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The Use of Food Samples from Sea Birds in the Study of Seasonal Variation
in the Surface Fauna of Tropical Oceanic Areas

MYRTLE J. ASHMOLE AND N. PHILIP ASHMOLE

ABSTRACT: Many parts of the tropical oceans appear to be relatively seasonless, but, because of the difficulty of sampling mobile and patchily distributed animals and the cost of oceanographic investigations, few data are available on the extent of seasonal changes. By regularly collecting regurgitations from sea birds, and identifying and measuring the food items, seasonal data could be obtained on the availability, size classes, and perhaps reproductive cycles of the fish and squid characteristic of the surface layer of tropical seas. Flying fish (Exocoetidae), juvenile tunas (Scombridae), and squid of the family Ommastrephidae are especially easily obtainable.

Experience gained during a recent study of the comparative feeding ecology of sea birds on Christmas Island (Pacific Ocean) makes it possible to assess the characteristics of bird species which affect their suitability for such study. Potentially useful species include terns (especially Sterna fascata, Anous stolidus, A. tenuirostris, and Gygis alba) and boobies (especially Sula sula). Samples could be obtained from several bird species in the same period, and a program could include sampling of inshore waters with the neuston net and making basic oceanographic observations. Investigations of this kind could be carried out economically on any of a large number of tropical oceanic islands.

IN ASSESSING the results of a study of the feeding ecology of some sea birds of Christmas Island, in the central equatorial Pacific, we attempted to make use of published information concerning seasonal variations in the fauna of the surface layer of the sea in this region. It soon became evident, however, that this type of information is very sparse, and that those workers who have made seasonal comparisons have often had to depend on data collected in different areas, in different years, or by different methods (see, for instance, King and Demond, 1953; King and Hida, 1957; King and Iversen, 1962).

The absence of information on seasonal variation in many tropical oceanic areas results mainly from the expense of running oceanographic ships, and the conflicting demands on their time, which generally prevent adequate sampling in a single area over a period as long as a year. Only in a few areas where there are important commercial fisheries are good seasonal data available. Even in these areas, however, there are generally few data on changes in the abundance of the forage animals which form the food of most sea birds and of many fish used for human food. This is because nets used for routine plankton sampling do not catch many nekton animals, and even modern nets like Isaacs-Kidd trawls catch few fast-swimming animals near the surface (King and Iversen, 1962; Pearcy, 1965).

It would be of considerable interest to obtain more information on the extent to which seasonal fluctuations in physical and biological characteristics actually occur in those parts of the tropical oceans which appear to be more or less constant throughout the year. For instance, ornithologists working on tropical islands in several different areas have found that among the sea birds breeding on a single island (or group) some species have evolved regimes under which individuals breed at intervals of less than a year, suggesting that seasonal variation in the environment is not of great importance to them.

1 Peabody Museum of Natural History, and Department of Biology, Yale University, New Haven, Connecticut 06520. Manuscript received January 23, 1967.
But on the same islands other species have annual breeding regimes, indicating that for them seasonal influences are sufficiently strong to outweigh the selective advantages of breeding at shorter intervals (Ascension Island: papers in Ibis 103b, 1962–63; Christmas Island: Gallagher, 1960; Ashmole, 1965; Ashmole and Ashmole, 1967; Ashmole, in press; Galapagos Islands: Léveque, 1964; Snow, 1965). Some advances are now being made in understanding the differences in feeding ecology which lead to dependence of different birds on different groups of prey species, but lack of knowledge of the importance of seasonal effects in populations of the various prey species prevents further progress. The reproductive cycles of oceanic fish and cephalopods in relatively seasonless areas are even less well understood, but are of both theoretical and practical importance.

The purpose of the present paper is to show that a very economical investigation of seasonal (and year-to-year) variation in the surface fauna of a tropical oceanic area could be carried out by making use of the sampling of the oceanic environment which is done by sea birds, and at the same time by collecting certain other data.

The method which we propose depends on the fact that tropical sea birds of many species are easy to catch and, when caught, will often regurgitate the whole or part of their latest meal. Regurgitations provide, on average, far more items in good condition than do stomachs of shot or netted birds and their collection does not appreciably affect the bird population. Regurgitations are stored in formalin and the individual food items identified and measured at leisure. Since the feeding methods of each species are reasonably constant, regular sampling on an adequate scale would permit detection of changes in the relative availability of different prey species. Furthermore, each of the bird species takes prey covering a considerable range in size, so that the data should reflect changes in the size-frequency distributions of the various prey species. Deductions could doubtless also be made about the timing of reproduction in some of the fish and squid species. The method could be used on almost any tropical island on which appropriate species of sea birds are available for a large part of the year, but the decision as to which bird species should be used for sampling depends on considerable knowledge of the ecology of the available species.

In the course of our study of the food of sea birds on Christmas Island during the period March 1963 to June 1964, we examined 800 samples (mainly regurgitations) from eight species of sea birds. We were mainly concerned with comparing the food of different species, and we did not have the opportunity to collect very large numbers of samples from any one species, so that our data are not suitable for detailed seasonal analysis. However, they do demonstrate the potentialities of the method. A complete account of the study is available in Ashmole and Ashmole (1967), and here we shall discuss only those aspects which are pertinent to the planning of a more general investigation, and in particular to the choice of bird species from which samples should be obtained.

The samples which we collected on Christmas Island consisted of entire or partially digested fish and squid, while two bird species also provided various invertebrates other than squid, mainly water striders (Halobates) and crustaceans. Nearly all the squid belonged to a single genus (Symplectotethis) of the family Omastrephidae, but the fish were distributed among 33 families. The state of the samples varied considerably, but there were fairly consistent differences among the bird species (Table 1). These differences resulted partly from the fact that in some species it was easiest to obtain samples from young birds which had previously been fed by adults, while in others it was easy to catch adults. The best samples were those obtained as the birds arrived to feed their chicks, while those obtained from roosting adults were generally more digested and thus the items were more often unidentifiable. It would be important, therefore, to plan future work in such a way as to obtain the food items as soon as possible after they were caught by the birds.

The usefulness of a particular species would depend largely on the ease with which large numbers of identifiable fish could be obtained from it, so we have calculated (Table 1) the number of fish which we were able to identify (to family level) per 100 samples collected. In the following short accounts of the most promising bird species we have also commented on the abundance of each species, the ways in which it
may be caught, the methods and zones which it uses in feeding, and the size of the animals which it obtains.

EVALUATION OF THE BIRD SPECIES

Of the eight bird species whose food was sampled on Christmas Island (Table 1), four would not be very suitable for marine biological investigations. It is time consuming to obtain samples from the Christmas Island Shearwater, Puffinus nativitatis Streets, the Phoenix Petrel, Pterodroma alba (Gmelin), and the Red-tailed Tropic-bird, Phaethon rubricauda Boddaert, and the number of identifiable fish which can be expected in 100 samples (Table 1) is rather low for all these species. The Blue-grey Noddy, Procelatyna cerulea (F. D. Bennett), provides large numbers of items per sample, but the populations on many islands are rather small, and the species is not widely distributed. Furthermore, it feeds close inshore on very small items which could probably be sampled more efficiently with a neuston net (David, 1965) towed behind a small boat. The other four species studied—the Sooty Tern, Sterna fuscata Linnaeus, the Brown Noddy, Anous stolidus (Linnaeus), the Black or Lesser Noddy, Anous tenuirostris (Temminck), and the White or Fairy Tern, Gygis alba (Sparrman)—all have certain advantages for regular study. Salient numerical details are given in Table 1.

Sterna fuscata (Sooty Tern)

This is the most abundant of all tropical sea birds, breeding in enormous colonies on islands in the tropics around the world (see Ashmole, 1963 for details of its breeding distribution and breeding seasons). The eggs are laid on the ground in the open, and sometimes there are as many as five nests per square meter. The birds may desert whole areas if they are disturbed too much at the start of nesting, but later they sit tightly and may be caught with a hand net. However, incubating birds rarely regurgitate when caught, and the only way in which large numbers of samples can easily be collected is to catch adults (with a long-handled hand net, or mist nets) as they arrive to feed their chicks, especially in the late afternoon, or to catch chicks shortly after they have been fed. Before breeding starts, a few regurgitations can be obtained by catching birds at night when they are roosting on the ground, but the samples are generally small and largely digested. On most tropical islands the species has one fairly short breeding season, but on Christmas Island and a few other central Pacific islands there are two breeding seasons each year.

Sterna fuscata catches its prey either while flying or by plunging to the surface, but it probably hardly ever submerges completely. It has been recorded as feeding at night (Gould, in press), but this probably occurs only when the moon is nearly full. It is an oceanic species capable of feeding hundreds of miles from land, even when breeding. However, the actual distance traveled regularly probably varies considerably from colony to colony.

Our 242 samples were mostly from adults feeding chicks. They contained, on the average, 5.6 items each, of which 60% were fish, 40% squid. On the whole, the samples were in good condition, and 79% of the fish were identified to the family level. This means that about 266 identifiable fish could be expected per 100 samples. The identified fish belonged to 21 families, the ones which occurred most regularly being Exocoetidae and Scombridae, Gempylidae, Serranidae, and Emmelichthyidae. The identified squid were nearly all Ommastrephidae. Of the fish, 93% were between 2 and 10 cm in length (measured to the base of the tail), while 98% of the squid were between 2 and 8 cm in mantle length. We obtained sufficient data from this species to suggest that important seasonal changes exist in the availability of certain fish families, but a more intensive sampling program would be necessary to demonstrate such changes convincingly.

In summary, the advantages of this species are that it is available in great numbers, and samples can easily be obtained; the samples are often in good condition, and contain a high proportion of identifiable items; Scombridae are especially well represented in the samples; and the feeding range of the species is such that it provides samples from a large oceanic area. However, one cannot determine precisely the area from which each sample comes, and it is not easy to obtain many samples at times when the birds are not breeding.


<table>
<thead>
<tr>
<th>ITEM</th>
<th>Phaethon subrubicunda</th>
<th>Puffinus nativitatis</th>
<th>Pterodroma alba</th>
<th>Sterna fuscata</th>
<th>Anous stolidus</th>
<th>Anous tenuirostris</th>
<th>Gygis alba*</th>
<th>Procelsterna cerulea</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean weight of bird (gm)</td>
<td>665</td>
<td>324</td>
<td>269</td>
<td>173</td>
<td>173</td>
<td>90.9</td>
<td>101</td>
<td>45.4</td>
</tr>
<tr>
<td>Mean number of items per sample</td>
<td>3.8</td>
<td>10.5</td>
<td>4.4</td>
<td>5.6</td>
<td>5.1</td>
<td>18.3</td>
<td>1.3</td>
<td>41.8</td>
</tr>
<tr>
<td>% composition by number</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fish</td>
<td>33</td>
<td>63</td>
<td>26</td>
<td>60</td>
<td>71</td>
<td>95</td>
<td>59</td>
<td>49</td>
</tr>
<tr>
<td>Squid</td>
<td>64</td>
<td>36</td>
<td>48</td>
<td>40</td>
<td>29</td>
<td>4</td>
<td>41</td>
<td>9</td>
</tr>
<tr>
<td>Other invertebrates</td>
<td>3</td>
<td>0.2</td>
<td>26</td>
<td>0.1</td>
<td>0</td>
<td>1</td>
<td>0.3</td>
<td>42</td>
</tr>
<tr>
<td>% of fish identified to family</td>
<td>55</td>
<td>20</td>
<td>1</td>
<td>79</td>
<td>67</td>
<td>27</td>
<td>87</td>
<td>38</td>
</tr>
<tr>
<td>% of squid identified to family**</td>
<td>100</td>
<td>62</td>
<td>24</td>
<td>88</td>
<td>100</td>
<td>71</td>
<td>100</td>
<td>74</td>
</tr>
<tr>
<td>Estimated number of fish identifiable to family per 100 samples</td>
<td>69</td>
<td>132</td>
<td>1</td>
<td>266</td>
<td>243</td>
<td>470</td>
<td>67</td>
<td>778</td>
</tr>
</tbody>
</table>

* When two figures are given for Gygis alba the upper refers to food samples carried in the bill and the lower to regurgitations.
** Some additional squid were tentatively identified.
Anous stolidus (Brown Noddy)

Anous stolidus breeds on many of the tropical islands where Sterna fuscata is found, but generally is less numerous. The birds are fairly easy to catch with a hand net at night, especially when there is no moon; mist nets could doubtless also be used, and unfledged young can be caught by hand. No general account of the breeding seasons of this species is available, but in many colonies breeding is probably less tightly synchronized than that of S. fuscata, while in some areas (including Christmas Island) individuals roost on the breeding islands even when they are not breeding.

A. stolidus uses feeding methods similar to those of S. fuscata, but sometimes also feeds while swimming on the surface; there is no evidence that it feeds at night. In contrast to S. fuscata, A. stolidus apparently does not normally feed more than about 50 miles from the colony, although the size of the zone utilized may be different in different areas.

Nearly all our 38 samples from A. stolidus were obtained from roosting adults early in the night, soon after they had returned from feeding. They contained, on the average, 5.1 items each, 71% of these items being fish, the remainder squid. Over half of the fish were identified to the family level, so that about 243 identifiable fish could be expected per 100 samples. The identified fish belonged to nine families, of which Exocoetidae, Scombridae, Holocentridae, and Gempylidae occurred most regularly. All the identified squid were Ommastrephidae. Of the fish, 94% were between 2 and 12 cm in length, while all but 1 of the 50 measurable squid had mantle lengths between 2 and 8 cm.

The advantages of A. stolidus as a sampler of the surface fauna of tropical seas are that the species is widely distributed, is available on some islands even outside the breeding season, and will often provide regurgitations when caught early in the night; its relatively limited feeding range means that animals obtained from it could normally be assumed to come from within 50 miles of the island. However, it is less abundant than S. fuscata and rather more difficult to catch.

Anous tenuirostris (Black Noddy)

This species (in which we include Anous minutus), although it breeds only on islands where bushes, trees, or cliffs are available to provide nest sites, often occurs in large colonies. Young birds often regurgitate when handled, but more consistent sampling can be carried out by catching roosting birds with a hand net early in the night, since on Christmas Island and many other islands some birds are present at all times of year.

A. tenuirostris feeds by the same methods as A. stolidus and S. fuscata; there is no conclusive evidence that it feeds at night. This species seems usually to feed even closer to its shore base than does A. stolidus: the Christmas Island birds fish very largely within 5 miles of the shore, but in some other areas (for instance Ascension Island, Atlantic Ocean) they go farther out to sea.

Our 110 samples, which were mostly regurgitations from roosting adults, contained on the average 18.3 items each. Of these items, 95% were fish, nearly all the remainder being squid. The regurgitations were often in the form of tightly-packed masses, many of the items being in a rather advanced state of digestion. We identified only 27% of the fish to the family level, partly because a large number of the fish were fry that we could not identify. Nevertheless, some 470 fish were identified per 100 samples. The identified fish belonged to 17 families, among which the most regularly represented were Exocoetidae, Gempylidae, Scombridae, Blenniidae, Holocentridae, and Emmelichthidae. The few identified squid were all Ommastrephidae. Of the fish, 98% were less than 6 cm long, and 77% between 1 and 4 cm. Of the few squid, 83% were between 2 and 6 cm in mantle length.

A. tenuirostris was the only species which showed any dramatic differences in the diet at different seasons. In May 1963 and June 1964 we found in the diet a far higher proportion of fish less than 2 cm long than were present in our other sampling periods.

This species has the advantages that it is abundant, easily caught while roosting, and on some islands is available all the year round; the samples provide large numbers of fish, and these
are from inshore waters; the small size of its prey would make study of its food an excellent complement to that of one of the larger species, for instance *A. stolidus*. Its main disadvantage is the difficulty of identifying many of the fish fry.

**Gygis alba** (White or Fairy Tern)

*Gygis alba*, another widespread tropical species, generally is less abundant than the preceding three species, but many tropical islands have populations of a thousand or more birds. The nests are dispersed, either in forks or hollows in branches of trees, on the tops of coral blocks, or on cliff ledges where these are available. *G. alba* differs from the other species in that the adults rarely regurgitate, and they carry food for the young in their bills. Hence the technique for obtaining food samples is different. The birds usually come quite close to a human intruder, even when carrying food, and may often be caught with a long-handled net; the food items dropped by the birds as they are caught can then be retrieved from the ground. Our samples were mainly obtained from adults in this way, although we also collected regurgitations from juveniles and from adults.

On Christmas Island *G. alba* breeds at all times of year. In many other areas, however, breeding is more seasonal and, since the individuals leave the colonies when they have finished breeding, it would be impossible to obtain samples at all times of year.

This species catches most of its prey in flight, and there is some evidence that it feeds extensively in the half light at dawn. It sometimes feeds close inshore, and most of the prey carried back to the young in the bill are probably caught fairly close to the colony; however, the species sometimes ranges hundreds of miles from land.

Among our 152 samples, those carried in the bill contained, on the average, 1.3 items each, while regurgitations contained 4.3 items. Fish made up 59% of the items, the remainder being squid. The samples were generally in excellent condition, and 87% of the fish were identified to the family level. Collecting only food carried in the bill, one could expect to obtain approximately 67 fish identifiable to the family level per 100 samples. However, all of these would be in excellent condition, so that further identification would be much easier than in most of the other birds. The fish which we identified represented 22 families, 5 of which were not found in the food of any of the other bird species. Blenniidae occurred most regularly, followed by Exocoetidae, Myctophidae, Scombridae, Gempylidae, and Gonostomatidae. Squid of the families Ommastrephidae and Enoploteuthidae were identified. Of the fish, 96% were less than 8 cm in length; the samples carried in the bill contained a lower proportion of small fish than did the regurgitations. Of the squid, 93% were between 2 and 6 cm in mantle length.

This species ate far more squid during one of our sampling periods than at other times, and during this same period the squid taken included Enoploteuthidae (*Abralia* sp.) which were not found in samples obtained in the earlier part of the study.

The main advantages of this species are the excellent condition of the items carried in the bill and the fact that a wide variety of prey are eaten. However, it is difficult to obtain many samples, since usually the populations are not very large, and some of the birds are too wary to be caught when carrying fish, so that a quantitative study would probably have to depend primarily on other species.

**Other Species**

The species just discussed are those with which we have most experience, but other species also might be used for sampling, and we have tried to indicate some of the criteria which should be used in deciding whether a given species would be appropriate. The only large species included in our study was *Phaethon rubricauda* (weights are included in Table 1), which takes large prey, but from which it is generally not easy to obtain many samples. The obvious additional candidates, available on many tropical islands, are the various species of frigate birds, *Fregata* spp., and boobies, *Sula* spp. We would reject the frigate birds on the grounds that they obtain some of their food by piracy, which complicates interpretation, and also the food generally is in poor condition. Of the three widespread tropical boobies, the Brown Booby, *Sula leucogaster* (Boddart), is mainly an inshore feeder, is rather difficult to catch, and
is not often available in large numbers. However, either the Red-footed Booby, Sula sula (Linnaeus), or the Masked (or Blue-faced, or White) Booby, Sula dactylatra Lesson, might be useful.

S. sula nests in colonies in bushes or trees, and regurgitates readily, at least when with young. The birds roost on many islands throughout the year; on Christmas Island, where the species nests on the main island, there is some breeding at all times of year. S. sula catches some of its prey below the surface by diving from a height, but has also been recorded catching flying fish in the air; it is thought sometimes to fish at night (Murphy, 1936). S. sula probably fishes mainly within a hundred miles of its home island (Murphy, 1936; Royce and Otsu, 1955, who almost certainly mistook S. sula for S. dactylatra). In a small series of samples from Oahu, Hawaii (Ashmole and Ashmole, in press) we found an average of nine items per sample, of which 64% were fish, 36% squid. Nearly 75% of the fish were identified, so that about 400 identifiable fish could be expected per 100 samples from this species. The fish found most frequently were Exocoetidae and Gymnophycidae, while all the identified squid were Ommastrephidae. Half of the fish were between 8 and 12 cm long, while there were appreciable numbers in the 12–16 and 16–20 cm groups; however, only a few squid with mantle length of more than 8 cm were present in our samples. The main advantages of this species are that it is available in some places throughout the year, and takes fish (and perhaps also squid) larger than any taken by the terns previously discussed.

We have had little experience with S. dactylatra, but relevant data have been presented by Dorward (1962). It would have advantages similar to S. sula, but probably ranges even farther from its breeding colonies.

**DISCUSSION**

It is clear that the use of analysis of the food of each of these bird species has certain merits, but also certain disadvantages. We suggest that valuable data could be obtained by making use of a group of bird species selected for the particular problem under investigation. For instance, to investigate the effects of seasons in the ocean around Christmas Island, it would probably be best to obtain a series of regurgitations, perhaps twice each month, from the three species Anous tenuirostris, A. stolidus, and S. sula. These samples would include animals ranging in size from less than 1 cm to at least 20 cm. The regurgitations from A. tenuirostris probably would represent sampling largely within 5 miles of the island, those from A. stolidus sampling largely within 50 miles, and those from S. sula might have been obtained as much as 100 miles away. On the other hand, for a long-term study concerned primarily with the detection of differences in the fauna of an oceanic area at the same season in a series of successive years, it would probably be more economical to collect samples from Sterna fuscata, choosing those months when this species has young. In any study, collection of samples from Gygis alba would be useful in providing animals in excellent condition and wide variety, to form the basis of a reference collection of the fish and squid available at the surface in the area.

If one is to use sea birds as samplers of their marine environment, it is important to have some understanding of the part which they play in the ecology of the surface layer of the sea. All the terns (including "noddies") considered here obtain their food within a few centimeters of the surface of the sea; boobies, Sula spp., tropic birds, Phaethon spp., and some shearwaters (Puffinus spp.), can penetrate a little deeper. Thus the terns should be sampling the fauna characteristic of the surface film, or "neuston." In fact, only one of the species for which we have data—the Blue-grey Noddy, Procellisterna cerulea—has a diet with a composition conspicuously similar to hauls made with the "neuston net" in the Indian Ocean (David, 1965): both contain large proportions of water striders (Halobates), pontellid copepods, and very small fish larvae. Among the other terns, only A. tenuirostris sometimes took many small fish larvae; and small crustaceans and Halobates were absent from the diet of all the larger species. Although there is little information available as to how many larger animals are normally present within a few centimeters of the surface during the day, observations suggest that, except for Procellisterna cerulea (and per-
haps *Gymnosoma* feeding at dawn on animals which visit the surface during the night, all the terns studied are dependent on schools of tuna and other predatory fish to drive fish and squid to the surface; many of the prey animals are caught by the birds while they are actually jumping out of the water in efforts to escape the predators below. The larger birds like *Phaethon rubricauda* and *S. sula*, which can penetrate the water to a depth of at least 1 meter, may be able to catch prey which are not disturbed by other predators, and so may be partially independent of the presence of predatory fish.

Tuna schools are by no means randomly distributed over the tropical oceans, but occur largely in those areas where the animals on which they feed are most concentrated. In an earlier paper (Ashmole and Ashmole, 1967) we have discussed the evidence that in the open ocean convergence at "fronts" produces local concentrations of plankton and nekton, even in areas where the overall density of organisms is very low, and that these concentrations attract tuna schools. The existence of large populations of sea birds—like *Sterna fuscata*—which can range great distances from their islands even when breeding, probably depends on the presence of rich feeding areas of this kind. Clearly a knowledge of the areas where the wide-ranging species are feeding will help in interpreting the data obtained by the analysis of their food. The inshore-feeding sea birds, on the other hand, make use of the concentrations of prey animals, and of surface-feeding tunas, which are often present in the lee of islands.

Thinking that there might be a close correspondence between the food of surface-caught tunas and the food of the birds, we studied records of stomach contents of Yellowfin Tuna, *Neothunnus macropterus* (Temminck and Schlegel), kindly made available by the Honolulu Biological Laboratory of the U.S. Fish and Wildlife Service. The data used were for Yellowfin caught at the surface within 10 miles of Christmas Island and neighboring islands, but in different years from our sampling of the food of the birds. We found that there were striking differences between the diets of the tunas and of the birds, even if the comparison was restricted to the birds which fed close inshore. The tunas took a far higher proportion of reef-originating fish than did any of the birds, and presumably this reflects the fact that tunas can quickly and easily change from feeding right at the surface to feeding at considerable depths or around reefs, while the birds must wait for their prey to come to the surface. After they have completed larval life, typical reef-inhabiting fish such as *Acanthuridae* evidently do not often come to the surface even when pursued, and so are rarely eaten by birds; however, they were eaten by the tunas in considerable numbers. (The pelagic larvae were also eaten by tunas; they may also sometimes be taken by birds, and it must be remembered that we were able to identify only a small proportion of the partly digested larval fish found in samples from *A. teniurostris* at certain times of year.) In contrast, Exocoetidae were unimportant in the diet of the tunas, but are of great importance in the diets of all the sea birds studied; probably the ability of these fish to escape submarine predators by flying renders them especially vulnerable to aerial predation by birds.

Attempts to sample forage animals near the surface of the central Pacific during the daytime, by means of oblique hauls with Isaacs-Kidd and other trawls, yielded so little material that they were abandoned in favor of night hauls, which produced catches containing far more organisms of generally larger size (King and Iversen, 1962). Although the greater number of organisms in night hauls partly reflects the movement to the surface layers at night of animals which are mesopelagic during the day, it is of interest that very few Exocoetidae, Scombridae, or Gempylidae, or squid of the family Ommastrephidae, were identified in either the day or night samples studied by King and Iversen. Since members of all these groups are commonly caught by birds feeding at the surface, it may be that they are such fast swimmers that they can generally dodge the nets (cf. Pearcy, 1965:266). Alternatively, they may be extremely patchily distributed, or so strictly confined to the surface that they are only rarely encountered by nets used in oblique hauls. In any case, it is clear that members of these groups are much more efficiently sampled by the birds.

In view of the commercial importance of tuna
fisheries, and consequent special interest in the biology of tunas, the effectiveness of tropical sea birds in catching juvenile tunas is worth emphasizing. King and Iversen (1962:301) said, "It was our hope that by means of midwater trawls we would capture juvenile tunas of lengths above 12 mm. which were able to elude the plankton nets. In 274 hauls made with the four midwater trawls described in this report we captured only six juvenile tunas, which ranged from 18 to 60 mm. in length." In contrast, in the 800 food samples which we obtained from birds on Christmas Island we found 247 young scombrids of which 166 were in 243 samples from Sterna fuscata. Of the latter group, 77 were examined in detail, and 69 proved to be Yellowfin Tuna. The scombrids from S. fuscata ranged from about 2 cm to 11 cm in length (measured to the base of the tail), but over 70% were between 4 and 8 cm. Those obtained in samples from A. tenuirostris included about a third which were less than 2 cm in length.

Since the birds eat mainly animals more than 0.5 cm in length, a program using birds to detect seasonal or longer-term changes in the environment could profitably be combined with other methods (such as use of the neuston net) of sampling the smaller organisms inhabiting the sea surface. If a version of this net could be arranged to fish clear of the bow wave of a small boat, it would permit quantitative sampling of the waters immediately around an oceanic island, to complement the sampling of larger animals, and a larger area, by the birds. The use of a small boat would of course also make it possible to obtain basic physical and chemical data requisite to an understanding of changes detected in the biota.

ACKNOWLEDGMENTS

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Sound Production and Associated Behavior in Triggerfishes

Michael Salmon, Howard E. Winn, and Nino Sorgente

Two Atlantic and five Pacific species of triggerfish produce sounds by movements of the pectoral fins against the side of the body. The behavior associated with sound production was observed in the field and in populations established in the laboratory. The sounds produced by all species when held by the hand underwater were analyzed and the pectoral fin–air bladder mechanism used to produce the sounds was studied principally by a series of ablation experiments.

It has been known for many years that triggerfishes are capable of producing sounds (Sørensen, 1884; Mobius, 1889). At least three possible mechanisms of sound production have been suggested: stridulatory mechanisms, consisting either of movements of the front teeth against one another in Balistes carolinensis, B. capriscus, B. vetula, and Melichthys piceus (Fish, Kelsey, and Mowbray, 1952; Moulton, 1958; Vincent, 1963) or of the first dorsal fin spine against underlying bones in B. erythrodon (Schneider, 1961); movements of the pectoral girdle bones against one another and the air bladder in B. aculeatus (Mobius, 1889); and "fluttering" or "drumming" of the pectoral fins against the side of the body in M. piceus, M. buniva, B. vetula, and B. carolinensis (Sørensen, 1884; Cunningham, 1910; Fish et al., 1952; Moulton, 1958). At the area of contact between the fin and body wall, the air bladder evaginated to form two bilateral lobes covered by a thin layer of integument and some enlarged scales, called the "tympanum" by Gregory (1933). A better term, the "drumming membrane," was used and illustrated by Moulton (1958). None of these proposed mechanisms of sound production have been verified experimentally.

Sounds produced by tooth stridulation in triggerfishes have been recorded underwater in the laboratory, and from fish feeding in the field (Moulton, 1958). Sounds produced by pectoral fin movements have most commonly been elicited from specimens held in the air, although Moulton (personal communication) has since recorded them from specimens underwater. Schneider (1961) and Tavolga (1965) concluded that pectoral fin sounds were not normally produced by triggerfishes under natural conditions in the field.

As a result of the above studies, there is considerable confusion as to the nature and operation of sound-producing organs in triggerfishes, as well as to the significance of the sounds themselves. This paper attempts to demonstrate that the pectoral fin–drumming membrane mechanism is used by several species, and that the sounds themselves are correlated with agonistic behavior in the field and the laboratory.

Materials and Methods

Hawaiian triggerfish (Rhinecanthus rectangularis, Melichthys buniva, M. vidua, Balistes bursa, and B. capistratus) were captured by hook and line, in fish traps, or by removing individuals from holes and ledges in the reef. All fish were captured from shallow waters (3–20 m) off the coast of Waikiki and Wai'anae, Oahu, from November to July, 1964–65. The fish ranged from 15 to 38 cm in total length. Individuals of the same species were hand-held underwater in fiberglass aquaria about 7.5 cm from an Atlantic Research Corp. hydrophone (LC-57) connected to a Uhlen 4000-S Report tape recorder. Tape speed during all
recordings was 18.75 cm/sec (7.5 in/sec). The tanks were 1.2 m × 0.6 m × 0.6 m deep, with a capacity of 758 liters. Water temperatures ranged from 21° to 25°C. Individual fish of the same species usually differed in size by no more than 7.5 cm.

All Bimini observations and experiments were carried out in November 1965 and January 1966. Specimens of _B. vetula_ and _M. piceus_ were captured at depths of 2–7 m by hook and line and recorded hand-held under water in concrete tanks, 1.8 × 0.9 × 0.6 m deep, using an Ampex (601) or Uher tape recorder. Specimens ranged from 18 to 26 cm in total length. The record level was adjusted so that sounds of normal fish peaked at no more than –1 on the VU meter of the Ampex, and at about the same level on the Uher (VU meter not calibrated).

A series of operations were carried out on _R. rectangularus, B. vetula_, and _M. piceus_. Sounds from fish were recorded before and after removal of part or all of the pectoral fin on one or both sides of the body. The role of the air bladder was determined by piercing the drumming membrane with a syringe and replacing most of the gas with water. The record level remained constant during all recordings (after an initial adjustment for each normal fish), so that relative changes in intensity of sounds produced by normal and operated fish could be measured. Only one recording system was used in any set of experiments. All fish were given at least 10 minutes to recover from handling and operations. No anaesthetic was used. The first five pectoral fin sounds produced by normal and operated fish were usually chosen for analysis. However, a few sounds of the fish were always masked by louder noises caused by tooth stridulation or violent contractions of the body.

These could be recognized easily and were not included. Therefore, only the first five pectoral fin sounds free of these disturbances were analyzed.

Sound durations were measured from oscillographs made with a Fairchild oscilloscope (701) and Grass Kymograph camera (C-4) at film speeds of 250 mm/sec. The effect of operations on the overall intensity of fish sounds recorded on tape was determined. A General Radio Co. Impact-Noise Analyzer (Type 1556-B) was connected to the output of the tape recorder and a peak sound pressure value was determined for the loudest of the first five pectoral fin sounds of a normal fish. The peak sound pressure of the same fish after the operation was also obtained. The peak value for the normal fish was considered as 0 decibel, while the value for the operated fish was considered as positive db (if the value exceeded that of the normal fish) or negative db (if the value was less than the normal fish). These changes in relative sound pressures (and all others mentioned below) were measured in db relative to 0.0002 microbar, but are not related to the original underwater sound pressures. Comparisons between pressure levels of normal and operated fish could be made because recordings were carried out at the same record level and with equal distances between the sound source and the hydrophone.

Relative sound pressures at various octave band frequencies were also measured from tape recordings. The output of a General Radio Co. Octave Band Noise Analyzer (Type 1558-A) was connected to the input of the Impact Analyzer. Sine wave signals of either 400 or 1000 Hz were applied to the input of the Octave Band Analyzer when in the "all pass" filter position, and with the preamplifier set to the 20 kHz weighting (essentially flat response from 20 Hz to 20 kHz). The Impact Analyzer was then calibrated to give a peak sound pressure value 3 db higher than the root mean square value shown by the Octave Band Analyzer for the sine wave. After calibration, the tape recorder output was connected to the input of the Octave Band Analyzer and readings for the fish sounds determined from the Impact Analyzer at various filter positions on the Octave Band Analyzer. The loudest of the first five sounds produced by each of ten normal fish in each species was measured, and considered as 0 db. Then, the sound pressures of the same sound in each octave band were compared to the level obtained for the unfiltered signal. The sound pressures of the filtered signal were always less than the total sound pressure, and this decrease was measured and expressed as negative db relative to the total sound energy.

The behavior of fish in the field was studied using SCUBA gear or, in clear waters, from
the surface. Observations were noted on submersible writing slates and behavior of fish was photographed with a Nikonos underwater camera. It was usually possible to sit on the bottom 1–2 m from individual fish, observe apparently normal behavior, and clearly detect by ear sounds correlated with pectoral fin movements.

Observations on two groups of 11 B. vetula were carried out in Bimini after establishing the fish in large, circular, concrete tanks 4 m in diameter and 0.6 m deep. Six shelters, constructed from building blocks, were placed around the tank periphery. A hydrophone was placed in the center of the tank. Color changes, sound production, and associated behavior were noted during a total of 6 hours of recordings on each group of fish, from 0900 to 1400 hours. Further observations and recordings were made in a fish pen 10 m × 6 m × 2–3 m deep (depending upon tidal conditions) in which 40–50 B. vetula and M. piceus were maintained.

RESULTS

The Pectoral Fin—Drumming Membrane Mechanism

The anatomy of the pectoral fin and drumming membrane in R. rectangulus is shown in Figure 1. The fin was composed of a single stout spine and the rays which supported most of the effective surface of the fin. The fin was supported at the base by a fleshy, muscular lobe. The drumming membrane was located just behind and partly above the fin, and was covered with thin scales. The anatomy of the area was essentially identical in all other species examined, differing slightly in the number and length of the rays and the surface area of the tympanum.

Movements of the pectoral fins during sound production by fish held underwater were also similar in all species. In R. rectangulus, the spine of the fin was pressed against the drumming membrane and moved back and forth across its surface when a sound was produced. As the spine was moved posteriorly, the rays were folded, then stretched taut as the spine was moved anteriorly. In B. vetula and M. piceus, the whole fin was moved across the drumming membrane, without folding of the rays. The number of back-and-forth sweeps of the fin across the drumming membrane varied from sound to sound within each fish, and ranged from one to seven movements in a series. Both pectoral fins appeared to complete these movements synchronously. Oscillographs of these sounds are shown in Figure 2.

No sounds resembling those of pectoral fin drumming could be detected from any fish when the fins were held immobile against the side of the body. Similarly, bilateral removal of the entire fin (rays, spine, and fleshy basal lobe) in eight fish of three species resulted in no further production of sounds.

The change in peak sound pressure of sounds produced by other operated fish, when compared with their own normal sounds, is shown in Figure 3 and analyzed statistically in Table 1. Removal of both the spine and rays of one pectoral fin (leaving the basal lobe intact) resulted in only slight reductions in sound pressure in three fish, and no change in two other specimens of R. rectangulus. When the same operation was performed bilaterally, sound pressures averaged about 16 db below those of normal fish. Removal of the spine from one pectoral fin in five specimens of R. rectangulus, B. vetula, and M. piceus had little effect on sound pressures; but, with the spines removed bilaterally, sound pressures averaged 13 db below those of normal fish. Unilateral or bilateral removal of the rays from the pectoral fin did

Fig. 1. External anatomy of the sound-producing apparatus in Rhinecanthus rectangulus. 1, Pectoral fin spine; 2, drumming membrane; 3, pectoral fin rays; 4, fleshy muscular lobe of pectoral fin.
not result in significant changes in sound pressure. When a small hole was made in the drumming membrane (but only a few bubbles of gas were allowed to escape from the airbladder), again there was no significant change in sound pressures. However, when the hole was held open with the syringe, allowing most of the gas to escape, sound pressures averaged 13.7 db below those of fish with only a small hole in the drumming membrane.

**TABLE 1**

**Peak Sound Pressures Produced by Triggerfishes after Operations on Parts of the Pectoral Fins and Air Bladder**

<table>
<thead>
<tr>
<th>Condition</th>
<th>Peak Sound Pressure1</th>
<th>S. D.</th>
<th>T-Value</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>One fin removed</td>
<td>-2.2</td>
<td>1.1</td>
<td>15.2688</td>
<td>0.005</td>
</tr>
<tr>
<td>Both fins removed</td>
<td>-16.4</td>
<td>3.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>One spine removed</td>
<td>-1.8</td>
<td>3.3</td>
<td>11.6792</td>
<td>0.005</td>
</tr>
<tr>
<td>Both spines removed</td>
<td>-13.0</td>
<td>2.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unilateral removal of rays</td>
<td>0.73</td>
<td>1.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bilateral removal of rays</td>
<td>-0.33</td>
<td>1.7</td>
<td>0.7067</td>
<td>0.5</td>
</tr>
<tr>
<td>Small hole in air bladder</td>
<td>-0.4</td>
<td>1.4</td>
<td>9.4785</td>
<td>0.005</td>
</tr>
<tr>
<td>Gas removed from air bladder</td>
<td>-13.7</td>
<td>5.3</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1 Sound pressures are expressed as positive db (above) or negative db (below) peak sound pressures of normal fish.
2 Experiments performed on *Rhinecanthus rectangulus* only.
Sound Production in Triggerfishes—Salmon, Winn, and Sorgente

CHANGE IN PEAK SOUND PRESSURE (Db re 0.0002 qbar) FROM LEVEL OF NORMAL FISH

Fig. 3. The change in peak sound pressures of operated fish from those of normal animals after various operations on parts of the sound-producing mechanisms. The pectoral fin consisted of a proximal fleshy muscular base and a distal stout spine and some rays. No sounds were detected when bilateral removal also included the muscular base (see text).

The effect of operations on sound durations of experimental fishes is shown in Table 2. In *M. piceus* and *B. vetula*, there was no significant change in sound durations of fish after unilateral removal of the pectoral fin rays or the spine, when compared with their own normal sounds. In *R. rectangulus*, operated fish tended to produce sounds of shorter duration than did normal fish. In all species, there was considerable variability in sound durations from normal and operated fish.

Octave band analyses of the sounds produced by all species are shown in Table 3. Sounds produced by pectoral fin movements ranged from below 75 Hz to below 9600 Hz in all species except *B. bursa*. This species, which was smaller than all others (total length under 20 cm), produced some sounds with measurable pressures above 9600 Hz. Most of the acoustic energy in other species was found between 150 and 1200 Hz, but there was considerable intra-specific variation not only between fish but also in consecutive sounds produced by the same fish.

Behavior Associated with Sound Production

All species but *B. capistratus* were observed in the field. When approached by a diver, about half the fish swam away rapidly. Other fish showed quite different behavior (Fig. 4). They swam in irregular paths, sometimes in wide circles, and then stopped by a hole or ledge in the reef. When again approached, the fish might
TABLE 2
Durations of the First Five Sounds Produced by Normal and Operated Triggerfishes

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>CONDITION</th>
<th>X</th>
<th>S. D.</th>
<th>T-VALUE</th>
<th>PROBABILITY</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhinecanthus rectangulus</td>
<td>normal</td>
<td>180</td>
<td>84</td>
<td>6.6667</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td>one spine removed</td>
<td>128</td>
<td>69</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>normal</td>
<td>179</td>
<td>53</td>
<td>7.1154</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td>rays unilaterally removed</td>
<td>149</td>
<td>46</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Melichthys piceus</td>
<td>normal</td>
<td>212</td>
<td>92</td>
<td>1.5473</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td>one spine removed</td>
<td>175</td>
<td>79</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>normal</td>
<td>185</td>
<td>76</td>
<td>0.7716</td>
<td>0.2</td>
</tr>
<tr>
<td></td>
<td>rays unilaterally removed</td>
<td>170</td>
<td>62</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Batistes vetula</td>
<td>normal</td>
<td>99</td>
<td>19</td>
<td>0.6867</td>
<td>0.5</td>
</tr>
<tr>
<td></td>
<td>one spine removed</td>
<td>93</td>
<td>21</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>normal</td>
<td>92</td>
<td>18</td>
<td>1.5472</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td>rays unilaterally removed</td>
<td>100</td>
<td>20</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

leave the area and continue swimming until another hole was found. Eventually, each fish entered a hole and extended its dorsal and ventral spines against the walls of the space. When attempts were made to grasp the fish and pull it from the area, a rapid burst of sound was produced. The sounds could sometimes be elicited by directing water currents into the area. No sounds were heard until currents were produced or until grasping attempts were made.

TABLE 3
Relative Distribution of Sound Pressure Within Octave Bands (Hz) in Sound Produced by Triggerfishes

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>75–150</th>
<th>150–300</th>
<th>300–600</th>
<th>600–1200</th>
<th>1200–2400</th>
<th>2400–4800</th>
<th>4800–9600</th>
<th>9600–19200</th>
</tr>
</thead>
<tbody>
<tr>
<td>Melichthys</td>
<td>-20.6</td>
<td>-13.8</td>
<td>-8.2</td>
<td>-5.8</td>
<td>-8.2</td>
<td>-16.1</td>
<td>-31.8</td>
<td>-</td>
</tr>
<tr>
<td>buniva</td>
<td>7–21</td>
<td>3–18</td>
<td>4–11</td>
<td>1–10</td>
<td>4–12</td>
<td>9–21</td>
<td>26–37</td>
<td>-</td>
</tr>
<tr>
<td>Melichthys</td>
<td>-8.3</td>
<td>-4.4</td>
<td>-6.8</td>
<td>-9.9</td>
<td>-11.7</td>
<td>-18.6</td>
<td>-23.6</td>
<td>-</td>
</tr>
<tr>
<td>vidua</td>
<td>4–11</td>
<td>1–6</td>
<td>2–12</td>
<td>3–14</td>
<td>7–23</td>
<td>10–27</td>
<td>13–38</td>
<td>-</td>
</tr>
<tr>
<td>Melichthys</td>
<td>-12.3</td>
<td>-4.9</td>
<td>-4.1</td>
<td>-8.7</td>
<td>-13.7</td>
<td>-20.5</td>
<td>-29.9</td>
<td>-</td>
</tr>
<tr>
<td>piceus</td>
<td>9–17</td>
<td>2–11</td>
<td>2–7</td>
<td>6–13</td>
<td>10–18</td>
<td>17–25</td>
<td>27–35</td>
<td>-</td>
</tr>
<tr>
<td>Balistes</td>
<td>-16.8</td>
<td>-9.7</td>
<td>-6.4</td>
<td>-8.0</td>
<td>-5.1</td>
<td>-10.1</td>
<td>-22.1</td>
<td>-24.1</td>
</tr>
<tr>
<td>Balistes</td>
<td>-8.4</td>
<td>-3.8</td>
<td>-4.5</td>
<td>-8.9</td>
<td>-11.7</td>
<td>-18.0</td>
<td>-25.4</td>
<td>-</td>
</tr>
<tr>
<td>capistratus</td>
<td>5–14</td>
<td>2–7</td>
<td>2–10</td>
<td>2–14</td>
<td>2–18</td>
<td>10–28</td>
<td>11–33</td>
<td>-</td>
</tr>
<tr>
<td>Balistes</td>
<td>-16.3</td>
<td>-10.1</td>
<td>-5.9</td>
<td>-3.0</td>
<td>-8.5</td>
<td>-12.8</td>
<td>-24.1</td>
<td>-</td>
</tr>
<tr>
<td>vetula</td>
<td>11–21</td>
<td>2–14</td>
<td>3–10</td>
<td>1–8</td>
<td>6–11</td>
<td>9–19</td>
<td>15–30</td>
<td>-</td>
</tr>
<tr>
<td>Rhinecanthus</td>
<td>-4.8</td>
<td>-4.8</td>
<td>-5.1</td>
<td>-11.2</td>
<td>-15.6</td>
<td>-23.0</td>
<td>-26.3</td>
<td>-</td>
</tr>
<tr>
<td>rectangulus</td>
<td>3–8</td>
<td>1–8</td>
<td>3–10</td>
<td>8–16</td>
<td>2–17</td>
<td>13–31</td>
<td>24–34</td>
<td>-</td>
</tr>
</tbody>
</table>

1 Data show mean and range of pressures at each octave band.
2 Numbers represent db below total sound energy, so that smallest reductions represent octave bands of greatest amplitude.
All fish stopped producing sounds a few seconds after attempts to dislodge them ceased. If pulled from the area, the fish continued to produce sounds until released. These observations are based upon the behavior of over 60 R. rectangulus, and at least 15 fish in the remaining species (excluding B. capistratus).

Most fish in the field were widely spaced, although in Melichthys sp. occasionally some were seen swimming in groups. In Balistes and Rhinecanthus, individual fish swam alone near the bottom, with only 5–10% of the fishes remaining near a hole or ledge in the coral for brief periods (5–30 minutes). On one occasion, 17 B. bursa were seen feeding on a small area of coral. Several large fish briefly chased smaller conspecifics away from the area, then returned to feed. The chasing was accompanied by a slight opening of the mouth and rapid, continuous volleys of pectoral fin drumming sounds. In two other cases, quite different behavior was observed during sound production. One fish approached another which had been hovering near a hole for several minutes. The "resident" and the "intruder" then slowly circled, simultaneously rising about 1–2 m off the bottom. Brief volleys of pectoral fin sounds were produced by both fish as they circled. In addition, the body coloration of both changed from the usual tan to a bright yellow. The intruding fish then swam away from the area. Brief chasing between conspecific R. rectangulus was also observed, but no sounds were detected.

On two separate occasions, individual B.
PACIFIC and when groups were observed, sometimes placed within conch), or crete consisted with aggressive fish, sometimes caused by chasing aggressive fish by B. vetula and M. piceus in the fish pen at Bimini. In three hours of recordings, sounds were produced at least once a minute. However, the large number of fish present made impossible the identification of the individuals involved. On four occasions, loud sounds were correlated with rapid chasing of one M. piceus by another across the length of the pen. In most recordings, presumably of sounds from both species, several sounds were produced in a series for up to a 9-second period. In a few cases, the sounds consisted of a loud burst.

Individuals of M. piceus in the circular concrete tank remained in the shelters for several days and only occasionally ventured into the open central area. This behavior was not comparable with that of conspecific fish in the pen or the field, and so only B. vetula was used for further observations. These fish adapted to the tank very quickly, i.e., they accepted food (fresh conch), produced sounds, and swam about the whole area within one hour after populations were established.

The most intense aggressive behavior occurred within the first 2–3 hours after the fish were placed in the tank. One fish in each of the two groups was dominant over all others. Chasing, sometimes accompanied by pectoral fin sounds, characterized the behavior of all aggressive fish. Submissive fish, usually smaller individuals, were dark or light brown in color. Most aggressive fish usually had bright yellow opercula.

A total of 134 aggressive interactions were observed, consisting of chasing of a conspecific by an aggressive fish. In 44 observations, the aggressive fish produced sounds by pectoral fin drumming just before or during the chase. Sounds were also produced during other less frequent interactions, i.e., when two fish circled slowly around one another for a few seconds (sounds produced by both fish in three observations); when one fish, after producing sounds, displaced a second fish from a shelter (12 observations); and when resident fish inside their shelters produced sounds in response to intruding fish (12 observations).

DISCUSSION

Pectoral fin movements against the drumming membrane appear to be responsible for production of sounds in three species of triggerfishes, representing three different genera. The data indicate that movements of the stiff pectoral fin spine across the drumming membrane contribute to most of the resultant sound pressure. The system must be extremely efficient, as removal of one spine or one pectoral fin lowered sound pressures no more than 2 db in any fish. The sounds of most normal fish peaked 22–25 db above background levels in the recording tanks, but we did not measure the absolute level of sound pressure in the water. Removal of both spines or most of the gas from the air bladder reduced intensities about 15–20 db. A very low level of sound remained when only the basal lobe of the fins was left intact. The acoustic energy released may represent muscle contraction sounds, or the sound of the base striking the side of the body.

Removing the gas from the air bladder resulted in a reduction in sound intensities, but it was noted that the operation had little effect on the frequencies contained in the sounds. In all species, the air bladder did not appear to emphasize any particular frequencies, and hence it probably does not function as a resonator. It may be that the air bladder acts chiefly as an efficient sound coupler to the water medium.

When the fleshy muscular lobe was held against the side of the body, or was removed, no detectable sounds were produced. Although no control was carried out for this specific operation, the data indicate that an intrinsic mechanism is not involved in sound production when fish of these species are hand-held underwater. It is possible, of course, that sounds may be produced by means of intrinsic mechanisms under other conditions.

Unilateral removal of the spine or rays did not affect duration of sounds in M. piceus or B. vetula. The results support the conclusion that the pectoral fins move synchronously on either side of the body during sound production.
In *R. rectangulus*, sounds produced after the operations were significantly shorter in duration than those of normal fish. However, when hand-held underwater for over a minute, even unoperated fish of this species gradually produced more abbreviated sounds. We believe that the effect after operations reflected this species-specific response to prolonged handling, and was not causally related to the operations themselves.

The octave band analyses of the sounds produced by seven species showed similarities in frequency spectra. Most of the acoustic energy was concentrated in the lower frequencies, as was shown by Moulton (1958) in his sonographic displays of sounds produced by *B. vetula* and *M. picens*.

Triggerfishes produced sounds in the field under conditions involving agonistic interactions. These sounds were quite loud and, when produced by a fish chased into a narrow hole in the reef, could function to startle a predator. Sound production under these circumstances is probably a behavior adaptation which, in addition to the bony plates and trigger mechanism, serves to promote survival of these relatively slow-moving fish.

Intraspecific aggressive behavior, with sound production, was infrequently observed in the field and only in two species (*B. bursa* and *B. vetula*). Triggerfish were usually observed swimming alone, and when they did meet conspecifics they were quite aggressive. Wide spacing between individuals seemed to be the normal social organization of each species at the time studied. Individual fish, observed from the surface, were seen swimming near the bottom, stopping occasionally to feed and inspect a ledge or hole in the reef. Sometimes a suitable hiding place was defended for a brief period. It may be that a fish which has found a suitable vacant hiding place nearby would be better able to escape from a predator. Several *R. rectangulus* consistently returned to the same hole when approached several times during a 2-hour period. It would be interesting to mark fish and determine if they swam regularly over a definite home range, returning at dusk to the same hole which would be defended as are territories by other vertebrates.

When placed in groups in the fish pen and in the circular concrete tank, Bimini species frequently produced sounds and, in *B. vetula*, showed color changes associated with aggressiveness by fish in the field. Under these conditions, interactions were more common due to the crowding of several fish within a small area. Sounds with correlated color changes were produced by individual fish when chasing one another, when defending their shelters, and when displacing other fish from the inside of the shelter.

Triggerfish sounds may function in other situations, particularly in reproductive behavior, but at present no information is available about these situations. The hand-held sounds show species-specific differences in duration, but little difference in frequency content. It is quite probable that temporal variation in the rate and intervals at which pulses are produced could carry information to distinguish between signals of different species, especially when the sounds are used in conjunction with changes in body coloration. Further study of these fish is certainly indicated.

**SUMMARY**

Triggerfishes produce sounds correlated with movements of the pectoral fins against the side of the body. The air bladder evaginates to form two bilateral lobes covered by thin scales at the area of contact between the fins and body wall. A series of operations were performed on these structures in *Balistes vetula*, *Melichthys picens*, and *Rhinecanthus rectangulus* in order to analyze their contribution to the sounds. The single stout pectoral fin spine contributed to production of most of the sound energy, but some was contributed by the fleshy muscular lobe of the fin. Removing the gas from the air bladder resulted in markedly reduced sound intensities. The sounds of these fish, and those of *B. capistratus*, *B. bursa*, *M. vidua*, and *M. buniva* were found to be quite similar in frequency spectra, with most of the acoustic energy below 1200 Hz.

Field and laboratory observations also were made on all species. The production of pectoral fin sounds during escape and aggressive behavior was described. In some species, these interactions were accompanied by color changes as well, usually in the aggressive or dominant fish.
REFERENCES

Cestode Parasites of Hawaiian Fishes

SATYU YAMAGUTI

The cestode parasites of Hawaiian fishes have never been investigated by previous workers. The specimens on which the present report is based have been collected along with parasites of other groups during our survey of Hawaiian fish trematodes. In this collection are represented four new genera, two of which belong to the Amphilcotylidae, and the others to the Parabothriocephalidae and Ptychobothriidae, respectively; the other already-known species are redescribed and figured in order to supplement earlier inadequate descriptions. All the larval forms, the identification of which is not easy, are reserved for a future study. The species described herein are listed below:

Amphicotylidae Ariola, 1899
1. Pseudobothrium xiphiados n. g., n. sp.
2. Pseudobothrioides lepidocybi n. g., n. sp.

Bothriocephalidae Blanchard, 1849
3. Bothriocephalus caranis n. sp.
4. Bothriocephalus manubriformis Linton, 1889

Parabothriocephalidae Yamaguti, 1959
5. Metabothriocephalus menpachi n. g., n. sp.

Ptychobothriidae Lühe, 1902
6. Alloptychobothrium spilonotopteri n. g., n. sp.

Lecanicephalidae Braun, 1906
7. Cephalobothrium acetabidis Shipley et Hornell, 1906

I wish to express my appreciation to the National Science Foundation for its extended financial support (GB-4480), to the professors of the University of Hawaii, and to Mr. Shunya Kamegai and Mrs. Ikuko Yamaguti, who helped me complete the present research.

1. Pseudobothrium xiphiados n. g., n. sp.

Habitat: Intestine of Xiphius gladius; Hawaii.


Description (based on two immature and two gravid specimens; one of the latter was cut into serial sections): Unless otherwise indicated, the following description is based on the gravid whole mount and serial sections. The largest specimen preserved in formol-alcohol is about 320 mm long by 6 mm wide. The type (which was fixed under cover glass pressure in Schaudinn's solution, stained with Heidenhain's hematoxylin, and mounted in balsam) is 40 mm in length, with maximum width of 4 mm in the greater posterior part, with the tapering posterior extremity appreciably truncated. In the immature paratypes the scolex is of the Enbothrium type in general appearance, 1.5-2.5 mm long by 2.1-3.0 mm wide, with a distinct apical disc notched on the median margin both dorsally and ventrally; each surficial proglottid is elongate oval to elliptical, 1.8 X 1.1 mm, widest at the posterior half, with a wide longitudinal median furrow tending to deepen posteriorly; its lateral margins may be distinctly crenulated. In the type the strongly flattened scolex is 3.8 mm long by 1.5 mm wide, its apical disc is about 1.0 mm in transverse diameter, and its median marginal notch is hardly recognizable. The neck is distinct, about 7 mm long by 1.5 mm wide in the type, more or less irregularly corrugated transversely. Proglottides are short, craspedote, with most of the cortex expanded transversely in the form of lamellae, 226 in number in the type, at the posterior extremity of which the last segment is only 0.28 mm long by 1.0 mm wide and contains paired, excretory vesicles 0.1 mm wide. In an immature paratype this last segment is 0.45 mm long by 0.7 mm wide, and is oc-

1 Hawaii Institute of Marine Biology, University of Hawaii. Present address: Beltsville Parasitological Laboratory, USDA, ARS, Beltsville, Maryland 20705. Manuscript received October 25, 1966. Contribution No. 275 from Hawaii Institute of Marine Biology, University of Hawaii.
cupied by wide, paired, sigmoid, excretory vesicles up to 0.2 mm wide; the latter vesicles unite in the median line and open outside 0.1 mm from the posteriormost margin. Dorsal and ventral longitudinal excretory vessels running at junction of lateral with middle third of proglottis or just medial to it near lateral end of medulla, ventral to genital ducts and lateral to nerve trunk in gravid proglottides. Nerve trunk dorsal to vas deferens and vagina. Inner longitudinal muscle bundles strongly developed throughout strobila, forming a distinct boundary between medulla and cortex.

Testes rounded or elongate, numerous, rather small, arranged in one layer or two in dorsal medulla, continuously from end to end, leaving part of medulla free where the ovary and uterus are situated. In the gravid proglottides the testes are atrophied as they approach the senile segments. In some sections one testis or two may lie exceptionally in the dorsal cortex immediately outside the inner longitudinal muscle bundles or among these bundles. Cirrus pouch pyriform, with thick muscular wall, 0.15–0.2 mm wide in the type, situated oblique-transversely, mostly in lateral marginal cortex, with its base extending into outer end of medulla or not, containing narrow convoluted ejaculatory duct and a bulbous cirrus, which opens at the tip of the pouch into the genital atrium. The cuticular lining of the bulbous cirrus forms a reticular basket-like structure (Fig. 1H), which is continued onto the ejaculatory duct, where the network is reduced and becomes so fine that it appears like cilia in cross section. Genital pore lateral, irregularly alternating.

Ovary transversely elongated along anterior median ventral margin of medulla, just inside inner longitudinal muscle bundles, up to 0.45 mm transversely in the type. Shell gland complex posterodorsalateral to oocapt, at median dorsal prominence of ovary. Uterus winding transversely dorsal to ovary, extending laterad into space between lateral ends of ovary and lateral testes; it may reach to the nerve trunk passing ventral to the outermost testes. Finally the uterus empties into the uterine sac, which lies in the ventral cortex in about the same sagittal plane as the dorsal collecting excretory vessel. Uterine pore wide, about one-third of proglottis width from lateral margin or a little more laterally. Eggs elliptical, comparatively thick-shelled, embryonated, 76–100 μ × 46–54 μ in sections. Vitelline follicles small, round, extending profusely in almost entire cortical parenchyma of marginal laminae. Vitelline reservoir inconspicuous, just ventral to shell gland complex. Vagina opening into genital atrium ventral to cirrus pouch; it is enlarged at its terminal portion, lined with smooth cuticle, the remaining portion is narrow, tubular, and lined with cilia.

**DISCUSSION:** This genus differs from the most closely related *Eubothrium* Nybelin, 1922, as shown in Table 1.

These morphological differences, combined with difference in host, are sufficient to justify

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**ABBREVIATIONS USED IN FIGURES**

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tr>
<td>b</td>
<td>bothrium</td>
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<tr>
<td>c</td>
<td>cirrus</td>
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<td>cf</td>
<td>collarlike fold</td>
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<tr>
<td>cp</td>
<td>cirrus pouch</td>
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<td>ds</td>
<td>ductus seminalis</td>
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<tr>
<td>cvp</td>
<td>cirrovaginal pore</td>
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<td>ds</td>
<td>dorsal vessel</td>
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<td>ej</td>
<td>ejaculatory duct</td>
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<tr>
<td>ex</td>
<td>excretory stem</td>
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<td>ga</td>
<td>genital atrium</td>
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<tr>
<td>gp</td>
<td>genital pore</td>
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<tr>
<td>il</td>
<td>inner longitudinal muscle</td>
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<td>mp</td>
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<td>nerve trunk</td>
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<td>sucker</td>
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<td>sph</td>
<td>sphincter of vagina</td>
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<td>u</td>
<td>uterus</td>
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<td>ud</td>
<td>uterine duct</td>
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<td>vitellarian</td>
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<td>vv</td>
<td>ventral vessel</td>
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**Figs. 1A–H.** *Pseudoebothrium xiphiod* n. g., n. sp. A, scolex of paratype, dorsoventral view; B, posterior extremity of holotype, ventral view; C, transverse section of anterior part of paratype; D, transverse section of immature proglottis of paratype; E, transverse section of mature proglottis of paratype; F, transverse section of gravid proglottis through ovary; G, transverse section of lateral portion of gravid proglottis through genital and uterine pores; H, same showing basketlike structure of lining of cirrus.
TABLE 1
DIFFERENTIATION OF PSEUDEUBOTHRIUM FROM EUBOTHRIUM

<table>
<thead>
<tr>
<th>CHARACTER</th>
<th>Eubothrium</th>
<th>Pseudeubothrium</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neck</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td>Median surficial furrow of strobila</td>
<td>present</td>
<td>absent</td>
</tr>
<tr>
<td>Vitellaria</td>
<td>may extend into inner longitudinal muscle layer or even into peripheral medulla</td>
<td>never extending into medulla</td>
</tr>
<tr>
<td>Uterine pore</td>
<td>midventral</td>
<td>submedian or sublateral, ventral</td>
</tr>
<tr>
<td>Vaginal pore</td>
<td>anterior to cirrus pouch</td>
<td>ventral to cirrus pouch</td>
</tr>
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</table>

The separation of the present genus from Eubothrium Nybelin, 1922.

**Pseudeubothrium** n. g.

**Generic Diagnosis:** Amphicotylidae, Amphicoelyinae Lühe, 1902. Scolex with an apical disc and elongate simple bothria. Strobila with distinct neck and very short, transversely extended, laminate, imbricated proglottides. No median furrow on each flat surface of strobila. Testes in dorsal medulla, continuous in median field except in ovarian region. Vas deferens convoluted in dorsal medulla. Cirrus pouch with thick muscular wall. Ejaculatory duct winding in cirrus pouch; cirrus swollen bulbously and lined with reticula basket-like cuticle which is continued onto the ejaculatory duct, where the network becomes reduced and appears like spinelets or cilia in cross sections. In cross sections of the cirrus the lining may appear like spines. Genital pore lateral, alternating irregularly. Ovary transversely elongated in ventral median medulla. Vitellaria confined to laminate cortex all around proglottis, never extending into medulla. Vaginal duct ciliated; vagina proper enlarged, with smooth cuticle, opening into genital atrium ventral to cirrus pouch. Uterine sac present, muscular; uterine pore ventral, submedian or sublateral. Eggs comparatively thick-shelled, embryonated. Paired excretory vesicles very conspicuous in posterior-most segment. Parasitic in marine teleosts.

**Type Species:** *P. xiphiados* n. sp., in *Xiphius gladius*; Hawaii.

2. **Pseudeubothrioides lepidocybii** n. g., n. sp. Fig. 2A–G

**Habitat:** Intestine of *Lepidocybium flavobrunneum*; Hawaii.

**Holotype:** U. S. Nat. Mus. Helm. Coll., S. Y. No. 373.

**Description** (based on a gravid type and two immature paratypes): Scolex elongate, 1.05 mm long by 0.47 mm wide in the type, with apical disc 0.47 mm wide and incised dorsally and ventrally, and an elongate, elliptical, simple bothrium on each flat surface; unsegmented neck portion about 1.0 mm long. Proglottides with salient posterior border; young proglottides wider than long; gravid ones wider than long, or as wide as long, 1.1–1.8 mm × 1.6–1.9 mm, nearly parallel-sided. Ventral excretory stem very wide throughout strobila, ventral to vas deferens and vagina, with transverse commissure at posterior end of each proglottis.

Testes small, round, distributed in medulla alongside excretory stem, confluent at posterior end of proglottis, very few, if any, in preovarian median field. Vas deferens describing an arcuate curve along vagina, passing transversely immediately in front of uterine sac and then running toward cirrus pouch. Cirrus pouch elliptical, up to 0.35 × 0.2 mm, lying obliquely between excretory stem and lateral margin; ejaculatory duct winding in cirrus pouch; no bulbous cirrus in strong contrast with *Pseudeubothrium xiphiados* n. sp. Genital atrium opening marginally near anterior end of proglottis on the same side as uterine pore, alternating irregularly from side to side.

Ovary bipartite, median, immediately in front of transverse excretory commissure. Uterine sac comparatively small, on pore side of median line near anterior border of proglottis, with inconspicuous ventral pore in immature proglottides. In gravid proglottides the uterus filled with eggs takes an arcuate course like the vas deferens and vagina, and finally opens into the uterine sac which is now an elliptical muscular
Figs. 2 A–C. Pseudeubothrioides lepidocybii n. g., n. sp. from Lepidocybium flavobrunneum. A, scolex of holotype showing excretory system, dorsoventral view; B, mature proglottis of holotype, ventral view; C, gravid proglottis of holotype, dorsal view.
structure up to 0.45 mm long by 0.2 mm wide. Ventral uterine pore at or just behind level of genital pore. The gravid uterus as a whole presents many more indentations than that of *Pseudenobothrium xiphiados*, which forms a rather compact mass. Eggs elliptical, large, 70–81μ × 35–42μ. Vitelline follicles small, distributed extensively in entire cortex. Vagina running alongside vas deferens, then along posterior margin of cirrus pouch, opening together with male pore at base of genital atrium.

**DISCUSSION:** This species differs from the most closely related *Pseudenobothrium xiphiados* n. sp. in the structure of the scolex and proglottides, in the absence of a bulbous armed cirrus, and in egg size. Of these differences the most outstanding is the difference in the structure of the proglottides. In the type species of *Pseudenobothrium* the laminate cortex of the proglottides is so conspicuous that it can easily be distinguished from the usual cortex of the present species. This difference appears to be of generic importance, so I prefer to assign the species in question provisionally to a new genus, *Pseudenobothrioides*, which is defined as follows:

**Pseudenobothrioides** n. g.

**GENERIC DIAGNOSIS:** Amphiocotylidae, Amphiocotylinae. Scolex with apical disc and elongate simple bothria. Strobila serrate, with distinct neck and nearly parallel-sided proglottides, without median furrow on each flat surface. Ventral excretory stems parallel, very wide, with transverse anastomosis at posterior end of each proglottis. Testes extending mostly along longitudinal excretory stems, continuous across median line immediately in front of posterior border of proglottis. Cirrus pouch with muscular wall containing convoluted ejaculatory duct; cirrus not forming a bulbous swelling. Genital atrium marginal, irregularly alternating from side to side, near anterior corner of proglottis. Ovary transversely elongated, bipartite, in median ventral medulla. Vitellaria confined to cortical parenchyma. Vagina opening immediately behind cirrus into genital atrium. Uterine sac present, muscular when fully gravid. Uterine pore submedian, ventral, on pore side. Eggs large, thick-shelled, not embryonated. Parasitic in intestine of marine teleosts.

**TYPE SPECIES:** *P. lepidocbyii* n. sp., in *Lepidocbyrium flavobrunneum*; Hawaii.

**BOTHRIOCEPHALIDAE** Blanchard, 1849

3. **Bothriocephalus carangis** n. sp.

Fig. 3A–E

**HABITAT:** Intestine of *Caranx belvolus* (type host, local name “black ulua”) and *Carangoides ferdau* (local name “ula”); Hawaii.


**DESCRIPTION** (based on eight, mostly gravid, mature specimens): Strobila 70–120 mm long, up to 2–5 mm wide when strongly flattened under cover glass, usually 1.0–1.5 mm wide, consisting of 170–230 primary segments and 15–30 or more secondary segments. Scolex longitudinally elongated, 1.0–1.6 mm long, with apical disc 0.25–0.45 mm in diameter, deeply incised laterally; bothria elongate oval in outline, up to 0.5–0.8 mm wide near posterior end, with thin smooth margin. Neck absent. Proglottides bell-shaped anteriorly, nearly parallel-sided posteriorly, with posterior margin slightly imbricated, or lateral margins slightly divergent. On each flat surface there is a distinct posterior median notch. Mature and gravid proglottides as long as wide, or longer than wide; the fused proglottides containing three sets of reproductive organs are longer than wide; proglottides with one set of reproductive organs are usually wider than long; senile end proglottis smaller than penultimate proglottis, longer than wide, convex on each side. Inner longitudinal muscle fibers rather weak in mature and gravid proglottides. Excretory system reticulate.

Testes round, divided into two medullary sublateral fields, apparently continuous from proglottis to proglottis, and interrupted in median field, 30–110 in number in each lateral field; this variation in number depends on the inadequate segmentation or fusion of proglottides, or on the degree of their maturity; generally speaking, the smallest number occurs in an immature, completely segmented, single proglottis; vas deferens convoluted close to base of cirrus pouch. Cirrus pouch elongate pyriform or claviform, provided with thick layer of inner circular and outer longitudinal muscle fibers,
0.2–0.35 mm × 0.08–0.11 mm, oblique to median axis of strobila, with its base alternating irregularly from one side of median line to the other, containing very narrow ejaculatory duct. Ejaculatory duct joining vagina just distal to vaginal sphincter to form a short cirrovaginal duct, which opens middorsally.

Ovary consisting of several lobes, rosette-shaped or bipartite, 0.15–0.35 mm wide, up to 0.45–0.55 mm wide in strongly flattened specimens, situated in median field immediately posteroventral to cirrus pouch. Vagina provided with a conspicuous bulbous sphincter just before uniting with ejaculatory duct, curved posteroventrally to join germiduct anterior to isthmus of ovary. Vitelline follicles diffuse in whole cortical parenchyma except marginal areas. Gravid uterus forming a few spiral turns and opening ventrally in median field anterolateral to base of cirrus pouch or level with it. Eggs oval, operculate, 60–68μ × 32–40μ in life; contained ovum unsegmented.

Figs. 3A–E. Bothriocephalus carangis n. sp. A, scolex of paratype from Caranx ferdau, ventral view; B, mature proglottis of holotype from Caranx belvolus, dorsal view; C, longitudinal section of paratype from Caranx ferdau; D, longitudinal section of mature proglottis of paratype from Caranx ferdau through genital pore; E, longitudinal section of mature proglottis of paratype from Caranx ferdau through uterine pore.
Discussion: This species differs from the most closely related Bothriocephalus scorpii (Müller, 1776), from Cottus scorpius and other marine fishes, in that the cirrus pouch is large and muscular and tilting so conspicuously to one side or the other from the median axis of the strobila that discrimination between the two species is not difficult. I have some doubt about the alleged occurrence of B. scorpii in Caranx or other pelagic carangids, because the type host is Cottus scorpius, which is definitely a benthonic fish.

4. Bothriocephalus manubriformis Linton, 1889

Fig. 4A–B

Habitat: Intestine of Makaira audax, Istiophorus orientalis, Istiompax orientalis, Tetraopterus angustirostris, and Xiphius gladius; Hawaii.

Description (based on several immature specimens and five gravid specimens): Strobila serrate, 25–334 mm × 0.35–3.8 mm; one specimen 130 mm long, comprising 420 primary...
segments and a large number of secondary segments. Scolex 1.7–2.8 mm long, with lateral bothria opening at anterior and posterior ends; apical disc, often prominent at center, 0.5–0.7 mm in transverse diameter, incised laterally. Proglottides campanulate, especially in anterior ones, which are medially notched both dorsally and ventrally; gravid proglottides wider than long, medially notched, 0.2–0.8 mm × 0.5–2.3 mm, with very prominent posterior border, always containing one set of reproductive organs unless pseudosegmented.

Testes arranged in one layer in two sublateral medullary fields, 25–50 or more in number on each side, not confluent in median field. Cirrus pouch elongate pyriform, 0.07–0.2 mm in diameter, usually slightly oblique, with strong circular muscles; vas deferens coiled around anterior end of cirrus pouch. Cirro vaginal pore dorsomedian, near posterior end of proglottis.

Ovary bipartite, divided laterally into several lobules, up to 0.3–0.5 mm in transverse diameter, at median posterior end of proglottis. Uterus sigmoid; uterine sac opening ventrally, rounded, up to 0.12–0.28 mm in diameter when distended with eggs, situated near anterior end of proglottis, usually only slightly to either side of median line. Eggs elliptical, operculate, 54–86 μ × 33–38 μ in balsam mounts. Vitelline follicles small, profusely distributed in entire cortical parenchyma except for median field, not continuous from one proglottis to the next; vitelline reservoir ovoid, situated behind ovary on the same side of the median line as the uterine pore. Vagina provided with sphincter just before joining ejaculatory duct.

**DISCUSSION:** This species is characterized by the lateral bothria being open anteriorly and posteriorly, and in the proglottides being campanulate. It occurs commonly in stiophorid fishes widely distributed in the Atlantic, Pacific, and Indian oceans.

**PARABOTHRIOCEPHALIDAE** Yamaguti, 1959

5. *Metabothriocephalus menpachi* n. g., n. sp.

**Fig. 5A–E**

**HABITAT:** Intestine of *Myripristis argyromus* (type host, local name “u’u” or “menpachi”), *M. chryseres* (local name “pau’u’u”) and *M. berndti* (local name same as that of type host); Hawaii.

**HOLOTYPE:** U. S. Nat. Mus. Helm. Coll., S. Y. No. 375.

**DESCRIPTION** (based on a fragmented type 120 mm long by 2.4 mm wide and two paraphyses, each of which is broken into several fragments; the following description is based mainly on the type): Scolex discoid at apex, which is depressed in the center, with an oval subapical bothrium 0.15 mm long by 0.13 mm wide on dorsal and ventral surface. Unsegmented neck uniform in width (about 0.1 mm in the type, in which the segmentation commences 2.65 mm behind the head end). Proglottides nearly parallel-sided, wider than long throughout strobila, with salient posterior border, which often may be constricted at pre-equatorial level. Inner longitudinal muscle bundles comparatively wide apart one from another (Fig. 5B). Dorsal and ventral excretory vessels running in lateral end of medulla, lateral to nerve trunk, ventral to terminal genital ducts.

Testes extending longitudinally medial to nerve trunk and longitudinal excretory vessels, 10–15 in number on each side. Vas deferens twisted, running outward immediately behind vagina. Cirrus pouch pyriform, small, 74–77 μ × 56–65 μ in immature proglottides; ejaculatory duct narrow, but swollen at base of cirrus pouch, opening with vagina on dorsolateral margin of proglottis at about pre-equatorial level, alternating irregularly from side to side.

Ovary transversely elongated near posterior margin of proglottis on pore side of median line, with compact mass of shell gland immediately behind. Uterine duct winding forward from behind ovary to uterine sac. Uterine sac rounded, almost median near anterior border of proglottis, opening midventrally. In fully gravid proglottides the uterus distended with eggs occupies the whole medulla with uneven outline. Eggs oval, operculate, rather thick-shelled, 77–90 μ × 49–63 μ in life; contained ova unsegmented. Vitelline follicles small, round, extending profusely in entire cortical parenchyma, continuous from proglottis to proglottis. Vagina running straight, obliquely anterolaterad from behind ovary toward com-
mon genital pore, lined with thick cuticle just before uniting with ejaculatory duct.

**Discussion:** This genus bears a certain resemblance to *Parabothriocephaloides* Yamaguti, 1934 in gross anatomy, but differs from it in that the scolex is provided on each flat surface with an oval bothrium, and in the distribution of testes, etc. From these differences it seems certain that the present genus, obviously parabothriocephalid in structure, represents a distinct genus, for which the name *Metabothriocephalus* is proposed, with the following diagnosis:

**Metabothriocephalus** n. g.

**Generic Diagnosis:** Parabothriocephalidae. Scolex not marked off from neck, with an indistinct apical disc followed on each flat surface by a small oval subapical bothrium surrounded by condensed tissue. Neck present. Strobila comparatively fleshy, with complete segmentation; proglottides wider than long throughout strobila, with salient posterior border and nearly parallel lateral margins. Inner longitudinal muscle bundles strongly developed anteriorly, though individual bundles are rather wide apart one from another. Testes medullary, in small number medial to excretory stems. Cirrus pouch reduced. Ejaculatory duct opening with vagina by a small common pore dorsomarginally at a pre-equatorial level, alternating irregularly from side to side. Ovary transversely elongated, not two-winged, slightly submedian (on pore side) near posterior end of proglottis. Uterine duct winding in median and submedian fields; uterine sac practically median, opening medially near anterior end of proglottis. Vagina straight, joining ejaculatory duct at genital pore. Vitellaria entirely cortical, diffuse, continuous from proglottis to proglottis. Eggs rather thick-shelled, operculate, with unsegmented ova. Parasitic in intestine of marine teleosts.

**Type Species:** *M. menpachi* n. sp., in *Myripristis* spp.; Hawaii.

**Ptychobothriidae** Lühe, 1902

6. *Alloptychobothrium spilonotopteri* n. g., n. sp.

**Habitat:** Small intestine of *Cypselurus spilonotopterus*; Hawaii.


**Description** (based on four immature and three gravid specimens; unless otherwise indicated the following description is based on whole gravid mounts and serial sections of gravid proglottides): Strobilas over 30 mm long are all gravid. Scolex arrowhead-shaped in lateral view, with edges markedly crenulated and enclosing deep longitudinal groove, 2.8 mm long, 1.7 mm wide dorsoventrally in the type; its apex blunt-pointed, two posterior ends widely divergent or hanging down, one on each side of strobila. Neck absent. Proglottides transversely elongated, 0.1 × 0.5 mm at anterior end directly following scolex, with posterior border somewhat craspedote or not; gravid proglottides very variable in length and width, ranging from 0.18 to 0.9 mm in length and from 0.9 to 2.2 mm in width, depending on the degree of pressure applied on cover glass. Transverse sections of unflattened gravid specimens fusiform, 0.4–1.7 mm wide, 0.1–0.5 mm thick, showing notches in dorsal and ventral midlines, corresponding to genital atrium and uterine pore, respectively. Cuticle thick, with striations at right angles to the surface. Inner longitudinal muscle bundles isolated in lateral fields, but forming a conspicuous layer outside as well as inside of layer of vitellaria in median and submedian fields, with distinct median break corresponding to genital and uterine pores. Dorsal longitudinal excretory stem with thicker walls than ventral stem, lying lateral to ventral stem, latter stems separated one from the other by uterine coils; two or more, narrower, ventral vessels are seen forming anastomoses.

Testes confined to submedian medulla im-
mediately dorsal to ventral medullary excretory anastomoses, in one layer or two; although their total number could not be determined, they are not numerous. Thin-walled vas deferens convoluted around base of cirrus pouch. Cirrus pouch subglobular, 0.16–0.2 mm × 0.13–0.2 mm, not very muscular, situated in median field, with its long axis nearly at right angles to body surface, containing somewhat muscular pars prostatica surrounded by prostate cells at its base and an axial cirrus, which is lined with corrugated cuticle and supported by numerous transverse muscle fibers. The distal end of the cirrus joins the vagina to form cirrovaginal pore which opens at the bottom of the mid-dorsal notch by a comparatively wide aperture.

Ovary arcuate, multilobulated, median, elongated transversely at base of proglottis, with its lateral ends curved posteriad or dorsad, 0.25–0.35 mm wide, up to 0.8 mm wide when extended; in cross sections a short lobe or two may be seen in the dorsal concavity of the ovary, where the vagina joins the germiduct arising from the dorsoposterior concave margin of the ovary. Vagina lined with thick cuticle and surrounded by dense layer of gland cells, running dorsad and backward windingly, opening into cirrovaginal pore alongside cirrus pouch. Vitelline follicles arranged in one layer all around between cortex and medulla, interrupted at notches where the uterus and cirrovaginal pore open, but continuous from proglottis to proglottis. Uterus winding a few times in median medulla from right to left and vice versa, not reaching to lateral medulla, distended with eggs when gravid, opening at small mid-ventral notch at about level of cirrovaginal pore (Fig. 6C). No uterine sac. Eggs subglobular to ovoid, not operculate, 34–51 μ × 23–37 μ in lactophenolglycerine jelly, relatively thick-shelled, each containing oncosphere.

Discussion: This genus differs from the most closely related Ptychobothrium Loennenberg, 1889, as follows: (1) bothrial edges are markedly crenulated; (2) the inner longitudinal muscle layer is divided by the vitellarian layer into two (outer and inner) layers; in Ptychobothrium the longitudinal muscle bundles are seen among or between the vitelline follicles, but not divided into two layers; (3) the vagina is very strongly developed and so long that it forms transverse windings; (4) the multilobulated ovary is curved dorsoposteriad at its lateral ends to form a conspicuous dorsal concavity; (5) the uterus does not extend as far laterad as in Ptychobothrium and does not form a uterine sac; (6) the uterine pore is midventral instead of submedian.

Recently, Cable and Michaelis described in the Proceedings of the Helminthological Society of Washington 34(1):15–17, 1967, a new cestode, Plicatobothrium cyseluri n. g., n. sp., from the Caribbean flying fish, Cypselurus babiensis. This worm resembles Alloptychobothrium spilonotopteri very closely, especially in the general shape of the scolex, the structure of the terminal genitalia, and the position of the vitellaria between the outer and inner layers of the longitudinal muscle bundles, but differs distinctly from the latter in that the ovary is V-shaped in dorsoventral view and the gravid uterine sac is conspicuously Y-shaped. The two species might be referred to the same genus, but until a detailed comparison of them is made on the whole mounts and sections, I prefer to regard them for the present as distinct not only specifically but also generically.

**Alloptychobothrium** n. g.

**Generic Diagnosis:** Ptychobothriidae. Scolex arrowhead-shaped in lateral view, compressed from side to side, with dorsal and ventral bothrial edges markedly crenulated. Neck absent. Strobila may be completely or incompletely segmented; proglottides wider than long, craspedote or not. Inner longitudinal muscle bundles divided by vitellarian layer into two (outer and inner) layers. Testes not numerous, in one layer or two, in submedian medulla immediately dorsal to ventral medullary excretory anastomoses. Cirrovaginal pore opening at bottom of middorsal notch. Ovary multilobulated, arcuate, transversely elongated, median, at posterior end.

Figs 6A–D. Alloptychobothrium spilonotopteri n. g., n. sp. A, scolex of holotype, lateral view; B, mature proglottis of paratype, dorsal view; C, transverse section of gravid proglottis of paratype through cirrus; D, transverse section of gravid proglottis of paratype through ovary.
of proglottis. Vitellaria continuous laterally and from proglottis to proglottis, but interrupted at notches, where the uterus and cirrovaginal pore open outside. Uterine coils confined to median field dorsal and anterior to ovary, not forming uterine sac before opening midventrally; eggs not operculate, containing subglobular oncosphere. Ventral longitudinal excretory stems anastomosing with narrower ventral vessels running longitudinally lateral to them. Parasitic in marine teleosts.

TYPE SPECIES: *A. spilonopteri* n. sp., in *Cypselurus spilonopterus*; Hawaii.

LECANOCEPHALIDAE Braun, 1900

7. *Cephalobothrium aetobatidis* Shipley et Hornell, 1906

Fig. 7A–D

HABITAT: Spiral valve of *Aetobatis narinari*; Hawaii.

DESCRIPTION (based on five immature specimens and a single mature specimen): Strobila 18.7 mm long in the mature specimen, comprising 144 craspedote segments; some of the posterior segments were detached during preparation of the whole mount. Scolex rounded quadrangular, 0.5 × 0.67 mm, occupied at its apex by a circular muscle pad 0.45 × 0.5 mm and dome-shaped in profile. The strong muscle bundles of the pad are converged toward the center, without forming a sectorial depression or lumen; these muscle bundles are continued backwards into the ensuing proglottides in form of inner longitudinal bundles delimiting the medulla from the cortex. Around the apical pad is a circular collar-like fold which is conspicuous in much younger individuals. The four suckers situated at the corners of the scolex are 0.13 mm in diameter and present typical sectorial structure. Neck absent. Immature and anterior mature proglottides wider than long, but posterior mature ones longer than wide, constricted at both extremities. The easily detachable posterior proglottides are elliptical, 0.5–0.8 mm × 0.4–0.55 mm, with the posterior end produced backward in form of an abruptly tapering truncate cone. The inner longitudinal muscle bundles are strongly developed in the anterior immature proglottides but, as they proceed backward, they become gradually thinner and wider apart one from another, and in the posterior mature proglottides they are reduced to a layer of very fine individual fibers. Excretory stems not seen.

Testes globular to oval, comparatively large (50–100 μ in diameter), 15–25 in number in mature proglottides, massed together, partly overlapping one another, in greater part of medulla between two lateral vitelline fields, leaving anteriormost and posterior parts of proglottis free. Vas deferens convoluted close to medial end of cirrus pouch. Cirrus pouch elongate pyriform or short claviform, 0.19 × 0.06 mm in the mature proglottis figured, lying transversely in pre-equatorial zone, nearly reaching median line, containing convoluted ejaculatory duct surrounded by gland cells (Fig. 7C) at base and eversible tubular ejaculatory duct distally. Cirrus, when everted, cylindrical, smooth, 60 μ × 20 μ in the proglottis figured (Fig. 7D), projecting backward along lateral margin of proglottis. Genital arium is clearly seen, when the cirrus is not everted, as a cuticular ring, into which the cirrus opens immediately in front of the vagina. The genital pore pre-equatorial, may be slightly depressed occasionally, alternating irregularly from side to side.

Ovary two-winged, 0.1 × 0.3 mm in the mature proglottis figured (Fig. 7D), situated near posterior end of proglottis, with shell gland complex immediately behind its isthmus. Vitellaria follicular, extending in lateral medulla between testes and lateral edge of inner muscle sheath from a little behind level of anterior extent of testes to ovarian wings, where the transverse vitelline duct passes inward on each side. The winding uterine duct running forward dorsal to the ovarian isthmus appears to open into the incipient uterus proper from

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Figs. 7A–D. *Cephalobothrium aetobatidis* Shipley et Hornell, 1906. A, scolex, apical view; B, same, lateral view; C, male terminalia, ovariocervical complex, and seminal receptacle, dorsal view; D, end proglottis, dorsal view.
the dorsal side a little anterior to the ovarian isthmus; the incipient uterus proper is seen as a wide, laterally crenulated lumen reaching to the base of the cirrus pouch. No eggs observed. The presence of a large elliptical seminal receptacle connected with the germiduct by a wide seminal duct, as shown in Fig. 7C and Fig. 7D, is one of the most important characteristics of this species.

**DISCUSSION:** Because the original description of this species by Shipley and Hornell is inadequate, no detailed comparison is possible between *Cephalobothrium aetobatidis* from Ceylon and the Hawaiian representative from the same host species, but from agreement in external anatomy there is no doubt that both are identical. The statement by Shipley and Hornell that the terminal "sucker" is round, with thickened edges, and their figure of the scolex appear misleading, because the apical muscle pad lacking a suckorial lumen is by no means a true sucker, and the collar-like circular fold encircling the apical pad is not shown in their figure.

**REFERENCES**


Distribution of Epifaunal Biomass on a Sublittoral Rock-Reef

WILLIS E. PEQUEGNA1

PREVIOUSLY the author reported on the quantitative distribution of epifaunal species and individuals and their zonation on a silstone reef located in the open ocean near Corona del Mar, California (Pequegnat, 1964). A marked top-to-bottom reduction in numbers of species and individuals was observed to exist on this reef, and these changes were related to a reduction of wave-induced water movements from the reef's upper to lower levels. Three observations pointed to the desirability of determining the distribution of biomass over the rock-reef: (1) the populations of some species were greatest on the reef's lower levels, (2) several of the largest species with relatively small numbers of individuals occurred here, and (3) there appeared to be a shift from a preponderance of suspension-feeders at the top toward increasing importance of deposit-feeders and scavengers at the base.

Accordingly, the objectives of the present study were: (1) to determine the quantitative distribution of biomass over the reef's surface, and (2) to relate the observed pattern to (a) position on the reef, (b) feeding types, (c) the frequency of occurrence of species on quadrats, and (d) the number of individuals per species.

The present study was supported by the Office of Naval Research and the Texas A&M Research Foundation. I also thank Dr. Claude E. ZoBell and Dr. Francis T. Haxo for laboratory space at the Scripps Institution of Oceanography.

STUDY SITE AND METHODS

Because descriptions of the study site and sampling methods used have been published elsewhere (Pequegnat, 1964), only a brief outline of them is given here. The rock-reef is located about 500 m offshore (referred to hereinafter as Reef 500) where, at mean sea level, its depth ranges from 9.5 m at the top to 18.5 m on the seaward bottom. Because the epifauna exhibits marked changes in composition down the reef, it has been subdivided into four zones. These zones, together with their general depth limits along the transect where the present sampling was done, are: Reef-top Zone, 9.5-12.5 m, where the important epifaunal feature is an incrustation formed by the rock oyster Chama pellucida; the Mid-reef Zone, 12.5-14.5 m, which supports a thick growth of calcareous ectoprocts; the Reef-base Zone, 14.5-16.5 m, where large sea urchins and deposit-feeding sea cucumbers predominate; and the Mixed-bottom Zone, 16.5-19 m, which is located on the adjacent sea bottom of sediments and rock slabs and which supports a mixture of infaunal and epifaunal species. In the following sections the term reef-proper will embrace the first three zones, while the term reef-complex will include the mixed-bottom as well.

All samples were taken under water through use of conventional Scuba techniques. Small species were sampled on the reef-proper from 0.1 m² quadrats, and from 0.25 m² quadrats on the mixed-bottom. Quadrats encompassing 1 m² were used to sample large species (gorgonians, sea urchins, and the like) on the reef-complex. The animals taken in samples were sorted into species, counted, and weighed dry. These general procedures were followed prior to drying: (1) mollusks were removed from their shells, (2) all tubiculous species were processed without tubes, (3) echinoderms, large decapods, and the like were decalcified, and (4) sponge and ascidian mats were picked free of motile species and rinsed free of sediments in filtered sea water.

Samples were taken during parts of 1958, 1959, and 1963. Unless specifically stated otherwise, all tabular data are based upon samples taken during all three years.

1Department of Oceanography, Texas A & M University, College Station, Texas. Manuscript received January 25, 1967.
GENERAL DISTRIBUTION OF BIOMASS

The epifaunal biomass is clearly concentrated on the upper levels of Reef 500. From the totals shown in Table 1, it is apparent that the mean biomass of the Reef-top Zone is about twice that of the Mid-reef Zone, seven times that of the Reef-base Zone, and 15 times that of the Mixed-bottom Zone. Analysis of variance of the differences in biomass among the zones of the reef-complex are highly significant at the 99% level (Tabular F (.01) = 5.70). Even though the biomass of the mixed-bottom region is a small fraction of that of the reef-top, it is large compared with that of many level-bottom communities. This is attributed to the quantities of debris and detritus swept from the reef by the strong water movements.

The top-to-bottom decline in biomass is consonant with the general decline of species and individuals, but these two entities need not be causally related. The fact that they are so related indicates that environmental conditions exist at the top of the reef and not at the base that favor the development of species whose biological characteristics include production of large standing crops. All of the largest producers of biomass attain maximum population densities on the reef's upper levels, and most of them are sessile or sedentary suspension-feeders. Among these, in descending order of biomass per m², are the sessile pelecypod Chama pellucida, a sponge mat composed of such amorphous sponges as Lissodendoryx noxiosa, the sedentary, plankton-feeding sea cucumber *Cucumaria lubrica*, and the burrowing date mussel *Lithophaga plumula*. The conditions that favor maximum development of their populations, such as ample supplies of suspended material and suitable water movements, are present only on the reef's upper levels.

BIOMASS AND FEEDING TYPES

On a weight basis, suspension-feeders predominate in all zones of the reef-complex (Table 1). They are followed in order by carnivores, scavengers, herbivores, and deposit-feeders. The principal carnivores are, in descending order of standing crop, the starfish *Pisaster giganteus*, various nemerteans, eunicid polychaetes, and gastropod mollusks. Among the principal scavengers are such crabs as *Parasen- thias taylori* and *Lophopanopenes leuconanus*, the ophiuroid *Ophioderma panamensis*, and the hermit crab *Pagristhes utreli*. The chief herbivores are the algalophagous sea urchins, the limpet *Megathura crenulata*, and such chitons as *Callistochiton crassiostratus*. The deposit-feeders are represented by the sea cucumbers *Parastichopus parvimensis* and *Leptosynapta albicans*, and the terebellid polychaete *Amphirite robusta*.

Table 1 reveals that on the reef-proper the mean weight of suspension-feeders decreases sharply from reef-top to base, as do the weights of carnivores and scavengers, though their decline is more gradual. Herbivores and deposit-

TABLE 1

<table>
<thead>
<tr>
<th>FEEDING TYPES</th>
<th>REEF-TOP</th>
<th>MID-REEF</th>
<th>REEF-BASE</th>
<th>MIXED-BOTTOM</th>
<th>MEAN WT.</th>
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<tr>
<td></td>
<td>g/m²</td>
<td>% wt.</td>
<td>g/m²</td>
<td>% wt.</td>
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<td>1120.4</td>
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<td>128.0</td>
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<td>117.1</td>
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<tr>
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<td>2.7</td>
<td>63.3</td>
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<tr>
<td>Deposit-feeders</td>
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<td>0.1</td>
<td>4.5</td>
<td>0.3</td>
<td>10.9</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td><strong>2585.2</strong></td>
<td><strong>1407.6</strong></td>
<td><strong>375.7</strong></td>
<td><strong>174.5</strong></td>
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</tr>
</tbody>
</table>

* The marked drop in total biomass between the mid-reef and reef-base zones is accounted for in part by lack of water movement and by feeding activities of sea urchins that destroy settling larvae.
feeders, on the other hand, exhibit a marked increase of biomass toward the bottom.

These patterns of biomass distribution on the reef and among the feeding types coincide well with expectations for those on a sublittoral rock-reef so situated as to have significantly higher values of water movement and suspended matter at the top than at the base (resulting from surface-wave propagation). I have already demonstrated that such a pattern of water movement exists on Reef 500 (Pequegnat, 1964). Suspension-feeders are favored by active water movement, whereas scavengers and deposit-feeders are benefited by calm waters at the reef-base that permit deposition of debris and detritus. Nevertheless, it is apparent that all feeding types are represented at every level on the reef. This permits the development of true communities that make effective use of the products of the primary producers. Some insight into the efficiency of this utilization of organic matter is revealed by the fact that the standing crop of deposit-feeders on the reef is little more than 1% that of the suspension-feeders.

**FREQUENCY OF OCCURRENCE ON QUADRATS AND INDIVIDUALS PER SPECIES**

The sublittoral epifauna displays a high degree of heterogeneity, i.e., a large percentage of species occur on a small per cent of quadrats, reflecting a poor fit of the Poisson distribution. This has a certain relationship to the production of biomass (Fig. 1). Of the 265 species of macroinvertebrates detected on the reef-proper, only 15 (6%) were found on 80–100% of quadrats (Group V), whereas 159 (60%) were found on only 0–19% of quadrats. But the latter group, even though 10 times as numerous as Group V, contribute only a tenth as much to the total biomass as do the 15 high-frequency species. Thus, the majority of species contribute very little to the standing crop biomass. Typical examples of each frequency group are: (I) the small gastropod *Seila montereyensis*, (II) the terebellid polychaete *Thelepus crispus*, (III) the holothuroid *Cucumaria lubrica*, (IV) the starfish *Pisaster giganteus*, and (V) *Chama pellucida*. The largest contributors to the biomass are suspension-feeders that of intermediate size, have a tendency to aggregate, are broadly adapted to the changing physicochemical factors on the reef’s vertical axis, and are either colonial or represented by large numbers of individuals.

Taking the species of the four most important noncolonial phyla on the reef-proper (viz., Mollusca, Arthropoda, Echinodermata, and Annelida), the mean number of individuals per square meter of those species occurring on 80–100% of quadrats is 283, while for the 0–19% group the mean drops to only 3. Apparently the multiplicity of microhabitats present on a rock-reef such as this favor highly adapted species whose small populations reflect the small area of each such habitat.

These findings may appear to support Turpae’s (1957) conclusion that the basic nature of marine benthic biocoenoses can be ascertained from the dominant species alone. Perhaps this conclusion is valid for level bottom communities, but lack of critical information precludes its immediate application to complex epifaunal assemblages. We need to know that species
selected as dominants on a standing crop basis retain this rank when secondary productivities can be calculated. Also, we need to be able to recognize successional stages in the sublittoral, for until we do it is impossible to assume that a small contributor to the biomass at one time interval is not an essential part of the community over a longer time-span.

REFERENCES


Compressional Wave Velocities in Basic Rocks

Nikolas I. Christensen

ABSTRACT: Compressional wave velocities determined by measurement of travel times of pulses at pressures to 10 kilobars are given for specimens of basalt. Variations of velocity with propagation direction are related to feldspar orientation and inhomogeneity in alteration of the specimens. Velocity differences reported for diabase, gabbro, eclogite, and basalt can be explained in terms of variation of density and mean atomic weight. The basalts have the lowest compressional wave velocities of basic rocks. The low velocities are a consequence of slight alteration, high mean atomic weight, and relatively low density.

Ultrasonic measurements of the elastic properties of rocks are required for the interpretation of seismic velocities. Comparisons of seismic velocities with laboratory-measured velocities provide the simplest and most direct evidence concerning the constitution of the earth's interior. It is surprising that with the abundant velocity data now available very little attention has been given to basaltic rocks at high pressures. In this paper compressional wave velocities are reported at pressures to 10 kb for three specimens of basalt. In addition to presenting new velocity data which may be important for oceanic crustal areas, this note is part of a continuing effort to understand the factors which influence the elastic properties of rocks.

MEASUREMENT TECHNIQUE

The technique for measuring the velocities was similar to that described by Birch (1960) and Christensen (1965); therefore it is described only briefly here. The specimens were cylindrical cores, ¾ inch in diameter and 2 inches in length, jacketed with a thin copper tube. Barium titanate transducers with natural frequencies of 1 Mc/sec were placed on the ends of the specimens and then backed by aluminum electrodes. Rubber tubing was used to seal the pressure fluid from the spaces between the sample, electrodes, and transducers. Rectangular electrical pulses of about 50 volts were applied to one transducer. The resulting mechanical pulse in the sample was received by an identical transducer and converted to an electrical signal which was amplified and displayed on a dual-trace oscilloscope. Transit times were measured by comparing the signal from the rock specimen with that through a variable mercury delay line displayed simultaneously on the oscilloscope.

Kerosene was used as the pressure fluid. Pressure was generated by the advance of a piston driven by a 6-inch ram into a cylinder with an outside diameter of 6 inches and an inside diameter of 1.5 inches. Pressure was measured by determining the change in resistance of a calibrated manganin wire gage. All measurements were made at temperatures between 20° and 30°C.

DATA

Compressional wave velocities and densities are given in Table 1. Velocities are recorded for each specimen from three cores cut in mutually perpendicular directions. The velocities are considered accurate to 1%.

The basalts were collected from the Triassic Hampden basalt near Hartford, Connecticut. Petrologically they are fine-grained tholeiitic basalts. Average grain size is about 0.2 mm. Modal analyses are given in Table 2.

DISCUSSION

Anisotropy in the basalts is related to variations in composition of the three cores from each sample and a subparallel orientation of plagioclase laths. Directions of low velocity in
TABLE 1

COMPRESSINAL WAVE VELOCITIES IN BASALT
(km/sec)

<table>
<thead>
<tr>
<th>SAMPLE</th>
<th>DENSITY (g/cc)</th>
<th>PRESSURE (kb)</th>
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<tr>
<td></td>
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<td>0.5</td>
</tr>
<tr>
<td>Basalt 1</td>
<td>2.91</td>
<td>5.8</td>
</tr>
<tr>
<td>Basalt 2</td>
<td>2.91</td>
<td>5.9</td>
</tr>
<tr>
<td>Basalt 3</td>
<td>2.88</td>
<td>5.6</td>
</tr>
<tr>
<td>Mean</td>
<td>2.90</td>
<td>5.8</td>
</tr>
</tbody>
</table>

TABLE 2

MODAL ANALYSES OF BASALTS
(Percentages by Volume)

<table>
<thead>
<tr>
<th>ROCK</th>
<th>PLAGIOCLASE</th>
<th>PYROXENE</th>
<th>MAGNETITE</th>
<th>CALCITE</th>
<th>SERICITE + CHLORITE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basalt 1</td>
<td>53.4</td>
<td>26.5</td>
<td>7.2</td>
<td>3.2</td>
<td>9.7</td>
</tr>
<tr>
<td>Basalt 2</td>
<td>54.2</td>
<td>25.3</td>
<td>6.9</td>
<td>3.0</td>
<td>7.6</td>
</tr>
<tr>
<td>Basalt 3</td>
<td>55.8</td>
<td>30.2</td>
<td>6.9</td>
<td>2.6</td>
<td>4.5</td>
</tr>
</tbody>
</table>

basalts 1 and 3 correspond to cores of relatively low density. The low densities are the result of slight alteration of pyroxene to chlorite and sericitization of plagioclase. No preferred orientation of minerals was observed in either sample. Petrographic examination of basalt 2 revealed a rough subparallel orientation of lath-shaped plagioclase crystals. Normals to the (010) twin planes of plagioclase concentrate in the direction of highest velocity. This is consistent with relatively high compressional wave velocities normal to (010) in single crystals of feldspar reported by Christensen (1966a).

Manghnani and Woollard (1965) have correlated elastic wave velocities in basalts at low pressures with glass content, olivine content, and volume percent of vesicles. The samples in the present study contain no microscopically visible glass or vesicles. Therefore, with the exception of a slight lowering of velocity due to alteration, the samples represent nearly maximum velocities for olivine-free basalts with tholeiitic composition. As will be considered in detail below, the basalts have lower velocities than other varieties of basic rocks. It is somewhat surprising that compressional wave velocities in several granites reported by Birch (1960) are close to the velocities of the basalts at equivalent pressures. The basalt velocities are also equivalent to partially serpenitized peridotites containing approximately 50% serpentine (Christensen, 1966b).

Birch (1961) found a difference in velocity of about 5% between the means for diabase and gabbro. This difference presented a problem since the reported densities were about the same, and diabase and gabbro are generally considered to be approximately equivalent in chemical composition. Birch (1961) and Christensen (1965) postulated that the discrepancy may actually be the result of differences in chemical composition of the two rock types.

The mean compressional wave velocity at 10
Compressional Wave Velocities in Rocks—Christensen

kb for the 9 cores of basalt is 6.34 km/sec. This is 0.52 km/sec lower than the mean reported by Birch (1961) for 15 specimens of diabase and 0.87 km/sec lower than the mean for 9 specimens of gabbro. The relatively low velocities of the basalts are due in part to their low densities. This is illustrated in Figure 1, where 10 kb velocities have been plotted against densities for eclogites, gabbros, diabases, and basalts reported by Birch (1960), Kanamori and Mizutani (1965), and this paper.

Birch (1961) has shown that compressional wave velocity is not a single-valued function of density, but also depends upon the mean atomic weight ($m$) of a rock. Birch's straight line solutions for mean atomic weights of 21 and 22 are shown in Figure 1. The points in Figure 1 suggest that important chemical differences (i.e., different values of $m$) which influence elastic properties may be present in basic rocks. Eclogites and basalts appear to have relatively high values of mean atomic weight. Lower values are suggested for diabases and gabbros.

Mean atomic weights calculated from chemical analyses are highest for basalts and eclogites and lowest for gabbros. In Table 3 values of $m$ have been calculated from average chemical analyses for basalts, gabbros, diabases, and eclogites. Since the mean atomic weight of a rock is usually a measure of its iron content (Birch, 1961), total iron contents calculated from the

![Fig. 1. Velocity at 10 kilobars versus density for basic rocks.](image)

reported percentages of FeO and Fe$_2$O$_3$ are also given for the rocks in Table 3.

Figure 1 and Table 3 show that Birch's correlation of compressional wave velocity with density and mean atomic weight holds remarkably well for basic igneous rocks. Basalt, which is free of glass and vesicles, falls near the line for $m = 22$. This agrees with chemical analyses of basalt. Laboratory measured velocities and chemical analyses of eclogite also suggest mean atomic weights near 22. Lower mean atomic weights and intermediate densities of gabbros and diabases produce compressional wave ve-

<table>
<thead>
<tr>
<th>ROCK</th>
<th>MEAN ATOMIC WEIGHT</th>
<th>PERCENT TOTAL IRON</th>
<th>REFERENCE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Norite</td>
<td>21.5</td>
<td>6.71</td>
<td>Nockolds (1954)</td>
</tr>
<tr>
<td>Pyroxene gabbro</td>
<td>21.6</td>
<td>7.33</td>
<td>Nockolds (1954)</td>
</tr>
<tr>
<td>Gabbro</td>
<td>21.7</td>
<td>6.83</td>
<td>Clarke (1966)</td>
</tr>
<tr>
<td>Olivine gabbro</td>
<td>21.7</td>
<td>7.70</td>
<td>Nockolds (1954)</td>
</tr>
<tr>
<td>Hornblende gabbro</td>
<td>21.8</td>
<td>7.99</td>
<td>Nockolds (1954)</td>
</tr>
<tr>
<td>Diabase</td>
<td>21.8</td>
<td>8.72</td>
<td>Clarke (1966)</td>
</tr>
<tr>
<td>Olivine diabase</td>
<td>21.9</td>
<td>9.03</td>
<td>Clarke (1966)</td>
</tr>
<tr>
<td>Tholeiitic olivine basalt</td>
<td>21.9</td>
<td>9.23</td>
<td>Nockolds (1954)</td>
</tr>
<tr>
<td>Tholeiitic basalt</td>
<td>22.0</td>
<td>9.05</td>
<td>Nockolds (1954)</td>
</tr>
<tr>
<td>Olivine-rich alkali basalt</td>
<td>22.1</td>
<td>9.74</td>
<td>Nockolds (1954)</td>
</tr>
<tr>
<td>Plateau basalt</td>
<td>22.1</td>
<td>10.10</td>
<td>Clarke (1966)</td>
</tr>
<tr>
<td>Alkali basalt without olivine</td>
<td>22.2</td>
<td>8.76</td>
<td>Nockolds (1954)</td>
</tr>
<tr>
<td>Alkali basalt</td>
<td>22.2</td>
<td>8.99</td>
<td>Nockolds (1954)</td>
</tr>
<tr>
<td>Eclogite</td>
<td>22.2</td>
<td>10.58</td>
<td>Coleman et al. (1965)</td>
</tr>
</tbody>
</table>
Locities which are higher than basalts and lower than eclogites. Lower velocities of diabases compared with gabbros are primarily related to differences in chemical composition.

ACKNOWLEDGMENTS
I am indebted to Professor Francis Birch for the use of the facilities at Hoffman Laboratory, Harvard University. Dr. Joseph Martinez contributed the samples of basalt for the study. The study was financed, in part, by the Advanced Research Projects Agency of the Air Force Office of Scientific Research through contract SD-88.

REFERENCES
Antarctic Ocean-Floor Fossils: Their Environments and Possible Significance as Indicators of Ice Conditions

CHARLES W. THOMAS

ABSTRACT: Seven Antarctic marine environments are examined with respect to their geology and to the skeletal remains of marine microorganisms. While all assemblages live in the same water mass, they vary significantly from place to place. Geology and oceanography of each locality appear to produce less effect upon the character of populations than do topography and bay ice. The latter features suggest a possible use of fossils as indicators of conditions of bay ice.

DURING THE ESTABLISHMENT by the U. S. Navy of permanent scientific bases in the Antarctic, from 1955 to 1957, coring and Orange Peel sampling of the ocean bottom was carried out under the general supervision of Dr. Willis L. Tressler, Senior Oceanographer assigned to U. S. Naval Task Force 43. This subdivision of command was responsible for the Navy's commitment in Antarctica. The author of this report was Chief of Staff.

General areas of ocean-bottom sampling considered in this paper are: Ross Barrier, McMurdo Sound, Hallett Inlet, Robertson Bay, Sabrina Coast, and Knox Coast. During the period of this study the Bay of Whales, once carved in the Ross Ice Shelf, was not extant, having been erased by iceberg-calving some time between 1947 and 1954. Since it was not possible to carry out sampling there, the Gould material, collected from the Bay of Whales in 1929 and analyzed by Warthin (1934), is considered in this paper.

The region represented in Gould's sampling is from the Bay of Whales to the Knox Coast (Clark Peninsula) (Fig. 1). This sector encompasses ca. 2,100 miles of the periphery of Antarctica, extending through ca. 90° of longitude. This continental periphery is washed by the Circumpolar Countercurrent, an easterly current generated by prevailing winds and directed by Coriolis force. Surface temperatures range from $-1.62^\circ \text{C}$ to $-2.13^\circ \text{C}$; bottom temperatures, from $-1.00^\circ \text{C}$ to $-1.85^\circ \text{C}$. The surface current attains velocities as high as 3 knots (author's observation).

THE STATIONS

Sampling was undertaken at the following stations:

Bay of Whales: In 1929 (when the Gould material was collected), the Bay of Whales was an indentation in the Ross Ice Shelf 13 miles long by 5 miles wide. During its life the embayment's shape and dimensions were constantly changing. As far as anyone knows, bay ice was swept out of the bay every year. Breakup generally occurred in January or February when winds produced waves which entered the bay and cracked the ice. The Gould collection of sediments was made at 78°34'S, 163°48'W in 548 m of water. The outer limits of the Ross Ice Shelf are known to fluctuate (Thomas, 1960) and an embayment (Discovery Inlet) once occupied the area where the sampling was made. However, this location now generally features hummocky sea ice during the greater part of the year. It is free of fast ice during the summer months.

Arrival Bay: This is a cove in Ross Island on the eastern side of McMurdo Sound. It is separated from Winter Quarters Bay (where Scott's "Discovery" was frozen in for two years) by Hut Point. Ross Island is of Tertiary orogeny and consists chiefly of beds of lava and tuff. Mt. Erebus, an active volcano, is situated on the northwest side and Mt. Terror (now extinct) on the northeast side. There

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are several vestigial cinder cones on the island. The bay ice does not renew itself perennially. For this reason the U. S. Naval Air Facility was located at Hut Point, where heavy aircraft could land on the bay ice the year around. The sample from this location was collected in 46 m of water two days after the icebreakers "Glacier" and "Northwind" removed bay ice of 5-m thickness.

Cape Hallett: (72°18'S, 170°20'E). The cape headland (elevation ca. 1,500 m) consists of beds of lava and tuff cut by many dikes and occasionally faulted. It forms the east side of Hallett Inlet, which is 8 nautical miles long. The west side consists of Precambrian metasedimentaries which are only slightly metamorphosed and cut by intrusives. From this side Mt. Sabine rises sheerly to an elevation of 3,617 m. The mouth of the inlet is distinguished by a flat, triangular, raised beach beneath the cape headland. Hallett Beach serves seasonally as a rookery for an estimated 205,000 penguins (Carl Eklund, Scientific Adviser for the U. S. Department of Defense, personal communication). It is here that the U. S.–New Zealand Scientific Base is located. In 1956 bay ice was moving out of the inlet on the eleventh of February. In 1957, breakup of the bay ice occurred a month earlier, due no doubt to icebreaker preparation of a staging area at the entrance. On January 5, 1957 bay ice exceeded 3 m in depth throughout the length of the inlet. Dependability of the bay ice for aircraft operations most of the year was an important factor in its selection as a base site. The sample considered herein was collected near the mouth of the inlet in 200 m of water.

Robertson Bay: This is an embayment 20 miles long at Cape Adare (71°21'S, 170°00'E). The environment has been described by Priestly (1923). In brief, it resembles McMurdo Sound and Hallett Inlet geomorphologically, in that it was formed by a fault. The east side is of Tertiary origin and the west of earlier origin.
On the east side lava beds are cut by dikes and sills, while on the west side metasedimentary beds are intruded and heavily folded.

Ridley Beach, at the foot of Cape Adare, is a larger-scale version of Hallett Beach and supports a correspondingly larger population of penguins. Borchgrevink wintered here in 1898. The hut erected by him and used by Scott's northern party in 1912 is still intact.

The sample was taken in 402 m of water off Pressure Bay, on the west-central side of Robertson Bay. According to Priestly and Wright (1922) the ice in this location (as the name implies) is hummocky and unstable. Catastrophic breaks caused by violent winds and glacial activity create turbulent sea ice conditions. The present author steamed to the head of Robertson Bay in January, 1956 without sighting a vestige of bay ice. At the same time, the south part of McMurdo Sound and Hallett Inlet were frozen solid.

**Sabrina Coast:** The coast is an ice barrier throughout its length. No embayments of any consequence are carved in it. The pack ice is perennial, with consolidated fields of hummocky ice persisting until November or December. It stays this way until April, when floes break up, and then coverage varies between close and loose pack. The sea bed was sampled at 65°61'S, 119°21'E in a depth of 586 m.

**Clark Peninsula:** This is a headland approximately 3 miles long by 2 miles wide (maximum). It has been described in detail by Hollin and Cameron (1961). At the distal end of the peninsula the inland ice terminates in a heavily morained area. Outcrops are basically highly metamorphosed sedimentaries with garnet inclusions. These rocks have been intruded by granites and scored by dikes and sills of hornblendeit, muscovite, and olivine, and by orthoclase and plagioclase feldspars.

Ice conditions at Vincennes Bay, wherein Clark Peninsula is located, are said to be turbulent with catastrophic breaks often producing open water in the winter. After breakup in the summer the area is kept generally ice-free by the Balaena Islets. These land masses dam the southwesterly drift of pack and glacial ice.

The bottom was sampled 450 m off Wilkes Station at 66°16'S, 110°34'E in 75 m of water. Organic remains in bottom sediments were exclusively diatomaceous.

**DISCUSSION**

An examination of sediment analyses (Tressler, 1957) shows the dominant material at each station: Kainan Bay (30 miles east of Bay of Whales)—feldspar, 50%; Arrival Bay—siliceous sponge spicules and small shell fragments, 100%; Hallett Inlet—shells, 30%; Robertson Bay—feldspar, 40%; Clark Peninsula—feldspar, 50%.

No analysis was made of the Sabrina Coast material.

Table 1 shows the incidence of skeletal remains of microorganisms in each of the locations sampled.

In his discussion of the Gould collection of Bay of Whales sediments, Warthin (1934) remarks, "Although foraminifera with secreted calcareous tests comprise one-sixth of the species, they make up only 7.2 percent of the individuals present. This condition is markedly different from that found by the *Terra Nova* expedition on the western side of the Ross Sea where 60 percent of the species collected were calcareous."

The foraminifera listed in the table which have calcareous tests comprise the following percentages of species and individuals at stations indicated:

<table>
<thead>
<tr>
<th>STATION</th>
<th>PERCENTAGE OF CALCAREOUS SPECIES</th>
<th>PERCENTAGE OF CALCAREOUS INDIVIDUALS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ross Barrier</td>
<td>2.0</td>
<td>7.0</td>
</tr>
<tr>
<td>Arrival Bay</td>
<td>67.0</td>
<td>92.0</td>
</tr>
<tr>
<td>Cape Hallett</td>
<td>82.0</td>
<td>75.0</td>
</tr>
<tr>
<td>Robertson Bay</td>
<td>30.0</td>
<td>25.0</td>
</tr>
<tr>
<td>Sabrina Coast</td>
<td>33.0</td>
<td>35.0</td>
</tr>
</tbody>
</table>

Ostracod carapaces were present only in the Arrival Bay and Cape Hallett sediments. Radiolarian skeletons, on the other hand, were absent in these sediments and present only in the Ross Barrier, Robertson Bay, and Sabrina Coast materials. Warthin (1934) mentioned the presence of radiolaria in the Gould collection from the Bay of Whales. They were not identified.

Bearing in mind that the Bay of Whales, Ross...
### Table 1
Table of Organic Remains

<table>
<thead>
<tr>
<th>SPECIFIC NAME</th>
<th>FORAMINIFERA</th>
<th>INCIDENCE OF OCCURRENCE</th>
<th>ROSS BARRIER</th>
<th>ARRIVAL BAY</th>
<th>CAPE HALLETT</th>
<th>ROBERTSON BAY</th>
<th>SABRINA COAST</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Rhabdammina discreta</strong> Brady</td>
<td>O</td>
<td>0</td>
<td>O</td>
<td>A</td>
<td>A</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Marisella cylindrica</strong> Brady</td>
<td>A</td>
<td>O</td>
<td>O</td>
<td>R</td>
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<td></td>
</tr>
<tr>
<td><strong>M. elongata</strong> Norman</td>
<td>R</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Saccammina sphaerica</strong> M. Sars</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td>R</td>
<td>O</td>
<td></td>
<td></td>
</tr>
<tr>
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<td>O</td>
<td>O</td>
<td>A</td>
<td>A</td>
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<td></td>
</tr>
<tr>
<td><strong>Bathysiphon filiformis</strong> M. Sars</td>
<td>R</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Psammophax fusca</strong> Schultze</td>
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<td>O</td>
<td>C</td>
<td>A</td>
<td>A</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>P. testudinaria</strong> Rhumbler</td>
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<td>O</td>
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<td>O</td>
<td></td>
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</tr>
<tr>
<td><strong>Psammophax conscia</strong> Rhumbler</td>
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<td>A</td>
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<tr>
<td><strong>Saccorbiza ramosa</strong> (Brady)</td>
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<tr>
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<td>O</td>
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<td></td>
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<tr>
<td><strong>T. spumosa</strong> Earland</td>
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<td>O</td>
<td>R</td>
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<td>O</td>
<td></td>
<td></td>
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<tr>
<td><strong>Pelosina elongata</strong> Wiesner</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td>A</td>
<td>R</td>
<td></td>
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<tr>
<td><strong>P. bicaudata</strong> Parr</td>
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<td>O</td>
<td>O</td>
<td>C</td>
<td>R</td>
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<td></td>
</tr>
<tr>
<td><strong>Reophax tubulata</strong> (Rhumbler)</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td>A</td>
<td>A</td>
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<td></td>
</tr>
<tr>
<td><strong>R. fusiformis</strong> Williamson</td>
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<td>O</td>
<td>O</td>
<td>C</td>
<td>A</td>
<td></td>
<td></td>
</tr>
<tr>
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<td>O</td>
<td>O</td>
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<td>A</td>
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<tr>
<td><strong>R. bulbosa</strong> Chapman and Parr</td>
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<td>O</td>
<td>O</td>
<td>O</td>
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<td></td>
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<tr>
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<td>O</td>
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<tr>
<td><strong>R. distans</strong> Brady</td>
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<td>O</td>
<td>R</td>
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<tr>
<td><strong>R. nodulosus</strong> Brady</td>
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<td>O</td>
<td>O</td>
<td>C</td>
<td>A</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>R. pilulifera</strong> Brady</td>
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<td>O</td>
<td>O</td>
<td>O</td>
<td>O</td>
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<td></td>
</tr>
<tr>
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<td>O</td>
<td>O</td>
<td>C</td>
<td>O</td>
<td></td>
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</tr>
<tr>
<td><strong>Hormosina orbicula</strong> Brady</td>
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<td>O</td>
<td>O</td>
<td>C</td>
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<tr>
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<td>R</td>
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<tr>
<td><strong>Trochammina ocbacea</strong> Williamson</td>
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<tr>
<td><strong>T. globigeriniformis</strong> Parker and Jones</td>
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<td>R</td>
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<tr>
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<td>A</td>
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<td>O</td>
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<td></td>
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<tr>
<td><strong>T. turbinata</strong> Brady</td>
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<td>O</td>
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<tr>
<td><strong>T. nana</strong> Brady</td>
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<td>O</td>
<td>O</td>
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<tr>
<td><strong>Ammodiscus incertus</strong> d'Orbigny</td>
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<td>R</td>
<td>C</td>
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<tr>
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<td><strong>Patellina antarctica</strong> Parr</td>
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**OSTRACODA**

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**RADIOARIA**

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Barrier, Robertson Bay, and Sabrina Coast environments are ones of unstable sea ice conditions, it seems significant that siliceous or arenaceous skeletal remains are dominant among organic material in the sediments. And it appears equally significant that calcareous shells are dominant in the sediments of Arrival Bay and Cape Hallett—where the sea ice cover is stable and smooth.

McKnight (1962) said, "...the calcareous benthonic populations (of foraminifera) are believed to be in areas of little or no bottom current, and the arenaceous populations to be in areas of either greater depths or bottom currents." McKnight attributed the high percentage of calcareous benthonic foraminifera to a lack of deposition of ice-rafted clastics, giving an apparent increase in production.

The evidence seems to support McKnight's postulation of ice-rafting, since feldspar dominates the sediments where sea ice is unstable. Tessler (1957) measured the thickness of unstable hummocky pack ice in the western Ross Sea in late October. He found that most of the ice scarcely exceeded 3–4 ft in thickness. It is indeed possible for an iceberg to plow through this kind of ice and to enter embayments such as Robertson Bay. But an iceberg cannot penetrate stable bay ice that is thick, to encroach upon an embayment.

In concurrence with McKnight's belief (1962) the evidence shows that calcareous shells are dominant in embayments where the ice-cover is stable and bottom currents are weak. This might well result in an "isolated" benthonic environment where the amount of bound carbonate enhances the production of calcareous shells. Since radiolaria are planktonic, it is unlikely that their skeletal remains will be found in embayments which are isolated from the body of the current.

**CONCLUSION**

From the foregoing it appears that knowledge of the amount of calcareous remains in the sediments of an unobserved Antarctic location would be of value in determining the suitability of the ice-cover for aircraft and staging operations. Moreover, such information is likely to be of even greater value to submarine stratigraphy and its application to paleo-oceanography.

**REFERENCES**


Preliminary Observations on the Fine Structure of Species of **Micromonospora** (Actinomycetales)

**DIANA D. KENNER**, **HANS-RUDOLF HOHL**, and **GLADYS E. BAKER**

The genus *Micromonospora* was first described by Ørskov in 1923 as a member of the Actinomycetales characterized by unicellular mycelium and the production of single, terminal conidia. The genus was little known for some time (Jensen, 1930), but subsequently the frequent occurrence of micromonosporae in soil (Jensen, 1932), lake bottoms (Erikson, 1941; Potter and Baker, 1956) and lake water (Potter and Baker, 1956), became well recognized. In spite of this wide acquaintance with the genus, the general morphology and cell structure is still not well understood and descriptions are sometimes at variance. The chemical composition of the actinomycete wall, including micromonosporae, (Erikson, 1947; Avery and Blank, 1951; Yamaguchi, 1965) is better documented than is the general morphology of the cell structure. Ultrastructure studies are few to date, and provide little detail (Agre, 1962; Leudemann and Brodsky, 1964). Both of these studies were concerned primarily with spores. A paper by Arai, Koyama, Kuroda, and Honda (1964) is more definitive for both mycelium and spores. It also includes some electron micrographs.

The small size of the mycelium and spores in the micromonosporae has made study with the light microscope difficult and, in part, accounts for the lack of critical morphological and cytological information. Waksman (1961) characterized the substrate or vegetative hyphae as straight or curved, branching, and without cross-walls. The lack of cross-walls has been accepted widely (Jensen, 1930; Erikson, 1941; Krasil’nikov and Agre, 1965), although in 1964 Arai et al. illustrated septa.

There is increasing recognition of the economic importance of the micromonosporae as sources of antibiotics (Leudemann and Brodsky, 1964; Weinstein, Leudemann, Oden, and Waggman, 1965) and as etiologic agents of disease in man (Castellani, De Brito, and Pinto, 1959). In view of this and of the discrepancies among reports on their structure, there is need for a consistent comparative study of the general cell structure and the process of spore production in the group. Consequently, studies at the ultrastructural level were undertaken for three species: *Micromonospora fusca* Jensen (isolated from Flathead Lake water, Potter, No. M-1012); *M. purpurea* Leudemann and Brodsky (NRRL No. 2953); and *M. sp.*, isolated from a foot lesion at the University of Miami. All cultures came from the collection of Dr. Louise F. Potter, Biology Department, Elmira College, Elmira, New York.

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**Fig. 1.** *Micromonospora fusca*, showing the electron-dense cytoplasm and fibrillar nucleoid. The two roundish masses probably represent prespores. × 32,000.

**Fig. 2.** Spore of *Micromonospora fusca*, showing the sculptured spore wall. × 26,000.

**Fig. 3.** *Micromonospora purpurea*, with septum and Y-shaped branching. × 25,000.

**Fig. 4.** *Micromonospora purpurea*, with prespore in form of a constricted and bulbous hyphal tip; Y-shaped branching as in Figure 3. × 22,500.

**Fig. 5.** *Micromonospora purpurea*, showing general cell morphology and septa of various thicknesses. × 22,500.

**Fig. 6.** Example of septate hypha in pathogenic *Micromonospora* spp. × 22,500.

**Fig. 7.** Longitudinal section through hypha of *Micromonospora purpurea*, demonstrating the frequent occurrence of septa. × 25,000.
Fine Structure of *Micromonospora*—Kenner, Hohl, and Baker
MATERIALS AND METHODS

Cultures were grown in broth on a Gyrotary shaker (New Brunswick Scientific Co.) at 200 rpm for three to four days. Sodium caseinate broth (Fred and Waksman, 1928) as modified by L. F. Potter (BBL No. 01-549) was the medium of choice. Fixation and embedding were performed according to the standard procedures of Kellenberger and Ryter (1958). Sections were cut on a Porter-Blum ultramicrotome and poststained with lead citrate. Electron micrographs were obtained on a Norelco EM 75 microscope.

RESULTS

The preliminary findings reported here demonstrate that the technique employed offers promise for its use in future investigations. All pictures taken clearly show the procaryotic nature of the three Micromonospora species: the nuclear areas are fibrillar and not surrounded by a membrane; the cytoplasm is densely granular and essentially devoid of lamellar organelles.

The hyphae of all three species sectioned (Figs. 1, 6, 7) show cross-walls or septa. These are particularly numerous in M. purpurea (Figs. 3, 4, 5, 7). Apparently there are no septal pores. Some branching was observed (Figs. 3, 4, 7). Spore formation seems to be initiated by the development of a heavy septum or plug within the hypha which isolates the apical end of the hypha as a roundish, somewhat enlarged structure filled with both cytoplasmic and nuclear material (Figs. 1, 4). The final spore (Fig. 2) has a sculptured wall. Wall sculpturing was shown by Leudemann and Brodsky (1964) on the spores of M. echinospora, but their pictures are completely devoid of inner detail.

DISCUSSION

Despite the preliminary nature of this report several points are worth emphasizing. The procaryotic nature of the cells has been established definitely for all three Micromonospora studied. Septa, which are particularly abundant in M. purpurea, are demonstrated clearly in all the strains considered: there should be no question of the occurrence of cross-walls in these three micromonosporae. The interpretation of the branched cells is less clear. This might be interpreted as true branching or as the result of anastomosis of two hyphae. Leudemann and Brodsky (1965) reported sectoring in colonies of M. carbonacea which represented sporulating and non-sporulating areas. They compared this to the well-known heterocaryotic behavior in fungi. Both anastomosis and sectoring are suggestive evidence which calls for confirmation in the entire group of micromonosporae.

SUMMARY

Electron microscope studies of three species of the genus Micromonospora were made to clarify the scanty and conflicting information about cellular structure in this group. All materials revealed clearly the procaryotic nature of the cells and the presence of definite cross-walls in the hyphae.

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An Account of the Species of *Polysiphonia* of the Central and Western Tropical Pacific Ocean

I. Oligosiphonia

**George J. Hollenberg**

**ABSTRACT**

Twenty-four tetrasiphonous species are described. The following species or varieties are new: *Polysiphonia anomala*, *P. apiculata*, *P. delicatula*, *P. flaccidissima* var. *decimera*, *P. flaccidissima* var. *iki*, *P. flaccidissima* var. *lopi*, *P. hawaiiensis*, *P. herpa*, *P. pokol*, *P. pokol* var. *longii*, *P. profunda*, *P. pseudovillum*, *P. quadrata*, *P. rubrobiza*, *P. setacea*, *P. sphaerocarpa* var. *distans*, *P. sphaerocarpa* var. *filifera*, *P. subtilissima* var. *abbottae*, *P. tenuis*, *P. tuberosa*, *P. scopulorum* var. *macrotichia*, *P. scopulorum* var. *minima*. The following new combinations are made: *P. saccorbiza* (Collins and Hervey) comb. nov., *P. sparsa* (Setchell) comb. nov., *P. scopulorum* var. *villum* (J. G. Agardh) comb. nov., *P. mollis* var. *tongatensis* (Harvey) comb. nov.

This paper includes the results of studies made in 1962 of Dr. Maxwell Doty’s collection of marine algae at the University of Hawaii, and of collections made by the author during 1948 in the Marshall Islands and in 1964–1965 of collections by Doty from widely scattered islands of the central and western tropical Pacific Ocean.

The taxonomically important features of the genus *Polysiphonia*, such as the number of pericentral cells, cortication, the nature and arrangement of trichoblasts, the origin of branches in relation to trichoblasts, and the nature of the spermatangial branches were pointed out in previous papers (Hollenberg, 1942a, 1942b, 1944, 1961) and still earlier by Falkenberg (1901) and others. Also it was previously recognized that the connection between the rhizoids and the pericentral cells bearing them is a feature of dependable taxonomic value. Not sufficiently recognized in earlier work on the genus is the nature of the apex of the rhizoids. In general the writer’s observations indicate that the length and abundance of rhizoids and whether or not the tip is digitate is a variable feature for a given species, dependent largely on the nature of the substratum and to some extent on the proximity of other plants or branches of the same plant. The degree of development of trichoblasts and their persistence is likewise a variable feature in most species.

On the other hand the development of multicellular rhizoids, by cutting off a series of cells from the apex, seems to be a more constant feature of considerable taxonomic importance. Although in some species gradations may occur, in general in mature rhizoids the apex is either clearly multicellular or simple to merely digitate in a given species when in contact with a firm substratum. Also the point of origin of rhizoids is characteristic for certain species. It was previously pointed out (Taylor, 1945:302) that the rhizoids arise mostly on the distal end of the pericentral cells (nearest the branch tip) in *P. bowei*, as they seem to do in all species of *Herposiphonia*, whereas in most species of *Polysiphonia* they arise on the proximal end or from the center of the pericentral cell.

Three species, *P. scopulorum*, *P. sparsa*, and *P. saccorbiza*, formerly considered as species of *Lophosiphonia* are included in this paper. In a former paper (Hollenberg, 1942a) it was concluded best to follow Setchell and Gardner (1903) in placing *P. villum* J. G. Agardh in the genus *Lophosiphonia* even though in a number of species of *Polysiphonia*, which are not chiefly prostrate in habit, erect branches com-

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1 Species with five or more pericentral cells will be treated in a later paper. This study was made possible through the support of research grant No. GB-2735 of the National Science Foundation.

2 University of Redlands, Redlands, California. Manuscript received January 17, 1967.
monly arise endogenously from the prostrate branches. The chiefly prostrate habit has often in practice been almost the sole criterion for distinguishing Lophosiphonia from Polysiphonia. Kylin (1956) emphasized another feature characteristic of many species generally placed in the genus Lophosiphonia, a feature which was included in the original description of the genus. This feature, the dorsiventrality of the shoot apex, is well exemplified in L. cristata Falkenberg, in which trichoblasts are unilateral. However, dorsiventrality may be determined by various factors in addition to the habit and manner of origin of erect branches from prostrate branches, or the unilateral branching of erect branches. In certain species of Polysiphonia short and more or less determinate erect branches arise cicatricgenously from spirally arranged primordia resembling scar-cells on the prostrate branches. Such prostrate branches are certainly not basically dorsiventral in spite of the seemingly dorsiventral habit. Furthermore, in certain species of Polysiphonia the first formed pericentral cell of a given segment is directly distal to or above the first formed pericentral cell of preceding segments. This is one type of dorsiventrality (unilaterality), and in such species the tetrasporangia likewise develop in a straight row rather than in a spiral arrangement as in most species. However, in species in which the tetrasporangia are in nonspiralling rows, the trichoblasts, if present, are spirally and not unilaterally arranged. In such cases one is at a loss to decide whether the apex of erect branches is radial or bilateral in construction unless one designates the determining feature or features.

Accordingly, the writer is presently of the opinion that the genus Lophosiphonia should include only those species which have the following features: (1) chiefly prostrate habit, (2) endogenous origin of erect, mostly simple, and more or less determinate branches from the prostrate branches; and (3) dorsiventral or bilateral apex of all branches, as evidenced by unilateral origin of either lateral branches or trichoblasts on the erect branches, or both.

In the following account when the positions of trichoblasts are described as 'one per segment' this indicates an arrangement in which more accurately a trichoblast or a scar-cell occurs on each segment not bearing a branch. It should also be noted that branches sometimes appear to arise in connection with trichoblasts when in fact they arise, as is frequently the case in P. tuberosa, in a delayed exogenous manner from the primordial cell which bears the trichoblast before the latter is shed.

The following symbols indicate the chief collectors of the materials studied: Da., E. Y. Dawson; D., Maxwell S. Doty, University of Hawaii; G., Malvern Gilmartin Jr., University of Hawaii; H., G. J. Hollenberg; T., and B., G. Hollenberg, Roy Tsuda, and R. Buggeln; L., C. R. Long, graduate student at the University of Hawaii; and T., Roy T. Tsuda, graduate student at the University of Hawaii at the time.

All D. collections were made by Maxwell S. Doty unless otherwise indicated. Further ecological data concerning collections at the University of Hawaii are given in his notebooks. Most of the dredged materials from Hawaii with Doty numbers were from collections made by Tetsue Matsui on the Pele Expeditions sponsored by Mrs. Mary Eleanor King and the Bernice P. Bishop Museum.

Relatively few dried herbarium mounts of Polysiphonia from the areas concerned are available for study. Furthermore, it is very difficult to make dependable determinations of most of these small algae from dried materials. Hence exsiccata have been studied to only a limited extent and mostly in the study of types or otherwise authentic material. Herbarium specimens examined other than types are indicated as follows: BISH, Bishop Museum, Honolulu, Hawaii; C, University of California, Berkeley.

The chief areas represented in the study are treated in the following sequence with the following approximate latitudes and longitudes: Midway Island (28°N, 177°W); Hawaiian Islands (19–28°N, 155–176°W); Johnston Island (16°N, 169°W); Line Islands (2–7°N, 157–162°W); Marquesas Islands (10°S, 140°W); Tuamotu Archipelago (25–16°S, 130–150°W); Phoenix Islands (5–7°S, 170–174°W); American Samoa (13–14°S, 168–170°W); Fiji Islands (15–21°S, 178°W to 176°E); Gilbert Islands (2–3°N, 172–177°E); Marshall Islands (4–14°N, 161–
171°E); Caroline Islands (4–8°N, 49–140°E); Philippine Islands (5–20°N, 120–127°E).

All types will be stored at the Smithsonian Institution, Washington, D.C. Isotypes or syntypes and hundreds of glucose microslide mounts representing nearly every listed collection and some not listed in the following account will be stored at the University of Hawaii.

Most of the species from the tropical Pacific area are small to minute. Species occurring in harbors and similar locations are somewhat larger. Those from small remote islands such as Johnston Island are notably smaller than those from larger land masses. It seems likely that availability of micronutrients may be a factor related to plant size.

**KEY TO THE SPECIES OF Polysiphonia**

1. With 4 pericentral cells .................................................................................................................. 2
2. With more than 4 pericentral cells (Part II of this study) ....................................................... \textit{P. baucockii}
2. Main branches corticated, at least at the base ............................................................................... 26
3. All branches without cortication ................................................................................................. 3
4. Rhizoids large, saccate, and prominently pigmented ................................................................... 4
5. Rhizoids not pigmented ............................................................................................................... 5
6. Chiefly erect from a basal tuft of rhizoids .................................................................................. \textit{P. rubrobriza}
7. Chiefly prostrate, with distributed rhizoids ................................................................................ \textit{P. saccorhiza}
8. Median parts of erect branches mostly 200µ or more in diameter ........................................... 6
9. Median parts of erect branches mostly 150µ or less in diameter ................................................ 9
10. Fruiting branches prominently narrowed at the base ................................................................. \textit{P. beaudetii}
11. Fruiting branches not prominently narrowed at the base .......................................................... 7
12. Commonly 3–5 cm high, with branches mostly widely divaricate and with branch tips more or less dichotomously branched .............................................................. \textit{P. hawaiensis}
13. Mostly less than 2 cm high, branches not widely divaricate ......................................................... 8
14. Segments in branch tips very short for many segments back of tapering apices; branching mostly alternate above ................................................................................................. \textit{P. sparsa}
15. Segments in branch tips otherwise; branching more or less pseudodichotomous at apices .................................................................................................................. \textit{P. sphaerocarpa}
16. Erect branches with a trichoblast, a scar-cell or a branch at every segment except those near the base of a branch .............................................................. \textit{P. tenuis} and \textit{P. delicatula}
17. With limited to extensive prostrate branches ................................................................................ 10
18. Attached by a basal tuft of rhizoids, with usually no creeping branches; plants epiphytic ........ \textit{P. tatatiari}
19. With prominent prostrate branches and with erect branches simple or with only a few lateral branches .................................................................................................................. 12
20. Chiefly erect and branched, with mostly limited prostrate branches ........................................... 16
21. With no scar-cells on prostrate branches .................................................................................. \textit{P. tenuis}
22. With scar-cells on prostrate branches ...................................................................................... 13
23. Scar-cells on prostrate branches divided into a group of small cells ........................................ \textit{P. herpa}
24. Scar cells mostly undivided ........................................................................................................ 14
25. Erect branches 50µ or less in diameter ....................................................................................... 15
26. Erect branches 100µ or more in diameter .................................................................................. \textit{P. poko}
27. Erect branches mostly less than 1 mm high, with relatively huge trichoblasts ......................... \textit{P. anomalä}
28. Erect branches commonly 2 or more mm high; trichoblasts relatively small ........................ \textit{P. delicatula}
29. Branches arising apically in connection with trichoblasts .......................................................... 17
30. Branches not arising in connection with trichoblasts ............................................................... 18
31. Trichoblasts colorless quickly deciduous; erect branches 1–3 cm high .................................. \textit{P. flacticidissima}
32. Trichoblasts brownish, relatively persistent; erect branches 3–6 mm high ........................ \textit{P. profundä}
33. Plants mostly of sheltered and often semibrackish water, more than 3 cm high; segments of median parts of erect branches mostly 2 or more diameters long ........................................ \textit{P. mollis}
34. Strictly marine plants of open water, less than 3 cm high; segments of median parts of erect branches mostly less than 1.5 diameters long .................................................. 19
35. Sublittoral plants, with branch apices abruptly acute to apiculate; tetrasporangia not protuberant ................................................................................................................... \textit{P. apiculata}

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19. Mostly littoral plants, with branch apices not abruptly pointed; tetrasporangia protuberant (in certain varieties) ........................................... P. sphaerocarpa

20. Rhizoids cut off by a cross-wall from the pericentral cells ........................................... P. sphaerocarpa

21. Rhizoids remaining in open connection with the pericentral cells ........................................... P. setacea

21. Mature rhizoids unicellular, although often digitate, arising mostly at the proximal end of the pericentral cells ........................................... P. setacea

22. Erect branches regularly branched ........................................... P. setacea

22. Erect branches mostly unbranched ........................................... P. setacea

23. Branches arising apically in a typically exogenous manner; erect branches commonly 1 cm or more high ........................................... P. setacea

23. Branches arising subapically in a delayed exogenous manner; erect branches mostly less than 1 cm high; prostrate branches frequently with tuberous portions ........................................... P. setacea

24. Segments of erect branches 1.2—1.5 diameters long in median parts; trichoblasts at intervals of 1—2 segments ........................................... P. pseudovillosum

24. Segments of erect branches mostly 0.5 diameter long or shorter; trichoblasts at intervals of 4—8 or more segments ........................................... P. quadrata

25. Plants of mostly brackish water, mostly 3 or more cm high, with numerous branches ........................................... P. subtilissima

25. Strictly marine plants, mostly saxicolous, and less than 1.5 cm high; erect branches simple or occasionally branched ........................................... P. scopulorum

Polysiphonia anomala sp. nov.

Figs. 1A, 1B, 1C

Extremely minute algae with creeping branches 30—40 μ in diameter, composed of segments 1.0—1.5 diameters long, attached by frequent unicellular rhizoids, which are cut off as separate cells from near the center of the pericentral cells; erect branches arising ciliate-ranously at frequent intervals, unbranched, to 1.5 mm high but mostly much shorter, similar to the prostrate branches, but with segments mostly shorter than the diameter; pericentral cells 4, erecticrate; trichoblasts on erect branches relatively huge to 1.1 mm long, arising one per segment in 1/3 spiral sequence, with 3—4 dichotomies and long tapering tips, mostly soon shed; scar-cells relatively large, 9—11 μ in diameter, occurring one per segment in 1/3 spiral sequence on prostrate as well as erect branches; tetrasporangia in short spiral series in the terminal parts of erect branches, which are prominently distended in fruiting segments; cystocarps ovate to slightly urceolate, 120—140 μ in diameter, with cells of the ostiolar rim not much enlarged, arising terminally on very short erect branches; spermatangial branches unknown.

Algae minitissimae, praecipue prostratae, ramos repentes 30—40 μ diam., per rhizoida unicellularia, ut cellulas discretas separata affixos, et ramos erectos cicatrigenosos, saepissime breviores quam 1 mm alt., habentes; cellulas pericentrales 4, erecticae; trichoblastae relative immensae, ad 1.1 mm alt., 3—4 dichotomias habentes, una in unoquaque segmento in ramis erectis, cito deciduae; cellulas-cicatrices magnae, una in unoquaque segmento, in 1/3 spira in ramis prostratis erecticae; tetrasporangia in serie spirali brevi in ramis erectis brevibus; cystocarpi ovati ad paululum urceolatos in ramis erectis brevissimis terminales; rami spermatangi alia ignoti.

TYPE: H. 48—1213.19, cystocarpic, growing on a species of Microdictyon, Amen I., Bikini Atoll of the Marshall Islands, July 7, 1948. It is represented by a glucose slide mount and fluid-preserved material.


P. anomala is commonly found on species of Microdictyon along with P. delicatula. Both species are delicate creeping forms. P. anomala differs from P. delicatula in the much shorter erect branches, huge trichoblasts, and much larger scar-cells, and in the procarps and cysto-
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carps arising on very short pedicels on the creeping branches.

It should be noted here that a very similar alga was collected by E. Y. Dawson, number 7472, tetrasporic, from Lake Surprise, Key Largo, Florida, May 28, 1949. The Florida alga corresponds closely with the Pacific species as far as known, with certain exceptions, namely:
(1) the Florida specimens are seemingly less firmly attached to the substratum; (2) trichoblast primordia or scar-cells do not occur regularly one per segment on the prostrate branches as they do in P. anomala, but at irregular and less frequent intervals; (3) the indeterminate (prostrate) branches are somewhat larger in the case of the Florida specimens; (4) tetrasporangia often occur in the indeterminate branches in series of 10–12 somewhat back of the apex.

In spite of these differences it seems best for the present to identify the Florida plant with P. anomala on account of the general features, and especially the short and more or less determinate erect branches arising from much more extensive creeping branches, the very large and much branched trichoblasts, and the rhizoids, which are cut off as separate cells from the pericentral cells.

Polysiphonia apiculata sp. nov.
Figs. 1D, 8, 9

Plants mostly sublittoral, epiphytic, up to 2.0 cm high, with a limited basal attachment by a number of unicellular rhizoids, which are cut off as separate cells from the basal end or middle of the pericentral cells; main branches 150–250–(320)μ in diameter, composed of segments mostly 0.5–1.0 diameter long; branching pseudodichotomous, replacing trichoblasts at intervals of 7–14–(20) segments; ultimate branches non-tapering for most of their length, but abruptly narrowed and more or less apiculate terminally; pericentral cells 4, eocorticate, trichoblasts mostly very rudimentary, occasionally 260–740μ long and 17μ in diameter at the base, with 3–4 dichotomies, arising one per segment in ⅓ spiral sequence, soon deciduous leaving very small scar-cells; tetrasporangia up to 60μ in diameter in slightly spiral series in the ultimate branches, whose segments are scarcely or not at all distended; pericarp globular, 240–320μ in diameter, composed of relatively large cells, with the cells of the ostiolar rim not much enlarged; spermatangial branches (immature) arising as a primary fork of a trichoblast.

Plantaephytinae, ad 2 cm alt., affixionem basalem praefinitam per rhizoeida, ut cellulas discretas separatas, habentes; rami principales plerunque 150–250μ diam., segmentis 0.5–1.0 plo breviora quam lata habentes; rami pseudodichotomii, intervallis 7–14–(20) segmentorum, pro trichoblastis substitutis; rami ultimi abrupte angustati, ad apicem plus minusve apiculati; cellae pericentralis 4, eocorticas; trichoblastae plerunque elementariae, 3–4 furcas habentes, una in unoquumque segmento in ⅓ spira enascente, max decidad; cellae-cicatrices minutas, tetrasporangia in serie paululum spirali, non protuberantia; cystocarpi globosi, cellulis orae ostiolaris vix amplificatis; stichidia spermatangialia ut furca primaria trichoblastae enascentia.

TYPE: D. 19127p, tetrasporic, dredged 10–14 fa, Pokai Bay, Oahu, Hawaii, July 30, 1959; represented by a glucose mount.

**Polysiphonia beaudettii** Hollenberg (1961:348)

**Figs. 1E, 17**

Plants epiphytic, to 4 cm or more high, with main erect branches to 700μ in diameter at the base, with distinct main axes and infrequent lateral branches, attached basally by a tuft of unicellular rhizoids with digitate tips and cut off by a cross-wall from the pericentral cells of 2–3 basal segments; pericentral cells 4, around a much smaller central cell, ecorticate, with segments in median parts of main branches 400–500μ in diameter and 0.5–0.6 diameter long with relatively thick walls; trichoblasts one per segment in 1/4 spiral sequence, with 3–4 dichotomies, mostly short but sometimes to 560μ long and about 18μ in diameter at the base and tapering to very delicate tips, often more or less persistent; all or nearly all fruiting branches cicatrogenous in origin, relatively short and prominently narrowed at the base; tetrasporangia to 80μ in diameter, in spiral series but not protuberant; cystocarps 270–320μ in diameter, slightly urceolate, with cells of the ostiolar rim not enlarged; spermatangial branches 200–240 × 45–60μ, usually with a sterile tip composed of 1–2 short cells, arising as a primary fork of a trichoblast.

**TYPE LOCALITY:** Isla Grande, Guerrero, Mexico.

**MATERIAL STUDIED:** HAWAIIAN ISLANDS—D. 19145AM1, D. 19116B1, D. 19116Q2, D. 19116R2, on other algae all dredged 20 fa, Pokai Bay, Oahu, Sept. 15, 1959; D. 19125C2, tetrasporic, cystocarpic, and spermatangial, on Amphirhoa sp., D. 19125L1, on Spyridia, dredged 13 fa, Pokai Bay, Oahu, July 29, 1959; PHILIPPINE ISLANDS—two collections by D. P. Abbott, one tetrasporic, on other algae, northeast coast of Sias I., Sulu Sea, Jan. 28, 1957; and the other tetrasporic, spermatangial, on Udotea sp., Faganak I., Turtle Group, Feb. 24, 1957.

The central and western Pacific specimens differ from the type in having trichoblasts regularly one per segment, in the lack of a creeping base, and in having much larger main axes. They agree with Mexican specimens in most other respects. In the original description of *P. beaudettii* the branches were described as "seemingly arising in connection with trichoblasts." They definitely do not arise in connection with trichoblasts in the case of the central and western Pacific specimens. Further collections will be needed to determine these points and to determine the correctness of the disposition of the specimens reported here.

**Polysiphonia delicatula** sp. nov.

**Fig. 1F**

Minute epiphytic algae, chiefly prostrate, with creeping branches 40–50(–80)μ in diameter with walls 5–6(–8)μ thick, composed of segments mostly 1.0–1.5 diameters long and attached at frequent intervals by unicellular rhizoids, which are cut off as separate cells from the center of the pericentral cells; with very short, terminal trichoblasts, one per segment, which are quickly deciduous; erect branches distinctly smaller to 2.5 mm high, with segments in median parts mostly 25–30μ in diameter, and 1.0–1.4 diameters long, arising cicatrogenously at distant intervals; lateral branches rare, arising in place of trichoblasts; pericentral cells 4, ecorticate; trichoblasts mostly very delicate, short and quickly deciduous, but occasionally persisting and up to 250μ long, with 2–4 semidichotomous branches and with a basal cell 6–7–(15)μ in diameter and 8–12 diameters long; trichoblasts mostly one per segment in 1/4 spiral sequence near branch tips; scar-cells about 6μ in diameter in corresponding positions on both prostrate and erect branches but often many consecutive segments with no scar-cells; tetrasporangia 25–30–(50)μ in diameter in short spiral series of about 10 toward the apices of erect branches whose segments are greatly distended; procarps 2–4 per erect branch, cystocarps and spermatangial branches unknown.

Algae epiphyticae minutae, praecipue prostratae, per rhizoidea unicellularia, ut cellulas discretas separata, affixa; rami erecti ad 2.5 mm alt., raros ramosi, 25–30μ diam., segmenta in partibus medius 1.0–1.4 plora longiora quam lata habentes, in intervallis remotis cicatrigone enascentes; cellulae pericentrales 4, ecorticateae; trichoblastae plerumque una in unoquaque segmento, delicatae, breves, cito deciduae; cellulace-cicatrices ca. 6μ diam, in rami et erectis et prostratis, plerumque una in unoquaque segmento; tetrasporangia plerumque 25–30μ diam, ca. 10 in serie brevi spirali, segmenta nultum distendentia; organa sexualia matura non observata.
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Type: D. 19116G2, cystocarpic, on Galaxaura sp., dredged 15 ft, Pokai Bay, Oahu, Hawaii, Aug. 1, 1959. It is represented by a glucose microslide.


This species resembles P. anomala, which see for distinctive features. It also resembles P. tuberosa, from which it differs in having mostly unbranched erect branches. It lacks the tuberous food-filled rhizome frequently present in P. tuberosa. From P. tenia it differs in being much more slender with much more reduced trichoblasts and considerably smaller scar-cells. As many as 90 segments occur in the erect branches of D. 11857.31 beyond a lateral branch.

Polysiphonia flaccidissima Hollenberg

Plants to 3 cm high from limited prostrate branches, attached by uncellular rhizoids cut off as separate cells from the proximal end of the pericentral cells; erect branches mostly less than 150 μ in diameter and with segments mostly 1.5–2.0 diameters long; lateral branches mostly at intervals of 6–10 segments, arising in association with trichoblasts; pericentral cells 4, ecoricate; trichoblasts delicate, unbranched or with 1–2 dichotomies, one per segment in ¼ spiral series, tetrasporangia one per segment in slightly spiral series somewhat distending the segments; cystocarps globular; spermatangial branches arising from a primary fork of a trichoblast, with or without a sterile tip.

Type Locality: Laguna Beach, Orange County, California. This species, originally described (Hollenberg, 1942b: 783) from southern California, is a variable species of very wide distribution.

P. flaccidissima var. flaccidissima Hollenberg

(Figs. 2A, 11

Plants 1–3 cm high with limited prostrate portions; median parts of erect branches 100–110–(170) μ in diameter and 1.0–1.5–(2.5) diameters long; walls thin and hyaline; main axes relatively distinct with laterals more or less distichous, arising mostly at intervals of 6 segments but often at intervals of 10 or more segments; branches slightly narrowed at the base; trichoblasts associated with branches unbranched or with 1–3 branches and up to 365 μ long; scar-cells on both erect and prostrate branches; reproductive structures characteristic of the species, but the spermatangial branches generally lacking a sterile tip.

Type Locality: Orange County, California.

Collections Identified: Hawaiian Islands—D. 1944T1, epiphytic, Port Allen, Kauai, dredged 5–13 ft, Sept. 12, 1959; M. 737, (as

Key to the Varieties of Polysiphonia flaccidissima

1. Erect branches mostly less than 1 cm high and less than 70 μ in diameter .................. 2
2. Erect branches mostly over 1 cm high and more than 70 μ in diameter .................. var. flaccidissima
3. Erect branches infrequent .................................................. var. lopi
4. Lateral branches at intervals of 4–10 segments ........................................ 3
5. Lateral branches mostly at intervals of 10 segments, prostrate branches well developed ... var. decimera
6. Lateral branches mostly at intervals of 4–6 segments, prostrate branches absent or poorly developed .................. var. iki
Fig. 2. A, Polysiphonia flaccidissima var. flaccidissima, branch apex. B, Polysiphonia flaccidissima var. lopi, branch apex. C, Polysiphonia flaccidissima var. iki, branch apex with young lateral branch and young cystocarp. D, Polysiphonia hancockii, habit sketch. E, Polysiphonia hancockii, branch with cystocarp. F, Polysiphonia hawaiiensis, branch apex with spermatangial stichidia. G, Polysiphonia herpa, prostrate branch with rhizoid showing multicellular apex.

**P. flaccidissima** var. *decimera* var. nov.1

Figs. 12

Minute algae, to barely 2 mm high from creeping branches to 55μ in diameter and with segments one diameter long or mostly shorter; erect branches similar with lateral branches commonly at intervals of 10 segments; trichoblasts 400–500μ long with 3–5 dichotomies, tapering to delicate apices, scar-cells large (to 10μ in diameter).

Algae minutae, usque ad vix 2 mm alt., e ramis repentibus ad 55μ diam., segmentis aequo longis ac latis aut plerumque brevioribus, enascentes; rami erecti repentibus similis, ramos laterales intervallis 10 segmentorum plerumque habentes; trichoblastae 400–500μ long., 3–5 dichotomias habentes, ad apices delicatos attenuatae; cellulae-cicatrices magnae (ad 10μ diam.).

**TYPE:** H. 65–82, sterile, growing on dead coral at a depth of 1–2 m, 20 m shoreward from the outer reef margin, north of North I., Johnston I., legit R. S. Jones, Apr. 22, 1965.

One additional collection, H. 65–85.1, on *Pocockiella*, Diamond Head Beach, Oahu, Hawaii, was made by Mitsuo Kajimura, May 4, 1965.

The diminutive size and the strong tendency for branches to arise at intervals of 10 segments are the distinctive features.

**P. flaccidissima** var. *iki* var. nov.

Figs. 1G, 2C

Minute, epiphytic algae, mostly less than 1 cm high, from a basal attachment with little or no prostrate portion; main branches 50–75μ in diameter; lateral branches few, at intervals of 4–6–(12) segments; scar-cells small but often pigmented; tetrarosporangia 40–50μ in diameter, in short, slightly spiral series; spermatic angial branches 116–190μ × 36–40μ with a short sterile tip of 1–2 cells; cystocarps seen were immature.

Algae minutae, epiphyticae, plerumque breviores quam 1 cm, ex affixione basali enascentes, parte prostrata minima vel nulla; rami principales 50–75μ diam.; rami laterales intervallis 4–6–(12) segmentorum enascentes; cellulariae-cicatrices parvae, saepe, autem, coloratae; tetrarosporangia 40–50μ diam., in serie brevi paululum spirali; rami spermaticangiales 116–190μ × 36–40μ, cactem breve sterile ex 1–2 cellulis compostum habentes; cystocarpi visi immaturi.

**TYPE:** D. 19145M1, tetrosporic, dredged 6–14 fa, Port Allen, Kauai, Hawaii, Sept. 12, 1959, is represented by a glucose mount. Additional material studied, all from the Hawaiian Islands: D. 19116C2, cystocarpic, on *Sargassum* sp., dredged 16–25 fa, Pokai Bay, Oahu, Aug. 1, 1959; D. 19144J1 and 19144Q1, spermangial, on *Liagora* sp., dredged 6–14 fa, along with the type.

This variety is named for its minute size (*iki* is the Hawaiian word for tiny). Otherwise it has the features of the species.

**P. flaccidissima** var. *lopi* var. nov.

Figs. 1H, 2B

To 7.5 mm high from prostrate branches 40–50μ in diameter; erect branches 30–45–(60)μ in diameter, of segments mostly 2 diameters long or longer, sparsely branched with 10–20–(30) segments between successive branches, which are gradually narrowed at the base; trichoblasts mostly short with 1 dichotomy, occasionally to 275μ long composed of 3–4 very long cells 3.5–4.0μ in diameter and relatively uniform in diameter throughout their length; mature reproductive structures not observed.

Plantae ad 7.5 mm alt., e ramis prostratis 40–50μ diam. enascentes; rami erecti 50–45μ diam. constantes e segmentis plerumque 2 plo longioribus vel plus quam lata, sparse ramosi, 10–20–(30) segmentis inter ramos successivis, ad basim gradatim angustatos; trichoblastae plerumque breves, unam dichotomiam habentes, interdum ad 275μ long., e 3–4 cellulis longis similis 3.5–4.0μ diam. compositae, relative uniforme diametro per longitudinem; structurae reproductive maturae non observatae.

**TYPE:** D. 10821, tetrasporic, cystocarpic, on a boat, just below the water line, Kanohe Bay,
Oahu, Oct. 7, 1953. The cystocarps are immature.

**ADDITIONAL COLLECTIONS:** Da. 19539, reef north of Sand I., Palmrya Atoll, Lide Islands, Oct. 18, 1958; G. 524.1, sterile, as a delicate thin fuzz over a dead coral branch in the lagoon at a depth of about 28 m, Eniwetok Atoll, Marshall Islands, Aug. 30, 1955 (the trichoblasts subtending the branches unbranched in these specimens); G. 592.1, sterile, from a depth of 8 fathoms in the lagoon at Eniwetok Atoll, of the Marshall Islands, Sept. 2, 1955.

This variety is characterized by its small and delicate nature and by the distantly placed lateral branches. *Lopi* is the Hawaiian word for thread.

**Polysiphonia hancockii** Dawson (1944:331)
Figs. 2D, 2E, 13, 14

Epiphytic algae to 1.5 cm high with main axes to 900 µ in diameter, attached basally by numerous rhizoids; median parts of main axes 500–600 µ in diameter, with segments \( \frac{1}{4} - \frac{1}{3} \) diameters long; pericentral cells 4, sparsely to completely but thinly corticated at the base of main axes and often slightly corticated in the major laterals; main axes mostly prominent, with somewhat distichous laterals of limited growth, but branching sometimes deliquescent (Fig. 2D); trichoblasts one per segment in \( \frac{1}{4} \) spiral sequence, mostly short, with 2–3 dichotomies, but occasionally to 700 µ long with 5–6 dichotomies, soon deciduous; scar-cells inconspicuous; branches arising independent of trichoblasts mostly at intervals of 6 segments; tetrasporangia to 70 µ in diameter, spirally arranged and protuberant, in repeatedly pseudodichotomous laterals; cystocarps globular to slightly urceolate, 280–400 µ in diameter, with prominently enlarged cells of the ostioral rim; spermatangial stichidia lanceolate, to 200 µ \( \times \) 45 µ, without a sterile tip, arising as a primary branch of a trichoblast.

**TYPE LOCALITY:** San Jose del Cabo, Lower California, Mexico.

**COLLECTIONS IDENTIFIED (all from the Hawaiian Islands):** D. 17400, spermatangial, Laie Pt., Oahu, Mar. 17, 1959; D. 19853C, tetrasporic, cystocarpic, spermatangial, near low tide level on rocks near the mouth of Halawa stream, Molokai, in water fresh to taste, Dec. 26, 1953; D. 20047.2, on wave-battered volcanic rock, Laie Pt., Oahu, legit R. Tsuda, R. Buggeln, and Gavino Trono, May 5, 1963; D. 22400, tetrasporic, D. 22401.1, tetrasporic, and D. 22410.1, tetrasporic, in intertidal algal turf, Papawai Pt., southwest of Maalaea Bay, Maui, legit H., T., and B., Apr. 19, 1965; D. 17184AC, D. 22534, cystocarpic, in algal turf, near Honokohau, Maui, legit H., T., and B., Apr. 20, 1965; D. 17197A11, Kalapana Beach, Kaimua Bay, Island of Hawaii, Feb. 27, 1953; D. 17333.1 on *Corallina* sp. \( \frac{1}{4} \) mile southwest of Opihikao, Puna, Island of Hawaii, Jan. 27, 1953; also a collection by C. M. Cook, Jr., cystocarpic, on *Gelidium* sp., Island of Hawaii, June 21, 1935.

**Polysiphonia hawaiensis** sp. nov.

*P. ferulacea* Menez (1964:209); *P. ferulacea* Segi (1863:980) (1951:209); non *P. ferulacea* Suhringar ex J. G. Agardh (1863:980)
Figs. 2F, 16, 41

Plants dull reddish brown, chiefly epiphytic, densely tufted, rigid 4.5–5.0 cm high from a limited prostrate base, attached by frequent unicellular rhizoids cut off by a cross-wall from the proximal end of the pericentral cells, occasionally with a discoid base composed of a tuft of rhizoids; rhizoids commonly with denticate tips; main erect axes mostly 300–500 µ in diameter, composed of 4 ecorticate pericentral cells and of segments mostly 0.5–1.0 diameter long, with the cells not tumid but having mostly straight outer walls; branches replacing trichoblasts, at first strongly curved toward the parent branch, but later oriented at a wide angle somewhat less than a right angle, little or not at all narrowed at the base; trichoblasts one per segment in \( \frac{1}{4} \) spiral sequence, mostly short and soon deciduous but sometimes well developed to 500 µ long with about 4 dichotomies, with apices not much tapered, 8–10 µ in diameter at the tips, up to 40 µ at the base, and with the short basal cell 1–1.5 diameters long; scar-cells small; mature tetrasporangia 60–90 µ in diameter, prominently spiralling in the ultimate branches which are not much distended; cystocarps globular, mostly 300–400 µ in diameter, with cells of the ostioral rim not much enlarged, spermatangial branches oblong-ovoid, arising
as a primary branch of a trichoblast, 200–250μ × 80–100μ with a relatively inconspicuous sterile tip consisting mostly of one small cell with a relatively thin wall.

Plantae praeipue epiphytice, conferte fruticulosa, ad 5 cm alt., e basi prostrata praefinita, per rhizoidea uncellaria, ut cellulas discretas separata, affixa; axes principales erecti 300–400μ diam.; cellularae percurrentes 4, erecto-carinae; segmenta partibus in medias ramorum erectorum 0.5–1.0 plo breviora quam lata; rami pro trichoblastis substituti, postremo late divergentes; sine axibus percurrentibus; trichoblastae una in unuoque segmento, in 4 spira, plerumque breves et mixt decidue; tetraropangia in ramis ultimis spiraliter ordinata; cystocarpi globosi; 300–400μ diam.; rami spermatangiales oblongo-ovoides, cacumen parum unicellare sterile, ut ramum trichoblastae primarium enascens, habentes.

**TYPE:** D. 18764, tetrasporic, cystocarpic, spermatangial, epiphytic on a species of *Sargassum* from shallow water, Sans Souci Beach Laboratory, Waikiki Beach, Oahu, Hawaiian Islands, legit G. J. Holleberg, Jan. 21, 1963. The species is very abundant at this locality.


Also referred to this species with some hesitatin

**Also referred to this species with some hesita

**Also referred to this species with some hesitation are the following:** D. 14697, tetrasporic, on *Sargassum* sp. Labrador, Tanjjang, Berlayar, Singapore, Jan. 25, 1965; W. H. Harvey, Alg. Ceylon No. 12, cystocarpic, spermatangial (as *P. binneyi* Harv.) on other algae, Rijksherbari

**A specimen identified as *P. ferulacea* f. implicata Tseng (1944:76) may prove to be a variation of *P. hawaiiensis*. Tseng does not indicate the height of his plant and efforts to obtain a loan of his Hong Kong specimens have met with no success.

Numerous herbarium specimens of this taxon, mostly from Oahu, are to be found in the Bishop Museum, Honolulu. Many of these have been annotated by E. G. Menez (1964) as *P. ferulacea*.

This alga has been commonly identified as *P. ferulacea* J. G. Agardh, which it resembles in a number of respects. From that species it differs chiefly in the widely divaricate branching, with percurrent axes, when present, lost in the terminal parts. Taylor (1960) describes the branching of *P. ferulacea* as "subflaccidate to virgate above." In a communication from Dr. Sven Sogngerup, Keeper of the Botanical Museum at Lund, Sweden, he mentions mounted specimens of *P. ferulacea* on sheets signed by J. G. Agardh. Two specimens, 40176 and 40181, are from "Vera Cruz, Liebmann," and in addition there are two specimens, 40178 and 40179 "from Guadaloupe, coll. Duchchassaing" accompanied by a mica preparation, 40180, "apparently from a cut-off part of one of them."
These specimens are labeled _P. ferulacea_ "in J. G.'s handwriting, followed by a mark of exclamation," leading Dr. Snogerup to conclude that they must perhaps be regarded as the type collection. Photographs of these specimens sent by Dr. Snogerup and one loose duplicate (40186) of "Vera Cruz Liebmann" represent plants with prominent leading axes especially in the upper parts, very unlike the dichotomously branched Hawaiian specimens.

If one accepts the view of Boergesen (1918: 277) that _P. brevioribundus_ Harvey is to be identified with _P. ferulacea_ J. G. Agardh, the figures of the former given by Harvey (1853: Tab. XVIB) represent a plant with strictly erect habit, with distinct percurrent axes and alternate branching, forming a penicillate tuft very unlike the Hawaiian plant. Furthermore, Boergesen gives the impression that the specimens he identified as _P. ferulacea_ are saxicolous, forming "together with Caulerpa . . . and other algae, low compact patches." The Hawaiian plants always seem to be epiphytic.

Finally, judging by descriptions and figure by Boergesen (1918:280, fig. 279) of the spermatangial branches of plants he identified as _P. ferulacea_, and also by spermatangial branches of various specimens from Florida and elsewhere in the southeastern United States, the writer is led to the conclusion that the male reproductive structures of the Hawaiian plants are short and stout (Fig. 2F) as are those of _P. ferulacea_, but differ from the latter in several respects: (1) they are considerably larger and more ovoid in form, rather than cylindrical; (2) there are fewer at a given branch tip, usually 2–3 present at any given time; (3) the sterile tip is much smaller, is neither globular nor thick-walled, and does not consist of two cells as is the case in _P. ferulacea_ as figured by Boergesen.

Polysiphonia herpa_ sp. nov.

_Lophosiphonia bermudensis_ Dawson, 1956: 59, fig. 65; non _Lophosiphonia bermudensis_ Collins and Hervey (1917:126), which is _Dipterosiphonia rigidus_ (Schousb.) Falk. Figs. 1/1, 2G

Chiefly prostrate algae, with the prostrate branches mostly 100–140μ in diameter and with segments 0.6–1.0 diameter long, attached by rhizoids which are cut off by a cross-wall from the proximal end or center of the pericentral cells and which commonly have multicellular discoid tips; erect branches to 3 mm high and 90μ in diameter, with segments mostly about 0.5 diameter long, arising cicatricenous, commonly at intervals of 4 segments and frequently in alternating pairs, one on either side of the prostrate branch, with one segment between members of a pair and 4 segments between corresponding members of successive pairs; erect branches with short segments, mostly unbranched or with one or two erect laterals from near the base; young branches at first strongly arched toward the prostrate branch; pericentral cells 4, corticate; trichoblasts on erect branches one per segment in 4 spiral sequence, mostly not well developed but occasionally to 1.3 mm and with 4–5 dichotomies, quickly deciduous, leaving relatively large scar-cells and commonly prominent wall scars at the point of abscission; trichoblasts on prostrate branches represented by exogenous primordia ("scar cells") only, most of which divide to form 3 or 4 small cells (branch primordia), from which the cicatri- genous branches later arise; reproductive structures not observed.

Algae praecipue prostratae, ramis prostratis plurumque 100–140μ diam., segmentis plurumque brevioribus quam lata, per rhizoidea, a cellulis pericentralibus per disseminatum separata, et cucumina multicellularia vulgo habentia, affixa; rami erecti ad 3 mm alt. et 90μ diam., segmentis plurumque ca. 0.5 plo breviore quam lata, vulgo non ramosis, inter- valli 4 segmentorum cicatrogenose et plurumque binatim enascentibus; cellulae pericentrales 4, corticate; trichoblastae in ramis erectis, una in unoque segmento, in 4 spira, mox deciduae; cellulae-cicatrices relative magnae, eae in cellulis prostratis ad cellulaver paras formandar plurumque divi- sae; structurae reproductivae non observatae.

**TYPE:** _D._ 11857.2, abundant in tufts on dead coral on the sea reef near Otetou, Raroa Atoll, Tuamotu Archipelago, leg. M. S. Doty and Jan Newhouse, Aug. 21, 1952. It is represented by glucose microslide mounts and abundant fluid-preserved material.

**ADDITIONAL COLLECTIONS:** HAWAIIAN ISLANDS—_D._ 19643DA, on a mollusc shell, dredged 8–10 fa, east side of Barber's Point,
off Ewa Beach, Oahu, Feb. 22, 1962; D. 19143R1, on other algae, dredged 31-32 fa, Penguin Bank, southwest of Molokai, Sept. 7, 1959; LINE ISLANDS—D. 20041, on mollusc shell, seaward reef flat, Christmas I., legit Ralph E. Palumbo, May 16, 1962; TUAMOTU ARCHIPELAGO—D. 11189.3, on dead coral, D. 11857.6, D. 11858.2, D. 11860C, all from lagoon transect, Otetou, Raroa Atoll, legit M. S. Doty and Jan Newhouse, Aug. 21, 1952; MARSHALL ISLANDS—D. 9586A, rock scrapings, D. 9599E, on Udotea sp., D. 9599GA, on Launercia sp., D. 9693B, on Halimeda sp., all on lagoon reef off Ine Village, Ine I., Arno Atoll, legit Leonard Horwitz, Aug. 17, 1951; H. 48–0914.15, on Microdictyon sp.; H. 48–0914.22, on Dictyosphaeria sp., H. 48–1091.13, on Pocockiella, outer reef, Arji I., Bikini Atoll, July 12, 1948 (probably all of these should be identified with this species although in some the segments are frequently more than one diameter long in both prostrate and erect branches, and rhizoids arise mostly at the proximal end of the pericentral cells); CAROLINE ISLANDS—D. 15989.3, on other algae, Helen Reef area, legit E. Menez, Aug. 28, 1960.

D. 11858.2 from sea reef near Otetou, Raroa Atoll, Tuamotu Archipelago, represents a variation in which the erect branches are up to 7 mm high with more laterals and with segments about 1 diameter long. A variant, H. 48–1091.13 from the outer reef of Arji I., Bikini Atoll, in the Marshall Islands has prostrate branches only 90μ in diameter and segments to 1.6 diameters long.

**Polysiphonia mollis** Hooker and Harvey

For synonymy see Hollenberg (1961:359), also *P. aquamara* Abbott (1947:212).

Fig. 43

Plants to 8 cm high, assurgent from limited prostrate portions attached by unicellular rhizoids, with or without lobed tips, cut off mostly from the proximal end of the pericentral cells by a cross-wall; 4 pericentral cells, eocarticate, with segments 1.5–3.0 diameters long in the main branches and with segments somewhat nodose at the ends; median parts of erect branches 120–180μ in diameter; branching pseudodichotomous and corymbose, with branches of many orders arising exogenously in place of, and not in connection with, trichoblasts, with mostly 6–8 segments between successive branches; branches gradually narrowed toward the base; trichoblasts one per segment in regular 1/4 spiral sequence, commonly 100–280μ long with 1–3 forks, but often poorly developed, soon deciduous, leaving scar-cells of moderate size; basal cell commonly considerably shorter than cells next above; tetrasporangia 60–80μ in diameter in slightly or prominently spiral series in the ultimate ramuli; cystocarps ovoid to globular up to 300μ in diameter; spermatangial branches measuring 140–270μ × 60–75μ, arising mostly as a primary fork of a trichoblast but sometimes as a secondary fork and sometimes bearing a short or longer sterile tip of 2–4 cells.

**TYPE LOCALITY:** Tasmania.

**COLLECTIONS STUDIED:** HAWAIIAN ISLANDS—D. 9765B, tetrasporic, cystocarpic, Sand I., Honolulu, Oahu, Jan. 27, 1956; D. 12386, 12389, from a pond-connecting channel, Conco nut I., Oahu, Feb. 5, 1954; D. 12684, D. 12689, tetrasporic, cystocarpic, spermatangial, Keeki Lagoon, airport side of Mokuaea I., Oahu, Dec. 30, 1954; D. 12792, mudflats in front of Kuliouou Beach Park, Oahu, June 10, 1955; D. 13356, on Natatorium floats, Waikiki, Oahu, Oct. 2, 1956; M. 704, tetrasporic, on Acanthophora, near old sugar mill, windward Oahu, July 7, 1961; M. 725, 739, tetrasporic, on concrete blocks under and near a seaward bridge, Ala Moana Park, Oahu, May 5, 1961; M. 758, 759, tetrasporic, cystocarpic, muddy area at Keeki Lagoon, Oahu, Feb. 27, 1961; I. Abbott 1535, tetrasporic, cystocarpic and spermatangial, as *P. aquamara*, legit C. J. Engard, Kuapa Pond, Oahu, Apr. 7, 1944; I. Abbott, as *Polysiphonia aquamara* spermatangial, “Salt Lake,” Oahu, July 2, 1945; TAHITI—Setchell 5213 (C. 261338), as *P. tongatensis* Harvey, legit W. A. Setchell and H. E. Parks, Port Phaeton, June 24, 1922; PHILIPPINE ISLANDS—a collection by D. P. Abbott, Siasi I., Jan. 28, 1957, a smaller and more slender form probably to be identified as *P. mollis var. tongatensis* (Harvey) comb. nov., is frequently found in sheltered.
water along with the typical form of the species. Also representative of this variety is H. 65—79.5 (D. 22567) from muddy bottom in shallow water of an ancient fish trap, southeast Molokai, Apr. 22, 1965.

**Polysiphonia poko** sp. nov.

Fig. 3A

Plants to 4 mm high, assurgent from prostrate branches attached by unicellular rhizoids which are cut off from pericentral cells by a cross-wall, mostly from the proximal end; prostrate branches and larger erect branches 90—140—(190)μ in diameter; pericentral cells 4, ecorcticate with segments mostly about 0.5 diameter long; erect branches mostly unbranched; all branches cicatrigenous, not narrowed at the base; trichoblasts not well developed or up to 500μ or more long and 20μ in diameter at the base with 3—4 dichotomies, arising one per segment in ½ spiral sequence; scar-cells on prostrate and erect branches; wall-scars often prominent; tetrasporangia spirally arranged in the branches, slightly distending the segments; cystocarps globular-ovoid, to 360μ in diameter with cells of the ostiolar rim not enlarged; spermatangial branches cylindrical, without a sterile tip; comprising a primary branch of a trichoblast.

Plantae ad 4 mm alt., assurgentae e ramis prostratis, per rhizoides uncinellularia, a cellulis pericentralibus per disseipimentum plerumque ab extremo proximali separata, affinis; rami prostrati et rami maiores erecti 90—140—(190)μ in diameter.; cellulae pericentrales 4, ecorcticatae, segmentis plerumque ca. 0.5 plo brevioribus quam lata; rami erecti vulgo non ramosi; omnis ramus cicatrigenus, ad basim non attenuatus; trichoblastae non bene evolutae aut usque ad 500μ vel plus long. et 20μ diam. ad basim. 3—4 dichotomias habentes, una in unoquaque segmento in ½ spira enascente; cellula-cicatrices in ramis prostratis erectisque; membrana-cicatrices saepe manifestae; tetrasporangia in ramis spiraliiter ordinata, segmenta paululum distendentes; cystocarpi globoso-ovoidi, ad 360μ diam., cellulæ orae ostiolis non dilatatis; rami spermatangiace cylindrici, sine cacumine sterilis, ramum primarium tricho-blastae comprehendentes.

**TYPE**: H. 65—113.1, cystocarpic and spermatangial, on dead coral, at a depth of 1—2 m, 20 m shoreward from the outer reef margin, north of North I., Johnston I., legit R. S. Jones, Apr. 22, 1965.

The Hawaiian name, meaning short, refers to the short segments. This species is close to *P. herpa*, from which it differs chiefly in the undivided scar-cells. It also lacks the multicellular tips of rhizoids common in *P. herpa*. It is in some respects similar to *P. sphaerocarpa*, differing in the mostly shorter segments in *P. poko* and in the unbranched erect branches of the latter.

This species also resembles *P. coatta* Tseng (1944), from which it differs in that: (1) the erect branches are mostly unbranched and seemingly exclusively cicatrigenous in *P. poko*, except for the assurgent origin of some of the erect branches from prostrate branches; (2) there is little or no evidence of coherence of erect branches by means of tentacular rhizoids as described for *P. coatta*.

**P. poko** var.*poko* var. nov.

Figs. 3A, 15

ADDITIONAL COLLECTIONS EXAMINED (those marked * are more slender, attenuate forms):

**HAWAIIAN ISLANDS**—D. 10361.1, on other algae, Poipu Beach Park, Kauai, Feb. 6, 1952; D. 19710C, a poor specimen from the intertidal flow of the reef flat, Kumimi, Molokai, Dec. 29, 1953; D. 22410.2, a very delicate form, Papawai Point, Maui, legit H., T., and B., Apr. 19, 1965; **JOHNSTON ISLAND**—H. 65—106.7, spermatangial, on dead coral at the type locality, legit R. S. Jones, Apr. 22, 1965; **LINE ISLANDS**—L. 2720.3*, in crevices of reef flat, Jarvis I., Nov. 17, 1964; L. 2782.2*, on wave-swept reef near the airport, Christmas I., Nov. 23, 1964; **TUAMOTU ARCHIPELAGO** (all legit M. S. Doty and Jan Newhouse, 1952); D. 11518.1*, on *Microdictyon* sp., outer reef edge, Akau, Raroia Atoll, Aug. 5; D. 11160B3, on reef near ship pass, Takeke, Raroia Atoll, July 9; D. 11189.4, on other algae, lagoon transect, Ngarumaoa, Raroia Atoll, July 12; D. 11509.1*, on dead coral, near Pakokota, Oneroa, Raroia Atoll, Aug. 5; D. 11553.1, on *Caulerpa* sp. under coral overhang of reef in front of Oneroa Village, Raroia Atoll, Aug. 5; D. 11585.1*, on dead coral, sea reef near Oetou, Raroia Atoll, Aug. 21; **PHOENIX ISLANDS**—L. 2416.5, on *Halimeda* sp., western reef of McKean I., Oct. 18, 1964; L. 2444.4*, on *Halimeda* sp. in sandy pool, northeastern reef of McKean I., Oct. 20, 1964; L. 2451.10*, on
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Fig. 3. A, Polysiphonia pokó, prostrate branch and bases of erect branches. B, Polysiphonia pokó, unnamed var., with young cystocarps and very delicate trichoblasts. C, Polysiphonia pseudovillum, apex of erect branch. D, Polysiphonia tuberosa, branch apex. E, Polysiphonia tuberosa, branch apex with delayed exogenous origin of a lateral in association with a trichoblast.

A collection by A. J. Bernatowicz, 53–358, from Bailey’s Bay, Bermuda, May 14, 1953, agrees in most details with the description given for this species, although the prostrate branches are somewhat more extensive and rhizoids have multicellular tips. No fruiting was observed in the Bermuda specimens.

A minute variant form of this species (Fig. 3b) is represented by H. 65–133 (Fig. 3b), cystocarpic, collected by R. S. Jones north of North I., Johnston I., Apr. 22, 1965. It is only 500μ high with erect branches to 75μ in diameter, with very delicate trichoblasts and with immature cystocarps on both erect and prostrate branches. No additional collections of this variant are available.

P. pokö var. longii var. nov.

Fig. 22

With the general features of the species but relatively coarse, with erect branches to 1.3 cm high and commonly with 1–3 unilateral branches, and with the tips of erect branches frequently functioning as stolons and forming new prostrate branches; tetrasporangial branches to 3 mm long and 115μ in diameter toward the base, mostly unbranched, and with 20–30 spirally arranged tetrasporangia, which are only slightly protuberant, and in some cases with evidence of at least as many tetrasporangia having been previously released from the lower segments.

Varietas propriae speciei generales praebeens, plantae, autem, relative grossae, ramis erectis ad 1.3 cm alt., et vulgo 1–3 ramos unilaterales habentibus, necnon cacuminibus ramosorum erectorum velut stoloni- bus saepe fungentibus et ramos prostratos novos for- mantibus; rami tetrasporangiales ad 3 mm long., et 115μ diam. ad basim, magna ex parte non ramosi, 20–30 tetrasporangia spiraliiter ordinata, vix protuber- antia ferentes, signa indicantia quod saltum totidem sporangia e segmentis inferioribus paulo ante liberata.

TYPE: L. 2709.1, tetrasporic, from exposed coral heads near breaking waves on the south- west reef of Jarvis I., Line Islands, Nov. 16, 1964; glucose slide mounts and fluid preserved material.

ADDITIONAL COLLECTIONS: Two are identi- fied with this species—L. 2703.1, tetrasporic, from exposed and protected parts of depressions and ridges on coral heads, near breaking waves, Jarvis I., Nov. 16, 1964; a collection by David Sigee No. 35 from Gan I., Addu Atoll, Maldives Islands in the Indian Ocean, July–Sept., 1964. One other collection is placed in this variety with some reservations, L. 2451.11, with matted algae, north shore of Gardner I., Line Islands, Oct. 23, 1964. In this the seg- ments of prostrate branches are as long or longer than broad (100μ in diameter) and have rhizoids with multicellular tips.

Polysiphonia profunda sp. nov.

Figs. 18, 20

Minute, epiphytic algae with prostrate branches attached by unicellular rhizoids with digitate tips cut off from the proximal end of the pericentral cells or sometimes with a basal group of rhizoids and no prostrate branch; 4 ecorticate pericentral cells slightly flattened tan- gentially, with segments mostly less than one but occasionally 1.5–2.0 diameters long and with stratified walls to 15μ thick and brownish in older parts; erect branches apparently of cicatrogenous origin; 125–145μ in diameter and 4–6 mm long, with few lateral branches; lateral branches arising in connection with trichoblasts or cicatrogenously at intervals of 20–30 or more segments; trichoblasts very slender, to 400 (500)μ long and 8–12μ in diameter at the base, with 3–4 forks, arising one per segment in ¼ spiral sequence, relatively persistent but when shed leaving small scar-cells 7–8μ in
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diameter; tetrasporangia 30–40 µ in diameter, in short series not much distending the segments; cystocarps globose, to 260 µ in diameter; spermatangial branches 175–200 µ × 45–50 µ arising as a primary fork of a trichoblast, usually with 1–2 short cells forming a sterile tip.

Algae minutae, epiphyticae, ramos prostratos, affixos per rhioida unicellularia, cacuminibus digitatis prædita, ab extremo proximali cellularum pericentralium separatæ, interdum, autem, aggregationem rhioideorum, ramos prostratos carentes, habentes; 4 cellularæ pericentrales ex corticatae tangentialiter subcomplanatae, segmentis plurumque brevioribus quam lata, interdum, autem, 1.5–2.0 longiores quam lata, et parietes stratificatos, usuque ad 15 µ crass. in partibus vetustioribus brunneolos, habentes; rami erecti, origine ut videtur cicatrigeni, 125–245 µ diam. 4–6 mm long., paucos ramos laterales habentes; rami laterales in associatione cum trichoblastis, aut cicatrigene, intervallis 20–30 vel plurium segmentorum enascentes, trichoblastae tenuissimæ ad 400 (500) µ long., 8–12 µ diam. ad basim, 3–4 furcas habentes, una in unoquoque segmento in spira enascente, relative persistentes, effusæ, autem, cellularæ-cicastriæ parvas 7–8 µ diam. relinquentes; tetrasporangia 30–40 µ diam., in serie brevi, segmenta paulum distententia; cystocarpi globosi, ad 260 µ diam., rami spermatangiales 175–200 µ × 40–50 µ ut furca primaria trichoblastae enascentes, 1–2 cellularæ breves, cacumen sterile formantes, plerumque habentes.

TYPE: D. 19116A11, cystocarpic, attached to a species of Galaxaura, dredged from 15 fath., Pokai Bay, Oahu, Hawaii, Aug. 1, 1959. It is represented by a glucose microslide mount.


This species is closest to P. flaccidissima in the origin of branches in relation to trichoblasts, and in its small size and delicate nature. From P. flaccidissima it differs in the relatively persistent trichoblasts, in the brownish color of the walls, and in the less frequent branches, terminal portions of erect branches having as many as 80 segments without a lateral branch.

Polysiphonia pseudovillum sp. nov.

Fig. 3C

Plants chiefly prostrate with creeping filaments to 60 µ in diameter, composed of segments 1.0–1.5 diameters long, attached by frequent unicellular rhizoids which are cut off from the proximal end of the pericentral cells by a cross-wall, and with a broad base in contact with the bearing cell although only a narrow pit-connection, and which may have digitate tips; erect branches arising cicatricigenously at frequent intervals, to 1 or up to 2.7 mm high and 40–60 µ in diameter, with segments about 1.5 diameters long, with slight constrictions at the nodes, and only occasionally with one or more laterals arising cicatricigenously in a pseudo-dichotomous manner; pericentral cells 4, ericatice and with a central cell scarcely half the diameter of the pericentral cells; walls hyaline, 5–8 µ thick; trichoblasts to 1 mm long, with mostly 4 dichotomies and very slender tips, and with a basal cell to 350 µ long and 18 µ in diameter, arising at irregular intervals in part but mostly one per segment in a spiral sequence in terminal parts of erect branches, tardily deciduous; scar-cells mostly one per segment on both prostrate and erect branches, but sometimes at intervals of two segments; tetrasporangia (immature) in short spiral series near the tips of branches; cystocarps ovoid to slightly urceolate, 150 µ broad and slightly longer than broad; spermatangial branches (only one seen) oblong, 220 µ × 58 µ, arising probably as a primary branch of a trichoblast.

Plantea præcipue prostratae, filamenta repentina ad 60 µ diam., e segmentis 1–15 pllo longioribus quam lata composita, affixa per rhizoidea unicellularia frequentia, per dissepimentum ab extremo proximali cellularum pericentralium separata, habentes; rami erecti intervallis frequentibus cicatricienascentes, plerunque 1 mm alt. aut paululo altaiores, segmentis ca. 1.5 pllo longioribus quam lata, ramis inter segmenta aliquantulum constrictis, parcis ramis cicatrigene enascentibus; cellularæ pericentrales 4, ericaticeae, cellula centralia multo minore quam cellularæ pericentrales; trichoblastae ad 1 mm long., ca. 4 dichotomias necon cellulam basalem ad 350 µ long., 18 µ diam., una in unoquoque segmento in spira in partibus terminalibus rumorum erectorum maxima ex parte oriente, habentes. Cellularæ-cicastriæ plurumque una in unoquoque segmento in mari et erectis et prostratis, interdum intervallis 2 segmentorum; tetrasporangia in serie brevi spirali; cystocarpi alian-
tulum urceolati, ad 150µ lat. et paululo longiores; rami spermaterangiales ut ramus primarius trichoblastae probabiliter enascentes.

**TYPE:** H. 65–52, tetrasporic, cystocarpic and spermaterangial, growing on dead coral at a depth of 1–2 m, and 20 m shoreward from the outer reef margin, north of North I., Johnston I., legit R. S. Jones, Apr. 22, 1965. It is represented by fluid preserved material and 6–8 glucose microslide mounts.

**ADDITIONAL COLLECTION:** T. 1393, spermaterangial, on top of a coral head at a depth of about 1 ft northeast of North I., Johnston I., Nov. 18, 1965.

The minute size and chiefly prostrate habit are features characteristic of *P. scopulorum* var. *villum*, but the rhizoids of *P. pseudovillum* are cut off as separate cells. Also the erect branches arise cicatricigenously in *P. pseudovillum* but endogenously in *P. scopulorum* var. *villum*.

**Polysiphonia quadrata** sp. nov.

*P. cocta* Tsuda (1964:11) not of Tseng (1944:71)

**Fig. 25**

Plants to 8 mm high, assurgent from creeping branches attached at frequent intervals by unicellular rhizoids which are cut off as separate cells from the proximal end of the pericentral cells and may have digitate tips; creeping branches 160–180µ in diameter, composed of segments 0.3–0.5 diameters long; assurgent erect branches 100–160µ in diameter, with segments mostly about 0.5 diameter long and gradually very short near the tapering apices; branches infrequent, replacing trichoblasts; pericentral cells 4, eocortic, mostly quadrate in external view, walls brownish and 8–10µ thick in older parts; trichoblasts arising at irregular intervals of 4–8 or more segments, very rudimentary with 2–3 dichotomies, quickly deciduous, leaving relatively small scar-cells; reproductive structures unknown.

Plantae ad 8 mm alt., a rami repetibus assurgentibus, affixa ex intervallis frequentibus per rhizoides unicellulares quae ut cellulara discribatur ad extremum proximali cellularum pericentralium separata et cacoquina digitata interdum habent; rami repetentes 160–180µ diam., e segmentis 0.3–0.5 plo brevioribus quam lata compositi; rami erecti assurgentibus 100–160µ diam., segmentis plerumque ca. 0.5 brevioribus quam lata neeon brevissimis prope apices attenuatis gradatis factis; rami infrequentibus, pro trichoblastis substitutis; cellularae pericentralae 4, eoticatae, extreminentiae visae plerumque quadrateae, parietes brunneolos, in partibus vetustioribus 8–10µ crass. habentes; trichoblastae interdum irregularibus 4–8 vel plurimis segmentorum enascentes, multum elementariae, 2–3 dichotomias habentes, cito deciduae, cellulæ-cicatricæ relative parvas relinquentis; structuræ reproductivæ ignotæ.

**TYPE:** D. 18774, collected by N. J. Cooper from below low water line on a reef just south of Rawanawi Village on the Marakei Atoll, Gilbert Islands, July, 1962.

**ADDITIONAL COLLECTION:** D. 18921.1, likewise sterile, was collected by the same person from the same general area, at a depth of 20–30 ft in a deep surge channel, July, 1962.

This species is very similar to a species with 5 pericentral cells to be described in Part II of this study. It differs, furthermore, in having mostly shorter segments in mature parts. The cells of *P. quadrata* plasmolyze readily in 20% glucose, due probably to the thinness of the walls of the relatively large pericentral cells of younger branches.

**Polysiphonia rubrobriza** sp. nov.

Figs. 4A, 4B, 32

Epiphytic algae to 8 mm high initially attached by a tuft of rhizoids from a basal cell and adjacent pericentral cells, later attached by additional rhizoids arising from prostrate stolon-like branches of limited extent emerging from the basal segments of primary erect branches; rhizoids to 125µ long, enlarged saccate to 110µ in diameter, thin-walled, deeply pink with numerous peripheral chromatophores about 3µ in diameter, arising as separate cells cut off from the pericentral cells and penetrating among the utricles of the host; pericentral cells 4, eoticate, with segments as long as broad or slightly longer; erect branches 75–100µ in diameter in the median parts, either endogenous or cicatricigenous in origin, pseudodichotomously branched above at intervals of (2)–5–10 segments, the branches arising independent of the trichoblasts; trichoblasts to 680µ long, with 2–4 dichotomies, arising one per segment in 1/4 spiral sequence in erect branches, and quickly deciduous; scar-cells on both erect and prostrate branches; treta-
Fig. 4. *A. Polysiphonia rubrorhiza*, showing saccate pigmented rhizoids arising from the base of erect branch, and from prostrate branches. From the type collection. *B, Polysiphonia rubrorhiza*, immature cystocarp (from type collection). *C, Polysiphonia saccorhiza*, prostrate branch with erect branch and saccate pigmented rhizoids. *D, Polysiphonia saccorhiza*, tetrasporic erect branch.
sporangia about 65μ in diameter in short spiral series in the ultimate branches; cystocarps globular with a suggestion of a bracket-like base produced by an extension of the short pedicel; spermatangial branches arising as a primary branch of a trichoblast.

Algae epiphytice ad 8 mm alt., e penicillo basali rhizoideorum saccatorum ruborum ad 125μ long. Quae hospitem penetrat et ut cellulae discrete a cellulis pericientalibus separaturn, enascentes; rami erecti 75–100μ diam., ramos laterales intervallis plerumque 5–10 segmentorum qui sine coniunctione trichoblastis enascent, habentes; cellulae pericientrales 4, ecoriciae, segmentis aequo longis ac latis aut longioribus; trichoblastae ad 680μ long., 2–4 dichotomias, una in unoquoque segmento in 1 spira in ramis erectis, habentes; cellulae-cicatrices in ramis et erectis et prostratis; tetrasporangia in serie brevi spirali in ramis ultimis innata; cystocarpi globosi; rami spermatangiales ut ramos primarius trichoblastae enascentes.

**TYPE:** D. 18740D, tetrasporic, cystocarpic and spermatangial, epiphytic on a species of *Codium* awash at Midway I., after a severe storm, and collected by C. H. Lamoureux, Dec. 16, 1962. It is represented by fluid-preserved material and several glucose microslide mounts. It is the only collection of this species.

The rhizoids of this alga are confusingly similar to those of *P. saccorhiza*, which was growing on the same host. From that species it differs in the chiefly erect habit in contrast to the chiefly prostrate habit of *P. saccorhiza*. Also the erect branches are much higher and branched, whereas the erect branches of *P. saccorhiza* are rarely if ever branched.

It may be that this is the same alga to which Cribb (1956:135) refers, when he mentions a "different *Polysiphonia on Codium*" with both inflated and non-inflated rhizoids. Along with the two Midway algae with inflated rhizoids were several specimens of a separate plant with non-inflated and non-pigmented rhizoids, which seem to be best identified with *P. savatieri* Hariot.

*Polysiphonia saccorhiza* (Collins and Hervey) comb. nov.

*Lophosiphonia saccorhiza* Collins and Hervey

(1917:127)

Figs. 4C, 4D

Epiphytic algae with prostrate branches 50–70μ in diameter and with segments 1.0–1.3–(2+) diameters long, attached by unicellular rhizoids cut off by a cross-wall from the center of the pericentral cells; rhizoids soon becoming prominently saccate, to 140μ in diameter in the saccate tips and to 500μ long, deeply pink with numerous discoid chromatophores about 1μ in diameter distributed around the periphery of the cell; all branches are prostrate or tend soon to become more or less prostrate except for the short erect reproductive branches, and all morphologically prostrate branches bear the saccate rhizoids, although many of the rhizoids do not penetrate the host tissue; branches arising endogenously and at intervals of mostly 6–12 segments; erect reproductive branches are up to 550μ high and about 40μ in diameter with segments 1.5–2.0 diameters long. They bear trichoblasts on upper parts, one per segment, which are mostly not well developed but are occasionally to 300μ long with 2 dichotomies; trichoblasts are soon shed, leaving scar-cells one per segment in 1 spiral sequence and often prominent wall-scars at the point of abscission; scar-cells infrequent on strictly prostrate branches; tetrasporangia 40–50μ in diameter, in short series in the erect branches, much distending the narrow segments; cystocarps 1–2 near branch tips, mature pericarps subglobular, to 210μ in diameter and 240μ long with cells well separated and tending to occur in transverse as well as longitudinal rows; spermatangial branches arising as a primary branch of a trichoblast.

A single collection D. 18739A, tetrasporic, cystocarpic, and male, epiphytic on *Codium* sp., was made by C. H. Lamoureux, Midway I., Dec. 16, 1962.

The Midway plants differ from the original description of the Bermuda plants in minor respects: (1) the erect branches are much shorter and are not noticeably contracted at the base; (2) the trichoblasts are not well developed; (3) the rhizoids usually do not penetrate the host, but are abundant on the preponderantly prostrate branches, or potentially prostrate laterals; (4) the rhizoids are somewhat smaller; (5) the cystocarps are larger (probably a matter of maturity).

Since these specimens of *P. saccorhiza* were found on the same host as was *P. ruborhiza*, and since the two entities have very similar saccate and pigmented rhizoids, the question
naturally arises as to whether they are distinct species. However, the growth habit is very different: *P. saccorhiza* is chiefly prostrate with relatively short unbranched laterals, whereas *P. ruborhiza* has few or no prostrate branches and is primarily erect, with much higher erect branches with several laterals.

*P. saccorhiza* was reported from southeastern Queensland by Cribb (1954). Later Cribb (1956) decided his plant was *P. platycarpa*. Since the Queensland plant lacked the trichoblasts and scar-cells, it can hardly be identified with the Midway specimens.

Howe (in Britton, 1918) states that *L. saccorhiza* occasionally grows somewhat free from the substratum. In the Midway specimens the prostrate branches may similarly grow free from the substratum, but their identity as prostrate branches is not lost. Howe states, furthermore, that the development of free branches suggests the genus *Polysiphonia* rather than *Lophosiphonia*. This indicates that he considered the prostrate habit as the chief distinguishing feature of *Lophosiphonia*, a view difficult to maintain.

It should be noted here that Doty and Menez (1960) reported the occurrence of pigmented rhizoids on a species of *Tiffaniella*. This alga was likewise epiphytic on a species of *Codium*.

*Polysiphonia savatieri* Hariot (1891:226)

Figs. 37, 38

Epiphytic algae, mostly 1 cm high or less, from a basal attachment or a briefly prostrate or assurgent base attached by unicellular rhizoids cut off by a cross-wall from the proximal end of the pericentral cell; pericentral cells 4, echinate, with segments in the median parts of erect branches, mostly about 1 diameter long; median parts of erect branches mostly 80–140 μ in diameter; all branches arising independent of trichoblasts mostly at intervals of 7–10 segments; trichoblasts one per segment in ¼ spiral sequence, with mostly 2–3 dichotomies, to 140 μ long, soon deciduous, leaving persistent scar-cells; tetrasporangia 53–60 μ in diameter in spiral series in the terminal branches which are usually considerably distended; cystocarps globular 130–145–(220) μ in diameter, to somewhat urceolate, with pericarp cells more or less isodiametric in surface view, and with ostiolar cells sometimes prominently enlarged; spermatangial branches 130–170 μ X 45–50 μ arising as a primary branch of a trichoblast with or without a sterile tip.

**COLLECTIONS STUDIED:** MIDWAY ISLAND—

D. 18727, sterile, on *Codium*, awash, legit C. H. Lamoureux, Dec. 16, 1962; HAWAIIAN ISLANDS—H. 65–15, on *Centroceras* in shallow water near Coconut I., Kaneohe Bay, Oahu, Mar. 20, 1965; H. 65–49.5, cystocarpic, on a small seagrass, Waikiki Beach, Oahu, Apr. 26, 1965; H. 65–86.1, tetrasporic, on Pocockiella, legit M. Kajimura, Diamond Head Beach, Oahu, May 1965; H. 65–50, tetrasporic, male, with very delicate trichoblasts, on *Codium*, on the bottom of a 2-ft pool at low tide, Wawamalu Beach, Oahu, May 1, 1965; D. 20144, on *Sargassum*, in tidepools, Kamoama, Puna, Island of Hawaii, Mar. 21, 1961; TUAMOTU ISLANDS—D. 11858.3, male, 11860B, tetrasporic, transect area, Otetou, Raroia Atoll, legit M. S. Doty and Jan Newhouse, Aug. 21, 1952; AMERICAN SAMOA—T. 262A, male, at high water line 20 m from shore, Nuuli Village, Tutuila I., Sept. 8, 1963; MARSHALL ISLANDS—D. 9603A, cystocarpic, male, on *Galaxaura*, awash at Ie Village, Ie I., Arno Atoll, legit Leonard Horwitz, Aug. 8, 1951; CAROLINE ISLANDS—D. 15586.3A, cystocarpic, male, on *Padina*, on the reef at Koror I., Palau Group, legit E. Menez, Sept. 5, 1960; D. 15654.8, tetrasporic, and D. 15656.1, male, cystocarpic, on *Sargassum*, on the reef at Pulo Anna I., legit E. Menez, Sept. 3, 1960; D. 23423, cystocarpic, on seagrass, on the reef near Utwa Village, Kusia I., legit E. Menez, July 17, 1960; PHILIPPINE ISLANDS—D. 18173.1, tetrasporic, cystocarpic, male, Mangagoy, Bislig, Surigao, legit E. Menez, June 29, 1958. Also several unnumbered collections by D. P. Abbott, 1957, as follows: on *Chaetomorpha*, tetrasporic, male, northeast coast of Siasi I., Sulu Sea, Jan. 28; on *Dictyota* sp., tetrasporic, cystocarpic, male, on sand flats, Laminusa, Siasi I., Sulu Sea, Jan. 29; on turtle grass east of Laminusa, Jan. 30; on other algae, tetrasporic, on reef west of Cagayan Sulu, Sulu Sea, Feb. 28; on other algae, tetrasporic, on reef, Pasig Bay, Balabac I., Mar. 1; on *Thallasia* and *Acanthophora*, tetrasporic, cystocarpic, Gnat Reef, Balabac I., Mar. 4.
A number of additional collections have been identified with this species with considerable misgivings. They are perhaps closer to P. *sphaerocarpa* as at present interpreted. A portion of the type collection of *P. savatieri* collected at Yokosuka, Japan by M. Savatier was examined through the kindness of the Natural History Museum, Paris. The plants of this collection

![Image](image-url)

**Fig. 5.** *A*, *Polysiphonia setacea*, tip of erect branch. *B*, *Polysiphonia setacea*, portion of an erect branch, showing oblique orientation of pericentral cells. *C*, *Polysiphonia setacea*, prostrate branch and rhizoid with enlarged apex and multicellular branches. *D*, *Polysiphonia sparsa*, portion of prostrate branch. *E*, *Polysiphonia sphaerocarpa* var. *distans*, tip of branch. *F*, *Polysiphonia subtilissima* var. *abbottae*, apex of branch with abundant trichoblasts (from type material).
are abundant epiphytes 1.3–2.0 cm high, each basally attached by a tuft of rhizoids with little or no prostrate portion. In most details the plants identified with P. savatieri in this paper agree with the type. They differ from the type in minor respects: (1) they are smaller and more delicate; (2) the segments are somewhat longer; (3) there are occasional prostrate branches; (4) branching is mostly more lax, with basal unbranched axis occasionally up to 33 segments long.

The similarities between P. savatieri, P. sphærocarpa, P. mollis, P. simplex (cf. Holldenberg, 1942b:782), and several other species in the genus are such as to raise questions concerning their distinctness. However, it seems best to continue to recognize them as distinct species for the present at least. A study of the early developmental stages of P. sphærocarpa and P. mollis might be helpful in determining whether or not P. savatieri is merely a fruiting developmental stage or an ecological form of one or more of these species. D. 19143T3, cystocarpic, is identified with P. savatieri even though it is only 2 mm high. It was growing on a species of Galaxaura and was dredged from 15 fa, at Ilio P't., Molokai, Hawaii, Sept. 7, 1959. This specimen may be merely a young but fruiting plant, or its minute size may be related to the habitat.

**Polysiphonia scopulorum** Harvey (1854:540)
**Lophosiphonia scopulorum** (Harvey) Womersley (1950:188)

Plants mostly 0.5–1.0 cm high from prostrate branches 50–85 μ in diameter and with segments mostly about 1 diameter long, attached by frequent unicellular rhizoids with digitate tips, which remain in open connection with the pericentral cells bearing them; erect branches similar to prostrate branches, mostly 40–60 μ in diameter, with segments mostly 1 diameter long but often shorter or longer, arising endogenously mostly at intervals of 2–3 segments, simple or with occasional lateral cicatrogenous branches; 4 pericentral cells, ectoricate; trichoblasts and scar-cells infrequent and limited mostly to the tips of erect branches, often short but commonly 200–400 μ long or longer; scar-cells not occurring in prostrate branches; tetrasporangia 40–45 μ in diameter, in straight series, sometimes greatly distending the segments; spermatangial branches arising from the entire trichoblast primordium or in pairs from the primary branches.

**Type Locality:** Fremantle, Western Australia.

**P. scopulorum** var. **scopulorum** (Harvey) comb. nov.

Figs. 6F, 30, 31, 33, 36

Mostly 5–8 mm high and with segments mostly shorter than broad; erect branches arising mostly at intervals of 2–3 segments from the prostrate branches and usually distinctly narrowed at the base (Figs. 30, 31). The rhizoids of this variety are sometimes finely and repeatedly branched (Fig. 31) or ornately discoid (Fig. 30) in the case of epiphytic specimens.

Examination of the type material kindly loaned from the herbarium at Trinity College, Dublin, leaves little doubt that numerous specimens from the tropical Pacific Ocean are to be identified with *P. scopulorum* var. *scopulorum*. From var. *villum* it differs in the coarser erect branches with consistently shorter segments and narrowed base. Also the erect branches are more

**Key to the Varieties of Polysiphonia scopulorum**

1. Erect branches mostly less than 1 mm high ............................................................. 2

1. Erect branches 5 or more mm high at maturity ............................................................. 3

2. Epiphytic algae with erect branches mostly less than 500 μ high, unbranched, and bearing relatively huge trichoblasts ............................................................. var. macrotrichia

2. Saxicolous algae with erect branches mostly more than 500 μ high, frequently branched, and bearing trichoblasts of more moderate size ............................................................. var. minima

3. Erect branches commonly arising at intervals of 2 segments, with segments in median parts mostly shorter than broad ............................................................. var. scopulorum

3. Erect branches mostly at distant intervals, with segments in median parts mostly longer than broad ............................................................. var. villum
commonly branched in var. *scopulorum* and arise at more frequent intervals (commonly 2–3 segments) from the prostrate branches. Tricho-

blasts are mostly larger and coarser in var. *scopulorum*. Further observations are needed to determine whether or not the paired arrange-

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ment of spermatangial branches (Fig. 6F) is a characteristic feature of this variety.


P. scopulorum var. villum (J. G. Agardh) comb. nov.

P. villum J. G. Agardh (1863:941); Lopho-
sphonia villum (J. G. Agardh) Setchell and Gardner (1903), Hollenberg (1942a: 535)

Fig. 7A

This variety is usually saxicolous and has erect branches mostly 5–8 mm high with segments mostly longer than broad, arising at intervals of mostly 4–6 segments. The branches are more slender than those of var. scopulorum, arise mostly at more distant intervals, and are not noticeably narrowed at the base.

Cribb (1956:138) places P. villum in synonymy with P. scopulorum, the latter having priority. A number of specimens from the Atlantic examined by the writer and most of those from the Pacific coast of the United States conform more closely to the description given for P. villum. The latter is retained as a variety.


A collection by Louis Williams, No. 910 from Cape Lookout, N. Carolina, Aug. 1946, likewise seems representative of this variety. A minute variant form is H. 65–25.1, with few or no trichoblasts. Half embedded in a coral crust, this specimen was dredged from a depth of 2–3 ft in Kanehoe Bay, Oahu, Hawaii, Mar. 20, 1965.

**P. scopulorum var. macrotrichia** var. nov.

Fig. 7C

Diminutive algae with creeping branches to 70µ in diameter, with segments 1.5–2.0 diameters long, attached by occasional to frequent unicellular rhizoids which are not cut off from the pericentral cells as separate cells; erect branches to 225µ high but mostly much shorter with segments mostly about 1 diameter long, arising endogenously at irregular intervals of about 8–10 segments; pericentral cells 4, ecticrate; trichoblasts one per segment in 4 spiral sequence on a few terminal segments of erect branches only, to 700µ long with 6–7 dichotomies and very delicate tips and with a basal cell to 170µ long and 20–28µ in diameter, mostly soon deciduous leaving relatively prominent scar-cells and wall scars; reproductive structures not observed.

Algae diminutivae, proprietates speciei basicas praebentes, ramis repentibus, autem, relative amplis, ad 70µ diam. et ramis erectis perumque brevissimis, intervallis 8–10 segmentorum enascentibus, paucas trichoblastas relative magnas ad 700µ long. Terrentibus,

**TYPE:** D. 11514A1, collected by M. S. Doty and Jan Newhouse from a depth of 3–4 ft in a reef channel north of Onorea, Raroia Atoll in the Tuamotu Archipelago, Aug. 5, 1952. It is represented by a glucose mount.

**ADDITIONAL COLLECTIONS:** D. 21079.1, tetrasporic, on other algae, Helen reef, Western Caroline Islands, legit E. Menez, Aug. 28, 1960; D. 23112.4, on Microdictyon sp. on a reef on the eastern side of Ifaluk and Falalap Islands, Caroline Islands, legit E. Menez, Aug. 10, 1960. The latter collection has the characteristic short erect branches from extensive creeping branches, but the trichoblasts are not large as in the type collection. More collections of this alga are needed to fully establish the distinctive features, especially reproductive features.

It is interesting to note that a very similar alga was collected by Dr. Harold J. Humm. It was attached to Batophora, at a depth of 15 ft, at Lower Matecumbe Key, Monroe County, Florida, Feb. 19, 1965. In most detailed features the Florida plant is close to the Raroia collection, differing chiefly in size. The diameter of the prostrate branches of the Florida specimens is more than twice as large as that of the Raroia plants, and the trichoblasts are about twice as long. However, this is in keeping with the generally diminutive nature of most *Polysiphonia* species from the central Pacific. The Florida plants were likewise sterile.

In its chiefly prostrate habit with very short erect branches *P. scopulorum* var. *macrotrichia* resembles *P. anomala* and *P. delicatula*, from which it differs chiefly in the rhizoids which remain in open connection with the pericentral cells.
Figs. 8–21. (Scale = 100μ, except as indicated.) 8, 9, Polysiphonia apiculata, vegetative branch tip. 10, Polysiphonia sphaerocarpa var. filifera, branch tips with immature tetrasporangia. 11, Polysiphonia flac-
cidissima, a delicate variant with branched trichoblasts associated with young branch. 12, Polysiphonia flac-
cidissima var. decimera, showing branching pattern (from the type collection). 13, Polysiphonia hancockii,
**Polysiphonia** of the Tropical Pacific, I—HOLLENBERG

**P. scopulorum** var. minima var. nov.

Figs. 6G, 7B, 34

Minute algae with creeping branches 40–50 μm in diameter, with segments mostly shorter than broad, attached by unicellular rhizoids which are not cut off from the pericentral cells as separate cells and which commonly have digitate tips; erect branches 200–300 μm (to 1 mm) high and 35–40 μm in diameter, unbranched or occasionally branched near the base, arising endogenously at frequent but irregular intervals, with segments mostly about 1 diameter long; trichoblasts commonly relatively large (to 750 μm with basal cell to 200 μm long and 28 μm in diameter), with 4–6 dichotomies, arising at irregular intervals on median parts and often one per segment in 1/3 spiral sequence in upper parts of erect branches, soon shed; scar-cells not present in prostrate branches; tetrasporangia 35–40 μm in diameter, somewhat protuberant, in straight or slightly spiralling short series in the erect branches; cystocarps globular to ovoid, to 150 μm in diameter, with cells of the ostiolar rim not enlarged; spermatangial branches oblong 115–145 × 40–45 μm, with a small sterile terminal cell and a stipe mostly 35–50 μm long but occasionally to 180 μm long, arising from the entire trichoblast primordium.

Algae minutae proprietates speciei generales prae- bentes, minores, autem, maxima ex parte, ramis pro- stratis 40–50 μm diam. et ramis erectis ad 1 mm alt., intervallis satis crebris endogeneenascentibus, et trichoblastis relative magnas ad 750 μm long., quae 4–6 dichotomias habent, ferentes; rami spermatangiales in stipitibus longioribus binatim producti.

**TYPE:** H. 65–113.4, tetrasporic, cystocarpic and male, consists of three glucose slides and fluid-preserved material. It was collected by R. S. Jones at a depth of 1–2 m, about 20 m shoreward from the outer reef margin north of North I., Johnston I., Apr. 22, 1965. It was growing on dead coral.

**ADDITIONAL COLLECTIONS:** D. 11859.2, sterile, on encrusting corallines, sea reef near Otetou, Raroia, Tuamotu Archipelago, collected by M. S. Doty and Jan Newhouse, Aug. 21, 1952; D. 23112.7, tetrasporic, on *Halimeda*, on reef at eastern side of Ifaluk I., Caroline Islands, collected by E. G. Menez, Aug. 10, 1960.

In the short segments this variety is similar to var. *scopulorum*, but it is a much smaller plant and more delicate and, unlike var. *scopulorum*, the spermatangial branches have a terminal sterile cell and at least sometimes long stipes (Fig. 7B). They may occur in pairs, as in *P. scopulorum*. This instance in which the stipe of the spermatangial branch was 180 μm long may not be representative of the variety.

**Polysiphonia setacea** sp. nov.

Figs. 5A, 5B, 5C

Chiefly saxicolous algae, relatively setaceous, commonly forming extensive patches to 1 cm high from prostrate branches attached by rhizoids, which are at first unicellular and cut off as separate cells mostly from the distal end of the pericentral cells, but at maturity mostly develop multicellular tips: erect branches to 1 cm high, arising mostly cicatriciously, mostly unbranched, composed of segments 65–70–(100) μm in diameter and 0.7–1.5–(2.0) diameters long with walls relatively thick (5–8 μm); pericentral cells 4, eocorticate; trichoblasts relatively coarse, with 1–3 dichotomies, mostly much reduced and quickly deciduous; scar-cells in upper parts one per segment in 1/3 spiral sequence but mostly at intervals of 2–3 segments below, and at intervals of 1–3 segments on prostrate branches; pericentral cells in erect branches commonly slightly oblique rather than in straight longitudinal rows; tetrasporangia in slightly spiral series, up to 30 in the series, in terminal parts of erect branches; somewhat dis- tending the segments; sexual plants unknown.

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upper portion of erect branch. 14, **Polysiphonia bancroftii**, tip of erect branch. 15, **Polysiphonia poko**, tip of erect branch with spermatangial stichidia. 16, **Polysiphonia hawaiensis**, with cystocarpic. 17, **Polysiphonia beaudettii**, with fruiting lateral branches. 18, **Polysiphonia profunda**, tip of erect branch showing origin of lateral branch in association with a trichoblast (from the type slide). 19, **Polysiphonia subtilissima**, tips of erect branches. 20, **Polysiphonia profunda**, tip of erect branch, with young cystocarp and persistent trichoblasts. 21, **Polysiphonia sphærocarpa** var. *sphærocarpa*, a slender form with tetrasporic branches narrowed at the base.
Algae praeципue saxicolaе, relative setaceaе, maculas amias ad 1 cm alt. et rami prostratis volugo formantes, per rhizoideaе quae primum unicellularia et ut cellularе discrete пlerumque ab extremо distali cellularum pericentrailum separatа, matura, autem, caccumina multicularillaria plerumque efficient, affixaе; rami erecti аd 1 cm alt. saeipius cиaticiгne ensacies, saeipius non ramosi, e segmentis 65–70(–100)μ diam, et 0.7–1.5(–2.0) longioribus quam lata, membranaе relative crassas (5.8μ) hабentibus, compositi; cellularе pericentrailе 4, ectоticaе; trichoblastae relative grossae, 1–3 dichотomias habentes, plerumque valide reductae et cito deciduae; cellularе-сisctricеs in partiibus superioribus, una in unoquoque segmentо in ½ spira, пlerumque, autem, intervallis 2–3 segmentorum infrа et 1–3 segmentorum in rami prostratis; cellularе pericentrailе in rami erectis vulgo paululum oblique et non in ordinibus rectis longitudinalibus; tetrasпораngia in serie aliqualium spiralii usque in ad 30 in serie, in particibus terminalibus ramosum erectorum; segmentа satis distendentes; plantaе sexuales ignотae.

Трype: D. 14696, on rocks in algal turf in a high tide pool near Koko Head Parking Area, eastern Oahu, легит E. Choy, Nov. 14, 1954.


A variant form is represented by G. 502, abundant on Halimeda sp. at a depth of about 19 m in the lagoon at Eniwetok Atoll, Marshall Islands, collected Aug. 29, 1955. It differs in the following respects: (1) scar-cells occur one per segment throughout; (2) the pericentral cells are hardly oblique; (3) the rhizoids arise ½ the length of the pericentral cell from its distal end; (4) the tips of the rhizoids are discolored, with a lobed apex to which the separate marginal cells are attached; (5) trichoblasts are unbranched or with a single branch and with a very long basal cell (to 240μ long); (6) the erect branches tend to arise in pairs with 4 segments between corresponding members of successive pairs. G. 781 is similar to the preceding in a number of the variant features. It was likewise growing on a Halimeda sp. at a depth of 5.3 m in the lagoon, Eniwetok Atoll. It was collected Sept. 7, 1955. D. 13464.1 likewise represents this variant form in most respects. It was collected from a basalt ledge on
the west lip of Pohoiki Bay, Puna, Island of Hawaii, Nov. 10, 1956.

Characteristic features of this low matted species are: the rhizoids with multicellular tips arising at the distal end of the pericentral cells, and the more or less oblique position of the pericentral cells, which are periclinally flattened.

**Polysiphonia sparsa** (Setchell) comb. nov.

*Lophosiphonia sparsa* Setchell (1926:103)

Figs. 5D, 23, 40

Epiphytic algae to 1 cm high from prostrate branches attached by relatively large unicellular rhizoids cut off by a cross-wall from the proximal end of the pericentral cells and often with finely digitate tips; plants relatively stiff, with 4-40 pericentral cells and segments mostly 0.2-0.5 diameter long and 200-280μ in diameter in median parts of main branches; trichoblasts one per segment in ½ spiral sequence; usually poorly developed but sometimes to 650μ long with 3-5 dichotomies and up to 9 cells in length of longest axis, with very delicate tips, soon deciduous, leaving small scar-cells and often prominent wall scars; branches arising independent of trichoblasts, with mostly 7-12 segments between successive branches; tips of branches acutely pointed; leading axes commonly distinct, the branching mostly not at all dichotomous, at least near apices; tetrasporangia 80-85μ in diameter, spiralling in the ultimate and subultimate branches and eventually distending the segments somewhat; cystocarps to 330μ in diameter, nearly spherical, with very short, broad attachment and pericarp of relatively large cells 30-40μ in diameter; spermatangial branches arising as a primary branch of a trichoblast without sterile tip.


Examination of the type of *Lophosiphonia sparsa* Setchell, kindly loaned from the herbarium of the University of California at Berkeley, leads the writer to conclude that the specimens listed above are to be identified with this species, which for reasons presented in the introductory paragraphs of this paper is more properly placed in the genus *Polysiphonia*.

It seems likely that specimens of this species have been sometimes identified as *P. ferulacea*. However, *P. sparsa* is a much smaller plant with much shorter segments especially in terminal branches, and has spermatangial branches without the sterile tips, seemingly characteristic of *P. ferulacea*.

**Polysiphonia sphaerocarpa** Boergesen (1918: 271)


Intertidal tufted algae mostly 0.5-1.5 cm high from prostrate branches of limited extent (80)-100-200μ in diameter, attached by unicellular rhizoids, which are cut off as separate cells from the pericentral cells; erect branches assurgent to cicatrogenous, mostly 100-180μ in diameter, with segments mostly 1.0-1.5 diameters long, pseudodichotomously branched in a somewhat flabellate manner; branches arising independent of trichoblasts, at intervals of 7-11 segments; pericentral cells 4, ecorticate; trichoblasts one per segment in ½ spiral sequence, 100-200-580μ long with mostly 3-4 dichot-
Figs. 22–36. (Scale = 100μ, except as indicated.) 22, *Polysiphonia poko var. longii*, tip of tetrasporangial branch of the type specimen. 23, *Polysiphonia sparsa*, vegetative branch tip. 24, *Polysiphonia sphaerocarpa var. filifera*, with spermatangial stichidia. 25, *Polysiphonia quadrata*, vegetative branch tip from the type
omies; scar-cells small, frequently present on prostrate branches; wall-scars rarely present at the former point of attachment; tetrasporangia to 70μ in diameter in spiral sequence in ultimate and subultimate branches; cystocarps globular, 250-350μ in diameter, with cells of the ostiolar rim distinctly enlarged; spermatangial branches cylindrico-conical 140-170-(290) × 40-60μ, mostly without sterile tips, arising as a primary branch of a trichoblast.

**TYPE LOCALITY:** St. Thomas Island in the Virgin Islands. As represented in the tropical Pacific Ocean this is a very variable species. It has been identified by Menez (1964) and other investigators as *P. pulvinata* (C. Agardh) J. G. Agardh (i.e., *Hutchinsia pulvinata* C. Agardh). According to Boergesen (1930:85), "Hutchinsia pulvinata* C. Ag., and most probably *Conerva pulvinata* Roth, both quoted by Montagne, have 6 pericentral cells, as pointed out by Bornet [1892:306], who probably examined Roth's specimens."

The writer examined five specimens from the Kützing herbarium identified as *P. pulvinata* C. Agardh. Cross sections showed that two of these have 6 pericentral cells. The other three have 4 pericentral cells. In none of the five specimens do the scar-cells occur regularly on each segment as in the various specimens from the tropical Pacific Ocean. One of those with 4 pericentral cells bears the notation "a communicat ex herbario J. G. Agardh."

The writer's observations and those of Boergesen seem to indicate that the specimens here-with identified as *P. sphaerocarpa* Boergesen cannot be identified with *P. pulvinata* (C. Agardh) J. G. Agardh.

Although *Conerva pulvinata* Roth has priority, Roth's specimens, unfortunately, are not available for study, having been destroyed during the second World War. On the other hand the writer examined a prepared mount and fluid-preserved material of the type of *P. sphaerocarpa* kindly loaned from the herbarium at the University of Copenhagen and found the Pacific specimens to agree in all basic details with the type of Boergesen's species, although the Pacific plants exhibit much more variability than Boergesen's description would indicate.

Taylor (1960) describes *P. sphaerocarpa* as "a reef plant growing in exposed places." Those so identified from the Pacific are of similar habitat. A number of collections by Dr. A. J. Bernatowicz from Bermuda, identified as *P. sphaerocarpa*, were found to correspond closely in most respects with the Pacific specimens, including the enlarged cells of the rim of the ostiole of the pericarp.

*P. sphaerocarpa* as described herewith seems close to *P. simplex* Hollenberg (1942b:782), but the latter plant is often larger and is basically prostrate, with assurgent branches, whereas *P. sphaerocarpa* is tufted erect with limited prostrate branches.

**KEY TO THE VARIETIES OF Polysiphonia sphaerocarpa**

1. Segments in median parts of leading branches mostly about 0.3 diameter long; trichoblasts well developed and relatively persistent ........................................... var. *filifera*
2. Segments in median parts of leading branches mostly about 1 diameter long; trichoblasts mostly less well developed and soon deciduous

2. Lateral branches abundant, at intervals of 5-12 segments ................................................................. var. *sphaerocarpa*

3. Lateral branches commonly at intervals of 20 or more segments ......................................................... var. *distans*
P. sphaerocarpa var. sphaerocarpa
Figs. 21, 26

MATERIAL EXAMINED (Those marked with an asterisk are more slender with segments often to 2 diameters long and with lateral branches slightly to distinctly narrowed at the base; see Figure 21): HAWAIIAN ISLANDS—D. 13355*, tetrasporic, cystocarpic, spermatangial, awash, Sans Souci Beach, Waikiki, Oahu, Oct. 2, 1956; D. 19121L, cystocarpic, dredged 15–26 ft, Pokai Bay, Oahu, Aug. 1, 1959; D. 19624, cystocarpic, Kahanaaki, Oahu, Jan. 27, 1962; a collection* by Isabella Abbott, tetrasporic, cystocarpic, on Laurencia sp. and corallines, Ewa Beach, Oahu, Mar. 17, 1946; H. 62–3, tetrasporic, cystocarpic, on Acathophora, Sans Souci Beach, Waikiki, Oahu, Dec. 12, 1962; a collection by G. F. Papenfuss, tetrasporic, Hanauma Bay, Oahu, Mar. 1, 1942; W. A. Setchell, 10403, cystocarpic, Mokuauia I., off the northeast coast of Oahu, July 14, 1924; D. 19738A2, tetrasporic, on rocks, Halena, Molokai, Dec. 27, 1953; D. 17184A1, southwest of Kaimu Bay, Island of Hawaii, Feb. 27, 1953; D. 17197A1, tetrasporic, with other algae, Kalapana Beach, Kaimu Bay, Hawaii I., Feb. 2, 1953; H. 65–6.5, tetrasporic, in algal turf, Kona District, Hawaii, legit M. Kajimura, Jan. 29, 1965; TUAMOTU ARCHIPELAGO—D. 11059.1*, tetrasporic, on coral reef opposite Ngarumuoa Village, Raroia Atoll, legit M. S. Doty and Jan Newhouse, July 8, 1952; AMERICAN SAMOA—all but the last legit R. Buggeln, 1964: T. 717, cystocarpic, on wave-washed basalt at the mouth of Faga Bay, Tutuila I., Aug. 21; T. 732, spermatangial, on Laurencia sp., wave-washed shore, Vista Bay, Tutuila, Aug.; T. 735B, tetrasporic, on wave-washed shore, Vatia Bay, Tutuila I., Aug. 1; T. 841, tetrasporic, cystocarpic, on wave-dashed shore, in small tidepools, Onenoa, Tutuila, Aug. 6; W. A. Setchell, 1068 (C. 237033), as P. tongatensis Harvey, legit F. A. Potts, from a buoy, Pago Pago Harbor, June 10, 1920; GILBERT ISLANDS—D. 18780, cystocarpic, P. fragilis as interpreted by Tsuda (1964) on the reef south of Rawanawi Village, Marakeai Atoll, legit M. J. Cooper, July, 1962; MARSHALL ISLANDS—H. 48–9514.2, tetrasporic, cystocarpic, on Boddelea sp., inner shore, Nama I., Bikini Atoll, July 15, 1948; CAROLINE ISLANDS—D. 23621, on the reef at Utwa Village, Kusiae I., legit E. Menez, July 17, 1960.

P. sphaerocarpa var. distans var. nov.
Fig. 5E

Plants as in the species but with intervals of (8)–20–25 or more segments between successive branches and with chromatophores mostly aggregated on the inner wall of the perisentral cells; trichoblasts relatively coarse, to 365μ long.

Plantae ut in species descriptae, intervallis, autem (8)–20–25 vel plurim segmentorum inter ramos successivos, et chromatophoris in pariete interiore cellularum perisentralium plerumque aggregatis; trichoblastae relative grossae, ad 365μ long.


ADDITIONAL COLLECTIONS: D. 19534, tetrasporic, cystocarpic, Hanauma Bay, Oahu, Apr. 6, 1952. A collection, III BA, spermatangial, by T. A. and Anne Stephenson, Plantation Keys, Florida, in 1957, seems identical in most details with the Pacific specimens, including the distant branches and the position of the chromatophores, although the branches are at somewhat closer intervals in the case of the Florida specimen. Stephenson III Bb from the same locality is very similar, although coarser, and the spermatangial branches terminate in a globular sterile cell very much like those figured by Boergesen (1918: Fig. 279) for a plant he identified as P. ferrulacea. This type of male structure has been seen several times in plants identified by the writer as P. ferrulacea, although the plants bearing them were in other respects distinct from P. sphaerocarpa.


Still another variant is represented by the following: D. 13014.2, male, on reef near
**Polysiphonia** of the Tropical Pacific, I—Hollenberg

Koloa, Oahu, Oct. 30, 1955; D. 17184AE, cystocarpic, on the southwest end of Kaimu Bay, Island of Hawaii, Feb. 27, 1953; D. 17332.1, immature male, 4 mile southwest of Ophihako, Puna, Island of Hawaii, Jan. 27, 1953; T. 749, T. 731, T. 732, spermatangial, and T. 755A all collected by R. Buggeln from coral and basalt, Vatia Bay, Tutuila I., American Samoa, Aug. 1964. This variant is characterized by segments of main branches, which are mostly less than 1 diameter long, and by relatively small spermatangial branches to 110μ long bearing a sterile tip composed of a single small cell 1–3 diameters long. In the latter respect this variant is similar to a specimen of *P. sphaerocarpa* collected by S. Carlquist at Grayson’s Cove, Saccora I., off the coast of Lower California, Mexico, May 4, 1955. However, in the Mexican specimen the sterile tips of the spermatangial branches are up to 280μ long and composed of 3–4 cells. Tsuda’s specimens from Samoa and the Mexican specimens are closer to var. *sphaerocarpa* in having short segments and in having intervals of 6–7 segments between successive branches. An unusual variant with respect to the spermatangial branches is represented by H. 65–66, cystocarpic and spermatangial, with very delicate trichoblasts and with spermatangial branches mostly very large and lanceolate in shape, with a short polysiphonous terminal extension, which bears short lateral trichoblasts (Fig. 26). This specimen was collected at Kahala Park, Honolulu, Hawaii, Feb. 25, 1963. It may represent a case of teratology. This variant is likewise closer to var. *sphaerocarpa* in other respects.

**P. sphaerocarpa** var. *filifera* var. nov.

Figs. 10, 24, 27, 28

Epiphytic or saxicolous with segments of erect branches mostly ca. 0.5 diameter long, with relatively long and persistent trichoblasts, and generally a more extensive prostrate branching system. The variety bears considerable resemblance to *P. pokos* but usually has much-branched erect branches, whereas the erect branches of *P. pokos* are mostly unbranched. Thus far this variety has been collected almost exclusively in the Hawaiian Islands, where it is very common.

Plantae epiphyticae aut saxicola, proprietates specie generalis habentes, segmentis, autem, ramorum erectorum ca. 0.5 brevioribus quam lata, trichoblastis relative longis persistentibusque, ramificatione prostrata plerumque ampliore.

**TYPE:** D. 22532, tetrasporic, cystocarpic, on algal turf near Honokohau, Maui, Hawaii, legit H., T., and B., Apr. 10, 1965.

**ADDITIONAL COLLECTIONS STUDIED:**

D. 20131, on other algae, Guam, legit E. Menez, Oct. 12, 1960; D. 12692, cystocarpic, male, on *Helminthoblastia*, at a very low tide level, Waianae, Oahu, legit Jan Newhouse and Henry Kekoaunui, Jan. 2, 1954; D. 12782, tetrasporic, cystocarpic, male, on *Chondria* sp., Haleiwa Army Beach, Haleiwa, Oahu, legit Elvin Fong, Apr. 25, 1955; D. 13442, tetrasporic, intertidal basalt, west lip of Pohoiki Bay, Puna district, Island of Hawaii, Nov. 10, 1956; D. 19315.1, cystocarpic, male, Makua Beach, leeward Oahu, Jan. 21, 1962; D. 17932.5, tetrasporic, cystocarpic, below low tide level at the east end of Maile Beach, Lualualei, Oahu, Apr. 11, 1959; D. 19618, tetrasporic, male, Kahanahai, Waianae, Oahu, Jan. 27, 1962; H. 65–61.5, cystocarpic, in algal turf, Wawamalu Beach, Oahu, May 1, 1965; a collection by G. F. Papenfuss, cystocarpic, male, between Halona and Kaloko, Oahu, Mar. 29, 1942; H. 65–3, tetrasporic, cystocarpic, male, upper littoral, opposite Kaneana Cave, leeward Oahu, Jan. 1, 1965; H. 65–8.5, tetrasporic, cystocarpic, male, upper littoral on basalt, northeast of Waiakea Bay, southeastern Oahu, Feb. 13, 1965; H. 65–10, tetrasporic, cystocarpic, on *Laurencia*, Makaha Pt., Oahu, Feb. 28, 1965; D. 22538.1, tetrasporic, male, in algal turf, basalt shore, southwest of Maalaea, Maui, legit H., T., and B., Apr. 19, 1965; D. 22423.1, tetrasporic and D. 22442, tetrasporic, cystocarpic, sandy beach near Camp Pecusa, Olowalu, Maui, legit H., T., and B., Apr. 19, 1965; D. 22484.1, male, basalt reef north of Kahana, Maui, legit H., T., and B., Apr. 20, 1965; D. 22549.2, tetrasporic, intertidal on *Pocockiella* growing on large boulders, Kahakuloa, Maui, legit H., T., and B., Apr. 21, 1965; D. 20165.1, tetrasporic, 1.3 cm high, with trichoblasts of variable coarseness, in algal turf in tidepools, Kamoamoa, Puna District, Island of Hawaii, Mar. 21, 1965 (somewhat larger and coarser than most of the collections of this variety); D. 20158, tetrasporic, on *Hypnea*, in tidepools, Kamoamoa,

Polysiphonia subtilissima Montague (1840:199)

Fig. 19

Plants to 4 cm high, from prostrate branches attached by relatively long, unicellular rhizoids, often with lobed tips, which remain in open connection with the pericentral cells; erect branches 70–130μ in diameter in median parts, with lateral branches arising independent of trichoblasts at intervals of 5–8–(14) segments, and with frequent endogenous branches arising from prostrate branches; segments in the main branches mostly 1.0–1.5 diameters long; pericentral cells 4, ecorticate; cell walls mostly thin and hyaline, except in lower parts where they may be considerably thickened, to 11μ; apical cells relatively large; trichoblasts infrequent and usually poorly developed and unbranched but occasionally to 400μ long, with 1–2 dichotomies, tapering to delicate tips, but relatively straight and stiff, soon deciduous leaving inconspicuous scar-cells; reproductive structures not observed in the materials studied.

Although usually sterile and smaller than the species elsewhere, Pacific specimens correspond closely to the features generally attributed to the species, except that the rhizoids although mostly long are not particularly coarse as described by Taylor (1960) for the species in Atlantic waters. Found mostly in slightly brackish water.

TYPE LOCALITY: Cayenne, French Guiana, northern South America. All but one of the collections identified with this species are from the island of Oahu, Hawaii. This probably indicates a lack of collections from suitable localities elsewhere.

P. subtilissima var. subtilissima

COLLECTIONS STUDIED: M. 710, 711 (BISH), at a depth of 4.3 ft, along the bank of Waipuhi stream, Kamehameha Highway bridge, near Kaneohe, Feb. 24, 1961; M. 727, 728A (BISH), from basalt rock wall, Waipuhi stream near Hauula School, Feb. 24, 1961; D. 14695, on rocks, south end of Salt Lake, Honolulu, Hawaii, early Jan. 1964; C. 696325, legit Cyril Crossland 6721, Marquesas Islands, 1923–24.

P. subtilissima var. abbottae var. nov.

Figs. 5F, 6A

With the features of the species but with longer segments (2–2.5 diameters long) in median parts of the main branches, with more slender main branches (50–70μ in diameter), and with abundant and relatively persistent slender trichoblasts to 600μ long and 6–9μ in diameter at the base, composed of relatively long cells, arising at intervals of 2–3–(12) segments; reproductive structures unknown.

Varietas proprietates speciei habens, segmentis, autem, longioribus (2.0–2.5 plon longioribus quam lata) in ramis principalibus qui tenuiores (50–70μ diam) et trichoblastas tenues ab undulantes relative persistantes, ad 600μ long., 6–9μ diam ad basim habent; trichoblastae e cellulis relative longis, intervallis 2–3–(12) segmentorum ensatibus compositae; stracturae reproductive ignotae.

The type and only known collection of this variety was collected from the shores of Salt Lake, Oahu, and reported by Isabella A. Abbott, No. 1757. The water in this pond was described by Abbott (1947) as nearly fresh. Abbott gave two figures (13A, B), but did not assign the plant to a definite species on account of the lack of reproductive structures. The habitat and the nature of the rhizoids strongly suggest placement in P. subtilissima. The most distinctive feature of the variety is the abundance of trichoblasts. Rhizoids remain in open connection with the pericentral cells and tend to arise in more or less whorled arrangement (Fig. 6A).

P. subtilissima Segi (1951:197) cannot be identified with Montagne’s species if the Hawaiian specimens and the specimens from the southeast coast of the United States mainland are properly identified. Segi’s Figure 8A shows rhizoids cut off as separate cells, a feature indicative of another species.

Polysiphonia tenuis sp. nov.

Figs. 6B, 6C

Minute algae with creeping branches 30–35μ in diameter, composed of segments about 1 diameter long and attached by unicellular rhizoids, which are cut off from the pericentral cells as separate cells; without scar-cells on the prostrate branches; erect branches to 2 mm high, unbranched, 28–35μ in diameter, with segments mostly 1.5–(2.0) diameters long, arising endog-
enously at frequent intervals; pericentral cells 4, erecticate; trichoblasts to 800μ long with 2–4 dichotomies and with basal cells to 260μ long and 30μ in diameter, and with very delicate tips, arising one per segment in terminal parts of erect branches but at intervals of 2–3 segments in lower parts; tetrasporangia in short spiral series near branch tips; cystocarps urceolate, 140–150μ broad and 190–220μ long, on the middle and upper parts of erect branches; spermatangial branches 100–130μ × 35–50μ, without sterile apices, arising from the entire trichoblast primordium.

Algae minuta ramos repentem 30–35 μ diam., compositae et segmentis ca. aequae longis ac lactis, habentes, per rhizoida unicellulare, ut cellulas discretas a cellulis pericentralibus separata, affixae; sine cellulis-cicatricibus in ramis prostratis; rami erecti ad 2 mm alt., non ramosi, 28–35 μ diam., segmentis 1.5–2.0 longioribus quam lata, intervallis frequentibus endogene nascentes; cellulae pericentrales 4, erecticate, trichoblastae ad 800 μ long., 2–4 dichotomias habentes, cellulis basilibus ad 260 μ long. atque 20 μ diam., una in unoquaque segmento in partibus terminalibus, intervallis, autem, 2–3 segmentorum in partibus inferioribus; tetrasporangia in serie spiralire brevi; cystocarpi urceolati, 140–150 μ lat. atque 190–220 μ long.; rami spermatangiales 100–130 μ × 35–50 μ, sine cacinibus sterilibus, e primordio toto trichoblastae ensascentes.

**Type:** H. 65–105.1 is the only collection. It is represented by 6 glucose mounts and some fluid-preserved material. It was growing on dead coral and was collected by R. S. Jones at a depth of 1–2 m and 20 m shoreward from the outer reef margin north of North I., Johnston Island, Apr. 22, 1965.

This is another minute plant resembling *P. scopulorum* in habit, in endogenous origin of erect branches, and spermatangial branches arising from the entire trichoblast primordium. From *P. scopulorum* it differs in the rhizoids which are cut off as separate cells and in the occurrence of tetrasporangia in spiral series. From *P. pseudovillum* it differs in the endogenous origin of branches and in the spermatangial branches.

**Polysiphonia tuberosa** sp. nov.

Figs. 3D, 3E, 39

Minute epiphytes with limited to extensive prostrate branches 45–80–(100) μ in diameter, frequently with local portions of prostrate branches conspicuously swollen and filled with what appears to be food reserves; attached by unicellular rhizoids cut off from the pericentral cells as separate cells; erect branches assurgent or endogenous, to 12 mm high and 50–65 μ in diameter with segments 1.5–2.0 diameters long, mostly with infrequent lateral branches, at intervals of 7–20–(30) segments; pericentral cells 4, erecticate; trichoblasts few and not well developed or frequently long (to 500 μ) and with 2–3 dichotomies and a basal cell up to 140 μ long; scar-cells at intervals of 1–2 segments on erect branches, mostly lacking on prostrate branches; erect branches mostly or all endogenous, lateral branches cicatrigenous, sometimes appearing to arise in connection with a trichoblast, when in fact the branch arises from the potential scar-cell bearing the still persistent trichoblast; tetrasporangia to 58 μ in diameter, in short straight series, much distending the segments; spermatangial branches arising as a primary branch of a trichoblast.

Algae epiphyticae minuta, ramos prostratis praefinitis ad late patentes, 48–80–(100) μ diam., horum partibus localibus manifeste tumuldis et, ut videetur, mutimento sepanso piens; plantae per rhizoida unicellulare, a cellulis pericentralibus et cellulis discretas separata, affixae; rami erecti assurgentem aut endogeni, ad 12 mm alt, 50–65 μ diam., segmentis 1.5–2.0 plo longioribus quam lata, plumque rarious ramos laterales, interdum, autem, aliquot ramos laterales intervallis 7–20–(30) segmentorum habentes; cellulae pericentrales 4, erecticate; trichoblastae paucae necnon male evolutae, aut saepse longae (ad 500 μ) et 2–3 divisiones atque cellulum basalem usque ad 140 μ long. praebentes; cellulae-cicatricis intervallis 1–2 segmentorum in ramis erectis, in ramos prostratis maxime ex parte carentes; rami erecti plerique omnesve endogeni, rami laterales cicatricine, interdum in assicuriente cum trichoblasta ut videtur ensascentes, cum enim rami et cellulara-cicatri ci potentiali trichoblastam etiam persistentem ferente, ensascent; tetrasporangia ad 58 μ diam., in serie brevi rectaque, segmenta multum distendientia; rami spermatangiales ut ramos primarius trichoblastae ensascentes.

**Type:** D. 19137 N1, sterile, dredged 15–20 fa, off Ilio Pt., Molokai, Hawaii, Sept. 7, 1959. Represented by a glucose slide mount.

**Additional Collections** (all from Hawaii): D. 19134 AC2, on Sargassum; D. 19134 H1, on *Amastia*, all from 25 fa near a channel buoy, Kanehoe Bay, Oahu, July 15,
1959; D. 19116Q1, on *Hypnea*, Pokai Bay, Oahu, Sept. 15, 1959; D. 1914QD1, from 31–32 fa, Penguin Bank southwest of Molokai, Sept. 7, 1959. A collection by Dawson No. 7472 from Lake Surprise, Key Largo, Florida, May 28, 1949, has a number of features in common with the Hawaiian specimens.

The minute size, delayed exogenous branching, and frequently tuberous prostrate branches are the chief distinguishing features of this species.

**Polysiphonia upolensis** (Grunow) comb. nov.  
Figs. 6D, 6E, 29, 35, 42

*P. tongatensis* var. *upolensis* Grunow (1873: 49)

Plants 1–2–(3) cm high from limited to extensive creeping branches attached by unicellular rhizoids, which often have finely digitate tips, and which are cut off as separate cells from the pericentral cells; rhizoids often conspicuously swollen in the middle, to 95 μ in diameter; prostrate branches 70–140 μ in diameter, composed of segments mostly 1.0–1.5 diameters long and slightly nodose; erect branches assurgent or arising cicatricenously from prostrate branches, 100–120 μ in diameter and composed of segments (1)–1.5–2.0 diameters long and usually not at all nodose, pseudodichotomously branched at wide angles below and narrower above, at intervals of 14–20–(50) segments, the branches arising exogenously, independent of trichoblasts or occasionally cicatricenously; pericentral cells 4, ecoricate; trichoblasts 200–340–(700) μ long, delicate, measuring 8–10 μ in diameter at the base, with 1–3–(4) dichotomies and with delicate tips, arising at intervals of (1)–2–3 segments in 1/4 spiral sequence, soon deciduous; scar-cells relatively small, on prostrate and erect branches, and with no obvious wall scars; tetrasporangia 60–80 μ in diameter in slightly spiral series in the ultimate and subultimate branches; cystocarps globular to slightly ovoid, 150–200–(275) μ in diameter, with cells of the ostiolar rim not noticeably enlarged; spermatangial branches 130–190 × 22–30 μ commonly with 1–2-celled sterile tips; arising as a primary branch of a trichoblast.

The type material from the Grunow Herbarium at the Natural History Museum, Vienna, was collected by Dr. E. Graeffe at Upolu, British Samoa. This material consists of six herbarium sheets on which are mounted 11 separate specimens accompanied by five glass microslide mounts (dried) and three sketches of detailed features, presumably by Grunow. Herbarium sheet 7778 probably is most representative of the collection and is reproduced in Figure 42A–F. It will be noted that two of the specimens are attached to leaves of a species of *Halophila*. Two were growing on *Halimeda* sp.

Examination of the type specimens reveals the same detailed features found in the numerous collections listed below. The plants of the type collection are 2–3 cm high, branches arise at intervals of 10–20 segments. Scar-cells occur mostly at intervals of 2 segments. Tetrasporangia occur in a slightly spiral series of 30–40 segments. The cystocarps are globular to 230 μ in diameter with cells of the rim of the ostiole not enlarged, and spermatangial branches are 200–220 μ long, lanceolate, with a small, mostly one-celled, sterile tip.


Da. 19532, 19539, tetrasporic, Palmyra Atoll, Oct. 1958; TUAMOTU ARCHIPELAGO—D. 11215.3, tetrasporic, D. 11217A, on a stump at a depth of about 5 ft, near the lagoon reef transect, Ngarumaoa, Raraio Atoll, legit M. S. Doty and Jan Newhouse, July, 1952; SOCIETY ISLANDS—D. 12103.1, cystocarpic, Arue Point, Tahiti, Sept. 15, 1952; collections by J. Randall; D. 14699, from the reef flat, Matavai Bay, Tahiti, Apr. 2, 1956 and D. 14700 from rocks at the water’s edge, Putepai Bay, Moorea, May 30, 1956; AMERICAN SAMOA—T. 678A, on Dictyosphaeria, in shallow water near shore, Vattia Bay, Tutuila I., legit R. Buggeln, Aug. 1964; T. 779.1, cystocarpic, male, in basalt tidepools near Onenoa, Tutuila I., legit R. Buggeln, Aug. 13, 1964; FIJI ISLANDS—D. 1212212, cystocarpic, on Caulerpa sp., Navavevu Cuvu, Singtoka, Viti Levu I., Sept. 22, 1952; GILBERT ISLANDS—D. 18897A, in a shallow passage between the lagoon and the ocean, Abemama Atoll, legit M. J. Cooper, July 1962; MARSHALL ISLANDS—D. 9215 B, tetrasporic, on coral, transect area, Ine Village, Arno Atoll, legit Leonard Horwitz, July 30, 1951; D. 18551.1, tetrasporic, Parry I., Eniwetok Atoll, Jan. 27, 1959; G. 608.1, tetrasporic, cystocarpic, male, G. 610, male, and G. 612, male, in the lagoon at a depth of 19 m, Eniwetok Atoll, Sept. 1955; CAROLINE ISLANDS (all legit Ernani Menez, June to Sept. 1960)—D. 15546.1, on Sargassum, D. 15556.1, cystocarpic, male, on Sargassum, D. 15557.1, tetrasporic, on Padina, D. 15559.2, tetrasporic, on Acanthophora, D. 15563.1 and 15566 on Padina, D. 15567.1, male, D. 15586.3B, tetrasporic, cystocarpic, on Padina, all eight collections from Koror I., Palau Group; D. 15576.1, cystocarpic, male, D. 15645.1, cystocarpic, D. 15656.1B, tetrasporic, on Sargassum sp., from Pulu Anna I.; D. 15721.2, D. 21737.1, tetrasporic, on dead coral, Mantapeitak I.; D. 21709.5 and D. 21838.1, tetrasporic from Epwellkapw, Ponape I.; D. 21796.5, tetrasporic, cystocarpic, eastern side of Peipalap Peak, Ponape I.; D. 21046, procarpic, south end of Moen I., Truk Islands; D. 23020, on coral pebbles on the reef at Utwa Village, Kusia I., D. 23207.4, on Microdictyon, south tip of Sorol I.; D. 15879.1 and D. 23854, tetrasporic, cystocarpic, Falas I., Truk Islands; PHILIPPINE ISLANDS—D. 18070A, cystocarpic, south of Sava wharf, Davao, Mindiniao, legit E. Menez, June 26, 1958; D. 18103A, on other algae at a depth of 3–6 ft, near Davao, Mindiniao, legit E. Menez, June 22, 1958; D. 18227A, on Avrainvillea, Davao, Mindiniao, June 24, 1958; several collections by D. P. Abbott, Feb.–Mar., 1958 as follows: on other algae, Tijitji Reef, Tawitawi I., Sulu Sea; tetrasporic, southeast shore of Faganak I., Turtle Group, Sulu Sea; male, on Tydemania, Laa, Tawitawi I., Sulu Sea; Calandorang Bay, Balabac; MARIANA ISLANDS—H. 65–75, awash at Agat, Guam, legit Mrs. Leonard Nelson, May, 1965. VIET NAM—Judging by Figure 60f. of Dawson (1954:455) it seems likely that his Polysiphonia sp., Da. 11329, is P. upolensis. A collection by Cyril Crossland 7259 (C. 792042), and Crossland 7153 (C. 791870) from Pa’ea, Tahiti, Jan. 1929, both identified as P. tongatensis, are P. upolensis, as is also a collection, July–Sept. 1964 by David Sigeo, No. 29D, from the lagoon reef of Gan I., Addu Atoll, Maldives Islands in the Indian Ocean.

This species is very common in the Caroline Islands and the Philippine Islands. It seems closest to P. sphaerocarpa from which it differs in the irregular distribution of trichoblasts and scar-cells, in the lack of enlarged cells on the ostiolar rim of the pericarp, in branches arising at more distant intervals, and probably in the sterile tip of spermatangial branches.

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Revision of the Genus *Pandanus* Stickman, Part 26

*Pandanus mayotteensis* from the Iles Comores

HAROLD ST. JOHN

Up to the present there has been known only one species of *Pandanus* in the Iles Comores, *P. maximus* Martelli (sect. *Pandanus*), indigenous to the Ilé Grande Comore. Now, there can be announced a second species from the islands, *P. mayotteensis* (sect. *Vinsonia*). The islands lie in the Mozambique Channel, about midway between Madagascar and Mozambique, Africa.

**Pandanus mayotteensis** sp. nov. (sect. *Vinsonia*)

Figs. 245, 245A, 246.

Nom. vern.: "doua," "pandanus panaché" (= foreign *Pandanus*).

**Diagnosis Holotypi:** Arbor 4–6 m alta 10 cm diametro, cortice brunneo sublaevi, radicibus fulturosis nullis, foliis 1.5–1.6 m longis 5.7–6.7 cm latis supra olivaceis infra pallidioboribus coriaceos in sectione mediiali cum 43–45 nervis paralleliis secundariis in dimidio quoque proxima basem cum nervis tertiiis transversis eis reticulis breviter oblongis formantiis supra latier sulcatis et cum plicis bis in sectione M-formatis laminis ligulatis sed in media ultima in apice 10 cm longo trigono subulato diminuientibus 10 cm ex apice 5 cm lato basi ampliicali inerni sed ex 10.5–15 cm marginibus cum serrae 0.7–1.3 cm longis 2–8 mm separatim albis sed apicibus brunneis, midnervo infra paene ad medium inerni, in sectione mediiali marginibus cum aculeis 0.5–0.7 mm longis 3–7 mm separatim subulatis adscendentibus valde adpressis albis, midnervo infra cum aculeis simulatibus sed 0.7–1 mm longis 4–7 mm separatim, in apice subulato marginibus et midnervo infra cum serrulis 0.3–0.5 mm longis 1.5–3 mm separatis, inflorescentia foeminea terminali cum syncarpio solitario erecto, pedunculo 35 cm longo 2 cm diametro recto 3-laterato cum bracteis foliosis paucis deciduis, syncarpio 15 cm longo 14 cm diametro globoso cum 55 phalangibus eis quando viridibus 5.3–5.5 cm longis 3.7–4.6 cm latis 3–4.4 cm crassis sed illis siccatis 4.5 cm longis (forsan partim ex animalibus editis) 2.8–4.1 cm latibus 2.2–3.2 cm crassis brunneis (geminis 5.6 cm latis et cum 6 loculis) cuneatis 5.6–angulosis "rubris" parte ⅔ supera libera lateribus planis apice depresse convexo (vel semiorniculati) laevi lucido quando submaturis sinu centrali brevi distincto 0.5–2 mm profundo quando maturis sinibus 5–6 mm profundis confluentibus, carpelis 3–6, stigmatibus 4–8 mm latis cordatis ad oblatore-reniformibus brunneis papillosis centripetalibus in phalangibus viridibus prostratis sed in illis siccis obliquis et salientibus, endocarpio supramediali brunneo osseo latilibus luidilibus 1 mm crassis intra laevibus et lucidis cum humeris, mesocarpio apicali cum fibris fortibus et medulla, mesocarpio basali fibroso et carnoso.

**Description of all Specimens Examined:** Trees 4–6 m tall, 10–35 cm in diameter; bark brown, fairly smooth; prop roots none (or when present to 70 cm long, 2 cm in diameter, remotely muricate); leaves 1.03–1.6 m long, 4.6–7 cm wide, above olive-green, below paler green, coriaceous, at midsection with 37–45 parallel secondary veins in each half; near the base with tertiary cross veins, visible on both sides, making a network of short oblong meshes; blade with a broad central furrow and two lateral pleats, thus M-shaped in cross section, almost linterrupt, but tapering in outer half to the trigonous subulate 10 cm apex, this 10 cm down 5 mm wide, the base amplexicau and unarmed, but beginning at 8–15 cm the margins with serrae 0.7–1.3 cm long, 2–8 mm apart, white with slight brown tips; on the underside the midrib unarmed almost to the middle; at midsection the margins with prickles 0.5–0.7 mm long, 3–7 mm apart, subulate, closely appressed ascending, white; the nearby midrib below with similar prickles but these 0.7–1 mm long, 4–7 mm apart; near the apex the margins and midrib with serrulations 0.3–0.5 mm long, 1.5–3 mm apart; pistillate inflorescence terminal, bearing the solitary syncarp erect on a straight peduncle 35 cm long, 1.7–2 cm in diameter, 3-sided, with a few deciduous leafy bracts; syncarp subglobosus, 15 cm long, 14 cm in diameter, bearing 38–55 phalanges, these when still green 5.3–5.7 cm long, 3.7–5.5 cm wide, 3–4.4 cm thick, but the fallen dried ones about 4.5 cm long (though it is likely that animals

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Fig. 245. *Pandanus mayotteensis*, holotype.  

*a, b*, Dry fallen phalanges, lateral view, × 1;  
*c*, fully grown but green phalange, lateral view, × 1;  
*d*, dry fallen phalange, longitudinal medial section, × 1;  
*e, f*, dry fallen phalange, apical view, × 1;  
*g*, fully grown but green phalange, apical view, × 1;  
*h*, carpel apex and stigma, apical view, × 4;  
*i*, carpel apex and stigma, lateral view, × 4;  
*j*, carpel apex and stigma, apical view, × 4;  
*k*, leaf base, lower side, × 1;  
*l*, leaf middle, lower side, × 1;  
*m*, leaf apex, lower side, × 1.

100
Fig. 245A. *Pandanus mayotteensis* St. John, from St. John 26,548. Top left, staminate inflorescence, × ¼; top right, staminal fascicle, × 10. Bottom left to right, leaf apex, lower side, × 1; leaf middle, lower side, × 1; leaf base, lower side, × 1.
had chewed off part of the base), 2.8–4.1 cm wide, 2.2–3.2 cm thick (but doubles 5.6 cm wide and with 6 cells), brown, cuneate, 5–6-angled, when mature “red,” upper 1/2 free, the sides flat, the apex low convex (or semi-orbicular), smooth, shining, when almost mature with apical central sinus short, separate, 0.5–2 mm deep, but when fully mature with the sinuses confluent and 5–6 mm deep; carpels 2–6; stigmas 4–9 mm wide, cordate to oblate reniform, brown, papillose, centripetal, on the green phalanges horizontal and flush, but on the dried fallen ones oblique and salient; endocarp supramedian, brown, bony, the lateral walls 1 mm thick, smooth and shiny within, with lateral shoulders; apical mesocarp with heavy fibers and continuous pith; basal mesocarp fibrous and fleshy.

STAMINATE PLANT (St. John 26,548): Tree 7 m tall, 10 cm in diameter, bark brown, with short conic spines; branchlets 3 cm in diameter; prop roots few, 1 m long, 4 cm in diameter; leaves 1.5 m long, 5.8 cm wide, similar to those of the pistillate trees except at midsection with 41 parallel secondary veins in each half, and there the margins with subulate-serrae 1.2–1.5 mm long, 3–6 mm apart; subulate apex 5 cm long and at base 4 mm wide; staminate inflorescence 50 cm long, pendent; peduncle 10 cm long, fleshy; bracts mostly white, the lowest floral one at base for 20 cm lance-elliptic, dilated, papyraceous, white, 6 cm wide, the apex 60 cm long, 4 cm wide, sword-shaped, coriaceous, green, with the margins and midrib below serrate; median bract 11.5 cm long, 5 cm wide, oblong-elliptic, white, papyraceous, the margins and midrib below fimbriate, the teeth subulate, 0.5–1 mm long, crowded; spikes about 13 and 5–12 cm long, 2 cm in diameter, dense; fascicles dense, 6–9 mm long, with 5–7 stamens; column 5–6 mm long, urmbellate; free filament tips 2.5–4 mm long, anthers 2.3–3 mm long, narrowly oblong, bearing a subulate projection of the connective 0.15–0.2 mm long.

HOLOTYPUS: Iles Comores, Ile Mayotte, 5 km SW of Mamoutzou, in forest along stream, 10 m alt, Aug. 19, 1961, H. St. John 26,549 (BISH).

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Fig. 246. Pandanus mayotteensis St. John, from holotype. Left, tree habit; right, leafy branch with fruiting syncarp.
SPECIMENS EXAMINED: Iles Comores, Ile Mayotte, poussant spontanément en groupes peu éloignés au bord des rivières, marais, généralement près de la mer dans des endroits humides, 21 août 1961, I. Ramadan (BISH); Ile Mayotte, Chiconi, Batrini, one tree left in coconut plantation, 8 m alt, Aug. 18, 1961, H. St. John 26,548 (BISH); Mayotte, 1847-1852, Boivin (P).

DISCUSSION: *P. mayotteensis* is a member of the section *Vinsonia*, as is its closest relative, *P. heterocarpus* Balf. f., of Rodriguez Island, a species with the phalanges 4-5 cm long, 3-4 cm wide, the apex dark green or purple and often with a red border at base; stigmas 3-4 mm wide; bark of trunk warty spiny; and the teeth of the leaf margins orange or red. *P. mayotteensis* has the phalanges 5.3-5.7 cm long, 3.7-5.5 cm wide, red; stigmas 4-9 mm wide; bark of trunk fairly smooth; and the teeth of the leaf margins white with slight brown tips.

The new epithet is formed from the name of the island Mayotte, with -ensis, the Latin adjectival place ending.
Revision of the Genus *Pandanus* Stickman, Part 27

*Pandanus* Novelties from Madagascar

HAROLD ST. JOHN

At the beginning of the eighteenth century *Pandanus* was found growing naturally on Madagascar. The first species from there were described by du Petit Thouars. Subsequent discoveries revealed that it was one of the three great centers of the genus, with 63 species.

With support from a grant by the National Science Foundation, the writer spent ten weeks in 1961 exploring the island for *Pandanus*. First a map showing all known localities for the accepted species was prepared. Then, three expeditions were undertaken in search of *Pandanus*, the route in all cases being to regions from which no previous collector had obtained specimens. As the genus is widespread on the island, the result of the search was the discovery of numerous additional species. Several of them are here described as new.

Section Acanthostyla

*Pandanus columnaris* sp. nov. (sect. Acanthostyla)

Figs. 247, 253 bottom, left and right.

Nom. vern.: "fan'dran."

Diagnosis holotypi: Arbor columnaris, trunco 20 m alto 25 cm diametro, cortice pallide bruneo cum spinis conicis, radicibus fulturosis nullis vel paucis eis 20 cm longis 1.5 cm diametro pallide bruneis et spinosis, corona anguste cylindrica in apice cum foliis magnis in spiris deinde infra trunco cum ramulis lateraliis secundariis brevisubaequalibus cum foliis minoribus angustis, foliis terminalibus 2 m et plus longis proxima basem 24 cm latis crassiter coriaceis supra midnervum sulcatis 2-plicatis, in sectione mediali cum 98 nervis parallelis secundariis in dimidio quoque proxima basem infra nervis tertiiis evidentis et reticulis breviter oblongis forariantibus, laminis ligulatis, in basi ex 16-17 cm marginibus cum spinis 3-5 mm longis 4-10 mm separatis basi incrassata sed apice subulato inferioribus recurvatis superiioribus adscendentibus, midnervo infra cum aculeis 1.5-2.5 mm longis 2-7 mm separatis subulatis adpresse adscendentibus, ramulis lateraliis medialiis brevibus 2-2.5 mm diametro bruneis in toto spinosis, foliis 1-1.2 mm longis 18-22 mm latis graciliter coriaceis supra obscure olivaceis infra pallide viridibus et glaucis subcurvatis non cassis supra late V-sulcatis 2-plicatis et ad apicem plicis acute serrulatis in sectione mediali cum 21 nervis parallelis secundariis nervis tertialiis nullis lamina ligulata in apice trigono subulato diminuente 10 cm ex apice 6-10 mm lato basi inermi amplificaui alba, marginibus basi ex 15 cm cum aculeis subulatis 0.5-1.2 mm longis 4-10 mm separatis vel cum serrulis albis cum apicibus bruneus, midnervo infrat longum vel ultra inermi, in sectione mediali marginibus cum serrulis 0.2-0.9 mm longis 2-4 mm separatis albis, midnervo infra inermi vel cum serrulis 0.1-0.2 mm longis 7-12 mm separatis albis, in apice marginibus et midnervo infra cum serrulis 0.3-0.5 mm longis 2-3 mm separatis albis, infrutescentia non visa sed dicet "in ramulis lateraliis et cum spicis luteis."

Phalangibus 20-22 mm longis 10-15 mm latiss 8-11 mm crassis obvoideis compressis 4-7-carpellatis parte 1/2 supera libera, stylis 6-7 mm longis acicularibus arcuatis in basi conica brevi affixis, stigmatibus 6-7 mm longis linearibus proximalibus papillosis, endocarpio in parte 1/2 supera osseoso bruneo lateribus 1-1.5 mm crassis intra laevibus et lucidis, seminibus 3.5-5 mm longis elipsoideis, mesocarpio apicali 3 mm longo cum fibris validibus longitudinalibus, mesocarpio basali fibroso et carnoso.

Diagnosis of holotype: Tree, columnar, the trunk 20 m tall, 25 cm in diameter; bark light brown, conic spiny; prop roots none or few and 20 cm long, 2.5 cm in diameter, light brown, spiny; crown narrowly cylindric, the apex with spirals of large leaves, but below them half or more than half of the length of the trunk with short secondary branchlets, all subequal, and bearing numerous small, narrow leaves; terminal leaves in spirals at apex of trunk, more than 2 m long, 24 cm wide near the base, thick coriaceous, furrowed above the midrib and the sides pleated, near the midsection with 98 parallel secondary veins in each half, near the base below the tertiary cross veins visible, forming short oblong meshes; blade

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Fig. 247. *Pandanus columnaris* St. John, from holotype.  

- **a**, Phalange, lateral view, × 1;  
- **b**, phalange, longitudinal median section, × 1;  
- **c**, phalange, apical view, × 1;  
- **d**, endocarp and seed cavities, transverse median section, × 1;  
- **e**, style and stigma, lateral view, × 10;  
- **f**, half of leaf base, lower side, × 1;  
- **g**, half of leaf middle, lower side, × 1;  
- **h**, leaf apex, lower side, × 1;  
- **i**, branchlet, × 1.
ligulate, at the tip narrowing into a short trigonous subulate apex which 10 cm down is 6–10 mm wide; near the base beginning at 16–17 cm the margins with spines 3–5 mm long, 4–10 mm apart, subulate from a stout base, the lower ones divergent, then the next slightly ascending; the midrib below beginning at 19 cm with spines 3 mm long, 4–8 mm apart, the base broad conic, the apex subulate, recurved; at midsection the margins with prickles 2–3 mm long, 3–10 mm apart, subulate, ascending; the midrib below with prickles 1.5–2.5 mm long, 2–7 mm apart, subulate, appressed ascending; on the subulate apex the margins and midrib below with subulate serrations 0.2–0.3 mm long, 0.5–3 mm apart, white; lateral branchlets 2–2.5 cm in diameter, brown, sharp conic spiny right up to the leaves; leaves 1–1.2 m long, 18–22 mm wide, thin, coriaceous, above dark olive-green, below pale green and glaucous, gently curved, not breaking across, above with a broad V-shaped furrow occupying the middle half, the lateral quarters pleated but horizontal, near the apex the two pleats sharply serrulate above, at midsection with 21 parallel secondary veins in each half, no tertiary cross veins, blade ligulate, narrowing near the tip to a trigonous subulate apex, this 10 cm down 6–10 mm wide, the base unarmed and amplexicaul, white, the margins near the base beginning at 15 cm with prickles 0.5–1.2 mm long, 4–10 mm apart, from serrulate to subulate, ascending, white, brown-tipped; midrib below unarmed to the middle or beyond; at midsection the margins with serrations 0.2–0.9 mm long, 2–4 mm apart, white; the midrib below unarmed or with serrations 0.1–0.2 mm long, 7–12 mm apart, white; on the subulate apex the margins and midrib below with serrations 0.3–0.5 mm long, 2–3 mm apart, white; pistillate inflorescence not seen, but reported to be "on the small, lateral branchlets, spicate, yellow." Phalanges 20–22 mm long, 10–15 mm wide, 8–11 mm thick, obovoid, compressed, 4–7-celled, upper ⅓ of body free; styles 6–7 mm long, acicular, outward arcuate, borne from a short conic base; stigmas 6–7 mm long, linear, proximal, brown, papillose; endocarp in upper ⅔ of body, bony, brown, the lateral walls 1–1.5 mm thick, the inner surfaces dark brown, smooth, shining; seeds 3.5–5 mm long, ellipsoid; apical mesocarp 3 mm long, sparse, with strong longitudinal fibers; basal mesocarp fibrous and fleshy.

**HOLOTYPE:** Malagasy Republika, Andasibe, ligne Cap Est, 20 km S of Antalaha, in remnant of coastal forest, infrequent, 5 m alt, 6 Sept. 1961, H. St. John 26,571 (BISH).

**DISCUSSION:** *P. columnaris* is a member of the section *Acanthostyla*, as is its closest relative, *P. mangokensis* Martelli, a species with the drupes 12–15 mm long, 7–9 mm wide, the body ovate-obpyramidal and 9–11 mm long; styles 1–3, and 4–5 mm long; endocarp "ad basim drupae sita"; terminal leaves 1.4–1.6 m long, 8 cm wide; leaves of lateral branchlets 80 cm long, and 1–1.4 cm wide. *P. columnaris* has the drupes 20–22 mm long, 10–15 mm wide, the body 14–15 mm long, broad obovoid; styles 6–7 mm long; endocarp in the upper ⅓; terminal leaves 2 or more meters long, 24 cm wide; leaves of the lateral branchlets 1–1.2 m long, and 1.8–2.2 cm. wide. The new epithet is the Latin adjective *columnaris*, columnar, and is descriptive of the shape of the crown of the tree.

**Pandanus pluriloculatus** sp. nov. (sect. *Acanthostyla*)

**Figs.** 248, 249, 250a, b.
**NOM. VERN.:** “fandran.”

**DIAGNOSIS HOLOTYPE:** Arbor 22 m alta 30 cm diametro, cortice obscure brunoceum spinis conicis, radicibus fulturosis plurumeque nullis, corona anguste cylindrica in apice cum spiris tribus foliarum gran-dium sed infra cum ramulis multis brevis aqua-libus cum foliis multis angustioribus et fractibus, foliis terminalibus 1.35–1.6 m longis 10–14 cm latis crassis coriaces V-sulcatas et proxima apicem 2-pli-catis in sectione mediali cum 79 nervis parallaxis secun-darisis in dimidio quoque, in foliis vetusis siccis nervis tertius transversis conspicuus et reticulis oblongis brevis formantibus, lamina ligulata supra olivacea infra pallide viridibus et glaucis, basi amplexicaulis inermi sed ex 10 cm marginibus cum aculeis 1–2.5 mm longis 2–5 mm separatis subulatis rectis vel arcuatis albis, midnervo infra ex 19 cm cum aculeis 1 mm longis 3–10 mm separatis subulatis apdresse reflexis fragilibus, in sectione mediali marginibus cum aculeis 1–2 mm longis 1–2.5 mm separatis crassae subulatis albis valde adscendentibus, midnervo infra cum aculeis 0.5–1 mm longis 2–4 mm separatis subulatis fragilibus albis apdresse adscendentibus, in...
Fig. 248. *Pandanus pluriloculatus* St. John, from holotype. *a*, Fruiting lateral branchlet, \(\times \frac{1}{2}\); *b*, leaf base of same, lower side, \(\times 1\); *c*, leaf middle of same, lower side, \(\times 1\); *d*, leaf apex of same, lower side, \(\times 1\); *e*, leaf apex of same, upper side, \(\times 1\).
apice marginibus et midnervo infra cum serrulis 0.2-0.3 mm longis 0.5-1.5 mm separatis albis, ramulis lateralibus cum foliis 71-83 cm longis 15-16 mm latis coriaceis supra obscure olivaceis infra viridibus et glaucis supra midnervum profunde V-sulcatis partibus lateralibus quadrangularibus horizontalibus et cum plicis duobus et eis per sectionem ultimum supra subulato-serratis, in sectione mediial cum 22 nervis parallelis secundariis nervis tertiiis nullis lamina ligulata sed in apice subulato contracta eo in puncto 10 cm ex apice 12 mm lato, marginibus ex 8.5 cm cum subulato-serrulis 0.3-0.8 mm longis 2-3 mm separatis albis, midnervo ex basi ad medium interni, in sectione mediial marginibus et midnervo infra cum aculeis 0.2-0.4 mm longis 1.5-4 mm separatis subulatis, in apice marginibus et midnervo infra cum serrulis 0.2-0.3 mm longis 0.5-1 mm separatis albis, infructescentia in ramulis lateralibus terminalibus, pedunculo 8-14 cm longo 1 cm diametro 3-laterato rhachidi 3-5 cm longo, syncarpis 3-4 congestis 5-9 cm longis 5-6.5 cm diametro plerumque ellipsoides sed eis minoribus ellipsoides vel globosis illis terminalibus maximis et cum 86-92 phalangibus in seriebus plerumque verticalibus, eis minoribus cum 32 vel pluribus phalangibus, phalangibus 27-29 mm longis cum stylis 14-20 mm latis 11-14 mm crassis cuneatis parte ½ supera libera (5)-6-angulosis laevisibis lucidis apice depressae conico et marginibus canaliculatis lateribus planis, stylis (2)-3-5-6) et 7-9 mm longis subulatis vel acicularibus in centro congregatis basi conica viridi 1-2 mm alta, stigmatibus 5-8 mm longis linearibus brunneis papillosis centripetalibus ad apicem non extensis, endocarpio mediiali osseo brunnneo 10 mm longo lateribus lateralibus 2 mm crassi intra laevisibis et lucidis, seminibus 5 mm longis ellipsoides, mesocarpio apicali medulloso et cum fibris longitudinalibus, mesocarpio basali fibroso et carnoso.

**DIAGNOSIS OF HOLOTYPE:** Tree, 22 m tall, 30 cm in diameter, bark brown, conic spiny; prop roots mostly none; crown narrowly cylindric, the apex with three spirals of large leaves,
but below them most of the length of the trunk with many, equal, short branchlets with numerous narrow leaves and spikes of fruit; terminal leaves 1.35–1.6 m long, 10–14 cm wide, thick, coriaceous, with a V-shaped furrow above the midrib and near the tip the sides pleated, at midsection with 79 parallel secondary veins in each half, on old dry leaves the tertiary cross veins well marked and making short oblong meshes, blade ligulate, above olive-green, below pale green and glaucous, near the base beginning at 10 cm the margins with prickles 1–2.5 mm long, 2–5 mm apart, subulate, straight or arcuate, white; the midrib below beginning at 19 cm with prickles 1 mm long, 3–10 mm apart, subulate, reflexed, appressed, weak; at midsection the margins with prickles 1–2 mm long, 1–2.5 mm apart, thick subulate, closely ascending, white; the nearby midrib below with prickles 0.5–1 mm long, 2–4 mm apart, subulate, appressed ascending, white, weak; on the subulate apex the margins and midrib below with serrulations 0.2–0.3 mm long, 0.5–1.5 mm apart, white; the narrow leaves of the lateral branchlets 71–83 cm long, 15–16 mm wide, coriaceous, above dark olive-green, below pale green and glaucous, the center half a deep V-shaped furrow above the midrib, the lateral
quarters horizontal and with two pleats that for the last few centimeters are subulate-serrate above; at midsection with 22 parallel secondary veins in each half, no tertiary cross veins, blade ligulate but contracted into a trigonous subulate apex which 10 cm down is 12 mm wide; near the base beginning at 8.5 cm the margins with subulate-serrulations 0.3–0.8 mm long, 2–3 mm apart, white; the midrib below unarmed to near the middle; at midsection the margins and midrib below with prickles 0.2–0.4 mm long, 1.5–4 mm apart, subulate; on the subulate apex the margins and midrib below with serrulations 0.2–0.3 mm long, 0.5–1 mm apart, white; the apex short subulate, and at the point 10 cm down 12 mm wide; the leaves of juvenile plants 3.63 m long, 18 cm wide; infructescence terminal on lateral branchlets; peduncle 8–14 cm long, 1 cm in diameter, 3-sided; rachis 3–5 cm long; syncarps 3–4, crowded, 5–9 cm long, 5–6.5 cm in diameter, mostly ellipsoid, but the smaller lower ones ellipsoid to globose, the terminal one the largest, and this one bearing 86–92 phalanges in mostly vertical rows, the smaller lower syncarps with as few as 32 phalanges; phalanges 27–29 mm long (including the style), 14–20 mm wide, 11–14 mm thick, wedge-shaped, upper ⅓ of body free (⅓ free including style), on the free apex the center depressed conic, its sides arising from a shallow depression or canal within the obtuse rim, (5)–6-angled, the surface smooth, shiny, the sides flat; the (2)–3–5–(6) styles 7–9 mm long, subulate or acicular, irregularly grouped near the center; green conic style base 1–2 mm high; stigma 5–8 mm long, linear, brown, papilllose, centripetal, not running to the apex; endocarp median in the body, bony, brown, 10 mm long, the lateral walls 2 mm thick, the inner surfaces smooth, shining; seeds 5 mm long, ellipsoid; apical mesocarp of pith and longitudinal fibers; basal mesocarp fibrous and fleshy.

**Holotypus:** Malagasy Republika, Andrapengay, 22 km N of Antalaha, cut-over swampy forest, 8 m alt., Sept. 7, 1961, H. St. John 26,572 (BISH).

**Specimens Examined:** Malagasy Republika, Andrapengay, same data as above, juvenile, H. St. John 26,573 (BISH).

**Discussion:** *P. pluriloculatus* is a member of the section Acanthostylata, as is its closest relative, *P. pseudobathiee* Pic. Ser., which has the pistillate spadix 23–35 cm long, 5–7 mm in diameter; syncarps 2–3, subglobose, 4–6.5 cm long, 3.5–5.5 cm in diameter; phalanges 1–(2–4)-celled, 26 mm long, 11–17 mm wide; endocarp in upper ⅔ and 14 mm long; and the leaves of the lateral branchlets 1 m or more in length. *P. pluriloculatus* has the peduncle 8–14 cm long, 1 cm in diameter; syncarps 3–4, mostly ellipsoid, but some lower ones globose, 5–9 cm long, 5–6.5 cm in diameter; phalanges (2)–3–5–(6)-celled, 27–29 mm long, 14–20 mm wide; endocarp median, 10 mm long; and the leaves of the lateral branchlets 71–83 cm long.

The new epithet is formed from the Latin plus, many; *loculatus*, with locules or carpels, and is given with reference to the more numerous locules of the compound ovary.

**Section Dauphinensis**

*Pandanus centrifugalis* sp. nov. (sect. *Dauphinensis*)

Figs. 251, 252, 253 top, left and right

**Nom. Vert.:** "hofa."

**Diagnosis Holotype:** Arbor 10 m alta 20 cm diametro, corona lata, cortice brunneo cum spinis coniciis multis, ramulis 8.5 cm diametro, cicatricibus foliarum 6 mm alitis, radicibus fulturosus nullis vel paucis et 1 m longis 2.5 cm diametro pallide brunneis cum spinis parvis remotis coniciis brevibus, foliis 1.58–1.65 m longis 9–11.6 cm latissimis coriaceis senis curvatis sed non fractis exulcidis supra olivaceis infra viridibus supra midnervum sulcatis anguste V-formatis sine plicis in sectione mediale cum 58 nervis parallelis secundaris in dimidio quoque nervis tertiiis evidentibus solum in basi laminis ligulato-gladiiformatis in apice trigono crassiter subulato diminuentibus eo 10 cm ex apice 6–14 mm lati basi amplexicauli interni alba et cum extensionibus lateralis 15–20 cm longis 1–1.5 cm latissimis integris membranaceis, marginibus ex 15–20 cm cum spinis 4–10 mm separatis deltoideis adscendentibus albis opaquis cum apicibus subulatis brunneis spinis biformatis majoribus 6–8 mm longis minoribus 3–5 mm longis, midnervo infra ex 25 cm cum spinis 3–4 mm longis 3–12 mm separatis inferioribus reflexis basibus latiter coniciis apicibus subulatis alterius adscendentibus, in sectione mediale marginibus cum spinis 3–5 mm longis 4–12 mm separatis irregulares biformatis majoribus vel minoribus latiter subulatis adscendentibus, midnervo infra cum aculeis 2.5–3 mm longis 6–15 mm separatis irregularibus arcuato-
Fig. 251. *Pandanus centrifugalis* St. John, from holotype. *a*, Syncarp, lateral view, $\times$ 1; *b*, bark of branchlet, $\times$ 1; *c*, bark of trunk, $\times$ 1.
Fig. 252. *Pandanus centrifugalis* St. John, from holotype. *a*, Sketch of infructescence, × 3; *b*, phalange, lateral view, × 1; *c*, phalange, longitudinal median section, × 1; *d–f*, phalanges, apical view, × 1; *g*, stigmas, apical view, × 4; *h*, half of leaf base, lower side, × 1; *i*, leaf middle, lower side, × 1; *j*, leaf apex, lower side, × 1.
Fig. 253. Top left, trunk of *Pandanus centrifugalis* St. John, holotype; top right, fruiting branch; bottom left, trunk and prop roots of *Pandanus columnaris* St. John, holotype; bottom right, trunk of same.
subulatis compressis, in apice marginaibus cum dentibus 0.7–2.5 mm longis 1–4 mm separatis irregulilibus biformatibus majoribus latiter arcuato-subulatibus adscendentibus albis cum apicibus minime brunneis olim bidentatis, midrerno infra cum subulato-serrulis 0.5–1 mm longis, inflorescentia foeminea terminali erecta spicata cum 9 syncarpiis in 3 seriebus, pedunculo 30 cm longo in apice 5 cm diametro clavato 3-laterato cum 2 bracteis basilariis foliaceis 80 cm longis 10 cm latis et cum basilariis binis caulinariis caducis, rhachide 18 cm longo, syncarpiis conregatis 12–15.5 cm longis 8.5–9 cm latis 6–7.5 cm crasis ovoideo-cylindris sed latere proximo plano cum 65–71 phalangibus in seriebus verticalibus, axili carnoso et fibroso, phalangibus 3–3.5 cm longis 2–3.1 cm latis 1.7–2.6 cm crasis aurantiiaco-luteis obovoides sed basi longiter cuneato-obpyramidalibus truncato parte ½ supera libera pyramidalibus-hemisphericis (5)–6-anguloso apice truncato vel vadoso concavo 7–10 mm lato orbiculari vel elliptico et cum (3–4)–5–7–(8) stigmatibus in margini circuli (rare cum stigmatum unico centrali), stigmatibus 1.5–2 mm longis brunneis papillosis horizontalibus superficialibus cordatis vel reniformibus vel cordato-ovatis plerumque centrifugalisibus sed paucis tangentialibus etiam paucis centripetalibus, sinibus 1 mm longis profundiis, endocarpo medio osseo bruneo lateribus lateralisibus 3–4 mm crassis intra laevibus et lucidis, seminibus 6–8 mm longis late ellipsoidis, mesocarpo apicali medulloso et cum fibris longitudinalibus, mesocarpo basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Trees to 10 m tall, 20 cm in diameter; crown wide; bark brown, with numerous, sharp conic spines; branchlets 8.5 cm in diameter; leaf scars 6 mm high; prop roots none or less commonly present and up to 1 m long and 2.5 cm in diameter, light brown, with small, remote, short conic spines; leaves 1.58–1.65 m long, 9–11.6 cm wide, thick coriaceous, gently down-curved but not breaking across, dull, above olive-green, below green, narrowly furrowed above the midrib, in section V-shaped but somewhat curving towards the margin, not pleated, at midsection with 58 parallel secondary veins in each half, no visible tertiary cross veins except at the very base, blade ligulate-sword-shaped, narrowing to a stout, trigonous, subulate apex, this at 10 cm down 6–14 mm wide, the base amplexicaul, unarmed, white, and with membranous, entire, lateral flanges 1–1.5 cm wide and 16–20 cm long, at base beginning at 15–20 cm the spines 4–10 mm apart, ascending, deltoid with subulate brown tips, otherwise opaque white, of two sizes, the major ones 6–8 mm long, the smaller ones 3–5 mm long; the midrib below beginning at 25 cm with spines 3–4 mm long, 3–12 mm apart, the first several reflexed subulate from broad conic bases, the later ones ascending; at midsection the margins with spines 3–5 mm long, 4–12 mm apart, irregular, large or small, broad subulate, ascending; the nearby midrib below with prickles 2.5–3 mm long, 6–15 mm apart, flat accurate subulate, irregular; on the subulate apex the margins with teeth 0.7–2.5 mm long, 1–4 mm apart, irregular, the smaller straight subulate and salient, white except for the slightly brown tip, the larger ones broad accurate subulate, ascending, occasionally bidentate; the midrib below with prickles 0.5–1 mm long, 2–5 mm apart, subulate-serrations; pistillate inflorescence terminal, erect, spicate, bearing 9 syncarps attached in three rows; peduncle 30 cm long, 5 cm in diameter, clavate, in section deltoid but the angles obtuse, subtended by two basal, persistent foliaceous bracts 80 cm long, 10 cm wide, and the stalk bearing two caducous bracts; rhachis 18 cm long; syncarps crowded, 12–15.5 cm long, 8.5–9 cm broad, 6–7.5 cm thick, in profile ovoid-cylindrical but the proximal face flat or nearly so, bearing 65–71 phalanges in nearly vertical rows; core fleshy and fibrous; phalanges 3–3.5 cm long, 2–3.1 cm wide, 1.7–2.6 cm thick, orange-yellow, obvoid but the base long cuneate obpyramidal, truncate, the upper ½ free, pyramidal-hemispheric, (5)–6-angled, the apical area truncate or shallow concave, 7–10 mm wide, circular or elliptic, (3–4)–5–7–(8)-celled, very rarely with one central stigma, normally with all on the margins of the apical circle or polygon; stigmas 1.5–2 mm long, brown, papillose, flush, horizontal, cordate to reniform to cordate-ovate, mostly centrifugal, but some tangential, and a few centripetal, prolonged beyond the central crease is a deep sinus about 1 mm long; endocarp median, bony, brown, the lateral walls 3–4 mm thick, the inner surface smooth, shining; seeds 6–8 mm long, broad ellipsoid; apical mesocarp of solid pith, traversed by longitudinal fibers; basal mesocarp fibrous and fleshy.

HOLOTYPE: Madagascar, Ile Sainte Marie, Lambountsira, 4 km S of Ambodifototra, forest remnant in cultivated fields, 4 m alt., Aug. 26, 1961, H. St. John 26,555 (BISH).
DISCUSSION: *P. centrifugalalis* is a member of the section *Dauphinensis*, as is its closest relative, *P. dauphinitionis* Martelli, a species with syncarps 18–20 cm long, cylindrical, bearing 100 or more phalanges; endocarp submedian; leaves 12 cm or more in width, and especially above tessellate and cross-veined; near the leaf apex the midrib below with crenate-serrations 9–12 mm apart. *P. centrifugalalis* has the syncarps 12–15.5 cm long, ovoid-cylindric, bearing 65–71 phalanges; endocarp median; leaves 9–11.6 cm wide, lacking cross veins except at the very base; and near the apex the midrib below with subulate-serrations 2–5 mm apart.

*P. centrifugalalis* is native to the thickly settled, offshore islet, Ile Sainte Marie. It is not a littoral species, but it occurs commonly on the coastal plain of the western or leeward shore on coastal sand flats or on upland lateritic soils or on basalt gravels near to or remote from the shore. It makes a good, vigorous tree that is persisting due to its ferociously armed leaves and stems, despite the nearly complete agricultural exploitation of the land for the culture of coconut, breadfruit, clove, mango, vanilla, papaya, and truck crops. There is no remaining virgin forest, though on rough or steep slopes there are patches of vigorous secondary forest, and *Pandanus* persists better than any other tree. The fruits have a pleasant fruity smell, and their phalange bases have a pleasant fruity incipient taste, but then are irritating. Only children, rats, and other animals eat them. The dried side strips of the leaves are used to plait floor mats, baskets, hats, etc.

The new epithet is the Latin *centrifugalalis*, being centrifugal, and is given in allusion to the orientation of the stigmas, which is very exceptional in the genus.

*Pandanus circularis* sp. nov. (sect. *Dauphinensis*)

Figs. 254, 255a, 255b top

Nom. vern.: "hoifa."

Diagnosis holotype: Arbor 12 m alta 20 cm diame.mt, cor. obscure bruneo cum spinis conicis, ramulis in apice 10 cm diam. tub. radiibus foliis 20 cm longis 1.5 cm diametro spinosis, foliis 2.35–2.6 m longis 14–15 cm latissi, rassiter coriaceis, sensim recurvatis apicibus caducis supra olivaceis infra viridibus et glaucis in sectione V-formatis in sectione mediiali cum 72 nervis parallelis secundaris in dimidio quoque nervis tertii olim ad basum evidentiis lamina gladiiformis in apice trigono crassiter subulato diminuuntibus eo 10 cm ex apice 8 mm lato basi inermi amplexicaulis alba et cum extensionibus lateribibus 16–20 mm latis 33 cm longis integris membranaceis, 26 cm ex basi marginibus cum spinis 5–6 mm longis 6–11 mm separatis crassioriter subulatis subarcuatis adscendentibus pallidis, midnervro proximo infra ex 30 cm cum aculus 2–2.2 cm longis 5–15 mm separatibus subulatis valide reflexis basi crassa, in sectione mediiali marginibus cum spinis 3.5–5.5 mm longis 5–16 mm separatris arcuato-subulatis compressis albidis adscendentibus, midnerva infra cum spinis simulantibus sed 12–16 mm separatris, in apice marginibus et midnerva infra cum subulato-serrulis 0.6–1.3 mm longis 1–2.5 mm separatris albis, infloroscentia formea terminalis erecta spicata cum 9 syn carpis in 3 seriebus affinis, pedunculo 36 cm longo in apice 5.5 cm diametro clavato 3-laterato in parte superiori cum 2 bracteis caducis, rhachidi 20 cm longo, syncarpiis 14–18 cm longis 9–10 cm latiss 7–8 cm crassis congratatis adscendentibus cylindrico-ovoideis sed latere proximo compresso cum 52–78 phalangibus, axili carnoso et fibroso, phalangibus 3.3–4 cm longis 2.7–3.8 cm latiss oboideis "luteis" in basi truncatis parte 4/3, supra libera oblasta obtuso-pyramidali (5)–6-angulosa concava ellipso apicali cum 4–9 stigmatibus (rariter stigmati unico minori centrali), stigmatibus marginalibus 1.5–2 mm longis ellipticis vel lanceolatis vel deltoideis plerumque centrifugalibus sed paucis tangentialibus vel enim centripetalibus, sinibus 0.5–1 mm longis profundis, endocarpo osseo bruno supramediali 14 mm longo lateribus 4–6 mm crassis infra laeves et lucidis, seminibus 8 mm longis ellipsoidales, mesocarpo apicali medulloso denso cum fibris longitudinalibus paucis, mesocarpo basali carnoso et fibroso.

Diagnosis of holotype: Tree, 12 m tall, 20 cm in diameter; bark dark brown, with conic spines; branchlets at apex 10 cm in diameter; prop roots few, 20 cm long, 1.5 cm in diameter, spiny; leaves 2.35–2.6 m long, 14–15 cm wide, thick coriaceous, gently down-curved, all mature leaves having lost their apices, above olive green, below green and glaucous, in section V-shaped, at midsection with 72 parallel secondary veins in each half, no visible tertiary cross veins except at the very base, blade sword-shaped, narrowing to a stout trigono subulate apex, this 10 cm down 8 mm wide, the base unarméd and amplexicaul, white, and with membranous, entire, lateral flanges 16–20 mm wide and 33 cm long, near the base beginning at 26 cm the margins with spines 5–6 mm long, 6–11 mm apart, very stout subulate, slightly arcuate, ascending, pale; the midrib below beginning at 30 cm with prickles 2–2.5 mm long, 5–15 mm
Fig. 254. *Pandanus circularis* St. John, from holotype. *a*, Phalange, lateral view, × 1; *b*, phalange, longitudinal median section, × 1; *c*, phalange, apical view, × 1; *d*, stigmas, apical view, × 4; *e*, half of leaf base, lower side, × 1; *f*, leaf middle, lower side, × 1; *g*, leaf apex, lower side, × 1; *h*, bark of trunk, × 1; *i*, branchlet, × 1.

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Pandanus circularis St. John, holotype. Left, base of trunk and prop roots; right, trunk and leaf bases.

Apart, subulate, heavy based, strongly reflexed; at midsection the margins with spines 3.5-5.5 mm long, 5-18 mm apart, flattened arcuate subulate, ascending, white; the nearby midrib below with similar spines but 12-16 mm apart; on the subulate apex the margins and midrib below with subulate-serrations 0.6-1 mm long, 1-2.5 mm apart, white; pistillate inflorescence terminal, erect, spicate, bearing 9 syncarps, these attached in three rows; peduncle 36 cm long, 5.5 cm in diameter at apex, clavate, in section deltoid, but the angles obtuse, the upper part with two caducous bracts; rhachis 20 cm long; syncarps crowded, ascending, 14-18 cm long, 9-10 cm broad, 7-8 cm thick, in profile cylindric-ovoid, but the proximal face flat or nearly so, bearing 52-78 phalanges in vertical rows; core fleshy and fibrous; phalanges 3.5-4 cm long, 2.7-3.8 cm wide, said to be "yellow," obovoid, the broad base truncate, upper $\frac{1}{4}$-$\frac{1}{3}$ free, oblate obtuse-pyramidal (5)-6angled, the apical area shallow concave, hexagonal to elliptic, bounded by a distinct rim on which are placed the 4-9 stigmas (though rarely there is a smaller, central one); marginal stigmas 1.5-2 mm long, elliptic to lanceolate or deltoid, mostly centrifugal, but a few are tangential, and rarely there is a centripetal one, the sinus a deep crack 0.5-1 mm long; endocarp bony, brown, supramedian, 14 mm long, the lateral walls 4-6 mm thick, the inner surfaces smooth, shining; seeds 8 mm long, ellipsoid; apical mesocarp of solid pith, traversed by a few longitudinal fibers; basal mesocarp fleshy and fibrous.

Holotypus: Malagasy Republika, Farankaraina, 14 km NE of Maroantsetra, wooded sandy flat near seashore, 2 m alt, Sept. 2, 1961, H. St. John 26,565 (BISH).

Discussion: P. circularis is a member of the section Dauphinesia, as is its closest relative, P. erectus St. John, a Malagasy species with the peduncle 53 cm long; phalanges 2.6-3.1 cm long, 1.5-2.2 cm wide, (2)-3-4-celled; endocarp lateral walls 1 mm thick; leaves 3.2-3.25 m long, 15-16 cm wide, at midsection with 83 parallel secondary veins in each half, and at
midsection the margins with prickles 1.5-2.2 mm long, and 5-11 apart. *P. circularis* has the peduncle 36 cm long; phalanges 3.5-4 cm long, 2.7-3.8 cm wide, 4-9-celled; endocarp lateral walls 4-6 mm thick; leaves 2.35-2.6 m long, 14-15 cm wide, at midsection with 72 secondary parallel veins in each half, and at midsection the margins with spines 3.5-5.5 mm long, 5-18 mm apart.

The new epithet is the Latin *circularis*, in a circle, a name given in reference to the placement of the stigmas on an apical circle or hexagon.


Figs. 255b bottom, 256, 257, 261 top left.

**Description from St. John 26, 579:** Tree 3-8 m tall, 15-20 cm in diameter, branchlets several, 12 cm in diameter below the leaves and clothed for some distance with marcescent leaf bases; crown broad; bark of trunk light brown, with a few conic spines or later with a few ascending rootlets; prop roots none; leaves
Fig. 256. *Pandanus dauphinensis* Martelli in Martelli & Pic. Ser., from *St. John* 26,579. *a*, Inflorescence, × ½0; *b*, syncarp, lateral view, × ½; *c*, phalange, lateral view, × 1; *d*, phalange, longitudinal median section, × 1; *e*, phalange, apical view, × 1; *f*, stigmas, apical view, × 4; *g*, half of leaf base, lower side, × 1; *h*, leaf middle, lower side, × 1; *i*, leaf apex, lower side, × 1.
Fig. 257. *Pandanus dauphinensis* Martelli in Martelli & Pic. Ser., from St. John 26,579. Top left, tree in dune hollow; top right, tree trunk; bottom left, tree branches; bottom right, infructescence.
1.85–2.73 m long, 16–17.5 cm wide near the base where the spines begin, 10–10.5 cm wide at the middle, thick coriaceous, gently curved, but breaking across about 2/3 of the way out, above olive-green, below light green, broad V-furrowed above the midrib, in the outer half the two lateral quarters horizontal but not pleated, at midsection with 70 parallel secondary veins in each half, no visible tertiary veins, blade sword-shaped, gradually tapering to the stiff, trigonous subulate apex, this at the point 10 cm down 9 mm wide, the base unarmèd, white, with entire lateral flanges 25–33 cm long, 12–17 mm wide, membranous margined, beginning at 26–34 cm up the margins with spines 4–7 mm long, 5–15 mm apart, the body conic, greenish, the apex subulate, dark brown, the lower ones divergent, the next ones somewhat ascending; the midrib below beginning at 40 cm up with spines 3–4 mm long, 7–12 mm apart, conic, acute, reflexed; at midsection the margins with spines of two kinds, the larger ones 3.5–5 mm long, 13–20 mm apart, arcuate heavy subulate serrae, white with brown tips, the alternating smaller ones 2–2.8 mm long, 12–17 mm apart, similar; the nearby midrib below with spines like the smaller marginal ones, 1.5–2 mm long, 6–15 mm apart; along the subulate apex the margins with subulate-serrae 1–1.9 mm long, 2–3 mm apart, and often doubly serrate; the midrib below with similar teeth 4–8 mm apart; infrutescence terminal, erect, bearing 11 ascending syncarps attached in 3 rows; peduncle 46 cm long, 5.5 cm in diameter at apex, distinctly clavate, 3-sided, with a few leafy bracts, these with an entire sheathing base, then a foliaceous blade 1.63 m long, 12 cm wide at base, tapering all the way to the subulate tip, the margins and midrib below with heavy white spines; rhachis 25 cm long; syncarps crowded, 17.5–21 cm long, 6–7.5 cm in diameter, cylindrical, obtuse, but the proximal face flat or nearly so, bearing 96–145 phalanges in mostly vertical rows; core fleshy and fibrous, 15–25 mm in diameter; phalanges 22–25 mm long, 16–23 mm wide, 14–22 mm thick (in a double 34 mm wide and with 11 carpels), still green, but apparently fully grown and as large as the old, fallen ones, becoming yellow, the lower part oblong, upper 1/3 free and oblate pyramidal ovoid, 6-angled, the apical area shallow concave, 6–11 mm wide, circular or elliptic, 3–7-celled, the stigmas always on the periphery; stigmas 1.5–2 mm wide, ovate to reniform or elliptic, brown, papillose, mostly centrifugal, but rarely a few tangential or centripetal, and prolonged beyond the central crease is a deep sinus 0.5–1 mm long; endocarp inframedian, 12–15 mm long, bony, dark brown, the lateral walls 1.5–3 mm thick, the inner surfaces smooth, shining; seeds 6–8 mm long, ellipsoid; apical mesocarp of continuous pith with a few strong longitudinal fibers; basal mesocarp scant, fleshy and fibrous.

**HOLOTYPUS:** Madagascar, "Est: C’est l’espèce la plus commune sur les dunes de la côte littorale de Fort-Dauphin, à Mananjary, Bas Matitanana, Oct. 1911 (Perrier de la Bathie, n° 11888)." (P).

**SPECIMEN HERE DESCRIBED:** Malagasy Republika, 2 km N of Fort-Dauphin, thicket on coastal sand dunes, with “voanat” (Sapotaceae), “hily” (*Helmiopsis Hily*), *Lycium* sp., and *Ipomoea brasiliensis*, 10 m alt, Sept. 22, 1961, H. St. John 26,579 (BISH).

**DISCUSSION:** *P. dauphinensis* is the type species of the section *Dauphinensis*. The type locality of the species is on the same coast as the collection here described in detail, but a few kilometers to the north. The two collections tally quite well, except that the holotype was described as with phalanges 3 cm long, and the syncarps 8 cm in diameter, but on the isotype (NI) the phalanges are 2.6–3 cm long. Ours are a little narrower, and the phalanges are 1/4 shorter. To be sure, ours were not fully ripe, yet they seemed nearly full-sized and their seeds and endocarp were well formed. They were as large as the fallen, weathered ones on the ground. Surrounding trees of other genera were much shattered by a cyclone five months previous, but as usual the *Pandanus* trees survived in good condition. It does not seem likely that all the phalanges seen on the many trees and all the mature, fallen ones would be uniformly smaller owing to the cyclone. In ours the carpels of the lateral phalanges were from 3 to 7.

Later, when in Paris, it was possible to study
the holotype of *P. dauphinenis*, Perrier de la Bathie 11,888. This consists of a dried fruit rhachis; a piece of a leaf 20 cm long, 11 cm wide, and one half of it continuing 55 cm more; a single syncarp 18 cm long, 7 cm in diameter, cylindrical but one side flat, complete except that about 9 phalanges have been removed. The phalanges are nearly all 24–26 mm long, only one near basal one on the narrow angular side is 3 cm long. Thus, it is clear that there are no significant differences between this holotypic collection from Bas Matitana and the writer’s from Fort-Dauphin, here illustrated.

The specimen here described was in a partly sheltered habitat, in a dune hollow, 75 m back from the beach. The others on dune crests or nearer the beach were wind battered and the syncarps were smaller. They were as small as 12 cm long, and 5 cm in diameter, but they had the same elongate oblong profile.

The inhabitants regularly gather the leaves, especially the larger ones borne by young plants, for the making of mats.

*Pandanus erectus* sp. nov. (sect. *Dauphinenis*)

Figs. 258, 259

NOM. VERN.: “hofa.”

DIAGNOSIS HOLOTYPE: *A*bor 15 m alta 25 cm di-
ametro, trunco erecto, ramis paucis adscendentibus proxima apicem 0.5–1 m longis 15 cm diametro, cortice brunneo cum spinis coniciis brevibus, radicibus fultuosos paucis 20 cm longis 1.5 cm diametro pallide brunneis spinosis, foliis 3.2–3.25 m longis 15–16 cm latis rigidos crassiter coriaceis erectis sed parte 3/4 ultima fracta et pendenti supra olivaceis infra palli-
dioribus et subglaucescens supra midnervum late V-sulcatitis ultra medium ultimum 2-plicatis, nervis paene eviden-
tibus sed in sectione mediali cum 83 nervis parallelos secundariorum in dimidio quoque lamina ligulata sensim in tertia ultima in apice crassiter trigono subulato di-
minuentibus eo in puncto 10 cm ex apice 5 mm lato basi amplificacli et inerni alba cum lateribus dis-
tenis 38 cm longis 2 cm latis membranaceis, margini-
bus ex 38 cm cum aculeis 2–3.5 mm longis 3–6 mm separatis subulatis infinis diversgentibus alteris adscen-
dentibus, midnervo infra per 90 cm inerni tum cum aculeis 1.5–2.2 mm longis 5–11 mm separatis arcuato-
sulatiis proxime adscendentibus albis cum apicibus brunneis, midnervo infra cum serrulis 0.6–1 mm lon-\ngis 3–7 mm separatis cum apicibus brunneis in apice marginibus et midnervo infra cum serrulis 0.2–0.9 mm longis 1–2.5 mm separatis, inflorescentia foeminea terminali erecta spicata cum 10 syncarpiis in 3 seriebus affixis, pedunculo 53 cm longo, in apice 6 cm di-
ametro 3-laterato in basi sustento cum 2 bracteis foliosis 1.7 m longis 8.5 cm latitis, rhachidi 23 cm longo, syncarpiis non visis, phalangibus 2.6–3.1 cm longis 1.5–2.2 cm latis 1.4–1.9 cm crasis “lutescenti-
bus” bovbovides vel late ita basi truncata parte à supra
libera semiorniculati (5)–6-angulosa apice concavo
elliptico 6–8 mm lato loculis (2)–3–4, stigmatibus plerunque in ellipsi 1–1.5 mm longo obliquo elliptico
plerunque centrífugibus sed sine sinu distali, endocarpio 15 mm longo supramediali osseo bra-
nneo lateribus 1 mm crassis intra laevibus et lucidis, seminibus 5–6 mm longis, mesocarpio apicali minori
sum medulla densa et fibris longitudinalibus, meso-
carpio basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree 15 m tall,
25 cm in diameter; trunk erect, unbranched
almost to the top, the few branches 0.5–1 m
long, 15 cm in diameter, strictly ascending;
bark brown, with short conic spines; prop roots
few, 20 cm long, 1.5 cm in diameter, light
brown, spiny; leaves 3.2–3.25 m long, 15–16 cm
wide, rigid, thick coriaceous, stiffly erect, but
the outer ones 1/4 breaking and pendent, olive-
green above, paler and somewhat glaucous be-
low, broadly V-furrowed above the midrib,
and beyond the middle with 2 lateral pleats,
the veins rather obscure but at midsection with
83 parallel secondary veins in each half, blade
ligulate, gradually tapering in outer third to
a stout, trignoson subulate apex, this about
10 cm down 5 mm wide, the base amplexicau-
lar, unarmed, white, with membranous, entire
lateral flanges 38 cm long, 2 cm wide; at base
beginning at 38 cm the margins with prickles
2–2.5 mm long, 3–6 mm apart, subulate, diver-
ing, then the upper ones ascending; the midrib
below unarmed for 90 cm; at midsection the
margins with prickles 1.5–2.2 mm long,
5–11 mm apart, arcuate subulate, closely as-
cending, white, with small brown tips; the
nearly midrib below with serrations 0.6–1 mm
long, 3–7 mm apart, brown tipped; on the
subulate apex the margins and midrib below
with serrulations 0.2–0.9 mm long, 1–2.5 mm
apart; infructescence terminal, erect, spicate,
bearing 10 syncarps attached in three rows;
peduncle 53 cm long, 6 cm in diameter at apex,
clavate, 3-sided, subtended by two basal, leafy
bracts 1.7 m long, 8.5 cm wide; rhachis 23 cm
long; syncarps seen only as remnants; phalanges
2.6–3.1 cm long, 1.5–2.2 cm wide, 1.4–1.9 cm
thick, said to be “yellow,” bovbovid or broadly
so, the base truncate, upper 1/5 free, semiornicu-
Fig. 258. *Pandanus erectus* St. John, from holotype.  

a, Phalange, lateral view, × 1;  
b, phalange, longitudinal median section, × 1;  
c–f, phalanges, apical view, × 1;  
g, stigmas, apical view, × 4;  
h, leaf base, lower side, × 1;  
i, leaf middle, lower side, × 1;  
j, leaf apex, lower side, × 1.
lar, (5)—6-angled, the apical area concave, 6—8 mm wide, polygonal or elliptic, (2)—3—4-celled, the stigmas mostly on the margin of the apical rim; stigmas 1—1.5 mm long, elliptic, oblique, mostly centrifugal, but lacking a projected sinus; endocarp 15 mm long, supramedian, bony, brown, the lateral walls 1 mm thick, the inner surface smooth, shining; seeds 5—6 mm long; apical mesocarp sparse, with dense pith and longitudinal fibers; basal mesocarp fibrous and fleshy.

HOLOTYPE: Malagasy Republika, Varingohitra, 5 km S of Maroantsetra, secondary forest, with "voapaka" (Uapaca Thonarsii), "nanto" (Sapotaceae), and "hintsina" (Afzelia bijuga), 5 m alt, 3 Sept. 1961, H. St. John 26,567 (BISH).

SPECIMENS EXAMINED: Malagasy Republika, Varingohitra, with same data, H. St. John 26,566 (BISH).

DISCUSSION: P. erectus is a member of the

Fig. 259. Pandanus erectus St. John, holotype. Top left, trunk and crown of tree; top right, prop roots; bottom left, trunk and bark; bottom right, infructescence with shedding phalanges.
section *Dauphinensis*, as is its closest relative, *Pandanus centripetalis* St. John, from Ilol Ste. Marie, a species which has the phalanges (3-4)-5-7-(8)-celled, 3-3.5 cm long, 2-3.1 cm wide; stigma 1.5-2 mm long; endocarp with lateral walls 3-4 mm thick; tree with wide crown; leaves 1.58-1.65 m long, 9-11.6 cm wide, at midsection with 58 parallel secondary veins in each half, and the margin beginning 15-20 cm from the base with spines 6-8 mm long. *P. erectus* has the phalanges (2)-3-4-celled, 2.6-3.1 cm long, 1.5-2.2 cm wide; stigmas 1-1.5 mm long; endocarp with lateral walls 1 mm thick; tree with few branches strictly ascending; leaves 3.2-3.25 m long, 15-16 cm wide, at midsection with 83 parallel secondary veins in each half, and the margins beginning 38 cm from the base with prickles 2-2.5 mm long.

In *P. erectus* but few of the phalanges fall to the ground, as most are caught and held in the leaf axils. Some germinate there, and may fall to the ground when the holding leaf falls. Several examples of this were observed on the collection *St. John* 26,566.

The new epithet is the Latin adjective *erectus*, erect, and is given in reference to the strictly ascending branches.

*Pandanus spicatus* sp. nov. (sect. *Dauphinensis*)

Figs. 260, 261 top right and bottom left

**Nom. vern.**: "vacoua madik" (= *Pandanus* small).

**Diagnosis of Holotype**: Arbor 8 m alta 15 cm diametro cum rami pluribus suberectis eis in apice 15 cm diametro et cum restis marcescentibus foliarum obtectis, cortice pallide brunneo cum spinis multis late conicus, radicibus fulturosis nullis, foliis 1.6-3.2 m longis 15-16.5 cm latis ligulatis crassiter coriaceis subulicidis supra obscure olivaceis infra olivaceis supra midnervum late U-sulcatis 2-apticis in sectione mediale cum 96-97 nervis parallelis secundaris in dimidio quoque nervis tertiis nullis laminae in apice valido trigono subulato subiter contracto eo 10 cm ex apice 18 mm lato basi amplexicauli inermi rosaces, marginibus ex 21-26 cm cum spinis 3-5 mm longis 4-16 mm separatis valide subulatis ex bosi conica lata ascendentibus infinis rosaces alteris subviridibus, midnervio infra ad medium vel ultra inermi, in sectione mediale marginibus cum spinis 3-3.5 mm longis 8-26 mm separatis valde arcuato-subulatis compressis valde ascendentibus viridibus cum apice breve brunneo et olim margine uno cum spinis brevioribus vel enim in parte inermi, midnervio infra in sectione mediali vel distancia parva ultra cum aculeis 1.5-2 mm longis 7-14 mm separatis subulatis subviridibus proxime ascendentibus, in apice marginibus et midnervo infra cum subulato-serris 0.7-1 mm longis 2-5 mm separatis, infructescentia terminali erecta cum circa 9 syncarpis in fascicula foliarum clausis et paene drupis omnibus retentis, pedunculo 20 cm longo 2 cm diametro carnoso, syncarps circa 9 cm longis et 7 cm diametro ovoides compressus cum drupis multisl, eis 20-26 mm longis 10-20 mm latis 10-17 mm crassis (sed in seminis 27 mm latis et 6-7-loculatis) licet luteus cum cneatis vel obvoideis 3-5-loculatis parte ¼ supra libera laevibus lateribus contiguis subplanis, stigmatibus 2-2.5 mm latis cordatis horizontalibus exproiectentibus brunneis papillosis circa apicem congregatis, inter stigmata licet cum valleculis vadois, endocarpio centrali 10 mm longo pallide brunneo osseoos lateribus lateralis 1.5-2 mm crassis intra transverse rugosis et cum projectione apicali in locula omnina, mesocarpo apicali cum fibris longitudinalibus fortibus, mesocarpo basali fibroso et carnoso.

**Diagnosis of Holotype**: Tree 8 m tall, 15 cm in diameter, with several suberect branches, these at apex 15 cm in diameter and long clothed with persistent leaf bases; dark light brown, with numerous broad conic spines; prop roots none; leaves 1.6-3.2 m long, 15-16.5 cm wide, ligulate, thick coriaceous, somewhat shiny, above dark olive-green, below olive-green, with a broad U-shaped furrow above the midrib and two lateral pleats, at midsection with 96-97 parallel secondary veins in each half, no visible tertiary cross veins, the blade abruptly narrowed to a stout trigonous subulate apex, this 10 cm down 18 mm wide, the base amplexicaul, unarmed, pink, but beginning 21-26 cm up the margins with spines 3-5 mm long, 4-16 mm apart, stout subulate, ascending from a broad conic base, the lowest pink, the next greenish, the midrib below unarmed to or beyond the middle; at midsection the margins with spines 3-3.5 mm long, 8-26 mm apart, heavy arcuate subulate, flattened, strongly ascending, green, with short brown tips, and not infrequently one of the margins has shorter spines or even in places is unarmed for a short span; the midrib below, beginning at or slightly above the middle, with prickles 1.5-2 mm long, 7-14 mm apart, subulate, closely ascending, greenish; near the apex the margins and midrib below with subulate-serrations 0.7-1 mm long, 2-5 mm apart; infructescence terminal, erect, bearing about 9 syncarps, concealed in the large plume of erect or ascending leaves which trap the
Fig. 260. *Pandanus spicatus* St. John, from holotype. *a–d*, Phalanges, lateral view, × 1; *e*, phalange, longitudinal median section, × 1; *f*, phalange, apical view, × 1; *g–h*, phalanges, median transverse section, × 1; *i*, stigmas, apical view, × 4; *j*, leaf base, lower side, × 1; *k*, leaf middle, lower side, × 1; *l*, leaf apex, lower side, × 1.
Fig. 261. Top left, Pandanus dauphinensis Martelli in Martelli & Pic. Ser., fruiting branch from St. John 26,579; top right, Pandanus spicatus St. John, holotype, view of trunk; bottom left, Pandanus spicatus St. John, holotype, branch with leaf bases; bottom right, Pandanus aridus St. John, holotype, two trunk bases, with prop roots.
Pandanus aridus sp. nov. (sect. Mammillarisia)  

**Figs. 262, 261 bottom right, 264 top left and right**  
**Nom. vern.:** "fandara."

**Diagnosis holopty:** Frutex multiramosa, caulisibus 7 m altis 4 cm diametro, cortice griseo acute spinoso, radicibus fulturosia paucis 20–30 cm longis 2 cm diametro, foliis 35–45 cm longis 16–20 mm latiss subcoriaceis gradatim arcuatis supra obscure olivaceis infra pallide viridibus et glaucis supra nudum angustie V-sulciis deinde planis in sectione mediali cum 17 nervis parallelis secundariis nervis tertio transversis nullis lamina ligulata sed dimidia ultima diminuienti in apice trigono subulato eo 10 cm ex apice 6.5 mm lato basi amplicauli et inermi alba sed ex 1.3–2 cm marginibus cum aculeis 2.2–3.3 mm longis 2.2–12 mm separatis deltioideo-subulatis adscendentibus albis sed apicibus brunneis, midnervo infra ex 3.5–4 cm cum aculeis 1.3–2 mm longis 4–11 mm separatis albis subulatis valde reflexis, in sectione mediiali marginibus cum aculeis 0.5–0.9 mm longis 7–13 mm separatis gracilibus subulatis divergentibus albis in apice subulato marginibus et midnervo infra cum subulato-serrulis 0.3–0.7 mm longis 1.3–4 mm separatis, inflorescentia foeminea terminali erecta cum sincarpio unico, pedunculo 8 cm longo 8 mm diametro 3-laterato folioso-bracteato et in apice cum 6 bracteis marcescentibus exteriori 2.5 cm longa 1 cm lata elliptica naviculari marginibus spinoso-fimbriatis, sincarpio 5.5–6 cm diametro globoso viridi cum 21 phalangibus eius 22–25 mm longis 12–23 mm latis 10–22 mm crassis obovoideis firme connatis parte 3 supra libera subpyramidali-conica 5–6-angulosa 2–4 loculatis apice lobato sinibus 0.5 mm profundiis, stigmatis 1–1.5 mm latiss cordatis obscure brunnweos papillosis centripetalibus horizontalibus minus elevatis concretis, endocarpio 13–14 mm longo supra mediali brunneo osseo solido obovodeo lateribus lateralibus 2 mm crassis intra pallidis laevibus lucidis, seminibus 6–8 mm longis ellipsoideis, mesocarpio apicati parvo medulloso et cum fibris paucis, mesocarpio basali carnoso et fibroso.

**Diagnosis of holotype:** Shrub with many stems, 7 m tall, 4 cm in diameter; bark gray, sharp spiny; prop roots few, 20–30 cm long, 2 cm in diameter; leaves 35–45 cm long, 16–20 mm wide, subcoriaceous, gently curving, above dark olive-green, below pale green and glaucous, above the midrib with a narrow V-shaped furrow, otherwise nearly plane, at midsection with 17 parallel secondary veins in each half, no tertiary cross veins, blade ligulate but the outer half tapering to a trigonous, subulate apex, this 10 cm down 6.5 mm wide, the base amplexicaul, unarmed, white, but begin-
Fig. 262. *Pandanus aridus* St. John, from holotype. *a*, Fruiting branch, $\times$ 1; *b*, phalange, lateral view, $\times$ 1; *c*, phalange, longitudinal median section, $\times$ 1; *d*, phalange, apical view, $\times$ 1; *e*, stigmas, apical view, $\times$ 4; *f*, leaf base, lower side, $\times$ 1; *g*, leaf middle, lower side, $\times$ 1; *h*, leaf apex, lower side, $\times$ 1.
ning at 1.3–2 cm the margins with prickles 2–2.3 mm long, 2–12 mm apart, deltoid subulate, ascending, white with brownish tips; the midrib below beginning at 3.5–4 cm with prickles 1.3–2 mm long, 4–11 mm apart, subulate, reflexed, close, white; at midsection the margins with prickles 1–1.8 mm long, 6–15 mm apart, subulate, arcuate ascending, white; the midrib below with prickles 0.5–0.9 mm long, 7–13 mm apart, slender subulate, divergent, white; on the subulate tip the margins and midrib below with serrulations 0.3–0.7 mm long, 1.3–4 mm apart; pinnate inflorescence terminal, erect, bearing a solitary syncarp; peduncle 8 cm long, 8 mm in diameter, 3-sided, leafy bracted, and at the apex with 6 marcescent bracts, the outer one 2.5 cm long, 1 cm wide, elliptic, navicular, the margins spiny fimbriate; syncarp 5.5–6 cm in diameter, globose, green, bearing 21 phalanges, these 22–25 mm long, 12–23 mm wide, 10–22 mm thick, obovoid, firmly connate, upper 1/3 free, slightly pyramidal conic, 5–6-angled, 2–4-celled, lobed about 0.5 mm deep between the apices of the carpels; stigmas 1–1.5 mm wide, cordate, dark brown, papillose, centripetal, horizontal, slightly raised, congregate; endocarp 13–14 mm long, supramedian, brownish, bony, massive, obovoid, the lateral walls 2 mm thick, the inner surfaces pale, smooth, shining; seeds 6–8 mm long, ellipsoid; apical mesocarp scant, of pith and a few fibers; basal mesocarp fleshy and fibrous.

HOLOTYPE: Malagasy Republika, Rano-mainty, 18 km E of Amboasary, W of Fort-Dauphin, dry and arid scrub with Euphorbia sp., Croton sp., 175 m alt, Sept. 26, 1961, H. St. John 26,582 (BISH).

DISCUSSION: P. aridus is a member of the section Mammillarisia, as is its closest relative, P. saxatilis Martelli, of northern Madagascar, a species with the phalanges 23–27 mm long, the upper 1/2 free; endocarp occupying almost the whole interior of the phalange; lower bract of the inflorescence 2 cm wide; prop roots none. P. aridus has the phalanges 22–25 mm long, the upper 1/3 free; endocarp 13–14 mm long, slightly supramedian, occupying about 2/3 of the interior of the phalange; basal mesocarp 7 mm long; lower bract of the inflorescence 1 cm wide; prop roots few, 20–30 cm long, 2 cm in diameter.

The new epithet is the Latin adjective, aridus, dry, and is given with reference to the dry forest habitat.

Pandanus connatus sp. nov. (sect. Mammillarisia)

P. acuminatus Hort. ex Wendl., Ind. Palm. 45, 1854, nomen nudum.


Figs. 263, 264 bottom left and right

NOM. VERN.: "vacoua madik" (= Pandanus small).

DIAGNOSIS: HOLOTYPE: Arboriformata 10 m alta 9 cm diametro, cortice bruno cum spinis conicas brevisbus, ramulis 2.5 cm diametro, radicibus fulturosibus nullis, foliis 90–109 cm longis 2–2.3 cm latis curvatis sed non fractis ligulatis subcoriaceis supra obscure olivaceais infras obseuro viridibus supra midnervum sil lonatis V-formatis et in media ultima 2-PLICATIS in sectione mediiali cum 23–27 nervis paralleliis secundariis in dimidio quoque nervis tertii solum in basi in tertii ultima sensim in apice trigono subulato diminu entibus eo in puncto 10 cm ex apice 6 mm lati basi amplexicaulis inermi sed ex 6–7.5 cm marginibus cum aculeis 1.5–2.5 mm longis 3–8 mm separatis crassiter arcuato-subulatis adscendentibus albis cum apicibus bruneis, midnervo infra per 4 partem inermi, in sectione mediiali marginibus cum serrulis 0.3–0.9 mm longis 3–7 mm separatis albis cum apicibus bruneis, in apice marginibus et midnervo infra cum serrulis 0.2–0.5 mm longis 1–3.5 mm separatis albis cum apicibus bruneis, finisinos utens in media terminalis, pedunculo 8 cm longo in apice 2 cm diametro clamato trigono folioso-bracteato, bracteis superis 4–5 cm longis 2.5–3 cm latis deltaeis subulatis ciliatis papillosulis quando sicis bruneis, syncarpio solutio 9.5 cm diametro globoso cum 79 phalangibus eis 3.3–3.5 cm longis 1.6–2.1 cm latiss 1.5–1.7 cm crasso connatis oblateoideis compressis 1.3–locu latiss 5–6-angulosus laevibus lucidis parte 1/2 supera libera lateribus liberis subcurvatis illis continguis planis, apicibus cum 2–3 stigmatibus cum vallecula 0.5 mm profunda subclausa, stigmatibus 1.5 mm diametro asymmetricalibus cordatis horizontalibus superficialibus pallide bruneis papillosulis, endocarpio 20–23 cm longo supramediali osseoso bruneo cum humeris medialibus latis lateribus 5–6 mm crassiss intras laevibus et lucidis, seminibus 10–12 mm longis lineari-elliptoidis, mesocarpo apicali medulloso et cum fibris paucis, mesocarpo basali fibroso et carnoso.

DIAGNOSIS OF HOLOTYPE: Tree-like, 10 m tall, 9 cm in diameter; bark brown, with short conic spines; branchlets 2.5 cm in diameter; prop roots none; leaves arching and recurving,
Fig. 263. *Pandanus connatus* St. John, from holotype. *a*, Fruiting branch, × ½; *b–c*, phalanges, lateral view, × 1; *d*, phalange, longitudinal median section, × 1; *e*, phalange, apical view, × 1; *f*, stigmas, apical view, × 4; *g*, leaf base, lower side, × 1; *h*, leaf middle, lower side, × 1; *i*, secondary and tertiary veins, near the leaf base, × 4; *j*, leaf base, lower side, × 1.
Fig. 264. Top left, Pandanus aridus St. John, holotype, two trunks; top right, fruiting branch; bottom left, Pandanus connatus St. John, holotype, trunk; bottom right, fruiting branch.
not breaking across, 90–109 cm long, 2–2.3 cm wide, ligulate, subcoriaceous, above dark olive-green, below bright green, with a broad V-shaped furrow above the midrib and beyond the middle with two lateral pleats, at midsection with 23–27 parallel secondary veins in each half, with tertiary cross veins only in the sheathing base, in the outer third the blade gradually narrowing to a trigonous subulate apex which 10 cm down is 6 mm wide, the base amplexicaul, unarmed, but beginning 6–7.5 cm up the margins with prickles 1.5–3.5 mm long, 3–8 mm apart, stout arcuate subulate, ascending, white with brown tips; the midrib below unarmed to the outer third; at midsection the margins with serrulations 0.3–0.9 mm long, 3–7 mm apart, white with brown tips; on the subulate apex the margins and midrib below with serrulations 0.2–0.5 mm long, 1–3.5 mm apart, white with brownish tips; pistillate inflorescence erect, terminal; peduncle 8 cm long, 2 cm in diameter at apex, clavate, trigonous, leafy bracted, the upper bracts 4–5 cm long, 2.5–3 cm wide, deltoid, subulate ciliate, papyraceous, drying brown; syncarp solitary, 9.5 cm in diameter, globose, bearing 79 phalanges, these 3.3–3.5 cm long, 1.6–2.1 cm wide, 1.3–1.7 cm thick, connate, oblanceoloid, compressed, 1–3-celled, 5–6-angled, the surface smooth, shining, upper 1/4 free, the contiguous sides flat, the free part with gently curving surfaces, when several-celled with a narrow, almost closed valley 0.5 mm deep; stigmas 1.5 mm in diameter, asymmetrically cordate, horizontal, flush, light brown, papillose; endocarp 20–23 mm long, supramedian, bony, brown, with broad median flanges, the lateral walls 5–6 mm thick, the inner surfaces smooth, shining; seeds 10–12 mm long, linear ellipsoid; apical mesocarp of dense pith and a few fibers; basal mesocarp fibrous and fleshy.

**Holotypus:** Malagasy Republika, near Jardin Botanique, Gravirage, 6 km SW of Joffreville, Montagne d’Ambre, 1,000 m alt, native forest, 14 Sept. 1961, St. John 26,578 (BISH).

**Specimens Examined:** Madagascar?, C. Gaudichaud (Fl, P); Madagascar, 1903, de Vilmorin (Fl).

**Discussion:** *P. connatus* is a member of the section *Mammillarisia*, as is its closest relative, *P. vanDamii* Martelli & Pic. Ser., a species of Madagascar which has the peduncle 18–20 cm long; phalanges 35–40 mm long, 20–28 mm wide, (2)–3–4–(5–7)-celled; endocarp 11–12 mm long, the apex irregularly convex; and the leaves 40 cm long, 2–5 cm wide. *P. connatus* has the peduncle 8 cm long; phalanges 33–35 mm long, 16–21 mm wide, 1–3-celled; endocarp 20–23 mm long, with a long, conic, central apex; and the leaves 90–109 cm long, 2–2.3 cm wide.

The binomials *Pandanus acuminatus* Hort. ex Wendl. and *Vinsonia acuminata* Gaud. ex Warb. were both nomina nuda. In the herbarium at Paris is a specimen with an original label by Gaudichaud, "*Vinsonia acuminata* Ch.G., mss. ?Madagascar?". It consists of six loose, somewhat eroded phalanges that well match those of *P. connatus*. A duplicate of this consists of 5½ phalanges (Fl). On the voyage of La Bonite, Gaudichaud obtained most of his Madagascar specimens by gift from A. Perpillé, formerly a gardener at the Paris Jardin des Plantes, later a voyager to the Seychelles and Nosy-bé, and then a colonist in Madagascar.

The new epithet is the Latin adjective *connatus*, joined or united, and is given with reference to the connate carpels.

**Section Microstigma**

*Pandanus subglobosus* sp. nov. (sect. Microstigma)

Figs. 265, 266.

**Diagnosis Holotypi:** Frutex, caule 5–7 m longo 3–4 cm diametro in media plus minusus horizontali cum radicibus fulturosus multii, cortice brunneo remote breviter spinoso, ramulis 7–8 mm diametro multii, horizontalibus vel adscendentibus, radicibus ful
turosus 2–3 m longis 2 cm diametro viridibus vel griseis murciatis, foliis 28–42 cm longis 4–7 mm latis supra viridibus infra pallide viridibus cum nervibus obscure viridibus in sezione mediali cum 8–9 nervis parallelis secundaris in dimidio quoque nervis tertii nullius supra midnervum late sulcatis explicatis lamina ligulata sed parte a ultima seminum in apice 10–15 cm longo compresso subulato diminuente eo 10 cm ex apice 2–3 mm lato basi amplexicauli inermi in toto viridi, aculeis omnibus albis translucentibus, ex 9–10 mm marginibus cum aculeis inferioribus 0.8–1.2 mm longis 1.5–3 mm separatis obliquiter deltoideis subadscendentibus sequentibus 1.3–2 mm longis 2–6 mm separatis arcuato-subulatis adscendentibus basibus deltoideis, ex 4–5 cm midnervum infra cum aculeis 0.5–0.6 mm longis 2–5 mm separatis arcautis subulatis adscendentibus, in sezione mediiali marginibus
Fig. 265. *Pandanus subglobosus* St. John, from holotype. 

- **a**, Fruiting branch, × 1; 
- **b**, drupe, lateral view, × 1; 
- **c**, drupe, longitudinal median section, × 1; 
- **d**, drupe, apical view, × 1; 
- **e**, stigma, apical view, × 4; 
- **f**, leaf base, lower side, × 1; 
- **g**, leaf middle, lower side, × 1; 
- **h**, leaf apex, lower side, × 1.

*lo cm.*
Fig. 266. *Pandanus subglobosus* St. John, holotype. *Top left*, leaning shrub and prop roots, and photo of M. Rabonary Rajaona, ingénieur, Service des Eaux et Forêts; *top right*, prop roots; *bottom left*, trunk and fruiting branchlets; *bottom right*, fruiting branchlets.
et midnervo infra aculeis 0.6—1 mm longis 2.5—4 mm separatis arcuato-sululatis adscendentibus, in apice subulato marginibus et midnervo infra cum subulato-serrulis 0.3—0.6 mm longis 1.5—3 mm separatis, infructescencia terminalis cum syncarpio unico, pedunculo 2—2.5 cm longo 3—4 mm diametro recto adscendentem cum bracteis terminalibus pluribus binis exterioribus cum basi 10—12 mm longis 4—10 mm latis distentis lanceolata naviculari lutea cum apice foliaceo 3—12 cm longo 2—2.5 mm lato in basi et subulato, syncarpio 3.5—4 cm diametro globoso cum (5)—6—(7) drupis viridibus et 16—21 mm longis 16—20 mm diametro subglobosis viridibus 1-carpellatis 3—5 angulosis parte infera cuneata cum lateribus planis parte à supera et plus libera laevi lucida; stigmat apicali horizontali 2—2.5 mm diametro orbiculari-cordato elevato pallide brunnneo papilloso, endospermum supramediali 13—14 mm lato ovoideo cum humere mediiali laterali lateribus laticarnosis 5—6 mm crassis intra pallide castanoe-brunneo laevi lucido, semine 5 mm longo 3 mm diametro obliquiter ellipsoidio, mesospermum apicali medulloso humido, mesospermum basali carnoso et fibroso.

DIAGNOSIS OF HOLOTYPE: Shrub, its main stem 5—7 m long, 3—4 cm in diameter, its vertical base usually decaying and vanishing, the middle section more or less horizontal, supported by numerous horizontal or ascending prop roots 2—3 m long, 2 cm in diameter, green to gray, muricate; leaves 28—42 cm long, 4—7 mm wide, above green, below pale green with dark-green veins, at midsection with 8—9 parallel secondary veins in each half, tertiary veins none, over the midrib with a broad, shallow furrow, then the sides gently down-curved but not pleated, blade ligulate but the outer 1/3 gradually long tapering into a 10—15 cm flattened, subulate apex, this 10 cm down 2—3 mm wide, base amplexicaul, unarmed, dark shiny green even where covered, prickles all white, translucent, at base beginning at 6—10 cm up the margins with prickles, the lowest ones 0.8—1.2 mm long, 1.5—3 mm apart, oblique deltoid, slightly ascending, then the next series 1.3—2 mm long, 2—6 mm apart, arcuate subulate from a deltoid base, ascending; beginning at 4—5 cm up the midrib below with prickles 0.5—0.6 mm long, 2—5 mm apart, arcuate subulate, ascending; at midsection the margins and midrib below with prickles 0.6—1 mm long, 2.5—4 mm apart, arcuate subulate, ascending; on the subulate apex the margins and midrib below with subulate-serrulations 0.3—0.6 mm long, 1.5—3 mm apart; infructescence terminal, bearing one syncarp; peduncle 2—2.5 cm long, 3—4 mm in diameter, straight, ascending, with several apical bracts closely subtending the syncarp, the two outer ones with the base 10—12 mm long, 4—10 mm wide, expanded, yellowish, lanceolate, navicular, bearing a folicaceous tip 3—12 cm long, 2—2.5 mm wide at base, subulate; syncarp 3.5—4 cm in diameter, globose, bearing (5)—6—(7) drupes, green (perhaps always so); drupes 16—21 mm long, 16—20 mm in diameter, 1-celled, subglobose, green, 3—5—angled, the lower section cuneate with flattened sides, slightly more than upper 1/3 free, smooth, shining; stigma apical, horizontal, 2—2.5 mm in diameter, orbicular-cordate, elevated, pale brown, papillos; endocarp supramedial, 13—14 mm long, bony, pale brown, broad ovoid, with median lateral flange, lateral walls 5—6 mm thick, within light chestnut-brown, smooth, shining; seed 5 mm long, 3 mm in diameter, oblique ellipsoid; apical mesocarp of moist pith; basal mesocarp fleshy and fibrous.

JUVENILE PLANT (St. John 26, 534): Stem 60 cm tall, 1.5 cm in diameter; leaves 45—55 cm long, 8—10 mm wide, at midsection with 10—11 secondary parallel veins in each half; near the base the principal marginal spines 4—4.5 mm long, 9—24 mm apart; midrib below unarmed to beyond the middle.

HOLOYPUS: Malagasy Republik, Amanionby, 20 km N.E. of Majunga, 2 km inland, low scrub forest of Terminalia sp. and Sideroxylon sp., on dry sand plain, 10 m alt, Aug. 8, 1961, H. St. John 26, 533 (BISH).

DISCUSSION: P. subglobosus is a member of the section Microstigma, as is its closest relative, P. oligocarpus Martelli, of the nearby plateau d’Antanimena, a species with the syncarp bearing 9 drupes; drupes 13—15 mm long, ovoid, the upper 2/3 free; endocarp in longitudinal section irregularly ovate; and the leaves 40—70 cm long. P. subglobosus has the syncarp with usually 6 drupes; drupes 16—21 mm long, subglobose, upper 1/2 free; endocarp in longitudinal section irregularly cruciform; and the leaves 28—42 cm long.

The new epithet is the Latin adjective, subglobosus, almost spherical, and is given in allusion to the shape of the drupes.
NOTES

A Eurasian Alga in Alaska¹

C. Peter McRoy

Specimens of the brown alga *Fucus inflatus* f. *latifrons* Foslod were collected in Izembek Lagoon (55°N, 163°W) on the Bering Sea coast of the Alaska Peninsula; these were preserved in the collections of the Department of Botany, University of Washington. Identification of the species was based on the description by Zinova (1953). This species has not previously been reported from the west coast of North America (Dawson, 1961:398). *Fucus inflatus* occurs in the lower intertidal of the arctic seas of Siberia and Greenland and to about 55°N in the North Sea (Zinova, 1953). On the Pacific coast of Asia, *F. inflatus* extends from the Arctic to about 45°N. The form *latifrons*, however, is known only from the White, Barents, and Norwegian seas; it has not been reported from the Pacific Ocean.

Scagel (1963) examined the distribution of benthic algae in the northeast Pacific Ocean in relation to oceanographic conditions, and found that several species could be used as oceanographic indicators. This record from Izembek Lagoon presents a discontinuous distribution that is not readily explained by the circulation of the surface waters of the Bering Sea and North Pacific Ocean (Zenkevitch, 1963:818–827).

The presence of a species requires its introduction as well as suitable conditions for growth. If the introduction of *F. inflatus* is a result of the circulation of surface waters, then, assuming favorable growth conditions, it should occur over a wide range of the Alaska coast. *F. inflatus* is a relatively conspicuous species. Since it has not been reported from other collections of Alaskan algae, it may not occur outside of a limited area of the Bering Sea coast.

Several mechanisms for the introduction of this alga into Izembek Lagoon can be conceived. The most interesting is the possible introduction by the several hundred thousand Stellar's Eiders (*Polysticta stellari*) that annually migrate between the arctic coast of Siberia and Izembek Lagoon (Jones, 1965). Future collections on both sides of the Alaska Peninsula should provide further evidence.

The assistance of Dr. R. E. Norris, Department of Botany, University of Washington, and Mr. R. D. Jones, Jr., Aleutian Islands National Wildlife Refuge, is gratefully acknowledged.

REFERENCES


A Variant *Aplysia californica*

**LINDSAY R. WINKLER**

**On July 6, 1960,** while on a routine collecting trip to Lunada Bay, Palos Verdes, California, I collected an unusual 19.5-cm sea hare. This sea hare had all the characteristic features diagnostic of *Aplysia californica* Cooper. In addition, however, a row of fleshy hornlike tentacles extended from 1 cm behind the posterior tentacles on the middorsal surface for a distance of 1.5 cm, after which the continuation of this line was outlined by a row of bumps extending caudad to its interception with the genital groove between the anterior ends of the parapodia. The specimen was transported live to the laboratory where it was observed and photographed (Fig. 1).

On this specimen the posterior tentacle measured 2.5 cm. Beginning anteriorly, the first three supernumerary tentacles measured 9, 7, and 8 mm, followed by a branched tentacle with a total length of 8 mm, each branch of which measured 3 mm. The most posterior tentacle was short, measuring only 3 mm in length.

Careful search of the Lunada Bay area at the time and on successive trips to the area during the next two years, though resulting in the capture and examination of hundreds of specimens, failed to produce others possessing aberrant tentacular configurations.

It is felt that this specimen is probably the result of an accident of development, in which cells normally destined to become tentacles were moved caudad to develop into supernumeraries. Credence may be lent to this hypothesis by the elongated incurve cavities on the right-hand side of tentacles 1 and 3, which suggest the "rolled-tube" effect which is normally seen in the posterior tentacle of the sea hare. Wong (Chi) and Wagner (1956) demonstrated morphological changes in snail tentacles after experimental irradiation with ultraviolet light. This may indicate a plasticity in snail tissues which, although not indicating any mechanism, could conceivably be remotely related to the present phenomenon.

It is not possible, however, to eliminate the possibility of the phenotypic appearance of a

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1 College of the Desert, Palm Desert, California 92260. Manuscript received December 18, 1966.
genetic mutation, though this seems unlikely for other considerations as well as the suggestion of non-bilaterality in the incurved cavities on tentacles 1 and 3.

The possibility of this specimen representing a new species would seem very remote. At most it seems only to further accentuate the variability of this plastic genus.

REFERENCE

THOMAS C. CHENG
Compatibility and Incompatibility Concept as Related to Trematodes and Molluscs

THEODORE CHAMBERLAIN
Littoral Sand Budget, Hawaiian Islands

G. C. MORRISON
Phytochemical Survey in the British Solomon Islands

ROY T. TSUDA and GAVINO TRONO, JR.
Marine Benthic Algae from Howland and Baker Islands

GEORGE J. HOLLENBERG
Species of the Red Alga, Polysiphonia, of the Tropical Pacific, II

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Polychaetous Annelids of the Marshall Islands

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EDWARD B. REED
Occurrence of the Copepod, Cyclops kolensis, in North America

WILLIAM A. GOSLINE
Considerations Regarding Evolution of Hawaiian Animals

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Contributions to Pacific biological and physical science will be welcomed from authors in all parts of the world. (The fields of anthropology, agriculture, engineering, and medicine are not included.) Manuscripts should be addressed to the Editor-in-Chief, PACIFIC SCIENCE, University of Hawaii, Honolulu, Hawaii 96822. Use of air mail is recommended for all communications.

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# PACIFIC SCIENCE

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The Compatibility and Incompatibility Concept as Related to Trematodes and Molluscs

Thomas C. Cheng

In this paper I propose to bring together significant facts already known to have some bearing on the mechanisms which govern or influence host compatibility or incompatibility during parasitism, to add information based on my own recent research, and to present some speculations.

From the broad viewpoint, host compatibility may be defined as the expression of the physical and physiological (including chemical) states of the host and parasite which enable the parasite to invade and carry out its life processes, including perpetuation of the species. Incompatibility refers to those factors which completely or partially prevent the establishment and normal development of the parasite. Both of these are highly complex phenomena influenced to one degree or another by a series of separate but commonly interrelated factors.

As working models from which we can seek evidence to support or reject various working hypotheses, we have chosen to examine the relationship between molluscs and digenetic trematodes, since this category of association, unlike a number of others, is an example of parasitism whether the definition of "parasitism" is couched in nutritional, pathological, ecological, or immunological terms. Molluscs, except in a very few unusual instances, serve as intermediate hosts for the Digenea, but this fact does not render them less appropriate as experimental tools. In fact, inasmuch as it is generally accepted that molluscs were the original hosts during the evolutionary adaptation to parasitism of the progenitors of modern day digenetic trematodes, one might expect to find the occurrence of certain adaptive mechanisms more firmly entrenched in them than in vertebrate definitive hosts. Furthermore, it is easier to simulate experimentally the natural environmental conditions of molluscs than those of vertebrates in captivity, and, with relative ease, one can test basic premises on a number of species from a variety of habitats, ranging from marine to fresh water, and from various attitudes.

It has long been known that compatibility and incompatibility need not be "all or none" phenomena, since both interspecific and intraspecific (or strain) differences do occur, as is indicated by the rate of parasite development, infectivity of the cercariae or metacercariae, the number of progeny produced by delayed polymorphy, etc. In fact, an understanding of the factors governing compatibility and incompatibility in turn most probably will provide answers for why these manifestations occur.

Since the initial host-parasite contact, the invasion process, the establishment of the parasite within the host, and the escape process are distinct aspects of a successful parasitic relationship (see the review by Cheng, 1967), one would expect factors correlated with all of these phases to contribute to some degree in regulating compatibility and/or incompatibility, and, indeed, available evidence indicates that this is so. In the following paragraphs are briefly reviewed those facts which support this concept. Space does not permit the citation of all the relevant literature; therefore, only selected studies are cited as examples.

Initial Host-Parasite Contact

Recently, Timon-David (1965) has again raised the question of the importance of host-
attraction in governing host-specificity in mollusc-trematode relationships. This topic, which has been critically reviewed by myself (Cheng, 1967), among others, is still a controversial one. The controversy is not whether host-attraction does occur since, in my opinion, the studies of Faust and Melenev (1924), Faust (1934), Faust and Hoffman (1934), Barlow (1925), Tubangui and Pasco (1933), Mathias (1925), Kloetzal (1958, 1960), Kawashima et al. (1961a), Campbell (1961), Davenport et al. (1962), Etges and Decker (1963), and MacInnis (1965) have demonstrated rather conclusively that attraction between miracidia and molluscs does occur. This is a subtle phenomenon, however, which is operative only within very restricted distances and can be observed only with the application of quantitative techniques. The controversy is over the question whether chemotaxis is in any way related to host-specificity and hence influences compatibility. Although the studies of Faust and Melenev (1924), Barlow (1925), Neuhaus (1953), and Etges and Decker (1963) suggest that miracidial attraction is host-specific, the results of Sudds (1960), Kawashima et al. (1961a), and Barbosa (1965) suggest that attraction of miracidia to a specific mollusc need not be correlated with subsequent compatibility.

Experiments carried out in our laboratory have revealed that the miracidia of Fasciola gigantica are stimulated by the plasma and tissue extracts of laboratory-raised Galba ollula, the natural host in Hawaii. These reactions, however, are not specifically elicited by G. ollula, since similar reactions were observed when miracidia were exposed to the plasma and tissue extracts of two other species of freshwater gastropods, Tarebia granifera mauniensis and Helisoma duryi normale.

In the first series of experiments, F. gigantica miracidia, between 15 and 25 minutes post-hatching, were placed in shallow Petri dishes (50 mm in diameter, 15 mm high) in which had been placed specific dilutions of the plasma or tissue extracts of H. duryi normale, T. granifera mauniensis, or G. ollula. Each dish was placed over a grid marked off in 2.54-mm squares. Using a 1/10-second-interval stop-watch and observing under a dissection microscope illuminated by indirect lighting, the swimming speed of a single miracidium was timed, recorded as seconds/2.54 mm, and later expressed as mm/sec (Tables 1 and 2). As controls, the swimming velocities of miracidia of similar age placed in distilled water were determined.

The six test media consisted of 1:10, 1:50, and 1:100 dilutions of molluscan plasma and similar dilutions of tissue extracts. Blood was collected from the molluscs' body sinuses by gently cracking the shell of each snail, without injuring the soft tissues, and permitting the blood to drain to the lower edge of an inclined Stender dish from whence it was rapidly collected with a hypodermic needle and syringe. The cellular components of whole-blood samples were removed by centrifugation. The tissue extracts were prepared by homogenizing the soft tissues of each snail in cc of distilled water after the tissues had been completely desanguinated and perfused with running distilled water for 15 minutes. After homogenization in an ice bath, the homogenates were centrifuged and the aqueous extracts collected were considered the 'concentrated' extracts.

All snails used were laboratory-raised and known to be parasite-free. The concentrated plasma and tissue extracts of each species were pooled and the desired dilutions were made from the pooled samples. All observations were made at 22 ± 1°C.

From the data presented in Tables 1 and 2, it is evident that all three dilutions of the plasma and tissue extracts of G. ollula (the natural host), H. duryi normale, and T. granifera stimulated F. gigantica miracidia to increase their swimming velocities. In addition, the miracidial swimming pattern was conspicuously altered. Miracidia in distilled water usually swim linearly, rotating along their longitudinal axes. Divergences from such a course were gradual rather than abrupt. When placed in plasma or extracts, their swimming behavior became erratic. They turned abruptly and frequently.

In the second series of experiments, 10 miracidia, 10–15 minutes post-hatching, were placed in small Petri dishes (60 mm in diameter, 13 mm high) which contained 10 cc of distilled water. In the center of each dish was placed an agar block of three mm³ which had been pre-soaked in concentrated plasma or tissue extracts of G. ollula, H. duryi normale, or T. granifera.
### TABLE 1
Comparisons of the Swimming Velocities of *Fasciola gigantica* Miracidia in Distilled Water (Controls) and in Three Dilutions of Molluscan Plasma (The Student's Test Was Employed to Determine Significances)

<table>
<thead>
<tr>
<th>MOLLUSCAN SPECIES</th>
<th>DISTILLED WATER (CONTROLS)</th>
<th>1:10 PLASMA</th>
<th>1:50 PLASMA</th>
<th>1:100 PLASMA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>NO. OF TRIALS</td>
<td>VELOCITY (MM/SEC)</td>
<td>NO. OF TRIALS</td>
<td>VELOCITY (MM/SEC)</td>
</tr>
<tr>
<td><em>G. olula</em>¹</td>
<td>40</td>
<td>0.79</td>
<td>25</td>
<td>1.65</td>
</tr>
<tr>
<td><em>H. duryi normale</em>²</td>
<td>101</td>
<td>1.96</td>
<td>81</td>
<td>2.70</td>
</tr>
<tr>
<td><em>T. granifera</em>³</td>
<td>60</td>
<td>2.30</td>
<td>60</td>
<td>3.5</td>
</tr>
</tbody>
</table>

1. The miracidia used were 25 minutes post-hatching.
2. The miracidia used were 18-20 minutes post-hatching.
3. The miracidia used were 15 minutes post-hatching.

### TABLE 2
Comparisons of the Swimming Velocities of *Fasciola gigantica* Miracidia in Distilled Water (Controls) and in Three Dilutions of Molluscan Aqueous Tissue Extracts (The Student's Test Was Used to Determine Significances)

<table>
<thead>
<tr>
<th>MOLLUSCAN SPECIES</th>
<th>DISTILLED WATER (CONTROLS)</th>
<th>1:10 EXTRACT</th>
<th>1:50 EXTRACT</th>
<th>1:100 EXTRACT</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>NO. OF TRIALS</td>
<td>VELOCITY (MM/SEC)</td>
<td>NO. OF TRIALS</td>
<td>VELOCITY (MM/SEC)</td>
</tr>
<tr>
<td><em>G. olula</em>¹</td>
<td>40</td>
<td>0.79</td>
<td>20</td>
<td>1.69</td>
</tr>
<tr>
<td><em>H. duryi normale</em>²</td>
<td>101</td>
<td>1.96</td>
<td>80</td>
<td>0.94</td>
</tr>
<tr>
<td><em>T. granifera</em>³</td>
<td>60</td>
<td>2.30</td>
<td>60</td>
<td>3.30</td>
</tr>
</tbody>
</table>

1. The miracidia used were 25 minutes post-hatching.
2. The miracidia used were 18-20 minutes post-hatching.
3. The miracidia used were 15 minutes post-hatching.
mauiensis for 10 hours. Although exact behavioral patterns exhibited by miracidia in the proximity of an agar block were determined, as well as the number of miracidia in each concentric zone at various time intervals, these results will not be reported at this time. Only the total number of contacts made by the miracidia per 5 minutes during the initial 10-minute period are reported (Table 3). The same number of miracidia placed in distilled water with untreated agar blocks served as controls. All observations were made at 22 ± 1° C.

From the data presented in Table 3, it is apparent that significantly more contacts were made between miracidia and plasma- and tissue extract-soaked agar blocks than with control blocks. The exception was in the case of T. granifera tissue extract-soaked blocks. It may be concluded then that the miracidia of F. gigantica respond to a velocity-increasing stimulant and an attractant in the plasma and tissue extracts of certain species of molluscs, and that these factors are not host-specific and need not indicate successful subsequent penetration and development. It is noted that the velocity-increasing stimulant and the attractant may be the same factor.

As has been pointed out in an earlier review (Cheng, 1967), the effectiveness of the "host factor" (a term introduced by Davenport (1955) to designate the stimulatory material of host origin) in guiding miracidia to their molluscan host is doubtful under certain circumstances. For example, Etges and Decker (1963) have pointed out that the naturally-occurring negative geotaxis and positive phototaxis of Schistosoma mansoni miracidia most probably eclipse the chemotactic effect of the "host factor." Even between these taxes, Chernin and Dunavan (1962) have demonstrated that the negative geotaxis is a more powerful determinant of miracidial behavior than is positive phototaxis. Thus, it is only under those conditions where naturally-occurring taxes guide the miracidia to the immediate proximity of the mollusc that the influence of the "host factor," which is operative only within short distances, is effective (Fig. 1).

Fig. 1. Diagrammatic drawing illustrating factors which can govern or influence miracidium-mollusc contact during the pre-invasion phase. The terms "tropism" and "taxis" are used interchangeably.
## Table 3

Comparisons of the Number of Contacts Between *Fasciola gigantica* Miracidia and Nonpresoaked Agar Blocks (Controls) and Blocks Presoaked in Concentrated Plasma and Tissue Extracts of Three Species of Snails (The Student’s Test Was Employed to Determine Significances)

<table>
<thead>
<tr>
<th>Molluscan Species</th>
<th>Control Blocks</th>
<th>Plasma-Soaked Blocks</th>
<th>Tissue Extract-Soaked Blocks</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. of trials</td>
<td>Mean no. of contacts (5 min.)</td>
<td>No. of trials</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>G. ocellata</em></td>
<td>40</td>
<td>1.55</td>
<td>60</td>
</tr>
<tr>
<td><em>H. duryi normale</em></td>
<td>117</td>
<td>1.65</td>
<td>117</td>
</tr>
<tr>
<td><em>T. grani</em></td>
<td>60</td>
<td>0.9</td>
<td>60</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Values are given as mean number of contacts per 5 minutes.
It should also be mentioned that it is highly doubtful if chemotactic forces are influential during the pre-invasion relationship between miracidia and pelecypod molluscs, since the ability of this group of molluscs to effect incurrents, through either their siphons or shell edges, undoubtedly results in the passive intake of miracidia via the currents (Fig. 1).

Besides innate taxes, the nature of the environment is known to determine whether attraction between mollusc and miracidium can be effective (Fig. 1). An excellent example of this has been contributed by Kawashima et al. (1961b). Earlier, these investigators (1961a) had demonstrated that, although the miracidium of Paragonimus obirai is attracted to three species of brackish water snails of the genus Assiminea (A. parasitologica, A. japonica, and A. latericea miyazakii), only one of the three, A. parasitologica, is a compatible host. A. latericea miyazakii is an incompatible host, while A. japonica can be infected experimentally but the level of infection is consistently low. Thus, it would appear that in nature some other factor or factors must be operative to bring about the selection of A. parasitologica by miracidia. It was subsequently shown, in a study of the locomotive speed and survival of P. obirai miracidia in various concentrations of NaCl, that the lower the salt concentration is the more active the miracidia become, with the optimum salinity being 0.25% NaCl or less. Concurrent studies on the ecology of the three species of snails revealed that the optimum salinity for A. parasitologica is 0.25%, that for A. latericea miyazakii is 0.4%, and that for A. japonica is 0.6%. These findings demonstrate that an environmental factor, salinity in this case, can serve as a mechanism determining host selection. Thus, these investigators have demonstrated that the influence of the molluscs' attractants can be masked by an ambient factor and have also revealed further evidence that attraction of miracidia to mollusc need not mean successful subsequent development.

Substances of host origin need not always enhance establishment of the parasite. Some may be inhibitory. For example, Cheng et al. (1966a) have demonstrated that the plasma of seven species of marine pelecypods, Mercenaria mercenaria, Mya arenaria, Crassostrea gigas, C. virginica, Tapes philippinarum, Mytilus edulis, and Modiolus demissus, will stimulate the cercariae of Himasthla quissetensis to encyst; as the result of the rapidity of this process in the instances of C. gigas and C. virginica, the cercariae are prevented from penetrating these oysters, especially C. gigas, and hence these pelecypods may be considered incompatible hosts (Cheng et al., 1966b). These findings demonstrate how in some instances a factor of host origin operative during the pre-invasion phase of host-parasite relationship could determine the incompatibility of the host.

It should be pointed out that the tissue extracts of the same seven species of pelecypods have a negative effect on H. quissetensis cercariae, reducing their life spans significantly. However, the fact that the cercariae are stimulated to encyst in M. mercenaria, M. arenaria, T. philippinarum, M. edulis, and M. demissus before the tissue component(s) could cause their death is believed to be responsible for the compatibility of those pelecypods as second intermediate hosts. This is because the cyst wall serves as a protective layer against continued contact with the tissue component(s).

Wright (1959) has suggested that the "host factor" may be in the form of species-specific substances incorporated in the body-surface mucus of molluscs; Kawashima et al. (1961a) have demonstrated that Paragonimus obirai miracidia are attracted to amino acid mixtures placed in cellophane bags; and MacInnis (1965) has found that butyric acid, galactose, L-cysteine HCl, and even 1.0 mM HCl will stimulate "contact with return" of over 80% of S. mansoni miracidia in an artificial test system. However, no direct evidence is yet available to indicate the nature of "host factors." Moreover, it should be pointed out that although organic molecules, possibly amino acids, fatty acids, and sugars, are the attractants, there is also some evidence which indicate that the pH or some other physical property of the host may be responsible, at least in part, for the attraction (Kawashima et al., 1961a) (Fig. 1). This most probably explains the attraction of S. mansoni miracidia for dilute HCl, as demonstrated by MacInnis.

In the case of those species of trematodes which do not include a free-swimming mira-
The invasion process

Because of obvious medical implications, considerable information is available about factors governing the penetration of cercariae into mammals and other vertebrate hosts. On the other hand, little is known about miracidial penetration into molluscs, either from the exterior or through the gut wall. Nevertheless, this barrier could be a factor determining compatibility or incompatibility.

Certain aspects of the processes involved during the successful penetration of *Lymnaea (= Limnaea) truncatula* and *L. auriculata* by *Fasciola hepatica* and *F. gigantica*, respectively, have been studied by Dawes (1959, 1960a, b, c). According to him, the miracidium first becomes attached to the molluscan host's integument by suctorial action resulting from application of the "cup" formed by the inversion of the anterior papilla assisted by mucus. This is followed by the secretion of cytolytic enzymes from "... the gut and the unicellular pharyngeal 'glands' into the 'cup.'" The subsequent enzymatic activity results in the lysis of the host's epithelial and subepithelial tissues. Only after the host's integument has been perforated does the parasite enter, but not before it has sloughed its ciliated epidermis. For this reason, Dawes considers the penetrating form to be a sporocyst and not a miracidium.

The question may be asked whether the miracidial cytolytic enzymes must be chemically specific for the integument of specific species of molluscs. If this is the case, the compatibility of enzyme to substrate could serve as a factor governing successful penetration, hence host-compatibility (Fig. 2). Indeed, Lie (1963) believes that the prevention of penetration of certain echinostome miracidia by unnatural snails is responsible for incompatibility.

In addition to the miracidium's cytolytic enzymes, Dawes (1960c) has expressed the view that the shedding of the ciliated epidermis by the miracidium, thus transforming it to a sporocyst, is a prerequisite for successful infection of the snail. This hypothesis has been challenged by Lengy (1962), who has demonstrated that *Schistosoma bovis* miracidia do not shed their ciliated epidermis prior to penetrating. Similarly, Maldonado and Metienzo (1947) demonstrated earlier that *S. mansoni* miracidia do not shed their plates until after successful penetration; and Heyneman (1966) has successfully initiated the infection of *Lymnaea rubiginosa* with *Echinostoma andyi* miracidia and of *Indoplanorbid exustus* with *Echinostoma malayanum* miracidia by inoculating these miracidia through the mantle via a minute hole drilled in the molluscs' shells, thus suggesting that the shedding of the miracidial epidermal plates is not a prerequisite to successful infection, at least in these species. It remains true, nevertheless, that certain species of fasciolid miracidia may shed their plates prior to penetration. Campbell and Todd

![Diagrammatic drawing illustrating factors which may govern or influence successful penetration of mollusc by miracidium.](image)
(1955), for example, have reported that Fascioloides magna miracidia shed their ciliated plates on the exterior after a brief contact with the molluscan host’s tissues, and Barlow (1925) has found the transformation of F. buski miracidia into sporocysts when bathed in “snail tissue juices.” I observed that F. gigantica miracidia shed their plates when placed in concentrated and 1:10 dilutions of the plasma of Galba ollulna, the natural host (Fig. 3, and in similar concentrations of the plasma of Helisoma duryi normale, an incompatible host, but not in the plasma of Tarebia granifera maniensis and Littorina pintado, both of which are also incompatible hosts. Similar phenomena were not observed when miracidia were placed in tissue extracts of all four species of snails, nor were they observed in greater dilutions of G. ollulna and H. duryi normale plasma. Thus, this phenomenon is apparently not related to host compatibility. Rather it suggests that miracidia which possess the innate ability to shed their epidermal plates prior to penetration can be stimulated to do so by some factor(s). Nevertheless, it would appear that the occurrence of the stimulatory factor(s) in the natural hosts could influence compatibility during this phase of host-parasite relationship, especially if Dawes’ contention is true among fasciolid trematodes (Fig. 2).

No information is yet available relative to the nature of the stimulatory factor(s); however, the fact that F. gigantica miracidia did not shed their plates when placed in extracts of desanguinated and aqueously perfused snails indicates that the factor is present in plasma rather than in tissue fluids.

It is also significant that F. gigantica miracidia were stimulated to shed their plates only in concentrated plasma and in a 1:10 dilution of plasma. This may be interpreted to mean that in nature the stimulatory effect would occur only when miracidia become intimately associated with or are in actual contact with the snail, since plasma, seeping from the wound resulting from the parasite’s lytic enzymes, would be rapidly diluted as it diffuses through the aqueous medium.

In addition to the shedding of epidermal plates, invagination of the apical papilla as well as the secretion of some substance, perhaps the lytic enzyme, were also noticed in F. gigantica miracidia exposed to plasma from G. ollulna and H. duryi normale (Fig. 4). Thus it would appear that the formation of the apical “cup” as well as secretion are stimulated not by physical contact but by some factor(s) present in the mollusc’s plasma (Fig. 2).

**ESTABLISHMENT OF THE PARASITE**

Successful establishment of germinal sacs (sporocysts, rediae, or both) within the mollusc implies that the form which has invaded the host will reach a suitable site, overcome the host’s internal defense mechanisms, be the target of host-elaborated growth and development-stimulating factors, be able to obtain its required nutrients, and at the same time not kill its host (Fig. 5). These requirements are considered separately.

**Reaching a Suitable Site**

Although tissue specificity still remains one of the unsolved problems in parasitology, it is a well-documented phenomenon. For example, for a large number of species among the Digenea the molluscan host’s hepatopancreas or gonads appear to be the preferred sites of normal larval development. This does not mean that aberrant parasites cannot develop in ectopic sites. Indeed, such exceptions to the rule are known. Investigations into the nature and development of larvae which grow at ectopic sites not only can provide insights into the physico-chemical requirements of these parasites but also can reveal some of the factors which inhibit or prevent the parasite from reaching its normal developmental site. A series of such studies is summarized to illustrate this point.

Among the Plagiorchioidea, the mother sporocysts of certain species are known to be attached to the external surface of their molluscan hosts’ alimentary tracts (Cort et al., 1954; Rankin, 1944; Leigh, 1946; Schell, 1961, 1962a; Cheng, 1961a, b; and others). Surrounding each of the daughter sporocysts arising from these mother sporocysts is a so-called paletot. The question is: what is the origin of this paletot? According to Cort and Olivier (1943), Cort and Ameel (1944), and Cort et al. (1954), the paletot is formed from the
Fig. 3. Photomicrograph showing *Fasciola gigantica* miracidium which has shed its epidermal plates after exposure to a 1:10 dilution of *Galba Pallida* plasma; 1 minute after exposure. se, Shed epidermal plates.

Fig. 4. Phase-contrast photomicrograph showing invagination of apical papilla of *Fasciola gigantica* miracidium and secretion of lytic enzyme(?) after exposure to concentrated *Galba Pallida* plasma. ip, Invaginated papilla; s, secreted material.

...multiplication of the cells of the mother sporocyst wall which invaginates and surrounds each daughter sporocyst. More recently Schell (1961, 1962a), who studied the sporocysts of *Haploometra intestinalis* and *Glypthelmins quieta*, has expressed the opinion that the paletot is not of parasite origin but represents an enveloping membrane which has resulted from the proliferation of the basement membrane surrounding the snail’s gut, thus preventing further invasion by the mother sporocyst beyond that space delimited by the intestinal epithelium on one side and the basement membrane on the other. If Schell’s observations are correct, the reason why mother sporocysts of *H. intestinalis* and *G. quieta* are found abutting upon their molluscan
hosts' alimentary tracts rather than between the hepatopancreatic lobules—as is the case with certain other plagiorchioid trematodes (Mattes, 1936; Maldonado, 1943; Cort et al., 1952)—is that the migration of these sporocysts becomes restricted by their hosts' basement membranes. Although the mother sporocysts of both H. intestinalis and G. quieta become successfully established at this site and produce daughter sporocysts, the migration of the mother sporocysts does become restricted. Schell (1962a) has stated: "In following the development of G. quieta it became evident that the thin basement membrane beneath the intestinal epithelium of the host snail plays an important role in protecting the snail from invasion by the parasite."

Is it possible, then, that certain species of trematodes, which could not undergo normal development at the site restricted by the basement membrane, would in this way be prevented from becoming established? Although examples of this, as far as I have been able to determine, have not yet been described among molluscular larval trematode relationships, the condition known as schistosome dermatitis caused by avian schistosome cercariae in human skin is an example of the inability of these cercariae to successfully penetrate the depth of the abnormal host's skin: being unable to survive in the surfacal areas of the skin, they die. In this connection, Lewert and Lee (1954), Lewert (1958), and Lewert and Mandlowitz (1963) have demonstrated that the physical and chemical natures of the basement membrane and ground substance do determine whether the entrance of invasive forms of helminths will be successful.

The evidence presented indicates that barriers, especially in the form of basement membrane and perhaps ground substances, situated in the path of invading trematode larvae could prevent them from reaching a satisfactory site for further development and thus serve as determinants of host incompatibility.

Host's Defense Mechanisms

What is known about the nature of internal defense mechanisms in molluscs, both cellular and humoral, has been reviewed in recent years by Stauber (1961), Cheng and Sanders (1962), Tripp (1963), and Cheng (1967). The role of molluscan leucocytes (amoebocytes or phagocytes) and fibrous elements in innate immunity by causing the encapsulation of trematode larvae, is well established. The results of Newton (1952, 1954), Brooks (1953), Sudds (1960), and others strongly indicate that encapsulation generally occurs around larvae in unnatural hosts. However, slight and restricted encapsulation may also occur around larvae in their natural hosts (Cheng and Cooperman, 1964; Probert and Erasmus, 1965; Schell, 1961, 1962a, b; Pan, 1965), but these extremely light capsules usually inflict little or no damage upon

![Diagram](image-url)
the parasites. On the other hand, the extensive capsules which surround parasites in unnatural hosts usually result in destruction of the parasites. The chemical basis for this destruction remains undetermined; nevertheless, it may be generalized that encapsulation by leucocytes and/or fibers resulting in death is by far the most effective form of innate defense mechanism in molluscs against incompatible trematode larvae.

Although supposedly innate humoral factors in molluscs have been reported by various workers (see the review by Cheng, 1967), their effectiveness as defense mechanisms against invading trematode larvae is unknown or uncertain. Recently, however, Heyneman (1966) has successfully demonstrated in transplantation studies that the inability of Echinostoma malayanum to become established in Lymnaea rubiginosa and of E. auxyi in Indoplanorbis exustus is due to "physiological rejection within snail tissues distinct from the factors responsible for failure of miracidia to attach to or penetrate the body wall of the nonadapted host." Although it would be tempting to interpret Heyneman's findings to indicate the occurrence of an innate humoral factor, the destruction of E. malayanum and E. auxyi larvae could very well have resulted from encapsulation. Unfortunately, follow-up histological studies which would confirm this conclusion are not available.

Two other examples of possible occurrence of innate humoral immunity which prevents the establishment of larval trematodes have been reported. Benex and Lamy (1959) showed that tissue extracts from the planorbid snail Planorbis cornensis will immobilize S. mansoni miracidia, and these French workers suggest that species of snails which are refractory to S. mansoni infection may possess "immune-like" immobilizing substances. Sadds (1960) has shown that Trichobilharzia elvae miracidia penetrate two abnormal hosts, Buliminae megasoma and Fossaria abrissa, the parasites die and begin to degenerate within 1.5–6 days, without any indication of a host tissue reaction. Again, it would be tempting to interpret these findings as indications of the presence of innate humoral immunity but, under the conditions of the experiments, other possible explanations cannot be completely ruled out.

Occasionally suggestions have appeared in the literature (Sogandares-Bernal, 1965) that snails at different ages present different degrees of susceptibility to infection by trematode larvae. Most, if not all, of these reports have resulted from either field studies (where the ages of snails have been estimated by their sizes) or qualitative assays of infectivity. Whether such age-correlated resistance is due to some innate humoral factor or even to a cellular factor remains unknown.

The only evidence of acquired cellular immunity I have been able to find is that presented by Barbosa and Coelho (1956). They demonstrated that, although Biomphalaria glabrata previously "cured" of Schistosoma mansoni infection can be reinfected, some tissue reaction involving leucocytes and fibrous elements is evoked in reinfected snails, a phenomenon not found in initial infections. This finding could mean that some type of incomplete acquired immunity exists in B. glabrata after the initial infection and is manifested during reinfection as cellular response.

The belief held by some workers that acquired humoral immunity can occur in molluscs stems primarily from the reports of Winfield (1932) and Nolf and Cort (1933). These investigators reported that the presence of Cotylurus flabelliformis sporocysts in varieties of Lymnaea stagnalis prevents almost all of the cercariae of this trematode from successfully penetrating and encysting as metacercariae. Later, Cort et al. (1945) repeated these studies and reported that the same phenomenon occurs in Stagnercola marginata angulata parasitized by C. flabelliformis sporocysts. They noted that the few cercariae which did succeed in penetrating were inhibited from developing into metacercariae unless they entered sporocysts and were thus presumably protected from the host's antibodies. On the basis of these reports, Culbertson (1941) concluded that "... it is clear that snails acquire an immunity after infection by trematodes..." Several later authors, especially Michelson (1963) and Cheng (1967), have cautioned that this generalization is unwarranted since, as of this date, the ability of molluscs to produce antibodies has not been conclusively demonstrated.

The results of two other studies suggest the
ocurrence of acquired humoral immunity. Chowaniec (1961) reported that only a small proportion of snails already harboring Fasciola hepatica could be infected with the same parasite, while most of the control snails could be readily infected. In the second study, Lie et al. (1966) demonstrated that only 5% of Lymnaea rubiginosa infected with one species of echinostome could be superinfected with a second, while 89% of uninfected control snails could be infected. In neither of these studies, however, were antibodies demonstrated. It is of interest that, in the case of L. rubiginosa, Lie et al. stated another possible explanation: young invading sporocysts of the second species are killed and ingested by the rediae of the first species.

The most convincing evidence of acquired humoral immunity in molluscs is that contributed by Michelson (1963, 1964), who demonstrated that Schistosoma mansoni miracidia-immobilizing substances occur in the tissue extracts of Biomphalaria glabrata infected with this trematode. Although Michelson found that his controls (extracts of other species of uninfected snails, extracts of snails infected with an acid-fast bacillus, an echinostome metacercaria, the nematode Daphnia pulex, and polystyrene spheres, uninfected B. glabrata, and water) all gave positive results, in no instance did the percentage of immobilization reach the level observed in extracts of S. mansoni-infected snails. Michelson cautiously states: "Although the suggestion that the immobilizing phenomenon might be associated with an antigen-antibody interaction is an appealing one, data are lacking to substantiate this hypothesis. The possibility that the immobilizing substance(s) might be related either to parasite-produced toxins or to products resulting from alternations in the snail's metabolism cannot be excluded."

It may be concluded, then, that innate cellular immunity appears to be the most efficient mechanism by which trematodes are prevented from developing in incompatible molluscs, although acquired cellular immunity may occur. The role of humoral factors, either innate or acquired, remains uncertain.

Influence of Host-Elaborated Growth- and Development-Stimulating or -Inhibiting Substances

This vast area of host-parasite relationships has hardly been touched. From what is known about the metabolic interaction between larval trematodes and molluscs, it is inconceivable that compatible hosts do not influence in some manner the growth and differentiation processes of their parasites and thus enhance their normal sequence of development, or, conversely, that incompatible hosts do not in some manner inhibit the normal developmental sequences of their parasites.

Meade and Pratt (1966) have reported that, when rediae of Metagonimoides oregonensis are experimentally transplanted from naturally infected Oxytrema silicula, in which the gonads had been destroyed, to young uninfected snails with healthy gonads, a certain number will survive but that differences are apparent between the transplanted rediae, their progeny, and those in naturally infected snails. They noted that the transplanted rediae more than doubled their natural size, "mucus and debris" were included in their caeca, and the enclosed metacercariae were no longer distinguishable. Burns and Pratt (1953) had shown earlier that the rediae of M. oregonensis give rise to both cercariae and metacercariae within their brood chambers and that no daughter rediae occur. Furthermore, although some metacercariae, released from transplanted rediae into the body cavities of acceptor snails, survived for up to 6 weeks, none of these were infective when fed to a known compatible experimental definitive host, the golden hamster. These uninfected metacercariae also exhibited some behavioral and morphological peculiarities. They displayed greater activity, their eyespots disappeared, and the prominent Y-shaped excretory vesicle which normally appears black was often enlarged and possessed fewer granules. Meade and Pratt are of the opinion that these differences in the transplanted rediae and metacercariae resulted from the influence of their new host's gonadal hormone(s). The same hormone(s) presumably was present at a very much lower level or not present at all in the original castrated hosts. Whether this conclusion is justified must await more direct evidence.
From the study cited above, it would appear that some host factor(s), perhaps hormones, in *O. silicula* with healthy gonads does disrupt the normal development of *M. oregonensis* rediae and metacercariae during the later phase of the relationship. The significance of this finding to our discussion is that it is an example of a host-elaborated substance which "inhibits" normal development and thus promotes incompatibility. The phenomenon reported by Meade and Pratt, however, does not appear to hold true in all transplanted mollusc-larval trematode associations. Chernin (1966), for example, has reported successful transplants of *S. mansoni* to armored snails, and daughter sporocysts from *B. glabrata* to acceptor snails of the same species which were followed by normal cercarial formation. Perhaps this difference can be explained by the fact that *M. oregonensis* includes a radial stage while *S. mansoni* includes sporocyst stages. It is well known that rediae inflict significantly more damage upon molluscs than do sporocysts. Thus, perhaps the donor *B. glabrata* is never completely castrated and *S. mansoni*, as the result of a long relationship with *B. glabrata* and exposure to its hormones, is not adversely affected by hormones during the latter phases of its development, as is *M. oregonensis*.

Another example of possible host-stimulated developmental alterations among larval trematodes has been reported by James (1964) and discussed by Cable (1965). James reported that the intramolluscan life cycle stages of the gymnothallid trematode *Paratrema homoeotenum* include a "primary germinal sac" with adult features, including an oral sucker, ventral sucker, pharynx, and bifid caeca, and a "daughter germinal sac" which is unique in that, in addition to the adult features found on the "primary germinal sac," it also possesses a bifurcate tail. The "daughter germinal sacs" increase in size and lose their tails while still within the "primary germinal sac." Further development does not occur until they rupture out of primary sacs. Daughter sacs then continue to develop in one of three possible ways: (1) most produce cercariae and metacercariae; (2) a few produce a second generation of "daughter germinal sacs"; and (3) very occasionally, cercariae, metacercariae, and second-generation "daughter germinal sacs" are produced in the same "daughter germinal sac." These larval stages are found in the haemocoelic spaces of the hepatopancreas and gonad of *Littorina saxatilis tenebrosa*. According to James, the "primary germinal sac" could be interpreted to be a metacercaria; while according to Cable, the "daughter germinal sac" could be considered a cercaria. Thus, the usual sequence of larval stages is reversed in *P. homoeotenum*. Since the usual life history pattern among related gymnothallids includes two molluscan intermediate hosts, both being marine pelecypods (see Stunkard and Uzmann, 1958), Cable has given the following as one possible explanation for this variation: "It may be significant that metacercariae of other gymnophalline species live in loose, even superficial association with their hosts whereas the species that James (1964) described invades the snail to the extent commonly seen in molluscs serving as the first intermediate host of trematodes in general. As a result, that species probably gets a double exposure of the most intimate sort to the tissues and body fluid of mollusks." This, of course, implies that the tissues and body fluids of molluscs may have influenced that unusual developmental sequence. Although in this instance the presumably host-stimulated developmental alterations do not affect the parasite deleteriously, it is conceivable that such changes could in certain instances deter or inhibit delayed polyembryony and thus render the host incompatible.

**Nutrient Requirements**

Available evidence indicates that trematode parasites utilize carbohydrates as their primary energy source. They acquire their carbohydrates in the form of glucose resulting from the degradation of the host's stored glycogen or, if there is no stored glycogen in the vicinity of their natural habitat, they utilize the mollusc's blood sugars (Cheng, 1963b). In addition to sugars, these larvae apparently utilize free amino acids from the mollusc's hemolymph and perhaps even from the surrounding host cells which are lysed or ruptured mechanically.

Lipids, in the form of short-chain fatty acids, are also taken up by germinal sacs, but are primarily stored rather than utilized in cercariae and in certain species in the walls of
germinal sacs. The current belief that these stored fatty acids are not utilized in energy production while within the mollusc's hepatopancreas stems from von Brand's (1931) belief that this environment is essentially anaerobic and hence is not conducive to lipid metabolism. The non-occurrence of aerobic metabolism in sporocysts and in rediae appears to be confirmed by the electron microscopic studies of Bils and Martin (1966), which revealed the absence of mitochondria in sporocyst and redial walls. On the other hand, mitochondria have been demonstrated in the wall of Parorchis acanthus rediae (Rees, 1966), and in the walls of Philophthalmus gralli rediae (Cheng and Hamamoto, unpublished data).

Cheng and Snyder (1962a, b; 1963), by employing histochemistry, arrived at the conclusion that glucose and fatty acids are taken up by sporocysts through their body walls. Electron microscope studies by Bils and Martin (1966) tend to corroborate this with the finding of conspicuous microvilli along the outer surfaces of sporocysts. In the case of rediae, Cheng (1962, 1963c) found that the ingestion of the host's cells is the primary method of nutrient acquisition, although some absorption may occur through the body wall also. This, again, appears to be corroborated by the finding of microvilli on redial walls by Bils and Martin (1966), Rees (1966), and Cheng and Hamamoto (unpubl.). For a detailed account of nutrient acquisition and contents of intramolluscan larval trematodes, see the reviews by Cheng (1963a, 1967).

Relative to the relationship between nutrition and compatibility and incompatibility, it may be asked whether the introduction of germinal sacs to some site within its natural molluscan host, or into a foreign host, where the physico-chemical nature of the host-parasite interphase prevents the uptake of nutrients could cause the parasite to fail to become established. For example, could the destruction of heavily encapsulated germinal sacs in incompatible hosts actually represent, at least in part, death due to starvation?

It is known that the rate of cercarial development is dependent upon the amount of food assimilated by the snail host and upon the number of larvae competing for the available nutritents in the snail, among other factors (Kendall, 1949). It would follow that, even if the host-parasite interphase is favorable for nutritional uptake but nutrients are not sufficiently available as the result of a poorly nourished host or because of competition between a large number of germinal sacs, normal development could not occur—and this would constitute incompatibility.

Lethality to Host

Surprisingly little information is available pertaining to the lethality of trematode larvae to molluscs. Some investigators (Rees, 1931; Kendall, 1964; and James, 1965) have suggested that during certain mollusc-trematode associations death of the host does not occur. Yet Schreiber and Schubert (1949) and Pan (1965), both working with B. glabrata parasitized with S. mansoni, have shown that a high incidence of mortality does occur. In fact, Schreiber and Schubert went as far as to quote a "half life" for parasitized snails. These known mortalities, however, cannot be considered to reflect incompatibility, since the parasites do develop normally and death, as Faust and Hoffman (1934), Schreiber and Schubert (1949), and Pan (1965) have pointed out, has resulted from the rapid multiplication of larvae and mass emergence of cercariae. From the available information, it would appear that the death of molluscs resulting from invasion by "pathogenic" trematodes is extremely rare. No indisputable examples have yet been reported, although Kendall (1950) has shown that Fasciola hepatica does inflict conspicuous deleterious effects on Lymnaea stagnalis, L. palustris, and L. glabra, but not on L. auriculata. The fact that mass mortality seldom occurs could be interpreted to mean that the defense mechanisms of molluscs are highly efficient.

It appears appropriate at this point to interject the following comment. Death of molluscs due to a pathogenic trematode infers extremely severe pathogenicity, a topic which has been reviewed recently (Cheng, 1967). Yet, despite known instances of drastic histopathological alterations in parasitized molluscs caused by trematode larvae, few proven cases of rapid and virulent deaths are known. This should serve as a warning to shellfisheries biologists and molluscan pathologists, who have been known to
draw unwarranted conclusions relative to the lethality of parasites, particularly helminths, based on histopathological studies.

ESCAPE PROCESS

Our present knowledge concerning the passive and/or active mechanisms employed by cercariae while escaping from their molluscan hosts is based primarily on studies carried out on the human-infecting species of schistosomes (see reviews by Probert and Erasmus, 1963; Cheng, 1967), although some information is available on Fasciola hepatica (Kendall and McCullough, 1951), Neodiplostomum intermediate (Pearson, 1961), and Cercaria X (Probert and Erasmus, 1965). All these studies have been concerned with the processes which make possible successful escape, and hence, in a manner of speaking, govern compatibility. On the other hand, if some factor or factors within the mollusc interfere with cercarial escape and thus prevent the parasites from continuing their normal course of development, this factor or factors may contribute to host-incompatibility. In seeking evidence for this hypothetical possibility, one should be cautious in distinguishing between consistent barriers, either structural or physiological, which prevent escape and in so doing endanger the perpetuation of the parasite species, and an occasional accidental arrest of the escape of a few cercariae. Examples of the latter include the report by Cheng and Cooperman (1964) that occasionally an escaping cercaria of Glypthelmins pennsylavienensis may accidentally migrate into the foot musculature of its snail host, Helisoma trivolvis, and become encapsulated, and the report by Pan (1965) that some escaping S. mansoni cercariae do become trapped in the loose vascular connective tissue of A. glabratu and die. Yet, in the latter case the frequency of this event suggests that it is a normal occurrence. If all of the cercariae were thus trapped, one could cite this as an example of incompatibility due to prevention of escape. It is of interest to note that if a similar phenomenon is not found in other mollusc-trematode associations, one might consider B. glabratu as being partially incompatible with S. mansoni as far as escape is concerned. Indeed, available information indicating the incompatibility of different strains of B. glabratu with strains of S. mansoni does suggest that this relationship is not completely free of factors favoring incompatibility.

SUMMARY

Compatibility between miracidia and molluscs may be determined prior to actual contact. In some instances this may be governed by the occurrence of host-specific "host factors" which stimulate and attract the parasite to a compatible host only. There is sufficient evidence to indicate, however, that the attractant need not be host-specific and need not indicate subsequent successful establishment and growth. Furthermore, ambient environmental conditions as well as innate taxes, when such occur, are generally stronger determinants of miracidial migration and behavior than are chemotactic forces. Thus, it is only when the other factors serve to bring miracidia into the immediate vicinity of the mollusc that chemotaxis becomes an effective attractant. There is also evidence which suggests that materials extruded from molluscs may inhibit rather than serve to enhance host-parasite contact.

In the case of miracidia which do not hatch until the eggs are ingested by the mollusc, the physical and chemical factors present in the host's gut can serve as determinants of compatibility or incompatibility.

It is possible that, during the invasion process, both the specificity of the miracidium's lytic secretions and the specificity of substances which stimulate the miracidium to shed its epidermal plates, secrete lytic enzymes, and invaginate its apical papilla could in some instances determine the compatibility of the host, especially if these are prerequisites of successful penetration.

Subsequent to successful invasion, the parasite generally has to reach a suitable site within the mollusc for further development. If this migration is prevented by some tissue(s), such as a basement membrane, incompatibility results. If such a barrier is absent or is overcome, the parasite must still overcome the host's internal defense mechanisms (immunity). From the information available, cellular immunity, both innate and acquired, occurs in molluscs; and it is primarily by the formation of capsules
comprised of leucocytes and/or fibers that incompatible trematode larvae are destroyed.

Since some indirect evidence suggests that substances of host origin, perhaps hormones, can alter the normal developmental pattern of intramolluscan trematode larvae, it is proposed that the absence of growth- and development-stimulating substances or the presence of growth- and development-inhibiting substances may be factors responsible for incompatibility.

Relative to the nutritional requirements of trematode larvae, their availability in the molluscs, as well as deficiencies in nutrients resulting from competition between larvae, could influence the compatibility of the association. Furthermore, the physico-chemical nature of the host-parasite interphase could influence the successful or unsuccessful uptake of nutrients and hence govern compatibility or incompatibility.

Finally, in order that the relationship be considered a completely compatible one, the parasite cannot destroy its host prior to its successful escape or the escape of its germ cell-bearing progeny. Thus, factors of parasite origin which are lethal to the host and factors of host origin which prevent escape must also be considered as determinants of incompatibility.

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The Littoral Sand Budget, Hawaiian Islands

THEODORE CHAMBERLAIN

ABSTRACT: Profile surveys were made across 80 selected Hawaiian beach and nearshore environments at quarterly intervals for one and one-half years during 1962–63. Also 70 additional beaches were measured at less frequent intervals. Using these profiles, supplemented by water-jet borings and measurements from aerial photographs, the total sand volume of each of the major Hawaiian beach systems was computed. The seasonal fluctuations of these volumes were also computed and related to the wave and littoral current regimes.

The volume of littoral sand was found to be considerably less than the volume for many sandy continental areas. About $4.0 \times 10^7$ cu yd of sand is held in beach reservoirs on the seven major islands of the Hawaiian group; most is concentrated on Kauai ($1.4 \times 10^7$ cu yd) and on Oahu ($1.0 \times 10^7$ cu yd). Individual beaches containing more than $1 \times 10^6$ cu yd are Keawanui on Niihau; Hanalei, Polihale-Barking Sands, and Kekaha-Nohili-Bonham on Kauai; Bellows-Waimanalo on Oahu; and Papohaku on Molokai. The beaches on the island of Hawaii hold the smallest volumes of sand.

Seasonal rates of erosion and accretion of beach sand reservoirs were found to be generally on the order of a few tens of cubic yards of sand per linear yard of beach per month. The higher rates were on exposed north and west coasts, with a maximum rate of several hundred cubic yards of sand per linear yard of beach per month recorded for Lumahai Beach, Kauai during 1962–63.

Beaches are not static but are continually changing their composition, structure, and volume—seasonally, yearly, or over longer periods of geologic time. Nor are these beach changes isolated phenomena. Rather, they are related, by a complex series of equilibria, with the rates of sand production, alongshore transport, and loss. Consequently, it is possible to consider a sand beach at any one moment in time to be a sand reservoir connected by certain exchanges of energy with its surrounding environment. Certain of the energy relationships between the beach and its surroundings will bring about a net increase in the volume of the beach: beach accretion. Other relationships will result in a net loss of sand from the beach: beach erosion.

In certain cases there may exist an equilibrium between accretion and erosion so that a constant beach sand volume is maintained. However, with most beaches this equilibrium is continually shifting so that the beach is continually in a state of flux, now accreting, now eroding. These fluctuations in the amount of sand held on the beach are most pronounced between seasons, reflecting the seasonal variations in the amount and types of wave energy that reach the beaches. However, diurnal, semidiurnal, and fortnightly fluctuations in beach sand volumes related to the tides, yearly and multi-yearly fluctuations related to long-period meteorological conditions, and noncyclic fluctuations, such as are caused by tsunami, are also common.

Along any stretch of coast the various factors affecting the amount of sand on the beach and in nearshore waters can be summarized, and, if the coast is in equilibrium (i.e., if a constant littoral sand volume is maintained), these factors can be quantitatively balanced against each other. Coastal streams and rivers, coastal ero-
sion, biological activities, wind, etc., may actively contribute sand; whereas paralic sedimentation (e.g., lagoonal, shallow neritic, transportation of sand into deep water via submarine canyons), the transformation of beach sand into beach rock, and wind are factors that are responsible for the loss of beach sand.

In any one locality certain of these processes may predominate. For example, in the Hawaiian Islands beach sand is primarily acquired through the biological activities of reef organisms, and is primarily lost by paralic sedimentation. Notwithstanding the particular processes involved, if the coast is in equilibrium there must exist a qualitative balance between the rate of sand production or input and the rate of sand loss. Quantitative considerations of these rates and their effects upon the beach and nearshore sand reservoirs give rise to the concept of a littoral sand budget, i.e., a quantitative balance under equilibrium conditions of the rates of change and volumes of beach and nearshore sand. Basically, the littoral sand budget can be divided into three separate parts: sand input, alongshore transport, and loss. However, a fourth consideration—time—must frequently be introduced due to the fact that, although short term rates of input, alongshore transport, and loss may not balance, the coast may yet be in perfect equilibrium over longer periods of time. For an example, high rates of sand input due to heavy flooding of coastal streams may not balance with the loss of nearshore sand over the same period of time, yet the fluctuations of this sand input may be such that over long periods of time the rates of sand input, alongshore transport, and loss are in equilibrium.

Considering beaches and coasts from the viewpoint of such a littoral sand budget, it can be shown that there exist certain stretches or units of coast along which the rates of sand input, alongshore transport, and loss are in equilibrium and between which there is little or no exchange of nearshore sediment. Typically, in the Hawaiian Islands these littoral units or littoral cells are separated by rocky promontories or long stretches of high, nearly vertical sea cliffs around which little or no sand is transported (Fig. 1).

**Discussion**

**Littoral Sand Reservoirs**

Sand-size material, contributed to the littoral sand budget by a variety of agents as discussed above, is transported into the nearshore zone, moves onto and along the beach, and after a rather long and complicated journey within the nearshore zone is finally transported out of that zone into deeper water, blown inland by the wind, or otherwise lost. Various reservoirs of sand therefore exist, corresponding to the various zones or environments through which the sand passes as it progresses toward its final depositional environment. Two types of sand reservoirs are common within the Hawaiian littoral cells: (1) the beach reservoir and (2) the nearshore reservoir, in turn composed of reef channel, reef flat, or river mouth.

**Beach Reservoirs (Comparisons):** Large volumes of sand are found between mean sea level and the upper limit of wave action on two of the seven major islands of the Hawaiian group, while on the other five the total volume is extremely small. Moreover, the average volume of the beach sand reservoir per mile of sandy coastline varies greatly from island to island. The subsurface base of the beach was determined by water-jet probing; essentially it is the contact between the beach and indurated rock or cobbles. The landward limit of the beach was taken as the upper limit of wave action as determined by the beach contact with growing vegetation, sea cliffs, windblown dunes, etc. The seaward edge of the beach is mean water level. As can be seen from Table 1, more than one-third of all beach sand in the Hawaiian Islands is found on the beaches of Kauai, and more than one-fourth, on the beaches of Oahu. Together these two islands hold 61.4% of the total beach sand found in the State of Hawaii.

In order to compare the intensity and/or nature of the littoral processes of the various Hawaiian islands, it is necessary to weigh the total beach sand reservoir of each island by some parameter, such as length of coastline, which in turn can be related to the zone or area over which the littoral processes are active. Table 1 gives the average beach reservoir vol-
ume per mile of total coastline and per mile of sandy coastline. Comparison of these figures shows that a real difference exists between the beach sand reservoirs of the various islands. The northwesternmost islands of Niihau and Kauai have the largest beach sand reservoir per mile of coastline. This large volume of beach sand is reflected in the intensity or magnitude of littoral processes not found on the remaining islands. From Niihau and Kauai there is a general decrease, in a southeasterly direction, in the volume of the beach sand reservoir per mile of coastline. The extremely low values for the island of Hawaii indicate the low intensity of the littoral processes that produce beach sand on that island.

The average volumes of sand contained in the beach reservoirs on the island of Niihau have been computed and are presented in Table 2. The larger reservoirs are found along the northwest coast, whereas the reservoirs along the eastern coast have very little beach sand.

By far the largest sand reservoir on Kauai is at Polihale (Table 3), although those at Hanalei, Lumahai, and Wailua beaches are also fairly large. Generally, the reservoirs are larger to the west and north, and smaller along the southeastern coast. Average beach sand reservoirs computed for the remaining portions of sandy coastline are presented in Table 4.

Table 5 shows that on Oahu the largest reservoirs lie along the eastern coast adjacent to the town of Waimanalo. Other very large volumes of beach sand are located at Kahana, Maili, and Sunset Beach. Average beach sand reservoirs computed for the remaining sections of the coast are presented in Table 6.

On Molokai more than 75% of all of the beach sand is found on the western coast, principally at Papohaku (Table 7). A lesser amount is found on the northern coast in the Moomomi District, and the least on both the
TABLE 1
BEACH SAND RESERVOIRS, HAWAIIAN ISLANDS

<table>
<thead>
<tr>
<th>ISLAND</th>
<th>TOTAL VOLUME 10^8 yd&lt;sup&gt;3&lt;/sup&gt;</th>
<th>MILES OF COASTLINE</th>
<th>VOLUME PER MILE TOTAL COASTLINE 10^8 yd&lt;sup&gt;3&lt;/sup&gt;</th>
<th>VOLUME PER MILE SANDY COASTLINE 10^8 yd&lt;sup&gt;3&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Niihau</td>
<td>3.96</td>
<td>43.0</td>
<td>92.2</td>
<td>208.7</td>
</tr>
<tr>
<td>Kauai</td>
<td>13.96</td>
<td>113.4</td>
<td>123.1</td>
<td>338.9</td>
</tr>
<tr>
<td>Oahu</td>
<td>10.28</td>
<td>129.0*</td>
<td>79.7</td>
<td>204.4</td>
</tr>
<tr>
<td>Molokai</td>
<td>2.95</td>
<td>105.9</td>
<td>27.9</td>
<td>134.9</td>
</tr>
<tr>
<td>Lanai</td>
<td>1.70</td>
<td>52.3</td>
<td>32.4</td>
<td>93.4</td>
</tr>
<tr>
<td>Maui</td>
<td>5.02</td>
<td>158.8</td>
<td>31.6</td>
<td>153.8</td>
</tr>
<tr>
<td>Hawaii</td>
<td>1.68</td>
<td>305.5</td>
<td>5.5</td>
<td>86.5</td>
</tr>
<tr>
<td>Total</td>
<td>39.56</td>
<td>av. 56.0</td>
<td>av. 174.4</td>
<td></td>
</tr>
</tbody>
</table>

* Excluding Pearl Harbor, Sand Island, and parts of Kaneohe Bay.

TABLE 2
BEACH SAND RESERVOIRS, NIIH AU

<table>
<thead>
<tr>
<th>COASTAL ZONE OR BEACH*</th>
<th>SUMMATION OF BEACH LENGTHS (yards)</th>
<th>AVERAGE SAND VOLUME† (10^3 yd&lt;sup&gt;3&lt;/sup&gt;)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Puuikole Pt.–Lehua Landing</td>
<td>1760</td>
<td>70.0</td>
</tr>
<tr>
<td>Lehua Landing–Palikoae</td>
<td>300</td>
<td>6.0</td>
</tr>
<tr>
<td>Palikoae–Keawanui</td>
<td>1760</td>
<td>17.6</td>
</tr>
<tr>
<td>Keawanui</td>
<td>7040</td>
<td>1689.0</td>
</tr>
<tr>
<td>Kaununui Bay</td>
<td>2640</td>
<td>396.0</td>
</tr>
<tr>
<td>Kaununui Bay–Paliuli</td>
<td>3520</td>
<td>140.8</td>
</tr>
<tr>
<td>Paliuli–Nonopapa</td>
<td>2000</td>
<td>360.0</td>
</tr>
<tr>
<td>Nonopapa–Makahauena</td>
<td>2640</td>
<td>211.2</td>
</tr>
<tr>
<td>Kamalino</td>
<td>100</td>
<td>6.0</td>
</tr>
<tr>
<td>Kahaino</td>
<td>100</td>
<td>6.0</td>
</tr>
<tr>
<td>Leahi</td>
<td>100</td>
<td>70.0</td>
</tr>
<tr>
<td>Kawaihoa–Oiamoi</td>
<td>1760</td>
<td>105.6</td>
</tr>
<tr>
<td>Oiamoi–Poonocone</td>
<td>1760</td>
<td>105.6</td>
</tr>
<tr>
<td>Poonocone–Poleho</td>
<td>2640</td>
<td>105.6</td>
</tr>
<tr>
<td>Poleho–Kii</td>
<td>3520</td>
<td>105.6</td>
</tr>
<tr>
<td>Kii–Puukola</td>
<td>1760</td>
<td>105.6</td>
</tr>
</tbody>
</table>

* Listed counterclockwise from northwestern coast of island.
† Volumes obtained from a single set of profiles in 1963, supplemented by aerial photographs and maps.

The largest beach sand reservoirs on Maui (Table 11) are found on the southwestern coast of Haleakala, on the northern coast near Sprecklesville, and along the western coast of West Maui (Table 12). The entire eastern coastal portion of East Maui is nearly lacking in sand.

The beach sand reservoirs are extremely small on the island of Hawaii (Tables 13 and 14); Waipio and Hapuna are the only beaches where the sand volume exceeds 100,000 cubic yards. The northwest section of the island, especially just south of Kawaihau, has the largest reservoirs. Along the flanks of Mauna Loa and Kilauea volcanoes few beaches are present.

NEARSHORE RESERVOIRS: The sand-size particles moving thorugh the littoral sand system may be deposited temporarily in one of several littoral environments other than that of the beach.

Reef Channel. Particles produced by the attrition of reef flora and fauna frequently are transported through a complex series of reef environments before being brought onto the beach, and even after reaching the beach they may be transported back and forth seasonally between the beach and reef before they are finally carried out of the littoral zone into deep water, or blown inland by the wind, or otherwise lost. Any channel or depression across the nearshore zone acts as a trap for this littoral sand.

Around the Hawaiian Islands the fringing
coral reefs are cut by numerous channels, some of which are surge channels that carry the water from the breaking waves up onto the reef flat. Other, often broader channels are frequently sites of old river courses across the reef (Fig. 2). Large volumes of sand are found in these channels. Most of the sand is newly formed material from the adjacent reefs and is in the process of being carried shoreward into the beach system. However, there exist definite sand circulatory patterns on the reefs, and some of the larger channels act as routes for the transportation of beach sand into deep water. Still others of the reef channels during certain seasons supply sand to the beach, and during other seasons receive sand from the beach so that a sand exchange system exists between the channels and the beach.

Notwithstanding the type or direction of movement, the sand found in the nearshore reef channels represents an important sand reservoir, the volume of which fluctuates seasonally,
TABLE 4
BEACH SAND RESERVOIRS, MISCELLANEOUS COASTAL ZONES, KAUAI

<table>
<thead>
<tr>
<th>COASTAL ZONE</th>
<th>SUMMATION OF BEACH LENGTHS (yards)</th>
<th>AVERAGE SAND VOLUME (10^3 \text{yd}^3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kalihiwai</td>
<td>4280</td>
<td>160.0</td>
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* Listed clockwise from northern coast of island.
† Volumes obtained from a single set of profiles in 1963, supplemented by aerial photographs and maps.

yearly, or otherwise, in response to waves and currents. An intimate and complex relationship exists between the various nearshore sand reservoirs and the beach reservoir; in some cases it can be shown that increases in the beach sand volumes are accompanied by decreases in the offshore reef channel reservoirs and vice versa.

The actual volume of the various reef channel reservoirs varies greatly. Surge channels extending up across the front of the reef may have a thickness of from 1 to 4 ft of sand and individual channels may contain several hundreds of cubic yards. Accurate volume measurements involving subsurface probing have shown that the summation of sand channel volumes along the entire front of a typical, small, Hawaiian reef between the depth ranges of —40 to —5 ft MLLW amounts to a sand reservoir of somewhat more than 50,000 cubic yards per linear mile of reef. On a large reef this volume may be nearer 200,000 cubic yards per linear mile.

The largest channels across the reef, some of which are ancient river courses, contain reservoirs of sand that are measured in millions of cubic yards. For example, the sand reservoir of the Halekulani Channel crossing Waikiki Reef, Oahu, has been measured and found to contain nearly 1/2 million cubic yards of sand within the depth range of 0–30 ft MLLW. Accurate measurements including subsurface probing of the sand channel reservoir in Poikai Bay, Oahu, indicate a reservoir volume of between 1 and 2 million cubic yards out to a water depth of 30 ft MLLW.

Reef Flat. There exist numerous shallow depressions on the reef flats surrounding the Hawaiian Islands. Many of these are measured in hundreds or in thousands of square yards, and quite a few are measured in hundreds of thousands of square yards. Most of the sand produced on the reef flat is transported onto the beach by being moved in a series of steps from one of these depressions, or sand pockets, to another. Consequently, the reef flat reservoirs also play an important role in the littoral sand budget.

Most of the sand reservoirs on the reef flat are shallow, sand thickness being measured in feet; individual sand pockets may contain only a few hundred or a few thousand cubic yards of sand. But when the sand pocket volumes are summed over an extensive reef, such as the Sprecklesville Reef, Maui, or the Waimanalo Reef, Oahu, the total indicates a reservoir of several millions of cubic yards of sand per square mile of reef.

These large volumes of sand located near shore and generally in water depths of less than 12 ft are very susceptible to varying wave and current conditions. Under certain wave conditions the rapid rates of accretion of the Hawaiian beaches is entirely due to the avail-
ability of this reef flat reservoir and the rapid transport of sand from it onto the beach.

River Mouth. Sand-size material derived from the erosion of the hinterland is transported by streams and rivers to the ocean. Following initial deposition at the mouth of the streams and rivers, much of the sand is moved along through the littoral system on and off the beach and eventually is carried out into deep water, blown inland, or otherwise lost.

In the Hawaiian Islands the largest river-mouth sand reservoir is off the Waimea River, Kauai. The exact volume of this reservoir is not known, but subsurface probings have shown that over an area of about one square mile off the Waimea River the sand thickness is greater than 20 ft. Consequently, a sand reservoir on the order of $10^7$ cubic yards is indicated.

Smaller river mouth reservoirs are found off several other Hawaii rivers, notably Hanapepe and Hanalei, Kauai.

**Selected Beaches.** Whereas an accurate volume measurement of the total beach sand reservoir for the Hawaiian Islands was fairly easily obtained, similar measurement for the total nearshore sand reservoir was not possible. The difficulty lay in obtaining a sufficient number of submarine measurements, compounded by surf and current conditions that in many localities prevented direct bottom measurements. Consequently, it was possible to measure only portions of the nearshore sand reservoir off certain selected beaches. The integration of these limited data over extended lengths of the coast is prevented by the extreme variability of the size of sand channels and sand pockets. At best the data can be used to indicate the relative vol-

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**TABLE 5**

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* Listed clockwise from northeast coast of island.
† Assumed value.

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*Littoral Sand Budget, Hawaii—Chamberlain*
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<th>COASTAL ZONE*</th>
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* Listed clockwise from northeastern coast of island.
† Volumes obtained from a single set of profiles in 1963, supplemented by aerial photographs and maps.

PACIFIC SCIENCE, Vol. XXII, April 1968

Table 6: Beach Sand Reservoirs, Miscellaneous Coastal Zones, Oahu

In Table 15 the nearshore sand reservoir computed in cubic yards of sand per linear yard of beach is given for 83 selected beaches in the Hawaiian Islands. Since it was impossible to measure this sand volume to a similar water depth off all beaches, the limiting depth of water is also tabulated. In most cases no sand existed seaward of the limiting depth so that the volumes listed represent the total nearshore sand reservoir per linear yard of beach for that particular beach. (In other cases, however, additional volumes of sand exist seaward of the limiting depth so that the volumes in some cases are minimal.)

The largest nearshore sand reservoirs on the island of Kauai are off the major rivers, Waihe, Hanapepe, and Waialua, and in Hanalei and Nawiliwili bays. The total nearshore sand reservoir around the island of Kauai is probably in excess of 25 million cubic yards of sand, i.e., more than twice the total beach sand reservoir for this island.

The largest nearshore sand reservoirs on the island of Oahu are in Kahana and Pokai bays. On this island, the total nearshore reservoir is probably approximately equal to the beach sand reservoir, i.e., 10^7 cubic yards.

Except for the reservoirs off Papohaku and Moomoni, very little nearshore sand exists around the island of Molokai. The total volume may be between 1 and 2 million cubic yards.

Table 7: Beach Sand Reservoirs, Selected Beaches, Molokai

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* Listed clockwise from the northeastern coast of island.
† Assumed value.
TABLE 8
BEACH SAND RESERVOIRS, MISCELLANEOUS COASTAL ZONES, MOLOKAI

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<th>AVERAGE SAND VOLUME† (10^3 yd³)</th>
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<td>72.5</td>
</tr>
<tr>
<td>Hale o Lono–Kapukuwahine</td>
<td>360</td>
<td>14.4</td>
</tr>
<tr>
<td>Kapukuwahine</td>
<td>1275</td>
<td>76.5</td>
</tr>
<tr>
<td>Kapukuwahine–Lauu</td>
<td>1100</td>
<td>66.0</td>
</tr>
<tr>
<td>Kamakaipo–Kaunalu</td>
<td>100</td>
<td>6.0</td>
</tr>
<tr>
<td>Kaunalu</td>
<td>150</td>
<td>12.0</td>
</tr>
<tr>
<td>Kaunalu–Papohaku</td>
<td>300</td>
<td>36.0</td>
</tr>
<tr>
<td>Papohaku</td>
<td>1550</td>
<td>775.0</td>
</tr>
<tr>
<td>Kepuhi</td>
<td>425</td>
<td>106.2</td>
</tr>
<tr>
<td>Kepuhi–Ilio</td>
<td>800</td>
<td>120.0</td>
</tr>
<tr>
<td>Kapalauoa–Kawaaloa</td>
<td>1725</td>
<td>69.0</td>
</tr>
<tr>
<td>Kawaloa</td>
<td>300</td>
<td>45.0</td>
</tr>
<tr>
<td>Moonomi</td>
<td>100</td>
<td>25.0</td>
</tr>
<tr>
<td>Puwahi</td>
<td>950</td>
<td>76.0</td>
</tr>
<tr>
<td>Kalaupapa</td>
<td>600</td>
<td>48.0</td>
</tr>
</tbody>
</table>

* Listed clockwise from northeastern coast of island.
† Volumes obtained from a single set of profiles in 1963, supplemented by aerial photographs and maps.

Around the island of Lanai the nearshore sand reservoirs are also very small. The largest is off Polihua but the total volume probably does not exceed 10^6 cubic yards.

On Maui large nearshore sand reservoirs exist in Hana Bay and off Honokahua and Kihei, and a total nearshore sand reservoir equal to the total beach sand reservoir seems probable, i.e., 5 × 10^6 cubic yards.

On Hawaii there are small nearshore sand reservoirs in Waipio Bay and off Kailua, Hapuna, and Kawaihae, probably not exceeding 10^6 cubic yards.

Seasonal Fluctuations

In tropical latitudes such as the Hawaiian area, the climatic year is not divided into four but rather into two natural meteorological seasons. Winter is well defined by the weakening of the northeast trade winds and the appearance of southwesterly winds. During the summer (April through November), strong trades blow from the eastern and northern quadrants, or transitional wind conditions exist.

During 1962–63 southwesterly or westerly winds dominated the local weather from November 1962 to April 1963 (Fig. 3). The remaining months of these two years, except for January and February, 1962, and December 1963, were exclusively under the influence of northeasterly trade winds.

The seasonal fluctuations of the beach sand reservoir for each of the 76 selected beaches as given in Tables 3, 5, 7, 9, 11, and 13, are summarized by island in Figure 4. Although the selected beaches represented in this figure do not include the entire beach sand reservoir, they are well distributed geographically on each island so that the total accretion or erosion as indicated, while not representing the total magnitude of change for each island, does represent quite accurately the direction of change, i.e., total island accretion or erosion.

On certain of the islands (e.g., Molokai and

TABLE 9
BEACH SAND RESERVOIRS, SELECTED BEACHES, LANAI

<table>
<thead>
<tr>
<th>BEACH*</th>
<th>SAND VOLUME, 10^3 yd³</th>
</tr>
</thead>
<tbody>
<tr>
<td>Halulu</td>
<td>7.7†</td>
</tr>
<tr>
<td>Hauola</td>
<td>18.4</td>
</tr>
<tr>
<td>Hulopoe</td>
<td>77.4</td>
</tr>
<tr>
<td>Polihua</td>
<td>532.8</td>
</tr>
</tbody>
</table>

* Listed clockwise from the northeastern coast of island.
† Assumed value.
TABLE 10
BEACH SAND RESERVOIRS, MISCELLANEOUS COASTAL ZONES, LANAI

<table>
<thead>
<tr>
<th>COASTAL ZONE</th>
<th>SUMMATION OF BEACH LENGTHS (yards)</th>
<th>AVERAGE SAND VOLUME† (yd³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kuahua–Halulu</td>
<td>2300</td>
<td>92.0</td>
</tr>
<tr>
<td>Halekulu–Hauola</td>
<td>5800</td>
<td>232.0</td>
</tr>
<tr>
<td>Haaula–Kapoho</td>
<td>10,700</td>
<td>428.0</td>
</tr>
<tr>
<td>Manele</td>
<td>500</td>
<td>30.0</td>
</tr>
<tr>
<td>Manele–Hulopoe</td>
<td>75</td>
<td>4.5</td>
</tr>
<tr>
<td>Polihau–Hale o Lono</td>
<td>1600</td>
<td>192.0</td>
</tr>
<tr>
<td>Hale o Lono–Kuahut</td>
<td>4800</td>
<td>192.0</td>
</tr>
</tbody>
</table>

* Listed clockwise from northeastern coast of island. † Volumes obtained from a single set of profiles in 1963, supplemented by aerial photographs and maps.

Lanai), where the distribution of the beaches is skewed toward one particular area, the fluctuations of the total beach reservoir reflect quite clearly the fluctuating wind, wave, and current conditions. However, on other islands (e.g., Kauai and Oahu) with nearly 360-degree distribution of beaches, erosion of the beaches along one coast may be accompanied by accretion of the beaches on the opposite side of the island due to the sheltering effects of the island itself. Under these conditions it is not possible to deduce the relationship between the beach reservoir and the meteorological and oceanographic conditions from the total island beach reservoir fluctuations. Individual beach sand reservoir changes must be studied.

RATES OF ACCRETION AND EROSION IN BEACH SAND RESERVOIRS: As can be seen from Table 16, there are several beaches on Kauai, notably Lumahai, where the rates of beach erosion and accretion are on the order of several hundreds of cubic yards of sand per linear yard of beach per month.

When the data are grouped according to island sectors, it can be seen that the effects of the winter storms are not the same in all island sectors (Fig. 5). Under Kona (southwesterly wind) conditions the northern beaches rapidly erode, but with the cessation of the westerly winds and the start of the northeast trades these same beaches rapidly accrete. The opposite is true of the beaches in the southern sector. With the commencement of winter storms, Polihale, Kekaha, Waimea, and the

TABLE 11
BEACH SAND RESERVOIRS, SELECTED BEACHES, MAUI

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Hana</td>
<td>23.8</td>
<td>16.3</td>
<td>22.6</td>
<td>19.6</td>
<td>18.2</td>
<td>23.1</td>
<td>20.6</td>
</tr>
<tr>
<td>Hamoa</td>
<td>32.3</td>
<td>48.6</td>
<td>47.0</td>
<td>32.3</td>
<td>31.0</td>
<td>43.6</td>
<td>39.1</td>
</tr>
<tr>
<td>Puu Olai</td>
<td>366.3</td>
<td>364.1</td>
<td>365.2</td>
<td>526.9</td>
<td>408.1</td>
<td>364.1</td>
<td>399.1</td>
</tr>
<tr>
<td>Makana</td>
<td>12.3</td>
<td>23.0</td>
<td>4.3</td>
<td>9.6</td>
<td>10.9</td>
<td>7.6</td>
<td>11.3</td>
</tr>
<tr>
<td>Keawakapu</td>
<td>44.1</td>
<td>52.2</td>
<td>60.3</td>
<td>10.8</td>
<td>48.6</td>
<td>63.0</td>
<td>46.5</td>
</tr>
<tr>
<td>Kalam</td>
<td>116.4</td>
<td>109.3</td>
<td>92.6</td>
<td>95.0</td>
<td>90.2</td>
<td>104.5</td>
<td>101.3</td>
</tr>
<tr>
<td>Kihei</td>
<td>294.2</td>
<td>217.9</td>
<td>188.0</td>
<td>118.3</td>
<td>226.1</td>
<td>217.9</td>
<td>210.4</td>
</tr>
<tr>
<td>Maalaea</td>
<td>250.6</td>
<td>226.0</td>
<td>191.8</td>
<td>231.2</td>
<td>194.5</td>
<td>248.9</td>
<td>232.8</td>
</tr>
<tr>
<td>Olowalu</td>
<td>264.0</td>
<td>221.8</td>
<td>209.4</td>
<td>262.2</td>
<td>169.0</td>
<td>213.0</td>
<td>225.2</td>
</tr>
<tr>
<td>Makila</td>
<td>2.4</td>
<td>2.4</td>
<td>2.2</td>
<td>1.6</td>
<td>1.6</td>
<td>4.6</td>
<td>2.5</td>
</tr>
<tr>
<td>Hanakao</td>
<td>85.5</td>
<td>34.5</td>
<td>25.5</td>
<td>43.5</td>
<td>22.5</td>
<td>30.0</td>
<td>40.3</td>
</tr>
<tr>
<td>Kaanapali</td>
<td>92.0</td>
<td>106.5</td>
<td>101.2</td>
<td>92.0</td>
<td>106.5</td>
<td>117.9</td>
<td>102.7</td>
</tr>
<tr>
<td>Napili</td>
<td>9.8</td>
<td>4.6</td>
<td>7.4</td>
<td>9.8</td>
<td>6.2</td>
<td>8.8</td>
<td>8.0</td>
</tr>
<tr>
<td>Fleming’s</td>
<td>53.5</td>
<td>66.5</td>
<td>71.5</td>
<td>57.3</td>
<td>82.5</td>
<td>59.5</td>
<td>65.2</td>
</tr>
<tr>
<td>Honokaa</td>
<td>31.8</td>
<td>45.2</td>
<td>48.6</td>
<td>48.6</td>
<td>46.9</td>
<td>46.9</td>
<td>44.7</td>
</tr>
<tr>
<td>Wai Paoo Kaio</td>
<td>104.0</td>
<td>123.4</td>
<td>76.6</td>
<td>104.0</td>
<td>92.9</td>
<td>84.0</td>
<td>97.5</td>
</tr>
<tr>
<td>Kahului Harbor</td>
<td>244.7</td>
<td>202.2</td>
<td>243.2</td>
<td>326.8</td>
<td>252.3</td>
<td>310.1</td>
<td>263.2</td>
</tr>
<tr>
<td>Papaula</td>
<td>148.4</td>
<td>176.4</td>
<td>165.9</td>
<td>125.3</td>
<td>149.1</td>
<td>129.5</td>
<td>149.1</td>
</tr>
<tr>
<td>Paia</td>
<td>44.2</td>
<td>39.8</td>
<td>44.2</td>
<td>36.8</td>
<td>42.0</td>
<td>53.7</td>
<td>43.0</td>
</tr>
</tbody>
</table>

* Listed clockwise from eastern coast of island. † Assumed value.
TABLE 12
Beach Sand Reservoirs, Miscellaneous Coastal Zones, Maui

<table>
<thead>
<tr>
<th>COASTAL ZONE*</th>
<th>SUMMATION OF BEACH LENGTH (yards)</th>
<th>AVERAGE SAND VOLUME† (10³ yd³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Opana–Hana</td>
<td>1300</td>
<td>52.0</td>
</tr>
<tr>
<td>Hana–Hamoa</td>
<td>600</td>
<td>54.0</td>
</tr>
<tr>
<td>Hamoa–Puu Olai</td>
<td>1100</td>
<td>44.0</td>
</tr>
<tr>
<td>Puu Olai–Makena</td>
<td>110</td>
<td>9.9</td>
</tr>
<tr>
<td>Keawakapu–Kalama</td>
<td>1550</td>
<td>139.5</td>
</tr>
<tr>
<td>Waiopulani–Maalaea</td>
<td>2724</td>
<td>408.6</td>
</tr>
<tr>
<td>Maalaea–Papawai</td>
<td>150</td>
<td>6.0</td>
</tr>
<tr>
<td>Papawai–Olowalu</td>
<td>1420</td>
<td>85.2</td>
</tr>
<tr>
<td>Olowalu–Launiupoko</td>
<td>1100</td>
<td>99.0</td>
</tr>
<tr>
<td>Launiupoko–Hahakea</td>
<td>4620</td>
<td>554.4</td>
</tr>
<tr>
<td>Hahakea–Hanakao</td>
<td>1300</td>
<td>90.0</td>
</tr>
<tr>
<td>Kaanapali–Napili</td>
<td>5300</td>
<td>477.0</td>
</tr>
<tr>
<td>Fleming’s–Honokahua</td>
<td>385</td>
<td>34.6</td>
</tr>
<tr>
<td>Waiee–Waiee Paiko Kaio</td>
<td>2830</td>
<td>113.2</td>
</tr>
<tr>
<td>Wai Paiko Kaio–Kahului</td>
<td>2400</td>
<td>141.0</td>
</tr>
<tr>
<td>Kahului–Sprecksville</td>
<td>2100</td>
<td>252.0</td>
</tr>
<tr>
<td>Sprecksville–Paia</td>
<td>1950</td>
<td>234.0</td>
</tr>
<tr>
<td>Paia–Opana</td>
<td>650</td>
<td>78.0</td>
</tr>
</tbody>
</table>

* Listed clockwise from northern coast of island.† Volumes obtained from a single set of profiles in 1963, supplemented by aerial photographs and maps.

Other beaches along the southwestern and southern coast begin to accrete, and with the return of the northeast trades they undergo erosion. The behavior of the eastern beaches is not as clear; during the duration of the study they were generally eroding, but the data are incomplete.

When the rates of accretion and erosion of 28 Oahu beaches (Table 17) were grouped into island sectors, the seasonal variation in the beach sand reservoirs was readily apparent (Fig. 6). With the commencement of winter Kona storms, the western beaches (leeward with regard to the northeast trades) erode rapidly. At the same time the beaches on the eastern side of Oahu accrete. With the cessation of the westerly storms and the return of the northeast trades, the process reverses. The northern beaches follow the same pattern as the windward ones, accreting under Kona conditions and eroding under normal trade wind conditions.

On Molokai, extremely rapid rates of change were measured at Kawaiola and Papohaku (Table 18). Because nearly the entire beach sand reservoir is concentrated along the western sector of Molokai, the total Molokai beach reservoir fluctuates in a manner similar to the western sector reservoirs of Oahu and Kauai. With the commencement of Kona storms the Molokai beaches erode, and, during the periods of northeast winds and waves, they accrete (Fig. 4).

On Lanai, low rates of change are indicated, except possibly at Polihua (see Table 19). Because the major beach reservoirs are on the western end of Lanai, the Lanai beaches also fluctuate in phase with those of Molokai and of the western sectors of Oahu and Kauai. With the commencement of Kona conditions, erosion occurs. Under the northeastern winds and waves the beaches accrete (Fig. 4).

TABLE 13
Beach Sand Reservoirs, Selected Beaches, Hawaii

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Waipio</td>
<td>372.3</td>
<td>198.0</td>
<td>120.1</td>
<td>169.0</td>
<td>242.9</td>
<td>71.3</td>
<td>195.6</td>
</tr>
<tr>
<td>Hilo</td>
<td>6.5†</td>
<td>4.0</td>
<td>4.5</td>
<td>5.5</td>
<td>6.5</td>
<td>5.5</td>
<td>5.4</td>
</tr>
<tr>
<td>Kaimu</td>
<td>16.0†</td>
<td>11.0</td>
<td>11.0</td>
<td>6.3</td>
<td>16.0</td>
<td>14.0</td>
<td>10.9</td>
</tr>
<tr>
<td>Punalau</td>
<td>8.8†</td>
<td>9.8</td>
<td>9.6</td>
<td>9.0</td>
<td>8.8</td>
<td>10.1</td>
<td>9.4</td>
</tr>
<tr>
<td>Hookena</td>
<td>15.0†</td>
<td>17.8</td>
<td>17.6</td>
<td>15.4</td>
<td>15.0</td>
<td>14.3</td>
<td>15.9</td>
</tr>
<tr>
<td>Kealakekua</td>
<td>3.5</td>
<td>3.5</td>
<td>2.3</td>
<td>1.4</td>
<td>1.6</td>
<td>1.9</td>
<td>2.4</td>
</tr>
<tr>
<td>Disappearing</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sands</td>
<td>1.8</td>
<td>3.8</td>
<td>3.4</td>
<td>0.8</td>
<td>0.7</td>
<td>2.2</td>
<td>2.1</td>
</tr>
<tr>
<td>Haruna</td>
<td>131.5</td>
<td>127.0</td>
<td>104.0</td>
<td>102.5</td>
<td>89.0</td>
<td>129.5</td>
<td>113.9</td>
</tr>
<tr>
<td>Kawaihae</td>
<td>4.6</td>
<td>4.1</td>
<td>4.5</td>
<td>4.1</td>
<td>4.1</td>
<td>3.4</td>
<td>4.1</td>
</tr>
</tbody>
</table>

* Listed clockwise from northern coast of island.† Assumed value.
TABLE 14
BEACH SAND RESERVOIRS, MISCELLANEOUS COASTAL ZONES, HAWAII

<table>
<thead>
<tr>
<th>COASTAL ZONE</th>
<th>SUMMATION OF BEACH LENGTHS (yards)</th>
<th>AVERAGE SAND VOLUME† (10^3 yd³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upolu–Pololu</td>
<td>100</td>
<td>12.0</td>
</tr>
<tr>
<td>Pololu</td>
<td>525</td>
<td>63.0</td>
</tr>
<tr>
<td>Pololu–Waipio</td>
<td>515</td>
<td>61.8</td>
</tr>
<tr>
<td>Hilo–Kaimu</td>
<td>300</td>
<td>18.0</td>
</tr>
<tr>
<td>Kaimu–Punalu</td>
<td>400</td>
<td>16.0</td>
</tr>
<tr>
<td>Punalu–Hookena</td>
<td>1000</td>
<td>120.0</td>
</tr>
<tr>
<td>Hookena–Na poopoo</td>
<td>30</td>
<td>2.4</td>
</tr>
<tr>
<td>Kealakekua–Disappearing Sands</td>
<td>200</td>
<td>24.0</td>
</tr>
<tr>
<td>Disappearing Sands–Hapuna</td>
<td>5500</td>
<td>825.0</td>
</tr>
<tr>
<td>Hapuna–Kawaihae</td>
<td>500</td>
<td>75.0</td>
</tr>
</tbody>
</table>

* Listed clockwise from northern coast of island.
† Volumes obtained from a single set of profiles in 1965, supplemented by aerial photographs and maps.

On Maui, rates of change are low, measured in a few cubic yards of sand per linear yard of beach per month (Table 20). Whereas most of the other Hawaiian islands are directly exposed to the waves generated by the southerly and westerly winds, Maui is protected in that quarter by the islands of Kahoolawe and Lanai, and a little to the northwest, by Molokai. Consequently, the refraction of waves around these obstacles, in addition to the direction of wave approach, plays an important part in determining the amount of energy reaching the coast. Because of this consideration the fluctuations of the various beach sand reservoirs do not show any simple relationship to the gross meteorological spectrum detailed in Figure 3. Relationships undoubtedly exist—since the seasonal volumes of the total beach reservoir show marked fluctuations, accreting during the winter storm and subsequently eroding under northwesterly winds and waves (Fig. 4)—but the exact nature of this fluctuation is not clear.

On Hawaii, rates are extremely low with the exception of Hapuna and Disappearing Sands (Table 21). But although the data are scattered and the total sand reservoir is low (lowest of all the islands) it is still possible to discern a pattern of behavior—similar to that for the western beaches of Oahu and Kauai—for Hapuna, Kawaihae, Kailua, and other western beaches. On the other hand during the winter storms of 1962–63, Waipio Beach accreted at the rate of about 9 cubic yards of sand per linear yard of beach per month, and, with cessation of the westerly winds and the com-
**TABLE 15**

**Nearshore Sand Reservoirs, Selected Beaches, Hawaiian Islands**

<table>
<thead>
<tr>
<th>Beach</th>
<th>Limiting Depth of Volume Computed (feet)</th>
<th>CU YD of Sand Per Linear YD of Beach*</th>
<th>Beach</th>
<th>Limiting Depth of Volume Computed (feet)</th>
<th>CU YD of Sand Per Linear YD of Beach*</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>KAUAI</strong></td>
<td></td>
<td></td>
<td><strong>MOLOKAI</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kalihiwai</td>
<td>30</td>
<td>1011</td>
<td>Halawa</td>
<td>12</td>
<td>31</td>
</tr>
<tr>
<td>Anahola</td>
<td>30</td>
<td>762</td>
<td>Kana</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Kapaa</td>
<td>6</td>
<td>16</td>
<td>Oneali</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td>Waialua</td>
<td>35</td>
<td>1092</td>
<td>Kapukuwahine</td>
<td>33</td>
<td>17</td>
</tr>
<tr>
<td>Nawiliwili</td>
<td>45</td>
<td>2674</td>
<td>Kamakaipo</td>
<td>10</td>
<td>0</td>
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* Volumes obtained from aerial photographs, seasonal profiles, and water-jet probings.
Fig. 4. Seasonal fluctuations in beach sand reservoirs, selected beaches, Hawaiian Islands.
### TABLE 16
**Rates of Accretion and Erosion on Selected Beaches, Kauai**

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* Rates of accretion (+) and erosion (−) in cubic yards of sand/yard of beach/month.
† No data.

### TABLE 17
**Rates of Accretion and Erosion, Selected Beaches, Oahu**

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* Rates of accretion (+) and erosion (−) in cubic yards of sand/yard of beach/month.
† No data.
### TABLE 18
**Rates of Accretion and Erosion, Selected Beaches, Molokai***

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</tbody>
</table>

* Rates of accretion (+) and erosion (−) in cubic yards of sand/yard of beach/month.
† No data.

### TABLE 19
**Rates of Accretion and Erosion, Selected Beaches, Lanai***

<table>
<thead>
<tr>
<th></th>
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</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(yards)</td>
<td>(3 mos.)</td>
<td>(3 mos.)</td>
<td>(4 mos.)</td>
</tr>
<tr>
<td>Halulu</td>
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<td>†</td>
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<tr>
<td>Hauola</td>
<td>400</td>
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<td>Polihua</td>
<td>1600</td>
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</table>

* Rates of accretion (+) and erosion (−) in cubic yards of sand/yard of beach/month.
† No data.

### TABLE 20
**Rates of Accretion and Erosion, Selected Beaches, Maui***

<table>
<thead>
<tr>
<th></th>
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<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>(yards)</td>
<td>(2 mos.)</td>
<td>(3 mos.)</td>
<td>(5 mos.)</td>
<td>(4 mos.)</td>
<td>(3 mos.)</td>
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<td>+0.3</td>
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<td>-27.0</td>
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<td>Makena</td>
<td>333</td>
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<td>+3.2</td>
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<tr>
<td>Keawakapu</td>
<td>900</td>
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<td>+3.0</td>
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<td>+10.5</td>
<td>+5.3</td>
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<td>Kalama</td>
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<tr>
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<td>-6.7</td>
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<td>+6.0</td>
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<td>+2.4</td>
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<td>+8.0</td>
</tr>
<tr>
<td>Napili</td>
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<td>+15.0</td>
<td>+15.3</td>
</tr>
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<td>Fleming's</td>
<td>200</td>
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<td>+2.4</td>
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<tr>
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<td>-13.3</td>
</tr>
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<td>Wai Paoko Kaio</td>
<td>1675</td>
<td>+4.0</td>
<td>+0.6</td>
<td>0</td>
<td>-0.2</td>
<td>0</td>
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<tr>
<td>Kahului Harbor</td>
<td>525</td>
<td>†</td>
<td>-29.6</td>
<td>+10.4</td>
<td>-5.2</td>
<td>-5.7</td>
</tr>
<tr>
<td>Kahului Harbor</td>
<td>1520</td>
<td>-14.0</td>
<td>+9.0</td>
<td>+11.0</td>
<td>-12.2</td>
<td>+12.7</td>
</tr>
<tr>
<td>Papaula</td>
<td>700</td>
<td>+20.0</td>
<td>-5.0</td>
<td>-11.6</td>
<td>+8.5</td>
<td>-9.3</td>
</tr>
<tr>
<td>Paia</td>
<td>433</td>
<td>-5.0</td>
<td>+3.3</td>
<td>-3.4</td>
<td>+3.0</td>
<td>+9.0</td>
</tr>
</tbody>
</table>

* Rates of accretion (+) and erosion (−) in cubic yards of sand/yard of beach/month.
† No data.
mencement of the northeast trades, began to erode.

**Littoral Transport**

The organic sand-size constituents of the Hawaiian littoral sands are produced across the entire width of the reef and are transported landward by series of tortuous channels across reef flats, and by depressions or pockets on the reefs themselves. On the beach and in nearshore waters they are mixed with inorganic terrigenous particles and moved along or on and off shore in response to waves and currents.

The lateral or alongshore transport of sand is limited, and alongshore transport distances of less than a few miles are the rule except in a few very cases, such as along the Manu Coastal Plain of southern Kauai, parts of southwestern Oahu, and the western coast of Molokai. Here the total volume of sand moving past a single point on the beach is appreciable, and the volume has been estimated by the U. S. Army Corps of Engineers to be approximately 20,000 cubic yards per year. But it is more likely that in most areas of the Hawaii coasts the alongshore transport is not even one-tenth this amount. Littoral cells generally are small and bounded by numerous rocky points and cliffs, and, as evidenced by the distribution of sand bodies within the cells and by underwater observations at the cell boundaries, very little sand escapes around the headlands and promontories that bound the cells.

Evidence indicates that within the littoral cells, however, there is an appreciable littoral transport of sand perpendicular to the coast. Our measurements show that several thousands to several tens of thousands of cubic yards of sand per mile of coastline are continually in motion, either moving on shore or off shore, as shown by rates of erosion and accretion, depending upon wave and current conditions. For example, during the Kona storms of the winter of 1962–63 nearly 2 million cubic yards of sand were eroded from the beaches between Pearl Harbor and Kaena Point, Oahu—an average of 62,000 cubic yards per mile of coastline. During the following spring and summer, 1.8 million cubic yards of sand were transported back onto those same beaches, or an average of 55,000 cubic yards of sand per mile of coast.

On the eastern coast of Oahu between Kahuku Point and Makapuu Head, more than 500,000 cubic yards of sand were eroded from the beaches during March, April, and May 1963, or an average of 10,000 cubic yards transported per mile of coast. During the period just prior to this erosion (November 1962–March 1963) 443,000 cubic yards were added to the same beaches, or more than 9,000 cubic yards transported per mile of coast. Similar rates of littoral transport were measured for the northern Oahu beaches.

For the transport of 50- or 60-thousand cubic yards of sand per mile of coast during a 2- or
3-month period, certain particular wave conditions are necessary. The commencement of steep Kona waves along the western sectors of the various Hawaiian islands activates beach erosion. When these waves cease running, the western beaches accrete. Accretion usually is accompanied by Southern Swell or near-quiescent conditions.

---

3 See Appendix, Hawaiian Wave Types.
CONCLUSIONS

1. Much of the littoral sand found around the Hawaiian Islands is held on the beach as a beach sand reservoir. The larger individual beaches may contain $10^6$ cu yd of sand between mean sea level and the landward edge of the beach. A more average volume for a typical Hawaiian beach is approximately $10^6$ cu yd. The largest beach reservoirs are Papohaku, Molokai ($10^6$ cu yd), Polihua, Lanai ($5 \times 10^5$ cu yd), and Polihale, Kauai ($3 \times 10^6$ cu yd).

2. More beach sand exists on the island of Kauai than on any other Hawaiian island ($1.4 \times 10^7$ cu yd). Oahu has the next largest total beach sand reservoir ($10^7$ cu yd). The average volume of the beach sand reservoirs...
per mile of coast for these two islands is $1.2 \times 10^6$ cu yd and $0.8 \times 10^5$ cu yd, respectively. The island of Hawaii has the smallest total beach sand reservoir ($1.6 \times 10^6$ cu yd) and the smallest volume per mile of coastline ($5.5 \times 10^6$ cu yd).

3. Large volumes of sand are found in the nearshore zone either on the reef flats in sand pockets and depressions, or in sand channels that cut across the reef, or in large sand deposits off the mouths of coastal streams and rivers. For a small reef area, measurements have been made showing that this nearshore sand reservoir out to a depth of -40 ft MLLW is on the order of $5 \times 10^4$ cu yd of sand per mile of coast. Within a similar depth range along coastal areas with large nearshore sand channels, volumes for the nearshore sand reservoir of $10^6$ cu yd of sand per mile of coast have been measured.

4. Seasonal fluctuations in the beach sand reservoir are very pronounced. Beach volume rates of change at several tens of cubic yards of sand per linear yard of coast per month have commonly been measured. Rates of change of up to $10^2$ cu yd of sand per linear yard of coast per month are not uncommon. During 1962–63 the highest beach volume rates of change occurred on the northern coast of Kauai, the western coast of Oahu, and the western coast of Molokai.

5. Fluctuations in the beach sand reservoir volume are particular for various sectors of the various islands, and are correlated with the amount and type of wave energy that reaches the beaches. Those beaches opening to westward are eroded upon the commencement of the westerly (winter) winds due to the arrival of the steep, high Kona waves commonly associated with those winds. During the summer period of northeasterly winds and waves, these beaches accrete. Beaches lying on the eastern or windward sides of the Hawaiian Islands are completely dependent upon the Northeast Trade Swell, and their beach sand volumes fluctuate accordingly. When the strength of the Northeast Trade Swell diminishes, as during the development of westerly winds, the eastern beaches accrete. During steep Northeast Trade Swell or North Pacific Swell these same beaches undergo rapid erosion.

6. The following data appear pertinent to the quantitative balancing of the littoral sand budget along the coasts of the Hawaiian Islands:

a. LITTORAL SAND SOURCES. An average sand contribution to an Hawaiian littoral cell may be $2-5 \times 10^5$ cu yd per mile of coast per year. Depending upon the locality, the following rates are applicable:

(1) Stream runoff. For Waimea, Kauai, perhaps $2.5 \times 10^4$ cu yd per year; for other Hawaiian streams, much less.

(2) Biological activity. No direct measurements; from consideration of littoral transport rates, an average of $1-5 \times 10^3$ cu yd of sand per mile of coast per year for well-developed reef areas.

(3) Coastal erosion. Locally, $10^2-10^3$ cu yd of sand per mile of coast per year.


b. LITTORAL TRANSPORT RATES

(1) Alongshore. Average: $2 \times 10^4$ cu yd per year. Locally, possibly as high as $10^4$ cu yd per year.

(2) Normal to shore. Measured values of $2 \times 10^4$ cu yd per mile of coast per month are common. Average is probably $5 \times 10^3$ cu yd per mile of coast per month.

c. LITTORAL SAND LOSSES

(1) Paralic sedimentation.

(a) Nearshore. Average, perhaps $2 \times 10^6$ cu yd of beach sand per mile of coast per year (attributional products of the beach sand: silt and very fine sand).

(b) Coastal progradation. Locally, $5 \times 10^6$ cu yd per year; average, $10^3$ cu yd per mile of coast per year.

(2) Wind. Locally, high rates of loss, perhaps $2 \times 10^3$ cu yd per mile of coast per year. On the leeward side, loss negligible.

(3) Beachrock formation. Small, perhaps $10^2$ cu yd per mile of coast per year.

7. To balance the littoral sand budget, the estimated average sand contribution within each littoral cell of $2-5 \times 10^3$ cu yd of sand per mile of coast per year must be balanced by the yearly loss from the littoral cell due to paralic sedimentation, wind, or beachrock formation. Rates of alongshore transport may also equal these rates if the alongshore-transported sand is destined to be removed from the littoral...
cell. The measured high rates of littoral transport normal to the beach \((2 \times 10^4\) cu yd of sand per mile of sandy coast per month) represent within-cell transport of an intermittent nature.

8. There is a definite decrease in the general intensity and magnitude of the littoral processes throughout the Hawaiian Islands from the northwest to the southeast. Both the absolute values of the littoral sand reservoirs and the rates of change of those reservoirs decrease continuously from Kauai to Hawaii. These phenomena can be partially explained by the increasing youth of the islands to the southeast and consequently the better development of reef platforms and fringing reefs on the older islands to the northwest. A larger reef structure would allow a greater biological production of sand and could account for the greater volumes of the sand reservoirs on the older islands and for the progradation of the shorelines to the northwest. Real differences may also exist in the total amount of wave energy reaching the individual Hawaiian islands.

APPENDIX
HAWAIIAN WAVE TYPES

Almost all of the energy that is available along the coasts of the Hawaiian Islands for deforming beaches and transporting sediment arrives in the form of ocean waves. These waves are generated in all parts of the Pacific Basin, some even in the South Indian Ocean, and, after a complex history, they arrive in the Hawaiian Islands exhibiting a wide variety of heights, lengths, periods, and velocities. At any one time several generating areas may be supplying waves simultaneously, and this consideration along with the seasonal activity of certain generating areas, the interaction of various wave trains, the attenuation of waves over long distances, and the effect of local winds and waves on distantly generated waves, all result in a very complex wave pattern along the coasts of the Hawaiian Islands.

It is suggested from a study of available wind and wave data that the entire yearly wave spectrum in the Hawaiian Islands can be represented by a few generalized wave types, typified by a specific range of wave heights, periods, and directions of approach (Fig. A-1).

1. Northeast Trade Wave. These waves may be present throughout most of the year, but are largest between April and November when they usually dominate the local wave spectrum. They result from the strong trade winds blowing out of the northeast quadrant over long fetches of open ocean. These waves typically have periods of from 5 to 8 seconds, and heights of between 4 and 12 ft. The direction of approach may vary from north through southeast, but the most frequent direction of approach is either from the northeast or from the east. Generally, northeast trade waves are present from 90 to 95% of the time during the summer and from 55 to 65% of the time in the winter months (Marine Advisers, 1963 and 1964; Moberly and Chamberlain, 1964).

2. Southern Swell. During the winter season in the southern hemisphere (the summer season in the Hawaiian Islands) strong winds blowing over long fetches produce very large waves in the region adjacent to Australia, Antarctica, and in the southern Indian Ocean. These waves, after traveling distances measured in thousands of miles, arrive in the Hawaiian Islands as low, long-period waves from the southern quadrant. Typically, Southern Swell can be identified along the Hawaiian coasts because of its low height (generally, 1–4 ft) and long period (generally, 14–22 seconds). The direction of approach is from the southern quadrant (Snodgrass et al., 1966). In a typical year, Southern Swell arrives in the Hawaiian Islands during 53% of the time, usually during the months April through October.

3. Kona storm wave. Kona storm waves are generated by the interim winds associated with local fronts or Hawaiian lows of extra-tropical origin, as discussed above under meteorological considerations. These waves are neither frequent nor consistent, as they are associated with erratic westerly winds. However, since these waves may develop to a large size and may approach the Hawaiian Islands in a direction opposite to that of the normal wind and wave regime, they are extremely important in relation to beach accretion and erosion and to nearshore water circulation. Kona storm waves may approach the Hawaiian Islands from any direction between the southeast and the west, but the larger waves are usually from the southwest.
Commonly, periods range from 8 to 10 seconds, and heights from 10 to 15 ft. In a typical year, Kona storm waves may be arriving in the Hawaiian Islands during 9.3% of the time, usually during the winter months.

4. North Pacific Swell. Waves produced by storms in the Aleutian area and by mid-latitude lows may arrive in the Hawaiian area throughout the year, but they are largest and most numerous during the period October through May. They may approach from the northwest, north, or northeast, and typically have periods of about 10–15 seconds and heights of 8–14 ft. Some of the largest waves reaching the Hawaiian Islands are of this type.

In addition to the above four representative
wave types into which the total yearly wave spectrum can be conveniently broken, there exist other wave types which are too difficult to identify or are insignificant to the nearshore zone and beaches, either because of their small magnitude or because of their infrequent occurrence. Foremost of these are Typhoon Waves, produced in the equatorial and southern latitudes during the passage of tropical storms. Usually, these waves approach from the southeast through the southwest and are most likely to occur in August and September.

ACKNOWLEDGMENTS

The author is indebted to the many field assistants employed on the Shoreline Project of the Hawaii Institute of Geophysics, of which this littoral study was a part, and especially to its director, Dr. Ralph Moberly.

The editorial assistance rendered by Mrs. Ethel McAfee in the revision of this paper in preparation for formal publication is gratefully acknowledged.

REFERENCES

A Preliminary Phytochemical Survey in the British Solomon Islands

G. C. Morrison¹

During 1964 and 1965, while the author was engaged on a project at Honiara, capital of the British Solomon Islands, the opportunity was taken to carry out a preliminary survey of the flora for the presence of alkaloids and saponins. The Forestry Department at Honiara is actively engaged in establishing a herbarium, but all the specimens collected for the herbarium are placed in ethanol. Such specimens are of no value for chemical tests.

It was necessary, therefore, for the author to collect plant material for this survey. Most of this material came from the main island of Guadalcanal. A sample of most of the specimens collected was lodged with the Herbarium at Honiara under the author’s name and collection number. This number is listed in the Table of Results, so that any interested person may obtain, by application to the Chief Forestry Officer, Honiara, verification of the genus and species and the date and place of collection.

The author is indebted to Dr. T. C. Whitmore, Forest Botanist, and Mr. G. Dennis, Herbarium Officer, both of the Forestry Department, Honiara, B.S.I.P., for their assistance in the problems of nomenclature, and to Mr. J. Berry of Honiara, who introduced him to jungle trails.

Preliminary Testing

Prior to departure from Sydney, some preliminary work was carried out on Australian flora to check the methods of extraction and the precipitating reagents for spot-testing. Following suggestions by Henry (1929), chopped-up plant tissue was extracted with mildly alkaline ether, petrol ether, chloroform, and ethanol, and also with Prollius fluid and hydrochloric acid (1% aqueous).

Of these solvents hydrochloric acid gave most consistently the best concentration of alkaloid. It also had the great advantage of simplicity for field laboratory work, and so the decision was made to use this solvent exclusively. Perhaps something was lost in so doing, but it is noted that Swanholm et al. (1960) state that the “information obtained by digestion with Prollius fluid appeared insufficient to warrant continued use.”

Visual estimation of the amount of precipitate formed from the extract by a reagent seemed to be the most suitable method for field work. This method was used by Webb (1949) and Swanholm et al. (1959). A review of these works, and of those of Henry (1929) and Bamford (1947), indicated that some alkaloids do not precipitate with some reagents. For example, betaine and caffeine do not show a precipitate with Mayer’s reagent. Moreover, because no one reagent is specific for alkaloids, it was decided to use a selection of reagents, seven in all. While this is a greater number than is usually employed for such testing, the extra work involved was negligible.

The following reagents were chosen: Mayer’s (potassio-mercuric iodide), Dragendorff’s (bismuth-potassium iodide), Hager’s (picric acid, 1% aqueous), Wagner’s (iodine in potassium iodide), Sonnenschein’s (phosphomolybdic acid), Scheibler’s (phosphotungstic acid), Marme’s (cadmium-potassium iodide).

In a series of preliminary tests on plant material known to be positively and negatively alkaloidal, the reagents appeared to work satisfactorily.

For the extraction of saponins boiling water was used. The extract was filtered, cooled, and subjected to the froth test. The extract was then made alkaline with sodium carbonate and again subjected to the froth test. The Liebermann-Burchard test was applied for further confirmation in some cases.

Methods Used

1. Extraction of Alkaloids

Fifty ml of dilute hydrochloric acid (1% aqueous) were placed in a 250-ml beaker on a
controlled-temperature hot-plate and maintained between 70° and 80°C. Sufficient chopped tissue to make a loose slurry (about 4–5 gm) was added to the acid and the temperature was maintained for 2 hours, with occasional stirring. The hot liquid was then filtered off and cooled. This gave 15–20 ml of fluid for testing.

In the main, leaf and stem tissue was used, although in some cases other parts of the plant were available.

2. Testing for Alkaloids

Four drops of the acid extract were placed in a watchglass and 2 drops of the reagent were added. The contents were mixed by gentle agitation and left for 10 minutes. The amount of precipitate formed in each watchglass was then estimated visually and a rating recorded for each. The ratings used were as follows:

0—no precipitate.
1—slight precipitate; usually requires close examination to see.
2—medium precipitate; readily discernible, although not prolific.
3—heavy precipitate; abundant.
4—extra-heavy precipitate; very flocculant, filling whole area covered by liquid.

After some experience, it was possible to disregard those precipitates which looked peculiar. For example, Wagner's reagent usually gave red or reddish precipitates and any other colours were suspect.

The plant material was extracted and tested as soon as possible after removing it from its parent plant. The normal delay was not greater than 48 hours, but in a few cases it was 96 hours.

3. Extraction of Saponins

A small quantity (1–2 gm) of chopped tissue was placed in about 25 ml of water. The mixture was brought to the boiling point and then allowed to cool for about 4 hours. The resulting extract was then filtered and the tissue discarded.

4. Testing for Saponins

About 10 ml of the filtered extract was shaken for about 30 seconds and allowed to stand undisturbed. The time taken for the froth, if any, to disappear was noted. If the froth persisted after 30 minutes, this was read as "saponin positive."

Another 10-ml portion of filtered extract was made alkaline with sodium carbonate and again shaken. If a froth persisted after 30 minutes, this was considered as "positive," and probably indicative of diterpene or triterpene acid.

RESULTS

Alkaloids

Using the method of estimation given above, it is clear that a maximum score of 28 is possible, and it was, in fact, obtained from some extracts. On the other hand, a score of 0 was not uncommon.

To set a score above which the plant is alkaloid positive and below which it is alkaloid negative is tempting, but this would simplify the interpretation. If a plant shows some precipitate in all seven reagents, then it very likely contains alkaloid, perhaps only in small quantities due to the season of the year or to the locality in which it was growing.

Unfortunately, phosphomolybdic and phosphotungstic acids are not as selective for alkaloidal substances as could be desired. In extreme cases the total score obtained for a plant was made up from its reaction to only these two reagents. This clearly rates as alkaloid negative, because there was no precipitate formed with any of the other reagents. In future surveys of this type, these two reagents could well be omitted without great loss. However, in Table 1 the precipitate scores from these two reagents have been included.

In Table 1 the plants tested are arranged alphabetically by families. The genus and the species are given where known; otherwise the author's collection number appears, in anticipation that identification will ultimately be made at the Herbarium in Honiara.

Names in parentheses are native names. The place and month of collection are also shown, together with the score and the number of reagents which produced precipitates (for example, 12(5) means a score of 12 derived from 5 reagents). The native names have been taken from the check list by Whitmore (1964). These are by no means authoritative and are offered as a guide only.
TABLE 1

RESULTS OF TESTS FOR ALKALOIDS AND SAPONINS IN PLANTS OF THE SOLOMON ISLANDS

<table>
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<tr>
<th>PLANT TESTED</th>
<th>COLLECTION NUMBER</th>
<th>PLACE AND MONTH</th>
<th>ALKALOID SCORE</th>
<th>SAPONINS</th>
</tr>
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<tbody>
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<td></td>
<td></td>
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<td>WATER</td>
<td>ALKALI</td>
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<tr>
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<td></td>
</tr>
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<td><em>Pseuderanthemum</em> sp. (malmalohenga)</td>
<td>102</td>
<td>H, Mar</td>
<td>22(7)</td>
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</tr>
<tr>
<td><em>Pseuderanthemum</em> sp.</td>
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<td>H, Mar</td>
<td>17(6)</td>
<td>—</td>
</tr>
<tr>
<td><em>Eranthemum</em> sp.</td>
<td>223</td>
<td>G, Aug</td>
<td>18(6)</td>
<td>—</td>
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<td><em>Graptotheca</em> sp.</td>
<td>232</td>
<td>P, Sep</td>
<td>15(7)</td>
<td>—</td>
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<tr>
<td><em>Clerodendron</em> inerme</td>
<td>228</td>
<td>B, Sep</td>
<td>20(7)</td>
<td>—</td>
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<td>ALANGIACEAE</td>
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<td><em>Alangium javanicum</em></td>
<td>176</td>
<td>M, Jul</td>
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<td>—</td>
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<td>AMARANTACEAE</td>
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<td><em>Vitex</em> sp.</td>
<td>106</td>
<td>G, Mar</td>
<td>5(4)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Stachytarpheta jamaicensis</em></td>
<td>110</td>
<td>G, Mar</td>
<td>15(5)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Clerodendron</em> sp. (teterau)</td>
<td>124</td>
<td>T, Apr</td>
<td>24(7)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Premna corymbosa</em></td>
<td>165</td>
<td>G, Jun</td>
<td>5(2)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Premna corymbosa</em></td>
<td>194</td>
<td>Giz, Jul</td>
<td>11(6)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Vitex negundo</em> leaf</td>
<td>254</td>
<td>G, Apr</td>
<td>12(4)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Tectona grandis</em> bark</td>
<td>267</td>
<td>H, Jan</td>
<td>20(7)</td>
<td>+</td>
<td>—</td>
</tr>
<tr>
<td><em>Gmelina arborea</em></td>
<td>272</td>
<td>H, Mar</td>
<td>15(7)</td>
<td>—</td>
<td>+</td>
</tr>
<tr>
<td>Vitaceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Leea</em> sp. leaf</td>
<td>113</td>
<td>H, Mar</td>
<td>3(1)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>(bora bora)</em> fruit</td>
<td></td>
<td></td>
<td>2(2)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Cayritia</em> sp.</td>
<td>207</td>
<td>H, Aug</td>
<td>2(2)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Cayritia</em> sp.</td>
<td>224</td>
<td>H, Aug</td>
<td>10(7)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Leea</em> sp.</td>
<td>245</td>
<td>W, Oct</td>
<td>3(3)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Zingiberaceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Tapeinochilus</em> sp.</td>
<td>185</td>
<td>MtA, Jul</td>
<td>15(7)</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

1 Abbreviations used for places: P-Poha River, Guadalcanal; SL-Skyline Rd., Guadalcanal; MtA-Mount Austen; H-Honiara; G-Guadalcanal Island; M-Matanikau River, Guadalcanal; T-Tetere; B-Benigi; W-White River, Guadalcanal; CE-Cape Esperance; V-Visale; Giz-Gizo Island; Auk-Auki, Malaita Island; Ten-Tenaru.

**Saponins**

For convenience, results of the tests for saponins have been included in Table 1 under three headings:

**Water**  
**Alkali**  
**L/B**

In the water and alkali columns, "+" means froth lasting for more than 30 minutes, and "—" indicates either no froth at all or froth having a persistence of less than 30 minutes. A blank in any column indicates that no test was done. In the L/B column the colour obtained is given. Blues are suggestive of steroids, whereas reds suggest triterpenoids.

**SUMMARY AND DISCUSSION**

The number of families represented by the specimens tested is 54 (within the limits of identification available).

**Alkaloids**

The following 32 families contain species which give positive tests for alkaloids. In this assessment, any score considered marginal has been recorded as positive. However, families represented by only one species have not been included unless the test is clearly positive. The first figure is the number of samples found positive, and the second figure is the number tested.

<table>
<thead>
<tr>
<th>Family</th>
<th>Samples Found Positive</th>
<th>Samples Tested</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthaceae</td>
<td>5/5</td>
<td></td>
</tr>
<tr>
<td>Amarantaceae</td>
<td>2/2</td>
<td></td>
</tr>
<tr>
<td>Apocynaceae</td>
<td>2/5</td>
<td></td>
</tr>
<tr>
<td>Aracaceae</td>
<td>1/1</td>
<td></td>
</tr>
<tr>
<td>Aristolochiaceae</td>
<td>1/2</td>
<td></td>
</tr>
<tr>
<td>Boraginaceae</td>
<td>1/3</td>
<td></td>
</tr>
<tr>
<td>Combretaceae</td>
<td>1/2</td>
<td></td>
</tr>
<tr>
<td>Compositae</td>
<td>2/7</td>
<td></td>
</tr>
</tbody>
</table>
Cucurbitaceae 1/2
Dioscoraceae 1/2
Euphorbiaceae 9/18
Flagellariaceae 1/1
Labiatae 1/2
Lauraceae 2/2
Leguminosae 23/30
Loganiaceae 2/2
Malvaceae 4/5
Melastomaceae 1/1
Meliaeae 1/1
Moraceae 4/8
Nyctaginaceae 1/1
Orchidaceae 1/2
Piperaceae 2/4
Polygalaceae 1/1
Rubiaceae 2/11
Rutaceae 1/2
Solanaceae 2/2
Sterculiaceae 4/5
Urticaceae 1/4
Verbenaceae 6/8
Vitaceae 1/4
Zingiberaceae 1/1

Acanthaceae 1/5
Amarantaceae 1/2
Apocyanaceae 1/5
Araliaceae 1/3
Boraginaceae 1/3
Compositae 2/6
Cucurbitaceae 1/2
Dioscoraceae 2/2
Euphorbiaceae 5/15
Goodeniaceae 1/2
Labiatae 1/2
Leguminosae 4/21
Liliaceae 1/4
Malvaceae 1/5
Passifloraceae 1/1
Polygalaceae 1/1
Rubiaeae 4/11
Sapindaceae 1/2
Solanaceae 1/1
Sterculiaceae 1/3
Verbenaceae 2/6

It would be of value to tabulate on a percentage basis the positive alkaloidal families. However, the number of species sampled per family is too small in some cases to permit this and could only lead to erroneous interpretations.

Similarly, a table to show, in descending order, the number of good alkaloidal species would also be misleading. This would show Leguminosae as the most promising whereas, in point of fact, species of Leguminosae were most prolific and easily collected.

However, one may be permitted the statistic that 58% of all families tested were alkaloid positive. This, of course, may only mean that the author was fortunate in collecting such specimens, and does not necessarily represent the ratio of alkaloidal to non-alkaloidal plants on Guadalcanal.

Saponins

The number of families represented by the specimens tested is 48 (within the limits of identification available).

The following 21 families contain species which gave positive tests for saponins. The first figure is the number of positives obtained (including L/B positives), and the second figure is the number of specimens tested in each family.

Of the total families tested for saponins, 42% gave a positive result either from water or alkali or the L/B test. In some cases the L/B test failed to show any colour, and these have been recorded as negative. In one case only (Apocynaceae) was the L/B test positive when both the water and the alkali froth tests were negative.

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WHITMORE, T. C. 1964. A Provisional Kwara'ae Check List to the Forest Flora of the Solomon Islands. Forestry Department, Honiara, Solomon Islands.
Marine Benthic Algae from Howland Island and Baker Island, Central Pacific

ROY T. TSUDA and GAVINO TRONO, JR.

Presented here is an annotated listing of the marine benthic algae collected by Mr. C. R. Long, under the auspices of the Pacific Ocean Biological Survey Program, Division of Birds, Smithsonian Institution, from two islands in the Central Pacific—Howland Island (0°48′N, 176°38′W) and Baker Island (0°12′N, 176°29′W).

A survey of the literature reveals no published papers on the algae from these two islands, although Degener and Gillaspy (1955), Degener and Degener (1959), and Dawson (1959) have reported on the algae of Canton Island, in the Phoenix Group, which lies approximately 400 miles southeast of Baker Island.

The collection numbers are those of Mr. Long, whom the authors thank for the opportunity to work on his collection. All specimens are deposited in the herbarium of Dr. Maxwell S. Doty, University of Hawaii.

CYANOPHYTA

Schizothrix calcicola (Ag.) Gomont, 1892:307; Drouet, 1963:275.

BAKER ISLAND: CRL 2395, in seep holes on NE end of island, brackish water, Oct. 14, 1964. The collection appears as gelatinous sheets about 5 mm in thickness, with the individual filaments about 2μ in diameter.

CHLOROPHYTA

Ulva fasciata Delile, 1813:153; Björk., 1940:10.


Enteromorpha kylinii Bliding, 1948:1; Bliding, 1963:103, fig. 61.

BAKER ISLAND: CRL 2367 and CRL 2368.2, on rusting machinery off SW beach, Oct. 13, 1964. The thalli of specimen CRL 2367 are about 12–15 cm high with proliferations occurring only at the basal portion. The base is approximately 70μ wide and increases to 225μ at the compressed terminal portion. The square to rectangular cells, about 9–15μ in diameter, are arranged in longitudinal rows and contain 2–3 pyrenoids per cell. Specimen CRL 2368.2, although listed here, seems to be more representative of E. tubulosa (Kütz.) Kützing in external appearance, but also possesses 2–3 pyrenoids.

Cladophora sp.

BAKER ISLAND: CRL 2369.4, in beachdrift on SW beach opposite wrecked landing craft, Oct. 13, 1964. The specimen, about 1 cm high, was found epiphytic on Hypnea sp. (CRL 2369.1). The thalli consist of irregular branches of uniform diameter, 140μ, with no predominant main axis present.

Dictyosphaeria cavernosa (Forsskål) Björk., 1932:2, pl. 1 (fig. 1); Egerod, 1952:350, figs. 1–g.


HOWLAND ISLAND: CRL 2190.3, on exposed...

Dictyosphaeria versiluvisi Weber van Bosse, 1905:155; Egerod, 1952:351, figs. 1a and 2b–k.


The filaments are clumped together, appearing as felt-like cushions. The erect filaments, about 110–140µ wide, attain a height of 2 cm, with the branches, if present, occurring only at the terminal portion. The walls are distinctly striated longitudinally.

Caulerpa serrulata var. typica f. serrulata (Weber van Bosse) Gilbert, 1942:15; Eubank, 1946:418.

HOWLAND ISLAND: CRL 2189, in crevices on exposed reef, July 23, 1964. The marginal serrations are at regular intervals throughout the untwisted fronds.

Halimeda spp.

Ten specimens were sent to Dr. L. H. Colinvaux, Department of Botany and Plant Pathology, Ohio State University, for a more critical study.

PHAEOPHYTA

Ectocarpus indicaus Sonder in Zollinger, 1854: 3; Børge, 1941:16, figs. 6–7.


Sphacelaria sp.

BAKER ISLAND: CRL 2369.4, in beachdrift on SW beach opposite wrecked landing craft, Oct. 14, 1964. A fragmentary specimen lacking propagulae is the only representative of this genus in the collection.

Dictyoza friabilis Setchell, 1926:91, pl. 13 (figs. 4–7), pl. 20 (fig. 1).

HOWLAND ISLAND: CRL 2324.3, in water-filled crevices on reef at NE point, Oct. 9, 1964.


BAKER ISLAND: CRL 2167, in beachdrift on south reef, July 21, 1964; CRL 2382.1, in pools on NE beach exposed at low tide, Oct. 14, 1964; CRL 2383.4 and CRL 2383.5, in drift in pools on NE point, Oct. 14, 1964. Specimens CRL 2167 and CRL 2383.5 are very similar to Taylor's circumscription of T. ornata var. ornata f. ecoronata Taylor, characterized by its prominent vesicle and lack of secondary rows of teeth. Specimens CRL 2382.1 and CRL 2383.4 are somewhat atypical forms in which the leaves possess only an occasional secondary tooth near the margin.

RHODOPHYTA

Gelidiopsis sp.

HOWLAND ISLAND: CRL 2324.3, in crevices on reef at NE point, Oct. 9, 1964; CRL 2342.2, in beachdrift on SE shore, Oct. 10, 1964; CRL 2333.1, in beachdrift on NW point of island, Oct. 10, 1964. The stoloniferous branches are attached to the substratum or to each other by means of short haptera-like attachment organs, giving rise to erect branches which may be simple or moderately branched. In cross section the cylindrical branches possess medullary cells up to 11µ in diameter, decreasing in size toward the periphery. The cortical cells are slightly elongated and radially arranged. The stichidia are intercalary, about 0.5 mm from the tip of the branch, and appear lanceolate in shape.

Jania capillacea Harvey, 1853:84 (Florida); Dawson, 1954:432, figs. 41a–b.

BAKER ISLAND: CRL 2369.2, in beachdrift on SW beach opposite wrecked landing craft, Oct. 13, 1964; CRL 2383.2, in shallow pool on NE


All specimens form small clumps about 1 cm high and always are found in association with other algae. The intergenicula are cylindrical, rather coarse, approximately 100–115μ thick, and about 5–8 diameters long. Branching is dichotomous to irregularly decussate and wide-angled, about 60°–90°. All specimens examined were sterile.

Jania micranthrodia Lamx., 1816:271; Dawson, 1956:49, fig. 2.


This alga forms hemispherical cushions to about 2.5 cm tall and 4 cm broad. It is often found in association with other algae. The erect branches are compact, basically dichotomous and decussate, but sometimes trichotomous or having several branches present on only one side of the main axis. Although basically dichotomous, the unequal spread of the branches gives the impression of a percurrent main axis. The conceptacles are antenniferous, with the anten- nae giving rise to branches which may bear other conceptacles.

Hypnea sp.

BAKER ISLAND: crl 2369.1, in beachdrift on SW beach opposite wrecked landing craft, Oct. 13, 1964. The only representative of this genus in the collection is a fragmentary specimen less than 1 cm in length. It is irregularly branched, with no distinct main axis present.

Lomentaria sp.

BAKER ISLAND: crl 2378, in sandy pool on NE reef, Oct. 14, 1964. A single specimen about 3 mm high with a slightly flattened thallus and irregular branching pattern was found in the collection. Five to six layers of small cortical cells about 6μ in diameter, with larger medullary cells about 30μ in diameter, were seen in cross sections.

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Ceramium gracillimum var. byssoidenum (Harv.)


BAKER ISLAND: crl 2378.2, in sandy pool on NE reef, Oct. 14, 1964. The specimens are characterized by the division of the nodal cortications at the lower third by a clear line, with the upper two thirds made up of angular cells cutting off smaller superficial cells, and the lower third made up of 1–2 tiers of horizontal cells; and also by the presence of whorls of spermatia found at the nodal cortication. However, our specimens possess whorls of long thin hairs originating from the upper portion of the nodal cortications. All specimens are antheridial.

Ceramium spp.


Lawrenzia nana Howe, 1920:566; Dawson, 1957:124, fig. 30.


HOWLAND ISLAND: crl 2324.3, in crevices on reef at NE point, Oct. 9, 1964.

The thalli, 2–3 cm high, anastomose in clumps due to the presence of rhizoidal haptera. In cross section the surface cells are radially elongated and arranged in a palisade. Our specimens (about 0.85 mm in width) are twice as wide as Howe’s specimen (0.45 mm wide).

REFERENCES


An Account of the Species of the Red Alga Polysiphonia of the Central and Western Tropical Pacific Ocean

II. Polysiphonia

George J. Hollenberg

ABSTRACT: Seven polysiphonous species are described. Three species are new: Polysiphonia dotyi, P. pentamera, and P. tsudana. P. bowei proves to be a very widely distributed species. P. exilis and P. tepida were previously known from the tropical Atlantic Ocean. P. homoia was previously known from the Pacific coast of Mexico. Of the polysiphonous species of Polysiphonia represented by the present study, none are corticated.

KEY TO THE SPECIES (continued from Part I)

26. Epizoic; erect branches 45–50μ in diameter ........................................ P. tsudana 27
26. Not epizoic; erect branches 100μ or more in diameter ........................................ 28
27. With 5 pericentral cells .............................................................................. 28
27. With 7 or more pericentral cells .................................................................... 29
28. Chiefly erect from a basal tuft of rhizoids; trichoblasts at intervals of 2–3 segments; segments of main branches mostly 1.5 diameters long or longer ........................................ P. homoia
28. Chiefly prostrate or decumbent; trichoblasts at intervals of 5 or more segments; segments of main branches 1 diameter long or shorter ........................................ P. pentamera
29. Trichoblasts and scar-cells at infrequent intervals; plants of estuaries and harbors .......... P. tepida
29. Trichoblasts and scar-cells commonly one per segment ..................................... 30
30. Pericentral cells in longitudinal rows; wall-scars relatively prominent where trichoblasts shed ................................................................. P. exilis
30. Pericentral cells in offset positions in successive mature segments ....................... 31
31. Rhizoids cut off as separate cells from the distal end of the pericentral cells; pericentral cells not tumid .......................................................... P. bowei
31. Rhizoids remaining in open connection with the pericentral cells; pericentral cells mostly tumid .......................................................... P. dotyi

Polysiphonia dotyi sp. nov.
Fig. 1A, 1B, 4, 5

Chiefly prostrate or sometimes clambering algae; prostrate and erect branches mostly 140–160μ in diameter; rhizoids unicellular with a broad open connection with the pericentral cells and with mostly discoid or occasionally multicellular apices; erect branches frequent, 0.5–1.0–(10) mm high, with segments mostly shorter than broad and tumid, especially above; lateral branches few, arising in association with trichoblasts; pericentral cells mostly 8–10, ecorticate, arranged in offset positions in successive segments; trichoblasts one per segment with a right hand spiral turn of one pericentral cell between successive trichoblasts, mostly rudimentary but occasionally to 1.2 mm long, with

Acknowledgments and designations used for collectors are given in Part I of this series (Pacific Science 22(1):56–98). The material collected by C. R. Long, and reported in Parts I and II of this account, was collected under the auspices of the Pacific Ocean Biological Survey Program conducted by the Division of Birds, Smithsonian Institution.

University of Redlands, Redlands, California. Manuscript received January 17, 1967.
4–6 unequal dichotomies, soon deciduous leaving small scar-cells in both prostrate and erect branches; tetrasporangia to 100μ in diameter, in spiral sequence near branch apices, considerably distending the segments at maturity; spermatangial branches 140–200 × 60–75μ, oblong with broadly rounded tips, arising as a primary branch of a trichoblast.

Planta proceptique prostratae aut interdum scandentes; rami prostrati erectique plerumque 140–160μ diam.; rhizoidea unicellularis, plerumque discoidea, interdum multicellularia; connectionem latam apertamque cum cellulis pericentralibus habentia; rami erecti non numerosi, 0.5–1.0–(10) mm alt., segmentis plerumque brevioribus quam lata, necnon tumidis, pracipue supra; rami laterales pauci, in associationem cum trichoblastis nascentes; cellulae pericentrales plerumque 8–10, eocitae, in segmentis successive ex ordine sitae; trichoblastae una in unoquoque segmento, per unam cellulam pericentralen inter trichoblastas successivas spiraliter versae; maxima ex parte elementariae, interdum, autem, ad 1.2 mm long., et 4–5 dichotomias inaequales habentes, mox deciduae, cellulas-cicatrices parvas in ramis et prostratis et erectis reliquentes; tetrasporangia ad 100μ diam., in spira prope apices ramorum, dum maturum segmenta aliquantum distendentes; rami spermatangiales 140–200 × 60–75μ, oblongi, in cacuminibus late rotundati, ut ramus primarius trichoblastae nascentes.


An unusual feature of this species is the broad open connection of the rhizoids with the pericentral cells. The writer is not aware of this feature occurring in any other species with more than 4 pericentral cells. A feature which it shares with only a few species, including P. bowei, is the offset position of the pericentral cells.

Polysiphonia exilis Harvey, 1853:47

Figs. 1C, 3C

Plants epiphytic or on dead coral, chiefly prostrate, attached by unicellular rhizoids, commonly with digitate or bulbous tips, cut off by a cross-wall from the center or proximal end of the pericentral cells, mostly short but occasionally as much as 2 mm long; pericentral cells mostly 9–11, around a relatively large central cell, eocitare, in straight rows longitudinally; walls to 20μ thick, often stratified; erect branches 3–6 mm high and 160–170μ in diameter, with segments mostly 0.5–0.75 diameters long, arising almost exclusively cicatriciously from the prostrate branches and having few or no lateral ramuli; trichoblasts on erect...
branched branches commonly well developed, as much as 2 mm long and 28–40μ in diameter at the base, with mostly 3–5 dichotomies, the final branches tapering to delicate tips; trichoblasts arising one per segment on erect branches, with 2 pericentral cells and approximately 1/4 spiral turn between successive trichoblasts, mostly soon deciduous but often relatively persistent, leaving small scar-cells and prominent wall-scars at the point of abscission; scar-cells on prostrate branches often 2 or more segments apart; tetrasporangia 50–65μ in diameter, in spiral sequence in the tips of erect branches, not much distending the segments; sexual plants unknown.

**TYPE LOCALITY:** Key West, Florida.


Examination of a fragment of the type, W.H.H.24, kindly sent from the Harvey Herbarium at Trinity College, Dublin, by Hilda Parks, reveals features which in detail correspond closely with those of the Pacific specimens, leaving little room for doubt concerning the identity of the latter, even though they are considerably smaller and with fewer lateral branches than the type. Another minor difference may be mentioned. The central cell is relatively small in the type material but is usually nearly twice as broad as the pericentral cells in the Pacific specimens.

A specimen which seems to be a variant of *P. exilis* is represented by D. 18713, collected by Charles H. Lamoureux, Midway I., Dec. 16, 1962, cast ashore following a heavy storm. The erect branches are unbranched and slightly smaller than those of other Pacific specimens of *P. exilis*. There are 14 pericentral cells. Trichoblasts tend to occur at intervals of 2–4 segments rather than on every segment, as is typical for the species. The plants were sterile.

**Polysiphonia homoia** Setchell and Gardner 1930:162; Hollenberg 1961:356

Fig. 2B

Plants flaccid, epiphytic, to 3 cm high, attached by a basal tuft of unicellular rhizoids, mostly with digitate tips and cut off by cross-walls from an original basal cell (spore?) and from adjacent pericentral cells; 5 pericentral cells, ecoricate, with walls thin and hyaline except near the base, and with segments in main axes to 2.5 diameters long and with clear dissepiments; main axis 100–420μ in diameter, of segments 1.5–2.5 diameters long; branches arising in connection with trichoblasts, at intervals of mostly 6–12 segments, slightly narrowed at the base; branching mostly pseudodichotomous; trichoblasts at irregular intervals, mostly 2–3 segments apart in 1/5 spiral sequence, up to 400–550μ long with 4–6 dichotomies and slender tapering tips, with basal cell very short and with the cell next to the basal cell about 15μ in diameter and up to 6 diameters long; tetrasporangia to 55μ in diameter, in short slightly spiral series, not much distending the segments; cystocarps slightly ovate to nearly globular and 200–240μ in diameter, with ostiolar cells prominently enlarged at maturity in comparison with cells immediately below them; spermamarginal branches measuring 200–275х40–45μ, arising as a primary fork of a trichoblast, without sterile tip.

**TYPE LOCALITY:** Guadalupe I., Lower California, Mexico.

Central Pacific collections are from the Hawaiian Islands only: D. 19144C1, on *Galaxaura* sp. dredged 6–13 fa, Port Allen, Kauai, Nov. 12, 1959; D. 19104E1, and D. 19104F1,
Fig. 2. *A*, Polysiphonia bowei, portion of a branch showing pericentral cells in offset positions, with two secondary pit connections with pericentral cells of adjacent segments; also showing the characteristically short basal cell of a trichoblast. *B*, Polysiphonia homoia, cystocarp (immature). *C*, Polysiphonia tsudana, tetrasporangial branch. *D*, Polysiphonia pentamera, apex of a branch, showing laterals and trichoblasts.
cystocarpic, on *Gracilaria*, 20–55 fa, Explosive Ammunition Area, Oahu, July 24, 1959; D. 19118A1, on *Cniospora* sp. 16–25 fa, Pokai Bay, Oahu, Aug. 1, 1959; D. 19134D1, on other algae, 25 fa, outside channel buoy, Kaneohe Bay, Oahu, July 25, 1959; D. 19135Z1, spermatangial, on *Hypnea* sp., 26 fa, Waialua, Oahu, Aug. 2, 1959; D. 19136F3, cystocarpic, 15 fa, Waialua, Oahu, Aug. 2, 1959; D. 19143T1, cystocarpic, on *Liagora* sp., 15 fa, Ilio Point, Molokai, Sept. 7, 1959.

This alga seems to be a plant of deeper water. It compares favorably in most respects with the description of the type and previously the only known collection of this plant. It differs in two respects: (1) the tetrasporangia are reported as occurring in straight series in the type material, and (2) the type is described as having a short sterile tip on the spermatangial branches.

*Polysiphonia howei* Hollenberg, in Taylor 1943:302; Hollenberg 1958:64.


Figs. 1D, 1E, 2A

Plants forming low dense mats on rocks, up to 1.5 cm high and to 7 cm or more in diameter; prostrate branches 100–170μ in diameter attached by unicellular rhizoids, with digitate to multicellular tips, often several per segment, each cut off by a cross-wall from the distal end of the pericentral cell; erect branches 100–150μ in diameter, arising exogenously at the tips of prostrate branches, or sometimes cicatricously, at intervals of 6–8 or more segments, at first strongly curved toward the apex of the prostrate branch, and bearing frequent, mostly curved, lateral branches; prostrate branches giving rise ventro-laterally to prostrate lateral branches in alternating positions on either side mostly 2 segments distal from each erect branch; 8–10 pericentral cells around a relatively large central cell, the pericentral cells, beginning 8 or more segments from the branch tip, shifting to offset positions, so that each pericentral cell is in contact at either end with 2 pericentral cells of the adjacent segment, with each of which it soon develops 1, or sometimes 2, secondary pit connections; segments in prostrate and erect branches mostly less than 1 diameter long; trichoblasts relatively coarse, to 600μ long and 28μ in diameter at the base, with short basal cells, even at maturity, and with about 4 dichotomies, not diminishing greatly toward the rounded tips, arising at no regular intervals but frequently, one per segment in 1/4 spiral sequence, at least in upper parts; tetrasporangia 45–55μ in diameter, in spiral series in the ultimate branches, not distending the segments; cystocarps ovoid, 175–200–(360)μ in diameter; spermatangial branches near branch tips 120–170μ long and 35–50μ in diameter on a sturdy 1-celled stalk, without a sterile tip, arising from the entire trichoblast primordium or frequently one from each primary branch of the trichoblast.

**TYPE LOCALITY:** Berry I., Bahamas.

**MATERIAL EXAMINED** includes the following:

Meñez, July 26, 1958; EAST INDIES (Siboga Expedition collections loaned from Rijksherbarium, Leiden, and identified by Mme. Weber v. Bosse as *Lophosiphonia obscura*)—Sta. 14, Kangean I., east of Java, Mar. 14, 1899; Sta. 165, Fausses Pisangs I., west of New Guinea, Aug. 20–22, 1899; Sta. 277, Dammer I., east of Timor, Jan. 9–11, 1900; Sta. 296, coast of Timor, Jan. 24–26, 1900; SINGAPORE—D. 16425A, on mangrove stems and roots at sea edge of mangrove swamp near Caltex refinery, Paudan Nature Reserve, Nov. 31, 1957; CEYLON—W. Ferguson, Ceylon Algae 239 (as *Lophosiphonia obscura*), Rijksherbarium.

The wide distribution of *P. howei* in the Atlantic and Pacific Oceans was previously reported by Hollenberg (1958:64). The present study extends the distribution westward to the Indian Ocean and shows that this species is common throughout the tropical Pacific. Furthermore, a collection by J. Feldmann at Roscoff, France, Aug. 25, 1946, is probably to be identified with this species. Erect branches arise in the characteristic exogenous manner from prostrate branches, and the specimens exhibit most of the detailed features of the species, although the rhizoids arise from the middle of the pericentral cells instead of from the distal end. Hence it seems probable that *P. howei* occurs also in southern Africa.

**Polisiphonia pentamera** sp. nov.


Fig. 2D

Plants epiphytic with prostrate branches 2–3 cm long and (115)–175–200μ in diameter, and with segments mostly shorter than their diameter, attached by unicellular rhizoids which are cut off from the pericentral cells by a cross-wall; assurgent erect branches to 3.5 cm high of a similar diameter and with segments about 1 diameter long in older parts and very short in younger terminal parts; branching mostly exogenous, sometimes cicatrogenous, pseudodichotomous and occasionally somewhat dichotichous, at relatively wide angles and at intervals of (6)–12–25 segments, the branches not constricted at the base, arising in connection with trichoblasts; pericentral cells 5, eccentric; walls hyaline, firm, and of moderate thickness, mostly but little constricted at the clear dissepsiments; trichoblasts mostly at intervals of 12–14 or more segments, with 3–4 dichotomies, quickly deciduous, leaving small scar-cells; tetrasporangia about 55μ in diameter in very long, slightly spiralling series up to 60 or 70 in the upper branches; sexual reproduction unknown.

Plantae epiphyticeae, ramos prostratos 2–3 cm long, et 115–175–200μ diam., segmentis plerunque brevi-oribus quam lata habentibus; per rhizoidea unicellularia quae a cellulis pericentralibus per dissepsimentum separantur affixa; rami erecti assurgentia ex 3.5 cm alt., rami prostratis diametro similes, segmenta in partibus vetoriusibus æque longa ac latá et in partibus iberius terminalibus brevissima habentibus; rami plerunque exoxeni interdum cicatrizare, pseudo-dichotomi et interdum satis distichti, angulis relative latis, intervallis (6)–12–25 segmentorum, ramos ad basim non constrictos, in associatione cum trichoblastis enascentibus; cellulae pericentrales 5, ecoriciatae; parietes hyalini firmi satis crassii, ad dissepsimenta saepissime vix constricti; trichoblastae plerunque intervallis 12–14 vel plurim segmentorum dispositione, 3–4 dichotomias habentem, cito deciduae, cellulas-cicatrices parvas relinquentes; tetrasporang'a ca. 55μ diam. 60–70 in serie longissima subsupciali in ramos superioribus; reproduco sexualis ignota.

**TYPE:** G. 524.2, tetrasporic, from a depth of 28 m, in the lagoon, Eniwetok Atoll, Aug. 30, 1955.

**ADDITIONAL COLLECTIONS:** HAWAIIAN ISLANDS—D. 19135W2, on other algae, dredged 26 fa, Waialua, Oahu, Aug. 2, 1959; GILBERT ISLANDS—D. 18937A, from a coral reef, Marakei I., legit M. J. Cooper, July, 1962, and identified by Tsuda (1964:11) as *P. fragilis* Suringar; CAROLINE ISLANDS—D. 21223.1, tetrasporic, creeping on a Padina sp., on a reef flat near the bridge between Kolonia and Jokai I., Ponape Group (6°58'N, 138°11'E), legit E. Meñez, June 25, 1960; EAST INDIES—two collections made on the Siboga Expedition and identified by Weber v. Bosse (1923) as *P. mollis*? Hooker and Harvey; Sta. 77, on other algae dredged 40–60 m, Borneo Bank, southeast of Borneo, June 12, 1899; Sta. 133, Lirung, Salibabu I., "flottant le long du bateau," July 25–27, 1899; VIETNAM—Da. 11277, tetrasporic, as *P. fragilis* Suringar, Ile de Tre; Da. 11278A, tetrasporic, as (*P. coarctata* Tseng) from Nhatrong, Feb. 16, 1952.
This species resembles *P. fragilis* Suringar as interpreted and figured by Okamura (1929, Vol. VI: Pl. 253, figs. 1–15). However, Okamura describes trichoblasts as arising one per segment. Segi (1951:231, as *P. forcipata* Harvey) describes and figures a similar plant with trichoblasts on every segment. *P. pentamerata* also resembles *P. polyphysa* Kützing, collected by Vieillard in New Caledonia, and figured in Kützing (1863, Vol. 13:20). *P. polyphysa* is described as having 5 pericentral cells and very short segments, but the branch apices are described as forcipate, and the pericentral cells as "valde inflatis."

*Polysiphonia tepida* Hollenberg 1958:65

*P. flabellulata* of Meñez 1964:219, (non *P. flabellulata* Harvey 1860:330); *P. dennudata* Taylor (1960) as concerns non-corticated forms

Fig. 3D, 3E

Plants 1–8 cm high, very soft and flaccid, assurent from a brief prostrate base attached by numerous unicellular rhizoids, which are cut off by a cross-wall mostly from the proximal end of the pericentral cells, which may have digitate tips and may be as much as 1.3 mm long; pericentral cells mostly 7, sometimes 6 in upper branches, or 8 at the base, eocriticate, with segments in median parts of main erect branches mostly 1–1.5 diameters long and 140–250μ in diameter; walls thin and hyaline or thick and stratified in lower parts; main axes not prominent, branching pseudodichotomously at wide angles up to 45 degrees below, at very narrow angles and somewhat distichous in upper parts, with 4–10 or more, but mostly 8, segments between successive branches; branches arising in connection with trichoblasts; trichoblasts commonly 1–2 between successive branches, often poorly developed, but sometimes well developed, 200–500μ long and with 2–3 forks and delicate tips, mostly soon deciduous, leaving small scar-cells; tetrasporangia 50–70–(95)μ in diameter, in short or longer straight series in the ultimate and subultimate ramuli; cystocarps subglobose and about 160μ in diameter, according to Meñez (1964:219). I observed only immature cystocarps; spermatangial branches not observed in the material examined, but described by Meñez as arising as a primary branch of a trichoblast.

**Type Locality:** Beaufort, North Carolina, United States mainland.

**Collections Examined** (all from the Hawaiian Islands): D. 9765A, tetrasporic, near the Army Gate, Sand I., Oahu, Jan. 27, 1952; D. 18020, tetrasporic, cystocarpic, Kaneohe Bay, Oahu, Oct. 10, 1953; D. 19756, tetrasporic, scraped from the hull of a boat in Ala Wai Yacht Harbor, Honolulu, Oahu, Nov. 14, 1951; H. 62–12, from an aquarium of sea water in which fish were being reared and fed the *Polysiphonia* for food, Sans Souci Beach Laboratory, Waikiki, Oahu, Dec. 3, 1962; an unnumbered collection, by I. A. Abbott, from Keawanui Pond, Molokai, Aug. 24, 1944.

A plant described and figured by Boergesen (1918:269, figs. 263, 264) may be *P. tepida*, although Boergesen's fig. 264 shows rhizoids in open connection with the pericentral cells.

*Polysiphonia tsudana* sp. nov.

*Polysiphonia* sp. of Tsuda 1965:21

Figs. 1F, 1G, 2C

Prostrate branches 40–62μ in diameter, composed of segments about 1 diameter long, attached by unicellular rhizoids, which are cut off by a cross-wall from the center or distal end of the pericentral cells; erect branches arising mostly cicatogenously at close but irregular intervals, to 4 mm high and 45–50μ in diameter, mostly unbranched, with segments 1 diameter long or less; pericentral cells 4 in the prostrate branches, 6–9 in erect branches, about the same size as the central cell, eocriticate, commonly of unequal length in a given segment and not strictly in longitudinal rows; trichoblasts infrequent and very rudimentary, but primordia (or scar-cells) commonly one per segment and in mostly 1/4 spiral sequence, except in tetrasporangial branches where they are unilateral; tetrasporangia about 36μ in diameter, one per segment in short, non-spiralling series, somewhat distending the segments; spermatangial branches (immature) lanceolate, to 65μ long, apparently without a sterile tip, on a very short, 1-celled pedicel, arising from the entire trichoblast primordium; cystocarps unknown.
Fig. 3. A and B, Polysiphonia? sp. (scale for B applies to A as well). C, Polysiphonia exilis, prostrate branch and erect branches. D and E, Polysiphonia tepida.

Algae minutaee, ramos prostratos 40-60μ diam. et segmenta aequa longa ac lata habentes, rami per rhizoidea unicellularia, ut cellulae discrete separata, affixi; rami erecti ad 4 mm alt., 40-50μ diam., plerunque non ramosi, segmentis plerumque ac longis ac latis aut brevioribus; cellulae pericentrales 4 in ramis prostratis et 6-9 in ramis erectis; trichoblastae rarae elementariaeque, primordiis vulgo uno in unoquoque segmento in ramis erectis prostratiisque, in spira ordinatis nisi in ramis tetrasporangialibus; tetrasporangia in serie brevi non spirali; rami spermatangiales et primordio trichoblastae toto enascentes; cystocarpi non observati; plantae in collo testudinis marinae colentes.

The spiral arrangement of trichoblasts and scar-cells, which are unilateral only on tetrasporangial branches, and the cicatrogenous origin of erect branches, are features which exclude this alga from the genus Lophosiphonia.

No additional collections are available for study, but no other species of Polysiphonia closely approximates the distinctive features of this alga, especially the epizoic habitat, the minute size, the variable number of pericentral cells, and the origin of spermatangial branches from the entire trichoblast primordium.

Polysiphonia ? sp.

Fig. 3A, 3B

Plants to 1 cm high with prostrate branches 200-220μ in diameter, attached by rhizoids
which are cut off as separate cells from the distal end of the pericentral cells and which may have multicellular tips; erect branches similar and slightly larger in diameter, arising endogenously or mostly catagenously at intervals of 6–8 segments, each erect branch mostly 2 segments and 1/4 right-hand turn from another branch or a branch primordium, the latter usually composed of several cells; pericentral cells 8–(9?) ecoricate, composing segments mostly less than half as long as broad, with pericentral cells not in longitudinal rows but in offset position, resulting in a more or less hexagonal shape of the pericentral cells as seen in surface view; erect branches in turn bearing short, somewhat arcuate laterals and primordia; trichoblasts to 700μ long, with about 5 dichotomies; arising at intervals of mostly 2–3 segments and 1/4 right-hand spiral, quickly deciduous, leaving scar-cells which quickly divide to form a cluster of small cells most of which remain as multicellular rudiments of potential branches; reproductive structures unknown.

A single collection, D. 17242.1, growing with a member of the Gelidiaceae, was collected by Jessie Kajimara at Ili Bridge, Halona, Oahu, Hawaii, Nov. 14, 1956.

This alga has very distinctive features, but the lack of reproductive structures makes its generic position uncertain.

REFERENCES


The Polychaetous Annelids of the Marshall Islands

DONALD J. REISH

This report is based upon collections made by the author at Eniwetok, Bikini, and Majuro atolls during the summers of 1956 and 1957. In addition, previous accounts of the polychaetes from the Marshall Islands, largely those reported by Hartman (1954), are incorporated in this study. The object of the field investigations was to prepare a reference collection of polychaetes for the Eniwetok Marine Biological Laboratory. Keys to the species within the families and references have been added as an aid to identification. The material upon which this study was based, including all holotypes and paratypes, has been deposited in the polychaete collections of the United States National Museum. A duplicate collection has been placed in the museum of the Eniwetok Marine Biological Laboratory. The author is indebted to Dr. Robert W. Hiatt for his assistance during the course of the field investigations.

Previous studies dealing with the polychaetes of the Marshall Islands include the account by Hartman (1954), who reported on material collected from Eniwetok, Bikini, Rongelap, and Rongerik atolls; Reish (1962a), who described a new species of Miconereis from Eniwetok Atoll; and Woodwick (1964), who described five new species of spionids collected by the author from Eniwetok, Bikini, and Majuro atolls. A total of 102 species, including some forms identified only to genus or family by Hartman, were previously known from the Marshall Islands. The Marshall Islands consist of 5 islands having no interior lagoon and 29 atolls (Emery, Tracey, and Ladd, 1954). Polychaetes have been collected thus far from 28 islands of 5 atolls: Eniwetok (14 islands) (Fig. 1), Bikini (6 islands) (Fig. 2), Rongelap (5 islands), Rongerik (2 islands), and Majuro (1 island) (Fig. 3).

MATERIALS AND METHODS

The collections upon which this study is based were made by the author from August 20 through September 14, 1956 (146 stations) and from June 29 through July 15, 1957 (77 stations). Three additional collections were made from the bottom of the lagoon at Eniwetok Atoll by Mr. Mike Chamberlain on September 15, 1957. The islands of Eniwetok Atoll visited in 1956 and 1957 were Parry, Eniwetok, Igurin, Rigilil, Bogombogo, Engebi, Aaraanibiru, Aniyanii, Japtan, and Bogen (Fig. 1). Collections at Enyu Island, Bikini Atoll, were made on September 6, 1956 (Fig. 2), and on Uliga Island, Majuro Atoll, on August 30, 1956 (Fig. 3).

The collecting procedure was similar at all islands. Transects were made of both the ocean and lagoon sides of the islands during low tide. Collections were made at the high tide, mid-tide, low tide, and surge zones. These collections consisted of individual specimens of polychaetes, algal clumps, sand, and pieces of corals, old coral heads, coralline algae, and of the coral reef itself. Generally one liter of material from each ecological niche at a site was preserved with formaldehyde in the field. The material was washed and sorted in the laboratory under a dissecting microscope. Subtidal collections of sand or pieces of coral were taken by swimming in depths of five meters or less. Polychaetes were taken from nearly every one of the 226 stations. Description of 85 of the 226 stations sampled are included in the paper by Barnard (1965).

Various names have been employed in the literature for the various islands of Eniwetok Atoll. The names employed by Dawson (1957) and by the Eniwetok Marine Biological Laboratory have been followed. Hartman (1954a) used the same names for those of the islands from which she made collections, with two ex-

1 The field work was made possible by the U.S. Atomic Energy Commission through the University of Hawaii and the Eniwetok Marine Biological Laboratory.

2 Department of Biology, California State College, Long Beach, California 90804. Manuscript received January 31, 1967.
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Fig. 1. Map of Eniwetok Atoll, Marshall Islands, showing collecting sites.

Fig. 2. Map of Bikini Atoll, Marshall Islands, showing collecting sites.

Fig. 3. Map of Majuro Atoll, Marshall Islands, showing collecting site at Uliga Island.

exceptions—Rujoru and Japtan which she called Rujiyoru and Munit.

DISCUSSION

In addition to the 102 species of polychaetes which have been reported previously from the Marshall Islands, 29 species, including 4 newly described, are herein reported from the Marshall Islands for the first time. Of the 25 species which have been described earlier, but which were previously unknown from the Marshall Islands, 13 are cosmopolitan forms. The distribution of 8 species has been extended from the Indian Ocean-Red Sea area.

Following is a list of the polychaetes newly-reported from the Marshall Islands arranged according to previous known distributional records:

COSMOPOLITAN SPECIES

- Eumida sanguinea
- Typosyllis prolifera
- T. armillaris
- Exogone verugera
- Sphaerosyllis pirifera
- Neanthes arenaceodentata
- Perinereis helleri
- P. cultifera
- Prionospio cirrifera
- Spio siliicornis
- Ctenodrilus serratus
- Capitella capitata
- Vermiliopsis glandigerus

SPECIES FROM INDIAN OCEAN-RED SEA GENERAL AREA

- Opistosyllis longicirrata
- O. australis
- Platynereis pulchella
- Perinereis nigropunctata
- Eunice australis
- Malacoceros (M.) indicus
- Heteromastides bifidus
- Axiothella australis

SPECIES FROM OTHER AREAS

- Typosyllis cirropunctata—Italy
- Opistosyllis brunnea—West Africa
- Scolelepis (S.) bonnier—France
- Salmacina incrustans—Mediterranean Sea
NEW SPECIES

Ceratocephala cordicola
Euchone eniwetokensis
Megalomma trioculatum
Serpula hartmanae

A total of 97 species are known from Eniwetok Atoll, 50 from Bikini Atoll, and 26 from Majuro Atoll. Hartman reported 17 species from Rongelap Atoll and 4 from Rongerik Atoll. The larger number of species reported from Eniwetok than from the other atolls is undoubtedly because of more extensive collecting there, and is not a reflection of any ecological difference. In general, more intertidal species of polychaetaes were collected from the ocean side of an island than from the lagoon side. This is probably because the greater area on the ocean side accounts for a greater diversity of ecological niches. The shallow water on the lagoon side of the islands apparently is quite rich in polychaetae species, judging from collections made in this zone at Parry Island. If the species from the shallow, subtidal lagoon waters are included with the intertidal ones, then a total of 44 species were taken from the lagoon side of Parry Island, as compared with 31 on the ocean side. Therefore it is likely that the number of polychaetaes known from the Marshall Islands could be increased by collections from the benthos of the lagoon and the subtidal region off the ocean side of the reef. The former zone can be studied by making dredge hauls and grabs, but collecting from the latter would be more difficult.

SYSTEMATICS

The polychaetaes known from the Marshall Islands are arranged systematically by families and alphabetically by genus and species. Keys to the known species are included under each family. References include, in so far as possible, citations to published figures of the species. The single most useful reference is the study by Fauvel (1953) on the polychaetaes of India.

Some abbreviations have been employed. Whenever Hartman (1954a) is referred to in the text, the date has been omitted. The abbreviation (O) and (L) refer to the ocean and lagoon sides of the island. The words “atoll” and “island” have been eliminated from the collecting data. Information on distribution has been condensed to single words or phrases.

Family Polynoidae

Key to the species from Marshall Islands

1. 12 pairs of elytra

1. 13 pairs of elytra ... Iphione muricata

1. 15 pairs of elytra

1. 18 or more pairs of elytra

2. One kind of dorsal setae

Lepidonotus argus

2. Two kinds of dorsal setae

Thornora jukesii

3. Elytra fringed for at least one-half circumference, with small papillae and large vesicle; ventral lamellae conspicuous

Patalepidonotus amplifera

3. Elytra with very little fringe, with small papillae; no ventral lamellae

Harmothoe imbricata

4. Conspicuous ventral lamellae giving appearance of elytra; setae entire

Gastrolepidia claverigera

4. No ventral lamellae; setae bifid

Hyperbalosydna striata

Gastrolepidia claverigera Schmardia

Fauvel, 1953, pp. 51–52, fig. 22 d–f; Hartman, 1954a, p. 630. Eniwetok: Parry (O), Aaraanbiru (O), and by Hartman at Elugelab (O). Bikini: Bokonfaauaku (O) by Hartman. Rongerik: Bock (O) by Hartman. Specimens of this commensal polynoid were taken from the holothurians Holothuria atria Jager, H. gyrifer (Selenka, Actinopygia mauritiana (Quay and Gaimard), and Stichopus horrens (Selenka). Indo-Pacific Ocean.

Harmothoe imbricata? (Linnaeus)


Hyperbalosydna striata (Kinberg)

Annelids of Marshall Islands—Reish

*Lepeidonotus* sp. cf. *L. argus* (Quatrefages)

*Paralepidonotus ampullifera* (Grube)
*Harmothoe ampullifera*. Fauvel, 1953, pp. 43–44, fig. 18 d.


*Thormora juksesii* (Baird)


*Rongelap*: Burok (O) by Hartman. Japan to New Zealand, west to Red Sea.

*Iphione maricata* Savigny

**Family Palmyridae**

*Palmyra aurifera* Savigny

**Family Chrysopetalidae**

KEY TO THE SPECIES FROM MARSHALL ISLANDS

1. Paleae with dentation on both sides; dorsal cirrus will develop; *Chrysopetalum eblersi* Gravier
2. Paleae with dentation on one side only; dorsal cirrus short, digitiform; *Bhawania goodei* Webster

*Bhawania goodei* Webster


*Eniwetok*: Lidilbut (O) and Bogon (O) by Hartman. Japan, Indo-Pacific Ocean, South Africa, Red Sea, and Bermuda Islands.

*Chrysopetalum eblersi* Gravier
Fauvel, 1953, pp. 78–79, fig. 36 a–d; Hartman, 1954a, p. 628. *Eniwetok*: Parry (L), Eniwetok (L), Iaurini (L), Bogomogo (O, L), Engedi (O), Aaraanibiru (O, L), Japten (O), and Bogen (O, L); from Rigili (O), Lidilbut (O), and Bogon (O) by Hartman. *Bikini*: Enyu (O, L). *Majuro*: Uliga (O). Indo-Pacific Ocean to Red Sea.

**Family Amphinomidae**


**Eurythoe complanata** (Pallas)
Fauvel, 1953, pp. 83–84, fig. 38 b–m; Hartman, 1954a, p. 628. *Eniwetok*: Parry (O, L), Iaurini (O), Bogomogo (O, L), Engedi (O), Aaraanibiru (O, L), Aniyaanii (O), Japten (O, L), Bogen (O). *Bikini*: Enyu (O, L). Majuro: Uliga (O). Additional reports from Eniwetok by Hartman include Lidilbut (O) and Bogon (O), several islands from Bikini, and from one island at Rongelap. Cosmopolitan in warm seas.

This species, known commonly as the fire-worm, is the largest and one of the most frequently encountered polychaetes from Eniwetok. It should not be picked up with the unprotected hand because the setae readily detach.

**Notopygos hispidus** Potts

**Pseudoerythoe oculifera** (Augener)

**Family Euphosinidae**

*Euphosine myrta* (Savigny)
628. Eniwetok: Lidilbut (O) by Hartman. Widespread from the Pacific Ocean, Indian Ocean, Red Sea, South Atlantic Ocean, and Adriatic Sea.

Family phyllodocidae

Key to the species from Marshall Islands

1. Prostomium with 4 antennae ............ 2
2. Prostomium with 5 antennae ............ 5
3. Proboscis with papillae in 12 rows
   Anaitides madeirensis
4. Blade of setae with spines along one margin
   Phylldoce marquesensis
5. Proboscis smooth .... Eunida sanguinea
6. Ventral cirri of segment 2 flattened and winged; shaft of setae with two curved spines .... Steggoa magalaensis
7. Ventral cirri of segment 2 not winged; shaft of setae otherwise .... Eulalia viridis

Anaitides madeirensis (Langerhans)

Eulalia viridis (Linnaeus)
Eulalia tenax Grube. Okuda, 1940, p. 8, fig. 4; Hartman, 1954a, p. 628
Eulalia viridis. Imajima and Hartman, 1964, p. 63

Reported from Bikini Atoll by Hartman. Atlantic Ocean, Mediterranean Sea, Arctic Ocean, Japan to Central Pacific Ocean.

Genetyllis gracilis (Kinberg)
Phylldoce gracilis Kinberg. Fauvel, 1953, p. 117.


Eniwetok: Parry (L), Igrurini (O). BIKINI: Phylldoce marquesensis? Monro

Phylldoce pruvoti Fauvel

Steggoa magalaensis (Kinberg)


Eunida sanguinea (Oersted)

Family hesionidae

Key to the species from Marshall Islands

1. Two antennae; palps absent
   Hesione genetta
2. Three antennae; palps present ............ 2
3. Some dorsal setae furcated
   Podarke angustifrons
4. Dorsal setae all capillary
   Leocrates chinesis

Hesione genetta Grube
Fauvel, 1953, p. 105; Hartman, 1954a, p. 628. Eniwetok: Bogombogo (O), Aniyaanii (O). Bikini: Enyu (O). Hartman reported this species from Eniwetok, Bikini, and Rongelap Atolls, but the specific islands were not given. Indo-Pacific Ocean.

Podarke angustifrons (Grube)

ENIWETOK: Parry (L), Aaraanbiru (L), Bogen (O). Indo-Pacific Ocean.

**Leocrates chinensis** Kinberg

Hartman, 1954a, p. 628; Imajima and Hartman, 1964, p. 82; Hartmann-Schröder, 1965, p. 94. ENIWETOK: Parry (L), Bogombogo (O), Engebi (O), and by Hartman from Lidilbut (O). BIKINI: Enyu (O). Circumtropical to subtropical.

**Family Pilargiidae**

**Ancistrosyllis rigida** Fauvel


**Family Syllidae**

**Subfamily Syllidae**

**Haplosyllis aberrans** Fauvel


**Haplosyllis spongicola** (Grube)


**Opistosyllis anstralis** Augener

Fauvel, 1953, p. 156, fig. 80 g–i; Imajima and Hartman, 1964, p. 120. ENIWETOK: Parry...
(O), Bogombogo (O), Engebi (O), Aaraanbiru (O), and Japtan (L). This is the first report of the species from the Marshall Islands. Japan, Australia, Gambier Islands, New Caledonia, Indian Ocean, and Marshall Islands.

**Opistosyllis brunnea** Langerhans

Fauvel, 1953, pp. 155–156, fig. 78 a-k. ENIWETOK: Parry (O,L), Eniwetok (O,L), Iegurini (L), Bogombogo (L), Engebi (O), Aaraanbiru (O). BIKINI: Enyu (O,L). This is the first report of the species from the Marshall Islands. Indian Ocean, Madeira Islands, West Africa, and Marshall Islands.

**Opistosyllis longicirrata** Moreno

Fauvel, 1953, pp. 154–155, fig. 77 f–i. ENIWETOK: Eniwetok (O), Iegurini (O), Rigili (O), Bogombogo (O), Engebi (O), Aaraanbiru (O,L), Aniyaanii (L), Bogen (O). BIKINI: Enyu (O). This is the first report of the species from the Marshall Islands. Central Pacific Ocean to Red Sea.

**Syllis gracilis** Grube


**Trypanosyllis zebra** (Grube)


**Trypsosyllis brachychaeta** (Schmarda)


**Trypsosyllis byalina** (Grube)


**Trypsosyllis variegata** (Grube)


**Typosyllis prolifera** Krohn

Fauvel, 1953, pp. 149–150, fig. 74 a–g. ENIWETOK: Eniwetok (O), Engebi (O), Bogen (O). This is the first report of the species from the Marshall Islands. Cosmopolitan.

**Typosyllis cirropunctata** (Michel)

Fauvel, 1923, pp. 266–267, fig. 99 n–p. ENIWETOK: Parry (L), Bogen (O). This species was previously known only from Naples, Italy.

**Typosyllis armillaris** (Muller)


**Subfamily EUSYLLINAE**

**Odontosyllis byalina** Grube

Monro, 1931, pp. 12–13, fig. 7; Hartman, 1954a, p. 629. ENIWETOK: Parry (L), Lidilbut (O) by Hartman. RONGELAP: Rongelap by Hartman. A total of 35 specimens were collected with the use of a night light on August 28, 1956. The water was 15 ft deep, and the bottom consisted of coral sand. These specimens were epitokes and were phosphorescent along their entire length. The specimens emitted their eggs or sperm in the laboratory. Fertilization and cleavage were noted that evening. No further attempt was made to follow the development of this species. Great Barrier Reef, Singapore, and Marshall Islands.

**Subfamily EXOGONINAE**

**Exogone verugera** Claparède


*Sphaerosyllis pirifera* Claparède


*Parasphaerosyllis indica* Monro


**Family NEREIDAE**

**KEY TO THE SPECIES FROM MARSHALL ISLANDS**

1. Peristomium with parapodia and setae; proboscis lacks paragnaths
   - *Micronereis eniwetokensis*

2. Paragnaths soft *Ceratocephala coralllicola*
3. Paragnaths horny
4. Paragnaths present only on distal ring of proboscis
   - *Ceratonereis*
5. Paragnaths present on both rings of proboscis
6. Prostomium with deep cleft between antennae
   - *Ceratonereis mirabilis*
7. Prostomium without cleft
8. Posterior neuropodial falcigers with terminal end fused to stalk
   - *Ceratonereis pachybaeta*
9. Posterior neuropodial falcigers not fused
   - *Ceratonereis costae*
10. All paragnaths conical
11. Some paragnaths transverse, or pectinate
12. Posterior notopodial lobes with homogomph falcigerous and spiniger setae
   - *Nereis zonata perisca*
13. Posterior notopodial with only spiniger setae

**8. A broad belt of paragnaths around the oral ring** *Neanthes arenaceodentata*

**8. Area VI with 2 or 3 paragnaths in a row** *Neanthes dawydovi*

**9. Transverse paragnaths on area VI**
   - *Perinereis*

**9. Pectinate paragnaths on maxillary ring**
   - *Platyneres*

**9. Paragnaths are conical, pectinate, and transverse**
   - *Pseudonereis*

**10. Area I of maxillary ring with a group of 4–12 conical paragnaths**
   - *Perinereis nigropunctata*

**10. Area I with 1–2 paragnaths**

**11. Tentacular cirri extend to 5–6 segments**
   - *Perinereis califera*

**11. Tentacular cirri extend to 8–9 segments**
   - *Perinereis belleri*

**12. Area VI with 1–2 curved rows of paragnaths; blade of falciger with pointed tip or slightly rounded**
   - *Platyneres dumerilii*

**12. Area VI with 1 row of paragnaths; blade of falciger broadly rounded**
   - *Platyneres pulchella*

**12. Area VI with oval cluster of pectinate paragnaths; known only from epitokal stage at Eniwetok**
   - *Platyneres polyclamal*

**13. Area V with 1 paragnath; area VI each with a large paragnath**
   - *Pseudonereis gallapensis*

**13. Area V lacking paragnaths; area VI each with a row of paragnaths**
   - *Pseudonereis anomala*

**Ceratocephala coralllicola**, new species

Fig. 4 (1–5)

Eight complete specimens were collected from Bogen Island at Eniwetok Atoll on September 12, 1956. They ranged in size from 5 to 20 mm in length and possessed from 38 to 112 setigerous segments. The holotype measures 12 mm in length, 0.5 mm in width, and possesses 90 setigerous segments. The prostomium bears four pairs of eyes in trapezoidal arrangement, with the anterior pair farther apart. The anterior part is crescent in shape and the posterior ones.
Fig. 4, 1–3. *Ceratocephala corallicola*, n. sp. 1, Parapodium of segment 14; 2, parapodium of segment 42; 3, parapodium of segment 76; 4, homogomph spiniger from notopodium; 5, heterogomph falcigerous seta from neuropodium.

6–9. *Euchone eniwetokensis*, n. sp. 6, Suspatulate seta from thoracic notopodium; 7, long-handed uncinus from thoracic neuropodium; 8, avicular hook from abdominal notopodium; 9, capillary seta from abdominal neuropodium.
circular. The prostomium also bears a pair of antennae and biarticulated palpi. Areas VI of the proboscis each bears a pair of conical papillae, and areas VII and VIII possess eight papillae in a single row. The other areas lack papillae. Three of the four pairs of peristomial tentacles are short, and the fourth pair is long. The first two setigerous segments are uniramous. Biramous parapodia begin with segment 3, with each ramus possessing a yellow to black aciculum. The parapodia of segments 14, 42, and 76 are shown in Figure 4, 1–3. The notopodium bears only homogomph spinigers (Fig. 4, 4). The neuropodium has superior homogomph spinigers and heterogomph falcigers (Fig. 4, 5). The pygidium terminates with two filiform cirri.

ECOLOGY: All eight specimens were collected from pieces of coral heads taken from shallow water at Bogen Island opposite the deep channel entrance between Parry and Japant islands. Along with C. corallicola, 20 other species of polychaetes were collected, the principle ones being Typosyllis brachycaeta, Eunice (N). gracilis, Palola siciliensis, and Polyphthibalmus pictus.

REMARKS: The genus Ceratonereis is known from eight species and subspecies (Hartman, 1959, 1960; Hartmann-Schröder, 1962). C. corallicola and C. edmondi Hartman (1954b) from Australia may be separated from the other known species by the possession of a single ventral cirrus rather than a bifurcated one. C. corallicola differs from C. edmondi by the absence of papillae on areas I to IV, and by the presence of two papillae rather than one on a side on area VI.

TYPE MATERIAL: Holotype and six paratypes in the U.S. National Museum.

Ceratonereis costae (Grube)
Fauvel, 1953, pp. 194–195, fig. 98 a–f; Hartman, 1954a, p. 629. Specimens unquestionably referred to this species were reported from an unspecified locality at Bikini Atoll by Hartman. Cosmopolitan.

Ceratonereis mirabilis Kinberg
Fauvel, 1953, pp. 200–201, fig. 103 a–c; Hartman, 1954a, p. 629. ENIWETOK: Parry (O,L), Eniwetok (L), Iurin (L), Rigili (O), Bogombog (O,L), Engebri (O), Aaraanbiru (O,L), Bogen (O), and also from Lidilibut (O) by Hartman. Cosmopolitan in the warmer seas.

Ceratonereis pachybaeta Fauvel
Fauvel, 1953, p. 196, fig. 99 a–h; Hartman, 1954a, p. 629. Hartman reported this species from Bikini Island at Bikini Atoll and from Rigoman and Rongelap Islands at Rongelap Atoll. Central Pacific Ocean to Gulf of Suez.

Neathes arenaceodentata (Moore)
Nereis arenaceodentata Moore, 1903, pp. 720–723, pl. 40, figs. 1–10.
ENIWETOK: Parry (O,L). A total of 24 specimens were collected; all but 5 were taken from the sandy mud found at the bottom of the trough of the domestic outfall sewer. The other collection came from sand at a depth of 15 ft from the lagoon side of Parry Island. This is the first report of the species from the Marshall Islands. Cosmopolitan.

Neathes dawydovi (Fauvel)
Nereis dawydovi Fauvel, 1937, p. 297–299, fig. 1 a–k.
ENIWETOK: Parry (O), Engebri (O), Aaraanbiru (O); also from Lidilibut (O) and from Rongelap Atoll by Hartman. Central Pacific Ocean to Indo-China.

Nereis zonata periscia Fauvel

Platynereis polyclasma Chamberlin
Fauvel, 1953, pp. 221–222, fig. 112 a–e; Hartman 1954a, p. 629. ENIWETOK: Parry (L). Hartman reported this species from Rongelap Atoll. A total of 40 epitokes were collected from two localities on the lagoon side of Parry Island.
with the use of the night light. The water was approximately 15 ft deep and the substrate consisted of white coral sand at both localities. On August 28, 1956, 13 females and 22 males were captured; 5 males were collected on September 3, 1956. Tropical Pacific Ocean and Indian Ocean.

Platyneris pulchella Gravier
Faurel, 1953, pp. 220–221, fig. 112 f–h. ENIWEOTOK: Parry (O.L), Eniwetok (O), Igerin (O), Rigili (O), Bogombo (L), Engebi (O), Aaraanbiru (O.L), Aniyaanii (O), Japtan (L), and Bogen (O). Bikini: Enyu (O.L). This is the first report of the species from the Marshall Islands. Red Sea, Persian Gulf, Arabian Sea, Indian Ocean, and Marshall Islands.

Perinereis belleri Grube

Eniwetok: Aniyaanii (L). This is the first report of the species from the Marshall Islands. Pacific, Atlantic, and Indian oceans.

Perinereis nigropunctata Horst
Faurel, 1953, p. 210, fig. 107 b–f. This is the first report of the species from the Marshall Islands. Indian Ocean, Malay Archipelago, and Marshall Islands.

Perinereis culifera Grube

Pseudonereis anomala Gravier

Pseudonereis gallapagensis Kinberg
Faurel, 1953, pp. 215–217, fig. 110 a–c; Hartman, 1954a, p. 629; Hartmann-Schröder, 1965, pp. 129–30. ENIWETOK: Parry (O), Bogombo (O), Engebi (O), Aaraanbiru (O), Aniyaanii (O), and from Lidilbut (O) and Japtan (O) by Hartman. MAJURO: Uliga (O, L). Tropical Pacific Ocean, Indian Ocean, West Africa, and Brazil.

Micronereis eniwetokensis Reish
Reish, 1961a, pp. 273–277, figs. 2–6. ENIWETOK: Parry (L), Igerini (O), and Aaraanbiru (L). This species is known only from these localities.

Family NEPHTYIDAE

Micronephys spharocirrata (Wesenberg-Lund)


Family Sphaerodoridae

Sphaerodorum pacificum Hartman
Hartman, 1954a, pp. 634–637, figs. 176 A, 177 I–J. ENIWETOK: Bogen (O) (1 specimen), and from Lidilbut (O) by Hartman. This species is known only from these localities on Eniwetok Atoll.

Family GLYCERIDAE

Glycera tesselata Grube

Family EUNICIDAE

KEY TO THE SPECIES FROM MARSHALL ISLANDS

1. Prostomium with 5 antennae .......... 2
2. Peristomium with a pair of cirri; branchiae present or nearly absent .......... 3
3. Peristomium without cirri; branchiae absent ............ Paramarphysa orientalis
3. Pectinate setae and acicular hooks present

*Ennica* 4

3. Pectinate setae and acicular hooks absent

*Palola siciliensis*

4. Branchiae present through a considerable region ........ Ennica, sensu latoir 5

4. Branchiae absent or nearly so

*Ennica* (Nicidion) gracilis

5. Acicular setae bidentate ..................... 6

5. Acicular setae tridentate ..................... 7

6. Branchiae begin at segment 24, with 6–10 filaments; sides of pectinate setae equal

*Ennica johnsoni*

6. Branchiae begin at segments 10–20, with 6–16 filaments; sides of pectinate setae unequal ............... *Ennica afrana*

7. Branchiae begin at segments 4–6 and extend throughout most of the length

*Ennica antennata*

7. Branchiae begin at segments 6–7 and are present only on the anterior third of the body ....................... *Ennica antennata*

*Ennica afrana* Peters

Fauvel, 1953, pp. 235–236, fig. 116 h–i; Hartman, 1954a, p. 629. ENIWETOK: Eniwetok (O,L), Igerini (O), Rigili (O), Engebi (O), Aaraanbiru (O,L), Aniyaanii (O,L), Japatan (O), and also Lidilbut (O) by Hartman. BIKINI: Enyu (O), and also Enrik, Yomyaran, and Namu (O,L) by Hartman. RONGELAP: Eniwetok by Hartman. Indo-Pacific Ocean and Red Sea.

*Ennica antennata* (Savigny)

Fauvel, 1953, p. 240, fig. 118 f–g; Hartman, 1954a, p. 629. ENIWETOK: Parry (O,L), Bogomogo (O), Engebi (O), Aniyaanii (L), and from Japatan (O) by Hartman. She reported this species also from Bikini: Namu (O); RONGELAP: Burok (O); RONERGER: Latoback. Indo-Pacific Ocean, Persian Gulf, and Red Sea.

*Ennica australis* Quatrefages

Fauvel, 1953, p. 240, fig. 118 h–l. ENIWETOK: Engebi (L). This is the first report of the species from the Central Pacific; it has been previously collected from Australia, New Zealand, India, Maldives Archipelago, Zanzibar, and Cape of Good Hope.

*Ennica johnsoni* Hartman

Hartman, 1954a, pp. 633–634, fig. 175 A–C, E–F. This species is known only from one specimen from Bikini Atoll.

*Lysidice collaris* Grube

Fauvel, 1953, p. 248; Hartman, 1954a, p. 629; Hartmann-Schröder, 1965, pp. 136–137. ENIWETOK: Parry (O,L), Eniwetok (O,L), Igerini (O), Rigili (O), Bogomogo (O,L), Engebi (O), Aaraanbiru (O,L), Aniyaanii (O, L), Japatan (O,L), Bogen (O), and also Lidilbut (O) by Hartman. BIKINI: Enyu (O,L), and by Hartman from Namu (O). MARJURO: Uliga (O). Japan, Indo-Pacific Ocean, Persian Gulf, and Red Sea.

*Nematoneres unicornis* Schmarda


*Ennica* (Nicidion) gracilis Crossland

Fauvel, 1953, pp. 243–244, fig. 122 a–f; Hartman, 1954a, p. 629. ENIWETOK: Eniwetok (L), Rigili (O), Japatan (O), and Bogen (O). BIKINI: Enyu (L), and by Hartman from Enrik. Warmer waters of Indo-Pacific Ocean.

*Palola siciliensis* (Grube)


*Ennica siciliensis*. Fauvel, 1953, pp. 241–2, fig. 121 e–m.

ENIWETOK: Parry (L), Eniwetok (O,L), Igerini (O), Rigili (O), Bogomogo (L), Engebi (O), Aaraanbiru (O,L), Aniyaanii (O, L), Japatan (O,L), Bogen (O), and also from Lidilbut (O) by Hartman. BIKINI: Enyu (O,L) and Yomyaran by Hartman. RONGELAP: Kabelle and Burok (O) by Hartman. Cosmopolitan, especially in warmer waters.

*Paramorphysa orientalis* Willey

Fauvel, 1953, pp. 247–248; Hartman, 1954a, p. 629. ENIWETOK: Eniwetok (L), Aniyaanii (L), Bogen (O), and reported by Hartman.
from Lidilbut (O) and Japtan (O), Bikini: Enyu (L). Warmer waters of Indo-Pacific Ocean.

Family LUMBRINERIDAE
KEY TO THE SPECIES FROM MARSHALL ISLANDS
1. Prostomium bluntly conical
   Lambrineris latreilli
1. Prostomium short, globular
   Lambrineris sphaerocephala

Lambrineris latreilli? Audouin and Milne Edwards
Lumbriconereis latreilli Audouin and Milne Edwards [sic]. Fauvel, 1953, pp. 266–267, fig. 134 m–r.
Hartman reported this species, with question, from the ocean side of Bikini Island, Bikini Atoll. Cosmopolitan in warmer seas.

Lambrineris sphaerocephala (Schmarda)
Notocirrus sphaerocephalus Schmarda, 1861, p. 116.
Lumbriconereis sphaerocephala (Schmarda). [sic], Fauvel, 1953, p. 267, fig. 135, c–f.
ENIWETOK: Lidilbut (O) by Hartman. Central Pacific Ocean to Indian Ocean.

Family ARABELLIDAE
KEY TO THE SPECIES FROM MARSHALL ISLANDS
1. Parapodia with heavy, projecting acicula; capillary setae with smooth margins
   Drilonereis major
1. Parapodia without projecting, heavy acicula; some capillary setae dentitions along part of one margin ............... Arabella mutans
2. Acicular setae with asymmetrical hood
   Arabella mutans
2. No such type of acicula Arabella mutans

Arabella iricolor (Montagu)
Fauvel, 1953, 224–225, fig. 140 a–h; Hartman, 1954a, p. 629. ENIWETOK: Parry (O,L), Eniwetok (O,L), Igarini (O,L), Japtan (O), Bogen (O), and from Rigili (L) by Hartman. Cosmopolitan.

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Arabella mutans (Chamberlin)
Fauvel, 1953, p. 275, figs. 140 i–l, 143 g–i; Hartman, 1954a, p. 629. ENIWETOK: Parry (O), Eniwetok (O), and reported by Hartman from Rigili (L) and Japtan (O). Cosmopolitan in the warmer seas.

Drilonereis sp. cf. D. major Crossland
Hartman, 1954a, p. 634. One specimen was taken from Namu Island (O), Bikini Atoll. Hartman stated that this specimen comes closest to D. major but differs in several respects.

Family LYSARETIDAE

Aglaurides fulgida (Savigny)

Family DORVILLEIDAE
KEY TO THE SPECIES FROM MARSHALL ISLANDS
1. Nuchal tentacle present; dorsal cirrus entire; acicular lobe broad
   Papilliodorvillea gardineri
1. No nuchal tentacle; dorsal cirrus jointed at end; acicular lobe narrow
   Dorvillea similis

Papilliodorvillea gardineri Crossland
Stauropses (Dorvillea) gardineri Crossland, 1924, p. 93, figs. 112–118. S. gardineri. Fauvel, 1953, p. 280, fig. 143 d–f.
ENIWETOK: Bogomogo (L) and Lidilbut (O) by Hartman. BIKINI: Enrik (O), by Hartman. Marshall Islands to East Africa.

Dorvillea similis Crossland
Hartman, 1954a, p. 629. ENIWETOK: Parry (L), Eniwetok (O,L), Rigili (O), Bogomogo (O), Japtan (O), and also from Bogon (O) and Lidilbut (O) as reported by Hartman. Gulf of Suez and Marshall Islands.
Family Orbiniidae

Naïneris sp.

Hartman, 1954a, p. 637. One small specimen agreeing with the description given by Hartman was taken from the ocean side of Bogon Island at Eniwetok Atoll. Hartman reported it from the ocean side of Bogon and Parry islands.

Family Spionidae

KEY TO THE SPECIES FROM MARSHALL ISLANDS

1. Fifth setigerous segment modified ... 2
2. Fifth setigerous segment not modified 8
3. Branchiae begin anterior to the fifth setigerous segment; neuropodial hooded hooks begin on setigerous segment 9
4. Branchiae present on segments 7–12; posterior neuropodial spines arranged in a cone 
   Polydora armata
5. Branchiae present on segments 10–26; posterior neuropodium with only capillary setae ....... Polydora tridenticulata
6. Prostomium without nuchal tentacles and eyes; special setae of fifth segment expanded distally with a hairy top and falcate hooks ....... Pseudopolydora reisi
7. Prostomium with nuchal tentacles and eyes ..................... 7
8. Prostomium with distinct frontal horns; branchiae on all but posterior segments
   Malacoceros (Malacoceros) indicus
9. Branchiae limited to few anterior segments .... Prionospio cirrifera
10. Branchiae present on nearly all segments ....................... 10
11. Bidentate hooded hooks present in neuropodium and neuropodium
    Scolelepis (Scolelepis) bonnier
12. Entire hooded hooks present only in neuropodium ... Spio filicornis

Malacoceros (Malacoceros) indicus (Fauvel)
Scolelepis indica Fauvel, 1953, pp. 313–314, figs. 165 g–m.
Malacoceros (Malacoceros) indicus (Fauvel).
ENIWETOK: Party (L). This is the first report of the species from the Marshall Islands. Tropical Pacific, Indian Ocean, South Africa.

Polydora armata Langerhans
Woodwick, 1964, pp. 147–148, figs. 2 (1–6). ENIWETOK: Eniwetok (O.L), Rigili, Engebi, Aaraanbiru, Aniyaanii, and Japant. BIKINI: Enyu. These specimens were identified and reported by Woodwick (1964). Cosmopolitan.

Polydora tridenticulata Woodwick
Woodwick, 1964, pp. 153–155, figs. 4 (1–5). ENIWETOK: Rigili (L), Engebi (L), and Japant (O.L). These specimens were identified and reported by Woodwick (1964). This species is known only from Eniwetok Atoll.

Prionospio cirrifera Wirén
Fauvel, 1953, p. 324, figs. 164 k–m. ENIWETOK: Parry (L), Bogombogo (O), and Aaraanbiru (O). Cosmopolitan.

Pseudopolydora antennata (Claparede)
Woodwick, 1964, pp. 148–151, fig. 2 (7–8); Imajima and Hartman, 1964, pp. 286–287.
Polydora (Carazzi) antennata Claparede.
Fauvel, 1953, pp. 316–7, figs. 166 i–m.

Annelids of Marshall Islands—Reish
ENIWETOK: Parry (O,L), and Eniwetok (O, L). MAJURO: Uliga. These specimens were identified and reported by Woodwick (1964). Atlantic Ocean, Mediterranean Sea, Arabian Sea, Indo-Pacific regions, South Africa, and Japan.

Pseudopolydora coralicola Woodwick
Woodwick, 1964, pp. 151–152, fig. 2 (9–12). ENIWETOK: Engebi (O). This species is known only from this locality.

Pseudopolydora pigmentata Woodwick
Woodwick, 1964, pp. 152–153, figs. 3 (4–6). ENIWETOK: Eniwetok (L) and Engebi (L). This species is known only from these collections as described by Woodwick (1964).

Pseudopolydora reishi Woodwick
Woodwick, 1964, p. 152, figs. 3 (1–3). ENIWETOK: Parry (O) and Engebi (L). This species is known only from this locality.

Scolelepis (Scolelepis) bonnieri (Mesnil)
Nerine bonnieri. Fauvel, 1927, pp. 35–36, figs. 12 f-o.
ENIWETOK: Rigili (O) and Japtan (L). This species was previously known only from France. Two specimens collected agree with the account of this species as given by Fauvel (1927).

Spio filicornis (Müller)
Fauvel, 1927, pp. 43–44, figs. 15 a–g. MAJURO: Uliga (O). This is the first report of the species from Marshall Islands. Cosmopolitan.

Tripolydora spinosa Woodwick
Woodwick, 1964, pp. 155–156, figs. 4 (6–9). ENIWETOK: Rigili (L) and Bogombogo (L). This species was described by Woodwick (1964) from these collections.

Family CHAETOPTERIDAE
KEY TO THE SPECIES FROM MARSHALL ISLANDS
1. One pair of tentacles
2. Two pairs of tentacles

Phyllochaetopterus 3
2. Two or three median segments; the notopodia of these segments separate and conical in shape . . . . Mesochaetopterus minutus

2. Five median segments with the notopodia of the first two aliform in shape and the last three cup-shaped . . . Chaetopterus sp.

3. Larger, 15 anterior segments; 3 smaller modified setae on the fourth segment; about 16 segments to mid-region

Phyllochaetopterus ramosus

3. Smaller; 10–18 or more anterior segments; 1 smaller modified seta on fourth segment; 5–28 segments to mid-region

Phyllochaetopterus socialis

Chaetopterus sp.
One incomplete specimen, which was similar to the one reported by Hartman, was taken from sand in 10 ft of water on the lagoon side of Parry Island, Eniwetok Atoll. This sandy area had a heavy concentration of two other members of the Family Chaetopteridae, Mesochaetopterus minutus and Phyllochaetopterus ramosus. Repeated attempts were made to secure additional material of Chaetopterus sp. without success. Hartman’s report was based on a single individual taken from the lagoon side of Rongelap Island, Rongelap Atoll.

Mesochaetopterus minutus Potts
Fauvel, 1953, pp. 342–4, fig. 178a; Hartman, 1954a, p. 629. ENIWETOK: Parry (O,L), Iurgini (L), Rigili (L), Bogombogo (O,L), Japtan (O), and Bogen (O). MAJURO: Uliga (L). Cosmopolitan in warmer seas.

Phyllochaetopterus ramosus Willey
Willey, 1904, p. 293, pl. 5, figs. 133–136. ENIWETOK: Parry (O,L), Rigili (L), Bogombogo (O), Aaraanbiru (L), Japtan (L). Hartman reported two specimens from Bikini Atoll which she believed were to be compared with P. ramosus. They differed from this species and the present account by the fewer number of segments to the anterior region and by a greater number of modified setae on the fourth segment. Ceylon and Marshall Islands.

Phyllochaetopterus socialis Claparède

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ENIWETOK: Parry (L) and Japtan (O). MAJURO: Uliga (O). Cosmopolitan in the warmer seas.

Family MAGELONIDAE

Magelona sp.

One specimen was taken from sand collected from 10 ft of water at the ocean side of Rigili Island at Eniwetok Atoll. The worm was small and in a poor state of preservation.

Family CIRRATULIDAE

KEY TO THE SPECIES FROM MARSHALL ISLANDS

1. One pair of palp; tentacular filament numerous 2
   2. Dorsal transverse tentacular filaments and lateral tentacular filaments begin at same segment .......... Cirratus sp.
   2. Lateral tentacular filaments begin anterior to dorsal transverse group
      Cirriformia seminicta

Cirratus sp.


Cirriformia seminicta (Ehlers)

Audouinia seminicta (Ehlers). Fauvel, 1953, pp. 330–1, fig. 174 c.


ENIWETOK: Parry (O,L), Eniwetok (O,L), Igurini (L), Rigili (O,L), Bogombogo (O), Engebi (O,L), Aaraanbiru (L), Aniyaanii (O), Japtan (L), and Bogen (O). Hawaiian Islands to Red Sea.

Dodecaceria laddi Hartman

Hartman, 1954a, p. 638, figs. 176 a–c, 177 d–h. ENIWETOK: Parry (O,L), Eniwetok (O,L), Igurini (O,L), Rigili (O,L), Bogombogo (O,L), Engebi (O,L), Aaraanbiru (L), Aniyaanii (L), Japtan (O,L), and Bogen (O), and also from Lidilbut (O) as reported by Hartman. BIKINI: Enyu (O,L). MAJURO: Uliga (O).

Dodecaceria laddi was described as having one pair of palpi and two pairs of tentacular cirri; Hartman also reported one specimen with only three tentacular cirri. Specimens from the present collection were observed possessing from two to four pairs of tentacular cirri. One specimen collected from Majuro Atoll on August 30, 1956, possessed swimming setae along its entire length. A pair of red eyespots was present on the dorso-lateral side of the prostomium of this worm. The possession of swimming setae is well known in D. concharam Oersted (Fauvel, 1927). Marshall Islands.

Family CTENODRILIDAE

Ctenodrilus serratus (Schmidt)

Hartman, 1944, p. 323, pl. 27, figs. 6–7. One specimen, measuring 1.0 mm in length, was taken from sand collected from 90 ft of water in the lagoon off Parry Island, Eniwetok Atoll. This is the first report of the species from the Marshall Islands. Known previously from Europe, West Indies, and the eastern Pacific Ocean, the distribution is herein extended into the central Pacific Ocean.

Family OPHELIDAE

KEY TO THE SPECIES FROM MARSHALL ISLANDS

1. Lateral gills present Armandia lanceolata
   1. Lateral gills absent Polyophtalmus pictus

Armandia lanceolata Willey


Polyophtalmus pictus (Dujardin)

Fauvel, 1953, pp. 360–1, figs. 187 1–o; Hartman, 1954a, p. 629; Imajima and Hartman, 1964, p. 309; Hartmann-Schröder, 1965, p. 149. ENIWETOK: Parry (O,L), Eniwetok (O), Igurini (O,L), Rigili (O,L), Bogombogo (O,L), Engebi (O,L), Aaraanbiru (L), Aniyaanii (L), Japtan (O,L), and Bogen (O), and reported by Hartman from Lidilbut (O). BIKINI: Enyu (O,L) and reported by Hartman.
from Namu (L). MAJURO: Uliga (O). This is one of the most commonly encountered polychaetes in the Marshall Islands. Cosmopolitan.

**Family capitellidae**

**KEY TO THE SPECIES FROM MARSHALL ISLANDS**

1. Posterior end terminates in anal plate **Heteromastides bifidus**
   1. Posterior end rounded .......................... 2
   2. Capillary setae begin at first segment posterior to prostomium; specialized genital setae in segments 8 and 9 of male **Capitella capitata**
   2. Capillary setae begin at second segment posterior to prostomium; no specialized genital setae ............................................. 3
   3. Hooks begin at setigerous segment 13; no branchiae .......... **Leiochrides? biceps**
   3. Hooks begin at setigerous segment 14; branchiae present ...... **Dasybranchus parryi**
   4. Anterior abdominal notopodia widely separated from one another **Dasybranchus caducus**
   4. Anterior abdominal notopodia close to one another ...... **Dasybranchus lumbricoides**

**Capitella capitata** (Fabricius)
Hartman, 1947, pp. 404–405, pl. 43, figs. 1–2; Imajima and Hartman, 1964, pp. 311–12, pl. 37, figs. a–g. ENIWE-TOK: Parry (L), Engebi (L). Only three specimens of this species were taken, two from a sediment bottle collector (Reish, 1961b) suspended for 28 days at one of the boat docks on the lagoon side of Parry Island. This is the first report of the species from the Marshall Islands. Cosmopolitan.

**Dasybranchus caducus** (Grube)

**Dasybranchus lumbricoides** Grube

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Bikini Atoll by Hartman. Widespread throughout Indo-Pacific Ocean.

**Leiochrides? biceps** Hartman
Hartman, 1954a, pp. 638–639, figs. 177 a–c. This species is known from only one incomplete specimen from Rigonman Island, Rongelap Atoll.

**Heteromastides bifidus** Augener
Fauvel, 1953, p. 368, figs. 192 a–b. ENIWE-TOK: Parry (O,L), Eniwe-Tok (O), Igarini (L), Rigili (L), Bogomogo (O), Engebi (O), and Bogen (O). MAJURO: Uliga (O). The distribution is herein extended into the central Pacific Ocean from Australia and India.

**Family arenicolidae**

**Branchiomaldane vincenti** Langerhans
Hartman, 1954a, p. 626.


Reported from the ocean side of Japant, Eniwe-Tok Atoll by Hartman. Atlantic and Pacific oceans.

**Family maldanidae**

**Axiothella australis** Augener
Fauvel, 1953, pp. 381–382, figs. 197 f–g. ENIWE-TOK: Parry (L), Rigili (O), Bogomogo (O), Aaraanbiru (O), and Bogen (O). BIKINI: Enyu (O). MAJURO: Uliga (O). The distribution is herein extended from Australia and India to the Marshall Islands.

**Family terebellidae**

**KEY TO THE SPECIES FROM MARSHALL ISLANDS**

1. Branchiae absent ....... **Polycirrus medius**
   1. Branchiae present .............................. 2
   2. Uncini set in single rows throughout thoracic region ............ **Thelepus** sp.
   2. Uncini set in double rows in at least part of thoracic region .......... 3
   3. Thoracic notosetae serrated at tip **Terebella ehrenbergi**
   3. Thoracic notosetae with smooth edges 4
   4. Branchiae filiform ....... **Leaena minuta**
   4. Branchiae arborescent ............ 5
5. Thoracic uncini pectinate *Loimia medusa*
5. Thoracic uncini avicular

*Eupolymnia trigostoma*

*Eupolymnia trigostoma* (Schmarda)

*Polymnia nebulosa* (Montagu). Fauvel, 1953, pp. 419–420, figs. 419 a–g (in part).


**Eniwetok**: Bogombogo (O, L). Reported from Bikini Atoll by Hartman. Indo-Pacific Ocean.

*Leaena minutata* Hartman

Hartman, 1954a, p. 639, figs. 178 E, H. This species was described from seven species collected from coral heads on the seaward side of Parry Island, Eniwetok Atoll. It has not been collected since.

*Loimia medusa* (Savigny)


*Polycirrus* sp. cf. *P. medius* Hesse

Hartman, 1954a, pp. 639–641. One specimen was reported from Enirik Island, Bikini Atoll by Hartman; it comes close to *P. medius* but differs in the nature of the ventral gland shield.

*Terebella ehrenbergi* Grube


**Eniwetok**: Parry (L), Igorini (O), Aniyau (L), and reported from Lidilbut (L) by Hartman. **Bikini**: Enyu (O). Indo-Pacific Ocean and Red Sea.

*Thelepus* sp.

One small specimen, agreeing with the generic diagnosis, was taken from an old coral head in 5 ft of water on the lagoon side of Parry Island, Eniwetok Atoll. It was in a poor state of preservation, so that a specific determination could not be made.

**Family SABELLIDAE**

**KEY TO THE SPECIES FROM MARSHALL ISLANDS**

1. Thoracic neuropodia with avicular uncini
2. Thoracic neuropodia with long-handled cromets

2. Branchiae borne on short stalk; pigmented patches arranged laterally throughout length


3. Thoracic with 8 setigerous segments; abdomen with 3 setigerous segments


3. Thoracic with 8 setigerous segments; abdomen with 13 or 14 setigerous segments, with the 6 posterior ones forming an anal depression


**Euchone eniwetokensis**

**Genus Euchone** Malmgren

**Euchone eniwetokensis**, n. sp.

Fig. 4 (6–9)

Two specimens were collected from 90 ft of water in the lagoon near Parry Island by Mike Chamberlain on September 14, 1957. These minute specimens measured 2.5 mm and 2.0 mm, including the branchial crown. Both specimens had 8 thoracic segments; one had 13, the other, 14 abdominal segments including the 6 segments comprising the anal depression.

The branchial crown is pinnate and the radioles are united with a membrane for one-third their length. Radioles number 3 and 4 on a side in one specimen and 3 each on the other.

The thoracic setae are simple capillary and subcapillary with a mucron in the notopodium (Fig. 4, 6), and number about 3–4 per segment each. Long-handled uncini (Fig. 4, 7) are present in the neuropodium and number about 5 per segment.

Abdominal notopodial setae are avicular hooks (Fig. 5, 8) and number about 30 per segment. Only simple capillary setae (Fig. 5, 9) are present in the neuropodium. The setae of the anal depression are the same as those in the more anterior abdominal segments.

**ECOLOGICAL NOTES**: The tube is unknown. These specimens were collected from 90 ft of
water from sand which was brought to the surface. Associated polychaetes with this species include *Typosyllis closterobranchia* Schmarda and *Micronephys sphæoricrâta* (Wesenberg-Lund).

**Remarks:** The genus *Euchone* is now known from 18 species (Hartman, 1951, 1959, 1965; Day, 1961; Reish, 1960, 1965), 9 of which have been reported from the Pacific Ocean. Previous localities from this ocean include Alaska, British Columbia, southern California, Okhotsk Sea, Kamchatka, and Japan. *Euchone* has not been collected previously from the central Pacific Ocean.

*Euchone eniwetokensis* is distinguished from the majority of the species in the genus by the small number of branchial filaments and the number of segments to the anal depression. It comes closest to *E. papillosa* (Sars), known from the Arctic-boreal region, since both species have only six segments to the anal depression. They differ in the total number of segments, the number of branchial filaments, and the length.

**Type Material:** The holotype and one paratype have been deposited in the U.S. National Museum.

*Fabricia bikini* Hartman
Hartman, 1954a, p. 641, figs. 178 a–d. Many specimens were collected from white coral sand at Bikini Island, Bikini Atoll, in 1950; it has not been taken since.

*Hypicomus phaetaenia* (Schmarda)

*Megalomma trioculatum*, n. sp.
Fig. 5 (1–10)

Five specimens, four of which were complete, were collected from three islands at Eniwetok Atoll. Two collections of one specimen each were taken from a sandy bottom in 3 m of water on the lagoon side of Parry Island on June 29 and 30, 1957. The collection of three specimens taken from algal holdfast on September 7, 1957, from the lagoon side of Engebi Island, was selected as type material. Specimens measured 7–14 mm in length including a branchial crown length of 2–3 mm; the holotype was 14 mm in length including a branchial crown of 3 mm. Four specimens had 8 thoracic, one had 9; abdominal segments numbered from 36 to 50 in complete specimens; the abdominal region consisted of 50 segments in the holotype.

Branchiae provided with 7–8 radiolose per side, the dorsal ones provided with large, dark eyes at the distal end (Fig. 5, 1); smaller eyes present near the tips of the other radiolose (Fig. 5, 2); the bars of the radiolose extend to near the tip of the radiolose. The branchial crown lacks pigmentation in preserved specimens. The collar extends from the mid-segmental line of the first setigerous segment anteriorly (Fig. 5, 3), forming a pocket on either side, to the lateral sides which have a slight notch, and ventrally to produce two triangular lobes that nearly touch one another along the mid-ventral line (Fig. 5, 4).

The notopodium of the first setigerous segment consists of about 8 single-winged capillary setae; neuropodial setae are lacking. Beginning with thoracic segment 2, the notopodium is provided with 3–4 single-winged capillary setae (Fig. 5, 5), and 5–6 subspatulate setae (Fig. 5, 6). Thoracic neuropodium provided with about 10 pennononed setae (Fig. 5, 7) and about 10 uncini (Fig. 5, 8); the abdominal notopodium with about 10 uncini (Fig. 5, 9) and the neuropodium with about 5 unequal double-winged capillary setae. The pygidium is provided with a dorsal triangular extension with a dorsal pair of eyespots.

**Remarks:** Twenty species have been assigned to the genus *Megalomma* (Hartman, 1959; Reish, 1963). *Megalomma trioculatum* belongs to that group of species which has eyes at the tips of all radiolose. It comes closest to *M. vigilans* (Claparède), reported as *Branchiomma vigilans* by Fauvel (1927) from the Mediterranean Sea. They differ in the nature of the collar; *M. trioculatum* lacks the membranous lobes at the base of the branchiae on the dorsal side in *M. vigilans*. *Megalomma vigilans* is a much larger species than *M. trioculatum*; it possesses about 150 segments, 20–25 pairs of radi-
Fig. 5, 1-10. *Megalomma trioculatum* n. sp. 1, Larger eye at the end of dorsal radiole; 2, smaller eye near tip of radiole; 3, anterior end, dorsal view; 4, anterior end, ventral view; 5, single-winged capillary seta from fifth thoracic notopodium; 6, subspatulate seta from fourth thoracic neuropodium; 8, uncinus from fourth thoracic neuropodium; 9, uncinus from abdominal notopodium; 10, double-winged capillary seta from abdominal neuropodium.

11-16. *Serpula barhamiae* n. sp. 11, Operculum; 12, bayonet seta from first thoracic segment; 13, capillary seta from first thoracic segment; 14, capillary seta from thoracic notopodium; 15, uncinus from thoracic neuropodium; 16, cup-shaped seta from abdominal neuropodium.
oles, and is 5–7 cm in length. The tube of *M. vigilans* is found among the dorsal setae of the polychaete *Aphrodite aculeata* Linnaeus. The specific name refers to the three types of eyes present.

**TYPE MATERIAL:** The holotype and two paratypes have been deposited in the U.S. National Museum.

**Family serpulidae**

**KEY TO THE SPECIES FROM MARSHALL ISLANDS**

1. Calcareous tube small and spirally coiled
   *Spirobranchus giganteus* .......................... 2
2. Operculum absent ................................. *Salmacina incrustans*
3. Operculum simple ................................. 4
4. Operculum compound ............................. 5
5. Central crown of operculum with pointed spines with lateral processes
   *Hydroides multiplinosa* .......................... 4
6. Operculum simple funnel
   *Serpula hartmanae* ............................... 4
7. Calcareous tube otherwise
   *Hydroides acuminate* ........................... 2
8. Operculum with a cylindrical or conical cap
   *Vermiliopsis glandigera* ........................ 3
9. Operculum with calcareous plate bearing branched spines
   *Serpula hartmanae* ............................... 4
10. Operculum with calcareous plate bearing simple spines
    *Salmacina incrustans* .......................... 2
11. Operculum present .............................. 3
12. Calcareous tube lacking lateral processes
    *Eupomatous albiceps* ........................... 5
13. Operculum compound ............................. 5
14. Calcareous tube lacking lateral processes
    *Hydroides multiplinosa* ........................ 4
15. Operculum simple funnel
    *Serpula hartmanae* ............................... 4

**Eupomatous albiceps** Grube

**Hydroides albiceps** (Ehrenberg) [sic]. Fauvel, 1953, p. 640, figs. 241 d–e.

**ENIWETOK:** Eniwetok (L), Rigili (L), Engebi (O.L.), Aaraanbiru (O), Aniyanni (L), Japtan (L), Bogen (O), and reported by Hartman from Lidilbut (O). BIKINI: Enyu (O). MAJURO: Uliga (O). The distribution is herein extended from the Mediterranean Sea and the Madeira Islands.

**Serpula hartmanae**, n. sp.

Fig. 5 (11–16)


Ten specimens were collected from seven stations at five islands at Eniwetok and Bikini atolls. They ranged from 10 to 15 mm in length and possessed about 80 setigerous segments, of which 7 comprised the thoracic region. The ocean side of Enyu Island at Bikini Atoll was selected as the type locality. Both the holotype and the single paratype measured 10 mm in length.

The anterior end bears 14 pairs of branchiae which have radioles for nearly their entire length. A funnel-shaped operculum (Fig. 5, 11) has 16–25 crenulations along its margin. A constriction occurs at the base of the funnel; two knobs are present at the junction of the funnel and opercular stalk. The operculum of the holotype has 19 crenulations. The collar is well developed except where it is separated at the mid-dorsal line. The collar is composed of two lateral and one ventral lobe. The ventral lobe is especially well developed. The collar margins overlap along the region of the mid-dorsal line in the region of the first and second thoracic setigerous segment.

The thoracic region consists of seven setigerous segments. The first thoracic segment bears 5 bayonet-type and 10 capillary-type setae (Figs. 5, 12 and 13). The notosetae of thoracic segments 2 to 7 are capillaries (Fig. 5, 14) and number about 12 per lobe. Thoracic uncini are provided with one larger and six progressively smaller teeth (Fig. 5, 15).

The abdominal region consists of about 75 setigerous segments. The abdominal uncini are similar to the thoracic uncini. The cup-shaped setae of the neuropodium possess one long spine and a serrated edge. Some of the posterior neuropodia are provided with simple capillaries.

The calcareous tube is white, circular in cross-section, and without ornamentation.
ECOLOGICAL NOTES: The majority of the specimens were collected from the ocean side of the islands. The tubes were attached to either corals or coralline algae. Hartman reported *Serpula* sp. from the ocean side of Lidilbut and Japtan Islands at Eniwetok Atoll.

REMARKS: The genus is known from about 16 recent species (Hartman, 1959; Pillae, 1960). *S. hartmanaе* can be readily separated from the majority of the known species in the genus by the small number of crenulations to its operculum. Three additional species are known to possess a small number of opercular crenulations: *S. watsoni* Willey (1905) with 25, *S. lo-biancoе* Rioja (1917) with 18–20, and *S. concharium* Langerhans (1880) with 18–22 crenulations. *S. hartmanaе* can be separated from *S. watsoni* on the basis of the long opercular funnel in the latter species; it can be separated from *S. lo-biancoе* by the asymmetrical operculum and the greater number of teeth and shape of the thoracic uncini in the latter species; it can be separated from *S. concharium* by the absence of a constriction at the base of the opercular funnel, by the fewer number of teeth and shape of the thoracic uncini, and by the presence of a dorsal ridge in the tube in the latter species.

TYPE MATERIAL: The holotype, one paratype, and additional material have been deposited in the collections of the U.S. National Museum.

*Spirobranchus giganteus* (Pallas)

Fauvel, 1953, pp. 462–463, figs. 252 a–g; Hartman, 1954a, p. 629. ENIWETOK: Parry (L), Engebi (O), Aaraanbiru (O), and by Hartman from Lidilbut (O). Only five specimens were collected by the author and all but one were attached to corals. Cosmopolitan in tropical seas, especially on coral reefs.

*Spirobranchus*, dextral and sinistral

Hartman, 1954a, p. 641. ENIWETOK: Parry (L), Eniwetok (O,L), Igurin (O), Rigili (O, L), Engebi (O), Aaraanbiru (O), Aniynanii (O,L), and Bogen (O,L). BIKINI: Enyu (O). MAJURO: Uliga (O). No attempt was made to identify these spirobids. These small coiled tubes were attached to rocks, corals, vermetid snails, other snails, and algae.

*Vermiliopsis glandigerus* Gravier

Fauvel, 1953, p. 467, fig. 242 k.

*Vermiliopsis* sp. Hartman, 1954a, p. 641. ENIWETOK: Parry (L), Igurin (O), Bogen (O), and it was reported as *Vermiliopsis* sp. by Hartman from Lidilbut (O) and Japtan (O,L). Cosmopolitan in the warmer seas.

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Annelids of Marshall Islands—Reish


The Folliculinids (Protozoa) of Ago Bay, Japan, and Their Relation to the Epifauna of the Pearl Oyster (Pinctada martensii)

DONALD C. MATTHEWS

Although the pearl oyster (Pinctada martensii) is widely dispersed throughout Japanese waters, that portion of Honshu south of Toba, in the many bays of Ise peninsula, excels as a favorable production center. This is largely because the cold Oya Shio (current) flowing south from the Kurile Islands meets the warm Kuro Shio between 35° and 40° N, sinks, and passes under it to well up again farther south, bringing an abundance of plankton. Thus, protected bays such as Ago, Matoya, and Gokasho provide an excellent environment for oysters and other filter-feeders to multiply. However, as the number of animals in the epifauna increases, available attachment sites decrease, and a sequential, complex epifauna develops on any suitable surface, whether glass plates or P. martensii imbricate scales.

Whereas some 50 species embracing many taxa (Protodonta, Porifera, Coelenterata, Nematoda, Polychaeta, Ostracoda, Harpactidea, Cumaacea, Amphipoda, Decapoda, Pycnogonida, Bryozoa, Mollusca, Echinodermata, and Tunicata) comprise this complex epifauna, the Polychaeta in particular, by the number and depth of their burrows, seriously affect the oysters’ well-being.

Korringa (1951) working on the epifauna of Ostrea edulis in the Oosterschelde, Holland, mentioned in his annotated list of species that folliculinids are among the first to appear, and he reasoned that because their growth and reproduction are so rapid they “... may be important as basic food for many members of the oysters’ epifauna.” Although Miyazaki (1938) made an extensive study of fouling organisms on shell-strings hung from rafts of Japanese oyster farms, interrelationships of species were not studied in detail.

The purpose of this paper is twofold: (A) to report the occurrence of folliculinids in Ago Bay, and (B) to determine whether folliculinids serve as food for P. martensii epifauna.

FOLLCULINIDS IN AGO BAY

Materials and Methods

In a combination of the methods of Moebius (1887), Miyazaki (1938), and Matthews (1962), shell collectors were suspended at various depths in Ago Bay from June through November, 1965, and sequential fouling periodically examined. Concurrently, folliculinids in the epifauna of living P. martensii, Pinna attenuata, and Chlamys nobilis suspended in baskets approximately one meter below oyster rafts of Ago Bay were similarly studied. Those readily identifiable folliculinids were figured and recorded, others were preserved and shipped to Honolulu for subsequent identification.

Results

The following folliculinids were obtained:

Ascobius sileni Hadzi, 1951, Slovenica Biology 2:114–122.


Figure 1A represents a ventral view of A. sileni taken at Ago Bay, June 21, 1965 from narrow cracks in the shells of Spirorbis sp. In such restrictive sites, the dorso-ventrally flattened lorica (f) seems attached throughout its length by a rather copious collectoderm (d). The lorica tapers rather gradually from its mouth (c) (almost devoid of collar) to the rounded and rather broad proximal end. Figure 1B represents a lateral view (left side) of A. sileni taken at the same time from spiral "chimneys" of the delicate, coral-like Bryozoa, Bugula dentata (Lamouroux) (see Utinomi, 1961:33, pl. 17, fig. 6) and from the smooth, "vertical" sides of Spirorbis sp. where attach-
Fig. 1. *Ascobius sileni*.

A, As viewed ventrally showing: a, left peristomal lobe; b, right peristomal lobe; c, mouth of lorica; d, collectoderm; e, spherical nucleus; f, lorica; g, spatulate foot.

B, As viewed from left side showing: a, position of left peristomal lobe; b, position of right peristomal lobe; c, collar; d, collectoderm; e, nucleus; f, lorica; g, non-spatulate-looking foot.
ment sites are not restrictive. In such instances, the lorica (Fig. 1B, f) is only slightly dorso-ventrally flattened and appears to be only partially attached throughout its length by the collectoderm (d). Thus, a short free neck is held above the substratum.

The length of the neck is difficult to measure since valves demarking neck from sac are absent. There are no longitudinal stripes, spiral whorls, rings, or extensions.

The species is further characterized by peristomal lobes of unequal length and breadth; the left (Fig. 1A, a and B, a) is always broader and longer than the right (b). Moreover, the left (Fig. 1B, a) is usually held at right angles to the longitudinal axis, whereas the right (b) is usually held vertically. In the hundreds of specimens observed, no finger-like projections were seen on the peristomal lobes.

The nucleus (e) is always spherical and appears as a mass of rather large granules in the posterior half of the extended body.

In specimens taken from restrictive areas (Fig. 1A) the dorso-ventrally flattened lorica (f) accentuates the spatulate nature of the foot (Fig. 1A, g), i.e., as the body contracts into a flattened lorica, the foot (g) is spread thinly into a broad spatula. However, when the lorica is not so dorso-ventrally flattened, the contracted body has more space and the foot (Fig. 1B, g) appears less spatulate.

Color: light greenish-blue through grey to colorless.


_Eufolliculina lignicola_ (Fig. 2) was first taken July 7, 1965 at Tatokushima from abandoned bamboo poles of oyster rafts. Although the smooth, hard surface of the internodes affords little opportunity for heavy _Limnoria_ sp. infestations, the nodes are riddled with their tortuous burrows and in these, but not restricted to them (see Matthews, 1963:438) were fully extended folliculins. In every respect these resembled those obtained from Douglas fir (_Pseudotsuga taxifolia_) frames (Matthews, 1962). Again, sac length, width, and height vary with site conditions. Crowding usually results in an abnormally shaped lorica whose sac (f) (up to 170µ) is often as long as the neck (e). And again, the neck, least affected by space restrictions, varies only between 130µ and 170µ with 5–7 spiral whorls (d). The nuclear components (e) vary widely; from what appears to be a more or less compact, spherical mass of 5 or 6 large granules to a "broken" string of 12 to 14 small beads. As in the Hawaiian representatives of this species, _E. lignicola_ in Ago Bay is a deep wine-red in reflected light and

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Fig. 2. _Eufolliculina lignicola_, as viewed from the ventro-lateral surface showing: _a_, left peristomal lobe; _b_, mouth of lorica; _c_, neck; _d_, spiral whorl; _e_, moniliiform nucleus; _f_, sac of lorica.
bottle-green in transmitted light. The peristomal lobes (a) are long (up to 118µ), without finger-like projections and are carried high above the almost collarless (b) distal end of the neck.


_Folliculinopsis annulata_ (Fig. 3A and B) was first taken at Tatokushima, July 6, 1965 on and in the calcareous tubes of _Spirorbis sp_. Whether free or crowded, all taper gradually from a rounded proximal end (f) to the distal end of the neck (a), resulting for the most part in a long, tube-like lorica with, superficially, no sharp line of demarcation between sac and neck. While certain necks are curved in conformity to attachment sites, most are surprisingly straight and held at an angle above the substrate.

What at first appears to be a cone is, in reality, two valves (d) shaped like a roof, whose ridge-pole (marking the position of closure) runs diagonally across the lorica, separating sac (f) from neck (b, c). The sac length is almost uniformly 275µ; the length of the neck varies only from 475µ to 500µ. Neck widths vary from 38µ to 50µ. Although no collars, longitudinal stripes, or spiral whorls are observed, the neck is characterized by light, "clean" bands (b) and dark, "dirty" bands (c), the latter formed by an accumulation of foreign, adhering grains.

The animal is further characterized by its long, narrow, peristomial lobes which, even in the contracted condition often reveal prominent, finger-like projections (e). However, none of these projections terminates in swollen drop-like bodies (Silén, 1947:50, fig. 59a). Size differences are frequently observed but the left peristomial lobe is as frequently reduced as the right.

The nucleus (g) is always moniliform and consists of 7–9 components.

The foot (b) is non-spatulate. Color varies from grey-green to almost colorless; however, both body proper and peristomial lobes possess pigment granules which may appear either red or green, depending on the light source used.
Halofolliculina annulata (Andrews, 1944)
Hadzi gen., 1951, Slovenica Biology 2: 152–153, fig. 25.
Parafolliculina annulata Andrews, 1944,
fig. 3.

Halofolliculina annulata (Fig. 4) was first taken at Tatokushima, July 9, 1965 from the valves of *P. martensi* and the calcareous tests of the acorn barnacle, *Balanus amphitrite* Brock. The Ago Bay representatives of this species follow in almost every respect the specific characteristics set forth by Andrews (1944).

The lorica is dorso-ventrally flattened. The length of the sac (f) is up to 200μ; its width, 150μ. The height of the sac rarely attains 50μ. The lorica, exclusive of the neck, is well cemented to the substratum by a rather extensive collectoderm (i). A narrow collar (a) is all that marks the rather plain neck (b). Unlike the one figured by Andrews (1944:323, fig. 3), no rings or spiral whirls are present. The ventral valve (d) is larger and better developed than the dorsal valve (c).

The peristomial lobes (e) lack finger-like projections and end rather bluntly. The nucleus (g) is non-moniliform and varies from 10μ to 13μ. The foot (b) is non-spatulate.

The living animal and its lorica vary from colorless to a rather deep brown. Old, empty loricae are invariably dark.

*Diafolliculina rotunda* Hadzi, 1951, Slovenica Biology 2:161–165, fig. 27.

*Diafolliculina rotunda* (Fig. 5A and B) was first taken at Tatokushima, July 10, 1965 on the valves of *P. martensi*. Not until some weeks later, however, was positive identification made. It is easily confused with the genus *Halofolliculina* which, as previously seen, also possesses the same general body shape, a spherical nucleus, no vestibule and well-developed valves.

The anterior end of *D. rotunda* viewed ventrally (Fig. 5A) discloses a rather broad collectoderm (a) and a short, almost circular neck (b) with valves (e, d). However, since the diameter of the neck may be only 30μ, valve determination (i.e., which is dorsal, which is ventral) is difficult. In Figure 5B (a lateral view of the right side) the valves are clearly seen. The rather short, thick, ventral valve (f) lies above the thin dorsal one (g) which often curves posteriorly. In related species (*D. similis*) the dorsal valve is often folded, but this condition is not seen in *D. rotunda* from Ago Bay.

The peristomial lobes are irregular, of average length and breadth, and without finger-like processes. The nucleus is spherical and measures up to 27μ in length and up to 24μ in breadth—a very prominent nucleus for such a small folliculinid.

As is true for many of the small folliculinids, the lorica and body vary from colorless to very light green.

*Lagotia expansa* (Levinsen, 1893) Hadzi, 1951,
Slovenica Biology 2:55–73, fig. 6a.

*Lagotia expansa* (Fig. 6) was first observed at Tatokushima, June 19, 1965 on the shell of the large Japanese oyster, *Pinna attenuata*. Literally thousands of folliculinids together with other species comprise the vast epifauna of this oyster. The genus *Lagotia* here contains...
The lorica (Fig. 6e) is approximately 500µ long of which perhaps half could be considered neck. Because no valves separate sac from neck, only 4 or 5 very indistinct spiral whorls (d) indicate where one leaves off and the other begins. The lorica therefore tapers only gradually from a rounded, attached, proximal end (g) to a morning-glory shaped distal end. The wide, delicate flare (a) is strongly marked by light and dark longitudinal stripes (b) which become indistinct posteriorly. No neck extensions are present. The width of the sac is 150µ, its height, 100µ.

The peristomial lobes (c) are long, even, and terminate bluntly without finger-like projections. The nucleus (f) is spherical, measuring up to 38µ in diameter. The foot (b) is non-spatulate.

The color, characteristic of members of this genus, is a deep blue-green. In reflected light the animal is bright red.


*Lagotia expansa* var. *depressa* was first taken at Tatokushima, June 19, 1965 on shells of the large Japanese oyster *Pinna attenuata*. More precisely, it was commonly found between the sacs and actually in the necks of *Lagotia* *gigantia*. Figure 7A shows *L. expansa depressa* (b) on the calcareous shell of *Spirorbis* sp. and on the operculum (a) of the living animal. To my knowledge, this is the first time that a folliculind has been reported attached to a moving part of a serpullid. Figure 7B is a ventral view and 7C, a ventro-lateral view. Both show the flattened lorica (d) with smoothly rounded proximal ends and typical longitudinal stripes (b) on short, distally flaring necks (a). The length, breadth, and height of the lorica fall well within the limits of those given by Hadzi (1951:81).

The peristomial lobes (c) are of even length and end bluntly without finger-like projections.

many closely related species which appear together in great abundance.\(^3\)

\(^3\) Silén (1947:47) stresses that species can only be determined by a study of abundant living material and Hadzi (1951:37) says, "We have, however, in practice, often only a few empty lorica and preserved in-

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**Fig. 5.** *Diasfolliculina rotunda.*

A. Ventral view of anterior portion of lorica showing: a, collectoderm; b, neck opening; c, ventral valve; d, dorsal valve.

B. Lateral view of anterior portion of lorica (right side) showing: e, neck; f, ventral valve; g, dorsal valve.
Lagotia gigantia (Dons, 1913), Dons 1934 gen. (Hadzi, 1951:81).

Although this may prove to be a form of *L. expansa*, certain characteristics of the Tatukushima material taken June 19, 1965 seem to set it apart. The sac (Fig. 8 e) although 350μ long seems too small for the long, almost perpendicular neck which may be up to 1038μ long and 138μ wide. Although as many as 4 spiral whorls (d) may be present, they are usually indistinct. Both the neck and its extension (e) possess wide, delicate flaring collars (a) up to 188μ in diameter, and light and dark longitudinal stripes (b). The peristomal lobes (f) vary widely. They are of equal size and may possess a single, almost median finger (i), a lateral finger (j), or a combination of one large and two or three small projections (k), or two large, finger-like projections (l).

The nucleus (g) is a spherical mass 15–20μ in diameter and again, because of intense overlying pigment, is difficult to see. The foot (b) is non-spatulate.

The color, so far as I could ascertain, was precisely like that of *L. expansa*—a very deep blue-green.

Lagotia spiroorbis (Dons, 1927:7) (see Hadzi, 1951:96).

Folliculinia spiroorbis Dons, 1912:73, figs. A–B, pl. 5; Fauré-Fremiet, 1936:1155, fig. 11.

Angustofolliculinia spiroorbis (Dons) (see Silén, 1947:63, figs. 77–82).

Representatives of this unique species (Fig 9A and B) were first taken at Tatokushima, September 13, 1965 on the shells of *Spirorbis* sp. Later, they were taken from many different habitats: *P. martensii*, *Pinna attenuata*, and *Chlamys nobilis*. These folliculinids are placed in the genus *Lagotia* simply because of the shape and form of the loric (f) and the spherical nucleus (e). Otherwise, there is considerable doubt whether the absence of a collar (b) and the presence of but one peristomal lobe (a) justifies this determination, especially when other *Lagotia* characters are lacking, i.e., color and longitudinal stripes, etc.

The necks of the specimens from Ago Bay, unlike those described and figured by Silén (1947:62, figs. 77–81), narrow gradually from
Folliculinids of Ago Bay, Japan—Matthews

75\(\mu\) to 48\(\mu\) (Fig. 9A, d). Only 4 or 5 spiral whorls (c) are present which mark off the neck region (d) from the rest of the lorica (f). The overall length of the lorica is 250\(\mu\) of which the neck usually makes up about half. No valves are present.

In every instance, only the left peristomal lobe (a) is present. This measures about 125\(\mu\) long when fully extended and varies from 12 to 25\(\mu\) in width. There are no peristomal projections. In the contracted animal (Fig. 9B) the peristomal lobe (a) is often curved. If the condition of but one peristomal lobe proves to be only a transitional stage, then these specimens

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Fig. 7. Lagotia expansa var. depressa.
A, a, Operculum of Spirobis sp.; b, calcareous shell.
B, Ventral view showing: a, delicate flare of collar; b, longitudinal stripes; c, peristomal lobe; d, flattened lorica; e, nucleus; f, non-spatulate foot.
C, Ventro-lateral view of same structures.
Fig. 8. Lagotia gigantia. Lateral view of right side and enlarged peristomal projections showing: a, delicate, flaring collar; b, longitudinal stripes; c, neck extension; d, spiral whorl; e, sac; f, peristomal lobe; g, nucleus; h, foot; i, j, k, l, variations of finger-like projections.
may rightfully belong to the genus Lagotia, if not, Silén (1947:63) is justified in creating his new genus (*Angustofolliculina*).

The nucleus (Fig. 9 A, e) is spherical and the foot (g) is non-spatulate. As previously stated, this material is not a deep blue-green but rather a light grey-green to almost colorless.

*Folliculina viridis* Fauré-Fremiet, 1936:1152, fig. 9.

*Folliculina ampulla* Dons, 1912:81, fig. C.

*Semifolliculina boecki* Dons, 1913:65.

*Folliculina viridis* (Fig. 10A and B) was first taken at Tatokushima, June 19, 1965 from the surface of *P. martensi* and the calcareous tests of the acorn barnacle, Balanus amphitrite Brock. The size and shape of the loria fall well within the limits previously prescribed for this species (Hadzi, 1951:37). The rather perpendicular neck (d) usually has 2 or 3 spiral whorls (c) ending just short of the narrow collar (b) but no longitudinal stripes.

The peristomal lobes (Figs. 10A and B, a) are equal, without finger-like projections and usually held quite high above the open neck. The nucleus (e) is spherical and the foot (f) non-spatulate even in highly contracted animals (Fig. 10B).

The color is the typical blue-green of this genus.


*M. andreusi* was first collected at Tatokushima, July 19, 1965 on shells of Spirorbis sp, comprising part of the epifauna of *P. martensi*. Later they were found on the valves of Pinna attenuata and Chlamys nobilis also taken in Ago Bay.

Figure 11 is a lateral view of the left side of *M. andreusi* taken from the epifauna of *P. martensi*. Although measurements vary considerably from one population to another, none are as large as those described by Hadzi (1938) nor as small as those described by Andrews (1950) for his Carrum Creek (Australia) material. Most fall well within the limits observed by Matthews (1953) for this species taken at Waimanalo Creek, Bellows Field, Oahu.

In the Ago Bay material, the sac (Fig. 11 f) is up to 136μ long and lies attached to the substratum. The neck (d), which rises some 200μ almost perpendicularly from the sac, is reinforced by 6 or 7 well-developed spiral whorls (e). The collar (b) is only slightly developed and beneath it are no indications of longitudinal stripes. No valves are present. Extensions are common. Common also are the presence of "new" swimmers locating in "abandoned" loricas; and it was not uncommon to see two or three completely metamorphosed folliculinids occupying the same loria.

The peristomal lobes (a) are long and slender and for the most part not provided with finger-like processes. When present, these projections
Fig. 10. *Lagotia viridis*.

A, Lateral view of right side of extended animal showing: *a*, peristomal lobe; *b*, collar; *c*, spiral whorl; *d*, neck; *e*, spherical nucleus; *f*, foot.

B, Ventral view of contracted animal showing same structures.

are small and not well developed. The nucleus (*e*) both in unstained and stained material is moniliform, with up to 20 small (3 or 4μ) beadlike components. The foot (*g*) is non-spatulate.

The color of the body is grey-green; the lorica, very light green to colorless. In no sense do even the darkest specimens approximate the deep blue-green of members of the genus *Lagotia*.

*Mirofolliculina limnoriae* (Giard, 1883) Dons, 1927 (see Hadzi, 1951:28–29).


*Mirofolliculina limnoriae* was first taken at Tatokushima, July 7, 1965 from *Limnoria* sp. living in the riddled nodes of abandoned bamboo poles of oyster rafts. Figure 12 is a ventral view of an extended animal and its lorica with lateral pouches (*d*). Although *M. limnoriae* from Ago Bay falls well within the limits of variation held for this species (Silén, 1947:57 and Hadzi, 1938:29), their position on *Limnoria* sp. and the degree of lorica branching differ from previously published accounts. Of 100 *Limnoria* sp. taken at random, only 16% had *M. limnoriae* on their exoskeletons. One of
Fig. 11. *Metafolliculina andreisi*. Lateral view of left side showing: a, peristomal lobe; b, collar; c, spiral whorl; d, neck; e, moniliform nucleus; f, sac of lorica; g, foot.

these had 4 *M. limnoriae* in a single row on the dorsal left side of the head with neck openings (b) pointing toward the mid-line and another had 2 *M. limnoriae* on the dorsal, right side of the head, with neck openings also pointing toward the mid-line. On still another, *M. limnoriae* was present on the dorsal, posterior margin of the head as well as on the dorsal surface of the pleotelson, and on 13 *M. limnoriae* was attached only to the dorsal surface of the pleotelson, but here again, their arrangement was random, affording only slight feeding advantage when the peristomal lobes (a) were extended above the short neck (c).4 Thus, the commonly held notion that the larval swimmer “selects” a site advantageous for the subsequent

4 This applies also to thousands of *M. limnoriae* examined from Hawaii.
metamorphosed, adult, sessile feeder, is placed in serious doubt. Perhaps the pleotelson, acting as a bulkhead, blocks the easy access of negatively phototropic swimmers and provides a suitable surface for lorica formation. But to date, this is mere conjecture. Only about 50% of the lorica had extensive lateral pouches.

The peristomal lobes (a) are without finger-like projections but, as mentioned by Silén (1947:59) are frequently bent forward. The nucleus (e) is always moniliform, although the number and size of beads vary considerably. The foot (f) is non-spatulate.

The color varies according to the amount and distribution of pigment grains, but in general it is a light, almost grey-green. The peristomal lobes when extended often appear rosy-pink.


*Folliculina gunneri* Dons, 1927:5

*Folliculinopsis gunneri* Fauré-Fremiet, 1936:1140.

*Pachyfolliculina gunneri* was first taken at Tatokushima, July 7, 1965 from the ventral

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**Fig. 13.** *Pachyfolliculina gunneri.*
A. Ventral view of contracted animal showing: a, collarless neck; b, cylindrical lorica.
B. Ventro-lateral view of left side showing: c, peristomal lobe; d, moniliform nucleus; e, non-spatulate foot.
side of *Limnoria sp.* living in the riddled nodes of abandoned bamboo poles of oyster rafts. Later, they were taken from the surface of *Spirorbis sp.* which formed part of the epifauna of *P. martensii*.

Figure 13A is a ventral view of a contracted animal taken from the unrestrictive surface of a *Spirorbis sp.* shell. In such instances, the lorica is cylindrical and terminates in a broad neck (b) and wide mouth (a). No collar, spiral rings, longitudinal stripes, or bands are present.

Figure 13B is a ventro-lateral view of the left side of an extended animal taken from a restrictive surface of a *Spirorbis sp.* shell. Here, the otherwise cylindrical lorica is bent in compliance to the restricted area; otherwise the general proportions are the same. In no instance did the lorica ever stand vertically (see Silén, 1947:48) as is usually the case in *Parafolliculina violacea*.

The peristomal lobes are usually equal, but sometimes the left (c) is slightly longer and perhaps broader than the right; finger-like projections are present. The nucleus (d) is always moniliform and composed of 8 or 9 beads of varying size. The foot (e) is non-spatulate.

The color varies from grey-green to bottle-green. The lorica may be yellowish-green to dark brown.

*Parafolliculina amphora* Dons, 1913 (see Hadzi, 1951:170–179, figs. 29 a–b, e–g and Silén, 1947:64–65, figs. 83–86).

*Parafolliculina amphora* (Fig. 14) was first taken at Tatokushima, September 22, 1965 on the interzooecial boundaries of the Bryozoan, *Schizoporella oenoebros* Ortman.

The measurements of the Ago Bay material fall well within the limits set for this species by other workers. Figure 14 represents a ventral view of a relaxed *P. amphora* taken from an unrestrictive lorica site. The division of the lorica into a short neck (b), vestibule (c) with valves (d), and sac (e) is clearly discernible. Especially significant is the extent of the collectoderm (i) which holds the lorica in a horizontal position, not vertical as in *P. violacea*.

The peristomial lobes (a) are of equal size and length and bear short, finger-like projections at their gradually tapering ends. The nucleus (f) is spherical.

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**Fig. 14.** *Parafolliculina amphora*. Ventral view of partially extended animal showing: a, peristomial lobe; b, short collar; c, vestibule; d, valves; e, lorica; f, nucleus; g, extent of foot (dotted area) when lorica excessively flattened; h, foot; i, collectoderm.

Silén (1947:25) mentions that in *P. amphora*, "the breadth of the attachment of the animal varies very much; it may be broad or as narrow as in most Folliculinidae (Figs. 83, 84)." Although Hadzi (1951:173) takes Silén to task for these figures, the width of the foot
(b) does increase as the building sites become more restrictive. In my Figure 14 the area within the dotted outline indicates the extent of the broadened foot (g). This type of foot attachment is encountered when the lorica is excessively dorso-ventrally flattened.

The color is light-green to grey-green.

*Parafolliculina violaceae* (Giard, 1888), Dons gen. (see Hadzi, 1951:188 and Silén, 1947:66).

*Folliculina violaceae* Giard, 1888:315.

*Parafolliculina violaceae* Dons, 1913.

*Parafolliculina violaceae* was first observed at Tatokushima, June 19, 1965 on practically everything collected, and, moreover, it was the most abundant folliculinid in Ago Bay. Because *P. violaceae* has been adequately described by many workers, only findings pertinent to the present study will be given here. Wide variations were observed in peristomal lobes (Fig. 15a) mouth (b), vestibule (c), valves (d), nucleus (e), and lorica attachment (f), and these variations seemed to be as much the result of the site chosen as the age of the "colony." As will be discussed subsequently, *P. violaceae* was one of the first organisms to appear on shell collectors and in such instances, even when space was not at a premium, the position assumed was always vertical.

The intense, deep red of this species in reflected light has been mentioned by other workers.

*Pebrilla paguri* Giard, 1888: Pl. 20.


*Pebrilla paguri* (Fig. 15A and B) was first taken at Tatokushima, September 13, 1965 from the dorsal side of the telson, uropods, and last two abdominal segments of the hermit crabs *Pagurus lanuginosus* de Haan, 1849, and *Pagurus samuelis* (Stimpson, 1857). These hermit crabs, at least for the month of September, were heavily infested (approximately 85%). In such cases of especially heavy infestation, folliculins were also found attached to the inner, upper region of the shell of *Tegula*

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5 Kindly identified by Dr. S. Miyake, Kyushu University, Faculty of Agriculture, Fukuoka, Japan.

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Fig. 15. *Parafolliculina violaceae*. Ventral view of partially extended animal showing: a, peristomal lobe; b, collarless opening of neck; c, vestibule; d, valves; e, spherical nucleus; f, collectoderm.
Folliculinids of Ago Bay, Japan—Matthews

rustica and, although a few were taken near its large opening, most were far removed from the opening, indicating that swimmers of this species, as well as attached adults, prefer little light.

Figure 16A is a ventral view of P. paguri showing the division of the horizontally attached lorica into a distal vestibular portion (e) with short neck (d) and wide collar (c), and a proximal portion (b) with a strong spur (i). Generally the length of the distal portion, including neck and collar, about equals the proximal portion including the spur, but occasionally either one may surpass the other. Almost without exception, the proximal portion is wider than the distal portion. Both Giard (1888:Pl. 20) and Fauré-Fremiet (1936:356, fig. 6) mention and figure a pronounced, transverse median wrinkle separating distal from proximal portions of the lorica. Superficially the loricae of the Ago Bay material likewise seem to be so demarked. However, a lateral view (Fig. 16B) drawn from many hundred specimens shows that the left, heavily reinforced invagination of the lorica (f) does not continue, even as a slight depression, across the ventral surface of the lorica. And while this disparity may one day justify the creation of a new species, perhaps it is best for the present to wait until the presence of this groove in previously described material is actually demonstrated.

The short but well-developed neck (d) possesses no longitudinal stripes, spiral whorls, bands, or closures.

The peristomial lobes taper distally and terminate bluntly without finger-like projections. When extended, the left (Fig. 16A, a) is commonly held at right angles to the longitudinal axis of the body, whereas the right (b) is commonly carried over the ventral surface, parallel to the longitudinal axis of the body.

The nucleus is moniliform and usually consists of 11 or 12 rather easily observed beads (g).

The non-spatulate foot is always attached at the bottom of the well developed spur (i) whose walls, like those of the lateral invaginations, are often strongly reinforced.

The living animal is bottle-green. The peristomial lobes and distal portion of the body are often lighter than the proximal portion. Especially is this evident in contracted, alcohol-preserved material.

FOLLCULINIDS AS FOOD FOR THE EPIFAUNA OF P. martensi

Material and Methods

Of the folliculinids forming a part of P. martensi epifauna, the following were suspect, prima facie, of prey-predator relationships:

Ascobion sileni

Bougla dentata, Spirorbis sp.

Folliculinopsis annulata

Lagotia expansa ...... Heterotanais sp.

L. expansa var. depressa

Spirorbis foraminosus, Heterotanais sp.

L. spirobri ...... Spirorbis foraminosus

L. viridis ...... Heterotanais sp.

Metafolliculina andrewsi

Balanus amphitrite, Heterotanais sp.

Parafolliculina amphora

Cymodoce japonica

P. violacea

Spirorbis sp., Balanus amphitrite, Heterotanais sp.

With two possible exceptions (Heterotanais sp. and Cymodoce japonica) the suspected predators were all filter-feeders. And, although these could not conceivably prey on the adult, sessile, lorica-protected folliculinids with which they were so closely associated, the possibility still remained that motile "swimmers" of folliculinids might be swept into the feeding currents of filter-feeders. With the exception of P. violacea (to be described subsequently) "swimmers" of these folliculinids were not available for feeding experiments. Therefore, living, attached folliculinids were removed from their lorica by gently tapping or applying pressure to the proximal end of the sac (Matthews, 1964:229). These were broken into tiny pieces and teased directly into the currents of suspected filter-feeders.

Most folliculinid pigment granules are easily discernible using low power, light microscopy, and their presence in digestive tract smears would clearly indicate predation. To this end, larger, suspected predators were dissected and the contents of their digestive tracts smeared
Fig. 16. *Pebrella paguri.*

* A. Ventral view of extended animal showing: *a*, left peristomal lobe; *b*, right peristomal lobe; *c*, collarless neck; *d*, neck; *e*, distal portion of lorica; *f*, lateral invaginations of lorica; *g*, component of moniliform nucleus; *h*, proximal portion of lorica; *i*, spur of lorica.

* B. Lateral view of left side of empty lorica showing: *f*, strengthened lateral invagination of lorica not complete ventrally.
and examined for pigment granules. Most, however, were too small to be dissected without micro-manipulators (which were not available) so the entire animal was squashed and examined under the microscope. No stains were employed and no permanent mounts were made.

Results

In every instance these tiny pieces were quickly carried toward the region of the mouth of a suspected predator but were as quickly rejected. Likewise, smears of digestive tract contents of large, dissected animals and squashes of entire animals too small to be conveniently dissected all failed to reveal folliculinid pigment granules. While it is true that the size of the pieces offered as food were probably too large to be accepted, smear and squash techniques should have disclosed "naturally" occurring granules had such been present. Not once in any of the suspected predators were folliculinid pigment granules observed.

Even in *P. violacea*, whose swimmers are among the first organisms to appear, no pigment granules were ever recovered.

At first sight, the situation seemed quite different in *Heterotaxia* sp. (a voracious isopod which temporarily abandons its mucous tube to search for food and then quickly returns to it for protection). It would accept the empty lorica quite as readily as the lorica-free body and quickly pull either into its mucous tube. However, digestive tracts of these animals failed to reveal either pieces of lorica or pigment granules, and only after days of searching were both found cemented together with debris in the wall of the mucous tube.

Even the large Umisemi, *Cymodoce japonica* (which the Japanese call the "locust of the sea," for they eat everything) fails to utilize either *P. violacea* or *P. amphora*, both of which occupy the same position on *C. japonica* that *Microfolliculina limnoriae* occupies on the gribble. In no instance, were folliculinid pigment granules recovered from their digestive tract contents.

Conclusions

Folliculinids, newly reported in Japan, are abundant in the epifauna of the Pearl Oyster, *Pinctada martensii* from Ago Bay, Japan, but while these may profit by their association with different types of filter-feeders it is doubtful if other members of the epifauna use folliculinids as food.

Acknowledgments

I wish to thank my sponsor, Dr. N. Kawamoto, who arranged housing accommodations at the National Pearl Research Laboratory, Kashikojima, and its director, Mr. Ohta, who provided research facilities at the Tatokushima Laboratory, Ago Bay. I am also grateful to the research staffs of these laboratories for their many kindnesses during these investigations. Credit to also due Mrs. Sally Oshiro, department secretary, who typed the manuscript and Mrs. Barbara Downs, department artist, who prepared the plates from my laboratory sketches.

References


The Occurrence of *Cyclops kolensis* Lilljeborg (Copepoda, Cyclopoida) in North America

Edward B. Reed

*Cyclops kolensis* was named by Lilljeborg in 1901; in the intervening 60 odd years, it has been infrequently reported in the literature. Kozinski (1933) noted that although *C. kolensis* is one of the most widely distributed species "in our region" it had been forgotten until recent years when he and Rzoska (1930) independently mentioned it in revisions of certain groups of *Cyclops*.

Judging from the list of synonyms prepared by Lindberg (1957) the name *C. kolensis* rarely has been incorrectly applied to other species. However, the reverse has occurred rather frequently; that is, animals which are actually *C. kolensis* have been assigned to other species. Apparently the most common misidentification has been to mistake *C. kolensis* for *C. vicinus* Uljanin. Less frequently it has been confused with *C. strenuus*; for example, Kiefer (1929) included *kolensis* as a doubtful synonym of *strenuus*.

The first evidence of *C. kolensis* on the North American continent appeared in some of the collections of the Canadian Arctic Expedition of 1913–1916. Marsh (1920) recorded finding in collections made at Bernard Harbour, N.W.T., and at Cape Collinson, Alaska, a number of freshwater cyclops with a spine formula of 2,3,3,3 but which in other features agreed with the description of *C. strenuus*. Marsh assigned his Canadian and Alaskan specimens to *C. vicinus* Uljanin 1875, noting that, because *C. kolensis* Lilljeborg and *C. minutus* Lilljeborg have the same formula of spines as does *C. vicinus* on the outer margins of the terminal segments of the exopodites of the swimming legs, he could see no reason for regarding these as distinct species (Marsh, 1920:11). Marsh also regarded *C. scutifer* as a synonym of *C. strenuus* on the basis that both have a spine formula of 3,4,3,3, thus obscuring the fact that both species occur in arctic North America.

Kozinski (1936) questioned the assignment of the North American specimens to *C. vicinus*, remarking that the furcal rami of *C. scutifer* and *C. kolensis* are similar, whereas the rami of *C. vicinus* are quite different from those of *C. scutifer*. Because Marsh had made his diagnosis chiefly on the basis of the spine formula, Kozinski (1936:225) believed it quite likely that the animals in question were *C. kolensis*.

Yeatman (1944) re-examined Marsh's collections, which had been deposited in the U. S. National Museum. He noted that the Alaskan specimens differed from *C. vicinus* in proportions of the furcal rami and in the relative lengths of some of the terminal furcal setae. Yeatman further noted that the shapes of the 4th and 5th thoracic segments of Marsh's specimens differed from *C. scutifer*, in which these segments are expanded. *C. kolensis* does not have expanded thoracic segments; the thoracic segments of *C. vicinus* are strongly expanded. However, in spite of these differences Yeatman (1944:84) believed that Marsh had correctly assigned his specimens to *C. vicinus*.

Rylov (1948:198), in giving the known distribution of *C. kolensis*, considered Marsh's specimens to belong to that species.

Lindberg (1956) revived the question and proposed *Cyclops kolensis alaskaensis* as a nomen novum for the Alaskan specimens. He noted (p. 117) that neither the form of the 4th and 5th thoracic segments nor the proportions of the furca as figured by Yeatman conform to the description of *C. vicinus* Uljanin. Lindberg (1957) further contrasts *C. k. alaskaensis* with *C. k. kolensis* on the basis of the figures and discussions of Marsh and Yeatman.

Until recently the only specimens of *C. kolensis* from North America were apparently

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2 Department of Zoology, Colorado State University, Fort Collins, Colorado 80521.
the few alcohol-preserved specimens and slides of dissected animals in the Marsh collections in the U. S. National Museum. Yeatman (1944) noted that the whole specimens were so thickly covered with ecto-commensal protozoans that details were difficult to observe. I also examined Marsh’s material and agree that it is difficult to study. Thus the availability of new specimens is of interest. Mrs. Mildred S. Wilson, Arctic Health Research Center, Anchorage, Alaska, forwarded some collections from Saint Matthew Island, Bering Strait. These collections were made by Dr. Robert Rausch and Reggie Rausch of the same Center. Dr. J. Kaff, Department of Zoology, McGill University, Montreal, sent several vials of Cyclops from the vicinity of Pt. Barrow, Alaska.

COMPARISON OF C. kolensis WITH C. vicinus

Four more or less consistent differences between C. kolensis and C. vicinus appear to be in (1) the shape of the posterior corners of the 4th thoracic segment, (2) the ratio of ramus length to width, (3) the ratio of inner terminal seta of ramus to outer terminal seta, and (4) the ratio of inner terminal seta to length of ramus.

Table 1 summarizes and compares these morphological features for the two species.

The antennules of both C. vicinus and C. kolensis typically have 17 segments, although Kozinski (1934) noted that specimens with 16 segments occasionally may be found. C. kolensis from Lake Baikal may have as many as 18 segments in the antennule (Lindberg, 1955). C. vicinus and C. kolensis share the same spine formula on the outer margins of the terminal segments of the exopods of the swimming legs —2,3,3,3. A chitinous ridge occurs on the dorsal surface of each furcal ramus.

Lilljeborg (1901) illustrated C. kolensis (Figs. 11 and 12) and C. vicinus (Figs. 16, 17, 18, and 19). The 4th thoracic segment of C. kolensis is but little wider than the genital segment and is figured with blunt laterally directed projections. The rami are about 5 times as long as wide; the inner terminal setae are slightly longer than the rami; the outer terminal setae are about two thirds the length of the inner. The seminal receptacle is shown as filling most of the genital segment.

The 4th thoracic segment of C. vicinus is shown with sharply pointed wings which are laterally and posteriorly directed. It is much

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<table>
<thead>
<tr>
<th>Cyclops kolensis</th>
<th>Cyclops vicinus</th>
</tr>
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<tbody>
<tr>
<td><strong>Posterior corners of the fourth thoracic segment</strong></td>
<td><strong>Posterior corners of the fourth thoracic segment produced and expanded into posteriorly directed wings</strong></td>
</tr>
<tr>
<td>rounded or produced laterally</td>
<td>1, 2, 3, 4, 8, 10, 11, 13, 15, 16</td>
</tr>
<tr>
<td>1, 6, 7, 11, 14, 15, 17</td>
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<tr>
<td><strong>Length of ramus 4 to 6 times the width</strong></td>
<td><strong>Length of furcal ramus usually 7 to 8 times the width</strong></td>
</tr>
<tr>
<td>1, 4, 7, 11, 14, 15, 17</td>
<td>1, 2, 3, 5, 7, 9, 10, 11, 13, 15, 16</td>
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<tr>
<td><strong>Inner terminal seta of ramus less than twice the length of the external terminal seta</strong></td>
<td><strong>Inner terminal seta of the ramus at least twice the length of the outer</strong></td>
</tr>
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<td>1, 4, 11, 14, 15, 17</td>
<td>1, 2, 3, 15, 7, 9, 10, 11, 13, 15, 16</td>
</tr>
<tr>
<td><strong>Inner terminal seta of the ramus less than the length of the ramus</strong></td>
<td><strong>Inner terminal seta of the ramus exceeding or equaling the length of the ramus</strong></td>
</tr>
<tr>
<td>1, 4, 7, 11, 14, 17</td>
<td>1, 2, 3, 5, 10, 11, 13, 15, 16</td>
</tr>
</tbody>
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---

a The numbered references are: 1, Borutzky 1960; 2, Dussart 1958; 3, Gurney 1933; 4, Herbst 1955; 5, Kiefer 1937; 6, Kozinski 1934; 7, Lindberg 1937; 8, Lint 1922; 9, Mann 1940; 10, Rylov 1935; 11, Rylov 1948; 12, Rozska 1930; 13, Sars 1918; 14, Kozlov 1963; 15, Lilljeborg 1901; 16, Uljanin, from Lint 1922; 17, Mazepova 1960.

b Seta equalling ramus.
c 6 times.
d Internal apical seta not as long as furca in C. kolensis alaskensis; internal apical seta exceeding ramus in C. kolensis kolensis.
e Internal seta much less than twice the length of the outer in C. vicinus kikuchi; internal 2 or more times the length of the external in C. vicinus vicinus.
wider than the genital segment. The rami are about 6 times as long as wide. The inner terminal setae are a little longer than the rami and twice the length of the outer. The seminal receptacle is pictured as not filling as large a portion of the genital segment as it does in *C. kolensis*.

**DESCRIPTION OF THE ALASKAN SPECIMENS**

Female. The total length exclusive of the furcal setae is 1.2–1.5 mm with most ranging from 1.3–1.4 mm.

The antennules of the St. Matthew Island specimens (about 15 were available for study) are either 16- or 17-segmented (Fig. 1). Considerable variation was observed in the number of segments of the antennules of about 15 Pt. Barrow animals: a few had 17; more frequently the number was either 12 or 11. Twelve-segmented antennules resulted from the incomplete separation of segments 12, 13, and 14, and 8, 9, 10, and 11 (Fig. 2). The joint between segments 11 and 12 was distinct in all cases. Eleven-segmented antennules resulted from fusion of the segments as in the 12-segmented antennules plus the failure of segments 3 and 4 to separate completely. Gurney (1933:48) indicates that in *C. strenuus* segment 3 of the 5th copepodite antennule gives rise to segments 3 and 4 of the adult, and he suggests further that segments 8, 9, 10, and 11 of the adult arise from segment 7 of the 5th copepodite and likewise segments 12, 13, and 14 of the adult derive from segment 8 of the copepodite. Gurney states (1933:59) that female *Cyclops* (species not indicated) possess a total of 43 setae and three aesthetes on each antennule. The antennules of the Alaskan specimens, whether 17- or 12- or 11-segmented, bore this number of setae and aesthetes.

The posterior corners of the 4th thoracic segment were either smoothly rounded or, more frequently, produced into laterally directed small processes (Figs. 10 and 11); in no instances were the corners expanded into wing-like shapes. All animals examined possessed a spine formula of 2,3,3,3 (Figs. 3–6).

To facilitate description of individual variability found in the Alaskan specimens and to aid in comparing them with forms of *C. kolensis* described in the literature, a series of animals from each locality was measured. Table 2 summarizes measurements of morphological features which have been used traditionally in working with *C. kolensis*.

In this study of variability, ratios of body parts often have been found to be more useful than absolute measurements. Therefore Table 3 was prepared. Because the ranges of ratios are based on means ± 90% confidence limits, the ranges have a confidence limit of 81%. The effect of treating two St. Matthew Island collections separately and combined is also indicated in Tables 2, 3, and 4.

Clearly, the Pt. Barrow and St. Matthew Island populations are referable to *C. kolensis* as characterized by the morphological features used in Table 1. How similar to each other are the Alaskan populations? This question is important in helping to understand the relationships of the North American forms to those reported from other regions. Figure 18 indicates that among the Alaskan animals those from Pt. Barrow tend to be larger than those from St. Matthew 809 which are, in turn, larger than St. Matthew 814 individuals. The exceptions are lengths of inner spines of terminal

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Figs. 3–9. Swimming legs of female *Cyclops kolensis*, St. Matthew Island, Alaska. 3, First; 4, second; 5, third; 6, fourth; 7, segment 3, exopodite, leg one; 8, segment 3, endopodite, leg one; 9, segment 3, endopodite, leg four. Scale a: Figs. 3, 4, 5, 6. Scale b: Figs. 7, 8, 9.
Cyclops kolensis in North America—Reed


Fig. 16. *Cyclops kolensis*, Canada. Female ramus.

Fig. 17. *Cyclops kolensis*, Poland. Female ramus.
### TABLE 2

**Measurements of *Cyclops kolensis***

<table>
<thead>
<tr>
<th>ITEM</th>
<th>NUMBER OF SPECIMENS</th>
<th>MEAN</th>
<th>STANDARD DEVIATION</th>
<th>STANDARD ERROR</th>
<th>CONFIDENCE LIMIT 90% OF MEAN</th>
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TABLE 3

Morphometric Ratios of *Cyclops kolensis* from Different Populations

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<th>INNER TERMINAL Seta :</th>
<th>INNER TERMINAL OUTER TERMINAL Seta :</th>
<th>INNER TERMINAL RAMUS</th>
<th>INNER TERMINAL LEG 4 :</th>
<th>INNER TERMINAL LENGTH :</th>
<th>INNER TERMINAL WIDTH :</th>
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<td>1.0 4.6-6.6</td>
<td>1.0 4.6-6.6</td>
<td>1.0 4.6-6.6</td>
<td>1.0 4.6-6.6</td>
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<td>1.0 4.6-6.6</td>
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<td>1.0 4.6-6.6</td>
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<td>1.0 6-1.1</td>
<td>1.0 4.6-6.6</td>
<td>1.0 4.6-6.6</td>
<td>1.0 4.6-6.6</td>
<td>1.0 4.6-6.6</td>
<td>1.0 4.6-6.6</td>
<td>1.0 4.6-6.6</td>
</tr>
<tr>
<td>Alaska (Marsh's material U.S.N.M.)</td>
<td>1.0 6-1.1</td>
<td>1.0 4.6-6.6</td>
<td>1.0 4.6-6.6</td>
<td>1.0 4.6-6.6</td>
<td>1.0 4.6-6.6</td>
<td>1.0 4.6-6.6</td>
<td>1.0 4.6-6.6</td>
</tr>
<tr>
<td>Poland (Kozminski's material U.S.N.M.)</td>
<td>1.0 6-1.1</td>
<td>1.0 4.6-6.6</td>
<td>1.0 4.6-6.6</td>
<td>1.0 4.6-6.6</td>
<td>1.0 4.6-6.6</td>
<td>1.0 4.6-6.6</td>
<td>1.0 4.6-6.6</td>
</tr>
</tbody>
</table>

Segment of endopod 4 (Pt. Barrow ca. equal to St. Matthew 809) and outer spine (St. Matthew 809, the longest). Quotients of inner seta ÷ outer seta, endopod ÷ inner spine, and for the Alaskan population inner seta ÷ ramus indicate no allometry (Fig. 19, panels C, F, D).

Means of different measurements are compared in Table 4. The two St. Matthew populations differed at a level of .001 in lengths of furcal rami, of endopod segment 3 on leg IV, and of outer spine on the segment. The Pt. Barrow animals were most like those of St. Matthew 809 and differed greatly (five measurements at .001 level and one at .05 level) from St. Matthew 814. Comparing Pt. Barrow animals with combined St. Matthew samples showed an intermediate condition.

COMPARISON OF PRESENT SPECIMENS WITH MARSH'S MATERIAL

The U. S. National Museum loaned the Cape Collinson specimens for examination. In all, nine slides labeled by C. D. Marsh and a small vial of whole specimens in alcohol were available. Slide 4438 (Marsh's number) contained six whole females, the other slides held dissected animals. Slides 4330 and 4334 are probably *Cyclops venustoides* Coker, although labeled *C. vicinus*. Slides 4331 and 4336 are marked *C. strenuus*, but on the basis of a 2,3,3,3 spine formula are most likely *C. kolensis*. Slide 4418 labeled *C. strenuus* is *C. scutifer*. Slides 4332, 4335 and 4337 are labeled *C. vicinus*. The least distorted animals on the slides were measured (Table 2).

The alcohol-preserved specimens were considerably distorted and covered with ecto-commensal stalked protozoans. The form of the thoracic segments agrees with the descriptions of *C. kolensis* but not of *C. vicinus*.

The ratios derived from measurements in Table 2 compare favorably with ratios of other Alaskan populations (Table 3). The evidence available indicates that Marsh's specimens should be referred to *C. kolensis* Lilljeborg. Although all of the Alaskan populations do exhibit some individual characteristics as a group they differ little from one another.

COMPARISON OF ALASKAN POPULATIONS WITH OTHERS DESCRIBED IN THE LITERATURE

Rylov (1948) and Herbst (1955) measured various body parts of *C. kolensis* from Siberia and Germany (Grosser and Plöner See). Their measurements have been included in Table 2. In comparing ratios (Table 3 and Fig. 19) the Siberian and German animals do not exhibit constant patterns in relation to the other popula-
TABLE 4

COMPARISONS OF MEANS OF DIFFERENT MEASUREMENTS, t VALUES AND DEGREES OF FREEDOM FOR VARIOUS POPULATIONS OF *Cyclops kolensis*

<table>
<thead>
<tr>
<th>POPULATIONS</th>
<th>RAMUS LENGTH</th>
<th>INNER TERMINAL SETA LENGTH</th>
<th>OUTER TERMINAL SETA LENGTH</th>
<th>SEGMENT 3 ENDOPOD LEG 4 LENGTH</th>
<th>INNER TERMINAL SPINE ENDOPOD LEG 4</th>
<th>OUTER TERMINAL SPINE ENDOPOD LEG 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pt. Barrow vs Germany</td>
<td>6.69*</td>
<td>-3.56†</td>
<td>3.81†</td>
<td>6.98*</td>
<td>4.73*</td>
<td>7.61*</td>
</tr>
<tr>
<td>St. Matthew 809 vs St. Matthew 814</td>
<td>5.7*</td>
<td>1.97</td>
<td>1.55</td>
<td>6.48*</td>
<td>1.99</td>
<td>9.52*</td>
</tr>
<tr>
<td>Pt. Barrow vs Siberia</td>
<td>0.71</td>
<td>2.21</td>
<td>5.23*</td>
<td>4.81*</td>
<td>2.26</td>
<td>4.39†</td>
</tr>
<tr>
<td>Pt. Barrow vs St. Matthew 809</td>
<td>5.00*</td>
<td>0.90</td>
<td>0.35</td>
<td>4.10†</td>
<td>0.02</td>
<td>-3.01‡</td>
</tr>
<tr>
<td>Pt. Barrow vs St. Matthew 814</td>
<td>6.58*</td>
<td>4.44*</td>
<td>6.90*</td>
<td>10.43*</td>
<td>3.04‡</td>
<td>5.01*</td>
</tr>
<tr>
<td>Combined St. Matthew vs Pt. Barrow</td>
<td>-7.22*</td>
<td>-2.52‡</td>
<td>-2.76‡</td>
<td>-5.64*</td>
<td>-1.21</td>
<td>-0.59</td>
</tr>
<tr>
<td>St. Matthew 809 vs Germany</td>
<td>1.57*</td>
<td>-2.95†</td>
<td>.42</td>
<td>2.00</td>
<td>2.50‡</td>
<td>13.67*</td>
</tr>
<tr>
<td>St. Matthew 814 vs Germany</td>
<td>-2.23*</td>
<td>-7.32*</td>
<td>5.92*</td>
<td>5.26*</td>
<td>-1.25</td>
<td>1.25†</td>
</tr>
<tr>
<td>Combined St. Matthew vs Germany</td>
<td>-0.95</td>
<td>-5.11*</td>
<td>-1.08</td>
<td>-1.25</td>
<td>1.24</td>
<td>3.37†</td>
</tr>
</tbody>
</table>

* Significant at .001 level.
† Significant at .01 level.
‡ Significant at .05 level.
tions, although there is a tendency Germany > Siberia > St. Matthew in regard to lengths of outer setae, endopods, and inner spines. The German animals had particularly short furcal rami and long inner terminal setae. The German population has a quotient $> 1$ for inner seta $\div$ ramus (panel D, Fig. 19) suggesting that the lengths of these structures do indeed differ from those of the other populations. There are a number of indications that the Siberian *C. kolensis* is similar to the Pt. Barrow specimens and to a lesser extent to the St. Matthew forms (Table 3 and 4, Fig. 18).

To further assess the variation shown by the five populations, six measurements were subjected to one-way analysis of variance. The results (Table 5) show that two values (lengths of furcal rami and outer spine) are significantly different at the .01 level and that the endopod lengths differ significantly at the .05 level. Inspection of Figure 18 suggests that much of the variation in furcal length may be due to the German animals. Analyzing furcal length after omitting the German specimens resulted in an $F = 4.63$, not significant at the .05 level. Likewise if the St. Matthew 809 animals are omitted, the $F$ value for the outer spine length is not significant at the .05 level.

Along with the specimens from the Marsh collections, the U. S. National Museum also loaned three specimens of *C. kolensis* from Lake Wigry, Poland, identified by Kozminski. Characteristics of the terminal seta, endopod, and rami of these animals are closer to those of the German specimens than they are to the Alaskan animals (Tables 3 and 4). The length of the abdominal segments (post genital) is $121\%$ of the furcal length.

In attempting to summarize the morphological variation shown by these populations, the German animals appear to possess long inner setae and short furcal rami, resulting in only the inner

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**Fig. 18.** Comparison of measurements of *Cyclops kolensis* from various populations. A, Length of segment 3, endopodite, leg four; B, length of inner terminal spine of segment 3, endopodite leg four; C, length of outer terminal spine of segment 3, endopodite, leg four; D, length of furcal ramus; E, length of inner terminal seta of ramus; F, length of outer terminal seta of ramus. Values in microns; thin vertical line is the range, heavy vertical line is the 90% confidence limit and horizontal bar is the mean.

Populations: a, Pt. Barrow, Alaska; b, Siberia (Rylov 1948); c, St. Matthew Island, Alaska (coll. 814); d, St. Matthew Island, Alaska (coll. 809); e, Grosser Plöner See (Herbst 1955); f, Canada (Marsh collections, U. S. National Museum); g, Lake Wigry, Poland (Kozminski collections U. S. National Museum).
seta to ramus length quotient exceeding unity.

Lindberg (1955) gives ratios of various body parts of *C. kolensis* from Lake Baikal and from a pond at Aneboda, Sweden. Four animals represent each locality. Means of some ratios from these populations are compared with each other and with those of animals from the Grosser Plöner See (Table 6). The Swedish and German forms differ most widely from each other. The Baikal and Swedish forms show the greatest similarity, which, in view of the great environmental differences, is unexpected.

Values of the ratios from Table 6 were subjected to analyses of variance (Table 7). Only two ratios had significant F values. These were length of outer medial terminal seta as percent of the length of the inner medial seta and the length of the inner medial seta as percent of ramus length.

Lengths of the medial furcal setae were not measured in the Alaskan specimens; however, using available measurements it is possible to make further comparisons among the present samples of *C. kolensis* and those recorded in the literature (Table 8). If the mean values only are considered, the German, Polish, Swedish, and Baikalense animals tend to have inner setae exceeding the ramus length and also to have long inner furcal seta as compared with the outer furcal seta. But the ranges overlap very broadly.

Mazepova (1961) studied *C. kolensis* from different habitats and found that it was morphologically homogeneous over its range with the exception of some bodies of water in Siberia. The northern form she considered to be *C. kolensis alaskaensis* Lindberg. She gave quotients of length of the last three abdominal segments: length of rami; Siberian animals were the only ones in which this value was over 100%, with a range between 100 and 150%. Two females from Pt. Barrow were checked for this quotient, which varied from 174 to 177%. Mazepova

---

**Fig. 19.** Comparison of ratios of measurements of *Cyclops kolensis* from various populations. A. Length of furcal ramus/ width of ramus; B, length of segment 3, endopodite, leg four/ width of same; C, length of inner terminal seta of ramus/ length of outer seta of ramus; D, length of inner terminal seta of ramus/ length of ramus; E, length of inner terminal spine, endopodite, leg four/ outer terminal spine, endopodite, leg four; F, length of segment 3, endopodite, leg four/ inner terminal spine same appendage.

Populations: a–g as in Fig. 18.
TABLE 5
SUMMARY OF ONE FACTOR ANALYSIS OF VARIANCE OF MEASUREMENTS OF Cyclops kolensis,
SAME POPULATION AS IN TABLE 4

<table>
<thead>
<tr>
<th>ITEM</th>
<th>SOURCE</th>
<th>SUM OF SQUARES</th>
<th>DEGREES FREEDOM</th>
<th>MEAN SQUARE</th>
<th>F VALUE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of segment</td>
<td>Main effect</td>
<td>1921</td>
<td>4</td>
<td>72.58</td>
<td>3.925**</td>
</tr>
<tr>
<td>3 endopod leg</td>
<td>Deviation</td>
<td>513</td>
<td>28</td>
<td>18.49</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>2434</td>
<td>32</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length outer spine</td>
<td>Main effect</td>
<td>2527</td>
<td>4</td>
<td>103.45</td>
<td>6.239*</td>
</tr>
<tr>
<td>endopod leg</td>
<td>Deviation</td>
<td>464</td>
<td>28</td>
<td>16.58</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>2991</td>
<td>32</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length inner spine</td>
<td>Main effect</td>
<td>1053</td>
<td>4</td>
<td>39.85</td>
<td>.637</td>
</tr>
<tr>
<td>endopod leg</td>
<td>Deviation</td>
<td>1635</td>
<td>28</td>
<td>62.50</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>2688</td>
<td>32</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length ramus</td>
<td>Main effect</td>
<td>8716</td>
<td>4</td>
<td>328.07</td>
<td>2.75**</td>
</tr>
<tr>
<td>Deviation</td>
<td></td>
<td>3445</td>
<td>29</td>
<td>119.28</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>12161</td>
<td>33</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length outer terminal seta</td>
<td>Main effect</td>
<td>3197</td>
<td>4</td>
<td>127.63</td>
<td>2.429</td>
</tr>
<tr>
<td>Deviation</td>
<td></td>
<td>1528</td>
<td>29</td>
<td>52.54</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>4725</td>
<td>33</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length inner terminal seta</td>
<td>Main effect</td>
<td>9227</td>
<td>4</td>
<td>318.45</td>
<td>1.598</td>
</tr>
<tr>
<td>Deviation</td>
<td></td>
<td>5777</td>
<td>29</td>
<td>199.22</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>15004</td>
<td>33</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Significant at .01 level.
** Significant at .05 level.

TABLE 6
RATIOS OF MEAN MEASUREMENTS OF Cyclops kolensis FROM THREE LOCALITIES

<table>
<thead>
<tr>
<th>ITEM</th>
<th>ANEBODA, SWEDEN VS LAKE BAikal</th>
<th>ANEBODA, SWEDEN VS GROSSER PLÖNER SEE, GERMANY</th>
<th>LAKE BAikal VS GROSSER PLÖNER SEE, GERMANY</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length outer seta as % length ramus</td>
<td>2.24**(0.05)</td>
<td>2.04**(0.05)</td>
<td>.598</td>
</tr>
<tr>
<td>Length inner seta as % length ramus</td>
<td>1.41</td>
<td>6.61**(0.05)</td>
<td>2.34**</td>
</tr>
<tr>
<td>Insert. lateral seta % length ramus</td>
<td>.578</td>
<td>0</td>
<td>-.142</td>
</tr>
<tr>
<td>Length med. inner seta % length ramus</td>
<td>.87</td>
<td>18.45**(0.01)</td>
<td>-.438</td>
</tr>
<tr>
<td>Width furca as % length ramus</td>
<td>1.26</td>
<td>3.09**(0.01)</td>
<td>-.205</td>
</tr>
<tr>
<td>Length inner seta as % outer</td>
<td>-.53</td>
<td>3.29**(0.01)</td>
<td>3.73**(0.01)</td>
</tr>
<tr>
<td>Length inner med. seta as % inner seta</td>
<td>-.33</td>
<td>4.37**(0.01)</td>
<td>2.46**(0.01)</td>
</tr>
<tr>
<td>Length outer med. seta as % inner med.</td>
<td>.236</td>
<td>-.61</td>
<td>-.688**(0.01)</td>
</tr>
</tbody>
</table>

* Data from Lindberg 1937.
** Significant at .05 level.

(1961) further noted that the 4th and 5th thoracic segments of the Siberian animals were relatively much wider than those of other C. kolensis examined.

ECOLOGY
Rzoska (1932) indicated that biological characteristics and ecological differentiation as well as morphological features should be of help in working out the systematics of the Cyclopidae. Unfortunately, there does not appear to be as much information on the ecology of C. kolensis and C. vicinus as on their morphology.

Apparently, C. kolensis is generally a cold water species. Kozinski (1933) reported that in Lake Wigry, Poland, C. kolensis is a dicyclic species with the maximum population occurring...
under the ice in February and March; a smaller population peak occurred in early summer. Later, Kozminski (1936) reported that C. kolensis appeared to thrive best in the eutrophic bays of Lake Wigry and in other eutrophic lakes of the region. In the open oligotrophic areas of Lake Wigry it occurred sparingly and seemed to avoid small dystrophic ponds. He also found that the species congregated in almost oxygen-free water near the bottom of Lake Wigry in February and March.

Herbst (1955) reported C. kolensis to be monocyclic with maximum numbers in March and April in Grosser Plöner See. Kozhov (1963) states that in Lake Baikal it occurs abundantly throughout the year in large bays and gulfs that are cooled by waters from the open lake. It occurs only during cold seasons in well sheltered bays which at other times apparently become too warm for it; however, he further states that in years when the water masses of the open lake become warmer than usual, C. kolensis spreads in increased numbers through all the open waters. Judging from the temperature data given by Kozhov the upper limit for the species is about 18°–20° C, and in Lake Baikal the optimum may be about 12°–14° C. Kozminski (1936) noted that Lilljeborg also recorded taking it in a shallow, relatively warm upland lake in July.

C. vicinus is reported to be a pond-dwelling species (Kozminski, 1934). Kiefer (1937) found sexually mature males and females in a small Manchurian lake in August. Rylov (1935) stated that C. vicinus occurs in the plankton of lakes and in small ponds. Gurney (1933) noted that in Britain the species is found in the plankton of "lakes and in small duck ponds" and seemed to be confined to eutrophic waters. Kozhov (1963) reported C.
**TABLE 8**

<table>
<thead>
<tr>
<th>POPULATION</th>
<th>LENGTH OF OUTER SETA AS % OF RAMUS</th>
<th>LENGTH OF INNER SETA AS % OF RAMUS</th>
<th>WIDTH OF RAMUS AS % OF LENGTH</th>
<th>INNER SETA AS % OF OUTER SETA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Siberia</td>
<td>37.1–70.6</td>
<td>52.2–102.5</td>
<td>15.05–28.6</td>
<td>109–187</td>
</tr>
<tr>
<td></td>
<td>50.6</td>
<td>72.4</td>
<td>20.5</td>
<td>143</td>
</tr>
<tr>
<td>Pt. Barrow</td>
<td>54.8–66.2</td>
<td>69.6–85.0</td>
<td>19.5–24.1</td>
<td>117–139</td>
</tr>
<tr>
<td></td>
<td>60.2</td>
<td>77.0</td>
<td>21.6</td>
<td>127</td>
</tr>
<tr>
<td>St. Matthew 809</td>
<td>45.7–83.3</td>
<td>70.3–101.2</td>
<td>24.1</td>
<td>88–213</td>
</tr>
<tr>
<td></td>
<td>67.7</td>
<td>85.5</td>
<td></td>
<td>126</td>
</tr>
<tr>
<td>St. Matthew 814</td>
<td>48.2–63.6</td>
<td>61.2–90.7</td>
<td>23.9–28.3</td>
<td>105–170</td>
</tr>
<tr>
<td></td>
<td>56.0</td>
<td>75.2</td>
<td>25.6</td>
<td>134</td>
</tr>
<tr>
<td>St. Matthew combined</td>
<td>52.8–73.1</td>
<td>67.0–94.6</td>
<td>24.0–27.1</td>
<td>99–165</td>
</tr>
<tr>
<td></td>
<td>62.7</td>
<td>80.3</td>
<td>25.5</td>
<td>128</td>
</tr>
<tr>
<td>Grosser Plöner See</td>
<td>63.1–70.7</td>
<td>99.6–113.7</td>
<td>17.7–19.8</td>
<td>148–170</td>
</tr>
<tr>
<td></td>
<td>66.7</td>
<td>106.6</td>
<td>18.7</td>
<td>159</td>
</tr>
<tr>
<td>Baikal</td>
<td>59.4–71.0</td>
<td>99.3–130.7</td>
<td>17.2–20.8</td>
<td>139–197</td>
</tr>
<tr>
<td></td>
<td>65.2</td>
<td>115</td>
<td>19.0</td>
<td>178</td>
</tr>
<tr>
<td>Aneboda</td>
<td>67.1–77.1</td>
<td>118–134</td>
<td>18.8–21.8</td>
<td>167–181</td>
</tr>
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<td></td>
<td>72.4</td>
<td>126</td>
<td>20.3</td>
<td>174</td>
</tr>
<tr>
<td></td>
<td>60.6–71.5</td>
<td>107–130</td>
<td>19.0–34.0</td>
<td>156–195</td>
</tr>
<tr>
<td></td>
<td>65.1</td>
<td>115</td>
<td>25.2</td>
<td>177</td>
</tr>
<tr>
<td></td>
<td>58.8–67.3</td>
<td>103–119</td>
<td>18.0–22.0</td>
<td>162–180</td>
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<td></td>
<td>65.3</td>
<td>113</td>
<td>19.8</td>
<td>173</td>
</tr>
<tr>
<td>Poland</td>
<td>72.7</td>
<td>118</td>
<td>16.3–24.3</td>
<td>133–193</td>
</tr>
<tr>
<td>Poland slides from</td>
<td>56.6–100.3</td>
<td>96–149</td>
<td>14.4–25.3</td>
<td>133–187</td>
</tr>
<tr>
<td>USNM</td>
<td>75.3</td>
<td>118</td>
<td>18.9</td>
<td>161</td>
</tr>
<tr>
<td>Marsh’s</td>
<td>46–59</td>
<td>63.9–85.0</td>
<td>17.2–24.3</td>
<td>123–156</td>
</tr>
<tr>
<td></td>
<td>53.4</td>
<td>74.7</td>
<td>20.6</td>
<td>140</td>
</tr>
</tbody>
</table>

**Distribution**

If Kozminski (1936) was correct in believing that Olofsson (1918) had specimens of *C. kolensis* from Spitzbergen, then it is known to occur in ponds there, in the New Siberian Islands, and in Alaska. Kozhov (1963) summarized records of the species in the Yeniesi and Angara drainages. Mazepova (1961) presented a map showing localities where it has been found. One belt of records runs from southern Sweden through Poland and Germany to Lake Baikal; a second belt follows the Arctic coast of Eurasia to Alaska.

Currently three subspecies of *C. kolensis* are recognized. *C. k. kolensis*, *C. k. baikalensis*, and *C. k. alaskaensis*. *C. k. baikalensis* was described as a new species by Vasilyeva (1950). Later Lindberg (1955) and Mazepova (1960) concluded that the form in Lake Baikal was not distinguishable from *C. kolensis*. Kozhov (1963) recognized *C. baikalensis* as an ecological subspecies. Lindberg recognized *C. k. alaskaensis* on morphological grounds and Mazepova (1961) concurred.
DISCUSSION AND CONCLUSIONS

The presence of *Cyclops kolenisis* Lilljeborg on the North American continent is established by the examination of new material. It seems unwise in our present state of knowledge to designate subspecies by formal trinomials. It is possible, by measuring enough morphological characteristics and selecting among them, to find at least one feature in which the animals of each lake differ from all others. Extended to the absurd conclusion each lake contains its own subspecies.

The effect of environment on the morphology of *C. kolenisis* is not clear from the evidence. Environmental factors, such as temperature, turbulence, and food, are believed to affect the morphology of some species of cyclopoid copepods. How true this may be for *C. kolenisis* cannot now be told. Animals living in ponds in Sweden exhibit several features in common with those dwelling in Lake Baikal; others living in nearby ponds on St. Matthew Island show features in common and also differences.

Species of supposed immediate common ancestry could be expected to share many features in common. Thus, if minor differences could be consistently associated with forms exhibiting reproductive isolation they would be sibling species—not subspecies. We cannot say whether or not different populations of *C. kolenisis* are reproductively isolated. Geographic separation and the fact that local differences are discernible would suggest that gene flow at least is restricted. The possibility of sibling species is not ruled out by present evidence. What does appear to be ruled out is the desirability of using subspecific names.

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Considerations Regarding the Evolution of Hawaiian Animals

WILLIAM A. GOSLINE

Interest in the biotas of oceanic islands is of long standing. There are several reasons for the continuing interest. One is the possibility that insular evolution may in some respects represent a small-scale model of what has occurred on continents. Another is that, despite all the work on the subject, the "hows" and the "whys" of insular evolution remain inadequately answered. Finally, there is the realization that, with the rapid decimation of native insular habitats, it will soon be impossible to study many aspects of the subject (Hubbell, 1967).

The general field of evolution in oceanic animals has been reviewed many times, most recently by Miller (1966) and Carlquist (1965). Zimmerman's summary (1948) for the Hawaiian terrestrial forms is classic. Here, I shall deal with only certain facets of the subject, and I shall cite only those references from the tremendous literature most pertinent to the matter at hand. This selective method of presentation has serious faults, but any attempt to be comprehensive would seem only to obscure the threads of thought that it is the purpose of the paper to present.

Recently, in writing of land plants, Carlquist (1966:433) has spoken of an "insular syndrome of interrelated evolutionary phenomena." Insofar as Hawaiian animals are concerned, what is more striking to me is the diversity of evolutionary results. Such variations occur not only between groups but within some groups as well. For example the evolution of the Hawaiian drepaniid finches has been very different from that of the sea birds.

This diversity of evolutionary results could be exemplified from various animals groups, most notably insects. However, I shall not deal with Hawaiian insects at any length, primarily because of unfamiliarity with them but also because at the present time they are the subject of an intensive continuing investigation (Zimmerman, et al., 1948—; Spieth, 1966:246). Rather, I shall emphasize the evolutionary problems of three Hawaiian animal groups: the inshore fishes, the achatinellid land snails, and the drepaniid finches. As an introduction to the problems involved the evolutionary status of these three groups in Hawaii is summarized briefly.

The Hawaiian inshore fishes (Gosline, 1958; Gosline and Brock, 1960) form part of a marine biota that is essentially similar to, but somewhat impoverished, as compared with that of the Central Pacific islands to the south and west. There are few conspicuous gaps in the Hawaiian marine biota, and, of those that do occur, at least one—the coral genus Acropora—was present in Hawaiian waters in the past (Menard, Allison and Durham, 1962). There seems to be a more or less constant infiltration of non-resident species into the Hawaiian marine biota today, some of which have become established (Doty, 1961), while some have not (Brock, 1948). Intentional introductions of purely marine forms into Hawaiian waters have been mostly unsuccessful. (By contrast, a number of introductions into areas of reduced salinity, e.g., Kaneohe Bay on Oahu, have done quite well.) One of the few that has succeeded, the "Marquesan sardine," has spread throughout the waters of the high Hawaiian Islands in a matter of a few years (Murphy, 1960). Endemism above the species level among Hawaiian fishes is dubious. However, about one third of the inshore species are represented by endemic forms. These can usually be distinguished from Central Pacific counterparts in 100% of the individuals (for some exceptions, see Gosline, 1955). Aside from a few expected correlations between morphological traits and the relatively cool Hawaiian water temperatures (see, for example, Strasburg, 1955), the morphological characters by which the Hawaiian endemics differ from their Cen-
central Pacific counterparts appear to be of a random nature. Within any family of fishes represented in Hawaii, the endemic forms are often the most abundant.

In striking contrast with the Hawaiian marine biota, the native terrestrial biota is highly disharmonic or unbalanced. Great groups of animals, e.g., the amphibians, were completely unrepresented, whereas others, e.g., the land snails and drepaniids, proliferated greatly. Not only new Hawaiian species, but also new genera and families evolved. Among the achatinellid land snails, the genus *Achatininella* is restricted to the island of Oahu, but some 100 allopatric forms have been described. No relation between the peculiarities of these forms and the environment they inhabit has ever been demonstrated. The drepaniid finches seem to have evolved in quite a different way. They inhabited all of the major islands of the Hawaiian chain and some of the smaller islands as well. The most notable differentiation within the group is in beak shape, which is associated with feeding habits (Baldwin, 1953). Several different drepaniids were often sympatric.

One of the main differences between the terrestrial and marine environments in Hawaii is in the amount of change caused by man. The terrestrial environment has been largely transformed, in part directly by man via agriculture, etc., but perhaps more by the indirect effect of animals and plants which man has introduced, intentionally or unintentionally. Many of these introductions have now replaced or are replacing the native biota and are directly or indirectly responsible for the restriction or extinction of native forms.

With this brief background, the question of evolutionary processes will be discussed.

Basic to the evolution (or lack of it) that will occur on any island is the matter of which organisms are there and which are not. To exist, an organism must first arrive, and it then must find an environment in which it can survive and reproduce. Both of these aspects depend in part on the isolation of the island—not isolation in terms of geographical-physical barriers alone, but in terms of these in relation to the ability of the organism to cross them.

The day when isolation could be considered a causal factor has long since passed. However, that it is a powerful controlling factor is generally recognized. This control acts in two related ways. First, it determines which organisms will get to an island and which will not. The selectivity of this filtering factor will increase with increasing isolation and hence will determine in part the extent to which the island biota resembles its parental biota. The greater the difference between these two biotas, the greater will be the change in biological selection pressures on any organism arriving on the island. This point will be discussed later.

Second, any species that establishes itself on an island should, at least for a while, be preserved from contamination by gene flow from the parental population. If the recent introduction to Hawaii of numerous species (e.g., the Marquesan sardine, the African snail, the garden spider, etc.) is any criterion, the initial immigrants can build up a population of millions of individuals in a few years. Beyond this point contamination from gene flow from a few subsequent immigrants will probably have little effect (Gosline, 1958). There are, however, certain important exceptions to this statement. If, in the process of building up a population from initial immigrants, the population becomes debilitated in some way or loses its ability to cope with diseases or parasites which later immigrants may bring with them, then subsequent immigration may matter a great deal.

Of factors actually causing insular evolution only two will be considered. One is natural selection, and the other the series of features associated with small population size.

It is generally agreed that differentiation proceeds more rapidly in animal populations on small islands than on large ones. The question is: to what extent is this caused by differences in the selective forces on small islands, and to what extent to factors associated directly with small population sizes. A rather large body of data suggests that many of the peculiarities of small-island forms are not directly selected by the environment. Two examples will suffice. Dowdeswell and Ford (1953 and elsewhere) have shown that on the larger islands of the Scilly group the spotting on the wing of the butterfly *Maniola jurtina* remains about as it
is on the adjacent Cornish mainland. On the small islands of the group, however, the number of spots on the wing of the females not only varies from island to island, but increases on some and decreases on others. Second, Mertens (1934:116) has pointed out that the same island may contain a dwarf form of one reptile and a giant form of another. It would be difficult to postulate environmental factors that would select animals in these ways.

If small-population forces are to be postulated for such differences, three possibilities must be considered. The first is the random loss of genes which may occur in small populations by genetic drift (Wright, 1931, etc.). Such a factor would presumably be operative in all small populations. A special case of genetic drift is the phenomenon often called founder effect. This merely expresses the fact that the original immigrants to an island are frequently few in number, and, whether or not they constitute a representative sample, they can bring with them only a small proportion of the alleles present in the parental population (see, for example, Zimmerman, 1948:122, 123). The third possible small-population factor is what Mayr (1954) calls internal selection. In large populations where each gene often has many alleles those which work best as heterozygotes will tend to be selected; on the other hand, in small populations there will be a larger proportion of homozygotes, and alleles which work best in the homozygotic condition will tend to be selected. Thus some shift in internal selection pressure between large and small populations would be expected.

These small-population factors, acting per se, should affect insular immigrants during those initial stages when the population is still small (Fig. 1). But there appears to be no known instance in which a change at this stage has been recorded (cf. Mayr, 1954). Furthermore, it is a generally accepted dictum that, other things being equal, the older the island the greater will be the differentiation in its biota; this implies continuous, not just initial, change.

Then how is the differentiation that occurs on islands, and more rapidly on small islands, to be explained? King (1955) conducted selection experiments for DDT resistance on two cultures of Drosophila melanogaster. After a dozen or more generations some degree of DDT resistance began to be built up in both lines. But, as judged from crossbreeding experiments, the resistance had been built up differently in the two lines. King (1955:314) states: "The manner in which a line could respond to selection was to some extent determined by the genetic nature of the sample from which it started, and having started along one certain road, it kept on. The inevitable sampling error which occurs when a line is taken from a larger population is very likely the anlage of the genetic individuality of the line. This is, of course, an example of the principle of genetic drift..." The second example is that reported on by Dobzhansky and Pavlovsky (1957). In this experiment ten cultures from a specially developed laboratory stock of Drosophila pseudoobscura were started with 20 flies each and compared after 17 months with ten other cultures that did not begin with a reduced number of individuals. Those stocks which had started with 20 flies showed more variation than the controls. Again, Dobzhansky and Pavlovsky conclude (1957:316): "Although the trait studied (gene arrangement in the third chromosome) is subject to powerful selection pressure, the outcome of the selection in the experimental populations is conditioned by random genetic drift."

One aspect of these experiments by King and by Dobzhansky and Pavlovsky may well be of importance for insular evolution. In both instances not only were the original samples small, but the selection that was exerted upon them was far different from the selection of the natural environment from which the flies came. It is as though the samples in the experiments were subjected to an intense selection pressure at right angles to the pressures to which the ancestral "wild" forms had presumably adapted themselves. Possibly some of the alleles intensely selected under the laboratory conditions had been of only peripheral significance to the wild stocks and hence variably represented in them. Such alleles would be more subject to sampling error among small founder populations drawn from the parental stock than those previously under intense positive selection pressure.
Insular selection pressures (except, perhaps, for species introduced by and dependent on man) are similarly at an angle to those exerted on the mainland parental form. Insofar as the island biota is different from that whence the immigrants came, it is inevitable that the biological selection pressures on islands will differ. Any immigrant to an island will leave behind at least some of the predators, competitors, diseases, and parasites that the parental mainland stock had to cope with. On the other hand the initial immigrants may well have to adapt to new forms of food, cover, etc. (This will be less true only in degree if a species arrives by a series of island hops.)

There is also evidence that selection pressures on small islands are likely to be more radically different than they are on large islands. Thus, on Manana Island, a small outlier of Oahu without domestic cats, the cat flea (Ctenocephalides felis felis) has developed an ectoparasitic existence on rabbits (Oryctolagus cuniculus) (Tomich, et al., in press). Again, in the Balearic Islands off Spain, Eisentraut (1949) showed that on the smaller outliers the food of lizards (Lacerta) differed considerably from that on the main islands. As the normal insect food became more restricted, these lizards added the normally avoided ants to their diets, and on very small islands ate even flower petals and young plant shoots.

Eisentraut believed that this change in diet had a direct metabolic effect resulting in the melanism frequently found in the small-island populations. To me (cf. Dowdeswell and Ford, 1955) it seems more likely that the morphological changes so frequently found in small populations are in part the indirect effect of altered selection pressures working with time on the, in part randomly, depleted gene pool of small populations. A gradual reintegration of such a gene pool in response to altered selection pressures would likely involve a change in phenotypic characters that are not themselves selected. Such an interpretation (cf. Mayr, 1954; Dobzhansky and Pavlovsky, 1957) seems to me to provide the best available explanation for the often rather heterogeneous differentiating characteristics of insular endemics, e.g., Hawaiian inshore fishes.

The main reason why the peculiarities of Hawaiian endemic fishes cannot, apparently, be attributed to small-population losses alone is that in many instances the Hawaiian endemics are not characterized by a simple increase in variability (as in Dobzhansky and Pavlovsky's flies) but rather by new and fairly constant characters entirely outside the range of variability of the ancestral populations (as in King's results). Presumably such characters must have arisen through a reintegration and/or evolution from the ancestral genetic system via direct or indirect selection. The same reasoning would seem to apply to at least some of Eisentraut's melanic lizard populations.

Judging by personal observation and common knowledge concerning recent successful terrestrial introductions of animals to the Hawaiian islands (see also Mead, 1961:180-182; Tomich, et al., in press), there is often (presumably following a longer or shorter period of small numbers) a tremendous initial build-up and "overshoot" in population number (Fig. 1). During my 18 years in Hawaii this has hap-

![Theoretical population size (above) and allele variety (below) plotted against time in a terrestrial animal that successfully immigrates into the Hawaiian Islands for the first time. A, Date of arrival; B, time when population becomes sufficiently large that small-population genetic factors will per se cause no further loss of alleles; C, initial peak of abundance; and D, subsequent equilibrium. For discussion, see text.](image-url)
pened with a garden spider (Argiope appensa) and the giant African snail (Achatina fulica), among the more conspicuous unintentionally introduced forms. If it can be assumed that this cycle happened in the past with our "native" biota, then certain postulates concerning selection pressures would seem to follow.

First, during the period of initial buildup of an introduced form, selection pressure must be very low. (Apparently the other members of the biota are not initially able to cope with or defend themselves from the new introduction.) However, at some point in the buildup, the population becomes excessive, after which it falls drastically to a new fluctuating equilibrium well below the previous maximum. The nature of the factor that sooner or later kills back the initial overshoot is unknown in any particular instance. There is no reason to believe it is the same in all cases, or that it may not be a combination of factors. What is important to the present argument is that after a period of relaxed selection during the population buildup a very severe selection pressure of some sort appears. Some of the various possibilities are as follows.

First, the animal may eat out the available food supply and then die of starvation. This apparently happened to the rabbits introduced to Lisianski Island (Bryan, 1942:192, 193), and almost but, perhaps significantly, not quite with the rabbits on Laysan (Warner, 1963:6, 7; cf. also Tomich, et al., in press).

On a larger island with a more varied biota a second possible situation might occur after the immigrant population had overeaten its original food supply. Assume that an immigrant adapts itself to an insular food supply as close as possible to that of its parental stock. Assume that, having adapted itself to this insular food source, the immigrant builds up a tremendous population under greatly relaxed selection pressure. At some point it will overshoot its new food supply and a severe competition for food will take place. This selection may preserve the best adapted individuals of the original immigrant type, if enough of the food supply is left. It may also preserve those individuals that have differentiated farthest in the direction of adapting to a new food source (Fig. 2). This theoretical possibility has been set up with the evolution of the Hawaiian drepaniid finches, with their various beak types, in mind.

Another possibility is that, following the initial population explosion, some factor other than food supply develops to keep subsequent numbers low. This could be disease or parasitism, some change in other environmental features, or some other factor which would lower the reproductive rate. That the reproductive rate may be diminished has been stressed by Lack (1954). Lack deals especially with changes in egg number in birds. But there is
another method, in plants at least, by which the replacement rate may be held in check. Rattenbury (1962:354) has said of New Zealand forms:

"Furthermore, the germination of seeds of many native species is a matter of extreme difficulty, as is evidenced by the sporadic appearance of seedlings which often seem to require special conditions for their development. Competent nurserymen have experienced great difficulty in germinating native seeds, often resorting to powerful treatments for breaking the dormancy. In many cases the viable period is very short."

Under conditions of severe interspecific competition, a reduction in the reproduction rate, however accomplished, would seem to be feasible only to the extent that it enables the species to raise a greater number of offspring (Lack, 1954). To drop below that rate would invite replacement by competitors (including possible subsequent immigrants of the same species). If, however, there is very slight interspecific competition, the reproductive rate might theoretically fall to and somewhat below the maximum possible replacement rate without immediate harm. In my opinion, this is what seems to have occurred in many forms among the native terrestrial Hawaiian biota.

If this is true, a species that experienced essentially no natural selection from infra- and interspecific competition during the initial increase might again avoid natural selection after an equilibrium had been reached. In the process, however, the species would of course lose its aggressiveness, especially as compared with subsequently introduced rapidly breeding forms.

Possible examples of a loss in fertility, apparently before any overpopulation has taken place, are provided by the Hawaiian hawk (*Buteo solitarius*) and the Hawaiian crow (*Corvus tropicus*), both of which are, and so far as known always have been, confined to relatively small areas of the single island of Hawaii. In view of the general adaptability of related mainland forms this geographic restriction is most difficult to explain. Possibly here we have a "depauperization of biotype" (Hultén, 1937) arising from small population effects. Such a "depauperization" of course could and probably often does result in a lowering of reproductive capacity.

Returning finally to the achatinellid snails of Oahu, it seems obvious from the isolation of many of the colonies of *Achatinella* (even before their extensive extermination by the introduced carnivorous snails *Englandina* and *Gonaxis*; see Krauss, 1964) that they were not spreading. Presumably they have only been developed from some more "aggressive" ancestral form (and/or a less dissected topography than exists today). But given the more recent isolation in separate colonies there seems to be no reason why, in the absence of further gene flow, each colony should not evolve in its own way as do so many other small populations, particularly land snails. A basically similar provisional hypothesis has been advanced by Carson (1966:405) to explain the formation of Hawaiian species of *Drosophilidae*.

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Notes on Indo-Pacific Scleractinian Corals, Parts 5 and 6

John W. Wells

Part 5
A New Species of Alveopora from New Caledonia

A number of specimens of poritid corals sent by Dr. R. L. A. Catala (Aquarium de Nouméa) included several species of Goniopora and Alveopora, among them a distinctive new form of the latter that is described below. All these corals came from the same site—Banc Gail in the lagoon of Nouméa at a depth of 35–40 m—and included the following species:

Alveopora allingi Hoffmeister
A. mortensi Crossland
A. catalai sp. nov.
Goniopora bernardi Faustino
G. duofaciat Thiel
G. sp. cf. G. Great Barrier Reef 6 of Bernard
G. sp. cf. G. irregularis (Crossland) (≡ G. octoformis Milne Edwards and Haime?)

The writer expresses his thanks to Dr. Catala for this material and for photographs of the living colonies.

Family Poritidae

Genus Alveopora de Blainville 1830

Alveopora catalai sp. nov.

Figs. 1–3

Corallum ramose, composed of gently-tapered blunt branches 5–12 mm thick, dividing about every 20 mm at approximately 30 degrees. Corallites cylindrical to subpolygonal, averaging 3.5 mm in diameter when fully developed, a few reaching 4.5 mm, their vertical axis diverging slightly from the axis of the branch. Mature calices slightly exsert, oval in outline, and slightly separated from each other. Corallite wall formed by a palisade of 12 trabecular pillars linked by stout synapticulae, the projecting tips of the pillars forming a prominent crown of spines. The 12 septa consist of vertical rows of trabecular spines projecting inward from the mural pillars. The tapered inner ends of the septa divide and fuse deep in the calices to form a loose, irregular axial tangle. The vertical row of spines of each septum in the inner or upper side of a mature calice is commonly strengthened by a vertical bar between each spine. Dissepiments sparse, represented by a few very delicate horizontal partitions deep in the calices. On older parts of branches the mural trabeculae become greatly thickened, often obliterating the spaces between them.

The polyps (Fig. 5) are typical of Alveopora—12 blunt tentacles expanding horizontally from the margin of the highly extensible column wall.

The arborescent growth form of this species alone distinguishes it from the 17 described species of Recent Alveopora from the Indo-Pacific, all of which are encrusting, submassive or gibbous, columnar, or clavate-ramose. None has slender branches with relatively large corallites. The nearest form is A. allingi Hoffmeister (1925: 81, pl. 23, fig. 2a, b, c) (25–30 m, Samoa; Great Barrier Reef; New Caledonia), a subcolumnar form with corallites of about the same size with similar development of mural and septal structures, but with calices normal to the surface of the lobate colonies.

 Locality: 35–40 m, Banc Gail, Nouméa lagoon, New Caledonia.

Reference

Figs. 1–3. *Alveopora catalai* Wells. 1 and 2, Holotype, ×1 and ×4; 3, expanded polyps, ×1 (photograph by R. Catala); Banc Gail, 35–40 m, Nouméa lagoon.

Figs. 4 and 5. *Blastomussa merleti* Wells. 4, Longitudinal section of corallite, ×4, Banc Gail, 35 m, Nouméa lagoon; 5, calicular aspect, ×4, outside barrier reef of New Caledonia, 40 m.

Fig. 6. *Cynarina lacrymalis* (Milne Edwards and Haime). Lateral aspect of septum, ×4, Banc Gail, 35 m, Nouméa lagoon.
Part 6
Further Note on Bantamia merleti Wells

Study of additional specimens of Bantamia merleti Wells 1961 sent by Dr. Catala shows that the writer's assignment of this coral to a position near Galaxea was erroneous, and that a new genus of the Mussidae is involved.

Family Mussidae
Genus Blastomussa gen. nov.

Colonial; colony formation by extratentacul ar budding from the edge-zone, producing small phaceloid tufts of erect cylindrical corallites. Corallite walls septothecal, costate, with narrow edge-zone and delicate epitheca. Septa stout, mossoid, composed of several fan systems each forming a low, rounded, lobulate tooth. Columella coarsely trabecular. Dissepiments (Fig. 4) coarsely vesicular, steeply inclined downward from the wall and rising axially.

Polyps (previously described by Wells) lacking organic connection in adult stage.

Type species: Bantamia merleti Wells 1961
Figs. 4 and 5

Having the characters of the genus as diagnosed. Corallites 10-12 mm in diameter with 24 non-uniting septa arranged 12/12.

The single holotype specimen described by the writer as a new species of Bantamia Yabe and Eguchi 1943 appeared to have septa with entire margins, a condition that suggested a systematic position near Galaxea. New topotype and other material, however, shows that the septa have the coarse lobate dentations (Figs. 4 and 5) characteristic of the mussids, especially Cynarina (Fig. 6).

Although Blastomussa resembles Bantamia in growth form and cylindrical corallites, the differences are more significant: the colony of Bantamia is less compact, the corallites are tortuous rather than regularly erect, the septa are smooth laterally (upper margins, whether dentate or not, unknown), the dissepiments are "delicate, but well-developed and usually horizontal." The relationship of Bantamia to Galaxea presumed by Yabe and Eguchi (1943), is still justified from the structures as now known, but the mussid affiliation of Blastomussa merleti is scarcely to be doubted.

Blastomussa is mainly distinguished from the other Recent colonial mussids (Lobophyllia, Symphyllia, Musa, Mussismilia, Isophyllia, Isophyllastrea, and Mycetophyllia), all of which increase by intratentacular budding, by its extratentacular budding and such lesser characters as the small size of the corallites and proportionally fewer septa. It compares most closely in septal structure to Cynarina, a larger, solitary form.

Localities: Banc Gail, 35-40 m, Nouméa lagoon (holotype and topotypes); and outer slope of barrier reef of New Caledonia, 40-50 m.

References
Notes on the Distribution of Wood-Boring Teredines in the Tropical Indo-Pacific

V. V. Srinivasan

Extensive work has been carried out on the taxonomy of the Teredinidae of the east coast of India, the Philippines, the Hawaiian Islands, and other areas in the Pacific (Becker, 1958; Daniel, 1956; Nair, 1961; Rajagopal, 1964; Saraswathi, 1964; Sivickis, 1928; Bartsch, 1921, 1922, 1927; Moll and Roch, 1931; Roch, 1935, 1940, 1955a, 1955b; Miller, 1924; Edmondson, 1941, 1942, 1946, 1959). Recently Turner (1966), in her "Catalogue of the Teredinidae," has redefined the genera and proposed a new system of classification. During a recent survey of the Teredinidae of the Hawaiian Islands it was possible for the author to collect material, study Dr. Edmondson's types, and draw conclusions on the possible mode of distribution of the teredines in the tropical Indo-Pacific area.

The study at Hawaii was based on collections at different sites on the island of Oahu, the island of Kauai and from Dr. C. H. Edmondson's type collections at the Bishop Museum in Honolulu. Also panels of Douglas fir and white pine were suspended at various depths at two different sites—one at Kewalo Basin, Honolulu and the other at Coconut Island, Kaneohe—and teredines were collected after an immersion period of about 3 months. Material from the Madras coast was collected from drift logs washed ashore on the Madras beach (Mylapore and Triplicane areas), from floating pieces of wood, from underwater wooden structures like piles and catamarans, and from test planks which were submerged in Madras harbour during 1965-1967. Specimens collected were identified using Turner's revised classification. The following are the species that occur on the Madras and Hawaiian coasts. Of the 18 species (11 of them new species) described by Edmondson, only 12 seem to be valid. Also, 27 species of teredines have been described from the Madras coast and these refer only to 13 valid species. The original names as well as synonyms (* from the Madras coast, ° from the Pacific islands) have been listed here.

Bankia carinata Gray
*Bankia (Bankiella) edmondsoni Nair
*Bankia (Bankiella) indica Nair
Bankia campanellata Moll and Roch
*Bankia (Bankia) bengalensis Nair
Bankia bipennata Turton
*Bankia (Plumulella) lineata Nair
*Bankia (Neobankia) lineata Nair
*Bankia (Neobankia) denticuloservata Daniel
Lyrodus pedicellatus Quatrefages
*Teredo (Teredo) indica Nair
*Teredo (Lyrodus) malaccana Roch
*Teredo (Teredo) madrasensis Nair
°Teredo (Teredo) honoluluenesis Edmondson
°Teredo (Teredops) diegensis and var. mid-wayensis Edmondson
Dicyathifer mannii Wright
*Teredo (Kuphus) mannii Wright
Teredora princesae Sivickis
*Teredo (Teredora) gregoryi Dall et al.
*Teredo (Teredora) minoris Nair
*Teredo (Dactyloteredo) diegenderichseni Roch
°Teredo (Teredora) gregoryi Dall et al.
Nototeredo edax Hedley
*Teredo (Psiloteredo) tondiensis Nair and Gurumani
*Teredo (Dactyloteredo) juttingae Roch
Uperrotus clavis Gmelin
*Teredo (Teredora) clava Gmelin
*Teredo (Teredora) vattanensis Nair and Gurumani
°Teredo (Teredora) rehderi Nair
Nausitora dunlopae Wright
*Bankia (Nausitora) madrasensis Nair
*Nausitora lanceolata Rajagopal
Teredo furcifera von Martens
*Teredo (Teredo) furcillatus Miller

1 Marine Organisms Scheme, Zoological Research Laboratory, University of Madras, Madras-5, India. Part of this work was carried out while the author held a F.A.O. (UN) fellowship in 1966. Manuscript received April 5, 1967.

2 Refer to Nair (1961) for earlier papers.
*Teredo (Teredo) parksi var. madrasensis Nair
°Teredo (Teredo) parksi Bartsch
°Teredo (Cornuteredo) bensoni Edmondson
Teredothyra smithi Bartsch
*Teredo (Nototeredo) nambudalaiensis Nair and Gurumani
*Teredo (Zopoteredo) bengalensis Nair
Teredothyra excavata Jeffreys
*Teredo (Teredothyra) linearis Nair
°Teredo (Teredothyra) palauensis Edmondson
°Teredo (Teredothyra) subicensis Edmondson

Bankia bipalmulata Lamarck
*Bankia (Bankia) bipalmulata Lamarck
°Bankia (Bankiella) sp.
°Bankia (Neobankia) hawaiensis Edmondson
°Bankia (Neobankia) konanensis Edmondson
Nautilus sp.
°Bankia (Nautilus) oahuensis Edmondson

Teredo bartschi Clapp
°Teredo (Teredo) bartschi Clapp
°Teredo (Teredo) biloensis Edmondson

Lyrodus medilobata Edmondson
°Teredo (Cornuteredo) medilobata Edmondson
Teredo triangularis Edmondson
°Teredo (Cornuteredo) milleri Dall et al.
Teredo fulleri Clapp
°Teredo (Zopoteredo) fulleri Clapp
Teredo clappi Bartsch
°Teredo (Zopoteredo) trulliformis Miller

From Table 1 it is clear that while 11 species of teredines are generally well distributed from Madras to the Philippine coast, the others are mostly confined to Hawaii and the Pacific, and are not represented in the rest of the areas. Of the seven species recorded from Hawaii, T. bartschi, T. clappi, and T. fulleri seem to extend farther and invade the Gulf of Mexico and the Caribbean while others are indigenous.

L. pedicellatus, T. princesae, T. furcifera, and T. excavata are known to occur not only along the Madras coast, in Southeast Asia, and near

---

**TABLE 1**

**The Distribution of Important Species of Wood-Borers in the Indo-Pacific Area**

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>INDONESIA AND PACIFIC ISLANDS</th>
<th>PHILIPPINES</th>
<th>HAWAII</th>
<th>OTHER ISLANDS*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bankia carinata</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Bankia campanulaea</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bankia bipennata</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lyrodus pedicellatus</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>1,2,3,4</td>
</tr>
<tr>
<td>Dicyathifer manni</td>
<td>X</td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Teredora princesae</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>2,3,4,5</td>
</tr>
<tr>
<td>Nototeredo edax</td>
<td>X</td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Uperotus clatus</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nautilus dunlopei</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>1,2</td>
</tr>
<tr>
<td>Teredo furcifera</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Teredothyra smithi</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Teredothyra excavata</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Bankia bipalmulata</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Nautilus sp.</td>
<td>X</td>
<td></td>
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<td></td>
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<tr>
<td>Teredo bartschi</td>
<td>X</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Lyrodus medilobata</td>
<td>X</td>
<td></td>
<td></td>
<td>1,7</td>
</tr>
<tr>
<td>Teredo triangularis</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lyrodus affinis</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Teredo fulleri</td>
<td>X</td>
<td></td>
<td></td>
<td>1,6,7</td>
</tr>
<tr>
<td>Teredo clappi</td>
<td>X</td>
<td></td>
<td></td>
<td>1,7</td>
</tr>
</tbody>
</table>

* The numbers in this column refer to species reported by Dr. Edmondson from the island of Samoa (1), Canton (2), Johnston (3), Midway (4), Wake (5), Christmas (6), and Palmyra (7).
the Philippine and Hawaiian islands, but also from Samoa, Canton, Johnston, Midway, Wake, Palau, Christmas, and Palmyra islands—all in the tropical Pacific. Hence these species are cosmopolitan in distribution. \textit{T. princesae} was collected from floating timber by the Vityas Expedition (from station No. 5209 in the Indian Ocean), and identified by the author.

While most of the species reported from Madras are from pelagic timber only a few have been successful in invading timbers from enclosed waters (\textit{L. pedicellatus} and \textit{T. furcifera} in Madras harbour; \textit{L. pedicellatus}, \textit{T. furcifera}, \textit{B. campanellata}, \textit{D. manni}, and \textit{N. bedleyi} in Pulicat Lake).

It may be of interest to note the records of occurrence of \textit{B. nordi} Moll (Rajagopal, 1964) and \textit{B. rochi} Moll (Rajagopaliengar, 1961) for the first time along the northeast coast of India at Calcutta.

The apparent discontinuity in distribution of some of the species in the Indo-Pacific area is probably due to non-availability of wood for transportation, lack of intensive collection efforts, or to hydrobiological factors like temperature and salinity which influence breeding. It is also possible that adults may not be able to tolerate wide ranges of temperature and salinity, and this may be a controlling factor for their successful establishment.

ACKNOWLEDGMENTS

My grateful thanks are due to Dr. G. Krishnan, Director, Zoological Research Laboratory, University of Madras, and Dr. A. Purushotham, Director, Biological Research, Forest Research Institute, Dehra Dun, for their encouragement. I wish to thank also Dr. Roland W. Force, Director, Bishop Museum for his unstinted help during my stay at Honolulu.

REFERENCES


Birds of Haleakala National Park, Maui, Hawaii

CHARLES F. YOCOM

FROM 4 JULY to 29 August 1963, I was able to observe birds on the Hawaiian Islands. Most of my observations are from the Island of Maui, where I worked on a study of feral goats in Haleakala National Park.

Most of the names of locations in the National Park are shown on the map (Fig. 1) which also shows elevations. The four types of cover found in the park and their percentages are: nonvegetative, 58%; brush, 39%; grass, 2.5%; and woodland, 0.5%. I hiked at least 300 miles over this terrain; so I had an unusual opportunity to observe the birds. Detailed information on the climate is presented by Feldwisch (1941) and Yocom (1964). Vegetation and plant communities are discussed by Ruhle (1959), Schwartz and Schwartz (1949), and Yocom (1964, 1967).

The following records are those of the author and include only observations made in Haleakala or on the road to the crater.

WHITE-TAILED TROPICBIRD OR KOAE (Phaethon lepturus): About a dozen sightings in Haleakala Crater, at elevations from 7,000 to 9,000 ft: 10 July, 1 on way to Haleakala; 16 July, 1 pair on west side of Kaupu Gap near cliff (possible nesting here); 31 July, 1 in flight near Paliku Pali; 6 August, 5 at Paliku; 8 August, 1 in flight over Paliku.

NENE OF HAWAIIAN GOOSE (Branta sandvicenlis): In 1962 several Nene were brought to a holding pen near Paliku Cabin, at about 7,000 ft elevation. These birds were allowed to fly from their holding pen as soon as new primaries developed after all old primaries were plucked from one wing. My observations are of Nene that were released in 1962. After 29 other Nene were brought in on 30 July 1963 and placed in the holding pen, birds from the release of 1962 returned to the immediate area. On 11 July, 1 seen flying east of Paliku; 15 July, 1 heard in morning at Paliku; 30 July, 2 flying near Paliku; 6 August, 1 female, which had been seen Oct. 1, 1962, now at pens; 7 August 1963, 3 now back at pens; 8 August, 5 now back at pens; as many as 10 seen a few days later.

AMERICAN GOLDEN PLOVER OR KOEA (Pluvialis dominica): The first plover was seen on 3 August, below Haleakala Headquarters in grassland. Other observations include the following: 12 and 13 August, 4 seen by Jim Lindsey along park road; 14 August, 2 along park road; 15 August, 10 in one flock along park road; 18 August, 6 in Haleakala Ranch lands; 22 August, 10 flushed from flat on top of Waikeheehia Kuike; 23 August, 12 flushed from lava between ancient Hawaiian trail and Silversword Loop; 23 August, 1 seen, others heard near Silversword Loop.

SHORT-EARED OWL OR PUEO (Asio flammensis): This owl is an active hunter in the grasslands of Haleakala and was noted to sail much like a Buteo hawk over the palis. On 11 July, 4 seen at Paliku; 12 July, 1 on pali above Paliku; 15 July, 1 (blond or light tan) flying over cliff at Paliku, 1 feeding back of Paliku cabin; 16 July, 1 on west pali of Kaupu Gap; 18 July, 1 mewing as it circled Paliku area; 31 July, 2 (1 blond and 1 with blond feathers in wing) at Paliku; 1 August, 1 in Kaupu Gap; 3 August, 1 in grassland, Haleakala Ranch.

APAPANE (Himatione sanguinea): My observations were all in the rainforest area near Paliku. On 11 July, 5 near Paliku; 12 July, 12–14 in Kipahulu Gap; 13 July, 3 in Kaupu Gap; 16 July, 2 feeding on red bloom of ohia tree in Kaupu Gap; 18 July, 2 in Kaupu Gap; 31 July, 1 feeding in mamane trees (yellow blooms), 1 juvenile at Paliku; 1 August, 1 adult and 1 juvenile feeding on mamane bloom; 8 August, 5 near Paliku; 21 August, 2 at
Paliku; 2 adults and 1 juvenile in wooded draw along Paliku Trail.

**Iiwi (Vestiaria coccinea):** This vermillion bird with black wings and tail is listed as very rare on Maui. I saw 4 in the rainforest area of Kipahulu and near Paliku. On 10 July, 1 at Paliku; 12 July, 2 in Kipahulu Gap; 1 August, 1 in a grove of ohia trees about 2/3 of the way up pali back of Paliku cabin.

**Amakihi (Loxops virens):** This small native greenish bird with no eye ring was seen in about the same areas as the Apapane and the Iiwi. On 10 July, 1 at Paliku; 12 July, 1 at Paliku cabin, and 3 at Kipahulu Gap; 13 July, 1 seen carrying food to young along fern lined goat trail on pali, 1 at Kaupo Gap; 14 July, one at Kaupo Gap; 18 July, 1 adult and 2 young near Paliku cabin, 3 at Kaupo Gap; 31 July, 1 in Paliku area; 1 August, 1 feeding on mamane bloom at Paliku; 22 August, 1 in wooded draw south of Paliku cabin.

**California Quail (Lophortyx californicus):** This introduced species was seen several times near Haleakala Headquarters, but none in the crater. The highest elevation at which I observed this species was 8,500 ft, on the Haleakala Rim Road, above the Park Headquarters on 18 August.

**Chukar (Alectoris graeca):** Many Chukars were seen on the floor of Haleakala Crater and on the pali, as high as 10,000 ft elevation. On 10 July, much sign; 16 July, heard calling from west pali of Kaupo Gap; 19 July, several heard calling from Holua cabin; 20 July, 21 near
Holua cabin, 2-weeks-old young seen near bracken fern, several heard calling from pali; 22 July, 1 female and 3 chicks (3½ weeks old) near Holua cabin; 26 July, 4 on rim of pali, Paliku, much sign along rim of Paliku (dusting bowls, droppings); 29 July, several heard calling in night at Kapalaoa cabin; 30 July, nest found (13 hatched eggs) east side of bunch grass, 150 yards out on floor of crater; 1 female and 7 young (4 weeks old) seen in wash south of Holua cabin; 2 August, 2 adults and 13 (half-grown) young on trail 2 miles from Paliku, also 1 adult and 11 young (one-third grown); 7 August, 6 on pali east of Paliku.

RING-NECKED PHEASANT (*Phasianus colchicus*): This bird seems well adapted to the mezic flora of Haleakala and was flushed from all of the palis. On 10 July, tracks seen near Paliku; 11 July, 2 at Paliku; 14 July, 1 near Kaupo Gap; 16 July, 1 pair flushed from Kaupo Gap, 2 males calling from Kaupo Gap, 3 flushed from Kaupo Gap, 1 female seen near cabin; 18 July, two males at Kaupo Gap; 21 July, 1 heard calling near Holua cabin; 31 July, 1 flew from 1,000 ft above to floor of Paliku; 2 August, 2 on crater floor; 7 August, 4 at Paliku; 21 August, 1 female and 2 young (half-grown) 1 mile from Paliku in Kaupo Gap; 22 August, 1 in Kaupo Gap.

SKYLARK (*Alauda arvensis*): Often seen high on the mountain rim and in the crater. On 10 July, 1 or more on way in to Haleakala; 20 July, 2 or 3 near Holua cabin, 1 calling as it flew over Holua cabin; 2 August, 2 near Kapalua Trail fork; 3 August, 25 + in grasslands, Haleakala Ranch on park road; 2 July, 1 on rim of Paliku.

RED-BILLED LEIOTHRIS (*Leiothrix lutea*): This introduced bird has adjusted to the rainy area in the National Park and was seen frequently near Paliku at over 7,000 ft elevation. On 10 July, some near Paliku cabin; 11 July, 4 or more at Paliku, 2 or more at Kaupo Gap; 12 July, heard singing; 13 July, 6 at Kaupo Gap; 18 July, individuals heard singing at Paliku, 2 at Kaupo Gap, 4 at Kaupo Gap; 18 July, 5 (1 carrying food) at Kaupo Gap; 29 July, 1 singing 1 mile west of Kapalaoa cabin; 31 July, heard singing in Paliku area; 20 August 1963, heard singing in Paliku area.

MOCKINGBIRD (*Mimus polyglottos*): This species is commonly seen at lower elevations outside the park. I assumed that the following sightings were of one bird that used a shrub-grass association, located on the floor of Haleakala Crater, at over 7,000 ft elevation. On 10 July, near Oili Puu; 2 August, near Kapalaoa Fork in Kipuka of Alii, mamane trees, mountain pilo, pukiwiki, bracken fern, evening primrose, and grasses; 9 August, 2 miles from Paliku.

INDIAN MYNA (*Acridothes tristis*): Although this is a common bird at lower elevations, the only one I saw in the park was observed feeding in a pasture at the base of Halemau Trail, on 20 July.

JAPANESE WHITE-EYE (*Zosterops japonica*): This species appeared to be distributed over much of the park. On 10 July, 1 near Puu Nae; 11 July, several near Kaupo Gap; 12 July, 5 at Paliku, 5 in grassy glade near Kaupo Gap; 13 July, several near Kaupo Gap; 14 July, several near Kaupo Gap; 18 July, several near Kaupo Gap, 20 or more (1 carrying food) near Kaupo Gap; 29 July, 1 seen 1.9 mile from Kapalaoa cabin; 31 July, several in Paliku area; 30 July, several in wash east of Kapalaoa cabin; 2 August, 2 near Kapalaoa Trail fork; 20 August, 2 in Kaupo Gap; 22 August, 2 in Kaupo Gap.

RICEBIRD (*Lonchura punctulata*): Only one ricebird was seen in the park, on 10 July, at Paliku.

HOUSE FINCH (*Carpodacus mexicanus*): Common in the park. By mid-July and August large flocks frequented the floor of the crater at 7,000 or more ft elevation. On 10 July, none noted at Paliku; 11 July, 2 seen at Paliku; 13 and 18 July, several at Kaupo Gap; 30 July, several in Kapalaoa area; 2 August, 150–200
along trail in mamane trees east of Puu o Pele; 20 August, several in Kaupo Gap; 22 August, 50 + near Paliku; 26 July, 2 on rim of Paliku; 29 July, 1 on rim of Sliding Sands Trail.

Other birds seen in the islands, but not in or near Haleakala National Park, included: Common Gallinule or Alae Ula (Gallinula chloropus) in a freshwater pond at Barber's Point, Oahu; American Coot or Alae Keokeo (Fulica americana) in a pond near highway between Kahului and Haleakala; Ruddy Turnstone or Akekeke (Arenaria interpres) at Maalaea, Maui; Black-Necked Stilt or Aeo (Himantopus mexicanus) in pond near Kahului; Hawaiian Hawk or Io (Buteo solitarius) at Kilauea and Kona, Hawaii; Spotted Dove (Streptopelia chinensis), Barred Dove (Goepelia striata), House Sparrow (Passer domesticus), and Cardinal (Richmondena cardinalis), all at lower elevations.

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Baker's Law and Dioecism in the Hawaiian Flora: An Apparent Contradiction

AMY JEAN GILMARTIN

ABSTRACT: Much evidence available in the literature supports the contention of H. G. Baker that self-compatibility is the rule in plants which have undergone long distance dispersal. However, in the Hawaiian flora there may be a high incidence of dioecism which represents an extreme form of outbreeding. Data are compiled which support the viewpoint of a higher than continental incidence of dioecism in the Hawaiian flora. A simple explanation is advanced for resolving the apparent contradiction between the higher percentage of dioecism and the isolation in the Hawaiian flora.

A high degree of self-compatibility is evidenced in plants which have undergone long distance dispersal (Baker, 1953, 1955, 1959a, 1959b). Stebbins (1957) suggested the term "Baker's Law" for this type of response to selection by the establishment of a closed breeding system. Self-compatibility which permits inbreeding increases the chances for a few individuals to establish themselves in an area new to their population. On the other hand, if they are subject to enforced outcrossing because of either a self-incompatibility mechanism at the chemical level (Baker, 1948) or because of the dioecious habit there would be less chance for success in establishment. This interpretation is well stated by Davis and Heywood (1963:376) under the heading, Long-Distance Dispersal: "Clearly if it is an inbreeding individual it will have a much better chance of being fertilized in the absence of pollen from another individual and of building up a new colony, than if it were an outbreeder depending on other individuals for pollen." Baker (1953) also makes the point that self-compatible species are not dependent upon insects for pollination, which insects might not be present in the new area.

Baker (1955) cites some examples where selection apparently has acted in preserving a self-compatible species which has been dispersed over long distances. Taylor (1954) studied the flora on Macquarie Island, a small isolated sub-antarctic island. He recorded thirty-five species of vascular plants, three of which are endemic. Recourse to the available geological information indicated to Taylor that the island had been completely covered by ice during the Pleistocene epoch. Therefore, the plants must have arrived sometime after the Pleistocene. He suggests that the three endemics have evolved in situ and notes that one of these, Coprosma pumila (Rubiaceae), is dioecious elsewhere in its range but on Macquarie Island is mainly monoecious.

An example of self-compatibility and long distance dispersal is available in the animal kingdom. Longhurst (1955) reports successful long distance dispersal in a self-fertilizing crustacean, Nostrostraca. He feels that this small crustacean has spread so successfully because of its characteristic small, light, easily dispersed eggs that do not hatch unless they are first subject to desiccation and because of their self-fertilizing habit.

Grant (1958) has found that many California annuals with self-incompatibility are represented in the Great Basin and other outlying areas by self-pollinating forms. Further evidence for Baker's Law is provided by the strand flora in Hawaii. It is generally accepted that strand plant species throughout the world are distributed by means of long distance dispersal. Indirect evidence for this is provided by McCaughey (1918). He estimates that of the littoral flora in the Hawaiian Archipelago, 30 per cent are endemic. His category, littoral, is in no way comparable to strand, including many more
species at great distances from the shore. Nevertheless, he found that only 30 per cent are endemic. This can be compared with the approximately 80 per cent endemics which have been estimated for the entire Hawaiian flora (St. John, 1946; Hillebrand, 1888). A more recent estimate (Stone, 1967) is that specific endemism could amount to about 96 per cent. This bespeaks rather continuous arrival of strand species by long distance dispersal. The percentage of dioecism in strand plant species from some low Pacific islands to the west of Hawaii was estimated by Long (1965, personal communication). Long concludes that less than 1.0 per cent of the strand plant species with which he is familiar are dioecious. The evidence from McCaughey (1918) supports the consensus that most strand plants have reached the shores upon which they are established by means of long distance dispersal. Long's estimates support the contention of Baker that long-distantly dispersed species are self-compatible.

In dealing with self-compatibility and dioecism it must, of course, be kept in mind that dioecism is not the only mechanism for producing outcrossing. However, it is easier to recognize self-incompatibility at the level either of dioecism or heterostyly than at the chemical level of self-incompatibility. Just because a species does not show dioecism is no indication that it does not have other mechanisms providing for outcrossing. Nevertheless, dioecism percentage does give an indication of percentage of outcrossing. Baker (1959a:181) writes, "... We might expect that the proportions of hermaphrodite species relative to those with separate staminate and pistillate flowers (particularly the dioecious species) will give at least a very crude indication of the prevalence of outcrossing."

An assumption which is fundamental to Baker's Law is that species that show a higher percentage of one breeding system under one set of conditions can change to another breeding system under a different set of conditions. Davis and Heywood (1963), Grant (1958), and Fryxell (1957) have emphasized that the degree of outcrossing in the same species may vary under different conditions from as much as 50 per cent to as low as 2–3 per cent such as occurs in cotton. In support of this is the experimental work of Jones (1932, 1934) who was able to produce a dioecious strain of Zea mays from a monoecious strain. A dioecious species of Mussaenda (Rubiaceae) appears to have evolved from a heterostylos form. Orn-duff (1966) states that dioecism has probably arisen from heterostyly in the Menyanthaceae. Taylor's (1954) observations on Coprosma pumila provide another example.

There seems to be abundant support both theoretical and observational for the thesis so well expounded by Baker that the breeding system is of the utmost importance in successful long distance dispersal. There is a clear relation between self-compatibility and long-distantly dispersed species. This is made possible because breeding systems are dynamic. The breeding system can change in a given species when there is selection for self-compatibility, as, for example, in an area where only a few individuals of a given population are present. This seems to occur, both toward the margins of a population's distribution and also in totally new areas which are attained by long distance dispersal.

**DIOECISM IN HAWAII**

Accepting the validity of Baker's Law, the question arises of how to explain the high degree of dioecism in the Hawaiian flora. Dioecism is certainly an outcrossing breeding system, and the Hawaiian Islands are isolated. The origin of the flora can be explained in one or both of the two possible ways: either (1) there has in the past been closer connection with other land masses, or (2) the plants arrived by long distance dispersal. Before attempting to show how Baker's Law can be equated with the high degree of dioecism in the Hawaiian flora, let us see if there actually is a high degree of dioecism relative to a continental flora.

Observations of botanists who have worked on continental floras and also that of Hawaii have led them to suspect that Hawaii has a disproportionate number of dioecious species (Carlquist, 1965, 1966a, 1966b). Tabulations of the dioecious species for the Hawaiian flora were made using Hillebrand's *Flora of the Hawaiian Islands* (1888), and for a continental flora using Munz's *Manual of Southern California Botany* (1935). Admittedly the sample which
I obtained for the circumscribed area in southern California is more complete than that for the Hawaiian Islands since a considerable number of species have been added to the indigenous Hawaiian flora as new discoveries of species were made since 1888. A much smaller number of additional indigenous species have been added to the flora of California since 1935. Nevertheless, Hillebrand's Flora is relatively complete. He included slightly more than 700 species among the indigenous phanerogams of Hawaii. St. John (1946) estimated that the indigenous phanerogams in Hawaii included 1,795 species and infraspecific taxa. If the species only are considered, it is very likely that there would be fewer than 1,200. The number of dioecious species in Hawaii (based on Hillebrand, 1888) and that of southern California (Munz, 1935) are compared in Table 1. Also compared is a bare representation of the flora of Ecuador, a tropical continental flora, the data for which are based on Diels' report (1938) of several months' collecting and include a total of only 658 species. This must represent a very small portion of the entire flora. Furthermore, Diels probably included a disproportionate number of species from the alpine region of the Andes where he spent more of his collecting time. Therefore, some reservations should be held in comparing the data on the flora from Ecuador with those of the other two floras. However, this information is included because it represents, perhaps poorly, both a tropical flora (as does the Hawaiian) and a continental flora (like that of southern California).

Table 1 indicates that the percentage of dioecism for the southern California flora is about 3 per cent and that of the Hawaiian flora about 5 per cent. This can be compared with figures of Yampolsky and Yampolsky (1922) which show 5 per cent complete dioecism for flowering plants of the entire world. If the number of dioecious species among the Hawaiian flora is incorrect it is very likely that the error was in underestimating dioecism. Hillebrand often was forced to describe species on the basis of inadequate specimens collected by someone else, and perhaps accompanied by poor notes. Thus, he was not always able to state whether a species was dioecious, monoecious, or hermaphroditic.

In compiling the data for Table 1, only those species clearly described as "dioecious" were included in that category. The percent of dioecism might have been higher if gynodioecism had been included. It is therefore safe to assume that the proportion of dioecious species in the Hawaiian flora is at least 5 per cent and very likely higher. The estimate of dioecism for the continental, temperate flora of southern California, as obtained from Munz's Manual, is probably much more accurate, and indeed it compares well with the estimate of Baker (1966, personal communication) for all of California—2.4 per cent. A two-by-two contingency table, chi square test for homogeneity was made for a comparison between dioecism in the two study areas, southern California and Hawaii. The results show that the difference in ratios is significant (P < .005). It is therefore extremely likely that a real difference exists in the amounts of dioecism in the two floras.

### TABLE 1

<table>
<thead>
<tr>
<th>AREA</th>
<th>TOTAL SPECIES</th>
<th>DIOECIOUS SPECIES</th>
<th>PER CENT DIOECIOUS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hawaii</td>
<td>730</td>
<td>39</td>
<td>5%</td>
</tr>
<tr>
<td>So. Calif.</td>
<td>2,355</td>
<td>67</td>
<td>3%</td>
</tr>
<tr>
<td>Ecuador</td>
<td>658</td>
<td>20</td>
<td>3%</td>
</tr>
</tbody>
</table>

1 Data compiled from Hillebrand (1888) for Hawaii, Munz (1935) for southern California, and Diels (1938) for Ecuador.

2 Only those species which are listed as dioecious are included; polypogamous or gynodioecious forms are not included.

**DIOECISM AND WOODY HABIT**

A comparison was then made to determine whether the difference in percentage of dioecism in the two areas might merely reflect the higher proportion of woody species in all tropical floras. Woody species are never annuals, and annuals do not usually have any sort of outcrossing mechanism. Baker (1959a) emphasized the point that there is a close association between outcrossing and perennial habit. Trees generally show outcrossing and heterozygosity (Baker, 1959a).

Table 2 presents the results of the compari-
sons between woodiness and dioecism in the three areas, Hawaii, California, and Ecuador. This comparison exposes an even greater difference between the floras of Hawaii and California. Based on the total number of woody species that could be tabulated from Hillebrand’s *Flora* and the number from Munz’s *Manual*, the percentage of those showing dioecism is 3 for California and 9 for Hawaii. The two-by-two contingency table indicates a significant difference ($P < .005$). The percentage of woody species showing the dioecious habit in the Hawaiian flora is so much greater than that in the Californian flora that one can be assured that some factor is responsible for the difference. It could not be merely random chance.

Our question—Is there a significantly higher percentage of dioecious species in the Hawaiian flora than in a continental flora?—can be answered in the affirmative on the basis of the samples from Hawaii and from southern California. Relative to the comparison of the percentage of dioecism in woody species in Hawaii and in Ecuador, the difference, while less, is still significant ($P = .005$). It is of interest to compare the present results with estimates of percentage dioecism from some other areas. Baker (1966, personal communication) has calculated that the approximate percentage of dioecious species in west tropical Africa was 3.2 per cent and for all of California, 2.4 per cent. Parsons (1958) found approximately 3.9 per cent dioecism for the Angiosperms of Australia. Milliner (1966, personal communication) estimated that approximately 20 per cent of the indigenous flora of New Zealand was dioecious.

### EVOLUTION OF DIOECISM IN HAWAIIAN PLANTS

The problem remains of explaining why there is a higher percentage of an outcrossing type of breeding system (dioecism) in Hawaii, an area that apparently can be attained only by long distance dispersal. The possibility of an alternative explanation for the origin of the Hawaiian flora will be discussed briefly later. Let us assume that at least a majority of the indigenous species now present either have arrived themselves by long distance dispersal or have evolved from ancestors that had arrived in this way. This is the more likely explanation. Fosberg (1948) suggests that if on an average one seed plant arrived and became successfully established every 20,000 to 30,000 years the present flora would be accounted for. His calculations are based on the number of indigenous species now present and the estimate of “...5–10 million years of above-water history for the entire Hawaiian chain.” This estimate is in line with the ones given today by geophysicists (Woollard, 1965) who suggest that the youngest island may be about 2 million years old and the older islands about 5 million years old.

To explain this apparent contradiction between Baker’s Law and high dioecism in Hawaii the author believes that the dioecious species present have evolved this habit *in situ* and are descended from species or strains that were hermaphroditic when they arrived and became established. That there has been time for this sort of change to dioecism to occur is evident. Approximately 80 per cent of the Hawaiian flora consists of endemics (St. John, 1946). These endemic species had time to evolve. Dioecism can occur quite rapidly. Jones (1932, 1934) experimentally produced a dioecious maize in four generations. Warmke and Blakeslee (1940) established a dioecious tetraploid race in a species of *Melandrium* (=*Lycnus*, Cariophyllaceae). H. Lewis (1966) has pointed out that differences in chromosome numbers between members of the same family in differ-

### TABLE 2
**Comparison of Dioecism and Woodiness in the Flora of Three Areas**

<table>
<thead>
<tr>
<th>AREA</th>
<th>TOTAL SPECIES</th>
<th>WOODY SPECIES</th>
<th>PER CENT WOODY OF TOTAL</th>
<th>WOODY AND DIOECIOUS PER CENT DIOECIOUS OF WOODY SPECIES</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hawaii</td>
<td>730</td>
<td>325</td>
<td>44%</td>
<td>32</td>
</tr>
<tr>
<td>So. Calif.</td>
<td>2,335</td>
<td>613</td>
<td>26%</td>
<td>22</td>
</tr>
<tr>
<td>Ecuador</td>
<td>658</td>
<td>282</td>
<td>42%</td>
<td>19</td>
</tr>
</tbody>
</table>

1 Data compiled from Hillebrand (1888) for Hawaii, Munz (1935) for southern California, and Diels (1938) for Ecuador.
ent areas may be the result of saltational speciation. That short term dioecism can occur very quickly is undeniable. This type of dioecism is present according to D. Lewis (1942) in those families that have only a few dioecious members. He feels that the majority of dioecious species show the short term type of dioecism that is controlled by few genes and is reversible, and he postulates that it is only within families like the Salicaceae that dioecism is irreversible. Yampolsky and Yampolsky (1922) estimated that about 75 per cent of all the families of the phanerogams have some dioecious species.

The percentage of families with dioecious species does not differ appreciably in the two study areas, Hawaii and southern California, being approximately 15 and 14 per cent respectively. In comparing these percentages with the estimate of 75 per cent by Yampolsky and Yampolsky (1922) caution is indicated in drawing conclusions. In neither of these two floras does the distribution of dioecious species per family seem to reflect the distribution for families of the world. While this could simply indicate that the sample in regard to species per family is inadequate here, it could also indicate that factors are at play in both these floras which are not generally found throughout the world.

If it is true that dioecism has largely, if not totally, evolved in situ in the indigenous dioecious species of the Hawaiian Islands, and the evidence is strong that it has, why has selection acted favorably toward dioecism? The answer would be that dioecism is a very effective mechanism for insuring outcrossing. Outcrossing produces heterozygosity, and heterozygosity provides more potential recombination types. In a small population, such as would exist shortly after the arrival and establishment of long-distantly dispersed species, the gene pool would be relatively small. Additional genotypes coming in from other populations would be rare indeed. A factor which favored outcrossing and the concomitant greater variability would probably be selected for. Lewis (1942) and Grant (1958) both have emphasized that the genetic system and its controlling factors are themselves subject to evolution. The factors making up a genetic system include mutation rate, chiasma frequency, meiosis, fertility, and, of course, the breeding system.

Whitehouse (1950), in emphasizing the importance of outbreeding to adaptation, has also suggested that when species are once adapted to a given situation the outbreeding mechanism may then be lost. Some current workers, studying small populations, seem to feel that self-pollination systems will be selected for and retained. Moore and Lewis (1965:113) write, "In a very small population genes promoting self-pollination would be at an advantage. Once established, an inbreeding race would become self-perpetuating." Apparently, however, if the selection pressure is great enough, the inbreeding system need not be self-perpetuating. Such a situation with strong selection pressure for an open recombination system would exist in the Hawaiian flora. The Hawaiian Islands include in a small area a large number of very different habitats. These habitats may change quickly because of the high rainfall producing landslides and because of volcanic effects. Different ecological niches are suddenly made available in such a situation. Baker (1953) has emphasized the greater advantage that an outbreeder has over an inbreeder in occupying a new niche.

DISCUSSION

The present author maintains, therefore, that selection pressure for an outcrossing breeding system has been very strong in Hawaii and has resulted in the survival of a higher percentage of dioecious species and survival of a lower percentage of hermaphrodite species, than are found in the North American continent. In the tropical continental flora there may be almost as high a percentage of dioecism as in Hawaii. The evidence is too flimsy to attempt to draw any conclusive comparisons between a continental tropical flora and an insular tropical flora. However, it would not be too surprising to discover that a flora such as that in Ecuador actually did show a percentage of dioecism somewhere between that of an insular tropical flora such as Hawaii and that of a continental temperate flora such as California. One would expect that in a continental tropical flora the selection pressure for dioecism, an outcrossing breeding system, might be less than in an isolated flora such as in Hawaii with a tropical climate and yet somewhat more than in a
temperate flora with a less changing landscape. The rainfall of southern California is such that land slides though they occur are not the rule. This is quite the opposite of the situation generally found in the tropics.

The foregoing interpretation has been based on the assumption that the flora of Hawaii has developed largely from species which arrived through long distance dispersal. Campbell (1919, 1933) felt that the Hawaiian Archipelago is a remnant of a much larger area which was once in more or less direct connection with the South Pacific. He maintained that the isolation occurred in early Tertiary and that the older genera are derived from the South Pacific before isolation, and that the younger genera such as those belonging to the Compositae arrived after isolation by long distance dispersal and largely from the east.

Skottsberg (1925) proposed that the flora of Hawaii represents the derivatives of an ancient antarctic continental flora. He speaks of a "Jurassic Hawaii" and apparently felt that such did once exist. The hypothesized sub-antarctic continent of Skottsberg and pre-Tertiary central Pacific land mass of Campbell are interesting conjectures. However, even if one assumes that they did occur, the Hawaiian Archipelago has been isolated for at least 5,000,000 years. Fosberg (1948) indicated that 5–10 million years would be enough time to account for the present flora, assuming one arrival by long distance dispersal on an average of once every 20,000 years.

If there is a high proportion of outcrossing in the species of the Hawaiian flora one would expect to find many polymorphic species. As Baker (1953) has pointed out, in outbreeding populations there is an almost continuous intergradation between different populations while in inbreeding populations there are much greater discontinuities between populations in both morphological and physiological characters. Nearly continuous intergradation between populations is frequently found in the Hawaiian flora. Hillebrand (1888:xxv) states, "A comparison of the Hawaiian flora with that of any other country brings out at once a striking difference in the great number of varieties in all the species of leading genera." And Fosberg (1948:107) commented, "The reputation for polymorphism enjoyed by Hawaiian plants has led taxonomists to avoid undertaking major problems on them." Polymorphism, inherent in outcrossing breeding systems, is further evidence for a truly high proportion of outcrossing. The outcrossing has been effected at least partially through dioecism which has developed in at least 14 different families in less than approximately 5,000,000 years.

**SUMMARY**

It is proposed that Baker's Law has been effective during the development of the Hawaiian indigenous flora. There is no reason to assume differently and there is good support for this view in the present structure of the Hawaiian flora. At the same time it can be demonstrated that there is a significantly higher percentage of dioecism in Hawaii than is found in continental floras. Dioecism is a very effective mechanism for outcrossing and in species in which it occurs there is assurance that an open recombination type is present. While self-incompatibility of hermaphroditic species occurs, the same plant family usually does not show self-incompatibility and dioecism. It is true that dioecism alone is not a measure of outcrossing in a flora since other outcrossing mechanisms occur. However, by estimating dioecism, one knows that outcrossing occurs at least as much as would be indicated by the proportion of dioecism. Thus, there is no reason to deny the applicability to the Hawaiian indigenous flora of Baker's Law of self-compatibility and long distance dispersal; yet there is an active outcrossing breeding system at work in Hawaii, where one would expect the contrary. The dilemma can be resolved if we recognize that the dioecious habit can develop relatively quickly and may then be perpetuated if it has greater survival value than hermaphrodisim. Several workers have experimentally produced dioecious species or races.

**ACKNOWLEDGMENTS**

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Characterization and Physiological Activity of Some Kawa Constituents

R. HänSEL

Kawa, the rhizome of Piper methysticum, has played an important role in the lives of the peoples of Oceania. This paper presents a review of our current knowledge of the kawa constituents—their molecular structure, their pharmacological properties, and their chemical and spectroscopic character.

AROMATIC CONSTITUENTS AND THEIR PHYSIOLOGICAL ACTIVITY

Piper methysticum Forster is a shrub in the family Piperaceae which occurs in Oceania. Its striking characteristics are long-stemmed, heart-shaped leaves, peculiarly knotty branches, and small flowers which lack a perianth and which form a dense inflorescence reminiscent of ears of grain. It is one of the bisexual members of the genus; apparently, however, only plants with male flowers exist. This necessitates vegetative propagation of the species. The original habitat of the plant is not known; perhaps it is New Guinea. From the rhizome, less often from a sprout, Polynesians and Melanesians prepare the so-called kawa, 'awa, or yangona drink, which is characterized by its peculiar sedative and muscle-relaxing effects. In order to understand the role which the kawa plant played in the life of these peoples one has to consider the endemic character of the flora of these regions. The flora of Oceania is markedly different from that of the Asian continent as well as from that of the American continent. Nature did not provide the Polynesians with intoxicants and stimulants of plant origin, substances of the types which were known to the peoples of Asia, Europe, and America. Most of the indispensable medicinal agents—such as opium, hashish, coca leaves, the Solanum drugs, digitalis, and Colchicum—of the peoples of the old world and of the American continent remained unknown to the Polynesians. Nor did they have alcohol.

They knew only one stimulant which at the same time was an effective medicine: 'awa. Apparently, 'awa for the Polynesians was a stimulant, an anesthetic, and an effective medicine. A plant of such importance, of course, also played a role in the religious life: kawa was the drink at religious ceremonies.

If one summarizes the numerous reports in the ethnological literature about the folk medicinal uses of the drug and translates them into modern scientific language, the following striking properties of kawa emerge (Lewin, 1886; Titcomb, 1948; van Veen, 1938): (1) It removes tension and anxiety. (2) It is an analgesic. (3) Small doses relax the muscles of the extremities, while larger doses paralyze through relaxation, without, however, causing a decrease in consciousness or will power. (4) The reversible relaxation or paralysis of the muscles of the extremities is not as pronounced as it is with curare; it also probably acts on the central nervous system. (5) The drug is active against various skin diseases. (6) Consumption of kawa may lead to photophobia.

Modern research has dealt with two major tasks: first, to recognize which constituents are responsible for the effects listed here; and second, to analyze the effects themselves through studies with experimental animals. The emphasis in the following discussion will be on pharmaco-chemical considerations. Results of pharmacological investigations will be treated only parenthetically.

The characteristic constituents of kawa

If one chews a piece of kawa, the tip of the tongue quickly becomes numb, as if one had chewed coca leaves. All of the early investigators associated kawa with cocaine, the local anesthetic principle of Folia coca. This association, later shown to be false, directed kawa research into certain channels. First, a belief persisted until very recently that kawa must have nitrogenous principles (alkaloids) as does coca. Every so often a report appeared which

1 Institute of Pharmacognosy, Freie Universität Berlin, West Germany. Manuscript received June 13, 1967.
claimed that alkaloids were actually demonstrated (only, however, on the basis of color reactions), but actual isolation of nitrogenous compounds has never been successful. The fact that the usual testing reagents for alkaloids are relatively non-specific was not taken into account. Especially ignored was the fact that the α-pyrones (which contain no nitrogen) can behave similarly to alkaloids in some of these tests (Farnsworth et al., 1962). Furthermore, L. Lewin, a toxicologist and pharmacologist in Berlin, who studied the drug intensively from 1880 on, was able to demonstrate that the anesthetic principle could be extracted from the plant with fat solvents, such as petroleum ether. Since that time, pharmacognostics and chemists have examined almost exclusively the lipid fraction of the plant.

**MOLECULAR BUILDING BLOCKS OF THE kawa LACTONES (PYRONES):** Nine lactones and two chalcones (i.e., eleven aromatic compounds) have so far been isolated from the plant. None of these occur as glycosides. We shall first consider the lactones, all of whose structures follow the pattern shown in Figure 1. The basic skeleton consists of 13 carbon atoms, 6 of them in a benzene ring. The benzene ring is linked by a 2-carbon bridge to an unsaturated 6-membered lactone. At first sight this lactone is reminiscent of sorbic acid lactones or of the bufadienolides which are cardiac-active glycosides isolated from the plant genus *Seilla* and from toads. However, an important difference should be noted. The kawa lactones contain a methoxyl group as part of an enol ether function, which strongly modifies the behavior of the lactone toward acids and alkalies, as compared with the bufadienolides and other known δ-lactones. In the kawa lactones we are dealing with masked enols of β-diketones. The chemical behavior of the kawa lactones is summarized in Figure 2 using kawain and dihydrokawain as examples (Borsche et al., 1914–1933).

**NATURALLY OCCURRING STRUCTURAL VARIANTS:** We have seen that the characteristic constituents of kawa are δ-lactones, which may be considered to be α-pyrones bearing a methoxyl group at carbon 4 and an aromatic styryl or phenylethyl moiety at carbon 6. The question arises what structural variants of this basic skeleton occur in nature. We can distinguish two groups of structural variants: (a) variance depending on the degree of saturation, and (b) variance depending on benzene substitution.

(a) We note that the molecule of the basic skeleton, the styryl-α-pyrones, contains three non-aromatic double bonds. If one assumes that in the biological environment, that is, in the plant, each of these three double bonds can be saturated independently, eight variants are conceivable which would differ from one another with regard to the degree of saturation. Theoretically, there is no difficulty in synthesizing all eight variants. Nature, however, seems to follow its own laws in that not all variants which are synthetically available in the laboratory occur in the plant; a certain limitation or choice exists. In our case the following situation obtains. The kawa plant lacks all those variants which contain the reduced double bond at carbon 3. To put this positively, all naturally occurring kawa lactones invariably contain in the molecule the enolic double bond. The number of structural variants which occur in the plant is therefore reduced to 4. Another phenomenon is present. The double bond at carbon 7 is reduced only when the double bond at carbon 5 is also in the reduced state. These relationships are summarized in Figure 3.

![Common molecular skeleton of the kawa lactones and their hypothetical precursor.](image-url)
(b) Nothing very remarkable can be said regarding the substituents on the benzene ring. In addition to unsubstituted derivatives we find the corresponding p-methoxy derivatives, dimethoxy derivatives, and dioxy-methylene compounds. No lactones occur in kawa which have a free hydroxyl group to which sugars could be linked to form glycosides. Lactones with a free or a glycosidically linked hydroxy group therefore do not occur. Of course we have no answer to the question why the kawa plant does not produce free phenols or glycosides. This may have to do with the excretion cells of the plant. A particular constituent, in order to be deposited in the excretion cells of the Piperaceae, must have a certain lipid solubility, a phenomenon which is well known from the constituents of essential oils. Substances with a free hydroxyl group, or even with glycosidically linked hydroxy groups, obviously do not have a suitable partition coefficient for deposition in the excretion spaces. Of course, the correlation may also be reversed: since the plant synthesizes many lipophilic end products, excretion cells are formed. Be that as it may, a correlation no doubt exists.

If we now combine the two possibilities for variation, (i) the degree of hydrogenation, that is, the number of non-aromatic double bonds, and (ii) benzene substitution, we arrive at a possible total of twelve structural variants (Table 1). Six of these have been known for a long time. We have worked out effective analytical separation and testing methods which will allow us to find additional lactones which might occur in the plant in trace amounts. We have synthesized all twelve structural variants and a few additional ones. Furthermore we have investigated kawa from various parts of Oceania, using samples from the island of Hawaii, the Fiji Islands, and from Samoa. As a result we now have the following picture. In addition to the six already known lactones we have demonstrated the presence of three additional derivatives so that today nine of a total of twelve pyrones are known as constituents of Piper...
Non-aromatic double bonds: 3

Theoretically possible variants: 8
- not hydrogenated: 1
- monohydrogenated ($\Delta_3$ or $\Delta_5$ or $\Delta_7$): 3
- dihydrogenated ($\Delta_{3,5}$ or $\Delta_{3,7}$ or $\Delta_{5,7}$): 3
- fully hydrogenated: 1

Naturally occurring (not hydrogenated, $\Delta_5$, $\Delta_{5,7}$): 3

Fig. 3. Hydrogenation stages of the kawa lactones.

methysticum (Klaproth, 1966). It is interesting that in both series of the unsubstituted lactones and of the p-methyl substituted ones we find three degrees of hydrogenation. In the dioxy-methylene derivatives one of the stages of hydrogenation is missing. It is the same one which, as the only representative of the series, occurs as a dimethoxy derivative. We do not know whether this vicarious occurrence of dimethoxy- and dioxy-methylene, or for that matter the entire $\alpha$-pyrone spectrum of the plant, is the result of evolutionary coincidence, or whether some day we shall be able to understand this development on causal biosynthetic grounds. However, let us not linger over fruitless speculations regarding the origin of the pyrone spectrum, let us rather ask in which way the plant constructs these substances. I shall not be able to offer direct proof for definite biosynthetic pathways since tracer studies or dynamic biochemical studies have so far not been carried out. The ideas of the biosynthesis of the kawa pyrones which I shall discuss are based on a comparative study of molecular structure and on reasoning by analogy which has derived justification from the fundamental agreement in the metabolism of all green plants.

IDEAS ON THE BIOSYNTHESIS OF THE KAWA PYRONES: Let us consider briefly the structure of the kawa pyrones from a biogenetic point of view. It is striking that the benzene ring is substituted in the manner in which we know it from the phenylpropyl compounds (cinnamic acids, lignanes, and coumarins). The synthesis of these $C_6-C_3$-compounds goes back to shikimic and prephenic acids. The remaining four carbon atoms in the molecule of the kawa pyrones show two alternating oxygen functions, a feature which is characteristic of substances whose biosynthesis indicates polyacetate chains, that is, acetate metabolism. We thus arrive at the picture that the kawa pyrones are an example of so-called mixed formation. They are formed from phenylpropanes and from acetyl coenzyme A building blocks and, if one considers numbers, from one phenylpropane and two acetate units:

$$C_6-C_3 + 2C_2 \rightarrow C_{13} \text{ (kawa pyrones)}$$

Such a scheme is outlined in Figure 4. Natural products which demonstrate such a mixed construction from phenylpropanes and acetates are no rarity in the plant kingdom. The most important representatives are the flavonoids, which are made up of one phenylpropane unit and three acetate units (Geissman and Hinreiner, 1952).

$$C_6-C_3 + 3C_2 \rightarrow C_{15} \text{ (flavonoids)}$$

The kawa pyrones therefore appear to be nothing but variants of flavonoids. Of course this holds only if one considers the metabolic physiological and not the analytical chemical point of view, since no flavonoid-like $C_{15}$-compounds are known with $\alpha$-pyrone structure. Flavonoids and kawa pyrones seem to have a common precursor. Kawa pyrones appear to be precursors of flavonoids with one less acetate unit. It is very remarkable that it was possible to discover in the kawa plant the pyrones which, so to speak, correspond to flavonoids, $C_{15}$-compounds which are analogs of $C_{13}$-compounds (Fig. 5) (Hänsel et al., 1963).

Up to this point our biosynthetic scheme assigns to the kawa lactones a given position in the flavonoid metabolism of plants. It does not explain why only certain degrees of hydrogenation occur in nature. The following biosynthetic scheme combines the observation on the occurrence of certain hydrogenation types and places
TABLE 1

STRUCTURAL VARIANTS OF THE KAWA LACTONES AND THEIR OCCURRENCE IN NATURE

<table>
<thead>
<tr>
<th>Benzene-substitution</th>
<th>Hydrogenation $\Delta_5$</th>
<th>Hydrogenation $\Delta_7$</th>
<th>Name</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>-</td>
<td>-</td>
<td>demethoxyyangonin</td>
</tr>
<tr>
<td></td>
<td>+</td>
<td>-</td>
<td>kawai</td>
</tr>
<tr>
<td></td>
<td>+</td>
<td>+</td>
<td>dihydrokawai</td>
</tr>
<tr>
<td>H$_3$CO</td>
<td>-</td>
<td>-</td>
<td>yangonin, $\Delta_5$-dihydmyangonin$^*$</td>
</tr>
<tr>
<td></td>
<td>+</td>
<td>-</td>
<td>tetrahydmyangonin$^*$</td>
</tr>
<tr>
<td>H$_3$CO</td>
<td>-</td>
<td>+</td>
<td>11-methoxyyangonin$^*$</td>
</tr>
<tr>
<td>H$_3$CO</td>
<td>+</td>
<td>+</td>
<td>methypticin</td>
</tr>
<tr>
<td></td>
<td>+</td>
<td>+</td>
<td>dihydromethysticin</td>
</tr>
</tbody>
</table>

* Symbols used: $^*$ Occurs in trace amounts in *Piper methysticum*.
--- Does not occur in *Piper methysticum*.

...it into a hypothetical biosynthetic scheme. In this scheme (Fig. 6) the paths which lead on one hand to kawai and on the other hand to yangonin branch already at the stage of the $\beta, \delta$-diketocarboxylic acid. Reduction of the $\delta$-keto group to an alcohol leads after cyclization to the enolic kawai and dihydrokawai. Enolization of the $\delta$-keto group, however, followed by cyclization leads to the dienolic yangonin. In order to arrive at the hypothetical (synthetically easily accessible, but not occurring in nature) 7,8-dihydmyangonin derivatives, the long conjugated system of yangonin would have to be interrupted. One therefore suspects that hydrogenation of the double bond at this point is not possible for energetic reasons. In the case of

![Diagram](https://example.com/diagram.png)

**Fig. 4.** A hypothetical scheme for the biosynthesis of the kawa lactones.
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Fig. 5. Biosynthetic scheme for the formation of yangonin and a C-15 chalone from a common precursor.

kawain, no long conjugated system is interrupted when the 7,8-double bond is reduced. The dihydrokawain derivatives indeed occur in nature.

**Physiological Activity of Kawa Pyrones**

The most intensive study of the pharmacology of the kawa pyrones has been carried out for some ten years by a team at the Pharmacological Institute of the University of Freiburg under the direction of H. J. Meyer. The most important observations on the effects of the kawa pyrones seem to be the following: intensification of barbiturate narcosis (Klohs et al., 1959; Meyer, 1962); analgetic effect (Brüggemann and Meyer, 1963); local anesthetic properties (Meyer and May, 1964); anticonvulsive effects (Meyer, 1964; Meyer and Meyer-burg, 1964; Kretzschmar and Meyer, 1965); spasmylytic effect (Meyer, 1965a); antymyotic effects (Hänsel, Weiss, and Schmidt, 1966).

I should like to make another general observation on the relationship between pharmacodynamic activity of the different kawa pyrones and their constitution. As far as animal experiments are concerned the lactones of the yangonin type, that is the dienolides, seem to be—within the usual dosages and as compared with enolides—pharmacodynamically inert.

In the enolides the effective optimum varies as a function of the hydrogenation of the double-bonded carbon 7 and of substitution in the benzene ring together with a dependence on the method of testing. For example kawain has the strongest effect as a local anesthetic, dihydromethysticin as a spasmylytic, and dihydrokawain as an intensifier of narcosis.

**INTENSIFICATION OF BARBITURATE NARCOSIS**

(Klohs et al., 1959; Meyer, 1962): When a pharmacologist has the task of testing pharmacologically little investigated substances for central sedative properties, he will probably measure first the toxicity of the substance and then the decrease in spontaneous motility. At a very early stage of the screening process he will check whether and in which way his substances will influence the effect of barbiturates. Substances with a central paralyzing effect intensify the effect of barbiturates and/or considerably prolong the effect. Dihydromethysticin (DHM) possesses to a particularly high degree this effect of intensifying barbiturate effects (intensifying narcosis). Let me cite an example (Meyer, 1962). After application of 150 mg/kg of hexobarbital sodium, white mice sleep on the average for 2 hours. If the animals are pretreated with 240 mg/kg DHM, they sleep after the
Fig. 6. Biosynthetic scheme showing various stages of hydrogenation.
The same dose of hexobarbital sodium for 27 hours. Enhancement of barbiturate narcosis is a property which is shared by a relatively large number of substances with central sedative properties. What is very impressive in the case of DHM, however, is the magnitude of the effect.

**ANALGETIC EFFECT:** Together with Brüggemann, a team under K. H. Meyer in the Pharmacological Institute of the University of Freiburg tested the analgetic effectiveness of the two kawa pyrones, DHK (dihydrokawain) and DHM. In the analgesic test according to Gross these two substances prove to be comparable in effect with dimethylaminophenazon. These results are summarized in Table 2.

**LOCAL ANESTHETIC PROPERTIES:** I have mentioned earlier that chewing crude kawa anesthetizes the tip of the tongue. This anesthetic effect is caused by DHK, a fact which has been known for a long time (van Veen, 1938). Again it was H. J. Meyer and his collaborators who carried out the detailed study of the local anesthetic properties using the testing methods of scientific pharmacology. It was shown, first, that not only DHK but that all the other kawa pyrones possess local anesthetic properties; however, not all pyrones have an equally strong effect. It was further demonstrated that the pyrones developed superficial anesthetic as well as infiltration effects. I shall mention a few details of the experiment on surface anesthesia (rabbit cornea) and the results. Most effective with respect to the degree of hydrogenation are the $\Delta^2$-dihydro derivatives, followed by the $\Delta^5,7$-tetrahydro derivatives; the non-hydrogenated yangonin homologues are ineffective. Unsubstituted derivatives are more effective than dioxyethylene substituted ones. Accordingly, the most effective compound in surface anesthesia is kawain which equals the effect of cocaine in the cornea test. Kawain and cocaine possess the same limiting concentration (equal to the smallest concentration which causes complete anesthesia in all animals) and equal length of anesthesia. The kawa pyrones are somewhat less effective in infiltration anesthesia. Of some interest for their evaluation is the fact that the kawa pyrones are very compatible with tissues and no danger of toxic resorption exists.

**ANTICONVULSIVE EFFECTS:** A cursory comparison of the total effect of kawa on man and of the pharmacological activity of the pyrones in the animal shows that kawa acts predominantly by central paralysis. In order to characterize in greater detail substances having a central paralytic effect, it is important to know toward which central nervous system (CNS) stimulants these substances act as antagonists. Furthermore, one needs to know whether they are capable of inhibiting tonic or clonic spasm components of electric shock.

Concerning the inhibition of electric shock, a whole series of well known and excellent drugs have been introduced into therapy and are frequently used as sedatives which inhibit at a given dose but which are toxic. A well known example of the statement that CNS sedatives are not necessarily effective inhibitors of electric stimulation is meprobamate. Other sedatives enhance, contrary to expectation, even the readiness for contraction; an example is reserpine. According to investigations, which again were carried out by the Freiburg team, DHM and DHK are contraction inhibitors. This inhibitory effect is qualitatively and quantitatively comparable with that of phenobarbital, pyrimidone, or diphenylhydantoin. Animal experiments have shown that DHM in particular may be considered a strongly effective anticonvulsant.

The behavior of the two kawa pyrones is peculiar toward chemical convulsive toxins, toward bemegride, pentetrazole, picrotoxin, and strychnine. Figure 7 shows the following: (i) Tonic bemegride and pentetrazole convulsions are activated within a given dose range (pre-administration of 20-45 mg/kg DHM). (ii) Tonic picrotoxin and strychnine convulsions are

<table>
<thead>
<tr>
<th>ANALGETIC AGENT</th>
<th>DOSE (mg/kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>morphine</td>
<td>2.5</td>
</tr>
<tr>
<td>dimethylaminophenazon</td>
<td>100</td>
</tr>
<tr>
<td>dihydrokawain</td>
<td>120</td>
</tr>
<tr>
<td>dihydromethysticin</td>
<td>140</td>
</tr>
<tr>
<td>acetylsalicylic acid</td>
<td>200</td>
</tr>
</tbody>
</table>

PACIFIC SCIENCE, Vol. XXII, July 1968
inhibited by preadministration of DHM, which is similar to electric convulsions. Strychnine convulsions are inhibited more strongly than are picrotoxin convulsions.

The curves would look very different if the inhibition of clonic convulsions had taken place instead of tonic convulsions. Toward clonic convulsions, which appear after application of the above-named convulsive toxins (bemegride, pentetrazole and picrotoxin) preadministration of DHM has essentially no effect. On the contrary, DHM enhances and prolongs strikingly the clonic convulsion phase. Especially by administration of DHM one effects long lasting strong convulsions with only rare and short-lived convulsion pauses (without DHM the convulsions show a more seizure-like character). The two kawa pyrones DHM and DHK (the latter has a weaker effect) are therefore capable of suppressing only incompletely the convulsions caused by chemical convulsive toxins since they can suppress only the tonic but not the clonic component. A remarkable exception is strychnine. In this case DHM and DHK are able to suppress both types of convulsion. It may be said that both pyrones demonstrate a definite anti-strychnine effect, which even surpasses the well known antagonism of phenobarbital toward strychnine.

If in conclusion we ask to which long-used therapeutics the kawa pyrones show the greatest similarity, we may quote H. J. Meyer who, in considering recent results which are not reproduced here, says, "Aside from certain peculiarities of their action the kawa pyrones show the characteristics of two anticonvulsants which have long maintained a leading role in epilepsy therapy, diphenylhydantoin and phenobarbital. The similarity with the action of diphenylhydantoin is somewhat more pronounced."

**Spasmolytic effect:** Dihydromethysticin was tested thoroughly for its spasmolytic action. In all experimental designs with smooth muscle organs and with organ systems, it proved more or less effective. An inhibition of spontaneous activity as well as a relaxing effect on muscle tone could be demonstrated. The mechanism of the action was predominantly designated as musculotropic (similar to papaverine).

**Antimycotic effect:** Anyone who has worked in a laboratory with aqueous plant extracts has observed that, if these aqueous plant extracts stand around for some time, they spoil. The extracts become inhabited by microorganisms. We observed some time ago that aqueous extracts of kawa do not spoil, at least not while they contain traces of kawa pyrones. In collaboration with the Institute of Hygiene and Bacteriology of Freie Universität Berlin we have studied the bacteriostatic properties of the kawa pyrones. The data (Table 3) are not complete since the investigations have not terminated. I shall mention the following preliminary results (Hänsel, Weiss, and Schmidt, 1966).

(i) The kawa pyrones do not act as bacteriostats. A large number of gram positive, gram negative, pathogenic, and apathogenic bacteria were tested and they developed uninhibited in nutrients containing pyrones.

(ii) On the other hand, certain kawa pyrones show remarkable fungistatic effects. It is well known that there exists a large number of bacteriostats but only a very small number of substances which are capable of inhibiting the growth of fungi. Among the fungi which show a high sensitivity particularly toward DHK are
such rugged types as *Aspergillus niger*. Perhaps the best known antibiotic which is effective against fungi is griseofulvin and it has absolutely no effect on *Aspergillus niger*.

(iii) The effect of the pyrones is very selective. Only certain genera of fungi, often only certain species, are attacked. Among the fungi which are completely untouched are the yeasts—pathogenic forms as well as the ancient wine and beer yeasts. Further investigations are designed to show whether among the fungi which are affected by the *kawa* pyrones are genera which are pathogens in man.

**CHEMICAL AND PHYSICAL PROPERTIES OF THE KAWA LACTONES**

**Chemical Behavior**

The characteristic constituents of *kawa* may be classified into two main groups. The first group, of which kawain is an example, is characterized by a single double bond in a 6-membered lactone ring. The second type, of which yangonin is an example, belongs to the series of dienolides. However both types may be considered either 6-membered lactones or 6-styryl-α-pyrone. The recognition that yangonin also possesses lactone character is however rather recent (Chmielewska et al., 1958). Earlier it was considered a γ-pyron and accordingly two series of characteristic *kawa* constituents were differentiated, the α-pyrones (lactones) and the γ-pyrones. It is obvious that the structural elucidation of yangonin provided some difficulties. In order to demonstrate these peculiar difficulties it is more useful to outline a synthesis of yangonin starting from the dimethyl derivative (yangonalactone) rather than to trace the historical development which eventually led to the correct formulation of yangonin. Methylation of the styryl substituted with triacetolactone (yangonalactone) with diazomethane leads to two isomeric methyl derivatives, one of which is identical with the natural product. The question remains which of the two isomeric methyl triacetolactones is identical with the natural product, the α- or the γ-pyron. Borsche (1914)

### TABLE 3

<table>
<thead>
<tr>
<th>TEST ORGANISMS</th>
<th>g/ml</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Trichothecium roseum</em></td>
<td>0.05</td>
</tr>
<tr>
<td><em>Alternaria porri</em></td>
<td>0.03</td>
</tr>
<tr>
<td><em>Penicillium funiculosum</em></td>
<td>0.02</td>
</tr>
<tr>
<td><em>(potential human pathogen)</em></td>
<td>0.008</td>
</tr>
<tr>
<td><em>Alternaria niger</em></td>
<td>0.005</td>
</tr>
<tr>
<td><em>Streptomyces griseus</em></td>
<td>0.005</td>
</tr>
<tr>
<td><em>Cryptococcus neoformans</em></td>
<td>0.005</td>
</tr>
<tr>
<td><em>(human pathogen)</em></td>
<td>0.005</td>
</tr>
<tr>
<td><em>Trichophyton tonsurans</em></td>
<td>0.005</td>
</tr>
<tr>
<td><em>(human pathogen)</em></td>
<td>0.005</td>
</tr>
<tr>
<td><em>Streptomyces purpureascens</em></td>
<td>0.005</td>
</tr>
<tr>
<td><em>Paecilomyces variotii</em></td>
<td>0.0035</td>
</tr>
<tr>
<td><em>Aspergillus niger</em></td>
<td>0.003</td>
</tr>
<tr>
<td><em>(potential human pathogen)</em></td>
<td>0.005</td>
</tr>
<tr>
<td><em>Chaetomium globosum</em></td>
<td>0.005</td>
</tr>
<tr>
<td><em>Trichophyton ferrugineum</em></td>
<td>0.001</td>
</tr>
<tr>
<td><em>(human pathogen)</em></td>
<td>0.001</td>
</tr>
<tr>
<td><em>Botrytis cinerea</em></td>
<td>(+)</td>
</tr>
<tr>
<td><em>Scleromyces breviscalis</em></td>
<td>(+)</td>
</tr>
<tr>
<td><em>(potential human pathogen)</em></td>
<td>(+)</td>
</tr>
<tr>
<td><em>Saccharomyces cerevisiae</em></td>
<td>(+)</td>
</tr>
<tr>
<td><em>Aspergillus tamarii</em></td>
<td>(+)</td>
</tr>
<tr>
<td><em>Aspergillus flavus</em></td>
<td>(+)</td>
</tr>
<tr>
<td><em>Fusarium solani</em></td>
<td>(−)</td>
</tr>
<tr>
<td><em>Candida albicans</em></td>
<td>(−)</td>
</tr>
<tr>
<td><em>Candida kruysi</em></td>
<td>(−)</td>
</tr>
<tr>
<td><em>Candida parakruysi</em></td>
<td>(−)</td>
</tr>
<tr>
<td><em>Candida parapsilosis</em></td>
<td>(−)</td>
</tr>
<tr>
<td><em>Candida tropicalis</em></td>
<td>(−)</td>
</tr>
</tbody>
</table>

---

2 The numbers are the minimum concentrations (g) of kawain per volume (ml) nutrient which completely inhibit macroscopically visible development of the fungus. (+) Indicates only growth inhibition at a concentration of 0.05 g/ml. (−) Indicates no effect at a concentration of 0.05 g/ml. (Hansel et al., 1966).
TABLE 4
SOME DIAGNOSTIC TESTS TO DISTINGUISH BETWEEN TAUTOMERIC α- AND γ-HYDROXYPYRONE METHYL ETHERS

<table>
<thead>
<tr>
<th>TEST</th>
<th>4-METHOXY-</th>
<th>2-METHOXY-</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>γ-PYRONE</td>
<td>γ-PYRONE</td>
</tr>
<tr>
<td>Basicity</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(a) ether-insoluble oxonium salt formation</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>(b) picate formation</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>IR carbonyl frequency</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(a) 1724 cm⁻¹ (α-pyrene)</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>(b) 1667 cm⁻¹ (γ-pyrene)</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Diels-Alder reaction</td>
<td>+</td>
<td>-</td>
</tr>
</tbody>
</table>

1 Chmielewska et al., 1958; Bullock and Smith, 1960.
2 Alder and Rickert, 1937.

Kawa Constituents—Hänsel

chose a γ-pyrole formulation for the following reasons.

By the action of alkali under mild conditions yagonin can be saponified to an acid and methanol, analogous to a methyl ester of a carboxylic acid. Kawain, on the other hand, the constitution of which was secured as an α-pyrole, behaved differently. Under analogous conditions kawain furnished no methanol, nor did kawaic acid which was produced by action of alkali. Borsche attempted to explain this striking difference in the behavior of kawain and yagonin in the following manner. Since the enol-ether linkage of kawain is not saponifiable, yagonin, which splits off methanol readily, cannot contain an enol-ether linkage. He therefore searched for a formula of yagonin which would combine an ester-like bound methanol with a cyclic structure (differing by one mole of water from an open chain ester). Borsche formulated yagonin as a γ-pyrole, which he also considered to be the "anhydride of the methanol ester of yagonic acid." Borsche's ideas are summarized in Figure 8. If we consider Borsche's yagonin formula in some detail, we are rather surprised that the following points did not concern him.

(a) Ring opening with alkali is generally effected more easily with α-pyroles than with γ-pyrones.

(b) Borsche's yagonin formula has the structural characteristic of an enol acetal. Acetals are generally more resistant to alkali than are esters and vinylogous esters (enol ethers). It appears to me that it would have been possible to arrive at the opposite conclusion that the alkali liability of the ring demands formulation of an α-pyrole.

In 1954 a Polish team reopened the question of the structure of yagonin. They systematically synthesized α-pyrones and the analogous γ-pyrones and investigated both types of compounds with IR and UV spectroscopy. IR spectroscopy in particular proved to be an excellent aid for distinguishing between the two isomeric pyrones. All γ-pyrones showed a carbonyl band at 6.0μ (1667 cm⁻¹), while the α-pyrene band appears at 5.8μ (1724 cm⁻¹), which is the characteristic band of unsaturated lactones.

These investigations made it apparent that the pyrones which occur in the kawa rhizome differ from one another by their substituents and by their degree of hydrogenation, and not,
as was originally assumed by Borsche, by being cyclic isomers (α- and γ-pyrones). If the new yangonin formula is correct, it should be possible by hydrogenation of the two double bonds to transform yangonin derivatives into dihydro-kawain derivatives. We (Werny and Hänsel, 1963) were able to demonstrate that this is indeed possible. Starting with naturally occurring yangonin we obtained by catalytic hydrogenation p-methoxydihydrokawain, the constitution of which was secured by an independent synthesis. These reactions are shown in Figure 9. One of the two double bonds in the ring is not attacked under the given conditions (palladium on carbon in ethyl acetate). This agrees with the observation that enol-ether double bonds are catalytically hydrogenated only with difficulty.

The actual cause, that is the mechanism, of the phenomenon which led Borsche to the wrong formulation of yangonin is still not known. Why is the enol-methyl ether of yangonin readily

![Chemical Structures](image)

**Fig. 9.** Transformation of yangonin in 5.6.7.8-tetrahydroyangonin and its identity with synthetic (±) p-methoxy-7.8-dihydrokawain (Werny and Hänsel, 1963).
saponified and methanol split off only with difficulty in the case of kawain? We may reduce this question to that of the alkali stability of the enol ethers of the two homologous acids (see formulas).

\[
\text{C}_6\text{H}_5-\text{CH} = \text{CH}-\text{C}(\text{R}) = \\
\text{CH}-\text{C(OCH}_3) = \text{CH}-\text{CO}_2\text{H} \\
\text{R = H} \quad (\text{kawaic acid}) \quad \text{no methanol} \\
\text{R = OH} \quad (\text{yangona acid}) \quad \text{methanol}
\]

Spectroscopic Characterization of the Kawa Lactones

So far in this paper we have seen that the characteristic constituents of kawa are substituted 6-membered lactones which may be classified into two main groups, with one or two double bonds in the ring, the enolides and the dienolides. We have seen further that these two main types may be distinguished by their behavior during alkaline hydrolysis. In the following section we will show that recognition of the hydrogenation type is achieved more quickly and more smoothly with the modern methods of IR, UV, and mass spectrometry.

IR spectra (Hänsel, Rimpler, and Langhammer, 1966): It is best to start with two simple model compounds, the methyl-triacetyl acid lactone and the dihydromethyltriacetyl acid lactone (DH-MTL), which we prepared for the first time. The IR spectra of these two model compounds are exceedingly clear in the region of carbon-carbon double bond frequencies. DH-MTL exhibits in this region a single strong band at 1622 cm\(^{-1}\) which accordingly has to be assigned to the enolic double bond at \(\Delta^3\). In MTL this band—probably because of conjugation of the two carbon-carbon double bonds—is shifted toward longer wave numbers by 26 cm\(^{-1}\). We therefore assign the band at 1566 cm\(^{-1}\) to the double bond at \(\Delta^3\). The assignment of one of the two hydrogenation types is also possible when the lactone rings are substituted by styryl or phenylethyl radicals. The band at 955–966 cm\(^{-1}\), which shows a \(\text{trans} \, \text{CHR} = \text{CHR} \) linkage, is well suited for the determination whether we are dealing with a styryl or a phenylethyl type. We dealt with a total of four hydrogenation types for which we were able to develop a simple infrared assignment scheme as shown in Figure 10. The relationships are simplified and numerous details are omitted.

MASS SPECTRA OF THE KAWA LACTONES (Pailer et al., 1965): Compounds of the yangonin type (Fig. 11) are best discussed first. We are dealing here with a conjugated system. There is no point in the molecule which facilitates the formation of energetically favorable fragments. We therefore find in this type of compound large molecular ions and little fragmentation. Repeated elimination of 28 m/e corresponds to two carbon monoxide molecules, which has been observed with coumarins. This is followed by elimination of a methoxyl group (m/e 157, 129). If we now proceed to the compounds of the kawain type (Figs. 12, 13), we notice the appearance of a peak which may be considered an elimination of cinnamaldehyde. In addition there is a peak which corresponds to the rest of the molecule which remains after cleavage of cinnamaldehyde (M - 132) = 98. In this case cinnamaldehyde represents only a small fragment while the fragment corresponding to aldehyde minus hydrogen is larger. This however is not true with the substituted derivatives. In these cases the aldehyde peak is of considerable magnitude and no carbon monoxide elimination takes place, which is observable in the unsubstituted derivative. Furthermore, the intensity of various peaks is somewhat dependent on the substitution pattern of the aromatic part of the molecule. The most striking peak in the spectrum of the compounds of the kawain type is the peak which corresponds to a benzyl or a tropylum ion. This means that quite unexpectedly cleavage takes place at a double bond. This is supposedly an artifact since presumably migration of the double bond precedes cleavage. Nevertheless, one can consider the possibility of a formal cleavage at positions with double bonds in the interpretation of the mass spectra. With substitution in the benzene ring the fragment is correspondingly displaced, that is, it is an indicator for the correct interpretation.

Finally, there remains the interpretation of substances belonging to the dihydrokawain type. It proceeds normally with formation of a tropylum ion. Cleavage p is the normal reaction of saturated lactones.
UV SPECTRA (Hän sel et al., 1967): Again it is best to begin with the basic lactone chromophore, the dihydromethyltriacetoacid lactone (DH-MTL). We are dealing here with an s-trans-fixed enone system, comparable to that of parasorbid acid (PSS). DH-MTL differs from PSS in the position of the maximum by an increment of 30µm, an effect which can be ascribed to the β-methoxy substituent (Fig. 14). The magnitude of the increment is in good
agreement with observations on other open chain enone systems. Since the enone system exists in the ring, where it is rigidly maintained in the energetically favorable $s$-trans conformation, the position and magnitude of the absorption change only insignificantly when we go to the corresponding open chain enone system. In other words, we can compare PSS with cis-crotonic acid and dihydromethysticin (DHM) with tetrahydromethystinic acid (Fig. 15). If we substitute the ring of DH-MTL with a phenylethyl or with a styryl radical instead of
a methyl group, we obtain two groups of natural kawa pyrones, the kawain and the dihydro-
kawain types. In the naturally occurring dihydro-
kawains, the two part chromophores—the benzene ring with its variable oxygen functions and
the DH-MTL moiety—are separated. The spectra of these substances may therefore be
interpreted as addition spectra of the two partial chromophores. This is graphically demonstrated
in Figure 16 for the spectrum of tetrahydroyangonin (p-cresol methyl ether + DH-
MTL). In contrast to the compounds of the dihydrokawain type we may consider that in the
naturally occurring kawains the two part chromophores (styril and DH-MTL moiety) have a
mutual effect on each other. In spite of this it is surprising that the spectra of this class of com-
pounds are also additive from given partial chromophores, that is, they may be predicted by
calculation from the corresponding cinnamyl alcohols and the DH-MTL. On the other hand,
measured and calculated spectra do not agree when, instead of the cinnamyl alcohols, the
aromatic chromophore is represented by other styril derivatives, such as allyphenols of the
anethole type.

A second large group of kawa lactones are not derived from DH-MTL but from MTL
itself. The two parent substances differ from each other by a double bond in the lactone ring.
The enone system is extended to a dienone
Fig. 16. UV spectra of (a) tetrahydropyronin, and (b) the addition spectrum of (1) p-cresol methyl ether + (2) DH-MTL.
system (Fig. 17). Generally, extension of an enone by an additional conjugated double bond causes a bathochromic shift of 30m\(\mu\) and an increase of the extinction coefficients in the UV spectra. In our case, the transition from DHMTL to MTL, the increment is 45m\(\mu\) and the change in intensity is in the opposite direction, that is, it is a decrease (hypochromic effect). Doubtless this apparent anomaly depends on the fact that the new double bond, which is part of the planar (pseudoaromatic) 6-membered ring, exists in the high energy s-cis-conformation. In agreement with this is the striking change in the spectrum when we compare substances with this cyclic chromophore with those which possess a formally identical but open chain chromophoric system. We are dealing here with a transition of a cyclic chromophore (with reference to the \(\text{C}_4-\text{C}_5\) single bond) which has s-cis-conformation to an open chain chromophore with the energetically preferred s-trans-conformation (Fig. 17). Changes of conformation of this kind which we have postulated have the described effect on UV absorption. If we substitute a hydrogen atom in the methyl group of MTL, we arrive at a \(\Delta_7\)-DH-yangonin, which is a type of \textit{kawa} pyrone that is readily accessible by synthesis but has not been found in nature. The UV spectra of these compounds are again additive from the partial chromophores of MTL and substituted toluenes.

The last group of structural variants with respect to degree of hydrogenation is the one in which the lactone ring is connected with the benzene ring by an ethylene bridge. The best known representative of this group is yangonin (\(R_1 = \text{OCH}_3, R_2 = \text{H}\)) (Fig. 18). Since we are now dealing with a fully conjugated system, the spectra are no longer simply predictable from partial spectra. The increment (\(\Delta\lambda\)) of the bathochromic shift is 164m\(\mu\) for the styryl radical in MTL, and the factor for the enhancement of the intensity of the band is approximately 4.4. The dienalide ring is certainly planar and we may formulate it as a pseudoaromatic system. With regard to position and intensity of the absorption band the pyrones agree with open chain triene acids as long as one takes into consideration the different conformations; however they differ markedly from the spectra of the analogously substituted stilbenes. Figure 18 shows further that spectra of triene acids and of their methyl esters do not agree with respect to position and intensity of the bands. Possibly the ester consists of mixtures of s-cis and s-trans conformers with respect to the single bond between the carbonyl carbon and the adjacent carbon. A study of models of these compounds, however, lends no support for possible steric hindrance.

**CONCLUSIONS**

From the rhizome of \textit{Piper methysticum} or \textit{kawa} a number of constituents have been isolated which are characterized by remarkable pharmacodynamic properties. One may ask why these substances with such remarkable properties have not found any use in modern therapy, for example, as an ataractic or an anticonvulsant. A precise answer to this question is not particularly easy. There are available a large number of chemical compounds, particularly among the readily available synthetic ones, which inhibit the central nervous system. Testing methods for such compounds are well worked out and are plentiful. The probability of finding therapeutically useful substances, therefore, is relatively great. This is particularly so since the sedative-hypnotic-narcotic property of a substance is not structurally specific. In fact, all substances with a given physical-chemical property, for instance, a given partition coefficient (relatively high lipid solubility), represent potential sedative-hypnotic agents. This means that in the case of hypnotic-narcotics one is not very dependent upon models in nature as is the case with other groups of drugs. To this must be

Fig. 17. UV absorption data of the MTL system.
Fig. 18. UV spectra of the yangonin type compounds and their open chain analogs.
added that we expect newly introduced therapeutics to be in some way superior to those which are already in therapeutic use. It appears then that such superiority has not been demonstrated for the *kawa* lactones.*

The further question arises: What is the intrinsic value of such a detailed investigation of the phytochemistry and pharmacology of a single plant? I shall not retreat by responding that every scientific investigation, regardless of the subject or the goal, carries with it its own justification. I should like to express the view that there is scientific justification in learning the chemical composition and the effects of an exotic plant which has played such an important role in the lives of the peoples of Oceania for thousands of years. To this may be added that natural products have always been models and examples for new medicinal agents in biochemical research. Even if this is not the case, as has been pointed out, for the sedative-hypnotic effect, it may perhaps be true for the other effects of *kawa*. Perhaps the *kawa* pyrones will stimulate chemists studying synthetic medicinal products to new research in the fields of epileptic agents, endoanesthetics, or oral antymycotics.

I should like to thank the Chemistry Department of the University of Hawaii for the opportunity to work in the chemistry laboratory during 1961 and Professor Paul J. Scheuer for his assistance with the preparation of the English manuscript.

REFERENCES


*In Germany, recently, kawain has been introduced into therapeutic use because of its muscle-relaxant and endo-anesthetic activity.
Gulls in the Central Pacific

Fred C. Sibley2 and Robert W. McFarlane3

Published information on the distribution of gulls in the central Pacific Ocean is limited to reports covering accidental or vagrant individuals of nine species. Reports for the central Pacific prior to 1961 were summarized by Bryan (1958) and Udvardy (1961), and all subsequent published records have appeared in The Elepaio, the journal of the Hawaiian Audubon Society (Walker, 1961; Bryan, 1962, 1964; Ord, 1962, 1963a, 1963b, 1963c, 1964). Papers by King (1955), Bourne (1965), and Fry (1966) present three gull records from other central Pacific islands.

Data collected through May 1966 increase our knowledge of gull distribution and provide the first quantitated information on gull occurrence in the Hawaiian Islands. The 41 specimens of eight species and 50 other sight records more than double the number of gull records from the central Pacific. Biweekly field reports from Kure Atoll provide the first positive information on arrival and departure dates. Most of the new records from the Hawaiian Islands have been summarized by Clapp and Woodward (in press) and those from the Line Islands and Phoenix Islands by Clapp and Sibley (1967).

During 1963 the Pacific Ocean Biological Survey Program (POBSP) of the Smithsonian Institution began a study of the central Pacific area emphasizing bird distribution and movements. Investigators of the POBSP have visited most of the islands between latitudes 30°N and 10°S and longitudes 150°W and 180°W (i.e., the Hawaiian, Line, Phoenix, and Tokelau islands), maintained year-round field stations on Kure and Johnston atolls, and accumulated thousands of hours of pelagic observations.

We are greatly indebted to all members of POBSP who assisted in the collection of these data and to Mrs. Roxie Laybourne and Dr. Lester Short, U.S. National Museum, who identified some of the specimens.

Records from the Hawaiian Islands

Ten species have been recorded in the literature: Larus argentatus, L. californicus, L. delawarensis, L. glaucescens, L. hyperboreus, L. occidentalis, L. philadelphia, L. pipixcan, and Rissa tridactyla as accidentals or occasional stragglers, L. nova-hollandiae as a zoo escapee and L. occidentalis as an introduction. Neither of the latter two species became established.

Table 1 presents data on all identifiable gull specimens collected through March 1966. In February and March of 1963, 12 gulls of three species were collected in the Leeward Hawaiian Islands. At least 8 other gulls were seen (6 on Midway and 2 on Kure), and 3 unidentifiable carcasses were found on beaches (2 on Midway and 1 on Kure).

During the period September 1963 to July 1965 from one to three observers were present on Green Island, Kure Atoll, and species observations were made continuously. The 3-mile perimeter of the island was patrolled at least every third day and special emphasis was placed on the sighting and collection of gulls. Although gulls roosted on an isolated sand bar west of the island, they spent part of every day on Green Island and it is unlikely that many were overlooked during the two years of observation.

No gulls were seen on Kure Atoll during the winter of 1963–1964 and none were seen on a trip to the Leeward Hawaiian Islands in March 1964.

During the winter of 1964–1965 at least 22 individual gulls were present on Kure Atoll. The number sighted during each 2-week period and the minimum number for that period are presented in Table 2. The daily variation in

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2 Present address: Bureau of Sport Fisheries and Wildlife, 1013 Sunset Place, Ojai, California 93023.
3 Department of Zoology, University of Florida, Gainesville, Florida.
# TABLE 1

**Gulls Collected in the Central Pacific by POBSP in 1963–1966**

<table>
<thead>
<tr>
<th>USNM NO.</th>
<th>ISLAND</th>
<th>DATE</th>
<th>SEX</th>
<th>WEIGHT IN GRAMS</th>
</tr>
</thead>
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<tr>
<td>493348</td>
<td>Kure Atoll</td>
<td>10 Mar 1963</td>
<td>♂</td>
<td>1120</td>
</tr>
<tr>
<td>493349</td>
<td>Kure Atoll</td>
<td>10 Mar 1963</td>
<td>♂</td>
<td>1570</td>
</tr>
<tr>
<td>493350</td>
<td>Kure Atoll</td>
<td>10 Mar 1963</td>
<td>♂</td>
<td>970</td>
</tr>
<tr>
<td>494367</td>
<td>Kure Atoll</td>
<td>20 Jan 1965</td>
<td>♂</td>
<td>1006</td>
</tr>
<tr>
<td>494371</td>
<td>Kure Atoll</td>
<td>8 Mar 1965</td>
<td>♂</td>
<td>948</td>
</tr>
<tr>
<td>494374</td>
<td>Kure Atoll</td>
<td>1 Apr 1965</td>
<td>♂</td>
<td>909</td>
</tr>
<tr>
<td>494375</td>
<td>Kure Atoll</td>
<td>10 Nov 1964</td>
<td>♂</td>
<td>1090</td>
</tr>
<tr>
<td>493351</td>
<td>Midway Atoll</td>
<td>25 Feb 1963</td>
<td>♂</td>
<td>940</td>
</tr>
<tr>
<td>493352</td>
<td>Laysan Island</td>
<td>12 Feb 1963</td>
<td>♂</td>
<td>—</td>
</tr>
<tr>
<td>493353</td>
<td>Lisianski Island</td>
<td>14 Feb 1963</td>
<td>♂</td>
<td>—</td>
</tr>
<tr>
<td>493346</td>
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<td>27 Feb 1963</td>
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<td>—</td>
</tr>
<tr>
<td>493347</td>
<td>Pearl and Hermes Reef</td>
<td>5 Mar 1963</td>
<td>♂</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td><em>Larus argentatus vegae</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(Herring Gull)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>493503</td>
<td>Johnston Atoll</td>
<td>7 Apr 1964</td>
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<td>365.8</td>
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<tr>
<td>493603</td>
<td>At sea, 12°41′N, 171°28′W</td>
<td>7 Mar 1964</td>
<td>♂</td>
<td>284</td>
</tr>
<tr>
<td>494981</td>
<td>At sea, 16°51′N, 169°40′W</td>
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<td>♂</td>
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<tr>
<td>493824</td>
<td>Christmas Island</td>
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<td>♂</td>
<td>414</td>
</tr>
<tr>
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<td>22 Mar 1964</td>
<td>♂</td>
<td>311</td>
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<tr>
<td>493826</td>
<td>Christmas Island</td>
<td>22 Mar 1964</td>
<td>♂</td>
<td>333</td>
</tr>
<tr>
<td>493827</td>
<td>Christmas Island</td>
<td>22 Mar 1964</td>
<td>♂</td>
<td>—</td>
</tr>
<tr>
<td>493947</td>
<td>Palmyra Island</td>
<td>24 Nov 1964</td>
<td>♂</td>
<td>312.6</td>
</tr>
<tr>
<td>494089</td>
<td>Baker Island</td>
<td>14 Feb 1964</td>
<td>♂</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td><em>Larus atricilla</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(Laughing Gull)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>493342</td>
<td>Pearl and Hermes Reef</td>
<td>5 Mar 1963</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>494343</td>
<td>Kure Atoll</td>
<td>22 Feb 1963</td>
<td>♂</td>
<td>479</td>
</tr>
<tr>
<td></td>
<td><em>Larus delawarensis</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(Ring-billed Gull)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>493344</td>
<td>Kure Atoll</td>
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<td>♂</td>
<td>1230</td>
</tr>
<tr>
<td>494365</td>
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<td>24 Dec 1964</td>
<td>♂</td>
<td>1483</td>
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<tr>
<td>494368</td>
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<td>♂</td>
<td>1270</td>
</tr>
<tr>
<td>494369</td>
<td>Kure Atoll</td>
<td>1 Mar 1965</td>
<td>—</td>
<td>1421</td>
</tr>
<tr>
<td>494370</td>
<td>Kure Atoll</td>
<td>7 Mar 1965</td>
<td>♂</td>
<td>1204</td>
</tr>
<tr>
<td>494372</td>
<td>Kure Atoll</td>
<td>9 Mar 1965</td>
<td>—</td>
<td>1248</td>
</tr>
<tr>
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<td>—</td>
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<tr>
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<td>—</td>
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<td>1515</td>
</tr>
<tr>
<td>494133</td>
<td>Lisianski Island</td>
<td>12 Mar 1965</td>
<td>♂</td>
<td>1700</td>
</tr>
<tr>
<td></td>
<td><em>Larus hyperborens</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(Glaucous Gull)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>494366</td>
<td>Kure Atoll</td>
<td>17 Jan 1965</td>
<td>♂</td>
<td>1575</td>
</tr>
<tr>
<td></td>
<td><em>Larus pipixcan</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(Franklin’s Gull)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>496203</td>
<td>French Frigate Shoals</td>
<td>4 Aug 1965</td>
<td>—</td>
<td>dried carcass</td>
</tr>
<tr>
<td>496505</td>
<td>Palmyra Island</td>
<td>13 May 1966</td>
<td>♂</td>
<td>—</td>
</tr>
<tr>
<td>496506</td>
<td>Palmyra Island</td>
<td>13 May 1966</td>
<td>♂</td>
<td>—</td>
</tr>
</tbody>
</table>
gull numbers and the collection of 5 individuals in early March, when no more than 3 were seen on any one day, would indicate a frequently changing population. Therefore more than 22 gulls may have visited the island during the winter. All sight identifications given in Table 2 are questionable since immature gulls are difficult to identify in the field. During two trips to the Leeward Hawaiian Islands, 6 gulls of three species were collected—5 birds in March and 1 in August.

Observers present on Johnston Atoll between July 1963 and March 1966 saw only 3 gulls, one of which was collected. In addition, 2 specimens were collected at sea, 11 miles and 300 miles south of Johnston Atoll.

No comparable data are available from the main Hawaiian islands, but since 1961 (during the winter months, December to March) observations of six species have been reported in The Elepaio (Walker, 1961; Bryan, 1962, 1964; Ord, 1962, 1963a, 1963b, 1965c, 1964).

Gulls probably occur irregularly during the winter on all of the Hawaiian islands but more frequently on the leeward than on the main islands. An unexplained fluctuation in numbers and species occurs from year to year. During the winters of 1962–1963 and 1964–1965, considerable numbers of gulls were present in the Leeward Hawaiian Islands; in 1963–1964, none. Larus argentatus and L. glaucescens, the most abundant species, were not equally common during the two good winters. In 1962–1963 L. argentatus outnumbered L. glaucescens eight to one, but in 1964–1965 the proportion was four to eight. Very few of the observations have been of adult birds, and there have been no summer observations of living birds.

<table>
<thead>
<tr>
<th>TABLE 1 (continued)</th>
</tr>
</thead>
<tbody>
<tr>
<td>USNM NO.</td>
</tr>
<tr>
<td>---------------</td>
</tr>
<tr>
<td>Larus schistisagus</td>
</tr>
<tr>
<td>(Slaty-backed Gull)</td>
</tr>
<tr>
<td>Rissa tridactyla</td>
</tr>
<tr>
<td>(Black-legged Kittiwake)</td>
</tr>
<tr>
<td>494373</td>
</tr>
<tr>
<td>494296</td>
</tr>
<tr>
<td>496205</td>
</tr>
</tbody>
</table>

Records from the Line and Phoenix Islands

Only three published records existed for the Line and Phoenix islands. King (1955) reported an immature Larus delawarensis on Christmas Island from 15–17 November 1953, Bourne (1965) reported the sighting of "a few" L. pipixcan at Fanning Island in December 1963, and Fry (1966) reported a L. occidentalis on Fanning Island in July 1965.

Three-yearly trips were initiated to the Phoenix Islands in 1963 and to the Line Islands in 1964. Gulls were seen once in the Phoenix group and on four trips to the Line Islands. All six specimens collected in 1964–1965 (four on Christmas Island, one on Palmyra, one on Baker) were L. atricilla and all six sight records for this period (two from Palmyra, four from Fanning) were referred to this species (Clapp and Sibley, 1967). In May 1966 two L. pipixcan were collected on Palmyra Island, Line Islands.

Discussion

Many authors have noted that gulls are generally absent from tropical oceanic islands. Their distribution is normally associated with continental areas or islands adjacent to large land masses, e.g., the Australasian region and the West Indies. Those gulls which habitually spend long periods at sea are restricted to the cold waters of the temperate and polar regions.
The Galapagos Islands, with two breeding species, would appear to be the only true oceanic islands in the tropical latitudes that boast breeding colonies of gulls. The westward extension of the cool Peru current, however, exerts considerable influence on the marine fauna of these islands and they cannot be considered ecologically typical of the tropics. Our field investigations reveal that gulls frequently reach islands of the central Pacific during the winter. In some years one or more species is present in considerable numbers. The lack of breeding gulls in these islands cannot therefore be attributed to lack of potential colonizers.

Gull distribution in the central Pacific is presented, by species, in Table 3. Analysis of their normal breeding and wintering ranges reveals no particular pattern of dispersal. All Herring Gulls collected from the Leeward Hawaiian Islands have proven to be Larus argentatus vega. This subspecies breeds only in Siberia and winters along the Asian coast of the Pacific, occasionally occurring on the American coast as far south as British Columbia. L. schistisagus occurs along the western Pacific shores from the Gulf of Anadyr to China and Formosa. Specimens of Rissa tridactyla, L. glaucescens, L. philadelphia, and L. hyperboreus could conceivably have originated from the North American coast. L. delawarensis and L. californicus breed in the plains of western North America and winter along the Pacific coast as far north as Washington and British Columbia. L. pipixcan breeds in the northern interior of North America. L. atricilla has the easternmost affinity, breeding on the Atlantic coast from Nova Scotia to Venezuela, the Gulf of Mexico, and southern California and Mexico on the Pacific coast, with some birds wintering on the Pacific coast from Mexico to South America.

The wide range in their probable origins and irregular appearance in the Hawaiian Islands suggests that wind drifting may be primarily responsible for their appearance.

Bryan (1964), Frings (1965a, 1965b), and Amadon (1965) have recently commented on possible factors restricting gull distribution. Frings presented several theories concerning the failure of gulls to colonize the Hawaiian Islands. These theories center on two main themes. The first is essentially non-adaptability to local food sources. He notes that gulls are essentially scavengers and depend on a rich source of dead or easily obtained food. Productivity of tropical waters is notoriously low and the molluscs and other invertebrates which are so abundant on the rocky beaches of the higher latitudes are almost totally absent. The second theme, and that which Frings believes most important, involves the functioning of the nasal glands and their role in salt excretion. He postulates that gulls must have access to fresh or brackish water.

<table>
<thead>
<tr>
<th>TABLE 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biweekly Gull Populations on Kure Atoll During the Winter of 1964–1965</td>
</tr>
<tr>
<td>DATE</td>
</tr>
<tr>
<td>---</td>
</tr>
<tr>
<td>Nov. 1–15</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>Nov. 16–30</td>
</tr>
<tr>
<td>Dec. 1–15</td>
</tr>
<tr>
<td>Dec. 16–31</td>
</tr>
<tr>
<td></td>
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<tr>
<td>Jan. 1–15</td>
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<td>Apr. 1–15</td>
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<tr>
<td>°N Latitude</td>
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</tr>
<tr>
<td>4°</td>
</tr>
<tr>
<td>2°</td>
</tr>
<tr>
<td>1°</td>
</tr>
</tbody>
</table>

+ - collected specimens
s - sight records only
1 - only species which have been substantiated by specimens are included. Sight records for these species on other islands are indicated.
for drinking purposes and that such water is usually totally lacking on Pacific islands.

Amadon replied to this article by pointing out that several species of gulls spend long periods at sea without suffering ill effects. He further argues that food availability would seem a more probable limiting factor. In addition, he postulates that competing tropical species and the apparent aerodynamic disadvantage of a gull over tropical oceans may also contribute to their lack of success.

Frings (1965a) cited a specimen of Larus argentatus which had washed ashore on Oahu and stated that most gulls arrive in the Hawaiian Islands in poor physical condition. This assumption is not supported by our data. Many gulls collected by POBSP personnel had considerable deposits of fat; the weights of these birds (Table 1) were within the range for immatures of each species; and all were wary and capable of strong flight. Although a large number of gulls visited Kure Atoll during the winter of 1964–1965, only one was found dead and it is believed to have died from gunshot wounds.

Not only were the Laughing Gulls from the Line Islands in good health, but there is some indication that they may have remained in the area for some months. Bourne (1965) reported a few "Franklin's Gulls" at Fanning Island in December 1963. These may have been the same birds observed and collected as Laughing Gulls (immature birds of the two species are very similar) in March 1964. An adult Laughing Gull in breeding plumage was seen over Palmyra in June 1964, and an adult in winter plumage was collected there in November 1964. On Johnston Island a Laughing Gull was present for two months before it was collected; a second bird which had been injured and apparently recovered was seen for almost two months before it disappeared.

Observations concerning the feeding habits of gulls in this area are fragmentary and inconclusive. The stomachs of most birds collected during the winter of 1962–1963 were empty or contained items obviously scavenged from garbage dumps. Gulls near Kure and Midway atolls habitually frequent the garbage dumps of the military facilities. The Laughing Gulls from the Line Islands contained local foods (analysis incomplete). While gulls as a group are voracious scavengers, many species are proficient at capturing live fish and other animals (Bent, 1921; Murphy, 1936).

Frings implied that all gulls reaching Hawaii fail to return to their place of origin and eventually die in the islands. However, those gulls which do reach the islands apparently do not remain long, and there are no summer records for gulls in Hawaii. Since they show no reluctance to depart, it would seem reasonable to assume they are not subjected to excessively stressful conditions at sea and probably will attempt to return to their normal summer range if navigational ability is unimpaired.

Since our observations recently have shown that some gulls arrive at the islands in apparent good health, and since Frings's birds were in poor physical condition, we are not able to agree with him that all gulls arriving at the islands after a long oceanic flight suffer from ionic imbalance and thirst, resulting in poor health, without the actual determination of body electrolytes.

Frings maintained that the salt glands of marine birds function primarily to rectify a given amount of sea water into a smaller amount of fresh water to satisfy their metabolic needs and that the elimination of excess salts ingested while feeding is to be considered a minor function. This view would seem to be contradictory to the reports of Schmidt-Nielsen et al. (1958) and Schmidt-Nielsen (1960) who found no evidence to support the hypothesis that sea birds must drink sea water in order to cover their normal needs for water. When his experimental birds were fed fresh fish the water content of the fish was more than adequate for the renal elimination of salts and nitrogen. He observed nasal secretion only after an osmotic load and never in fasting birds or after ingestion of fish or fresh water.

Frings pointed out that gulls are unable to concentrate sodium chloride in their salt gland secretion to the degree known in albatrosses and petrels (800–1100 meq/l). He feels, therefore, that gulls are unable to exist for long periods without recourse to fresh or brackish water. It would seem, however, that the salt-eliminating capability of the two species of gulls tested by Schmidt-Nielsen (Larus argen-
tatus, 600–800 meq/1; L. marinus 700–900 meq/1) is sufficient to allow them to exist on sea water (500–550 meq/1) even if their diet was restricted to isotonic marine invertebrates. Brewster (1883) even reported a captive Kittiwake (Rissa tridactyla) which refused fresh water but drank salt water eagerly.

Even if gulls did require a source of fresh or brackish water, this is available on most of the Hawaiian islands and on several of the Line islands. Many of the main Hawaiian islands have a high annual rainfall and permanent bodies of fresh or brackish water. Palmyra Island, although a low-lying atoll, has over 100 inches of rain a year, and there are enough pools of fresh water to support a population of toads (Bufo marinus). Washington Island also has over 100 inches of rain which maintains a large fresh water lake in the interior of the island. Thus we believe that the known physiological capabilities of gull salt glands are sufficient evidence to reject the theory that the salt glands are a limiting factor in the adaptation of gulls to these islands.

The failure of gulls to colonize tropical islands remains a puzzle. We have presented evidence that a number of species may winter in the central Pacific, and we have questioned several theories concerning their failure to establish breeding colonies in this area. Part of the answer may lie in the ease with which gulls arrive at, and presumably depart from, the islands. With the exception of the Laughing Gull, all of the species recorded from these islands breed at more northerly latitudes. Rather than being accidental (i.e., lost) birds, they may represent irregular migrants. Perhaps the question is not why gulls have failed to colonize tropical islands, but why migrants rarely establish breeding populations on their wintering grounds.

**SUMMARY**

Data collected from February 1963 to May 1966 by the Pacific Ocean Biological Survey Program on gull distribution in the central Pacific are presented. The 41 specimens and over 50 sight records indicate that Larus argentatus and L. glaucescens are the most frequent visitors in the Hawaiian Islands, L. atricilla and L. pipixcan in the Line Islands. Wind drifting is presumed to be primarily responsible for the arrival of gulls on central Pacific islands.

Gulls do not necessarily arrive at the islands in poor condition as previously believed, nor do they seem to remain on any one island for long. Garbage dumps are an important food source in the Hawaiian Islands but gulls in the Line Islands survive without access to any but local foods. Evidence is presented to show that a gull’s salt glands are not a limiting factor in its survival on central Pacific islands.

It is proposed that gulls are irregular winter visitors to the Hawaiian Islands and that most of them return to their nesting grounds.

**REFERENCES**


Gulls in Central Pacific—Sibley and McFarlane


Calanoid Copepods from Midwater Trawl Collections Made in the Southeastern Pacific Ocean

GEORGE D. GRICE AND KUNI HULSEMANN

In addition to the fishes and faster swimming invertebrates (euphausiids, squids) usually obtained in midwater trawl collections, relatively large species of copepods are also frequently captured. Aside from Sewell's (1929) report of copepods found in six midwater collections made in the Indian Ocean, it has only been in recent years that midwater trawl samples have been more or less systematically analyzed for copepods. From the Florida Current off Miami, an area in which the copepods have been studied fairly extensively, Owre and Foyo (1964) reported that 21 calanoid species were found only in collections made by the Isaacs-Kidd midwater trawl (Isaacs and Kidd, 1953). Of these, 11 represented new records for the area. In the southwestern Indian Ocean, De Decker and Mombeck (1965) using both vertical plankton net and midwater fish trawl found 274 species of copepods. Of these the fish trawl accounted for 115 species including 43 which were not found in the plankton net collections. In the western Indian Ocean Grice and Hulsemann (1967) studied a series of 30 plankton net and 21 midwater trawl collections obtained between 18°N and 40°S. In the midwater trawl collections were found 64 species not present in the plankton net collections, including representatives of all eight species of the family Megacalanidae. It thus appears that midwater nets constitute a valuable additional means of sampling the calanoid copepod fauna in an open ocean area, and it is hoped that those interested in copepods will examine any available midwater trawl samples.

The samples examined in this study were obtained in the southeastern Pacific Ocean during Cruise 13 of R/V "Anton Bruun" by means of a 10-ft Isaacs-Kidd midwater trawl. They were collected at intervals along a transect of stations extending seaward from Valparaiso, Chile, for a distance of approximately 1,000 nautical miles between 33°S and 34°S (Table 1). Of the 29 trawl collections examined, 18 sampled within the upper 1000 m and the remaining 11 sampled greater depths. A total of 904 calanoid copepods were removed from the samples aboard ship and subsequently identified in our laboratory.

In all, 78 species of calanoid copepods belonging to 11 families (Table 2) were identified. In general, these are widely distributed species and most of them occur also in the deeper waters of the Atlantic and Indian oceans. Comparing these observations, for example, with a series of midwater trawl samples collected in the Indian Ocean (Grice and Hulsemann, 1967) we find that 68% (53 species) of the species from the southeastern Pacific are also present in the Indian Ocean. Furthermore, 81% of the species occur also in the Atlantic. Of the 78 species we found, 13 have previously been reported from the waters adjacent to the coast of Chile (Fagetti, 1962); 7 have not previously been reported from the Pacific Ocean (these are marked with an asterisk in Table 2); and 6 other species, Bradycalanus typicus A. Scott, Enchaeta gracilicandana (A. Scott), Enchaeta weberi (A. Scott), Euchirella formosa Vervoort, Euchirella indica Vervoort, Lophotrix gigas (A. Scott), have been reported only from the Malay Archipelago. Also found in the collections were 6 new species and the hitherto undescribed adult female and undescribed male of 2 other species. Descriptions of these 8 species are given below.

1 Contribution No. 1934 from the Woods Hole Oceanographic Institution. This study was supported by National Science Foundation Grants GB3479 and GB6052 and by the Southeastern Pacific Biological Oceanographic Program. Manuscript received April 26, 1967.

2 Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543.

3 The help of Dr. Giles Mead and his scientific party who secured the samples is gratefully acknowledged.
TABLE 1

List of Stations

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* Depth determined by depth telemeter (D) or wire angle (W).

as well as remarks on the distribution and
taxonomy of 11 other species. Type specimens
have been deposited in the U.S. National
Museum.

Bradyacalanus typicus A. Scott, 1909

Remarks: The specimens are considerably
larger (10.33–15.16 mm) than the one
originally described by Scott (1909), who
reported the length as 9.00 mm. One adult fe-
male reported by Vervoort (1946) measured
11.00 mm. Sewell (1947) found a stage V
copepodid believed to be Bradyacalanus typicus
in the Gulf of Aden, and Ovree and Foyo (1964)
described a stage IV copepodid of this
species from the Florida Current.

Megacalanus princeps Wolfenden, 1904

Remarks: Two females and two males were
found that belong to the var. inermis Sewell. At
station 54 there was one female with a crested
forehead which is believed to belong to this
species since no other differences were observed.
The total length of this specimen is 10.33 mm.

Batheuchaeta enornis n. sp.

Figs. 1–13

Occurrence: Station 6, 1 female.

Diagnosis: Female. Body elongate. Length of
deymen and furca contained 5.7 times in
cephalothorax. Head and first thoracic segment
incompletely separated, fourth and fifth thoracic
segments fused. Anterior portion of head
rounded without trace of a spine or crest.
Rostrum absent. Posterior lateral margin of last
thoracic segment rounded and slightly pro-
duced. Abdomen 4-segmented. Genital segment
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<td>A. simplex Sars</td>
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* New record for Pacific Ocean.
** Species being described elsewhere by T. S. Park (in press).

with conspicuous, slightly asymmetrical lateral swellings. First antenna consisting of 24 free segments, segments 8 and 9 fused, reaching end of cephalothorax. Segments 7, 8, 13, 17, 20, 23, 24 each armed with 1 large, smooth seta; first segment bearing 2 long, plumose setae. Endopod of second antenna smaller than exopod, exopod consisting of 7 segments. First maxilla with 10 spines on first inner lobe, 0 setae on second inner lobe, 1 seta on third inner lobe, 1 seta on second basal segment, 6 setae on endopod, 11 setae on exopod, and 9 setae on outer lobe. One seta each on third to fifth lobe of second maxilla developed as spine. Second basipodal segment of maxilliped nearly twice the length of first segment. Exopods of first to fourth swimming feet 3-segmented. Exopodal segments of first foot indistinctly separated from each other. Each of the segments bearing 1 external spine. Endopod of first swimming foot consisting of 1 segment. Endopod of second swimming foot 2-segmented, of third foot 3-segmented; fourth foot broken short. Posterior side of second basipodal segment of fourth foot smooth. Terminal spine of exopods (intact only on left second and right third swimming foot) strong, denticulate. Fifth feet absent. Total length 9.00 mm. Holotype: USNM 120526.

The male is unknown. Remarks: The genus Batheuchaeta was established by Brodsky (1950) to accommodate one species, B. lamellata, which he found in the northwestern Pacific. The female of the new species proposed here, B. enormis, differs from the description of the genus given by Brodsky in the following points: The genital segment is slightly asymmetrical, it is symmetrical in Batheuchaeta; the posterior margins of the abdominal segments are smooth, they carry teeth in Batheuchaeta; the second maxilla carries 3 spines, 1 each on lobes 3 to 5, Batheuchaeta has one spine each on lobes 4 and 5 only.

**Euchirella speciosa** n. sp.

Figs. 14–19

Occurrence: Station 29, 1 female.


Remarks: Euchirella speciosa closely resembles E. formosa Vervoort, E. indica Ver-
Figs. 1–13. *Batheuchaeta enormis* n. sp., female. 1, Dorsal view; 2, lateral view; 3, fourth and fifth thoracic segments and abdomen, dorsal view; 4, fourth and fifth thoracic segments and abdomen, left lateral view; 5, fourth and fifth thoracic segments and abdomen, right lateral view; 6, second antenna; 7, second maxilla; 8, second maxilla, other side; 9, distal end of maxilliped; 10, proximal segment of maxilliped; 11, first foot; 12, second foot; 13, fourth foot (incomplete).
voort, and *E. venusta* Giesbrecht in the absence of a crest, the number of spines on the first basipodal segment of the fourth foot, and the number of setae on the lobes of the terminal segment of the endopod of the second antenna. *E. speciosa* is distinguished from these three species by the presence of 2 swellings on the left side and the nearly straight right side of the genital segment when seen in dorsal view.

*Gaetanus brachyrurus* Sars, 1907

**Remarks:** The first basipodal segment of the maxilliped carries a lamella on its external side as is the case in many species of *Gaidius*. Such a lamella is also present in three females of *Gaetanus brachyrurus* found by us previously in the Indian Ocean (Grice and Hulsemann, 1967). This lamella is not mentioned in the description of the species by Sars (1907, 1925).

*Gaidius inermis* (Sars, 1905)

**Synonymy:** *Gaetanus inermis* Sars, 1905, p. 12; Sars, 1925, p. 64, pl. 19, figs. 3–5; Rose, 1929, p. 19; Wilson, 1950, p. 231.

**Remarks:** According to Vervoort’s (1952a, 1952b) revised definitions of *Gaidius* and *Gaetanus*, the species described by Sars as *Gaetanus inermis* is transferred to the genus *Gaidius*.

Single females of *Gaidius inermis* were reported from the northeastern Atlantic (Sars, 1925; Rose, 1929) and one female, which was identified by Sars (Wilson, 1950), from off Peru. The male is still unknown.

*Pseudochirella limata* n. sp.

Figs. 20–25

**Occurrence:** Station 27, 1 female.

**Diagnosis:** Female. Body elongate, dilated in the oral region. Anterior portion of head slightly obtuse in dorsal view. Strong 1-pointed rostrum directed downward and slightly backward. Head and first thoracic segment separated by fine line, fourth and fifth thoracic segments separate. Posterior margin of fifth thoracic segment produced covering half the genital segment. Left side of fifth thoracic segment with minute spine. Abdomen consisting of 4 segments. Genital segment smooth, only little protruded ventrally. In dorsal view nearly symmetrical, right side slightly swollen near distal margin. Widest part proximally, behind which is abruptly narrowed portion. Patch of hair on ventral side of anal segment, also on inner margins of furca. Flat, rounded teeth dorsally on distal margin of second and third abdominal segments. First antenna consisting of 23 free segments, segments 8 and 9, and 24 and 25 fused. First antenna reaching end of furca. Endopod of second antenna two-thirds length of exopod. Exopod consisting of 7 segments. Outer lobe of terminal segment of endopod with 6 large and 1 small setae, inner lobe with 6 large and 3 small setae. Endopod of first swimming foot 1-segmented, exopod 3-segmented, segments 2 and 3 incompletely separated. Endopod of second foot 2-segmented, exopod 3-segmented. Posterior side of first basipodal segment of fourth pair of swimming feet equipped with row of 16 spines, decreasing in size toward inner side. Total length 7.33 mm. Holotype: USNM 120528.

**Remarks:** *Pseudochirella limata* shows relationship to *P. lobata* (Sars), but in the latter species the fifth thoracic segment is more protruded and does not carry a spine, and the genital segment is widened distally instead of proximally.

*Pseudochirella tuberosa* n. sp.

Figs. 26–33

**Occurrence:** Station 3, 2 females; station 10, 1 female; station 20, 1 female; station 40, 3 females; station 41, 2 females; station 54, 2 females; station 59, 4 females.

**Diagnosis:** Female. Head and first thoracic segment incompletely fused. Fifth thoracic seg-
Figs. 26–33. *Pseudochirella tuberosa* n. sp., female. 26, Lateral view; 27, anterior end of head, dorsal view; 28, posterior end of thorax and abdomen, dorsal view; 29, posterior end of thorax and abdomen, left side; 30, posterior end of thorax and abdomen, right side; 31, genital segment, right side; 32, second antenna; 33, fourth foot (exopod missing).

Figs. 34–40. *Euchaeta regalis* n. sp., female. 34, Dorsal view; 35, lateral view; 36, rostrum, lateral view; 37, abdomen, dorsal view; 38, abdomen, right lateral view; 39, first foot; 40, second foot.
ment small without spines, separated from fourth segment by fine line. Genital segment asymmetrical, right side with large swelling. Rostrum strong, 1-pointed, curved downward and backward. First antenna consisting of 24 free segments, segments 8 and 9 fused; reaching to distal end of genital segment. Endopod of second antenna slightly longer than half the length of exopod, outer lobe of terminal segment of endopod with 7 setae, inner lobe with 9 setae. Endopod of first swimming foot 1-segmented, exopod 2-segmented with 3 external spines. Endopod of second swimming foot 2-segmented, exopods of second to fourth feet and endopods of third and fourth feet 3-segmented. Posterior surface of first basipodal segment of fourth swimming foot with 6–8 rather strong spines. Total length 5.42 to 6.50 mm. Holotype: USNM 120529.

REMARKS: Pseudochirella tuberosa resembles P. gibbera Vervoort and P. mawsoni Vervoort, but is distinguished from these by its 2-segmented exopod in the first swimming foot and the characteristic shape of the genital segment.

Undeuchaeta major Giesbrech, 1888

REMARKS: The first basipodal segments of the fourth pair of swimming feet of 28 females were examined. Most of them have 2 or 3 small spines on these segments. In only two specimens are the spines absent. The size of the females varies from 4.66 to 5.25 mm.

The genus Undeuchaeta is defined as having no spines on the first basipodal segment of the fourth swimming foot. In other respects (e.g., the structure of the genital segment), however, these females agree with the description of U. major. The present specimens are also similar to but smaller than Pseudochirella incisa (Esterly). The synonymy of this species has been discussed by Grice (1964). Pending re-examination of Giesbrecht’s type specimen we will propose neither an emendation of the generic description nor a transfer of U. major to another genus.

Euchaeta barbata Brady, 1883

REMARKS: The total length of one female Euchaeta barbata from station 5 is 10.16 mm which is the size of the closely related E. farrani With. Our female, however, is identified with E. barbata because the second external spine on the third exopodal segment of the second swimming foot overreaches the end of the segment, as is pointed out by With (1915).

Euchaeta dubia Esterly, 1906

REMARKS: One male Euchaeta dubia was found at station 10. It measures 8.00 mm in length. Tanaka (1958) reported the length of the male of this species (as Pareuchaeta comosa) as 7.25 mm, Vervoort (1963) as 6.80 and 7.10 mm, and Grice and Hulsemann (1967) as 6.35 mm. The tooth mentioned by Vervoort as being present in the incision of the bifid lamella on the exopod of the left fifth foot is absent in our specimen. It is also absent in Esterly’s (1906) and Tanaka’s (1958) figures of this species as well as in a male found by Grice and Hulsemann (1967) in the Indian Ocean.

Euchaeta pavlovskii (Brodsky, 1955)

REMARKS: Euchaeta pavlovskii was described from specimens obtained in the Bering Sea and Kuril-Kamchatka Trench. Our findings of this species extend its geographical range to the eastern South Pacific and its size range to 9.33–10.83 mm in length. Brodsky’s (1955) specimens measured 10.4–10.8 mm. It may be added here that the first antenna of E. pavlovskii consists of 24 free segments (segments 8 and 9 are fused) and reaches the posterior margin of the second thoracic segment.

Euchaeta pseudotonsa Fontaine, 1967

REMARKS: One female Euchaeta pseudotonsa was found at station 23 and two females were found at station 43. Fontaine (1967) considers the range of this species to be restricted to the Atlantic Ocean. Re-examination of the specimens reported by us in an earlier paper (Grice and Hulsemann, 1967, sample no. 22) as E. tonsa revealed that one female is E. pseudotonsa. Thus, our records indicate that this species occurs in all three oceans.

Euchaeta regalis n. sp.

Figs. 34–48

OCCURRENCE: Station 2, 2 females; station 3, 1 female; station 16, 1 female; station 20, 1 female; station 40, 9 females, 1 male; station 41, 3 females; station 54, 3 females.
Figs. 41–48. Eucbaeta regalis n. sp., male. 41, Dorsal view; 42, lateral view; 43, rostrum, lateral view; 44, abdomen, left lateral view; 45, abdomen, right lateral view; 46, fifth feet (distal end of right exopod missing); 47, fifth feet, another view; 48, distal end of exopod of left fifth foot.

Figs. 49–52. Eucbaeta vorax n. sp., female. 49, Rostrum, lateral view; 50, fourth and fifth thoracic segments and abdomen, left lateral view; 51, genital segment, dorsal view; 52, exopod of second foot.
DIAGNOSIS: Female. Body slender. Length of abdomen and furca contained 2.5 times in cephalothorax. Head and first thoracic segment separate. Fourth and fifth thoracic segments fused. Rostrum of moderate size, pointed downward and forward. Posterior lateral margin with patch of hair, in lateral view rounded, in dorsal view smoothly rounded. Abdomen consisting of 4 segments. Genital segment long and slender; in dorsal view almost symmetrical, moderately widening on both sides of proximal half, becoming slender again in distal half. Genital swelling produced ventrally; in lateral view the posterior part more produced than the anterior due to the shape of the genital flaps. Posterior margins of abdominal segments smooth. Anal segment very short. First antenna reaching to fourth thoracic segment, consisting of 23 free segments (8 and 9, and 24 and 25 are fused). First and second exopodal segments of first swimming foot incompletely separated. External spine of second exopodal segment of second foot almost reaching tip of first external spine of third exopodal segment. Total length 8.50-9.41 mm. Holotype: USNM 120530.

Male. Body slender. Abdomen contained 2.3 times in cephalothorax. Rostrum small, slender, directed downward and somewhat backward. Forehead in side view rounded. Head and first thoracic segment fused as are fourth and fifth thoracic segments. Posterior lateral margin of last thoracic segment asymmetrical: left side rounded, protruded; right side shorter, bluntly triangular. Abdomen consisting of 5 segments. Right side of first abdominal segment slightly longer than left. Anteriorly there is a dorsal button, somewhat set off toward the right side; there is also a V-shaped ridge. The distal margins of second to fourth abdominal spine carry flat, rounded teeth. Anal segment very small. First antenna reaching end of genital segment; consisting of 22 free segments (segments 8-10, and 24 and 25 are fused). Fifth feet longer than abdomen. Endopod of right fifth foot as long as first exopodal segment which carries a tubercle in about its middle. Distal end of exopod broken off. Endopod of left fifth foot small, curved. First exopodal segment of left fifth foot flattened, second segment carrying a recurved tooth. Inner distal end of this segment prolonged into a slender lamella with smooth outer margin; inner margin beset with row of teeth separated into proximal and distal portion. Finely striated finger-shaped process about as long as toothed lamella. Hairless tubercle bilobed. Pointed third exopodal segment only slightly longer than toothed lamella bearing the usual patch of hair. Total length 8.50 mm. Allotype: USNM 120531.

REMARKS: The female *Euchaeta regalis* is similar to *E. dubia* Esterly, *E. hanseni* With, and *E. sarsi* Farran. It is readily distinguished from these species by the more slender abdomen and the peculiarly shaped genital protuberance. The male of *E. regalis* shows close affinities to the males of *E. dubia* Esterly and *E. hanseni* With. It differs from the male of *E. dubia* in the absence of hyaline spines on the posterolateral margin of the last thoracic segment and in the structure of the toothed lamella on the left fifth foot. This lamella is spoon-shaped and smooth on the external margin. The lamella of *E. dubia* has a bifid apex and carries teeth on the external as well as on the internal margin. In the male of *E. hanseni* the lamella bears teeth also along the external margin.

*Euchaeta vorax* n. sp.

Figs. 49-52

OCCURRENCE: Station 21, 1 female.

DIAGNOSIS: Female. Body and abdomen slender. Length of abdomen and furca contained 2.2 times in cephalothorax. Head and first thoracic segment separated by a fine line, fourth and fifth thoracic segments fused. Rostrum slender, pointed downward and forward. In lateral view posterior lateral margin of fifth thoracic segment slightly angular, with patch of hair. Hair also present on posterior lateral margin of same segment. Abdomen con-

Figs. 53-59. *Euchaeta weberi* (A. Scott). male. 53, Dorsal view; 54, lateral view; 55, rostrum, lateral view; 56, posterior end of thorax, left lateral view; 57, posterior end of thorax, right lateral view; 58, distal end of exopod of left fifth foot; 59, distal end of exopod of left fifth foot, another view.

Figs. 60-62. *Xanthocalanus pinguis* Farran, female. 60, Endopod of second maxilla (8.91 mm specimen); 61, fifth foot (8.91 mm specimen); 62, fifth foot (8.00 mm specimen).
sisting of four segments. Groups of hair present on ventral side of third segment near distal margin and of anal segment. Genital segment little shorter than the two following combined. Genital protuberance protruded ventrally. Lateral flaps flanking the genital opening small. In dorsal view genital segment slightly asymmetrical. Proximal third of segment slender, distal two-thirds dilated. Segment with small knob on dorsal side and ridge on left side. First antennae broken short. First and second exopodal segments of first swimming foot incompletely separate. External spines of second foot long; external spine of second segment overreaching insertion of first spine on third segment; first spine of third segment reaching insertion of second spine, second spine overreaching end of segment. Total length 7.25 mm. Holotype: USNM 120532.

REMARKS: *Euchaeta vorax* is similar to *Euchaeta gracilicauda* (A. Scott). It differs, however, in the somewhat shorter abdomen, the asymmetrical and wider genital segment and the longer external spines on the exopod of the second swimming foot.

**Euchaeta weberi** (A. Scott, 1909)

Figs. 55–59

DIAGNOSIS: Male. Body slender, length of abdomen and furca contained twice in that of the cephalothorax. In dorsal view cephalon triangular anteriorly. Rostrum small, pointed downward. Head and first thoracic segment and fourth and fifth thoracic segments fused. Posterior lateral margins rounded, asymmetrical; left side slightly more produced than right side. Small spine on both sides near dorsal margin. Abdomen consisting of 5 segments. Genital segment slightly asymmetrical with small ridge on right dorsal side. Posterior margins of second to fourth abdominal segments with small spines. First antenna reaching beyond genital segment. Fifth pair of feet longer than abdomen. Right endopod styliform, just exceeding first segment of exopod in length. Left endopod 2-segmented. One tubercle in about middle of left first exopodal segment. Second exopodal segment prolonged into spoon-shaped lamella equipped with teeth along the distal and outer margins, the larger teeth being located distally. Finger-shaped process about as long as lamella. Tubercle at base of third exopodal segment haired. Third exopodal segment exceeding lamella and finger-like process in length, pointed at the apex, and with the usual tuft of hair. Small tooth present near base of finger-like process. Total length 6.41 mm.

REMARKS: The species A. Scott (1909) described from the male as *Paraechaea tuberculata* was considered by Vervoort (1957:76) to be the male of *Euchaeta weberi* (A. Scott). Tanaka (1958) synonymized *P. tuberculata* with *E. tonsa* Giesbrecht. Fontaine (1967) transferred the males which were described as *P. tuberculata* by A. Scott and referred to *E. tonsa* by Tanaka to a new species, *E. scaphula* Fontaine. There was no male of this species in our samples.

The male characterized above and presented as the hitherto undescribed male of *Euchaeta weberi* differs from *E. scaphula* mainly in the shape of the toothed lamella on the exopod of the left fifth foot, the distribution of the teeth on this lamella, and the presence of only 1 tubercle on the first exopodal segment of the left fifth foot. *E. scaphula* has 2 tubercles and 1 small spine on the first exopodal segment of the left fifth foot.

**Xanthocalanus pinguis** Farran, 1905

Figs. 60–62

REMARKS: Two female specimens belonging to the genus *Xanthocalanus* were found at station 27. Their total lengths are 8.00 mm and 8.91 mm. We are referring them to *X. pinguis* Farran, although the terminal segment of the fifth foot in the larger specimen is longer than the second segment, and the terminal segment of the fifth foot in the smaller specimen bears only 3 spines. There are 4 spines on the fifth foot of the larger specimen. The first antennae of both females consist of 24 free segments, with segments 8 and 9 fused, as reported by Tanaka (1960). The terminal part of the second maxilla is provided with sensory appendages of various sizes.

**Lophothrix gigas** (A. Scott, 1909)

Figs. 65–74

DIAGNOSIS: Female. Body elongate, slender. Abdomen contained 5 times in cephalothorax. Cephalon and first thoracic segment separated
Copepods in Southeastern Pacific—Grice and Hulsemann

by fine line, fourth and fifth thoracic segments incompletely fused. Head in dorsal view tri-
angularly rounded, in lateral view with low crest. Posterior lateral corner of last thoracic
segment broadly triangular ending in a point. Fifth thoracic segment and ventral portion of
fourth with pitted surface. Rostrum large, directed downward and backward; swollen in
its distal half, tapering into two separate points. Genital segment about as long as the rest of
the abdomen produced ventrally, slightly overhanging second abdominal segment. Furcal rami
short, divergent. First antenna 24-segmented, segments 8 and 9 incompletely fused, reaching
third abdominal segment. Exopod of second antenna slightly longer than endopod. Second
maxilla distally with sensory appendages. Exopods of first to fourth swimming feet 3-seg-
mented; endopod of first foot 1-segmented, of second foot 2-segmented, of third and fourth
feet 3-segmented. Second and third endopodal

segments of second to fourth foot armed with
spines on their posterior sides. Fifth foot 3-seg-
mented. Terminal segment bearing 4 setae; 1
originating in the middle of the outer margin,
1 on the inner margin near the distal end, and
2 on the distal end. Inner seta nearly 3 times
the length of outer seta. Total length 7.91–
8.66 mm.

REMARKS: The large size, the pointed fifth
thoracic segment, and the shape of the fifth pair
of feet distinguish *Lophothrix gigas* from all
other species in the genus.

Vervoort (1965) recognized that the
immature male described by A. Scott (1909) as
*Brachycalanus gigas* belongs to the genus
*Lophothrix*. Vervoort mentions also that he
found an immature male and an adult female
of *Lophothrix gigas* in the "Snellius" collection.
We obtained seven females of this large species.
After kindly comparing drawings of one of our
females with the female from the "Snellius"
collection, Vervoort (in litt.) informed us that these specimens were identical. Since a description of the female of *L. gigas* has never been published we have presented a diagnosis of the female here.

*Lophothrix similis* Wolfenden, 1911

**Remarks:** Since its description by Wolfenden (1911), *Lophothrix similis* has not been reported again. Wolfenden's specimen was found in the South Atlantic, and therefore the females reported here constitute the first record for the Pacific Ocean. Our specimens range in size between 7.08 and 7.41 mm, which is larger than that reported by Wolfenden (5.5 mm).

It should be added here that the posterior lateral margin of the fifth thoracic segment is rounded and protruded, as in *L. frontalis*. No mention is made of this in the original description.

**REFERENCES**


Copepods in Southeastern Pacific—Grice and Hulsemann


—— 1965. Pelagic Copepoda. II. Copepoda Calanoida of the families Phaennidae up to and including Acartiidae, containing the description of a new species of Aetideidae. Atlantide Rept. 8:9–216, figs. 1–41.


Host Specificity, Settling, and Metamorphosis of the Two-tentacled Hydroid *Proboscidactyla flavicirrata*

Richard D. Campbell

The colonial hydroid *Proboscidactyla* has been found only on the leathery tubes of marine sabellid worms (Uchida and Okuda, 1941:433; Hand, 1954; Brinckmann and Vannucci, 1965:367). Nothing is known about the means by which this specific commensal association arises. In this paper I present observations on planula settling and metamorphosis, which indicate that larvae are caught in the tentacles of the sabellid worm and transferred to the rim of its tube.

**METHODS AND MATERIALS**

Medusae of *P. flavicirrata* (Brandt) were dredged in East Sound, Orcas Island, Washington at a depth of 15 meters, on August 16-18, 1964. Most specimens contained ripe gametes. Medusae kept in glass dishes without feeding shed and fertilized many eggs for three or four days at about 5 AM. Developing larvae were kept in sea water at 17°C, changed every 24 hours.

To test the influence of substrate on settling, five glass dishes of sea water were prepared with the following: (1) 3 sabellid worm tubes from which the worms had been removed; (2) 3 tubes with worms; (3) 3 worms in glass tubes; (4) some perisarc of obelia, and (5) sea water only. About 50 one-week-old planulae were pipetted into each dish. Observations were made during the following 8 hours, and at intervals over the next 8 days.

Studies on metamorphosis were made on planulae which had settled on a tube (see below), and which were transferred to a microscope slide where they completed metamorphosis.

**OBSERVATIONS**

Planula settling and metamorphosis took place only on tubes containing sabellid worms, regardless of whether the tubes were natural or artificial. No settling occurred on tubes without worms, or on other surfaces.

Several hundred planulae were kept in clear glass dishes for 18 days. During this period none metamorphosed or settled.

Observations on the behavior of the planulae and sabellid worms during the settling process indicated the role of the worm. Initiation of the settling process began when a planula was caught in the ciliary currents of the sabellid's radioles (tentacles). In the vicinity of the radioles these currents are much swifter than the planula's swimming movement; therefore, the planula must be considered as a passive participant in initiating this association. However, when the planula does contact the worm, nematocysts discharge and anchor the planula (Fig. 1). The physical attachment is clearly indicated when a single planula binds to several adjacent pinnules, clumping them.

The next stage in the settling process involves the transfer of the planulae from the radioles to the rim of the tube. This is mediated through retractions of the worm into its tube, which

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**Fig. 1. Proboscidactyla flavicirrata.** Planula (arrow) attached to two pinnules (p) of a sabellid worm. Printed from 16 mm film. Scale: 0.5 mm.
scrape the planulae off onto the rim. This transfer was also made possible by a stickiness of the planulae, which developed after the contact with the worm. At least 20 minutes elapsed between attachment to the pinnules and transfer to the tube rim, and most retractions of the worm were unsuccessful in achieving this transfer. Probably the elapsed time represents the time required for secretion of an adhesive material.

Accidental contacts between the swimming planulae and the worm tube were refractile, and had no effect on the activity of the planulae. However, after a planula had been transferred normally to the tube it would undergo metamorphosis even if removed from the tube.

The visible onset of metamorphosis occurs about 6 hours after settling. Figure 2 shows the mature planula before attachment. Nematocysts are more abundant at the anterior end. The planula is characteristically spindle shaped. Figure 3 shows a planula several hours after attachment, as the first visible signs of metamorphosis become apparent. There is a loss of refractile quality of the endoderm at the future oral pole. This reflects the formation of a well delineated high columnar epithelium which is characteristic of the hypostome of the adult polyp. Also at this time the mouth has begun to form. The animal in Figure 4 shows a protrusion in the body wall below the hypostomal region. This evagination becomes a single tentacle, which elongates rapidly (Fig. 5).

Within several hours another protrusion is seen developing on the body wall (Fig. 5). It always develops after the tentacle has been initiated, and usually after the tentacle has elongated. It is always on the same side of the body as the tentacle, and is generally situated in the middle of the body. This protuberance develops into the "foot" (Campbell, 1967) which may be homologous with the stolon tip in other hydroids. The segment of polyp posterior to the foot adheres to the substratum, secretes a very fine perisarc, and becomes the stolon. The foot marks the anterior extent of the attachment to the substratum, and the distal portion of the polyp remains erect from the substratum.

During the next 24 hours, the observed, single-tentacled polyps began to glide along the substratum. The polyp column posterior to the "foot" elongates during polyp movement, becoming a stolon. Figure 6 shows a polyp just beginning its movement. The stolon elongates not by terminal extension, for the aboral end remains fixed with respect to the substratum (or it may actually move in the direction of the polyp). Elongation is apparently due to stretching by the advancing polyp. The mechanism of this advancement was not determined, but the movement appeared similar or identical to that of mature polyps (Campbell, 1967). It was always oriented in the direction of the tentacle and foot.

About 30 young polyps were raised for more than a week during which time they were fed sabellid eggs. None of them during this time developed a second tentacle. Of about 250 metamorphosing polyps studied, however, 2 possessed two tentacles just after metamorphosis (Fig. 7). The formation of these paired tentacles was not observed.

After metamorphosis, the young polyps on the worm tube were not oriented with respect to the axis of the tube, although the majority were right at the edge of the tube. Movement carried some further from the rim. The behavior of these young polyps was not observed for a longer time, and so it is not known whether all of them were capable of forming colonies.

**DISCUSSION**

Interaction between the worm and the planula appears to be a prerequisite to settling in *Proboscidactyla flavicirrata*. Since planulae deprived of contact with worms did not undergo metamorphosis during the more than 2 weeks of observation, the contact itself is probably a stimulus for metamorphosis. It is possible that nematocyst discharge is a direct part of this stimulation. These conclusions explain how the close association between the hydroid colony and worm tube, and the polyp's initial position on the rim of the tube, may arise. It would be interesting to know if other species of worms or other animals, which must also draw *Proboscidactyla* planulae into contact with themselves, similarly stimulate the planulae to settle and undergo metamorphosis. If there were a species specificity involved, this intricate interaction could present an explanation of the specificity
Figs. 2–7. Proboscidactyla flavicirrata. Fig. 2. Mature planula; scale: 0.1 mm. Fig. 3. Planula metamorphosis, 3 hours after contact with sabellid worm; hypostomal endoderm (b) has differentiated; n, nematocyst; scale: 0.1 mm. Fig. 4. Planula metamorphosis, 4.5 hours after contact with worm; t, tentacle rudiment; scale: 0.1 mm. Fig. 5. Metamorphosis nearly complete, 7 hours after contact with worm; f, rudiment of "foot"; scale: 0.1 mm. Fig. 6. Beginning of migration; f, "foot"; tissue to the left of foot represents stolon (s), which in this case has stretched to about 3 times its original length; scale: 0.1 mm. Fig. 7. Newly metamorphosed polyp possessing two tentacles; small protrusion at left is the "foot"; scale: 0.1 mm.

The initial attraction of the planula to the worm site, however, appears to be quite non-specific, involving water currents set up by the branchial cilia. In this respect the commensal specificity resembles that of Hydractinia for shells inhabited by hermit crabs: Schijfsma (1935:290–302) and Cazaux (1958:2195), showed that there is no attraction of the Hydractinia planula by the hermit crab, but rather that settling is apparently stimulated by particular conditions of waterflow across a hard substratum, conditions which are frequently presented by a hermit crab shell in its habitat of swiftly moving water.
Proboscidactyla metamorphosis resembles that of other hydroids, despite the unusual final morphology of the polyp. Metamorphosis occurs only after settling, which apparently provides a trigger for the development of polyp features. Settling occurs on the future aboral surface. Mouth, tentacles, and the hypostomal dome are the first structures to appear, followed by the formation of the stolons more proximally on the stalk.

A striking feature of the newly metamorphosed Proboscidactyla is its ability to move across the substratum. Adult polyps have this same behavior pattern (Campbell, 1967), which is essential to colony maintenance. The movements can be interpreted in terms of stolon elongation with the polyp residing near the stolon tip.

While in the mature Proboscidactyla colony movement is directed distally along the worm tube, thus maintaining the polyp on the edge of the tube as it is elongated, the movement of the newly metamorphosed larvae was not oriented with respect to the tube in the cultures observed. Thus, in some instances this movement carried the polyp father from the tube rim. This may be unusual behavior associated with laboratory conditions, or it may be a normal event which has an unappreciated selective advantage.

The adult Proboscidactyla polyp has two tentacles. The newly metamorphosed larvae observed generally possessed only one. Although the identity of the medusoid and polyp generation of this species has not been established by complete life cycle studies in the laboratory (the most complete data are given by Uchida and Okuda, 1941:435–439), the identity appears very probable. Presumably either these young polyps were abnormal, or a second tentacle arises later. However, another possible explanation for the single tentacle is that only those polyps developing asexually, during colonial expansion, have two tentacles; single-tentacled polyps may generally start colonies.

**SUMMARY**

Planulae of the hydroid Proboscidactyla flavicirrata are caught in ciliary currents of sabellid worm radioles, attach to these radioles by means of nematocysts, and are scraped off onto the rim of the leathery tube as the worm retracts. This explains how Proboscidactyla colonies may become initiated on this site, and may explain why the colonies are not found elsewhere.

Metamorphosis, apparently triggered by interaction with the worm, is generally typical for hydrozoans except that the final morphology is unusual. A young polyp moves across the substratum, stretching the proximal end into a trailing stolon.

Most of the newly metamorphosed polyps observed had only one tentacle, although polyps in natural colonies normally have two.

**REFERENCES**


Two New Calycophorae, Siphonophorae

ANGELES ALVARÍNO

The new species here described were observed in the plankton collections obtained by the NAGA Expedition (1959–1961) in the South China Sea and the Gulf of Thailand.

Family ABYLIDAE L. Agassiz 1862

Subfamily ABYLOPSINAE Totton 1954

Genus Enneagonum Quoy and Gaimard 1827

Diagnosis: Superior nectophores with opening to nectosac next to dorsal wall of hydroecium at the base of a large triangular basal facet. Bract cuboidal; somatocyst with apical horn and two short stubby ventrolateral branches. Gonophores with five prominent teeth; dorsal, one lateral and one ventral ridge incomplete; deep pocket beneath the apophysis (Sears, 1953).

The genotype E. hyalinum Quoy and Gaimard 1827, for which only the superior nectophore, bract, and gonophores are known, is well described by Sears (1953), together with the synonyms.

Enneagonum searsae n. sp.

Holotype: USNM No. 52701

Paratypes: USNM No. 52702

Etymology: Named for Dr. Mary Sears in appreciation of the privilege of working with her.

Description: Represented by only the bract and gonophores. Its bract is a truncated square pyramid; thus the top is a perfect square, with four lateral ridges prolonged at the base to a length almost equal to the height of the pyramid. Therefore, the bract is cuboidal, with a top square facet, two lateral trapezoidal facets (anterior and posterior), and the other two sides with a huge arch emphasized by the extension of the ridges. Most of the entire basal part is the opening of the hydroecium (Fig. 1A,B).

The somatocyst in the bract is like that in E. hyalinum, formed by two swollen ovoid lateral branches and the conspicuous apical diverticulum.

The gonophore is a complicated bell, with the dorsal and lateral teeth more prominent than in E. hyalinum gonophores. These teeth are emphasized by ridges like wings and by strong serrations. Pocket deep. (Fig. 1C,D.)

The illustrations of the bract and female gonophore (Fig. 1), together with those of the superior nectophore, bract, and gonophores (male and female) for E. hyalinum (Fig. 2), make it easy to compare the morphological characteristics of these two species. The size of the bells of the siphonophores is variable; therefore, only the size of the whole specimen is given in the legends for the illustrations.

Distribution: See Table 1.

Family DIPHYIDAE Quoy and Gaimard 1827

Subfamily SULCULEOLARINAE Totton 1954

Genus Sulculeolaria Blainville 1834

Diagnosis: The nectophores are smooth and round. The lateral canals of the posterior nectophores make a loop from the ring canal to the upper part of the nectosac walls. The anterior nectophores lack the hydroecium cavity. In contrast to the genus Lensia, which does not present looped canals, the anterior nectophores have lateral longitudinal ridges and also have a shallow hydroecium cavity.

The genus Sulculeolaria is represented by the following seven species, the synonyms for which appear in Totton and Bargmann (1965).

S. angusta Totton 1954
S. bigelowi (Sears) 1950
S. biloba (Sars) 1846
S. chuni (Lens and Riemsdijk) 1908
Fig. 1. *Enneagonum searsae* n. sp. *A*, Left dorsal view of bract (7 mm high, ridges 11 mm long); *B*, ventral view of bract; *C*, female gonophore, left view (2.7 mm high); *D*, female gonophore, right view.
Fig. 2. Enneagonum hyalinum Quoy and Gaimard. A, Superior nectophore (8 mm high); B, bract, right view (4 mm high); C, female gonophore, left view (2.5 mm high); D, female gonophore, right view; E, male gonophore, left view (2.5 mm high); F, male gonophore, right view.

TABLE 1

Distribution of Enneagonum searsae n. sp. in the South China Sea and the Gulf of Thailand (NAGA Expedition)

<table>
<thead>
<tr>
<th>CRUISE</th>
<th>DATE</th>
<th>TIME</th>
<th>STATION</th>
<th>POSITION</th>
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<th>DEPTH OF BOTTOM (METERS)</th>
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### TABLE 2
**Differential Morphological Characteristics of Superior Nectophores for the Species of Sulculeolaria**

<table>
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<tr>
<th>SPECIES</th>
<th>SOMATOCYST</th>
<th>BASAL PLATES</th>
<th>LATERAL CANALS</th>
<th>COMMISSURAL CANALS</th>
<th>OSTIAL TEETH</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. angusta</em></td>
<td>small</td>
<td>both with round pointed distal edges</td>
<td>none</td>
<td>none</td>
<td>none</td>
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<tr>
<td><em>S. bigelowi</em></td>
<td>small</td>
<td>exceptionally large and wide lamellae</td>
<td>extend to near the summit of nectosac; ventral canal divides in two short branches before entering ring canal</td>
<td>none</td>
<td>none</td>
</tr>
<tr>
<td><em>S. biloba</em></td>
<td>short ovoid, longest axis oblique</td>
<td>long, bilobed</td>
<td>extending to near upper 1/4 of nectosac; reaching to midlength of nectosac; one small branch at top of loop, length variable according to size of nectophore</td>
<td>none</td>
<td>none</td>
</tr>
<tr>
<td><em>S. brintoni</em></td>
<td>long</td>
<td>2, mitten-shaped, with free finger to the center, locking</td>
<td>extending near upper 1/4 of nectosac</td>
<td>left canal shorter than right, which joins ventral canal</td>
<td>2, like fingers at dorsal side</td>
</tr>
<tr>
<td><em>S. chuni</em></td>
<td>long, but shorter in small specimens</td>
<td>short, rounded</td>
<td>extending to top 1/3 of nectosac</td>
<td>none</td>
<td>none</td>
</tr>
<tr>
<td><em>S. monoica</em></td>
<td>small</td>
<td>divided, with one tooth near sagittal margin in proximal part</td>
<td>to top 1/3 of nectosac</td>
<td>to posterior 1/3 of nectosac</td>
<td>5 in total; 3 dorsal, 2 lateral</td>
</tr>
<tr>
<td><em>S. quadrivalvis</em></td>
<td>long, reaching to midlength of nectosac</td>
<td>2 wings, with notch locking them together</td>
<td>to near summit of nectosac</td>
<td>to posterior 1/3 of lateral canals</td>
<td>4 in total; 2 dorsal, 2 lateral</td>
</tr>
<tr>
<td><em>S. turgida</em></td>
<td>small</td>
<td>2 halves</td>
<td>to near summit of nectostac</td>
<td>to posterior 1/3 of lateral canals</td>
<td>none</td>
</tr>
</tbody>
</table>

*S. monoica* (Chun) 1888  
*S. quadrivalvis* Blainville 1834  
*S. turgida* (Gegenbaur) 1853

The ostium of the nectophores of *S. monoica* and *S. quadrivalvis* presents teeth, five in the former and four in the latter. In the other five species, the ostium has smooth borders.

*Sulculeolaria brintoni* n. sp.  
**HOLOTYPE:** USNM No. 52703  
**PARATYPES:** USNM No. 52704
ETYMOLGY: Named after my colleague Dr. Edward Brinton, scientist in the NAGA Expedition.

DESCRIPTION: Appeared to be represented by only the anterior nectophores. These bells presented two teeth in the dorsal part of the ostium. The teeth are long and cylindrical, like fingers, and are inclined toward the opening of the nectosac (Fig. 3). The mouth plates are of mitten shape. They lock together at the middle by the free finger protuberance in such a way that the left mitten locks with the finger to the outer part, and the right mitten to the inner part, that is, toward the opening of the nectosac.

The somatocyst is long and thin, reaching up to near the midlength of the nectophore.

The commissural canals reach up to the posterior third of the length of the lateral canals. The ventral canal either joins the right commissural canal (Fig. 3) or goes straight to the point at which both commissural canals meet.

The anterior nectophores of the seven other species of the genus Sulculeolaria are illustrated (Fig. 4) for comparison with those of S. brintoni n. sp. The size of the bell is variable; for instance, the superior nectophores of S. monoica ranged in length from 5 mm to 22 mm. Therefore, again, only the specimen size is given in the figure legends.

The differential morphological characteristics of the superior nectophores of the eight species of the genus Sulculeolaria are summarized in Table 2.

DISTRIBUTION: See Table 3.

REFERENCES


——— 1931. Siphonophorae from the Arcturus
Fig. 4. Superior nectophores of other species of Sulculeolaria, for comparison. A, S. angusta, left view (4.5 mm high); B, S. bigelowi, left view (7 mm high); C, S. biloba, right view (13 mm high); D, S. chuni, right view (10 mm high); E, S. monoica, left view (13 mm high); F, S. quadrivalvis, right view (12 mm high); G, S. turgida, left view (11 mm high).
### TABLE 3

**Distribution of Salpuleolaria brintoni n. sp. in the South China Sea and the Gulf of Thailand (NAGA Expedition)**

<table>
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<th>TIME</th>
<th>STATION</th>
<th>POSITION</th>
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———. 1954. Siphonophora of the Indian Ocean, together with systematic and biological notes on related specimens from other oceans. Discovery Rept. 27:1–162.

The Associates of Four Species of Marine Sponges of Oregon and Washington

Edward R. Long

ABSTRACT: Four species of sponge from the coasts of Oregon and Washington were studied and dissected for inhabitants and associates. The four species differed in texture, composition, and habitat, and likewise, the populations of associates of each differed, even when samples of two of these species were found adjacent to one another. Generally, the relationships of the associates to the host sponges were of four sorts: (1) inquilinism or lodging, either accidental or intentional; (2) predation or grazing; (3) competition for space resulting in "co-habitation" of an area (i.e., a plant or animal growing up through a sponge); and (4) mutualism. Fish eggs in the hollow chambers of Homaxinella sp. represented fish-in.sponge inquilinism, which is the first such instance reported in the Pacific Ocean and in this sponge. The sponge Halichondria panicea, with an intracellular algal symbiont, was found to emit an attractant into the water, which Archidoris montereyensis followed, in behavior experiments, in preference to other sponges simultaneously offered. A total of 6,098 organisms, representing 68 species, were found associated with the samples of Halichondria panicea with densities of up to 19 organisms per cm² of sponge tissue. There were 9,581 plants and animals found with Microciona prolifera, and 150 with Suberites lata.

Sponges frequently serve as hosts for many plant and animal associates. The relationships of such organisms vary from loose lodging or inquilinism to mutualism, a close type of symbiosis. The first account of sponge symbiosis was that of Radcliffe (1917) in which he reported the goby Garmannia spongicola living within unidentified sponges off North Carolina. Other early reports include those of Vosmaer (1911) who found invertebrates in the canals of tropical sponges, and Ridley and Dendy (1887) who found a very abundant oscillatory alga in Halichondria panicea.

Perhaps the most significant reports concerning sponge symbioses were those of Pearse (1933, 1949) who described the inhabitants of various Caribbean sponges, Gudger (1935) who found many fish living in Atlantic sponges, and Forbes (1964, 1966) who described the mutualistic relationship between the sponge Stellata grubii and the oyster Ostrea pernollosis from the Gulf of Mexico. Caullery (1952), Dales (1957), Nicol (1964), and Henry (1966) have summarized the symbiotic relationships of marine animals and included in their descriptions many previous reports of sponge symbioses. The following is a description of the associates of four species of sponge, three subtidal and one intertidal in Pacific Northwest marine waters.

METHODS AND MATERIALS

Because the sponges studied occupied varied habitats, the methods of collection differed. Microciona prolifera and Suberites lata, which were subtidal, were obtained with scuba. They were pulled or scraped off their substrate and immediately placed into zippered plastic bags which were sealed underwater. Halichondria panicea, which occurred intertidally upon unprotected rocks, was scraped off the rocks by use of the fingernails and placed into plastic bags. Homaxinella sp. was collected from 10 to 15 fathoms with an otter trawl. The collected specimens were subsequently taken to the laboratory.

to recover the associates. The sponges were pulled apart and examined under a binocular microscope (120 ×). The inhabitants found were preserved in AFA for further examination and identification. The results are summarized in Table 1.

**OBSERVATIONS AND EXPERIMENTS**

*Suberites lata*

*Suberites lata* occurred in Hood Canal, Washington, in a distinct zone of its own at a depth of 5–10 meters (MLLW) on nearly vertical rocks that were lightly covered with a fine mud. The water conditions in this narrow inlet were quite stable and calm.

The consistency of the sponge was very tough and impenetrable. It harbored very few organisms. The 15 samples studied had 150 associates, representing 25 species and 6 phyla. The densities of the associates varied from 0.001 to 0.03 (mean 0.1) organisms per cm³ of sponge (Table 1). The sparsity of inhabitants was most likely due to the toughness of the sponge. The predominant organisms were the small spionid polychaete *Polydora socialis* which was found in every Hood Canal sample, the gammarid *Aonides columbiana*, the ectoproct *Crista* sp., and unidentified, filamentous green algae.

*P. socialis* was the only organism actually living within the sponge, the remainder were simply attached to the surface. The larger animals, such as the crabs, were usually found hiding among the convolutions and contortions of the sponge.

One clump of *S. lata* was found in an unprotected rocky coast situation at Yaquina Head, Oregon. It harbored only a few more organisms than the Hood Canal samples. The organisms found on the Yaquina Head sample were those of the local community.

**Microciona prolifera**

*Microciona prolifera* was found attached to subtidal rocks in Willapa Bay, Washington. This sponge was erect, branching, and bushy, sometimes forming a mass of branches 1 foot or more in diameter and 6 or 7 inches high.

*M. prolifera* provided a place to live for many animals and plants; the population density varied from 0.27 to 3.64 (mean 0.80) organisms per cm³ of sponge. The organisms most commonly found were the gammarid *Corophium acerosum*, various caprellids, the polynoid *Harmothoe imbricata*, the sabellid *Sabella media*, and the anemone *Dianemone luciae*. The 15 samples of sponge dissected harbored 9,581 organisms of at least 52 species from 9 phyla. The most common and abundant of this array were the amphipods *Corophium acerosum* and various caprellids.

The majority of the inhabitants were found attached to the surface of the sponge and relatively few were found within the sponge tissue. Some of the amphipods, sabellids, nereids, and nematodes occurred within the sponge. It was apparently difficult for the associates to penetrate into the tough and fibrous *M. prolifera*.

Due to the branching and bushy morphology of the sponge, mud often collected on it and this mud harbored many of the associates that were found. Therefore, there is a question whether the associates were attracted to the

| TABLE 1 | Average Thickness, Volume, Total Associates, and Density of Population for Samples of *Suberites lata*, *Microciona prolifera*, and *Halichondria panicea* |
|---|---|---|---|---|
| **Species of Sponge** | **No. of Samples** | **Average Thickness (cm)** | **Average Volume (cm³)** | **Average Total Associates** | **Average Density** |
| *Suberites lata* | 14 | 4.5(3-7) | 503(195-820) | 10(1-59) | 0.2(0.001-0.8) |
| *Microciona prolifera* | 15 | 5(2-13) | 394(24-2,340) | 640(21-1,883) | 1.2(0.27-3.64) |
| *Halichondria panicea* | 33 | 1(0.5-3) | 104(20-540) | 188(18-670) | 1.8(0.126-19.14) |
sponge itself or to the mud collected thereupon. The fact that relatively clean samples of the sponge also harbored many associates indicated that there was a definite attraction to it. Other species of sponge occurring near or upon M. prolifera were completely devoid of associates, suggesting that the associates preferred M. prolifera.

**Halichondria panicea**

**GENERAL OBSERVATIONS:** *Halichondria panicea* occurred as an encrusting sheet 1–5 cm thick upon unprotected rocky coast areas in violent surf. It was green in its upper layers and yellow below, the coloration being due to an intracellular single-cell alga.

*H. panicea* harbored many associates of a great variety. A total of 6,098 organisms of 68 species were found in 32 samples with densities of population of from 0.26 to 19.0 (mean 1.15) organisms per cm². The most common associates were amphipods (*Jassa falcata* and caprellids); the barnacles *Balanus glandula* and *B. nubilis*; the isopods *Dynamene shearei* and *D. dilata*; and the coralline alga *Corallina gracilis*.

The relationships of these associates to the sponges varied considerably. The associates can be grouped in four general headings: (1) those that were caught in the sponge as larvae and subsequently matured; (2) those that were on the sponge accidentally at the time of collection; (3) those that grew simultaneously with the sponge on the same substrate; and (4) those that clung to the sponge because it was abundant and provided purchase.

Such organisms as algae, hydroids, ectoprocts, some crabs, barnacles, mussels, and some molluscs and annelids probably were caught among the sponge spicules as planktonic larvae and, having survived digestion, developed into adults thereupon and therein. Many of the nereids, large crabs, caprellids, gammarids, and fish were found by chance upon the particular sponge collected when they were feeding or using it for temporary shelter. It is most likely that some of the algae (e.g., *Microcladia borealis*) grew simultaneously with the sponge.

Several animals were grazing on the sponge. *Acmaea asmi*, *Mopalia lignosa*, *Oedognathus inermis*, *Pachycheles radiis*, *Cancer productus*, and, particularly *Archidoris montereyensis* were found to have *H. panicea* spicules in their stomachs.

The only possible examples of truly mutualistic associations were those concerning the intracellular algae of *H. panicea* and the cleaning action of the crustacea associated with *H. panicea*, as well as with *Suberites lata* and *Microciona prolifera*. The algae may have provided needed oxygen or other nutrients to the sponge. The sponge without algae could survive, but it usually appeared as thin, rubbery sheets. The numerous crustacea fed on the material which collected upon the sponge.

Generally, the samples of *H. panicea* from different areas harbored the same species, and the various members of the community were usually found in the same proportions from sample to sample. However, the exact composition of the sponge communities varied enough among the samples to suggest that a given individual community was related to the fauna of the immediate area.

**EXPERIMENTS:** Sponges of similar consistency living immediately adjacent to *Halichondria panicea* normally had very few associates of any kind, while the clumps of *H. panicea* were well provided with associates. Also, when the nudibranch *Archidoris montereyensis* was placed into a laboratory tank upon a piece of *Suberites lata* downstream from *H. panicea*, the animal would invariably crawl to the *H. panicea*, indicating a chemotaxis toward the *H. panicea*.

An apparatus similar to that of Davenport (1950) was set up to determine if there was a chemical attraction of *A. montereyensis* to *H. panicea*. The apparatus consisted of a series of waterways which gave the nudibranchs a choice between water passing over *H. panicea* and *Suberites lata*. The majority of the nudibranchs always moved toward the *H. panicea* water outlet: 9 individuals of 15, 10 of 15, 13 of 15 in the three experiments went to the *H. panicea* outlet. None ever moved to the *S. lata* outlet.

*Homaxinella* sp.

This sponge had much the same shape as *Microciona prolifera*, but it was branched fewer times, and its branches were thicker and hollow. *Homaxinella* sp. occurred at a depth of 20–30 meters off the Oregon coast.
The hollow branches were found to contain clusters of 20–30 fish eggs with living embryos inside. The eggs were probably those of a small blenny or goby that normally deposits its eggs within sponges. All the eggs found died before hatching.

Assuming that these eggs are from a sponge-dwelling fish, this example of fish-sponge inquiline is the first recorded for Homaxinella sp. and for the Pacific Ocean.

**DISCUSSION**

The four species of sponge studied showed great variation in the community of associates found. These variations were due to the different habitats of the sponges and also to different properties of the sponges that acted as attractants and inhibitors. Other species of sponge adjacent to those studied harbored fewer associates, probably because they lacked factors that attracted the associates, or they possessed something that discouraged them.

In comparing Halichondria panicea, Microciona prolifera, and Suberites lata, which occurred in progressively deeper waters, the community of associates was progressively more stable, consistent, and predictable and its composition fluctuated less from sample to sample. The intertidal H. panicea showed great variation in community density and composition, indicating that these parameters were related to the fauna of the immediate area. When two species of sponge (e.g., S. lata and H. panicea) occurred next to each other, the tougher, more impenetrable species harbored fewer associates.

The majority of associates did little harm to the host sponge. The numerous crustacea may have benefited the sponges by cleaning them. Such a relationship can be considered mutualistic. The intracellular algae of H. panicea were also probably mutualistic with the sponge. The most deleterious associate was Archidoris montereyensis, which, along with other predators, fed voraciously on H. panicea. Some of the tube worms and amphipods associated with M. prolifera caused minor structural damage to the sponge. The sponge-dwelling fish whose eggs were deposited within Homaxinella sp. obviously benefited from the water currents and shelter of the sponge, while it did not appear to inhibit the growth or function of the host.

**CONCLUSIONS**

Four species of sponge from the coasts of Oregon and Washington were studied for associates. A large number and great variety of associates were found. The great numbers of sponge associates suggests that sponges are important to the ecology of the numerous associates. The relationships of these associates fall into four general categories: (1) inquilineism, or lodging, within or upon the sponges; (2) coexistence of two organisms on the same substrate as a result of simultaneous growth; (3) predation or grazing; (4) mutualism.

The 32 samples of Halichondria panicea harbored 6,098 organisms, representing 68 species, with a mean density of 1.15 organisms per cm³ of sponge. The 15 samples of Microciona prolifera had 9,581 associates with a mean density of 0.80 organism per cm³. The 14 samples of Suberites lata had 150 associates at a mean density of 0.1 organism per cm³ of sponge.

Significant differences in composition and density among the sponge communities were attributed to the different habitats of the species studied, and to differences in the exudates and consistencies of the species of sponge. The nudibranch Archidoris montereyensis, which frequently occurred on Halichondria panicea, exhibited a distinct preference for that species in laboratory experiments.

The tubular sponge Homaxinella sp. harbored the eggs of a fish, which was assumed to be an unidentified, sponge-dwelling inquiline.

**ACKNOWLEDGMENTS**

Space and facilities were provided by Prof. Ivan Pratt at his laboratories in Corvallis and at the Marine Science Center, Newport. The following persons provided identifications of many of the sponge associates: Dr. Joel Hedgpeth (insects), Dr. J. Laurens Barnard (amphipods), Mr. Danil Hancock (annelids).

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Ecological Factors on Manana Island, Hawaii

P. Quentin Tomich,1 Nixon Wilson,2 and Charles H. Lamoureux3

ABSTRACT: A 25-ha islet occupied by seasonally nesting sea birds, feral rabbits, and house mice is considered. Rabbits presumably modified the unknown original vegetation in their 70 or more years on the island and reached an equilibrium with a plant cover composed largely of a few hardly introduced grasses. A total of 28 species of higher plants has been recorded from the island, only 6 of which are native to Hawaii. Rabbits occur in low to moderate numbers, sustained by a food source that is enriched by bird guano and subject to annual drought. Average body weight of the mouse is remarkably heavy at 19.5 g. Data on biological and food habits are presented for both mammals. Among 13 species of ectoparasites of birds and mammals are two unusual host adaptations: of the cat flea, Ctenocephalides felis felis, to Oryctolagus cuniculus, and of the Oriental rat flea, Xenopsylla cheopis, to Mus musculus. Rabbits appear not to be detrimental to the nesting of birds, and their control or extermination is discouraged at present. The scientific importance of the island’s unique ecosystem is stressed, and proposals for its intensive study are outlined.

Most of the lands in Hawaii were altered rapidly, in the hundred years or so following initiation in 1778 of sustained contact with outside cultures, through agricultural development and the spread of introduced plants and herbivorous animals. Then there came a period of lessened disturbance simply because purposeful exploitation of land was diminished and because controls were exercised over some major pest species. In the past 50 years, many new balances have emerged among lands, plants, and animals. However, Hawaii is now in a second era of resource development that threatens to overrun not only the lands touched little or not at all by earlier disruptions, but also those which have achieved new levels of ecological stability. This is a universal problem that is not peculiar to Hawaii. Its solution lies in the exercise of wise resource development based on present, as well as future, needs. Lands with prominent natural attributes often serve their highest use only when left undisturbed. Pro-

1 Plague Research Unit, State Department of Health, Honokaa, Hawaii 96727.
2 Bernice P. Bishop Museum, Honolulu, Hawaii 96819.
3 Department of Botany, University of Hawaii, Honolulu, Hawaii 96822. Manuscript received August 4, 1967.

proposals for their manipulation should be preceded by careful study of each individual case.

This paper is concerned with Manana (Rabbit) Island which lies about 1.3 km off the southeast tip of Oahu, Honolulu County. Its principal occupants are a depauperate flora, large numbers of seasonally nesting sea birds, a colony of feral rabbits, and house mice. Since 1945 this island has been a Territorial and State bird reservation whose security from unauthorized landings is now vested in the State Department of Land and Natural Resources. The basis for this status is that Manana has been one of the main nesting grounds for the Noddy Tern, Anous stolidus (L.), and the Sooty Tern, Sterna fuscata L., two species highly valued by fishermen in locating schools of aku, Katsuwonus pelamis (L.), the principal commercial fish of Hawaiian waters. The terns and aku prey on the same species of forage fish, crustaceans, and squids (Gosline and Brock, 1960).

Some ornithologists and conservationists have recommended destruction of the rabbits on Manana as an undesirable invader, in an attempt to enhance and possibly enlarge the colonies of terns and other birds, notably the Wedge-tailed Shearwater, Puffinus pacificus (Gmelin). In 1962 a program of rabbit extermination was
initiated, and poisoning and shooting were carried out on several occasions. For lack of manpower and at the request of interested parties the program was discontinued in 1964.

The purposes of this paper are to review the biological history of Manana, to present some new data on its plant-animal relationships, and to outline a possible course for determining what management practices, if any, should be applied to the island—specifically, whether or not the program of rabbit extermination should be renewed. Principal objections to a policy of rabbit extermination at this time are that little if any evidence is available to show that bird-rabbit relationships are other than harmonious, and that the rabbit in many generations of survival under restrictive conditions has earned a place in the Hawaiian fauna as a resource of importance to science (Tomich, 1965).

As a first step in the project, the authors were permitted to join an expedition to Manana on February 29-March 1, 1964 led by D. H. Woodside of the State Division of Fish and Game. This brief trip allowed some insight into the present status of the vegetation, the vertebrate fauna and certain parasitic elements of Manana ecology. Additional data were gathered on trips to the island by Lamoureux in October 1953 and March 1955, and by Wilson in July 1963, and from interviews with D. H. Woodside and others.

HISTORICAL ASPECTS

Manana is an ancient tuff cone, 25-ha in area (Fig. 1). In the northwest sector of the island is a shallow crater whose broad floor is some 20 meters above sea level. The crater rim is low on the northwest side but rises to a peak of 110 meters on the southeast side. In the northeast sector a remnant of a second crater opens to the sea on the east side. Its bottom contains a series of tide pools. Seaward slopes of Manana vary from low beach terraces to

Fig. 1. Manana Island as seen from the east. Coconut palms (Cocos nucifera) and low vegetation are visible in the main crater at right. (Photo by U. S. Marine Corps, January 1966.)
high precipitous cliffs. The southerly outer slopes of the main cone have been eroded into several steep valleys, presumably by intermittent streams. Bryan (1935) and Richardson and Fisher (1950) have given brief but detailed descriptions of the island. Its physical features have not changed appreciably in historic times. The island has suffered few attempts by man to use or modify it for his own purposes. However, the introduction of rabbits at some unknown date prior to 1900 and the establishment of exotic species of plants have undoubtedly changed the original vegetation. In World War II Manana was used as a bombing and strafing target (Green, 1942). Small shells are still found occasionally in its loose soils, although the Navy Department has made some effort to remove these potentially dangerous missiles (Woodside, personal communication).

Because of its easy access, Manana may have been occupied frequently as a fishing station by the Hawaiians. Records of visits for the purpose of studying the flora and fauna are relatively few. Bryan (1935) reported on insects, vegetation, and miscellaneous topics; Munro (1945, 1950) briefly described the vegetation. Richardson and Fisher (1950) made repeated observations on its birds for nearly two years, and also published a list of plants. Other notes, mainly on birds, have accumulated over the years from the excursions of the Hawaii Audubon Society and have been published in their official journal, the Elepaio.

**FLORA AND VEGETATION**

Collections of plants made on Manana on several occasions provide some information on changes in the flora during the past 40 years (Table 1). A thorough search of the Bernice P. Bishop Museum herbarium has revealed no specimens from Manana collected earlier than 1927; therefore no record is available of the island's flora before the introduction of rabbits. The earliest published information was supplied by Bryan (1935). He reported that Marie C. Neal had compiled a list of 21 species of higher plants from Manana during four trips up to August 1934, but he mentioned only 8 of these species by name in his account. However, 18 species are represented in the 1930 and 1934 collections.

In all, 28 species of higher plants have been found growing on Manana, and at least 18 of these were present at the time of our survey in 1964. Richardson and Fisher (1950) reported only 7 of these 28 species. It is likely that others were actually present, for they did not consider their list as necessarily complete. Of the 7 plants listed for 1950, none is a native Hawaiian species, while 3 of the 18 found in 1964 are native.

Munro (1945, 1950) discussed conditions on Manana between 1937 and 1941, and noted that the soils which have developed on the western slopes of the island and on the crater floor supported a "heavy cover" of introduced grasses and weedy herbs. He noted that the coconut trees were very small in 1941, but he did not give the date of planting. Richardson and Fisher (1950) indicated that the vegetation began to dry up in late May or early June, and by July all the vegetation was "brown and sear."

The most heavily vegetated parts of the island in 1964 were the floor of the main crater and the outer gentle slopes on the southwestern side of the island. In both places a fairly deep rich soil has developed from the decomposed tuff mixed with guano. On the upper south slopes, the upper inner slopes of the main crater, and the outer slopes on the north, east, and west, little or no soil has accumulated except in scattered pockets and cracks in the tuff, and few plants are present. The failure of soil to develop on these slopes is probably related to their steepness and their exposure to strong trade-winds. As the tuff decomposes in these areas, it falls or is blown away, either to lower vegetated areas or into the sea.

The vegetation of the crater floor (Fig. 2) consisted mainly of *Trichachne insularis*, a bunch grass about 1 meter tall, and *Nicotiana tabacum*, an erect herb from 1 to 2 meters tall. Scattered here and there were *Lycopodium esculentum*, *Ageratum conyzoides*, *Boerhavia diffusa*, *Setaria verticillata*, and *Cenchrus echinatus*. A few plants of *Portulaca oleracea* were found in the eastern portion of the crater floor, and one large shrub of *Sida cordifolia* grew near the northern edge of the crater floor. About 30 trees of
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Symbols used: *, Native Hawaiian species.

X, Specimens available.

Cocos nucifera, some as tall as 8 meters, grew on the crater floor, and many of these were producing fruit in 1964.

The vegetation of the outer southwestern slopes (Fig. 3) differed from that in the crater. The dominant plants were Setaria verticillata and Cenchrus echinatus, mostly 0.5 meter or less in height. Occasional shrubs of Tephrosia purpurea occurred here, along with several plants of Boerhavia diffusa. Scattered clumps of Chloris inflata were found also on these slopes; Nicotiana tabacum was occasional. Toward the lower part of the slopes Atriplex semibaccata was abundant. Two trees of Cocos nucifera grew on the western part of these slopes.

Dactyloctenium aegyptium was restricted to the sandy beach at the base of the slopes. One tree of Prosopis pallida was growing high up in the largest valley on the south side of the island. In this same valley were several flowering plants of Argemone glauca, and seedlings of this species were found also on the beach at the mouth of the valley.

One mature shrub and a few seedlings of Pluchea odorata were found in soil pockets just below the crater rim on the outer southwest slopes, and a few plants of Sonchus oleraceus grew in soil pockets on the crater rim.

MAMMALS

Oryctolagus cuniculus

The principal resident vertebrate of Manana is the European rabbit, Oryctolagus cuniculus (L.). Identification is confirmed by a flat skin and skull in the Bishop Museum, collected August 27, 1934 by E. H. Bryan, Jr., by two fresh specimens collected by State Fish and Game personnel on August 31, 1961 and examined by K. Wodzicki, and by a series of seven museum specimens prepared from material collected on the 1964 expedition.

The population probably has descended from one or more importations of mixed domestic breeds of several colors. Escaped or planted stocks of domestic rabbits sometimes revert in coloration to the wild type (Thomsen and Evans, 1964), and this is apparently the case with the population on Manana. It now resembles the wild European rabbit, which has
Fig. 3. Outer southwest slopes of Manana Island. Dominant grasses are sandbur (Cenchrus echinatus) and bristly foxtail (Setaria verticillata); shrubs include ahulu (Tephrosia purpurea) as dark patches in middleground, and wild tobacco (Nicotiana tabacum) scattered in foreground. (Photo by K. Wodzicki, February 29, 1964.)

typically an agouti dorsal color with reddishness behind the ears. The throat puff and lower abdominal patches are buff-colored; ventral parts, inclusive of the tail, are otherwise generally white (Fig. 4). However, traces of domestic color traits are still evident in the rabbits on Manana. One of the 1961 specimens was a male with patches of white on both forelegs. Of 13 rabbits examined in 1964, 2 males had similar markings: one a white paw (Fig. 5) and the other an entire white foreleg. These appear to be expressions of the genetic Dutch pattern.

Rabbits have been on Manana for 70 years and perhaps longer. One anonymous writer (1901) stated that, "A few of the small rodents (sic) were taken there many years ago by some party or parties unknown and now they are innumerable." There have been reports in the literature suggesting that species other than Oryctolagus cuniculus may have been introduced to Manana, but none of these reports is well founded in fact. W. A. Bryan (1915) listed the rabbit under the misnomer of Lepus, the genus of hares, but perhaps properly referred to the animals as a "mongrel breed." De Vos et al. (1956) quote a letter from Ernst Schwarz to the effect that, "A hare, believed to be of Russian origin (species unknown), is found ... off Oahu." A partial source of Schwarz' information may be Bryan's notation of Lepus. Watson (1961) states, "The Manana rabbits closely resemble the American cottontail in color and ear length and it is conceivable that these rabbits are in fact cottontails (Sylvilagus spp.)." The source of his information is not given; however, it is known that Watson did not see the rabbits himself.

Several brief notes record the status of the population through the years. The anonymous writer (1901) reports that, as he approached Manana by boat, "Almost every foot of the ground is seen to be occupied by a rabbit; in fact, it is one of the most thickly populated rabbit colonies in the world. ... They have so denuded the place of all edible vegetation that they are obliged to subsist on small shell fish which they find along the beach. ... Mr. John Cummins has several hundred of them killed off every year, the meat being salted down and eaten as required."

W. A. Bryan does not indicate whether his report in 1915 that Manana was thickly populated with rabbits was the current condition, or
whether he was merely paraphrasing the 1901 statement. A few years later, rabbits may have been plentiful because a note from the Territorial Division of Forestry (Anon., 1919), which apparently had charge of the island then, said, "In March, 1918, 3 chauffeurs were arrested for going to Manana and killing rabbits without a permit..." E. H. Bryan, Jr. records 3 rabbits seen on the August 25–26, 1934 expedition and that they were seemingly in good condition. Vegetation at that time was considered doing well. The next report is by Richardson and Fisher (1950) who made 14 half-day trips to Manana between October 1946 and August 1948. They saw from 2 to about 30 rabbits per trip, with the maximum number observed in June 1948. Wodzicki notes (in litt.) that on August 31, 1961 the landing on Manana was made for about an hour at mid-day, and 5 or 6 rabbits were seen, including the 2 collected. On October 27 of the same year, 15 rabbits were shot as a part of the extermination program (Woodside, personal communication). These scattered records indicate a large early rabbit population on Manana and later populations stabilized at low to moderate levels.

On the February 29—March 1, 1964 trip, rabbits were seen commonly. As the party climbed into the main crater at 4:30 PM, several rabbits were on the dry grassy slope above the beach. Two hunters moving in advance shot two of them among the tobacco plants. Here, as within the crater, the rabbits had burrowed in the friable soil. There seemed to be no distinction between old burrows seasonally used by various birds and those used by rabbits. Thousands of prenesting Sooty Terns milled day and night over the island. At night small numbers of them, as well as of Wedge-tailed Shearwaters, settled, and some were banded by a party of ornithologists also visiting the island. In the crater, by 6:00 PM, the hunters shot and recovered 11 more rabbits. Each person who entered the crater reported seeing several rabbits, in spite of the shooting. Here the vegetation was still quite green, and Trichacme insularis was seeding heavily. After dark only a few rabbits were noted, even with the aid of lights. The population for the island may have been as many as 100 juveniles and adults. This would be a fairly large number to be supported by the vegetation, which covers about 10 ha. Heavy rains later in March were effective in extending the growing period into summer, and thus replenishing the food supply.

Rabbit pellets were noticeably scarce on February 29, 1964, in relation to the observed abundance of rabbits. Pellets found, except for
the occasional fresh deposit, had a roughened and weathered appearance. These phenomena were explained when we observed at night that the cosmopolitan terrestrial isopod, *Porcellio laevis* Latreille, swarmed over the rabbit pellets and fed on them. Often a single pel-let had several *Porcellio* on it and was rolled about as the isopods shifted position. Thus the destruction of rabbit feces is hastened and the usual methods of censusing rabbits by pellet counts cannot be applied to the Manana population.

Three male body weights were 2189, 1695, and 1670 g and three females weighed 2055, 1970, and 1640 g, indicating a similar weight in the two sexes. Average weight for the six rabbits was 1870 g. Paunched weight averaged 73.6% of the live weight. A male and female collected in August 1961 weighed 2284 and 2087 g, respectively. Paunched weight averaged 70.4% as heavy. Both were fat, rating at 3 and 2, respectively, on a scale of 0 (none) through 3 (heavy). The rabbits observed in 1964 were in good flesh but not fat. On the same scale a pregnant doe registered 1, and four others 0 for an average of 0.2. Five males were 1 and one was 0, for an average fatness of 0.8.

The population had just passed a peak of reproduction. All five adult does were lactating, averaging 2.2 on a scale of 0 through 3. One doe was about 10 days pregnant and showed the least mammary tissue (rated at 1). Corpora lutea were counted easily in the pregnant doe as 8R-1L. Eight embryos were implanted in the right uterine horn, none in the left. Another doe had distinct black uterine scars 4R-0L and corpora lutea 7R-1L, suggesting a 50% pre-implantation or early resorption loss. No other scars were found. Uteri of the four parous does definitely were inactive as flabby flattened structures 5 to 7 mm wide. The reproductive rate was seemingly high. These data on corpora lutea, embryos, and placental scars show that litter size may average about 6.0 (allowing for a 25% loss before birth of shed ova and early-stage embryos).

The testes of one adult male weighed 2.7 g and the cauda epididymides had visible tubules indicating the presence of sperm. In another buck testes were larger than this, in two they were of similar size, and in two they were smaller. At least four and perhaps all of the six males were in breeding condition. Regression may have been in progress. That the four parous does were sexually inactive suggests that the breeding season was nearly terminated. Each of the party who crossed the crater reported seeing small young rabbits. The smaller of two juvenile females collected weighed 352 g and was still nursing, for it had a small mass of curds in the stomach.

Age structure offers some clues about the population. Of 12 rabbits classified by age, 5 were less than 10 months old (2 were juveniles), 5 were from 15 to 26 months, and 2 were 33 to 38 months. The criteria used were those of Taylor (1959) which employ the progressive closure of skeletal epiphyseal sutures. These three age groups are spaced at approximately yearly intervals and imply that breeding may normally occur yearly in a season extending from November to April. A rabbit attains adult size at the age of 4 to 5 months.

Because the rabbits on Manana must depend on the few foods available, it is almost mandatory that they eat all palatable plants within reach. The rabbits taken in 1964 all had full intestinal tracts. Reingestion, as described by Meyers (1955) and by Rowley (1956), was evidenced by soft pellets which made up 10% to 40% of the stomach contents of at least seven rabbits. None had other than hard rectal pellets, showing that reingestion takes place earlier in the day than the 4:30 to 6:00 PM period in which the rabbits were shot.

Thorough mastication and the second pas-sage of food through the alimentary canal usually makes identification of food items a tedious process requiring specialized techniques. We were fortunate to have collected a male (2759) which had lost its fourth and fifth upper cheek teeth on one side, resulting in malocclusion and uneven wear of all other cheek teeth. He swallowed most of his foods whole, allowing their easy identification (Table 2). Comparative data for the other rabbits are given in Table 3.

Grass fragments composed over half the identifiable materials in all seven animals, although volumetric measurements were not

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4 All mammal specimen numbers refer to the catalog of P. Q. Tomich.
TABLE 2
Food Items in Stomach of Rabbit 2759 with Poor Dental Occlusion, from Manana Island, Hawaii

<table>
<thead>
<tr>
<th>PLANT</th>
<th>PARTS EATEN</th>
<th>% BY VOLUME</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atriplex</td>
<td>Leaves and stems</td>
<td>18</td>
</tr>
<tr>
<td>semibaccata</td>
<td>Seeds in utricles</td>
<td>27</td>
</tr>
<tr>
<td>Nicotiana</td>
<td>Whole flowers, leaf fragments</td>
<td>30</td>
</tr>
<tr>
<td>tabacum</td>
<td>Seeds and parts of capsules</td>
<td>3</td>
</tr>
<tr>
<td>Grasses</td>
<td>Leaves and stems cut in</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>5-10 mm lengths</td>
<td></td>
</tr>
<tr>
<td>Lycopersicon</td>
<td>Whole fruits, pulp, seeds and</td>
<td>7</td>
</tr>
<tr>
<td>esculentum</td>
<td>skins</td>
<td></td>
</tr>
<tr>
<td>Portulaca</td>
<td>Seeds</td>
<td>trace</td>
</tr>
<tr>
<td>oleracea</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>100</td>
</tr>
</tbody>
</table>

TABLE 3
Food Items in Stomach and Rectal Pellets of Seven Rabbits with Good Dental Occlusion, from Manana Island, Hawaii

<table>
<thead>
<tr>
<th>ANIMAL NO.</th>
<th>FOODS IDENTIFIED</th>
</tr>
</thead>
<tbody>
<tr>
<td>2754</td>
<td>Grass stems and leaves</td>
</tr>
<tr>
<td>2755</td>
<td>Grass fragments; Portulaca oleracea leaves</td>
</tr>
<tr>
<td>2756</td>
<td>Grass fragments; P. oleracea leaves; Lycopersicon esculentum leaves</td>
</tr>
<tr>
<td>2757</td>
<td>Grass fragments; Nicotiana tabacum seeds; Atriplex semibaccata fruits</td>
</tr>
<tr>
<td>2758</td>
<td>Grass fragments; L. esculentum leaves</td>
</tr>
<tr>
<td>2760</td>
<td>Grass fragments; N. tabacum seeds; P. oleracea seeds</td>
</tr>
<tr>
<td>2761</td>
<td>Grass fragments; P. oleracea leaves</td>
</tr>
</tbody>
</table>

made. This is in contrast with rabbit 2759, in which grasses comprised only 15% of the stomach contents on a volumetric basis. There seem to be at least two explanations for these differences. Animal 2759 may have had different food preferences because of the poor condition of his teeth, or may have eaten less grass than the other animals because of his possibly restricted range on the outer slope of the island. He appeared undernourished but not thin; prepared skeletal parts were fat-free compared to those of six other rabbits, and in flexing the thawing body for skinning, two legs were broken under little pressure. This was the oldest rabbit examined and probably an outcast who never ventured onto the main crater floor. Mykytowycz (1964) reports well-defined territoriality in the wild rabbit as well as a social hierarchy among males. On the other hand, grasses have many thick-walled lignified cells which are not digested readily, and are more likely to pass through the intestinal tract than such thin-walled unlignified materials as tomato fruits and tobacco flowers. Rabbit 2759 was able to digest little of its poorly chewed food, for the rectal pellets contained seeds of salt bush, tomato, tobacco, and purslane, as well as large pieces of grass stems, tobacco capsules, and tomato skins—virtually all the items eaten, except for tomato fruit pulp and tobacco flowers. Rabbits with good occlusion have reasonably complete digestion of many food materials other than grass fragments, so that recovered materials are often mostly grass fiber. Perhaps a combination of differences in local availability of foods and inefficiency of their use account for the differences in food residues between rabbit 2759 and the others. Animal 2757, a female, was the only other rabbit in which salt bush was identified. She was the other member of the 33- to 38-months age class.

Most fragments of grass could not be identified as to genus, but those which could be identified proved to be either Cenchrus or Triebachne. These were the two most common species on Manana at the time of the study, and unless there is great preferential feeding by the rabbits, one would expect them to occur most commonly in the food materials sampled.

Munro (1950) reported that rabbits on Manana were eating roots of Boerhavia tetrandra (= diffusa). This plant has a large fleshy taproot which is a good source of food, but no identifiable fragments of it were recovered from the rabbits we studied. However, such material probably would be digested readily and would be difficult to detect. Rabbits had gnawed the bark from some erect woody stems of Nicotiana tabacum and had also scratched the soil from some of the plants, barring the roots which were then gnawed (Fig. 6).

Aside from Atriplex semibaccata, which grew only on the lower, outer slopes of the main
crater, all foods identified from each rabbit examined were available to rabbits living in any of the vegetated parts of the island. However, there are differences in abundance of the food plants; for example, *Trichache insularis* is very common within the crater, but uncommon on the outer slopes. We suspect that the rabbit population is more concentrated in the heavily vegetated main crater than in any other part of the island, and that individually the rabbits may be quite localized. Shifts in range, with the rise and recession of forage plants and of number of rabbits, are quite likely.

*Mus musculus*

The house mouse, *Mus musculus* L., is the only other mammal on Manana. Rats are not now present and never have been reported. Mice possibly have inhabited the island longer than rabbits, through early accidental introduction by Hawaiians. Tinker (1938) was apparently the first to report *Mus* on Manana, but he offers no detailed information. Richardson and Fisher (1950) briefly discuss this species.

On February 29—March 1, 1964, we found mice commonly active in late afternoon and at night along the beach, on the slopes above the beach, and in the main crater. Fifteen traps set overnight caught three mice, and three others were caught easily by hand at dusk and at night. Mice seen in full daylight early in the morning were noticeably wary.

One mouse was a juvenile weighing 5.4 g; the others were adult. A male weighed 20.0 g, and three females were 22.4, 18.2, and 17.3 g, for a mean weight of 19.3 g (the fifth adult was partly eaten by ants). These are remarkably large mice for Hawaii. For example, on the island of Hawaii adults range generally from 9 to 14 g, and seldom reach 17 g (Tomich, unpublished). A parallel case is reported by Berry (1964) in Scotland.

Reproductive data on the mice from Manana were as follows. The male was in breeding condition, three females were lactating and one female was parous-inactive. One had just borne a litter, as was shown by six prominent uterine scars; another was in estrus. From this small series, it appears that reproduction was at a high level in a mature population, and that weanling offspring were just appearing above ground. Two museum specimens were preserved.

The stomach contents of six mice were examined but identification of foods was difficult. Because of thorough mastication and digestion, very few recognizable fragments remained (Table 4). It was not possible to estimate relative volumes of different foods consumed, nor to compile a list of all materials used by the mice. We conclude, however, that the mice tend to subsist on foods such as seeds, fruits, and insects rather than coarse bulky stems or leaves.

**ECTOPARASITES**

Parasites of isolated animal populations are expected to be few in number of species be-
TABLE 4
FOOD ITEMS IN STOMACHS OF SIX MICE FROM MANANA ISLAND, HAWAII

<table>
<thead>
<tr>
<th>ANIMAL NO.</th>
<th>FOODS IDENTIFIED</th>
</tr>
</thead>
<tbody>
<tr>
<td>2746</td>
<td><em>Nicotiana tabacum</em> seeds</td>
</tr>
<tr>
<td>2747</td>
<td>Grass stems, leaves, and fruits; insect fragments</td>
</tr>
<tr>
<td>2748</td>
<td><em>N. tabacum</em> seeds; grass fruits</td>
</tr>
<tr>
<td>2749</td>
<td><em>Atriplex semibaccata</em> fruits and bracts; anthers of grass flowers</td>
</tr>
<tr>
<td>2750</td>
<td><em>N. tabacum</em> seeds</td>
</tr>
<tr>
<td>2751</td>
<td><em>N. tabacum</em> seeds</td>
</tr>
</tbody>
</table>

cause host chains are often incomplete and the colonizing stock may have been relatively parasite-free. In spite of these limitations, remarkable adaptations may occur if a parasitic species is pressed for survival. Such adaptations are found among the ectoparasites of birds and mammals on Manana. A total of 13 species are recorded, with two collections of Mallophaga from birds identified only as to genus. Of these, 6 species are primarily parasites of mammals and 7 are primarily parasites of birds. The ectoparasites of mammals are much better known than those of birds because the two species of mammals have been examined more thoroughly than the numerous species of birds.

DIPTERA
HIPPOPOTRICIDAE

*Olfersia aenesens* C. G. Thomson
6 ♀ ♀, ex *Anocephalus stolidus* and/or *Sterna fascata*, July 17, 1963
1 ♀, ex *Oryctolagus cuniculus*, Feb. 29, 1964

This hippoboscid is a common parasite of oceanic birds of the families Phaethontidae and Sulidae (Pelecaniformes) and Laridae (Charadriiformes). There are previous records of this species from Manana, and the specimen reported by Bryan (1935) as *Olfersia spinifera* was reidentified as *O. aenesens* by Maa (1962). During the summer months when large numbers of sea birds are nesting on the island, this species can be seen flying about and may be caught easily by sweeping with an insect net.

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The specimen collected from a rabbit is certainly an example of straggling which probably resulted from the close association of rabbits and birds on the island. The fate of adult flies during the winter months when sea birds are absent from the island is unknown.

SIPHONAPTERA
PULICIDAE

*Pteolepides felis felis* (Bouché)
3 ♂ ♂, 2 ♀ ♀, ex *Oryctolagus cuniculus*, Aug. 31, 1961
80 ♂ ♂, 114 ♀ ♂, ex *Oryctolagus cuniculus*, Feb. 29, 1964
*C. f. felis* seldom has been reported from *O. cuniculus*, and the only records of which we are aware are those of Cable (1943), Seddon (1947), Hopkins and Rothschild (1953), Mykytowycz (1957), and Smit (1957). The last author lists the occurrence on *O. cuniculus* in England as accidental. Mead-Briggs (1961; 1963) examined over 53,000 fleas collected from rabbits in England without finding *C. f. felis*.

Of the 13 rabbits collected on Manana, 8 were examined for ectoparasites. Conditions were such that it was impossible to collect all of the fleas seen and it is estimated that only about one-third of those on the 8 animals were collected. Cat fleas were very common on the body but were found only rarely on the head of the rabbits. The greatest concentrations were on the back of the neck.

The finding of large numbers of cat fleas on rabbits on Manana indicates this species is capable of maintaining itself on this host under certain conditions. This is the first recorded instance of a naturally occurring population of *C. f. felis* on feral *O. cuniculus*. The flea could have been introduced to Manana on the rabbits or at various times by dogs or cats brought ashore by fishermen.

The *C. f. felis* from Manana might be a suitable strain for laboratory culture inasmuch as its host, the rabbit, is more convenient to maintain than other hosts. Dogs or cats have been used (Smith and Eddy, 1954; Hudson and Prince, 1958) but necessitate more care and space than would rabbits. Attempts have been made to rear cat fleas on laboratory and wild
rats and mice; however, none has been successful (Elbel, 1951; Wang, 1960; Kir' yakova, 1961; Haas, 1966).

**Echidnophaga gallinacea** (Westwood)

1 ♂, 35 ♀, ex *Oryctolagus cuniculus*, Aug. 31, 1961

94 ♂ ♀, 289 ♀, ex *Oryctolagus cuniculus*, Feb. 29, 1964

The stick-tight flea has been reported previously from *O. cuniculus* in Australia (Seddon, 1947; Hopkins and Rothschild, 1953; Mykytowycz, 1957). On Manana this flea was found in clusters of 10–12 on the upper eyelids of some rabbits and singly inside the ears of others. Most of the fleas came from the heads of freshly shot rabbits.

*Austromenopon paululum* (Kellogg and Chapman) sens. lat.

1 ♀, ex *Puffinus nativitatis*, July 17, 1963

**Austromenopon sp.**

2 ♀, 1 N, ex *Sterna fasciata*, July 17, 1963

**Austromenopon sp.**

4 ♀, 1 N, ex *Anous stolidus*, July 17, 1963

**Philopteridae**

**Quadriceps birostris** (Giebel)

1 ♂, 3 ♀, ex *Sterna fasciata*, July 17, 1963

**Trabeculus hexacon** (Waterson) sens. lat.

1 ♂, ex *Puffinus nativitatis*, July 17, 1963

Mallophaga spend their entire lives on the host, and their geographic distribution generally coincides with that of the host. For this reason factors limiting the distribution of other ectoparasites seldom are important to the Mallophaga.

*Q. birostris* has been reported under the name *Nirmus gloriosus* from Laysan in the Hawaiian chain (Kellogg and Paine, 1910).

**Metastigmata**

**Argasidae**

**Ornithodoros capensis** Neumann

7 ♂ ♀, 2 ♂, from under rocks, Mar. 30, 1963

*O. capensis* is confined to sea birds and has a world-wide distribution. Studies have revealed *O. capensis* to be a complex of two species which are identifiable with certainty only in the larval stage (Kohls et al., 1965). The above record is considered in the broad sense of the species.

Kohls et al. (1965) recently listed one larva of this species from Manana. This was collected from *Anous stolidus* on November 24, 1946 by L. Kartman. It and the following species were among the specimens Kohls (1957) listed as "off terns on islands near Oahu . . ." (Kohls, personal communication).
Ornithodoros denmarki Kohls, Sonenshine and Clifford

This species is listed from Manana on the basis of two larvae recorded by Kohls et al. (1965) with the same data as the one larva listed for O. capensis.

A new virus has been found recently in this species, giving it added importance as a potential disease vector (Hughes et al., 1964; Philip, 1965).

PROSTIGMATA
CHEYLETIDAE

Cheyletiella parasitivorax (Mégnin)
1 ♂, ex Oryctolagus cuniculus, Feb. 29, 1964

C. parasitivorax is found on leporids throughout the world and has been reported from this host in the wild. According to some authorities this mite is a predator on Listrophoridae rather than a parasite of the rabbit. It was not known from Hawaii prior to its discovery on Manana.

ASTIGMATA
LISTROPHORIDAE

Listrophorus gibbus Pagenstecher
1 ♂, 13 ♀♀, 3 NN, ex Oryctolagus cuniculus, Feb. 29, 1964

This species is a common parasite of both wild and domestic O. cuniculus and has been reported from many parts of the world. This is the first record of its occurrence in Hawaii.

Listrophorus musculus Wilson and Lawrence
3 ♂♂, 10 ♀♀, 1 N, ex Mus musculus, Feb. 29–Mar. 1, 1964

Hawaii is the only known locality for this fur mite. It is remarkable that an animal so common and widespread as the house mouse, and probably examined as frequently as any other rodent for ectoparasites, should be host to such a restricted and, until recently, undescribed mite. It is very common on Mus in Hawaii and has been reported from Honolulu, Oahu and Honokaa and Kukuihaele, Hawaii (Joyce, 1959; Wilson and Lawrence, 1967).

PSOROPTIDAE

Myocoptes musculus (Koch)
4 ♂♂, 14 ♀♀, ex Mus musculus, Feb. 29–Mar. 1, 1964

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M. musculus is a common parasite of wild and laboratory mice throughout the world and has been reported from Hawaii by Joyce (1957). It is more abundant on mice on Manana than the few specimens indicate; however, because of its small size and the condition of the hosts when examined it was difficult to estimate the degree of infestation.

ENDOPARASITES

While no endoparasites were identified specifically from 2 rabbits examined in August 1961, or from 13 in February 1964, it seems desirable to report the procedures used and findings made. Cursory examination of viscera revealed no nematodes, trematodes, or cestodes. Rectal pellets preserved in alcohol, and dry fecal pellets collected from the ground, proved unsatisfactory for the determination of coccidial oocysts or helminth ova. Distorted cyst-like objects were present and additional effort should be made to identify them from new material. Rectal or freshly defecated pellets exposed to air for three days before fixation in dilute formalin (but kept damp to allow sporulation of coccidia), should provide suitable study samples. Sieving and microscopic search of intestinal contents, and similar critical examination of the blood, gall bladder, liver, and other organs, is recommended for a complete appraisal of rabbit endoparasites. There are several definitive studies of the internal parasites of the European rabbit (Bull, 1958; 1960; 1964) which can be applied directly to the situation on Manana.

The 6 mice likewise were negative for endoparasites and further attention should be paid to this species.

DISCUSSION

It is of primary significance that the sea birds, rabbits, and vegetation of Manana have reached an obvious degree of mutual ecological adjustment. The unknown original vegetation undoubtedly suffered greatly soon after it was exposed to rabbits, and events in its change to the present complex may have unfolded as follows. The large rabbit population present at the time of the brief early record of Manana (Anon., 1901) probably existed at most about
10–15 years after establishment of rabbits. This great number of animals almost certainly was generated and sustained by an original reserve of woody shrubs and creepers, and other plants. Such species as *Scaevola taccada* and *Ipomoea pes-caprae* that are common on similar offshore islets (e.g., Mokulua) reasonably could be expected to have occurred on Manana. Their absence from the more than 35-year record of plants on Manana may well be a result of their extermination and subsequent exclusion by rabbits. Parallel conditions of depletion have been observed on Laysan and Lisianski (Watson, 1961). Perhaps on Manana the pattern of destruction was modified and prolonged by a heavy bag of rabbits taken periodically for meat, annual seasonal recovery of the vegetation, and a series of unusually wet years. Whatever the details, the result is what we see today, a reasonable equilibrium between a low to moderately dense rabbit population and vegetation composed predominantly of hardy introduced grasses and forbs.

Rainfall at Makapuu Point, Oahu, 2.4 km from Manana, averages 597 mm per year (U.S. Weather Bureau, 1964), close to the 635 mm estimated for the open ocean in this region (Blumenstock, 1961), and is therefore useful as a reference to precipitation on Manana. Of the annual rainfall 77% falls between October and March, and so the April-to-September period is typically arid. Watson (1961) has suggested that on islands with rainfall regimes such as this, periodic (normally annual) droughts result in a drastic reduction of the rabbit population, which enables the vegetation to, "recover sufficiently to survive." The present annual cycle seems to be as follows. During the dry season (summer) the vegetation dies back, and the rabbit population declines considerably. Seeds have been produced and are present on the ground. When the rainy season begins (early winter), the seeds germinate, seedlings become established, and regrowth of perennials occurs before the rabbit population increases. In the winter an adequate food supply is available, but onset of the next dry season results in a return to conditions of food shortage and decline in numbers of rabbits. Drought, accompanied by recession of the vegetation, may be the strongest limiting factor for this population. However, the European rabbit does not need free water to drink and by remaining deep in its burrows in the heat of the day it minimizes transpiration loss. In pen experiments on water deprivation, rigid selection occurs, but a few rabbits survive (Hayward, 1961). The strain on Manana may have faced drastic drought conditions several times in the long period of its adaptation and may be capable of behavior resembling estivation.

In the three wet seasons of October to March, from 1961 through 1964, rainfall was normal or above normal. There were no winter droughts. These conditions support the likelihood of the results that there was a regular November-to-April breeding season during these three years as derived from age classification of 12 rabbits collected in 1964. The driest period was June through September 1963 when only 38 mm of rain fell (half of the normal for these months), and the wettest was in March through May 1963 when 866 mm fell (five times normal). Because of the rapid percolation of water through volcanic soils and the high rate of evaporation at the latitude of Hawaii, repeated moderate rains are ideal for normal growth of most plants on Manana. Distribution of rainfall in time, therefore, may be more important than total precipitation for any year.

In addition to their effective control of the vegetation by grazing, rabbits are capable of contributing to seed dispersal. Several animals had plant reproductive structures entangled in their pelage. Thorough combing of one skin yielded many spikelets with subtending bristles from *Setaria verticillata*, some spikelets of *Cenchrus echinatus*, and one spikelet of *Chloris inflata*. Rabbits must disseminate plants from one part of the island to another, but, because of the small area, other means of transport also could account for the fairly uniform distribution of plant species.

Because our study has been limited to a review of the scanty history of conditions on Manana, brief sampling of the present flora and fauna, and interpretations of the few data available to us, we are not in a position to make a final judgment on what management practices should be adopted. It is apparent immediately, however, that Manana does support a great many nesting oceanic birds each year in the presence of rabbits. We concur with Richardson and Fisher (1950) that bird-rabbit
relationships do not seem particularly significant, but we hasten to add that this may be because they have never been probed deeply. For instance, it is conceivable that the rabbits affect the vegetation in such a way that favorable conditions for nesting by certain birds are maintained. Nesting colonies of Sooty Terns, which one of us (Lamoureux) has observed on several of the Leeward Hawaiian Islands, tend to be in more open areas covered with grasses and low herbs, rather than in areas covered with shrubs. It is quite possible that the presence of the rabbit on Manana contributes to the relative scarcity of shrubs there. In turn, the selective development of the rabbit strain on Manana may have been guided by a vegetation richly fertilized with bird guano, infusing in it a vitality sufficient to permit at least a bare survival of the rabbits in times of crisis. Without question, the ecology of birds, rabbits, and vegetation on Manana is complex, and very likely there are key interdependencies not realized at this time.

A decision now to eliminate rabbits because of some presumed interference with nesting of birds would be premature. We recommend, instead, an intensive program of ecological study to embrace particularly birds, rabbits, and vegetation. Because of the unique relationships observed between some species of ectoparasites and birds and mammals, careful attention should be paid to all of the fauna. The following immediate suggestions are made for projects that would lead gradually to an understanding of the island's more prominent ecological relationships.

1. Construction of a 20 × 50 m (open) and several 2 × 2 m (covered) exclosures to test the responses of vegetation in the absence of rabbits and the presence of birds only, and in the absence of both.

2. Establishment of permanent vegetation transect points and periodic recording of vegetation changes by photographic and other means.

3. Monthly or quarterly population estimates of birds, rabbits, and mice, with particular regard to season of year and condition of vegetation. The mark and release of trapped mammals would allow access to information on age composition, nutritional condition, reproductive cycles, and ectoparasite infestation of the populations.

4. Behavioral studies of rabbits and birds, with particular attention to social relationships of rabbits to surface- and burrow-nesting birds.

5. Study of energy relationships to determine the degree of dependence of the vegetation, and hence the rabbits, upon bird guano as a primary nutritive source.

The possible importance of the rabbit strain on Manana as an experimental animal in particular problems of medical or biological research should not be overlooked (Thomsen and Evans, 1964), and a thorough study of the population as it is related to other populations of the species in Hawaii and in the world is a need of special significance.

Further intentional introduction to Manana of organisms of any sort in the near future is not recommended. Ecological studies should be carried out with as little disturbance as possible of the present biota. The ecosystem on Manana has much scientific potential in its present condition and is within easy reach of the intellectual center of the state. This value will increase in time and in proportion to the effort made to understand and interpret this singular Hawaiian resource.

**ACKNOWLEDGMENTS**

The authors are particularly indebted to Dr. Kazimierz Wodzicki, former Director of the Ecology Section, D.S.I.R., New Zealand, for his sustained interest in the rabbits of Manana, for encouraging the present project, and for advice and assistance during the 1964 visit to the island. David H. Woodside arranged the trip, skillfully directed our landing and departure in rough weather, and gave us much assistance from his extensive knowledge of Hawaiian fauna. Ronald L. Walker and William J. Voss rendered valuable aid during the expedition. Dr. Theresa Clay and Dr. C. M. Clifford identified the Mallophaga and Metastigmata, respectively, and P. C. Bull provided advice and services in the search for internal parasites of rabbits. Dr. R. W. Strandmann visited Manana in March 1963 and collected ectoparasites, the records of which he placed at our disposal.
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The Determination of a Series of Ages of Hawaiian Volcanoes by the Potassium-Argon Method

JOHN G. FUNKHOUSE, I. LINUS BARNES, AND JOHN J. NAUGHTON

Geologically speaking, the Hawaiian Islands are perhaps the most thoroughly studied group of oceanic islands in the world. Because of their relative petrological and structural simplicity, they constitute an example where an intensive application of the techniques of geology and geophysics may be expected to yield significant results particularly relevant to volcanology. An example of a thorough effort of this type was reported by McDougall (1964) who measured the relative ages of the surface lavas of most of the older volcanoes of the islands using the potassium-argon method of geochronology. We would like to report additional age measurements obtained by the same method, with a concentration of our effort on the Waianae Volcano on the island of Oahu. A scattering of measurements made on samples from other sites also is tabulated.

METHODS AND RESULTS

The argon measurement equipment and techniques developed by the Berkeley group (Everden and Curtis, 1965) were employed in the work. Ultrahigh vacuum methods were necessary for measurements on these young materials of relatively low potassium content. Potassium was analyzed by flame photometry.

The results of the potassium-argon age work on Hawaiian extrusive rocks are given in Table 1. The over-all precision of the ages reported herein is estimated to be approximately 11% (standard deviation). The uncertainty for each age is based on the experimental errors and the effect of the correction necessary for air argon contamination.

The ages of the different members of the Waianae Range are in general agreement with those of McDougall (1964). However, this investigator reported an age of 8.36 my for a biotite fraction separated from the Mauna Kuwale rhyodacite. This age appears to be abnormally high in view of the present work which indicates that Mauna Kuwale is contemporaneous with the upper member of the Waianae volcanic series. A possible cause of this discordance relating to included excess radiogenic argon has been discussed elsewhere (Funkhouser, Barnes, and Naughton, 1966).

DISCUSSION

The results obtained from HK-123, a vesicular olivine basalt classified as Lower Waianae, are clearly anomalous. The high degree of air argon contamination for this specimen contributes to the large uncertainty; however, this does not fully explain the wide variation in the results. Thin-section examination as well as microscopic inspection of hand samples and granular fractions indicated no abnormal mineral components or alteration products. The basalt contains a large number of very small vesicles which probably contain entrapped air. This is substantiated by the lower air argon correction for HK-123-3 which was ground to 100-180 mesh while the other two samples were analyzed as 10-16 mesh fractions. Of course, this sample could be 7-12 my old, but there is no confirmation from geological field evidence or other potassium-argon dates. The ages obtained for HK-142, a Lower Waianae olivine basalt, also show a range greater than that predicted from experimental uncertainties and the atmospheric argon correction.

1 Chemistry Department and Hawaii Institute of Geophysics, Hawaii Institute of Geophysics Contribution No. 221. This work was supported by the National Science Foundation under grant NSF GP-140. Manuscript received September 5, 1967.
2 Present address: Earth Science Department, State University of New York at Stony Brook, Stony Brook, New York.
3 Present address: B28 Physics Building, National Bureau of Standards, Washington, D.C.
### TABLE 1

**Potassium-Argon Ages of Hawaiian Extrusive Rocks**

<table>
<thead>
<tr>
<th>Sample, Rock Type or Mineral, and Location</th>
<th>K, %</th>
<th>Ar(^{40}) (Radiogenic), cc/gm \times 10^{-7}</th>
<th>Ar(^{40}) (Air), % of Total Ar</th>
<th>Age \times 10^6 yrs</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Upper Waianae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HK-121. Mauna Kuwale rhyodacite (average of 11 determinations of minerals and whole rock)</td>
<td>1.32–6.03</td>
<td>1.32–10.5</td>
<td>75–89</td>
<td>2.3 ± 0.4</td>
</tr>
<tr>
<td>HK-119-1. Dike through HK-121</td>
<td>1.43</td>
<td>1.71</td>
<td>49</td>
<td>3.3 ± 0.2</td>
</tr>
<tr>
<td>HK-119-2. Dike through HK-121</td>
<td>1.43</td>
<td>1.90</td>
<td>50</td>
<td>3.0 ± 0.2</td>
</tr>
<tr>
<td>HK-143-1. Feldspar from flow overlying HK-121</td>
<td>0.206</td>
<td>0.348</td>
<td>91</td>
<td>4.3 ± 1.1</td>
</tr>
<tr>
<td>HK-122-3. Flow underlying HK-121</td>
<td>0.885</td>
<td>0.810</td>
<td>88</td>
<td>2.3 ± 0.5</td>
</tr>
<tr>
<td>HK-122-4. Flow underlying HK-121</td>
<td>0.885</td>
<td>1.081</td>
<td>84</td>
<td>3.1 ± 0.5</td>
</tr>
<tr>
<td>HK-122-5. Flow underlying HK-121. Calcite removed</td>
<td>0.911</td>
<td>0.838</td>
<td>91</td>
<td>2.3 ± 0.6</td>
</tr>
<tr>
<td>HK-124-1. Whole rock</td>
<td>1.07</td>
<td>1.22</td>
<td>38</td>
<td>2.9 ± 0.1</td>
</tr>
<tr>
<td>HK-126-1. Feldspar</td>
<td>0.272</td>
<td>0.235</td>
<td>80</td>
<td>2.2 ± 0.2</td>
</tr>
<tr>
<td>HK-126-2. Whole rock less feldspar</td>
<td>0.970</td>
<td>1.019</td>
<td>87</td>
<td>2.7 ± 0.1</td>
</tr>
<tr>
<td>HK-132-1. Feldspar</td>
<td>0.238</td>
<td>0.207</td>
<td>65</td>
<td>2.2 ± 0.1</td>
</tr>
<tr>
<td>HK-132-2. Whole rock</td>
<td>0.697</td>
<td>0.717</td>
<td>42</td>
<td>2.6 ± 0.1</td>
</tr>
<tr>
<td>B-1. Whole rock</td>
<td>1.02</td>
<td>1.12</td>
<td>47</td>
<td>2.8 ± 0.1</td>
</tr>
<tr>
<td><strong>Middle Waianae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HK-145-1. Whole rock</td>
<td>0.512</td>
<td>0.735</td>
<td>80</td>
<td>3.7 ± 0.4</td>
</tr>
<tr>
<td>HK-145-2. Whole rock</td>
<td>0.512</td>
<td>0.712</td>
<td>77</td>
<td>3.5 ± 0.3</td>
</tr>
<tr>
<td>HK-146-1. Whole rock</td>
<td>1.11</td>
<td>1.33</td>
<td>39</td>
<td>3.0 ± 0.1</td>
</tr>
<tr>
<td>HK-146-2. Whole rock</td>
<td>1.11</td>
<td>1.26</td>
<td>39</td>
<td>2.9 ± 0.1</td>
</tr>
<tr>
<td><strong>Lower Waianae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HK-123-1. Whole rock</td>
<td>0.441</td>
<td>2.82</td>
<td>97</td>
<td>16.1 ± 13.6</td>
</tr>
<tr>
<td>HK-123-2. Whole rock</td>
<td>0.441</td>
<td>1.09</td>
<td>98</td>
<td>6.2 ± 6.2</td>
</tr>
<tr>
<td>HK-123-3. Whole rock. Fine powder. Zeolite removed</td>
<td>0.435</td>
<td>1.94</td>
<td>93</td>
<td>11.2 ± 3.9</td>
</tr>
<tr>
<td>HK-142-1. Whole rock</td>
<td>0.209</td>
<td>0.360</td>
<td>83</td>
<td>4.3 ± 0.6</td>
</tr>
<tr>
<td>HK-142-2. Whole rock</td>
<td>0.209</td>
<td>0.409</td>
<td>82</td>
<td>4.9 ± 0.6</td>
</tr>
<tr>
<td>HK-142-4. Whole rock. Treated with HF</td>
<td>0.264</td>
<td>0.332</td>
<td>83</td>
<td>3.2 ± 0.4</td>
</tr>
<tr>
<td>HK-144-1. Ewa drill core. Whole rock</td>
<td>0.522</td>
<td>0.820</td>
<td>88</td>
<td>4.0 ± 0.8</td>
</tr>
<tr>
<td>HK-144-2. Ewa drill core. Whole rock</td>
<td>0.522</td>
<td>0.722</td>
<td>90</td>
<td>3.5 ± 0.8</td>
</tr>
<tr>
<td>B-2. Whole rock</td>
<td>0.70</td>
<td>1.49</td>
<td>45</td>
<td>5.4 ± 0.3</td>
</tr>
<tr>
<td><strong>Samples from other Hawaiian Sites</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HK-127-1. Whole rock. Nihoa Island</td>
<td>0.416</td>
<td>1.25</td>
<td>56</td>
<td>7.5 ± 0.4</td>
</tr>
<tr>
<td>HK-107-1. Whole rock. Necker Island</td>
<td>1.04</td>
<td>4.66</td>
<td>57</td>
<td>11.3 ± 0.6</td>
</tr>
<tr>
<td>B-3. Whole rock nepheline basalt. Moilili, Oahu</td>
<td>1.02</td>
<td>0.35</td>
<td>88</td>
<td>0.9 ± 0.5</td>
</tr>
<tr>
<td>B-5. Dike edge. Glass. Koolau Volcano, Oahu</td>
<td>1.52</td>
<td>1.79</td>
<td>76</td>
<td>2.2 ± 0.3</td>
</tr>
<tr>
<td>B-4. Whole rock. Trachyte. Puuwaawaa, Hawaii</td>
<td>4.18</td>
<td>0.64</td>
<td>79</td>
<td>0.4 ± 0.3</td>
</tr>
<tr>
<td>B-5. Whole rock hawaiite. Laupahoehoe, Mauna Kea, Hawaii</td>
<td>1.89</td>
<td>0.43</td>
<td>73</td>
<td>0.6 ± 0.3</td>
</tr>
<tr>
<td>B-6. Phlogopite mica from B-5</td>
<td>5.50</td>
<td>6.34</td>
<td>44</td>
<td>2.8 ± 0.1</td>
</tr>
</tbody>
</table>

* Samples prefixed by "B" were analysed at Brookhaven National Laboratory, New York, and previously reported as an abstract (Naughton and Schaeffer, 1962).
The basaltic dike (HK-119) cutting through the rhyodacite (HK-121) yields a high age relative to its host formation. The low air argon contamination in this specimen precludes any convenient overlap of ages within experimental error. The single determination on the feldspar (HK-143) from the flow overlying the rhyodacite should also be less than 2.3 ± 0.4 my. The feldspar phenocrysts were handpicked from a weathered specimen and treated with hydrofluoric acid to remove the more easily soluble altered layers. Microscopic examination of these indicated pure plagioclase crystals with no alteration or contamination evident. The high atmospheric argon correction creates a large potential uncertainty in the 4.3 my date, and it is possible that an even greater error than acknowledged exists due to alteration not revealed by examination. It is also possible that these samples (HK-119 and HK-143) contain an excess of radiogenic argon. Damon, Laughlin, and Percious (1967) noted 0.56 × 10^−7 std. cc/g excess argon in large plagioclase phenocrysts from a very young basalt, and 2.3 × 10^−7 std. cc/g excess argon from the chilled border of a young basaltic dike. It is believed that the discordance in age shown between whole-rock sample B-7 and its constituent mica, B-8, is an example of mica giving an anomalously older age due to excess radiogenic argon present in inclusions, as in the samples from the Mauna Kuwale rhyodacite noted above.

HK-144, a sample from a core taken from the 1081-foot level of the Ewa I drill hole at Barber’s Point, Oahu, is listed as a Lower Waianae sample, although H. T. Stearns has stated, on topographic grounds, that it might come from a flow from Koolau Volcano, the other major volcano of the island of Oahu. The variability in the degree of air argon contamination among the different samples is worth noting. Bake-out temperatures and time cannot be correlated with the quantity of air argon in each sample. A relatively large amount of air argon was present in the apparatus during the initial gas extractions but any corrections for this would lower the atmospheric correction of HK-121 (whole rock) to a minimum of approximately 80%. In general, certain minerals have been found to hold inherently less air than others. This phenomenon apparently holds true for different whole-rock samples as well, and is probably related to the degree of microvesiculation of the basalts. The differences between feldspar separates and whole-rock samples is mostly attributable to the residual air argon in the extraction system which would predominate when smaller total quantities of radiogenic argon are released.

The two specimens in which feldspar and whole-rock ages can be compared indicate a possible loss of radiogenic argon from the plagioclase, yet Evernden and James (1964), and Livingston, Damon, Manger, Bennett, and Laughlin (1965) have reported that volcanic feldspars are quite retentive, especially for young rocks. It is most probable that during the 23–28 hours of bake-out at 210°–240°C some of the radiogenic argon was lost by diffusion, or that the lower ages are coincidental and result from experimental error.

Nihoa (Bird) Island is approximately 150 miles west-northwest of Kauai while Necker Island is about 180 miles beyond Nihoa. The ages of 7.5 my and 11.3 my, respectively, for these island remnants are not surprising considering the progression of age of the islands (McDougall, 1964).

The paucity of data and the uncertainty in the age determinations preclude any generalizations regarding the duration of island growth or volcanism except to note that volcanic activity of the Waianae Volcano appears to have spanned well over two million years.

REFERENCES


A Geological and Ecological Reconnaissance off Western Oahu, Hawaii, Principally by Means of the Research Submarine "Asherah"\textsuperscript{1}

Vernon E. Brock and Theodore C. Chamberlain\textsuperscript{2}

ABSTRACT: In November 1965 a combined geological and ecological reconnaissance of the sea floor off western Oahu was undertaken using a variety of methods and techniques to maximize both the range and reliability of the information obtained. Bottom topography and fish concentrations were surveyed with a precision echo sound recorder for which the transducer was towed in a streamlined housing below the research ship. Photographic bottom surveys were also made with an automatic stereo-camera system, and some bottom dredging and trawling were undertaken to secure samples of the bottom and the biota. Direct visual observations were also made using a small research submarine largely in the depth range of 25–180 meters.

The dominant geological features were a series of submerged, wave cut, largely sand covered terraces separated by rocky escarpments. The major terraces were an upper one terminating seaward at approximately 60 meters, an intermediate one from 70 to 120 meters, and a deep one beginning from a shoreward depth of 180 meters or deeper.

Patterns of littoral sand movement were observed to be southerly in the region between Kaena Point and Kepuhi Point with a substantial movement offshore. It was estimated that approximately 10,000 cubic yards of calcareous sand move seaward and are deposited annually on the inner portions of the deep terrace.

Associated with the escarpments were large and discontinuous aggregations of fish and, on the upper and intermediate terraces, extensive beds of the clam Pinna muricata. The observed patterns of distributions may be a response to the localized accumulation of food. Organisms which make nocturnal vertical migrations in adjacent deep water may be swept shoreward by surface currents and become trapped on the terraces. The collection of planktonic organic material in the thermocline where the water increases rapidly in density with depth may be a mechanism for the localized accumulation of particulate food of value to the clams.

The simultaneous use of a variety of observational techniques in an area provided non-identical and independent observations of the same situations. This served to confirm the information obtained and to add new and significant detail.

During November of 1965 a reconnaissance of the sea floor geology and of the marine ecology off western Oahu, Hawaii was made using a remotely operated stereo-camera system, a precision echo sounding recorder, biologic and geologic dredges, and, most importantly, a two-man deep-diving research submersible vehicle.

Surface support was supplied by the University of Hawaii’s 90-ft research vessel, the "Teritu." The intent of the investigation was to make a series of direct observations of the geomorphology and the biota by means of the submersible vehicle and to correlate with these observations data collected at the same time and in the same area by means of conventional, indirect data-gathering techniques (submarine photography, biologic and geologic dredging, etc.). The experiments were successful: 15 deep dives were made with the research submarine, most to 180

\textsuperscript{1} Contribution 283, Hawaii Institute of Marine Biology. Manuscript received September 12, 1967.

\textsuperscript{2} Department of Oceanography, Hawaii Institute of Geophysics, University of Hawaii, Honolulu, Hawaii 96822.
meters; 500 black and white and an equal number of color photographs were taken, some from the remote surface controlled stereo-camera, some from the submarine; 20 bathymetric profiles were run normal to the coast by the "Teritu" and numerous geological and biological specimens were collected from the terraces and escarpments by the various dredges and trawls. The following report summarizes these data and compares their relative merits for geological and biological reconnaissance surveys.

AREA OF INVESTIGATION

The area of investigation was chosen mainly with the intent of selecting oceanographic and meteorologic conditions that would be optimum for handling a small, research submarine. Since the submarine diving operations necessitated surface towing of the vehicle, and since the replenishment of compressed air, recharging of the battery bank, and maintenance required moving alongside the mother ship, a leeward coast was necessary. Secondary requirements in the selection of the area of investigation were connected with the land-based logistical support of the entire operation over a 10-day period.

Because of the prevailing easterly tradewinds and the resulting near permanency of a lee coast along western Oahu, it was possible to meet the above requirements in an area of intensely interesting submarine features and a poorly known biota. Consequently a 14-kilometer length of coast along western Oahu, from Kaena Point to Kepuhi Point, was chosen for the reconnaissance (Figs. 1 and 2). This area provided ideal lee operating conditions during November; it was within 1/2 hour by boat from Pokai Bay, a replenishment harbor just to the south; it was a single isolated geological unit or cell in regard to the littoral circulation of sand; and

Fig. 1. Location chart.
it contained numerous, well developed submarine terraces and escarpments that could be correlated with the ancient anticyclonic circulatory pattern that dominates the North Pacific Ocean. Within a few hundred miles of the Hawaiian Islands the surface currents all set toward the western quadrant, generally with a drift of about 1/2 knot. As this large mass of water flows past the Hawaiian Islands it breaks up on the downstream side of the islands into large, semi-permanent eddies, some cyclonic and others anticyclonic. Superimposed upon these eddies, and in some cases completely dominating the surface circulations, are strong tidal currents.

About 10 miles off western Oahu the surface water appears to consistently move south, in conformation with the general flow of water from the east through the Kauai Channel, and join the circulation of an anticyclonic eddy about 20 miles in diameter located about 20 miles directly offshore at southwest Oahu (Latham, 1967). The velocity of the near-Oahu portion of this eddy was measured by Latham and found to be about 1/2 knot to the south.

Nearer shore the surface currents have been found to reverse themselves semi-diurnally in accordance with the tides. During flood tides there is generally a flow of water to the south just west of Kaena Point, and to the southeast, south of the point. These currents have been measured at about 1 1/2 knots (Latham, 1967). However, immediately adjacent to the coast, both north and south of Kaena Point, there is a persistent drift of water of 1-2 knots that follows the coastline to a convergence point some few miles west of Kaena Point. These northwest-setting currents are more intense during ebb tide and have been measured at a maximum of 5 knots (Laevastu et al., 1964).

During the diving operations with the "Asherali" a nearly constant set to the north and west was encountered. The drift of this current varied, but 1/2 knot was not uncommon even to depths of 180 meters.

WAVES: Wave energy reaching the western coast of Oahu can be approximately represented by four wave types related to predominant...
meteorological conditions within the Pacific Basin:

(1) *Kona Wind Waves*: Generated by local westerly storms; period 7 seconds, direction of approach SSW, height 2.4 meters, frequency of occurrence 9.5%, generally during the winter months.

(2) *North Pacific Swell*: Generated by the passage of low pressure areas across the Northern Pacific Basin; period 13 seconds, direction of approach NNW, height 3.4 meters, frequency of occurrence 89%, generally during the winter months.

(3) *Southern Hemisphere Swell*: Generated by low pressure areas in the Southern Hemisphere; period 15 seconds, direction of approach S, height 0.9 meters, frequency of occurrence 53%, entirely during the summer months.

(4) *Tradewind Waves*: Generated by the easterly tradewinds; period 8 seconds, direction of approach E and NE, height 2.4 meters, frequency of occurrence nearly 100% but, due to the sheltering effect of Oahu, of minor importance in the area of investigation.

The currents that lie within the breaker zone, and which are of prime importance in the alongshore transport of littoral sand, are dependent upon the wave regime and consequently vary greatly in direction and speed. Waves from the northwest quadrant (generally North Pacific Swell) create southeastwardly flowing currents; waves approaching from the southwest quadrant (generally Southern Hemisphere Swell and Kona Wind Waves) produce currents flowing toward the northwest. Current speeds vary from less than $\frac{1}{10}$ knot to about $\frac{1}{2}$ knot.

**Thermal Structure**: The island of Oahu centered at 21°30' north latitude is in tropical water with a permanent surface isothermal layer. The long term (1936–1956) average temperatures within a 250-mile radius of Oahu are given in Table 1, together with the range for depths from the surface to 2000 meters.

It will be noted from Table 1 that the greatest range in temperature occurs between 200 and 300 meters. These are the depths where the thermocline is ordinarily found. However, the thermocline fluctuates in depth depending upon

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**Table 1**

<table>
<thead>
<tr>
<th>Depth in Meters</th>
<th>Temperature (°C)</th>
<th>Temperature Range (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>24.6</td>
<td>2.2</td>
</tr>
<tr>
<td>50</td>
<td>24.1</td>
<td>2.5</td>
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<tr>
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<td>16.7</td>
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</tr>
<tr>
<td>300</td>
<td>12.4</td>
<td>3.7</td>
</tr>
<tr>
<td>500</td>
<td>8.2</td>
<td>2.7</td>
</tr>
<tr>
<td>800</td>
<td>4.8</td>
<td>0.6</td>
</tr>
<tr>
<td>1000</td>
<td>4.2</td>
<td>0.7</td>
</tr>
<tr>
<td>1500</td>
<td>2.8</td>
<td>0.2</td>
</tr>
<tr>
<td>2000</td>
<td>2.1</td>
<td>0.2</td>
</tr>
</tbody>
</table>

*From Dr. B. C. Heezen.*

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the stirring effects of the wind or lack thereof, and the depths through which it fluctuates will show a greater temperature range than depths above or below. A protected lee area such as the Waianae coast of Oahu, because of reduced strength of the prevailing tradewinds, may have a shallower mixed layer. During the “Asherah” dives in this area, the location of the thermocline was inferred by noting the depth at which both visual ranges were minimal and the greatest apparent concentration of particulate matter occurred. On this basis the thermocline was between 70 and 100 meters. No vertical temperature profiles were obtained at the time of the diving operations.

**Geologic**

The main Hawaiian islands lie toward the southeastern limit of the Hawaiian Ridge, a large, positive, geomorphic feature built up of shield-shaped basaltic domes along a 1,600-mile fissure in the north-central Pacific Ocean. Neither the age nor the geologic history of the Hawaiian Ridge is well known, but recent investigations have indicated a Tertiary age for most of the Ridge, with a developmental sequence starting in the northwest and proceeding to the southeast. The growth of the Ridge has been accompanied by large scale subsidence; superimposed upon this subsidence have been major Tertiary and Quaternary eustatic sea level fluctuations due to tectonic deformation of the Pacific Basin and intense
continental glaciation. The result of these positive and negative shifts of sea level has been the formation of numerous marine terraces, reef horizons, and beaches, now found at various positions from several thousands of feet below to several hundreds of feet above the present sea level.

Oahu, the center of population and site of the present investigations, is the third largest of the Hawaiian Islands with an area of 604 square miles. The island was built up above sea level by the emergence and coalescing of two large volcanoes, the Koolau Volcano on the east and the Waianae Volcano on the west. Today the remnants of these two volcanoes form the Koolau and Waianae mountain ranges respectively, between which lies the Schofield Plateau, a flat, low plateau consisting of alluvious and thinly-bedded lava flows. On the north and south flank of the island are wide coastal plains.

Along western Oahu, the geology is completely dominated by the deeply eroded remnants of the Waianae Volcano. The center of volcanic activity of this volcano was a caldera near Kolekole Pass at the head of Lualualei Valley. From this caldera and from the rift zones extending from it, large amounts of fluid lava were extruded over many millions of years. The older extrusions were thin, fluid, pahoehoe flows; the later flows were massive, adesitic aa.

The main extrusive activity of the Waianae Volcano terminated several millions of years ago; the cessation of major eruptions was followed by deep erosion of the volcano and later by a few secondary eruptions of small magnitude near the caldera. During the initial period of erosion the major valleys were formed; some, such as Lualualei, were graded to stands of the sea over 600 meters below the present sea level. With subsequent and continued subsidence of Oahu these major valleys were drowned, and eventually thick sections of reef, lagoonal, and beach sediments were deposited.

The present geomorphology of the western coast of Oahu is dominated by the deeply eroded valleys described above. Between these valleys, sharp spurs extend down to the sea and offshore as submarine ridges. These spurs and their offshore extensions act as effective barriers to the alongshore transport of nearshore sand and other sediment. Consequently the nearshore environment is divided into littoral units or cells between which little exchange of sand occurs, and within which the amount of sand produced is in equilibrium with the amount of sediment lost from the cell. Contributions of littoral sand are from coastal streams and from the disintegration of calcium carbonate skeletal remains on the reef flats; losses of littoral sand are by offshore sedimentation into deep water, and to a lesser extent by paralic deposition and by the landward migration of beach dunes.

The coastal zone between Kaena and Kepuhi points, the area of the present study, is essentially one large littoral cell; there appears to be very little nearshore sand transport around either point. The cell is dominated by the large Makua Valley located in the center of the cell; the major reservoir of beach sand is located at the mouth of this valley. Above sea level there are probably no fewer than four well-developed ancient sea level stands preserved, the most pronounced at +8 meters. Below sea level there are at least five additionally preserved sea level stands, at -18, -55, -90, -550, and -1100 meters (Stearns, 1966:23).

Bio logic

The nature of the sea floor in the area of investigation has been described elsewhere. As an environment it is a series of sand-covered terraces paralleling the trend of the coast and backed by discontinuous escarpments. In places, the sand covering on the terraces is thin and the epifauna scant, even where the rock is bare due possibly to sand scouring. This is most apparent in shallow water from 10 to 30 meters in depth. In depths of 30 meters or less there are some areas with a vigorous growth of hermatypic corals. There are extensive beds of the clam Pinna muricata on the sand-covered terraces in depths between 35 and 100 meters, and occasionally on rocky areas numerous vasicform coral colonies, possibly a Montipora, are found in 60 to 80 meters of water.

The sand-covered terraces, other than areas of Pinna beds, have little apparent life. Some dredging on the terraces resulted in the collection of numerous heart urchins Brissus latecavinitus. There were also very few fishes over the
terrace. The escarpments had in general an abundant fauna of fishes and invertebrates.

Areas of some of the terraces have a scattered covering of rubble with attached algae as deep as 90 meters. Algae also were noted on the escarpment areas. Where the escarpment was deeper than 90 meters it appeared to lack algal growth and had a poorer epifauna as compared with the escarpments in shallower water. At all depths, in holes and small caves, an abundant fauna was noted of fishes and invertebrates characteristic of their environment.

RECONNAISSANCE TECHNIQUES

"Asherah" Operations

To obtain the maximum amount and the highest quality of scientific data during the investigations it was felt that, simultaneously with the use of the "Asherah," other techniques should be employed to measure biologic and geologic parameters. Consequently, while the "Asherah" was diving, the "Teritu" was engaged in bathymetric or photographic surveys or geologic and biologic dredging operations in the same general area. (For equipment specifications see the appendix.)

The "Asherah" was moored each night alongside the "Teritu" off Makua Valley. During the night her batteries and compressed air tanks were recharged. The daily procedure was to take the "Asherah" in tow with a 16-foot power boat early each morning and proceed to the proposed diving locality. Upon reaching the diving site the "Asherah" was released, made ready for diving, and boarded. Each dive lasted for 2 to 3 hours and generally two dives were made a day. During the time the "Asherah" was actually under water she was accompanied on the surface by a 13-foot power boat with which she maintained direct and continual communications. From November 1 through November 5, 15 dives were made.

Remotely Controlled Stereo-Photography

While the "Asherah" and her accompanying small boats were actually engaged in diving operations, the "Teritu" was also employed in data collection. Each area transversed underwater by the "Asherah," as well as additional interesting areas, were photographed from the surface by the "Teritu." Edgerton, Germeshansen and Grier cameras were used, depth-controlled by a pinger unit mounted on the camera frame and monitored by the Precision Echo Sonic Recorder aboard the "Teritu." A stereo-(double-)camera arrangement was employed, and both black and white and color film were used. In all, 500 pairs of photographs were taken at depths of 120 to 300 meters.

Echo Sounding

Numerous continuous echo sounding profiles were made by the "Teritu" prior to, during, and subsequent to the "Asherah" dives. The equipment used consisted of an EDO echo sounder towed outboard in a Braincon streamlined housing and a GIFFT recorder (Precision Echo Sonic Recorder). Because of the high degree of sensitivity of the recording unit, it was possible to record fish schools and micro-relief on the various submerged terraces, and consequently the echo sounding profiles were instrumental in determining the diving localities for the "Asherah." Twenty of the best echo sounding profiles are shown in Figures 3a-3d, their localities in Figure 1; these records form the basis for the bathymetric chart shown in Figure 4. Three of the echo sounding profiles (Nos. 4, 10, and 11) show excellent examples of fish populations, and consequently are reproduced in Figures 5, 6, and 7.

Geologic Dredging

Numerous attempts to dredge rock from the various marine terraces and escarpments were made by the "Teritu." Heavy pipe dredges with chain briddles were used connected to the ship by ¾-inch steel wire, but the light "A" frame and sheaving system of the "Teritu" prevented heavy strains being put on the system. Dredging on the outer edge of the Penguin Banks Shelf, just north of Kepuhi Point, recovered reef rock fragments with freshly broken surfaces. These samples came from depths of from 50 to 60 meters and probably represent the outcrops marking the boundary between the Penguin Banks and Mamala shelves. Similar reef rock fragments were obtained at depths of 120 meters on the Mamala shelf off Makua Valley.

Attempts to break rock off the major escarpment between the Mamala and Lualualei shelves
met with failure. In each case the ship had to be backed to recover the dredges and the cutting edge of the dredge was frequently bent.

**Trawling**

A standard shrimp try trawl was tested as a collecting device in the general area of the "Asherah" operations, but deeper and south of the area off Pokai Bay. The trawl was hauled twice in about 350 meters of water and took a scant catch with a good deal of damage to the net. The echo sounding record had indicated a smooth bottom. The tension on the cable reached one ton, overloading the ship's generator. A new net was rigged and shot in a sand channel off Pokai Bay which was presumed to be free of obstructions. The gear was towed perpendicularly to the trend of the coast offshore beginning in 20 meters of water and ending in about twice that depth. A large catch was taken of nearshore fishes, including a female *Dasyatis hawaiensis* whose weight must have exceeded 100 kilograms even though the fishing time was quite short. Again the net was badly damaged.

Both the dredging and trawling operations indicated that the "Teritu" was quite inadequate for this use.

**MARINE GEOLOGY**

**Geomorphology**

The submarine geomorphology between Kaena and Kepuhi points, is dominated by a series of marine terraces separated by escarpments. From the "Asherah" it was possible to discern at least three distinct levels:

1. An upper level terminating seaward at a depth of approximately 60 meters.
2. An intermediate level extending from about 70 meters down to approximately 120 meters.
(3) A deep level extending from about the diving limitation of the "Asherah" (180 meters) seaward. These marine terraces observed from the "Asherah" correspond fairly well with the submarine terraces recorded by Ruhe et al. (1964) in their careful analysis of the shorelines and submarine terraces of Oahu. It is known from work done by Stearns (1966) and by Ruhe et al. (1964) that a shoaler terrace also exists in the depth range of 5–18 meters, but this terrace was above the general working range of the "Asherah" during the present investigation.

It is not the purpose of this paper to attempt to refine on the depth limitations computed by Ruhe for each of the submarine terraces around Oahu. Interested readers should refer to his work cited above or to several of H. T. Stearns' works on the same subject. However, it is our purpose to describe certain features of these terraces that lay beyond the ability of these earlier workers because of the previous lack of means for direct visual observation.

The most striking feature of the submarine geomorphology off northwestern Oahu as observed by the "Asherah" was the escarpment between the lower and intermediate terrace levels (here equated to the Lualualei and Mamala shelves, 247–932 meters and 75–124 meters, respectively, of Ruhe et al., 1964). After viewing firsthand this major escarpment and the submarine terraces it separates, it seems no wonder that the depth determinations for the various shelves around Oahu have such a wide range: the near vertical nature of this escarpment prevents accurate determinations of its features by echo sounding, it is cut in many places by wide sand channels that grade gently

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Fig. 3b. Bathymetric profiles Nos. 6–10. See Figure 1 for locations.
from one terrace to another, and the escarpment is almost completely buried by nearshore sand for almost one-half its length—from Makua Point to Kepuhi Point.

Figure 2 shows the relationship of this deeper escarpment to the upper terrace levels and generally to the land topography. Figure 9 shows a detailed picture at a point slightly north of Makua Valley. Generally this escarpment between the Lualualei and Mamala shelves is much more pronounced in the area north of Makua Valley. In places it is perfectly vertical for over 30 meters with caverns and indentations in the lower levels and in some localities large boulders at the base. The amount of sand in the offshore zone increases to the south (as explained in the section on Littoral Processes below), and this increase in offshore sand partially masks the base of this escarpment and, far to the south near Kepuhi Point, completely obliterates it. Starting at about Makua Valley, large spillways or canyons cut through the escarpment and, together with the sand spilling over the rim and fragments from the escarpment itself, form immense talus slopes (Fig. 9). On most of the dives directly to 180 meters the "Asherah" alighted on a 10°–15° talus slope which dropped off seaward into darkness and extended upward and shoreward to the base of steep cliffs or over broken outcrops of rock to the Mamala Shelf.

In the area of investigation it would be almost impossible to fix the depth of the inshore edge of the Lualualei Shelf by means of echo soundings: the sand and talus deposits are probably tens of feet in thickness and completely bury the inner portion of the shelf. Just south of Kaena Point, where the base of the escarpment is covered with large boulders, the depth is approximately 186 meters. These boulders most probably are the remnants of a boulder beach; together with the near vertical escarpment above them they possibly represent the strand line and sea cliffs for a very prolonged stand of the sea. The age of the Lualualei Shelf is not known, but its possibly warped and tilted surface (Ruhe, 1964) and the recovery from it of a possible Miocene fauna (Menard, Allison, and Durham, 1962) would indicate mid-Tertiary. Irrespective of the absolute age, a long period of stability of the sea level is indicated by the massive nature of the escarpment observed from the "Asherah." A continuation of this escarpment can be traced around most of western and southern Oahu.

The upper edge of the escarpment described above terminated abruptly in a nearly horizontal marine terrace. The seaward or deeper edge of this terrace generally was encountered at depths of about 120 meters, but ranging from approximately 100 to 140 meters in depth. Landward the terrace continued for hundreds of meters, finally terminating against a very broken line of irregular outcrops. Figure 8 is a representation of this intermediate terrace (here referred to as the Mamala Shelf) at a depth of about 90 meters. The nature of the outcrops defining its inner edge is shown as well as some of the surface features of the shelf. The outcrops themselves were very interesting as many had large caves in their seaward sides and were 3 to 6 meters in height and perhaps twice that in diameter. A definite delineation of these outcrops, generally parallel to the shoreline, could be seen. A representation of this delineation is attempted in Figure 8.

It was possible to trace the Mamala Shelf landward in some areas to depths of less than
70 meters, but usually landward of about 75 meters another terrace level commenced, probably equated to the Penguin Banks Shelf of 55 meters depth as defined by Stearns (1966). The inner edge of this shelf was not explored with the "Asherah."

Both the Mamala and Penguin Banks shelves were very flat and, approximately south of Makua Valley, were covered extensively with patches and channels of sand. These masses of sand were generally irregular but connected into river-like masses 30 or more meters in width, which continued across the shelves and through cuts in the escarpments down to the diving limit of the "Asherah." On the Mamala and Penguin Banks shelves, the sand channels and sand patches were rippled; generally the ripples were elongated normal to the channel axis irrespective of the meandering of the channel. Usually the sand bodies were not below the general level of the shelves, except where the sand bodies passed through the various escarpments.

**Lithology**

Due to the limitations of the "Asherah" it was not possible to collect rock samples at the time visual observations were made. Nor was it possible to use heavy rock dredging gear aboard the "Teritu." Consequently, an adequate lithologic sampling program could not be undertaken.

Nevertheless, rock samples were dredged
from the escarpment between the Penguin Banks and Mamala shelves. These samples were all well indurated reef limestone. No basaltic cobbles nor pebble-size fragments nor basaltic outcrops were seen on the Penguin Banks or Mamala shelves.

The rounded boulders observed at the base of the escarpment between the Lualualei and Mamala shelves and the escarpment itself appeared to be basalt, though no samples were taken of either. Fragments of basalt were numerous in the channels cutting through this
escarpment and on the talus-like slopes on the inner edge of the Lualualei Shelf.

**Nearshore and Offshore Sedimentation**

Generally the coastal area between Kaena and Kepuhi points (herein called the Makua Cell) is one littoral unit or cell, that is, a zone in which the beaches are essentially in equilibrium, and the sand produced within or transported into the cell is just balanced by the sand lost to deep water sedimentation (Chamberlain, in press). Very little sand is transported around either Kaena or Kepuhi points.

The sand, nearshore and on the beach, is continually shifting in response to the wave and current regime, both on and offshore and alongshore. But usually there is a net, yearly, alongshore transport of sand to the south under the influence of the North Pacific Swell—high, powerful waves arising from the northwest gradient more than one-half of the time. These are mainly winter waves, and consequently most of the southward transport of sand takes place during that season.

As a result of these littoral processes, the sand-size particles, produced on the reef or carried onto the beaches from the hinterland by the intermittent streams of the area, are carried southward in the littoral cell and piled up on the southernmost beaches, and offshore against the northern side of Kepuhi Point.

The dives in the "Asherah" revealed that by no means all of the nearshore sand moves within the surf zone and on the beach to the south, but rather, a very substantial amount moves directly offshore, across the various marine terraces and escarpments into deep water. In Figure 2 an attempt is made to indicate these patches and channels by which sand is moved directly offshore.

The sand-size particles that make up the beaches, and the nearshore and offshore sand bodies between Kaena and Kepuhi points are of various composition and from various sources. Generally the sand is of medium grain-size and well sorted. Most of the constituents are remains of reef organisms; a small percentage of lithogenic components are present in the form of crystal grains of olivine and
weathered basalt fragments. Samples from the area of Keawaula Beach have shown the organic constituents to be mainly the remains of benthic Foraminifera, with lesser amounts of fragments of Mollusca and calcareous algae; various amounts of coral and echinoid debris are also present (Moberly and Chamberlain, 1964:137). A general discussion of the constituents of
Hawaiian beach sands can be found in the report by Moberly et al. (1965).

As can be seen from the composition, most of the sand-size particles are produced in the nearshore zone by disintegration of reef-associated organisms. Their route of transportation is unknown but probably complex. Some of the particles move onto the beaches and, as the beaches are eroded and accreted during the year, the particles migrate onshore and offshore, but year after year they are set in the direction of net alongshore transport, that is, to the south. Just north of Kepuhi Point, thick, extensive sand deposits attest to this southerly migration. During periods of intense northwesterly waves, strong littoral currents deflected seaward by Kepuhi Point as they flow southward, probably carry large quantities of this material nearshore and offshore, where it completely buries the various offshore terraces and escarpments at least down to 180 meters, the diving limitation of the "Asherah." A similar littoral cell a few miles to the south (Kahe) has been well studied and shows a similar nearshore sand circulatory pattern (Chamberlain and Marine Advisers, 1964).

The masses of sand lying on the Penguin Banks and Mamala shelves, and the accumulations of calcareous sand on the inner edges of the Lualualei Shelf at the base of the deeper escarpment must be explained in a somewhat different manner. It is quite possible that little of this sand has ever been on the beaches. Most of it, except that in the larger channels connected to the nearshore zone, is probably produced in situ on the deeper terraces, and by some process, yet unclear, it progresses seaward across the shelves, eventually spilling down onto the Lualualei Shelf. The larger sand channels on the deeper terraces may well be located relative to strong, offshore currents that develop within the Makua Cell during periods of storm. But most of the sand observed from the "Asherah" is moving slowly downslope under the influence of gravity, disturbed occasionally by the orbital velocity of large waves in the unidirectional flow of periodic bottom currents. Where the escarpments are very steep, for example, between the Mamala and Lualualei shelves, the calcareous sand simply spills over the escarpment edge and falls down upon various ledges and finally upon the inner edge of the Lualualei Shelf.

The quantity of sand within the Makua Cell has been estimated previously at approximately $5 \times 10^5$ cu yd (Chamberlain, in press). However, in light of the observations made from the "Asherah," this estimate is probably too low by a factor of two, perhaps even by an order of magnitude. Assuming this amount (say, $10^6$ cu yd) to be a sand reservoir essentially in equilibrium with the present geologic and oceanographic conditions, then the yearly addition of new sand to this reservoir must be balanced by the yearly loss of sand from the reservoir. The yearly production or input of sand-size particles per length of coast along western Oahu is not known, but from the analyses made just to the south at Kahe, the total yearly production, or introduction, of sand into the Makua Cell is probably less than 10,000 cu yd. Nevertheless, since the principal loss of sand from the Makua Cell is to deep water sedimentation, this figure means that approximately 10,000 cu yd of sand are deposited yearly onto the inner portions of the Lualualei Shelf. The distance that this sedimentation extended out onto the Lualualei Shelf could not be ascertained from the "Asherah" due to depth restrictions, but sand-size particles were photographed on the shelf down to below 600 meters.

**Benthic Ecology and Fish Communities**

Information on the kinds, distributions, and associations of organisms were obtained through four more or less complementary investigations: (1) by dredging and trawling, (2) by precision echo sounding, (3) by submarine photography with an automatic camera system, (4) direct observations from a research submarine.

The submarine was limited to depths of 180 meters or less and, while the other methods of investigation were not thus limited, the discussions concern observations from about 180 meters to about 25 meters. Few observations were made in water shallower than this. The nature of the bottom and its topography is described in detail in the section on geomorphology. Considered as an environment the area comprised two major biotopes: terraces, gen-
eral sand covered, and rocky areas, either outcrops of reef rock or near-vertical rocky escarpments separating the terraces. Of the latter, the important ones were a line of outcrops and low escarpments at 70 meters and massive escarpments with crests at 120 meters or deeper, paralleling the coast. Associated with the rocky areas were an abundance of fishes and in places a rich epifauna also.

The Communities of the Rocky Areas

Figures 5, 6, and 7, reproducing the actual sounding traces of the bottom, also show, more faintly and somewhat separated from the bottom, traces of what were subsequently demonstrated to be concentrations of fish. These were located generally at or above escarpment crests or over outcrops of reef rock. These concentrations of fish were investigated by cruising in the “Asherah” near the sea floor, along and across the escarpments near where the soundings were made. In addition, photographic transects were made both obliquely to the trend of the coast and at a right angle. These ran from shallow to deep water in order to minimize direct contact of the camera system with the bottom.

The visual observations made from the “Asherah” provided a dramatic contrast to the photographic ones obtained with the automatic camera system. Visual observations confirmed the indication given by the echo sounding record in finding major, but highly discontinuous, concentrations of fish associated with the escarpment crests. This was not true of the photographic transects. Fish were photographed on only a few frames of the hundreds exposed, and those photographed were species that commonly rest on the bottom or swim very near the bottom. The greatest number of fish were photographed in a few instances when the camera system was in contact with the bottom, being dragged along so that photographs were taken parallel with the sea floor.

Observations from the “Asherah” on the relative abundance of some species, suggested that the fish community associated with outcrops of reef rock at about 70 meters differed from that associated with the deeper escarpment crests further offshore at depths of 120 meters or more. The damselfish Chromis verater appeared to be the most abundant species about the outcrops of reef rock. The little bass Caesioperca thompsoni was common in small loose schools on the face of these outcrops. Hemitrechus acuminatus was also common, frequently as individuals, but sometimes in small groups. The surmullet Parupeneus bifasciatus was also common near the basal portion of the outcrops or around rocks in the vicinity, but not in schools.

The angel fish Holocanthus arcticus was observed as scattered individuals over rocky areas, usually very close to the bottom. The most abundant butterfly fish observed was Chaetodon miliaris; however this species was less numerous than the damsel fish Chromis verater in the rocky outcrop environment. See Figure 8.

Both Naso hexacanthus and Seriola dumerilli were observed in schools at both the outcrops of reef rock and the escarpments. The schools of Naso appeared to be smaller and more open in the shallower water. Naso schools above the crest of the deep escarpments, near large aggregations of Chaetodon miliaris, had the following characteristics. The schools were roughly spherical, about 3 to 7 meters across, and moved slowly between 5 and 15 meters off the bottom. The individual fish appeared to be 35 to 70 cm in length and swam rather closely together.

Seriola dumerilli were observed in roving schools of a few dozen fish. Individual fish in the schools were estimated to be larger than 70 cm and less than 150 cm in length.

Mention has been made of aggregations of Chaetodon miliaris above the crests of the escarpments. These occurred over a relatively small area of bottom, usually less than 50 meters across, which was somewhat elevated (by 5 meters or less) above the general height of the escarpment crest. The aggregation, or school, extended upward into the water column from 15 to 40 meters. Individual fish were 12 to 25 cm in length and appeared to be separated by distances of 0.5 to 2 meters or more apart. The fish were close to the bottom but confined to the rocky elevated portions. They did not occur down over the face of the escarpments and the diameter of the aggregation appeared to be less with increased distance from the bottom. The individual fish were in easy motion, both vertically and horizontally, but the aggregation as a
whole appeared to be fixed over a specific area of the bottom. It is this feature which suggests that the large number of fish be considered an aggregation rather than a school. See Figures 5, 6, 7, 8, 9, and 10.

The schools of *Naso hexacanthus* also appeared to be oriented with respect to the aggregation of *Chaetodon miliaris* but not nearly as tightly as the latter appeared to be oriented to the sea floor topography. The *Naso hexacanthus* schools were located peripherally to the aggregation of *Chaetodon miliaris* and over the terrace rather than beyond the face of the escarpments. However, schools of the deep water snapper *Etelis carbunculus* did occur peripherally in relation to the *Chaetodon miliaris* aggregation at the level of the terrace, or deeper in open water beyond the escarpments. This species was not observed in shallower water, but it was also observed near the crest of the escarpments or beyond in deeper water where no aggregations of *Chaetodon miliaris* occurred.

These aggregations did not occur continuously along the crests of the escarpments, but appeared to occur wherever an elevated rocky area broke the crest profile. While the face of the outcrops of reef rock had had an abundant population of fish, there was a scant population along the face of the escarpments. The commonest species was an unidentified priacanthid-like fish that appeared to dwell in shallow holes on the face of the escarpments at distances of 10 meters or more apart. Small carangids were occasionally observed at all depths studied on or beyond the face of the escarpments. There were cavities of various sizes in the rocky areas. Those of apparent depth were usually thickly crowded by myripristids and holocentrids. *Holocentrus scytheops* or a species very much like it appears to be common. Spiny lobsters were also common and, while no certain identification of the species was made, *Panulirus japonicus* would at least be anticipated to occur since it appears to be commoner in deeper water within the range of scuba. Spiny lobsters were sighted in depths greater than 140 meters. A large moray eel, resembling *Gymnothorax flavimarginatus*, was seen at a depth of 150 meters adjacent to a cavity in the rock.

**The Terrace Community**

For the most part the terraces were covered by sand with little apparent epifauna. Fish were also largely absent. A large school of kawakawa (*Euthynnus yaito*) was observed, apparently foraging over a rubble- and sand-covered area about 150 meters deep. The fish were very near the bottom, less than a meter above it. Rays, probably *Dasyatis hawaiensis* and certainly *Aetobatus narinari*, were not infrequently sighted on or over sandy areas. A very large *Dasyatis hawaiensis* was taken in a small trawl at a depth of less than 50 meters off Pokai Bay from a sand bottom, and dredging at between 150 and 75 meters largely in sand north of Kepuhi Point resulted in an abundant catch of the heart urchin *Brissus latecarnatus* and many fragments of shells from the hatchet clam *Pinna muricata*. While the heart urchin is normally buried in the sand and is therefore not detectable visually, very extensive beds of the clam were observed from the "Asherah" and by submarine photographic transects off western Oahu and elsewhere in depths between 35 and 100 meters. One such clam bed observed from the "Asherah" was at least 500 meters across.
Subsequently, a bed which had an extent of more than 1500 meters was photographed during a submarine camera transect in an area between Maui and Lanai at a depth of 70 to 80 meters. As is characteristic for this genus, the clams were buried deeply in the substrate with the lip of the shell protruding. Individual clams were close together, appearing to be almost in contact.

The Neritic Community

Observations of the biota thus far have concerned benthiic organisms, and suggest that distributions of fish are related to bottom topography. Very few fish were observed high above the bottom. However, concentrations of plankton and particulate matter, possibly organic, were observed from the "Asherah" well above the bottom and also near it, at depths of 70 to 100 meters. It was assumed that these concentrations, causing a substantially reduced visual range, were located at the bottom of the mixed layer, at the thermocline. Temperature measurements were not taken to confirm this assumption.

Discussion

The ecological observations from the "Asherah" together with the data obtained by echo sounding, submarine photography with automatic cameras, and trawling and dredging suggest the existence of two major biotopes—the terraces, and the rocky outcrops and escarpments—and that each of these contains two recognizable subdivisions. For the terrace biotope these are: (1) the sand-covered flats, and (2) the extensive beds of Pinna muricata, which could be better characterized as a bioenosis. Its investigation would likely be rewarding.

The biotope of rocky outcrops and escarpment includes two subdivisions—the outcrops of reef rock characterized by Chromis verater and the less abundant Caesioperca thompsoni, and the escarpments characterized by large aggregations of Chaetodon miliaris and small schools of Etelis carbunculus, as well as other species. The observed patterns of distribution are difficult to understand in detail, but two general hypotheses are proposed, in part to provide a basis for future investigations of these matters. One hypothesis concerns the bathymetric distribution of Pinna muricata, and the other, the aggregations of Chaetodon miliaris and associated species.

Occasional specimens of Pinna muricata are found in quite shallow water, essentially just below the low tide level. The shallowest beds observed from the "Asherah" were about 38 meters deep, and SCUBA divers have reported beds as shallow as 25 meters. The deepest beds observed from the "Asherah" off western Oahu were at about 100 meters. This may not, of course, represent the downward extension of the range of this species. As shown in Table 1 the average temperature to and including depths of 100 meters is from 24.6°C to 22.3°C, with a low temperature of 20.0°C at 100 meters. At 200 meters the average temperature is 16.7°C with a range of plus or minus 4.7°C. This is the maximum range for the water column. The temperature variation is less in either shallower or deeper water, becoming markedly less for depths in excess of 500 meters. There may be an association between the depths of abundant occurrence of Pinna muricata and the lower part of the mixed layer. Pinna is a filter feeder, and the lower part of the mixed layer may have a higher concentration of organic particulate material since such material, unless mobile, tends to settle. The sinking rate would decrease at the bottom of the mixed layer because of an increase in density of the water. As mentioned earlier a marked reduction in visual range was sometimes noted at depths between 70 and 100 meters. Upon going deeper the transparency of the water increased abruptly, with a change in visual range from 10–15 meters to 40 meters or more. If the lowest portion of the mixed layer did have a higher concentration of particulate food, the bathymetric range through which it passed may be the bathymetric range of the clam beds, with a possible additional qualification that the decrease in temperature with depth may establish an independent lower limit to the distribution of the clam.

The striking aggregations of Chaetodon miliaris observed over certain topographic features of the deep escarpment must relate to some essential advantage that this behavior provides in this locality. Chaetodon miliaris is the commonest butterfly fish in Hawaiian waters and was considered to be a coral reef fish. Its abundant occurrence in depths of 120 meters
and more was surprising. However, with the exception of *Etelis carbunculus*, *Caesioperca thompsoni*, *Chaetodon tinker* and possibly *Holocentrus scythrops* and one or two others, the list of fish species observed from the "Asherah" (see Table 2) are common either in nearshore reef environments or in near-surface waters. With a few additions, the fish fauna at depths to 180 meters was essentially a selected portion of a nearshore reef fish fauna.

Many of the species of fish listed in Table 2 are normally found about rocky areas in shallow.
water and apparently find both shelter and food in a rocky environment. Chaetodon miliaris is such a species in nearshore areas. It is possible that Chaetodon miliaris occurs in major aggregations well off the bottom in the deepwater environment as a response to a plankton feeding regime. Isaacs and Schwartzlose (1965) suggested that vertically migrating zooplankton are swept over shoal areas such as banks during the night when they move upward in the water column, and then are trapped against the bottom on their downward migration with the approach of day. They may be thereby especially vulnerable to predation by fishes. A mechanism of this nature would not, however, explain the highly discontinuous distribution of fish laterally along the crest of the escarpments. It is also difficult to see what advantages would accrue through aggregating upwards of 40 meters above the bottom, in some instances over a rocky area not more than 5 meters above the average height of the escarpment crest.
Aggregations of fish do occur over rocky mounds on a much smaller scale in shallower water. Immature Dascyllus albisella do this over individual coral heads and seek concealment in the branches of the coral when alarmed. However, it is unlikely that the very large aggregations of Chaetodon miliaris use for shelter the features of bottom topography above which they aggregate. This statement would also apply to Chromis verater.

Fish concentrations on or over banks and in the vicinity of oceanic islands have long been noted by fishermen. Tuna fishermen in the eastern tropical Pacific have found concentrations of tuna in the vicinity of offshore banks regularly enough to make such topographic features of special interest (Bennett and Schaefer, 1965).

Four hypotheses have been offered to explain the apparent greater abundance of marine life about such topographic features, three of which would apply to banks as well as islands. The margins of continents, under many circumstances, would have similar effects on the abundance of marine life. The four hypotheses, which are not mutually exclusive, are as follows: (a) nutrients from land runoff (Gran, 1931); (b) vertical movement of water transporting nutrients into the euphotic zone (Moore, 1949); (c) increased productivity through the growth of benthic algae in relatively shallow depths (Sargent and Austin, 1949); (d) the trapping of deep scattering layer organisms (Isaacs and Schwartzlose, 1965).

A discussion of the first three of these possible mechanisms, which involve means by which the primary production is increased, is presented by Jones (1962) in connection with the discovery of larger standing crops of zooplankton as the Marquesas Islands are approached.

The pattern of fish concentrations as observed off western Oahu seem to accord best with a food resource which may be provided by the trapping of deep scattering layer organisms as suggested by Isaacs and Schwartzlose (1965). However, if this is the correct hypothesis, the observed relation among topographical features, fish concentrations, and deep scatters is a complex one, and is affected by elements that are not obvious.

CONCLUSIONS

1. At least three well-defined terraces were discernible from the “Asherah” (Fig. 1): (a) the Lualualei Terrace deeper than 180 meters, (b) the Mamala Terrace at depths of 70 to 120 meters, and (c) the Penguin Banks Terrace shoaler than 70 meters.

2. Vertical and near-vertical rock escarpments separate the Mamala Terrace from the Lualualei Terrace. In many places these escarpments were over 35 meters high and north of Maku Valley there were areas of rounded boulders at their bases; in some areas caves were present (Fig. 9). Between the Penguin Banks Terrace and the Mamala Terrace a broken line of reef rock outcrops extended up above the level of the terraces. These outcrops were from 5 to 10 meters in height and generally aligned parallel to the shore (Fig. 8).

3. Associated with these bottom structures were communities of the benthic biota. There appeared to be two major biotopes, the terraces and the rocky outcrops and escarpments. Each of these biotopes was separable into two portions based on the presence or absence of dominant species.

The terraces were largely sand covered, rather barren of fishes or obvious benthic fauna except for extensive beds of a hatchet clam Pinna muricata, which were both extensive enough and dense enough to constitute a biocoenosis.

The escarpments lying between the Lualualei Terrace and the Mamala Terrace had at irregular intervals large concentrations of fish associated with features of the crest. Concentrations of fish were also observed with the reef rock outcrops between the Mamala Terrace and the Penguin Banks Terrace. These concentrations appeared to differ significantly in both dominant species and the proportions of other species.

4. The majority of the species of fish and those most abundant within the range of depths observed from the “Asherah” were species common or abundant in shallow water.

5. Offshore transport of calcareous sand was evident to the diving limit of the “Asherah” (180 meters). On the Mamala and shoaler shelves, large sand “channels” and interconnected sand patches were present (Figs. 1 and
3). Seaward these sand channels spilled over the Lualualei escarpment or through gullies in that escarpment down into the Lualualei Terrace. In most places the inner edge of the Lualualei Terrace was buried with thick masses of nearshore calcareous sand mixed with escarpment talus of pebble and cobble size (Fig. 9).

6. The amount of offshore sand increased markedly from north to south; near Kepuhi Point all of the escarpments and terraces were completely buried and a single sand slope of about 5° extended from 25 meters to the depth limit of the “Asherah.”

APPENDIX

EQUIPMENT SPECIFICATIONS

"Asherah"

The research submarine “Asherah” was leased from the Electric Boat Division of General Dynamics for a period of one week. Accompanying the submarine was a 3-man operating and maintenance crew and equipment to keep all systems functioning. She was 17 feet long with a spherical pressure hull 5 feet in diameter at the anterior end attached to a cone-shaped afterpart which was floodable and housed batteries, compressed air tanks, and ballast tanks.

She was rated for a maximum depth of 600 feet and for an operating period of 10 hours. Other data include:

- Crew: 2, an operator and an observer
- Propulsion: 2 side-mounted, 2-hp motors
- Power: 24-volt storage batteries
- Life support: 48 man-hours endurance (CO₂ absorbent and compressed oxygen)
- Viewports: six 5-inch minimum diameter, 90° truncated cone, 2-inch-thick plexiglass; and one 2-inch skylight of 1-inch plexiglass in hatch
- Weight in air: 8,500 pounds

Through a “pinger” mounted on the hull of the submarine and a directional hydrophone on board the 13-foot power boat, the approximate position of the “Asherah” was monitored throughout a dive.

Where the nature of the diving investigation permitted, the dive was begun at its deepest point, that is at 180 meters, in order to get the submarine down into cool water as soon as possible. This was desirable since in near-surface waters the temperature inside the craft, together with 100% humidity, made her uncomfortable. For this reason, near-bottom observations were taken from deep to shallow water. Both the operator and the scientific observer aboard the vehicle used the viewports and exchanged information on their observations. In addition, a portable tape recorder was used to record what was seen; however, because of the ambient noise level, the tapes were difficult to understand on playback. Photographs in monochrome and color were taken through the viewports with cameras impervious to moisture such as the Nikons. While the “Asherah” had an external automatic camera, this was in operating condition for only a few of the dives near the termination of the program. While few of the photographs were of good quality, many were adequate to confirm visual observations.

Stereo-Photographic Equipment

The following photographic equipment, purchased from Edgerton, Gerneshausen and Gier, Inc., 160 Brookline Avenue, Boston, was used throughout the “Asherah” diving operations: two 35-mm cameras, Model 200; light source, Model 210; and camera mount, Model 240.

A pinger system monitored by the “Teritu’s” echo sounding recorder was used to record the camera’s distance from the bottom. Its components consisted of a driver (Model 220), and a transducer (Model 221).

The entire camera system, including pinger, was powered by silver cell batteries.

Kodak TRI-X film was used for all black and white photography, Ectochrome MS film for all color photography.

Echo Sounding Equipment

The echo sounding equipment used aboard the “Teritu,” and by means of which the bathymetric profiles were made, consisted of: GIFFT Transceiver: 800 watts peak power at 12 kilocycles, ALPINE Precision Echo Sonic Recorder (PESR), and BRAINCON towed “V” Fin incorporating an EDO transducer.
Geologic Dredges

The rock dredges were made of 1/4-inch iron pipe, 14 inches in diameter and cut into 3-foot lengths. An iron grating was welded across one end and a 4-foot chain bridle attached to the other end. The cutting edges of the dredges were sharpened and tempered.

REFERENCES


Studies on the Internal Defense Mechanisms of Sponges

I. The Cell Types Occurring in the Mesoglea of *Terpios zeteki* (de Laubenfels) (Porifera: Demospongiae)

*Thomas C. Cheng, Herbert W. F. Yee, and Erik Rifkin*

It is well known that various morphological types of free cells occur in the mesoglea of sponges. Collectively, these cells are generally designated as amoebocytes since they are all assumed to be capable of amoeboid movement although their functions may vary. According to Hyman (1940), in those poriferan species in which there are much mesoglea and relatively few cells, the mesenchyme, that is, the mesoglea together with the cells embedded therein, may be referred to as the collenchyma, while in those in which there are numerous cells, the mesenchyme may be designated as the parenchyma. The mesenchyme of the species under consideration may be considered parenchymatous. A search of the literature pertaining to the mesenchymal cells of sponges reveals that a variety of names have been coined to designate the various cell types (Tuzet, 1932; de Laubenfels, 1932; Wilson and Penney, 1930; and others). This practice has led to considerable confusion for those interested in cell homologies and analogies. During our investigation of the parenchymal cells of *Terpios zeteki* (de Laubenfels), we have found the designations used by Minchin (1900), Galtsoff (1925), and Hyman (1940) categorizing the free cells as archaeocytes, collencytes, chromocytes, thesoocytes, and scleroblasts, to be the most useful. Therefore, we have used these names for the cells encountered in *T. zeteki*.

Our interest in poriferan collenchymal or parenchymal cells stems from inquiries into the types of internal defense mechanisms occurring in sponges, whether in response to abiotic factors or microorganisms, including parasites. Although studies of this nature, particularly the various aspects of cellular defense mechanisms (leucocytosis, phagocytosis, pinocytosis, and encapsulation) have been examined extensively among the higher coelomate invertebrates, especially the Mollusca and Arthropoda, very few comparable studies have been carried out among the Porifera. In this paper are described the various types of free amoebocytes normally found in the parenchyma of *T. zeteki*, and the ratio of each type of cell present is reported.

We are grateful to Dr. Sidney J. Townsley for identifying the sponge used in this study.

MATERIALS AND METHODS

*Terpios zeteki* is one of the two or three most abundant species of sponges in Hawaii (de Laubenfels, 1950). Specimens collected from pilings at Ala Wai Yacht Harbor, Honolulu, were brought into the laboratory and maintained in aerated filtered sea water with a salinity of 35 ‰ at 20°C. The parenchymal cells were examined by two methods: in histological sections, and in smears of living tissues.

Histological sections of *T. zeteki* were prepared by fixing segments of whole sponges, each approximately 1 cm in length, for 12 hours in 10% neutral formalin. These were subsequently dehydrated via a closely graded ethanol series, cleared in xylene, and embedded in high temperature paraffin (melting point 56°C). The sections were cut at 10μ and stained with Harris’ hematoxylin and counterstained with eosin. After the morphological characteristics of each type of cell found in the mesoglea were determined, comparable cells were sought in smear preparations of small pieces of living sponges, each piece measuring approximately 0.5 cm³. Examinations of living dissociated
parenchymal cells were made as these revealed certain distinguishing characteristics not readily observable in stained sections. For example, the pseudopodial movements of each type of cell and their cytoplasmic inclusions, especially the pigments of chromatocytes, were clearly visible only in living cells. The dimensions of the cells were determined from living cells by use of a calibrated ocular micrometer.

The percentages of the total number of parenchymal cells represented by each cell type were determined in the following manner. Uniform suspensions of dissociated cells of 10 sponges were made in filtered sea water. Samples of such suspensions were examined with a phase-contrast microscope equipped with a Whipple-Hausser ocular micrometer to facilitate counting. During the counting procedure, the first hundred cells recognized as ameboocytes native to the mesoglea encountered in the squares were recorded by type. A total of 23 counts were made.

RESULTS

Descriptions of Cell Types

The architecture of Terpios zetek is of the leuconoid type. The viscous mesogleal layer fills the spaces between the flagellated chambers and canals and is tightly packed with cells and spicules. The most abundant type of cell is the small spherical collencyte, each measuring 0.003 mm (0.002–0.004 mm) in diameter (Figs. 1–5). When examined in histological sections, many of the collencytes possess fine pseudopodia which are fused with those of adjacent cells to form a netlike syncytium (Fig. 19) with independent cells intermingled with it. In preparations of dissociated cells, however, collencytes generally round up, appearing as minute spheres which are not interconnected. Occasionally one is seen producing one or more fine pseudopodia (Fig. 4). In hematoxylin-and-eosin stained sections, the cytoplasm of collencytes is agranular and is either chromophobic or only slightly eosinophilic while the nucleus is homogeneously slightly hematoxyphilic. These cells are limited to the parenchyma although occasionally collencytes have been observed free in the water canals, particularly excurrent canals. When dissociated living collencytes are observed under the light microscope, the cytoplasm appears clear but the nucleus is extremely difficult to define. When examined with phase-contrast microscopy, however, each nucleus appears to be homogeneous and rounded. On a few occasions the nuclei of collencytes have been observed dividing although the exact mitotic figures have not been studied (Fig. 5).

The second most abundant type of parenchymal cell is the rounded to ovoid archaeocyte which measures 0.006 by 0.005 mm (0.004–0.007 by 0.004–0.007 mm) (Figs. 6–11). This type of cell appears either rounded or with a lobose pseudopodial projection in histological sections. Many of them enclose a rather large globule to ovoid hematoxyphilic body that measures 0.003 mm in greatest diameter and which when observed in the living state proved to be a yellowish-green symbiotic zooxanthella with a distinct bright red stigma. In addition to the zooxanthella, each archaeocyte includes a rounded nucleus with a distinct nucleolus, and some include cytoplasmic inclusions which vary in size, while others include one or two vacuoles. The cytoplasm of these cells is faintly eosinophilic while the nucleus is hematoxyphilic. It should be noted that very rarely the pseudopods of two adjacent archaeocytes may be fused to form a two-celled syncytium. In addition, archaeocytes are occasionally found free in the water canals, primarily the excurrent canals. When examined in the living state, archaeocytes are either spherical or ovoid. Approximately 45–50% of those encountered include endosymbiotic zooxanthellae. The cytoplasm may be clear or with a few hyaline inclusions. These cells have been observed to produce a single lobopodium (Figs. 9, 10). Occasionally some have been observed undergoing what appears to be division (Fig. 11); this, however, is not a common phenomenon. Approximately one out of 60 cells is dividing.

The third type of parenchymal cell encountered in T. zetek is believed to represent theocytes. Each of these measures 0.007 by 0.006 mm (0.005–0.010 by 0.004–0.009 mm). According to Hyman (1940), theocytes are nutrient-enclosing cells. The exact chemical nature of the cytoplasmic inclusions of what we are designating as theocytes has not been determined although the consistent occurrence of these
Figs. 1-18. Cell types found in the parenchyma of *Terpios zeteki*. Drawn from living material.
1-5. Collencytes. Notice the fine filament-like pseudopod in 4 and the dividing collencyte in 5. (Scale A)
6-11. Archaeocytes. Notice the presence of a symbiotic zooxanthella (a) in 7-10, the formation of pseudopods in 9 and 10, and a dividing cell in 11. (Scale B)
12-14. Thesocytes. Notice two types of cytoplasmic inclusions, the larger bodies (r), and extremely small granules. (Scale C)
15. Scleroblast. Notice the intracytoplasmically developing spicule (ds). (Scale D)
16-18. Chromocytes. Notice the pigment granules (pg) in all the cells depicted and the formation of a pseudopod in 18. (Scale E)
Fig. 19. Syncytially arranged collencytes embedded in the mesoglea of Terpios zeteki. Drawn from section stained with hematoxylin and eosin. Notice unconnected collencytes intermingled with syncytially arranged ones.

inclusions, which resemble stored nutrient globules, suggests their functional nature. There are two types of cytoplasmic inclusions. The more predominant is the form of relatively large globose bodies each measuring approximately 0.002 mm in diameter. The second type is in the form of small granules which are barely visible under the light microscope. The larger globules in living cells do not give a positive test for glycogen when stained with Lugol's iodine but, when stained with Sudan Black B, only some give a positive test for lipids. In H and E stained sections, the cytoplasm of thecsocytes is eosinophilic. Some of the larger inclusion bodies are also eosinophilic, others appear yellowish, while still others are chromophobic. Among the smaller granules, some are eosinophilic while others are colorless. The nuclei, each measuring approximately 0.002 mm in diameter, are strongly hematoxyphilic with distinct chromatin granules but no visible nucleoli. When observed in the living state, the larger inclusions vary from yellowish to colorless, while the smaller granules range from colorless to dark brown.

The fourth type of parenchymal cell includes the chromocytes or pigment-bearing cells (Figs. 16–18). Actually two types of chromocytes, based on the color of the pigments present, are distinguishable: those enclosing red, and those with black, pigment granules. Both types of cells are of the same size, measuring 0.004 by 0.003 mm (0.002–0.005 by 0.003–0.005 mm). These cells are distributed primarily in those regions of the mesoglea situated near the body surface of the sponge. Undoubtedly it is the red pigment-bearing chromocytes that give T. zeteki its reddish surface color and the black pigmented ones that give certain areas their blackish color. Each cell includes a nucleus, measuring 0.0008 mm in diameter, with distinct chromatin granules but no visible nucleolus. The pigment granules are more or less evenly distributed through the cytoplasm. In H and E stained sections, these pigment granules are deeply hematoxyphilic. Living chromocytes are capable of amoeboid movement (Fig. 18).

Skeleton-secreting cells or scleroblasts are rarely encountered in T. zeteki. Examination of sections of 10 sponges revealed only two, while in the numerous smear preparations examined, only nine scleroblasts, all silicoblasts (silicious spicule-forming cells), were observed. These cells, measuring 0.005 mm in greatest diameter, are quite similar to archaeocytes except for their slightly larger nuclei, which are devoid of nucleoli, and the presence of a developing spicule in each (Fig. 15). The young spicule is noncellular, colorless, and refractile. Its shape is generally elongate, with knobs at one or both terminals. In addition to the nucleus and young spicules, two types of cytoplasmic inclusions occur. The first is in the form of ovoid hematoxyphilic globules which are generally located near the nucleus. The second is represented by extremely minute colorless granules randomly distributed in the cytoplasm (Fig. 15).

Cell Counts and Ratios

A total of 23 differential counts were made of the cell types in T. zeteki by the method described earlier. The data are tabulated in Table 1.

**DISCUSSION AND CONCLUSIONS**

From our examination of both histological sections and dissociated cells it is evident that the parenchymal cells of Terpios zeteki can be identified as belonging to five cell types: collencytes, archaeocytes, thecsocytes, chromocytes, and scleroblasts. These can be distinguished by their dimensions, cytoplasmic inclusions, and other characteristics. It is of interest to note that collencytes, which represent the most abundant type of cell, are capable of forming syncytia by the fusion of their fine pseudopodia. A similar
phenomenon has been reported by Tuzet (1932) who described what she termed "stellate cells" in *Regiera elegans* (Bwk.) and *R. similans* (Johnston) with anastomosing pseudopods. It is uncertain whether Tuzet's "stellate cells" are homologous with *T. zeteki* collencytes, as she reported the presence in the former of a granular nucleus containing a nucleolus. As we have noted, nuclei of *T. zeteki* collencytes are agranular and without visible nucleoli. Similarly, Wilson and Penney (1930), who examined *Microciona prolifera* Verrill, and de Laubenfels (1952), who studied *Iotrochota birotulata* Higgin, have reported that many of the mesenchymal (parenchymal) cells in these sponges are connected by fine protoplasmic processes. Specifically, Wilson and Penney stated: "The space not occupied by canals, flagellated chambers, and skeletal fibers is filled with a tissue here designated as mesenchyme. It consists of abundant cells of several kinds, very many of which are connected together by intercellular strands. . . ." This situation, although superficially similar, is definitely different from that found in *T. zeteki*. In this sponge, collencytes are connected only with other collencytes and have not been observed to fuse with any other type of cell. Van Weel (1949), in a study of the freshwater sponge *Spongilla prolifera* Annand, has also reported syncytially arranged "indifferent cells" with faintly stained clear cytoplasm, and which may be without a nucleolus. His "indifferent cells" are believed to be comparable to our collencytes. It is proposed that the collencytes of *T. zeteki* represent the basic type of structural cell *in situ* and provide a firm network which, together with the spongins and spicules, add stability to the integrity of the parenchyma. The "stellate cells" of *Regiera* spp., as described by Tuzet (1932), and the "indifferent cells" of *S. prolifera*, as described by van Weel (1949), appear to serve the same function. It is noted, however, that not all of the collencytes of *T. zeteki* are fused. Independent collencytes also occur. It is also of interest to note that the

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Total 1330 512 286 163 9

Mean ± S.D. 57.83 ± 5.39 22.26 ± 5.54 12.43 ± 4.82 7.09 ± 3.68 0.39 ± 2.2
intercellular connections between collencytes are extremely fragile and are readily broken. Such connections are not found in smear preparations.

As stated, archaeocytes, which also occur in relatively large numbers in *T. zeteki*, are often found to include zooxanthellae. It is of interest to note that according to McLaughlin and Zahl (1966), the terms "zoochlorellae" and "zooxanthellae" are not generic designations but their contemporary meanings are primarily coloristic. Zooxanthellae are yellowish to greenish-brown algal cells, while zoochlorellae are pale to bright green cells. Those found in *T. zeteki* archaeocytes are yellowish-green and therefore are designated as zooxanthellae.

The occurrence of symbiotic algae, zooxanthellae or zoochlorellae, in sponges has been known since the investigations of Weber and Weber-van Bosse (1890), Koorders (1902), van Trigt (1919), Rodriguez (1930), van Weel (1949), and others. The sponge cells enclosing such algal cells have been designated by a variety of names. As examples, van Weel (1949) refers to the cells of *Spongilla proliferans* as "amoebocytes with symbiotic algae" (abbreviated "ASA") and infers that they are different from "phagocytes," and Rodriguez (1930) refers to such cells in *Spongilla lacustris* Johnston as "amoebocytes." An examination of the descriptions of these host cells has convinced us that such cells should all be designated as archaeocytes in that they all are relatively large, are capable of producing lobose pseudopodia, possess prominent nuclei with nucleoli, and may include cytoplasmic granules and vacuoles. In fact, Pourbaix (1933), in reviewing Rodriguez' work, has referred to these cells as archaeocytes.

It may be significant that symbiotic algal cells are found only in archaeocytes and not in other types of cells. Our studies on the phagocytic roles of the various types of parenchymal cells in *T. zeteki*, which will be published at a later date, indicate that archaeocytes are much more active and efficient in phagocytizing foreign materials. According to Rodriguez, the algal cells enter sponges via the flagellated choanoocytes and are later transferred to parenchymal amoebocytes (=archaeocytes). As the result of finding algal cells in the process of being digested within archaeocytes, van Trigt (1919) concluded that the relationship between the alga and the sponge is not a completely compatible one; however, van Weel (1949) has shown that sponges, in his case *Spongilla proliferans*, are associated with only one species of alga, in his case *Plenococcus vulgaris*, thus suggesting specificity, and having found few examples of intracellular digestion of *P. vulgaris*, he disagrees with van Trigt that the relationship is not totally compatible. Van Weel is of the opinion that only dying or dead algae become digested. Our examination of zooxanthellae within *T. zeteki* archaeocytes revealed very few instances of intracellular digestion and we tend to agree with van Weel that the relationship is one of compatible symbiosis, most probably mutualism as defined by Cheng (1967).

The nature of the cytoplasmic inclusions of *T. zeteki* thesoocytes remains essentially unknown. Our preliminary studies indicate that the larger globules do not represent glycogen. On the other hand, certain ones give a positive test for lipids. It is of interest to note that Pourbaix (1934) has reported that the nutrient reserves in certain cells comprising the gemmules of *Ephydatia fluviatilis* Lamouroux are not glycogen but may be proteinaceous, probably a glycoprotein. In addition, he has found unidentified lipid globules. Similarly, van Weel (1949) reported that no glycogen occurs in the cells of adult *Spongilla proliferans* except in oocytes and that fats occur in what he termed "phagocytes." Our findings confirm the presence of lipids and the absence of glycogen in the nutrient-storing cells of sponges. Furthermore, it is possible that those globules which do not give a positive stain with either Sudan Black B or Lugol's iodine may represent glycoprotein granules. This, however, is pure speculation and needs histochemical confirmation.

Our finding of intracellular formation of spicules in the few scleroblasts encountered indicates that in *T. zeteki* the spicules are formed intracellularly, at least initially, although the exact mechanisms involved remain to be determined.

As we have stated, our interest in the parenchymal cells of sponges stems from inquiries into their roles as associated with cellular internal defense mechanisms. With the estab-
lishment of the types of cells in *T. zeteki*, it is now possible to examine the phagocytic role of each type. Furthermore, with the establishment of the normal ratios of each type of cell, we now have the baseline for determining whether increases of all or certain types of amoebocytes occur when challenged with foreign materials. These studies are currently in progress.

**SUMMARY**

The parenchymal cells of the sponge *Terpios zeteki* were studied both in histological sections and in smear preparations. Five distinct morphological types can be recognized. These are readily identified as collencytes, archaeocytes, thesocytes, chromatocytes, and scleroblasts. The dimensions and morphological characteristics of each type are given. An endocyttoplasmic symbiotic *zooxanthella* occurs in the archaeocytes of *T. zeteki*. Counts revealed that collencytes are the most abundant of the five cell types. Many of these are syncytially arranged *in situ*. Archaeocytes are the next most abundant, followed by chromatocytes, thesocytes, and scleroblasts. Intracytoplasmic spicule formation was observed in scleroblasts. Having defined the cell types and ratios occurring in the mesoglea of *T. zeteki*, it is now possible to examine the role of each as associated with phagocytosis and other forms of internal cellular defense mechanisms.

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Lamellate Structures in the Nucleolus of the Cellular Slime mold *Acrasis rosea*

HANS R. HOHL and SUSAN T. HAMAMOTO

During a study on the morphogenesis of *Acrasis rosea*, a cellular slime mold, we have encountered lamellar structures appearing as part of the nucleolus of spores and stalk cells in the fruiting body. This report describes in detail these structures, their occurrence, and their possible nature.

MATERIALS AND METHODS

*Acrasis rosea* originally obtained from Dr. A. Kahn, Syracuse University, was grown on Difco cornmeal-dextrose agar supplemented with 0.1% yeast extract (Weitzman, 1962) with *Rhodotorula mucilaginosa* as food organism. Myxamoebae and fruiting bodies were most successfully prepared for electron microscopy by one of the following two methods: (1) Fixation for 1 hour in osmium vapor, followed by 1 hour in 2.5% phosphate-buffered glutaraldehyde at pH 7.3, and post-fixation for 1 hour in 1% phosphate-buffered osmium tetroxide at pH 7.3. (2) Fixation for 1/2 hour in Karnovsky's (1965) cacodylate-buffered glutaraldehyde-paraformaldehyde at pH 7.0, diluted to 1/4 (personal communication from Dr. S. Ito, Harvard University), followed by fixation in 1% Palade's osmium tetroxide at pH 7.3 for 1/2 hour. For both methods dehydration was carried out in ethyl alcohol followed by propylene oxide, and the specimen was then embedded in epon. In some cases the tissue was incubated in 0.5% uranyl acetate in 70% ethyl alcohol for 1/2 hour during dehydration. Sections were cut on an LKB ultramicrotome, post-stained in lead citrate and viewed in a Hitachi HU-11A electron microscope.

For demonstration of RNA, glutaraldehyde-paraformaldehyde fixed (1/2 hour, 4°C, pH 6.0) samples were treated with 0.7 mg/ml RNAase (heated for 10 minutes at 90°C prior to use). After incubation, the cells were washed with 5% trichloracetic acid for 30 minutes at 0°C, postfixed in osmium tetroxide, and embedded as described above.

For histochemical purposes at the light-microscope level the cells were fixed for 10 minutes in acetone at 4°C. The cells were stained for (1) RNA using pyronin Y according to Kurnick (1955), for (2) DNA and RNA with acridine orange followed by fluorescence microscopy, and for (3) protein with mercury bromphenol blue following the procedure outlined by Pearse (1960). Controls were treated with DNAase or RNAase (Loh and Soergel, 1965) before staining.

RESULTS

The nucleolus of the myxamoebae of *Acrasis rosea* appears to be built from three morphologically distinct components. The most striking, and the one of particular interest for our discussion, consists of a series of roundish masses of granular material (Figs. 1 and 2). These masses are either dispersed as separate units within the nucleus (Fig. 2) or condensed into large aggregates (Fig. 3). Each mass is made up of a large number of electron dense granules which stain heavily with lead citrate and are comparable in size to cytoplasmic ribosomes. The granules are more densely packed at the periphery of each clump, the central part of which then appears as a light core revealing a somewhat fibrous matrix.

The second component has not been observed frequently. It appears as an intensely stained, homogeneous body containing electron transparent cavities and is always situated within the first component (Figs. 1 and 5). The third component of the nucleolus consists of a large
Fig. 1. Part of a cell of *Acrasis rosea* showing nucleus (NU) with two components of the nucleolus (1,2) as described in the text. × 25,000. The black bar in all pictures represents 1µ.

Fig. 2. Nucleus of *Acrasis rosea* with components 1 and 3 of nucleolus. Note lighter and darker areas within component 1. × 20,800.

Fig. 3. Example of component 1 aggregated into a large mass. Cytoplasmic invagination (I) and nuclear evagination (E) are seen at upper left. × 20,000.
roundish mass of finely granular material somewhat more dense than the rest of the nucleus but considerably less dense than the first component (Fig. 2).

In the resting stages, that is, in the stalk cells and the spores, the first granular component often contains lamellar elements which are stacked in parallel fashion (Fig. 4). The number of lamellae per stack has been observed to vary from 1 to 12. The lamellae can be flat or curved, may cross through the middle of the granular component (Figs. 4 and 5), or may follow its contour (Figs. 6 and 7). Yet they never extend beyond the granular mass. The lamellae are separated by a constant distance of approximately 150 Å. The constant thickness of the lamellae together with the constant spacing conveys to the whole structure a regularity of appearance (Fig. 4).

Each lamella consists of a single layer of granules (Figs. 1, 6, and 7) apparently identical to the granules making up the first component (Figs. 1, 2, and 8). In fact, the layers are often continuous with the granular component (Figs. 8 and 9) and are always closely adjacent to it. Oblique sections through the stacks provide additional evidence that the layers are built from granules and not, for example, from a filamentous component (Fig. 8). Furthermore, we see that the granules are not oriented in any particular way but are packed rather tightly, though randomly, within the planes.

By applying the histochemical tests described, ribonucleoprotein-containing areas can be demonstrated within the nucleus comparable in size and location with the components described at the electron microscope level. This suggests that the granular masses contain ribonucleoprotein and are probably aggregates of ribosomes or ribosomal precursors. The nucleolus has been shown to be a source of ribosomes (Birnstiel, Chipchase, and Hyde, 1963). Our best evidence supporting this idea is obtained from the electron microscope study of RNAase treated cells in which the granular component has largely faded (Fig. 10).

**DISCUSSION**

The lamellae described in this report bear a certain resemblance to the "core" structures of spermatocytes (Moses, 1956) as well as to the chromatid bodies in parasitic protozoa and in germ cells of plants and animals (Barker, 1965). In the case of the "cores" a close similarity can be noted between the outer layer of the complex cores described by Schin (1965) and our lamellae. In both cases the layers are granular, show continuity with the nucleolus, and are often attached to or partly surrounded by the latter (Schin, 1965; Guénin, 1965). In the case of *Acrasis*, however, all the other components of the "core" structure are lacking; also, the cells are at a resting stage and no division of cells or nuclei occurs.

In the chromatid bodies of *Entamoeba invadens*, granules identified as ribonucleoprotein particles also are arranged in layers. A closer examination of those lamellae reveals, however, that the granules within the layers form helices (Siddiqui and Rudzinska, 1963) and thus differ from the arrangement described here for *Acrasis*.

All of these examples demonstrate the capacity of ribonucleoprotein granules to assemble into orderly structures. In our case particularly, we attribute this to a process of spontaneous self assembly within or at the periphery of a highly concentrated mass of granules in a state of low metabolic activity.

The fact that the lamellae have so far been observed only in resting cells, and then not with regularity, indicates that they do not represent an organelle involved in an essential function.

**SUMMARY**

Lamellate structures have been demonstrated within the nucleoli of spores and stalk cells of the slime mold *Acrasis rosea*. The lamellae, numbering up to about 12, are separated from each other by about 150 Å and are arranged in a parallel fashion to form stacks which either cross the main nucleolar mass or line it peripherally. Each lamella is composed of a single layer of granules apparently identical to the ones making up the bulk of the nucleolus. The granules are fairly tightly but randomly packed within the layer. The lamellate structures are interpreted to represent an arrangement of ribosomal type particles formed from a concentrated pool of particles by a process of self assembly.
Acrasis rosea Nucleolus—HOHL AND HAMAMOTO

Fig. 4. Nucleolus of *Acrasis rosea* with a series of parallel lamellae transversing it. × 16,000. The black bar in all pictures represents 1μ.

Fig. 5. Massed component 1 of nucleolus with lamellar material in between portions of mass. × 22,000.

Fig. 6. Nucleolus with lamellae along contours. Lamellae are sectioned tangentially in parts. × 22,000.

Fig. 7. Nucleolus with peripheral lamellae. × 22,000.
Fig. 8. Higher magnification of lamellar material cut obliquely. The lamellae appear to be made up entirely of granules and seem to be continuous with dark mass of component 1 (arrow). $\times 56,000$. The black bar in all pictures represents 1 μ.

Fig. 9. Continuity between lamellar material and component 1 of nucleolus (arrows). $\times 53,000$.

Fig. 10. Nucleus after treatment with RNAase. The nucleolar masses have largely faded. $\times 20,000$
We would like to thank Dr. Hans Ris for advice and Dr. Philip Loh for the use of the fluorescence microscope.

REFERENCES


A New Polyclad Turbellarian Associating with a Hermit Crab in the Hawaiian Islands

Stephen Prudhoe

At the request of Dr. Ernst S. Reese of the University of Hawaii the writer has studied seven specimens of a polyclad turbellarian found in the shells of Trochus sandwichensis occupied by the hermit crab Calcinus latens in Kaneohe Bay, Oahu, Hawaiian Islands. According to Dr. Reese (in litt.) the worm wraps itself around the abdomen of the crab and usually occurs deep in the spiral cavity of the molluscan shell. When dislodged from its shelter and placed in a dish of water together with the crab in its shell, the worm tries to re-enter the shell, but only one case was actually seen of the worm entering. The frequency with which this association occurs is about one per 25–30 crabs, but a particularly high incidence of four worms to 60 crabs was found on March 7, 1967, in the same location in Kaneohe Bay.

Apparently the polyclad has not been found in the shells of other hermit crabs, Calcinus laevismanus and Cibanarius zebra, associating with Calcinus latens, although the three species use Trochus sandwichensis shells, and the only ecological difference between them is that Calcinus latens extends further down into the sub-tidal than does either of the other two species.

The present specimens undoubtedly belong to the genus Emprostethobaryx and appear to represent a new species. They were first noticed by Dr. Reese's research assistant, Mrs. Anne Phillips Rasa, and the writer has much pleasure in naming the species after her.

The writer would like to thank Dr. Reese for giving him the opportunity of examining the worms, and for providing information on their behaviour. The type specimens are deposited in the collections of the British Museum (Natural History).

Emprostethobaryx rase sp. nov. (Figs. 1–3)

In life, the worms are light reddish brown to tan, with somewhat paler margins, but when preserved in glycerine-alcohol the body is whitish, with the dorsal surface in mature specimens being faintly mottled with brownish spots which appear to be ovaries lying beneath the wall of the body. The seven specimens available are in varying stages of development. Of the two largest mature specimens, one measures 20 mm in length and 6.5 mm in maximum width, and the other 18 mm long and 7.0 mm wide. The body is elongate oval in outline and tapering somewhat at both ends. It is dorso-ventrally flattened and measures about 1 mm in maximum thickness. No tentacles or indications of them have been made out. The cerebral organ is relatively small and lies in the median line at about 2.5 mm from the anterior margin of the body in the larger specimens.

The eyes, which are not numerous, are very small and mainly submarginal in the anterior region of the body. A few, however, lie in the cerebral area. The submarginal eyes form a band extending posteriorly to a level close behind the cerebral organ. The eyes occurring in the region of the cerebral organ are disposed in four groups (Fig. 2). Two of the groups are located one on either side of the cerebral organ; each consists of a pair of eyes, and these may be regarded as the tentacular eyes. Sometimes the tentacular eyes divide, and therefore three or four eyes may be seen in one group. The other two groups, each containing from three to five eyes arranged more or less in a row in front of the cerebral organ, may be considered as the cerebral groups, which lie more ventrally in the parenchyma than the tentacular eyes.

In a complete specimen stained with Mayer's pararaine there is a submarginal area around the whole body which stains a deeper hue than the rest of the body wall. From serial sections

1 Department of Zoology, British Museum (Natural History). Manuscript received June 27, 1967.
it has been ascertained that the differentiation of a submarginal zone is due to the presence of numerous subcuticular gland cells, which open on the ventral surface of the body. These cells appear to contain a material that is deeply stained by eosin, and when secreted onto the ventral surface of the body it probably has adhesive properties.

The mouth opens into the middle region of the pharyngeal chamber, which is very small, measuring only about 0.6 mm in length in the larger specimens. The pharyngeal chamber lies immediately behind the cerebral organ and shows no indication of possessing lateral pockets. It opens into a backward directed intestine, situated in the median line and extending into the hinder region of the body. Throughout its length, the intestinal trunk bears numerous lateral branches which divide but do not appear to anastomose.

The male genital pore is situated near the hinder extremity of the body, and the male copulatory complex lies entirely in front of it. The testes are small and follicular, and occur only in the ventral parenchyma, adjacent to the subepidermal musculature. They are distributed in the median and submedian fields from about the level of the pharynx to near the copulatory complex. They open into a common sperm duct which lies in the median line, ventrally to the intestinal trunk. This sperm duct extends from a short distance behind the pharynx into the hinder region of the body. It has thin walls and opens into a seminal vesicle. The latter is elongate, has thick muscular walls, and is lined with a ciliated epithelium. Although sperm is massed in the common sperm duct, none is present in the seminal vesicle. A short ejaculatory duct runs from the seminal vesicle to open into the prostatic organ, which is a little larger than the vesicle. The prostatic organ is pyriform and possesses a thick muscular wall investing a tall glandular epithelial lining. This lining is smooth, as in other members of the genus Emprosthopharynx. Passing through the musculature of the prostatic organ and opening into its epithelium, there are several collecting tubes of unicellular glands lying in the surrounding parenchyma. The prostatic organ opens directly
into a relatively stout, conical, penis-papilla, which occupies much of the antrum masculinum.

The ovaries are very much larger and more numerous than the testes. They lie dorsally to the testes and are distributed in the area between the cerebral organ and the copulatory complexes and extend into the submarginal regions of the body, thus having a greater area of distribution than the testes. The female genital pore lies immediately behind the male opening. It opens into a simple vagina, which extends antero-dorsally, but above the male antrum it turns sharply and runs posteriorly for a short distance. The antrum femininum (or vagina externa) is very short, while the "shell" chamber (vagina media) is relatively long, extending to the dorsal curve. The "shell" chamber is lined with a tall glandular epithelium. The "shell" glands are numerous, surrounding the "shell" chamber and forming a pair of ala-like areas extending out from the chamber on both sides. The posteriorly directed portion of the vagina (the vagina interna) is short, and into its inner end open a pair of uterine canals. These canals extend anteriorly on both sides of the seminal canal to the pharyngeal region of the body.

Hitherto, only three species of the genus *Emprosithopharynx* Bock, 1913 have been recorded: *E. opisthoporos* Bock, 1913, from the Galapagos Islands and Panama; *E. vanhooffeni* Bock, 1931, from the Cape Verde Islands and Morocco; and an "extremely minute" and undetermined species of this genus mentioned by Bock (1925:61) from the Gilbert Islands.

The species described here differs from *E. opisthoporos* in possessing fewer cerebral and tentacular eyes, in having an elongate and not a bulbous seminal vesicle, and in the fact that the sperm canal is not bifurcated in the hinder half of the body, as it is in the latter species. *E. vanhooffeni* is clearly very closely related to the present form but may be differentiated principally by its smaller size, by the distribution and greater number of eyes, and by the presence of a penis stylet.

It is interesting to note that the specimens of *E. opisthoporos* recorded from Panama by Bock (1925:61) were found in the "houses" of the pagurid *Petrochirus californiensis* from two different localities. Unfortunately, these specimens were not described morphologically,
but figures of them, in which are shown the number and arrangement of the cerebral eyes, as well as the elongate contour of the seminal vesicle, suggest that the worms are, in these features, more comparable with the present form than with the type specimen of *E. opisthoporos*. It seems possible, therefore, that only one species of *Emprostopharynx* inhabits the "houses" of pagurids in the eastern Pacific, and that it is different from the free-living form occurring in the Galapagos.

REFERENCES

Revision of the Genus *Pandanus* Stickman, Part 28
The Australian Species Published by Robert Brown

HAROLD ST. JOHN

When still a young man, Robert Brown served as botanist upon the exploring expedition under Capt. Matthew Flinders which in 1802–1805 surveyed the coasts of southern, eastern, and northern Australia. His collections included specimens of *Pandanus* from the tropical eastern and northern coasts. Two of them he published as new species, and they were the first representatives of the group to be made known from Australia. His manuscript, written on the trip, contains good and lengthy descriptions of these novelties, but when published in 1810 these were drastically condensed to a very few descriptive words for each. These two, *Pandanus pedunculatus* and *P. spiralis*, have been maintained by most subsequent botanists, but have been given very diverse application, all of which interpretations were in reasonable agreement with their brief diagnoses. Type specimens of both are still in the British Museum, and they are here illustrated and described at length, to help Australian botanists understand these first Australian species.

Section *Eydonxia*

Figs. 267–269

Expanded diagnosis of lectotype: "Trunk often 3.3–4 m tall, terete, unarmed, decumbent at base, as thick as a person’s thigh, often scaly from leaf bases, bearing prop roots; leaves in three spirals, strongly imbricate, keeled, the margins with ascending spines, the midrib below with the lower spines reflexed or alternately reflexed and ascending, or more commonly the midrib unarmed; pistillate inflorescence solitary, ovoid, bracteate" (*fide* Brown’s mss.); phalanges 5.8–6 cm long, 7.8–8.8 cm wide, 6.3–7.7 cm thick, suborbicular but with the base broad truncate, obtusely 5–6-angled, the lateral sutures wanting, the sides gently convex, not mortised, mostly developing numerous longitudinal dark cracks, upper 3/4 free, the apex semiorbicular, smooth, shining, when dried pale, yellowish brown, apical central sinuses mostly 0, but a few 0.1–1 mm deep, straight, dark, or in age splitting and brown, forming a conspicuous superficial tessellate pattern; carpels 19–23, subequal, the apices rounded to form part of the semiorbicular phalange apex, though essentially low convex, each carpel apex has perceptible ridges radiating to the angles, and the few most central ones are very oblate pyramidal or retuse around the summit, but the marginal and near marginal ones have a tiny concave platform distal of the stigma; stigmas 1.5–2 mm wide, reniform to cordate, "whitish," turning brown, papillosic, centripetal, the inner flush or slightly tilted centrally, the outer raised and divergent; proximal sinus a broad crack running 1/2–1/2 way to valley bottom; endocarp centering in lower 2/5, bony, massive, the lateral walls 10–13 mm thick, bearing lateral shoulders; mesocarp forming in the apex of each carpel a cavity crossed by a few longitudinal fibers and with transverse membranes; basal mesocarp scant, fleshy and fibrous, 3–7 mm long.

Staminate plant (*Brown 5,799 in part*): Staminate inflorescence subtended by numerous foliaceous bracts, sword-shaped, the outer green and foliaceous, the inner progressively more white, the lower 45 cm long, 5 cm wide, the uppermost 10 cm long, 5 mm wide, all with subulate prickly margins and midrib below, at least towards the tip; staminate spikes numerous, 4–7.5 cm long, 3–3.5 cm in diameter, dense, cylindric; fascicles of stamens 1.5–2.5 mm long, bearing 10–35 stamens; column 6–10 mm long, stout; free filament tips 2–3.5 mm long;

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1 B. P. Bishop Museum, Honolulu, Hawaii 96819, U.S.A. Manuscript received March 7, 1964.
Fig. 267. Pandanus spiralis R. Br., from lectotype. a, Phalange, apical view, × 1; b, phalange, lateral view, × 1.
Fig. 268. *Pandanus spiralis* R. Br. *a*, Phalange, longitudinal median section of lectotype, × 1; *b*, staminate inflorescence, from *Brown 5,799*, × 1/4.
Fig. 269. *Pandanus spiralis* R. Br., from *Brown* 5,799. Staminate fascicle, X 10.
anthers 4–5 mm long, 0.5 mm wide, almost linear, at apex bearing a subulate prolongation of the connective 0.3–0.4 mm long.

LECTOTYPE: Iter Australiense, 1802–5, R. Brown 5,799, the pistillate tessellate part (BM), but, as his manuscript reveals, this is more precisely: Gulf of Carpentaria, [Queensland, Wellesley Group of Islands], Island C [Allen I., Island Bay], Nov. 22, 1802, R. Brown 5,799, but only the two phalanges with broad tessellate apices (BM).

SPECIMENS EXAMINED: Australia, same data, the stamine inflorescence, R. Brown 5,799 (BM, K).

DISCUSSION: *P. spiralis* is a member of the section *Eydouxia*. It was one of the first two species discovered in Australia. Though remarkably distinct, it has had varied treatment, perhaps due to the brevity of the original description. Solms-Laubach (Linnaea 42:79, 1878) listed it with the Species Dubiae. Balfour (Linn. Soc., J. Bot. 17:56, 1880–1878) made it a synonym of *P. odoratisimus* L. f., as did Warburg (Pflanzenreich IV, 9:46, 1900, and Bentham & von Mueller (Fl. Austral. 7:149, 1878). It was reestablished by Martelli (Webbia 4(1):31, 90, 94, 1913; 4(2):t. 13, fig. 1–2, 1914).

Various more recent collections from more or less distant localities have been identified as *P. spiralis*, but all, it seems, incorrectly so. S. T. Blake (Austral. J. Bot. 2:130, 1954) stated that Martelli’s published illustration was drawn from Hulse’s collection from Escape Cliffs. That was implied by the wording of Martelli’s legend: "*P. spiralis*: Australia, Cliff. (H. M. ex H. Brit. Mus.)."

However, the specimen referred to: Northern Territory, Escape Cliffs, Hulls [an error for W. Hulse], (Mel.), has the phalanges 6.6–7.9 cm wide, has only 8–9 carpels, the central apical sinuses 1.5–3 mm deep, the apical mesocarp cavities 8–11 mm long, suborbicular; and the stigmas 4–5 mm long or wide. This specimen is now determined as *P. convexus* St. John (Pacif. Sci. 15:182–184, fig. 10, 1961) and is easily distinguishable from *P. spiralis*. Martelli’s illustration of *P. spiralis* does not agree with the *Hulse* collection of *P. convexus*, but on the other hand it does exactly agree with the broad, many carpelled, unlobed phalanges that are the lectotype of *P. spiralis* R. Br., and it is evident that Martelli really made the drawing from Brown’s type. Apparently there are no subsequent collections of *Pandanus* from the Wellesley Islands in the Gulf of Carpentaria.

Martelli’s illustration of *P. spiralis* (Webbia 4(1):t. 13, fig. 1–2, 1913) showed as Figure 1 an oblique lateral view of a phalange exactly like the larger of the two still in the British Museum of Natural History. His Figure 2 shows a median longitudinal section of a similar phalange. This halved phalange was not found in 1963 in the London herbarium material.

Brown’s collection of fruiting *P. spiralis*, still in the British Museum, is a mixture. Besides the lectotype, discussed above, it also contained fruits of a very different species which will be described as *P. Brownii* St. John.

Section *Pandanus*

*Pandanus Brownii* sp. nov. (sect. *Pandanus*) Fig. 270

**DIAGNOSIS**: Holotypi: Solum 2 phalanges, eis 5.9–6.2 cm longis 7.2–8.8 cm latiss 4.5–4.7 cm crassis angustae vel late flabellatis compressis cum 6 angulis majoribus et carpelis omnibus in fuga salientibus et aliquis cum 2–3 fugis longitudinalibus brevibus et valleculis solum in medio lateribus laevibus lucidis curvatis parte ½ supra libera apice rotundato suturis lateralis omnibus profundis et prominentibus et aliquis in basi extantibus, siniibus apicalibus centralibus 3–4 mm profundis in centro V-formatis subrectis sed deinde recurvatis, carpellis 19–29 plerumque in 3 seriebus eis centralibus oblate pyramidalis-semiorbiculatis illis marginalibus cum stigmatibus in margine apparentibus et cum regione lato concavo subverticillare distali, siniibus proximalibus ½–2/3 ad fondam extantibus, stigmatibus 2–3 mm latiss reniformibus plerumque prostratis eius centralibus horizontalibus illis marginalibus extraobtusitis, endocarpio solido 4 cm longo paene submediali osseoso majore majore magnocolorato lateribus centralibus 10–11 mm crassis intra circum-striatis lucidis, seminibus 15–18 mm longis ellipsoidis, mesocarpio apicali dulculluso dense cum fibris longitudinalibus, sed non in sectionibus partitis, mesocarpio basali parvo fibroso et carnoso.

**DIAGNOSIS OF HOLOTYPE**: It consists of 2 phalanges only; phalanges 5.9–6.2 cm long, 7.2–8.8 cm wide, 4.5–4.7 cm thick, narrowly to broadly fan-shaped in outline, compressed, with 6 major angles and each carpel salient and
Fig. 270. Pandanus Brownii St. John, from holotype. a, Phalange, lateral view, $\times$ 1; b, phalange, longitudinal median section, $\times$ 1; c, phalange, apical view, $\times$ 1.
forming another ridge and some of the carpels with 2–3 short longitudinal ridges and valleys only at midsection, the sides smooth, shining, curving, upper 1/2 free, apex rounded, all lateral sutures deep and prominent and several of them extending to the very base; central apical sinuses 3–4 mm deep, V-shaped at center, then recurving, nearly straight; carpels 19–29, mostly in 3 rows, the central ones oblate pyramidal-semiorbicular, the marginal ones with the stigmas appearing marginal and with a broad concave, nearly vertical surface where the outer side reaches the stigma, and a few of the carpels with the stigma slightly remote from the margin which bears a small distal concavity; proximal sinus running 1/2–3/4 way to valley bottom; stigmas 2–3 mm wide, reniform, mostly flush, the central ones horizontal, the marginal ones flush but facing outward; endocarp massive, 4 cm long, slightly submedian, bony, dark mahogany-colored, the lateral walls 10–11 mm thick, the inner surfaces striate ringed, shining; seeds 15–18 mm long, ellipsoid; apical mesocarp of dense pith, traversed by longitudinal fibers, but not forming perceptible carpellary cavities or structures; basal mesocarp scant, fibrous and fleshy.

HOLOTYPUS: Australia, Iter Australiense, 1802–5, R. Brown (BM).

DISCUSSION: P. Brownii is a member of the section Pandanus, as is the most similar species, P. Delesserti Warb., a species known only from the type collection, published by Gaudichaud without description as Ejdouxia Delesserti and said to come from Bourbon Island. No one has found it there since, and the detailed and careful monograph of the Mascarene species by Vaughan and Wiehe discredits it, and leads us to believe that the species is native elsewhere. It has 19 carpels in 3 rows in the fan-shaped phalange, 4.2 cm long, 6.5 cm wide, 4 cm thick, compressed, flabellate in outline; central apical sinuses little more than creases 0–1 mm deep; stigmas 4–6 mm long, cordate shield-shaped, and all that still remain are obtuse (none acute as shown in Gaudichaud’s pl. 18, fig. 7–8). The holotype (p) consists of a single phalange. P. Brownii differs in having the phalanges of 19–29 carpels, 5.9–6.2 cm long, 7.2–8.8 cm wide, 4.5–4.7 cm thick; central apical sinuses 3–4 mm deep, V-shaped; stigmas 2–3 mm wide, reniform. Species of this general type are known only from Australia; so it is concluded that P. Delesserti Warb. is probably an Australian species of which Gaudichaud obtained the specimen from some other botanist.

The holotype of P. Brownii was mixed with the lectotype of P. spiralis R. Br., from Allen Island, Wellesley Group, Gulf of Carpentaria, Queensland, Australia. The type collections of both of Brown’s two new species, P. spiralis and P. pedunculatus, contain mixtures of other species. It appears that either he or his successors who accessioned his herbarium considered each a variable species and added to the boxes other loose fruits which they considered similar. There is no implication that this new species and P. spiralis were collected at the same locality. In his manuscript (British Museum) he also has a description of a species from Endeavour Straits, which he called P. odoratisimus L. f., but no separate specimen of this is now found in his herbarium in London. There is such a specimen of Brown’s collecting now in Edinburgh. It is labeled “Pandanus odoratisimus ? North Coast.” It is a good stamine inflorescence of a species in the section Pandanus, but it cannot be more precisely identified.


Fig. 271

EXPANDED DIAGNOSIS OF LECTOTYPE: "Tree 4–5.3 m tall; trunk erect, 1.3–2.6 m tall, below the middle bearing at an acute angle, prop roots that are terete, roughened by remote, small tubercles; branches divaricate, sometimes reclining; leaves in terminal, loose fascicles, broad sword-shaped, above green, below glaucous, striate with fine but prominent veins, the margins ascending denticulate almost to the base, the keel retrorsely roughened scarcely up to the point 1/3 from the apex; syncarp solitary, terminal, pedunculate, nodding, ovate-globose, of the size of a human head or somewhat more elongate, bearing numerous compact phalanges," (this much extracted from Brown’s manuscript); phalange 7.6 cm long, 4.7 cm wide, 3.9 cm thick, pyriform, 4-angled, the sides gently convex, smooth, shining, of the 7 lateral sutures 5 are sealed but 2 are narrow and
evident to the base of the free part of the phalange; carpels "9–11," but 10 on the single lectotype, their apices ovoid, the marginal ones with a small, oblique, deep, concave platform; central apical sinuses 4–5 mm deep, straight, V-shaped; stigmas 1–2 mm wide, elliptic to reniform, centripetal, very oblique, brown, papillose; proximal sinus a short slit, running ⅛–⅛ way to valley bottom; endocarp apparently supramedian, but the single phalange was not cut for examination.

LECTOTYPE: Australia, "(T.) v. v.," and his manuscript adds: Sandy Cape, Hervey's Bay, [north end of Great Sandy I., Queensland], July 31, 1802, R. Brown 5,799A, the phalange 7.6 cm long, with ovoid carpel apices (BM).

DISCUSSION: P. pedunculatus is a member of the section Pandanus, though Brown's first identification of it was as P. odoratissimus L. f. His manuscript, obviously written in the field, since he recorded, "lect: July 31: descr. Augt. 3," is of 23 lines and is reasonably detailed, but his published diagnosis was of 12 words, of which 8 were descriptive. Of these the only significant ones were "phalangibus 8-18-locularibus : apice conico-lobato; ..." The species was accepted and given a vague, generalized description by Bentham & von Mueller (Fl. Austral. 7:149, 1878). It was likewise accepted by I. B. Balfour (1878), Warburg (1900), and Martelli (1913). The latter (Webbia 4(1):1. t. 1–7, 1913) extended the range from Australia to the Loyalty Islands, the Solomon Islands, and the Bismarck Islands, and illustrated the fruits from each area. Each has a different and distinctive appearance. The Australian one was actually drawn, not from Brown's type, though he had studied the British Museum collections, but from a specimen collected by F. von Mueller, labeled merely "Australia." This, as represented in Martelli's herbarium, is a single phalange 5.7 cm long, 4.9 cm wide, broadly obvoid, the scarcely convex apex nearly as wide as the middle; carpels 25 and their apices mostly conic, but a few outer ones ovoid-conic, the central apical sinuses 5–7 mm deep. The present writer does not consider it conspecific with P. pedunculatus, nor should it be used as a standard to represent that species. It is here redetermined as P. Blakei St. John. The three collections cited by Martelli from Melanesia are also extraneous, but do not need a detailed discussion here.

Martelli's classification of members of the large and difficult section Pandanus fluctuated from his early view that it contained only a widely dispersed littoral species which could not be called P. odoratissimus L. f., as that name must be used for an aggregate species; to the view that there were many separate species; to the view that there was one major species, P. tectorius, under which many varieties could be recognized; to the view that this should be called P. odoratissimus L. f.; and then to reverse swings to one of his previous views. Martelli never printed any general key to the species or taxa he accepted. He long studied Pandanus and published on it over a span of 30 years, and his work was good, but in it there are certain inconsistencies. As regards P. pedunculatus, the writer finds it to be exclusively Australian, and he has not seen any more recent collections to match the type, and no one has taken it again from the type locality.

Bentham wrote (Fl. Austral. 7:149, 1878), "I found no specimen in Brown's Herbarium, ..." but he did find one without label which he identified as P. odoratissimus L. f. The printed label form for Brown's collections was prepared, and collection (or species) numbers were assigned, by J. J. Bennett when he accessioned the herbarium into the British Museum. Hence, it is likely that the specimen here accepted as the type of P. pedunculatus was the one which Bentham had called P. odoratissimus.

The collection Brown 5,799A is of three phalanges. First, the one just described and here made the lectotype. Second, a phalange 4.7 cm long, 5 cm wide, 4 cm thick, subglobose, broad-based; carpels 10, their apices oblate pyramidal and the marginal ones with a small, concave distal platform; central apical sinuses 2–3 mm deep, and the valleys very wide V-shaped. Third, is a transverse median section 1 cm thick of a phalange with 14 carpels which seems to be identical with no. 2. These last two are surely different from the lectotype, and do not agree with the details of Brown's diagnosis, "phalangibus ... apice conico-lobato; basi subangustata." Hence, they are here excluded. They may represent Brown's collection from En-
deavour Strait, Island C, Oct. 30, 1802, which he included in his unpublished manuscript as *P. odoratissimus* L. f., and described with equal detail, but did not publish or list. In the Kew Herbarium there is a sheet with a staminate inflorescence, marked, "ex Herb. R. Brown," and an old label with, "New Holland, North Coast." Since its staminate columns are shorter and the spikes narrower, it does not seem to represent Brown’s *P. spiralis* from the Wellesley Islands, Gulf of Carpentaria, or *P. pedunculatus* from Sandy Cape on the east coast. It may be what he called *P. odoratissimus* from Endeavour Strait. There is no fruiting collection paired with this, and so it must be left undetermined.

Now we return to the consideration of the
mixed collection representing Brown's *P. pedunculatus*. It is possible that, when Brown consolidated his small study set, kept apart while on the expedition, with the ones shipped to London in casks, or when Bennett later sorted and labeled the specimens, the shorter, broad-based phalanges were dumped in the box with the lectotype of *P. pedunculatus*. In any case, they are different, and are here excluded, as not tallying with the diagnosis of that species.
Cyrtandra megistocalyx (Gesneriaceae), a New Species from Oahu, Hawaiian Islands

Hawaiian Plant Studies 28

HAROLD ST. JOHN

One's work seems never done. Though in 1966 the writer published (Bishop Museum, Bull. 229) a monographic account of twenty-five years of study of Cyrtandra, he now presents, as a supplement, one more species from the island of Oahu, Hawaiian Islands.

Cyrtandra megistocalyx sp. nov. (Sect. Cyldrocalces)

Fig. 1

Diagnosis holoty: Frutex 2 m alta, caule 2 cm diametro, ramulis glabris viridibus tum bruneis quadrangularibus teretibus in sicco contractis, cinctibus separatis 2.5–3 mm altis scutelliformibus stramineis suberosis, cinctibus fasciis 5, novellis subadpressis brunei-pilosis, ramulis foliosis 2–4 mm diametro subteretibus cito glabris, internodis 5–25 mm plerumque 15 mm longis, folii oppositis non aggregatis adscendentibus sed veistioribus paucis divergentibus inaequalibus in 5–10 nodis superis affixis, folio uno paris cuiusque 1/8–1/2 minori, petioliis 15–36 mm longis gracilibus in juviente adpresser brunei-pilosis sed tum glabris, laminis 5–20 cm longis 14–45 mm latis chartaceis oblanceolatis cuneatis decurrentibus in apice subito subacuminato supra glabris et obscure lucidis viridibus infra in midnervo adpresso brunei-pilosis et in nervis lateralibus minime pilosulis parte 1/4 ultima remote crenato-serrata, nervis lateralibus 8–17 in quoque late rectis adscendentibus tum proxima marginem interconnectis et ramulis in serris salientibus, cymis 1-floriferis sparse brunei-pilosis ex axillis foliosis, pedunculis 2–3 mm longis et in flore divergentibus, pedicelis in flore 2–6 mm longis in fructu 7–14 mm longis sparse brunei-pilosis, bracteiis duobus caducis 2.5–3 mm longis lanceolatis subadpressis brunei-pilosis densiter ad marginem sparsiter in dorso, alabastris 26–27 mm longis in vivo extra remotissime brunei-pilosi intra densiter adpresso brunei-pilosi fusiformibus corpore oblanceolato rostro 8–10 mm longo adscendentis arcuatius vel subsignoideis, lobis 5 subcommatis sed in apice labia supera cum 3 papillis et labia infera cum 2 papillis brevissimis, corpourae et parte infera rostri in flore in sinu 10 mm longo aperiens et ex eo flore exserto, calycibus 25–27 mm longis et a fructu

immaturo caducis, corollis 28 mm longis in vivo albis extra glabris tubo 20 mm longo sed in fawce capitati-glandulosi-puberulentis cineati-cylindrici in parte mediiali in 40° deflecto in basi 3 mm diametro in medio 5 mm diametro in fawce 8 mm diametro et 5 mm lati, limbo bilabiato, labia supera in 80° ab axile deflecto, lobis binis 6 mm longis 7 mm latis suborbicularibus intra in parte 1/2 infera capitati-glandulosi-puberulentis, labia infera 3-lobata lobis binis lateralis 8 mm longis 8.5 mm lati oblongi-suborbicularibus simulante puberulentibus, loba infera 9 mm longa 8.5 mm lata latitiera elliptica pagina supra supra capitati-glandulosa excepta ad apicem et infrar, staminibus binis inferis perfectis filamentis in tubo 4 mm ex basi adnatis parte libera 2.5 mm longa valida spiritaliter curvata, antheris 3.5 mm longis convinventibus oblique et asymmetricae lati-ovatis, connectivco simulante, staminodis binis lateralis in tubo 6 mm ex basi adnatis parte libera 0.3 mm longis antheroidea 0.7 mm longo translucenti, staminodeo supra simulante sed in tubo in 5.3 mm adnato, stylo 9.5 mm longo tereti glabro, stigmata cum lobis binis 3.5 mm longis 2.5 mm latis ellipticos in late 1/2 connatis, ovario 7 mm longo lineari-lanceolato glabro basi cum disco cupulato 1.8 mm alto cincio, baecis 15 mm longa 9 mm diametro ellipsoidalis alba rostrata (bacca immatura 23 × 8 mm), seminibus 0.4–0.5 mm longis 0.23–0.25 mm diametro ellipsoides mellasscis sed apicibus umbonatis bruneis corpourae cum reticulis cellulosi polygonatis elanghtatis 1/3 tum longis quam semine.

Diagnosis holoty: Shrubb 2 m tall; stem 2 cm in diameter; branchlets glabrate, green to brownish, quadrangular terete, shrinking on drying; leaf scars separate 2.5–3 mm high, shield-shaped, stramineous, corky; bundle scars 5; young shoots covered with subappressed brown pilosity; leafy branchlets 2–4 mm in diameter, nearly terete, quickly glabrate; innernodes 5–25 mm, mostly about 15 mm long; leaves opposite, not crowded, ascending, but a few older ones diverging, unequal, one of each pair being 1/8–1/2 the smaller, borne at the 5–10 upper nodes; petioles slender, 15–36 mm long, in youth appressed brown pilose but later glabrate; blades 5–20 cm long, 14–45 mm wide, chartaceous, oblanceolate and cuneate decurrent at base, the apex abruptly subacuminate, above

1 Botanist, B. P. Bishop Museum, Honolulu, Hawaii 96819, U.S.A. Manuscript received July 20, 1966.
Cyrtandra megistocalyx—St. John

Fig. 1. *Cyrtandra megistocalyx* St. John, from holotype. *a*, Habit, × ½; *b*, bud, × 1; *c, d*, flower, × 1; *e*, pistil, × 2; *f*, fruit, × 1; *g*, apex of calyx, × 4.
glabrous and dark shiny green, below finely
appressed brown pilosulous on the midrib and
slightly so on the lateral veins, the outer three-
quartors coarsely remotely crenate serrate, the
lateral veins 8–17 on a side, straight, ascending,
then near the margin the tips inarching and
branches salient in the serrae; cymes 1-flowered,
from the leafy axils, sparsely brown pilose;
peduncle 2–3 mm long, diverging in flower;
pedicels 2–6 mm long in flower, 7–14 mm long
in fruit, sparsely brown pilose; the paired bracts
of the pedicel 2.5–3 mm long, caducous, lance-
olate, brown subappressed pilose, sparsely so
on the back, densely so near the margins; buds
26–27 mm long when fresh, without very
remotely brown pilose, within closely appressed
brown pilose, fusiform, but the body oblanceo-
loid, the beak 8–10 mm long, ascending and
acute or subsigmoid, the 5 lobes almost com-
pletely fused, but at apex of the upper lip there
are 3 minute tips like rounded nipples, and 2
shorter ones of the lower lip, the body and
lower part of the beak at anthesis opening by a
distal slit 10 mm long, through which the
corolla protrudes; calyx 25–27 mm long, cadu-
cous from the young developing fruit; corolla
28 mm long when fresh, white, glabrous with-
out, the tube 20 mm long, glabrous except for the
throat which is capitate glandular puberulent,
cuneate-cylindric, but at mid-point deflected at
40° from the axis of the lower tube, at base
3 mm in diameter, at the middle 5 mm, at the
throat 8 mm high and 5 mm wide, limb 2-
lipped, 5-lobed, upper lip spreading at 80° to
the axis of the throat, the two lobes 6 mm long,
7 mm wide, suborbicular, within capitate glandu-
lar puberulent on lower half; lower lip 3-
lobed; the two lateral lobes 8 mm long, 8.5 mm
wide, oblong suborbicular, with similar glandu-
lar puberulence; lower lobe 9 mm long, 8.5
mm wide, broadly elliptic, the upper surface
capitate glandular except near the tip and below;
the two lower stamens perfect, their filaments
adnate to the corolla tube to within 4 mm of the
throat, the free portion 2.5 mm long, stout, spirally upcurved; the two perfect anthers
3.5 mm long, connivent, obliquely and asym-
metrically broad ovate, the connective similar
in shape; the two lateral staminodia adnate to
the corolla to within 6 mm of the throat, the
free filament tips 0.3 mm long, bearing an
antheroid tip 0.7 mm long, translucent; the
upper staminodium similar but attached 0.7 mm
lower down on the corolla tube; style 9.5 mm
long, terete, glabrous; the two stigmatic lobes
3.5 mm long, 2.5 mm wide, elliptic, connate 75%
way up the proximal side; ovary 7 mm long,
linear lanceoloid, glabrous, the base surrounded
by a cupulate disk 1.8 mm high; berry (a ripe
one) 15 mm long, 9 mm in diameter, ellipsoid,
white, rostrate by the base of the style (one im-
mature berry is larger, 23 × 8 mm); seeds
0.4–0.5 mm long, 0.23–0.25 mm in diameter,
ellipsoid, honey-colored but the umbonate ends
brown, the body covered with elongate poly-
gonal cellular reticulations 1/3 as long as the
seed.

HOLOYTUS: Hawaiian Islands, Oahu, Ka-
hana, Waiahole Ditch Trail, Gulch no. 17,
moist wooded gulch among Metrosideros, rare,
800 ft alt., May 2, 1954, H. St. John 25,297
(BISH).

DISCUSSION: C. megistocalyx is a member of
the section Cylindrocalyces, as is its closest
relative, C. paludosa Gaud. var. paludosa, a
plant with the cymes 1–7-flowered; peduncles
3–14 mm long; pedicels 6–21 mm long; bracts
3–8 mm long; calyx 10–20 mm long at anthesis,
splitting into 2 lips and 5 lobes 2–10 mm long;
corolla tube glabrous; anthers 2 mm long, the
connective asymmetrically broad ovate; style
6–8.5 mm long; and the stigmatic lobes 3 mm
long. C. megistocalyx has the cymes 1-flowered;
pedicules 2–3 mm long; pedicels 2–6 mm long
in flower; bracts 2.5–3 mm long; calyx 25–27
mm long at anthesis permanently united and
the 5 lobes represented only by minute nipple-
like tips; corolla tube capitate glandular puber-
ulent in the throat; anthers 3.5 mm long, the
connective circular; style 9 mm long; and the
stigmatic lobes 3.5 mm long.

The new epithet is formed from the Greek
adjective megistos, larger; and the noun calix,
cup or calyx, and is given with reference to
the large-sized calyx.
NOTE

Theophrastaceae, a Family Wrongly Attributed to the Hawaiian Flora

Benjamin C. Stone

A curious error in the stated distribution of a family of flowering plants, the Theophrastaceae, is found in two leading American textbooks of plant taxonomy, Lawrence's "Taxonomy of Vascular Plants" and Benson's "Plant Classification," both of which attribute the family to the Hawaiian as well as to the American tropical flora. Lawrence (1951:657) states (after the description of the family Theophrastaceae): "A family of 4 genera and about 60 species of the American tropics and Hawaiian Islands." Benson (1957:205) states: "The family consists of four genera occurring in the American Subtropics and Tropics and in Hawaii." Since no representative of the family occurred anywhere in Hawaii as far as I knew, I made an attempt to track down the origin of such an attribution, which proved rather simple. Jacquinia aurantiaca Ait. is credited to the Sandwich Islands by DeCandolle (1824-1873) in the Prodromus (8:150), and is also listed in the Index of Hillebrand's "Flora of the Hawaiian Islands" (1888); but on page 282 of that work is stated (in a short footnote after Embelia pacifica) the phrase, "most probably erroneously." Hillebrand continues: "It [i.e., Jacquinia] was supposed to have been collected by Menzies in 1796. The genus Jacquinia is entirely confined to America and easily to be distinguished from Myrisine and Embelia by the monopetalous corolla, which is furnished at the sinuses with sterile staminodial appendages, in the manner of Sapota, the fruit being a berry with several small angular seeds."

The explanation evidently lies in the mislabelling of a specimen of Jacquinia collected supposedly by Menzies and cited by DeCandolle. I have not seen this specimen but presumably it originated from some part of tropical America; it is most improbable that DeCandolle could have mistaken any authentic Hawaiian plant for this genus.

Intensive exploration of the Hawaiian Islands since Hillebrand's day has failed to yield any member, or even possible relative, of the Theophrastaceae; so it seems clear that the range of the family is in fact exclusively American. No member of the family appears even in cultivation.

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The Geology of the Manu‘a Islands, Samoa

GARY D. STICE and FLOYD W. MCCOY, JR.

ABSTRACT: The Manu‘a Islands are a group of three islands—Ta‘u, Ofu, and Olosega—that were built by volcanic activity along the crest of the easternmost portion of the Samoan Ridge. Ta‘u Island represents the largest volcanic center, where aa and pahoehoe flows of non-porphyrity basalt, olivine basalt, picrite basalt, and feldspar-phryic basalts constructed a volcanic shield more than 3,000 feet above sea level. The present-day total thickness of this volcanic material is over 12,000 feet, as measured from the ocean floor to the summit of Ta‘u, Lata Mountain (3,056 feet). Dips of the lava flows frequently exceed 30°, but average 20–25°. Summit collapse formed a caldera that became partially filled with ponded lavas and pyroclastic deposits which accumulated to a thickness of over 1,000 feet. From the summit area, two rift zones radiate to the northeast and northwest, the latter coinciding with the trend of the Samoan Ridge. Two smaller shields are located along these rift zones. Following a period of extensive erosion, the northeast corner of the island was built out by dunite-bearing lava flows, upon which the village of Fitiiuta now stands. A tuff complex containing large dunite xenoliths and coral blocks extended the northwest corner of the island near the village of Faleasao, burying a former sea cliff.

Ofu and Olosega islands represent a complex of at least six volcanic cones aligned along the regional rift of the Samoan Ridge. Two of these cones developed as shields that later coalesced and buried the older cones of largely pyroclastic material. The shields are composed mainly of aa and pahoehoe flows of non-porphyrity basalt, olivine basalt, and picrite-basalt, with hawaiites occurring in the uppermost portion of the shield on Ofu. More than 11,000 feet of volcanic material are represented by these shields, as measured from the ocean floor to the present-day summits of Ofu at Tumu (1,621 feet), and of Olosega at Piumafua (2,095 feet). These summits represent the approximate former summits of both shields. Average dips of the lava flows are 10–20°, locally becoming considerably steeper. Summit collapse of both shields produced Calderas, one on northern Ofu and another off northwestern Olosega near Sili Village. The caldera on northern Ofu was partly filled by the ponding of olivine basalt, hawaiite, and ankaramite lava flows. The floor of the other depression, Sili caldera, lies offshore and may never have been exposed above sea level. Following a period of quiescence and erosion probably contemporaneous with that on Ta‘u Island, recent volcanism built a lapilli tuff cone, the remnants of which form Nu‘utele and Nu‘usilaelae islets. Volcanism has continued to the present day with a submarine eruption reported between Olosega and Ta‘u islands in 1868.

Narrow fringes of calcareous beach deposits and fringing coral reefs nearly surround each of the three islands. High cliffs around the islands are the result of marine erosion. Benches at +15 and +5 feet above present sea level may indicate former higher stands of sea level.

THE SAMOAN ARCHIPELAGO lies about 2,200 miles southwest of Honolulu and about 500

1 Hawaii Institute of Geophysics Contribution No. 233. Manuscript received October 26, 1967.
2 Hawaii Institute of Geophysics, University of Hawaii, Honolulu, Hawaii 96822.
3 Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543.
the largest island in Eastern Samoa, lies about 60 miles west of the three small Manu’a Islands (14°–15°S, 169°W), and Rose Atoll, the easternmost island of Samoa, which is approximately 100 miles east of the Manu’a Islands.

The islands of Samoa are located along the crest of a submarine ridge which extends over 300 miles from Savai’i to Rose Atoll and trends approximately S 75° E. Apparently this ridge, hereafter called the Samoan Ridge, is the topographic expression of a regional rift along which the various volcanoes in the archipelago have erupted. That portion of the ridge between Tutuila and the Manu’a Islands is offset to the north but has nearly the same trend, S 70° E, as the western portion. It seems most likely that the ridge at one time was continuous, but it has been offset by later left lateral displacements. If the Tonga Trench were extended only 100 miles north, it would intersect the Samoan Ridge near the offset.

Tutuila is separated by normal oceanic depths of greater than 10,000 feet from Upolu to the west and the Manu’a Islands to the east. Thus, three major volcanic piles are aligned along the Samoan Ridge: (1) Savai’i (700 mi² above sea level) and Upolu (450 mi² above sea level), which may have been two piles that gradually merged; (2) Tutuila (53 mi² above sea level); and (3) Manu’a Islands (19 mi² above sea level).

In addition, Rose Atoll (less than 1 mi² above sea level) is the only remaining surface expression of a fourth volcanic pile atop the Samoan Ridge. In a very general way then, volcanic activity moved from east to west, whereas in the Hawaiian Islands and the Society Islands (Williams, 1933) the volcanic activity was from west to east. There have been historic eruptions on Savai’i and Upolu (Kear and Wood, 1959), as well as an historic eruption in the Manu’a Islands (Friedlander, 1910).

Friedlander (1910), the first geologist to visit the Manu’a Islands, thought that Ofu and Olosega were remnants of a single volcano and that the embayments to the north and south represented two central craters of collapse that nearly coalesced. He pointed out that the lavas of Ta’u were relatively recent in age and that the scarp on the south side of the island was formed by a caldera collapse. He also thought that the present sea cliff on the southern shoreline of the island was the vestige of further collapse. Friedlander was given an eye-witness account of a submarine eruption that occurred around 1866 between Olosega and Ta’u.

Daly (1924) spent a few days on a reconnaissance of the Manu’a Islands, during the course of his more complete study of Tutuila, and made the following observations:

(1) The western slope of Ofu and the eastern slope of Olosega largely preserve the constructional profiles of a volcanic cone.

(2) Cliffs of approximately 300 feet have been cut into the islands by the sea, whereas
the much higher (1,500–2,000 feet) curvilinear precipices on the north and south central shores suggest an origin in a double eversion through (a) volcanic explosion, (b) faulting into a sink analogous to Kilauea or Mokuaweoweo in Hawaii, or (c) large-scale landsliding due to foundering of large parts of the volcano. The first hypothesis he considered improbable, but he could not decide whether the foundering was due to collapse both to the north and to the south, or to landsliding.

(3) The lavas of Ta’u are relatively fresh, whereas deep weathering has laterized the flows on Ofu and Olosega.

From only one or two days’ observations, Stearns (1944) produced a remarkably accurate geologic sketch map of the Manu’a Islands. He divided the rock units into pre-caldera volcanic deposits, a dike complex and post-caldera volcanic deposits. In disagreeing with Daly’s statement that the Ofo-Olosega volcano was a cone of the explosive type, Stearns stated that pyroclastic beds are no thicker or more numerous than around the main vents of many basaltic volcanoes. According to Stearns, the steeply dipping pre-caldera lavas of the Ofo-Olosega cone indicate that they plunged into deep water and mantled a steep-sided submarine cone, probably largely of pyroclastic material, the calderas being formed in part by collapse over a magma reservoir and in part by landslides of the steep underlying ash beds. He also suggested the possibility that the 2,000-foot cliff on the north side of Ta’u may be due to faulting related to another caldera offshore.

Machesky (1965) conducted a gravity survey of the Manu’a Islands. The results of this work showed a Bouguer anomaly of up to +290 milligals over the center of the main caldera on Ta’u Island. The highest Bouguer anomaly on Ofu and Olosega islands (+310 milligals) was recorded over an intrusive gabbro plug at Fatuaga Point on eastern Ofu. Contouring of the corrected gravity anomalies shows a general concentric decrease away from these two centers.

GEOL OGY OF TA’U ISLAND

Nature and Distribution of Rock Types

GENERAL STATEMENT: Lavas issuing from vents on the crest of the Manu’a Ridge gradu-
ally built above sea level to form Ta’u Island. The history of the early shield-building stage is not revealed in the present exposures, but there was probably a long period of relatively quiet, frequent thin lava flows emanating from rift zones which steadily built up a basal shield volcano, as in the Hawaiian Islands. The lavas which built the main shield of Ta’u Island above sea level are exposed in the 1,400-foot escarpment that extends to the summit of the island, Lata Mountain (3,056 feet). The rocks comprising this shield, hereafter called the Lata shield, belong to the Lata formation.

The summit of the shield collapsed to form a caldera, and somewhat more explosive eruptions from cinder cones within the caldera and on the flanks of the volcano continued to build up the island. However, the eruptions were not as frequent during this stage, and erosion became more effective. There are local erosional unconformities in the lower sections exposed on Ta’u Island, indicating a long history of intermittent lava flows even before the formation of the caldera.

Two smaller shields built out the northeastern and northwestern portions of the island. The Tuna Island, on the northwest, is located along the regional rift zone. Luatele shield is part of a minor rift zone extending down the northeastern slope of the main Lata shield. These smaller shields are composed mainly of thinbedded olivine basalt pahoehoe flows with average dips of 5–10°. The summits of both shields collapsed to form depressions which were partly filled by deposits of subsequent volcanism. Small pit craters are associated with both the Tuna and the Luatele shields. The Tuna and Luatele formations are composed of the rocks of their respective shields, including the deposits within the collapsed areas.

After the formation of these shields volcanism probably subsided considerably and erosion became more pronounced. The lava flows were so infrequent that a sea cliff about 200 feet high developed around Ta’u Island. Post-erosional lava flows occasionally spilled over this cliff from cones on the flanks above it; in two places, extensive post-erosional volcanism built large areas of land in front of the sea cliff.

On the northwest corner of the island the Faleasao Formation consists of a tuff complex, approximately 1 mi² in area, which buried the
sea cliff. On northeastern Ta’u the historic village of Fitiiuta is located on post-erosional lava flows comprising the Fitiiuta Formation, which have built out a platform of nearly 1 mi² seaward of the old sea cliff. Even though the lavas in this area appear to be quite young, they probably were erupted at least 1,500–2,000 years ago, prior to settlement by the Polynesians, because, according to Samoan legends, Fitiiuta was the first village to be settled in these islands and possibly in all of Samoa. There are no Samoan legends that mention volcanic eruptions on Ta’u Island.

Thus, the rocks exposed on Ta’u Island can be placed in the following units, in approximate order of decreasing age (see legend for Ta’u Island, page 434):

1. Lata Formation
   a. extra-caldera member, consisting of pre-caldera and post-caldera deposits of the Lata shield, the latter including both pre-erosional and post-erosional volcanism
   b. intra-caldera member
2. Tunao Formation
3. Luatele Formation
4. Faleasao Formation
5. Fitiiuta Formation
6. Intrusive rocks, mainly basaltic dikes associated with Lata caldera
7. Sedimentary deposits, including alluvium, landslide debris, beaches, marshes, and so forth

EXTRA-CALDERA MEMBER OF LATA FORMATION: The lava flows and pyroclastic deposits associated with the building of the Lata shield were erupted prior to, during, and after collapse of its caldera. Those rocks not deposited within the caldera itself belong to the extra-caldera member of Lata Formation. Pre-caldera rocks are exposed in the high fault scarp on the southern part of the island. The base of the volcano is about 9,000 feet below sea level, giving a total vertical thickness of about 12,000 feet. Because of the dense vegetation on the flanks of the shield, it is impossible to distinguish pre-caldera lavas from the post-caldera lavas which form most of the surface of the Lata shield. However, the rocks cut by deep valleys on the north shore are certainly pre-caldera lavas, although late flows may have filled the floors in a few of these valleys at lower elevations. Therefore pre-caldera lavas, since they cannot be distinguished from post-caldera lavas, are not mapped separately except in a few areas where exposures are adequate.

Some of the post-caldera vents are shown on the geologic map (Fig. 2); undoubtedly there are many others that were not discovered in the dense jungle. Lava flows associated with these vents are extremely difficult to delineate. The youthful appearance of numerous post-caldera cinder cones and the fact that many flows are found spilling over the sea cliffs indicates that the post-caldera volcanism was in part contemporaneous with the post-erosional volcanism at Fitiiuta and at Faleasao. Judging from the consistent height of the sea cliff surrounding the entire island, there must have been an extensive period of volcanic quiescence after the formation of the Tunao and the Luatele shields. Therefore, post-caldera volcanism was more active prior to the formation of the sea cliff and again after its development. Lavas from the post-caldera cones on the Lata shield flowed over the sea cliff. Few can be traced to their source, and no major erosional unconformity like that represented by the lave-mantled sea cliff can be found to separate pre-erosional lavas from post-erosional deposits on the upper flanks of the Lata shield. Wherever possible, post-caldera cones and lava flows, whether pre-erosional or post-erosional, are mapped separately from the rest of the post-caldera rocks. Lavas that have flowed over the sea cliff, as well as the vents from which they were erupted, are obviously post-erosional.

The contact between the extra-caldera rocks of the Lata shield and those of the Tunao shield (shown on Fig. 3) is based on the topographic expression of the two shields, because there is no petrographic distinction between rock types. The contact between post-caldera rocks of the Lata shield and lavas of the Luatele shield is also based on topography. Even though the Luatele lavas are quite characteristic, soil cover and dense jungle obscure outcrops along most of the contact.

The extra-caldera lavas are dominantly olivine basalt with lesser amounts of picrite-basalt and feldspar-phryic basalt at low elevations. Aa and pahoehoe flows are interbedded, with aa flows
Fig. 2. Geologic sketch map of Ta'u Island, showing offshore topography. Bathymetric interval: 600 feet.
Fig. 3. Detailed geologic map and cross section of Ta'u Island.
EXPLANATION OF SYMBOLS

- Normal fault showing downthrown (D) side.
- Eroded fault scarp showing downthrown (D) side, approximately located.
- Buried fault scarp, approximately located.
- Contact, definitely located.
- Contact, approximately located.
- Dip and strike of beds.
- Horizontal beds.
- Dike.
- Intermittent stream.
- Coral reef.

CONTOUR INTERVAL 200 FEET

(For explanation of symbols, see Legend on following page.)
LEGEND FOR TA’U ISLAND

CALCAREOUS SEDIMENTS
Modern beaches (Qb) composed of unconsolidated fragments of marine organisms. Beachrock is frequently present.

NONCALCAREOUS SEDIMENTS
Alluvium (Qa), including talus, landslide debris at the base of cliffs, and stream deposits. In areas behind constructional beaches marshes (Qm) sometimes occur.

FITIUTA FORMATION
Lava flows (Qfl) of basalt and olivine basalt forming the bench at Fitiiuta. An associated cinder cone (Qfc) is mapped separately.

FALEASAO FORMATION
Undifferentiated tuff complex (Qft) of palagonitized vitric-crystal lapilli tuff, breccia, and occasional horizontal lava flows from at least three main cones centered at Faleasao, To’a, and Fa’asemene Coves.

MAJOR EROSIONAL UNCONFORMITY

LUATELE FORMATION
Thin pahoehoe flows (Qlp) of olivine basalt and picrite-basalt have built Luatele shield on the northeastern portion of the island. The depression formed by collapse of this shield was partly filled with volcanic deposits (Qtc) of red vitric-crystal ash, lapilli tuff, and olivine basalt lava, some of which contain dunite xenoliths. Associated cinder cones (Qtcc) are mapped separately where possible.

TUNOA FORMATION
Lava flows (Qte) of basalt and olivine basalt have built Tunoa shield on the northwestern portion of the island. The depression formed by collapse of this shield was partly filled with ponded lavas (Qle). Associated cinder cones (Qtcc) and Recent lava flows have been mapped separately. Usually the pre-caldera lavas and the post-caldera lavas cannot be separated and are mapped together as extra-caldera deposits. The pre-caldera member (Tle) consists of lava flows of olivine basalt, picrite-basalt, basalt, feldspar-phric basalt, and hawaiite with occasional beds of tuff. Most of these rocks have been mantled by post-caldera deposits (Qle) of olivine basalt, picrite-basalt, basalt, and hawaiite which were erupted from cones on the flanks of Lata shield. Where possible, late cinder cones (Qlec) and Recent lava flows have been mapped separately. A dike complex intruded pre-caldera (?) rocks at Laufuti.

PLIOCENE
PLEISTOCENE
RECENT
predominating in the upper part of the section. The flows at low elevations on the north slope dip 15–20°, but the uppermost layers have steeper dips of 25–35°. Near the summit the dips of these upper flows decrease to less than 15° in the high fault scarp on the southern part of the island. On the eastern and western slopes of the Lata shield and the north side of its caldera, the present ground surface also conforms to the lava flows, dipping about 15° away from the summit.

The extra-caldera member contains numerous erosional unconformities, which seem to increase in number up-section, but no profound unconformity was noted. The change to steeper dips up-section apparently was a gradual one, accompanying a decrease in volcanism and a corresponding increase in the rate of erosion of the former slope.

The olivine basalt lavas generally contain phenocrysts of olivine approximately 2–4 mm in diameter. Most of the basalt lavas contain phenocrysts or microphenocrysts 1 mm or less in diameter. Approximately one-third of the olivine basalt lavas contain plagioclase microphenocrysts 1 mm or less in diameter. A few flows exposed in the sea cliff on the northern shore between 'Ao'aauli Stream and Lepula contain plagioclase crystals up to 5 cm long. The massive portions of these flows are only 0.5–2 feet thick, but are separated by layers of clinker up to 7 feet thick. The flows are composed almost entirely of plagioclase phenocrysts with little groundmass to bind them together and therefore are very friable. A 30-foot section of these flows is exposed at the base of 'Ao'aauli stream valley and another 60-foot section only about 200 feet upstream. In several places higher in the section, thin massive central portions of aa flows only 1–2 feet thick are associated with clinker beds up to 8 feet thick; these flows generally have steep dips (30–35°), which may account for the large accumulation of clinker. One tuff bed and a soil horizon were found at about 1,200 feet elevation in 'Ao'aauli stream valley. The section up Avatele Stream, given in Table 1, is characteristic of the extra-caldera member.

Some of the larger Recent post-caldera cones of the Lata shield are Lepu'e, Olomatimu (Fig. 4, middle photo), Olomanu, and Olotania on the northwest flank, and Sa'umane and a line of four or five cones near Tafetafe on the northeast flank. Most of the lavas issuing from the post-caldera cones are olivine basalt or picrite-basalt. Vesicular basalt and hawaiite are less common. Dunite inclusions approaching 2 inches across are found in some lavas. Rarely, some augite occurs along with the olivine in these inclusions. Near the vents cinder and often welded spatter occur. The olivine basalts typically have phenocrysts of olivine approximately 2–4 mm in diameter. Plagioclase microphenocrysts approximately 1 mm in diameter are usually found in the basalts, olivine basalts, and hawaiites. The flows range from 2–3 feet up to 15 feet in thickness. Aa flows are predominant, although pahoehoe flows are occasionally found.

**TABLE 1**

| STRATIGRAPHIC SECTION OF EXTRA-CALDERA MEMBER, LATA FORMATION, UP AVATELE STREAM |
|------------------------------------------|--------------------------|
| TOP                                      | THICKNESS (feet)         |
|                                          |                          |
| Nonporphyritic, dense gray hawaiite dipping 28°N |                           |
| Red vitric ash lying unconformably on an older erosional surface and dipping 31°N | 1                       |
| A series of aa flows of olivine basalt and olivine crystals 1–3 feet thick separated by clinker beds 2–6 feet thick, dipping approximately 15°N | 25                      |
| No exposures                             | 100                     |
| Aa flow of basalt dipping S5°W, apparently poured over fault scarp to form an angular unconformity with underlying aa flows | 5                       |
| A series of thin (0.5–1.5 feet) aa flows containing abundant plagioclase laths up to 5 cm long separated by clinker beds up to 7 feet thick (dip = 28°N) | 50                      |
| A series of thin (0.5–1.5 feet) aa flows of basalt with occasional olivine phenocrysts separated by clinker beds 0.5–4 feet thick (dip = 26°N) | 20                      |
| Total thickness of section               | 226                     |

**INTRA-CALDERA MEMBER OF LATA FORMATION:** After formation of the caldera on the Lata shield, lava flows and pyroclastic deposits of the Lata intra-caldera member accumulated within the depression. They are separated from the volcanic rocks of the Lata extra-caldera...
member by normal faults bounding the caldera. Intra-caldera lavas include picrite-basalts (both ankaramites and oceanites), olivine basalts, hawaiites, and possibly one or two flows of mugearite. In addition, there are extensive deposits of ash and lapilli tuff. The flows vary from 5 feet to more than 30 feet in thickness. Nearly horizontal ash beds cover much of the remaining caldera floor.

The caldera was only partly filled. At least

Fig. 4. Ta'u Island. Top: Looking north into the Lata caldera toward Lata Mountain (A), the curved cliff (B) between the benches at 'Ele'elea and Afuatai, the bench at Tali'i (C).

Middle: Looking east toward the cliff bounding the Tunoa depression (A), Olomatimu (B), and Lepu'e (C) craters in background, the old sea cliff behind Ta'u Village (D), which has been buried by the Falesaso tuff cone (E).

Bottom: Looking northwest toward the nearly horizontal lava flows of the Fitiuta formation, which have been built out in front of the old sea cliff cut into the Luatele shield.
two and possibly three normal faults formed major benches on the caldera floor. The highest bench, at the base of the fault scarp that rises vertically 1,370 feet to Lata Mountain, is composed of a sequence of approximately horizontal pahoehoe flows. Interdigitated with them is a bed of ash 3–4 feet thick which is composed of individual laminae less than 0.5 inch thick. The ash is basaltic glass. The flows both overlying and underly the ash are 1–4 feet thick and are mostly vesicular olivine basalts with some oceanites. The vesicles in several surface flows of the caldera floor are filled with limonite-stained clay. These vesicle fillings may be the result of alteration and deposition by rising gases and hot solutions in the vent area of the volcano, or simply the result of ordinary weathering and poor drainage of nearly horizontal flows, although in other volcanic rocks in the Manu'a Islands, the vesicles are not filled.

**TUNOA FORMATION:** The small shield on northwestern Ta'u was built predominantly by thin-bedded pahoehoe flows and less abundant interbedded aa flows with average dips of less than 10°. The summit of this shield collapsed, and the central depression was partly filled by ponded lava flows and pyroclastic deposits. Subsequently, the western portion of the shield has been eroded away so that it is nearly bisected by a sea cliff. The formation is named after Tunoa Ridge, a curvilinear escarpment approximately 200 feet high which forms the eastern rim of the collapsed area.

The shield-building lava flows are mainly aphanitic basalt with some flows of olivine basalt and at least one 10-foot-thick flow of oceanite, but they are too deeply weathered to reveal much detail in composition and structure. The floor of the depression, on the other hand, is covered by pahoehoe flows with well-preservedropy surfaces and tumult, and by some aa flows still fresh in appearance. Most of these lavas are vesicular olivine basalt with feldspar microphenocrysts less than 1 mm long. At least five vents were located on the floor of the depression; undoubtedly there are others, but the dense vegetation makes their discovery more or less accidental. The vents are low cinder cones less than 30 feet high and about 200 feet in diameter. Some of the flows from these cinder cones contain small dunite xenoliths, which are usually less than 1 cm across. Two 10-foot-thick pahoehoe flows containing dunite xenoliths are exposed in the sea cliff behind Ta'u Village. Underlying these lavas is a pala gonitized tuff bed of unknown thickness.

The southern half of the cinder cone that stands on the northern edge of the escarpment near Tulatula is missing. Either half of the cone has slumped down the cliff during or after its formation, or it has been eroded back at about the same rate as the fault scarp. The former explanation seems more likely, because the cinder cone should erode much more rapidly than the lava flows exposed beneath it. The western wall of the pit crater at Fogapo'a has either been eroded away or been cut off by faulting during the collapse of the shield. Because the floor of the pit crater is at the same elevation as that of the Tunoa depression, it was probably filled in by later lavas ponding within this larger collapsed area.

**LUATELE FORMATION:** As at Tunoa, a secondary shield on the northeast side of the island has collapsed to form a depression known to the Samoans as Luatule. On the topographic map of the Manu'a Islands, published in 1963 by the U. S. Geological Survey, this place is erroneously called "Judd's Crater," but no one on the island knows it by that name. Therefore, this depression will be referred to as Luatule. The lava flows and pyroclastic deposits that form this shield comprise the Luatule formation.

The Luatule shield is made up almost entirely of thin-bedded pahoehoe flows of vesicular olivine basalt containing olivine phenocrysts up to 4 mm in diameter. Only one dunite xenolith about 0.5 inch across was found in the lavas. The flows of this shield vary in thickness from less than a foot to 3 or 4 feet. The dip ranges from 3–4° near the summit to 6–8° farther down the flanks.

The collapsed area is only about 0.3 mile in diameter, and at its deepest point is 400 feet deep. The depression has been partly filled with ponded lavas, but the nature and thickness of these deposits were difficult to determine due to poor exposures. Less than 500 feet northeast of Luatule is a small pit crater, Lualaitiiti,
which is approximately 200 feet in diameter and about 200 feet deep. Exposed in the walls of this pit crater are thin-bedded shield-building pahoehoe flows.

Luatele flows are also exposed in the old sea cliff behind Fitituita Village. In the cliff along the north coast of the island the contact between the Luatele lavas and those from the Lata shield was not found because of poor exposures. However, the topography and outcrops of the characteristic lavas inland from the cliff indicate the approximate location of the contact, as does the composition of talus boulders at the base of the cliff.

The western boundary of the Luatele lavas has been masked by the eruption of a post-caldera cone, Sa’umane Crater, located near the edge of the sea cliff. Oceanite occurs at the vent, and the flow itself is an olivine-rich, vesicular basalt. Flows from this cone, as well as from the Luatele shield, all seem to predate the sea cliff. Nearby, however, a few of the youngest Lata lavas have flowed over the sea cliff near Siua Stream.

**FALEASAO FORMATION:** The area on the northwest corner of the island, including Faleasao Village and extending east beyond Si’u’lagic Point to Tulatula, is a complex of two or three tuff cones. One of these cones is centered at Faleasao, another at To’a Cove, and probably a third, smaller one at Fa’asemene Cove. Coral fragments included in the tuff indicate that the eruptions came from vents cutting through a contemporary or relict fringing coral reef; they were therefore probably formed near sea level. The cones grew above sea level and covered the old sea cliff. Pisolites on the surface of the beds on the south flank of the Faleasao cone, at the northern end of Ta’u Village, indicate that rain accompanied the eruption and are evidence for subaerial deposition.

At Tulatula, the Faleasao tuff appears to have buried a sea stack of thin-bedded pahoehoe basalt flows that are unconformably overlain by a thicker flow of oceanite. These lavas most likely are part of the Tuna’a shield. Offshore bathymetry suggests that the base of the tuff complex is about 600 feet below sea level, indicating that the Faleasao Formation is at least 1,100 feet thick.

The rock making up most of the formation is a vitric-crystal lapilli tuff of basaltic composition. Most of the lapilli are accidental, but some are accessory. Blocks and bombs also occur in the tuff, particularly in the area around Fa’asamene Cove, where the blocks increase both in number and size, sometimes measuring over 2 feet in diameter. Along the northeast part of that cove, oceanite boulders more than 15 feet in diameter are found, but they are probably remnants of a small flow ponded within the Faleasao tuff cone.

Although magmatic bombs occur in many different areas, they are particularly abundant in the cliff behind Faleasao Village. Bombs up to 4 inches in diameter and associated bomb sags are exposed in thin beds, 0.5 inch to 1 foot thick, in the southeast portion of the inner crater wall. In this same area, the pulsating activity which built the cone is recorded in rhythmically graded beds, which are approximately 2 feet thick. At least four or five of these beds are exposed; each unit grades from lapilli tuff into fine-grained tuff. Overlying this series is a bed of volcanic breccia approximately 3 feet thick.

Breccia occurs elsewhere in the formation and is especially abundant around Fa’asamene Cove. The point between Fa’asamene and To’a coves contains an exposure of the crest of a palagonitized tuff cone overlain by breccia with an unpalagonitized, black ash matrix. The breccia is mostly accidental basalt and some picritic basalt. The blocks usually range in size from about 1 to 4 inches, although some are as large as 6 feet in diameter. Lapilli of dunite, coral, and palagonitized tuff are included within the black ash matrix, and some of the blocks of basalt contain dunite xenoliths.

Dunite xenoliths up to 2 inches in diameter are found in the lava blocks included in the breccia near Fa’asemene Cove. Dunite is also found as separate inclusions ranging from 0.1 inch to more than 6 inches in diameter. These nodules of dunite are extremely abundant on the westernmost part of the cone at Si’u’u’i Point. The dunite is essentially 100 per cent olivine, though a few augite crystals were found. Coral blocks up to 4 inches in diameter were also found at Si’u’a’i Point. Smaller fragments less than 1 inch across were found in the cliff.
behind Faleasao Village and on the east side of Sī'ulagi Point.

FITIUATA FORMATION: Post-erosional lavas which erupted from at least two vents and extended the northeast corner of Tā'u Island beyond the old sea cliff comprise the Fitiuita formation (Fig. 4C). Fitiuita Village is situated on these flows. The fresh appearance of numerous tumuli on the lava surfaces indicates a Recent age. The sea is eroding a 150-foot-high cone, Maluatia Hill, revealing its internal structure. The cone is composed of cinder, beneath which a sequence of thin-bedded pahoehoe flows and thick lenses of red cinder extends from about 90 feet down to 30 feet above sea level. This sequence is in turn underlain by a polygonally jointed flow 30–40 feet thick. The pahoehoe flows conform somewhat to the topography of the hill, but with a gentler dip. Therefore, they probably came from the same vent, and may have been an earlier part of the eruption that ejected the overlying cinder. Cinder and scoria indicate the proximity of another vent inland to the southwest, near the base of the old sea cliff behind the village. This vent, along with Maluatia Hill, the Lualaititi pit crater, and the central depression of the Luatele shield, lie along a line trending N 41° E from the caldera of the Lata shield.

The Fitiuita lavas are almost entirely pahoehoe flows of olivine basalt. These lavas are aphanitic to finely porphyritic with phenocrysts of olivine 1–4 mm in diameter and plagioclase of less than 1 mm. The lavas contain abundant dunite xenoliths ranging from less than 0.1 inch to 0.3 inch across. Nearly all of the inclusions are entirely olivine; augite is rare.

INTRUSIVE ROCKS: The only exposure of a major intrusive complex on Tā'u Island is a swarm of dikes and sills near the mouth of Laufuti Stream on the southern side of the island. Several dikes also crop out parallel to the cliff at Vailolo'atele near the southwestern tip of the island. Only a few widely scattered radial dikes were found in the high escarpment on southern Tā'u. Most of the dikes are less than 2 feet thick; none were found to exceed 4 feet. Many of them were magnetic enough to deflect a compass needle.

Virtually all of the hundreds of dikes exposed along Laufuti Stream strike N 70°–90° W and dip 80°–90° S. Most are only 2 or 3 feet thick. They are composed of dense basalt and olivine basalt, and a few are oceanite. Some of the dikes are vesicular, indicating that they were intruded near the surface. The selvage is usually less than 1 inch thick. Sometimes vesicles are concentrated near this chilled contact zone. A few multiple dikes are exposed in the steep sides of Laufuti stream valley, about 100 yards from its mouth. Olivine basalt sills were found associated with the dike complex. The sills are usually about 2 feet thick and have a maximum lateral extent of less than 30 feet. Only two or three small radial dikes were seen exposed in the northern wall of the 1,300-foot fault scarp.

A dozen or so thin (1.5–2 feet) dikes are exposed in the cliff between Papaotoma and Sī'ufa'alele points, at the southwest corner of the island. These dikes parallel the cliff which merges with the sea cliff at Tali'i, 0.6 mile to the northeast. In the same area at the base of the cliff, a Recent vent has extruded pahoehoe basalt flows which form Lotoaiese Point. The horizontal flows of olivine-rich basalt on Leatu-toga Point only 0.1 mile north are probably from the same source. Apparently the lava has flowed out over the reef.

NONCALCAREOUS SEDIMENTARY DEPOSITS: Rock waste forming the talus at the base of the old sea cliff is the most prominent noncalcareous sediment. Much of the talus has been deposited by landslides, but many boulders have become dislodged one at a time, rolling down to the base of the sea cliff. Generally the talus is heavily covered with vegetation. The alluvium deposited by the streams is a similar type of rock waste, except for the absence of soil and vegetative cover. Boulders up to 10 feet in diameter comprise the bulk of the alluvial deposits. These boulders, especially the larger ones, usually are from the dense portions of aa flows; most of them are picrite-basalt.

The cobbles and pebbles in the stream beds have usually been formed by chipping and breaking of the boulders. Most of the granules in the stream bed occur as angular chips of non-vesicular or poorly vesicular flow rock. Less frequently the granules are large pheno-
crysts of olivine, augite, or plagioclase. Some of the finest gravels are made up almost entirely of plagioclase phenocrysts as, for example, in 'Ao'auli stream bed downstream from exposed flows containing plagioclase phenocrysts up to 2 inches long.

**Calcareous sedimentary deposits:** Most of the coastline of Ta'u Island is fringed by long, narrow beaches that are usually 40-100 feet wide at mean sea level. Beachrock composed of cemented calcareous sand is common on these beaches near sea level and offshore. A fringing coral reef nearly surrounds the island.

Sand samples collected at sea level from most of the beaches around the island and offshore at Ta'u and Faleasao villages vary in median grain size from 0.29 mm to 3.50 mm. Nearly all of the samples are well sorted (only 4 of 43 analyzed samples had \( \phi > 1.3 \)). Samples from the beach and the reef flat at Ta'u Village are very well sorted, possibly due to the strong currents of up to 3.8 feet/second that flow periodically across this reef.

The noncalcareous material in these samples is mostly lithic fragments of lava rock with occasional mineral grains of olivine, augite, and magnetite. The calcareous material is mainly fragments of calcareous algae, foraminifera, coral, mollusk shells, and crustacean skeletons in approximate order of abundance. Samples from Faga on northern Ta'u have the highest percentage of noncalcareous grains, up to 32 percent. Several streams along this coast provide abundant volcanic detritus. Most other beaches on Ta'u contain more than 95 per cent calcareous material. The highest calcareous content (over 99 per cent \( \text{CaCO}_3 \)) was found in sand collected from Tufu on the southeastern tip of the island.

**Major Structures**

Ta'u Island represents the remnant of a constructional dome with two lesser shields located along northwest- and northeast-trending rift zones. The northwest rift zone, along which lie the Tunoa shield and the Faleasao tuff complex, extends seaward to Ofu and Olosega islands as the regional Samoan Ridge. Bathymetric data (Fig. 2) indicate a dozen or more volcanic cones located along the crest of this ridge; one cone erupted about 1866 (Friedlander, 1910).

Water depth over the ridge crest nowhere exceeds 750 feet, and in places the water is only 125 feet deep. Midway between Ta'u and Olosega islands, there may be a rift zone that trends approximately north-south, cutting across the Samoan Ridge. The northeast rift zone, along which lie the Luatele shield, the Fitituta lavas, and a line of cones on the flank of the Lata shield, continues at least 3.6 miles offshore, beyond which soundings are sparse.

The caldera apparently was not formed at the exact summit of Lata shield but was located slightly to the south. The beds on the southeast and west sides of the shield have an average dip of about 15°, conforming to the ground slope in that area. Within the collapsed summit area, two major benches are present—a higher one at Afuatai, and a lower one at 'Ele'elesa (Fig. 4, *top photo*). The lower bench contains three large pit craters and at least one cinder cone (see Fig. 3). The upper bench is covered with thin-bedded, horizontal layers of oceainite and olivine basalt with a few small areas that are mantled by a 3-foot bed of fine-grained tuff with laminae less than 0.5 inch thick. No vents or pit craters were seen on this bench.

Because of the relatively steep (10-17°) seaward dips of the beds at Li'u and Tali' i and the series of faults paralleling the sea cliff, the bench at Afuatai and the narrower benches to the southwest at Leavania and Tali' i, and to the southeast at Li'u, probably represent the former summit of the volcano which has dropped vertically as much as 1,300 feet. The lower bench at 'Ele'elesa and Leatutia, the pit craters and the cinder cone, probably represents the original caldera of the volcano. If so, the caldera was a little more than a mile in diameter and was partly filled with volcanic material to its present depth of 300 feet. Later collapse has dropped the adjacent summit area to form the present bench at Afuatai, as well as the Leavania-Tali'i and the Li'u slopes. These areas have therefore been shown on the geologic map as extra-caldera deposits (Fig. 3).

The offshore soundings (Fig. 2), though very sparse, also suggest the possibility of large-scale foundering on the southern slopes of Ta'u Island. The ridges on the east and west sides of the depression slope downward about 15° from their summit to the ocean floor, for a
total relief of about 12,000 feet. The caldera apparently has no southern rim, but seaward from it is a huge depression or "valley" that extends to more than 8,000 feet below sea level. The numerous small faults in the two large, seaward-sloping, downfaulted blocks at each side of the caldera could have resulted from tension produced by gravity collapse on the southern slope of the volcano (Figs. 3 and 5). On the north coast, however, the dips of the subaerial lavas are about the same as the bathymetric slope, and so there is no need to postulate extensive slope failure there.

The sea cliff along the south coast may be a fault line scarp. The dikes, described above, and the numerous faults parallel to the coastline, support this conclusion. Perhaps the area of gravity collapse (Fig. 5) contains a series of steep faults below sea level. Near the mouth of Lauftuti Stream there are two small normal faults which offset some of the dikes in the dike complex; these dikes strike N 60° E and dip 39° S with a 5-foot vertical displacement.

It is possible that the Lauftuti dike complex, the dikes exposed in the cliff between Papatoma and Si'ufa'alele points, and the vent at Lotoaise Point are related to normal faulting due to gravity collapse, rather than being associated with rift zones or the caldera of the Lata shield. A gravity collapse of such magnitude could force magma from its chamber to the surface via avenues formed by tensional faulting and fracturing of the collapsed area. If this gravity collapse did occur, it probably was not a single short event, but took place slowly over a long period of time, perhaps even continuing at the present time. Some residents of Tā'u state that they feel earthquakes every few years.

The crescent-shaped cliff bounding the Tunoa depression (Fig. 4, middle) suggests an original circular depression typical of calderas. If the escarpment is projected seaward the diameter of the depression is approximately 1.5 miles. The escarpment varies from 200 to 300 feet in height and has an average slope of about 34°. The southern end of the scarp merges with the slope of the Lata shield, late flows of which apparently have buried the southern slope of the Tunoa shield. No indication of the seaward prolongation of the escarpment was found in the sea cliff south of Tā'u Village, where it might be expected to occur, nor is the northern seaward extension of the escarpment exposed, because the sea cliff there has subsequently been buried by eruptions of the To'a tuff cone. Gravity measurements (Machesky, 1965) show no anomalous high such as is commonly associated with Hawaiian calderas (Strange, Woollard, and Rose, 1965). Nevertheless, the attitudes of the beds both within and outside the depression are evidence for partial filling of the depression produced by shield collapse. Cinder cones at the top and base of the escarpment, as well as the pit crater at Fogapo'a, indicate that faulting associated with the collapse of the Tunoa shield provided avenues along which magma was forced to the surface.

*Fig. 5. Schematic diagram illustrating "gravity collapse" and possible associated volcanic activity.*
The northeast rift zone of Taʻu, along which the Luatele shield, Lualaititi pit crater, and at least two vents at Fitiuta are perfectly aligned (Fig. 2), extends to more than 5,000 feet below sea level. Four or five extra-caldera cones are also aligned along a radial rift just to the south, but there is no indication of a submarine ridge continuing offshore.

**Geomorphology**

**Streams and Valleys:** The radial drainage pattern of the original Lata shield is still present today, although somewhat modified by faulting and later volcanism. Faleiulu Stream, for example, is a radial stream on the Lata shield, but where it encounters Tunoa shield, it is deflected to the north. Daly’s statement (1924:132), “The deepest gorge observed is about 5 meters in depth,” is correct for most of the island. However, along the northern coast, Avatele, Matautuʻao, and ‘Aoaʻauli streams have cut deep valleys into pre-caldera flows where apparently no later post-caldera volcanism occurred. ‘Aoaʻauli and Matautuʻao streams have cut canyons more than 300 feet deep, and Avatele Stream locally is more than 600 feet lower than the adjacent ridges. The entire island would probably have been similarly dissected had there been no post-caldera volcanism.

The lowermost 1,000 feet of Laufuti Stream on the southern coast is the only perennial drainage on Taʻu Island. Laufuti stream valley has been cut into the dike complex, tapping springs that are fed by ground water trapped there by the relatively impermeable dikes. The rate of discharge for this stream is on the order of thousands of gallons per minute, even during periods of minimum rainfall. The upper portion of the stream flows only after heavy rains, but because of the high rainfall (probably well over 200 inches per year in this area), water remains in small ponds and pools which contain large freshwater eels.

None of the streams on the island is sufficiently mature to have a floodplain. Alluvium is present only in the narrow stream beds and is not extensive enough to be mapped separately. Many of the stream beds contain boulders up to 12 feet in diameter.

**Beaches and Coasts:** Marine erosion during a long period of volcanic quiescence cut a sea cliff approximately 200 feet high around Taʻu Island. On the north central coast where pre-caldera lavas are exposed the sea cliff cannot be distinguished because marine erosion was subordinate to stream erosion. On the south central coast the cliff is locally as high as 1,200 feet and appears to be partly a fault-line scarp. The sea cliff is buried under the Faleasao tuff on northwestern Taʻu, and the Fitiuta lavas have built out in front of the sea cliff on northeastern Taʻu. Some of the post-erosional lavas of the Lata shield have spilled over this sea cliff.

Most of the coastline on Taʻu Island consists of beaches less than 100 feet wide. Foreshores slope 10–13°. Vegetation usually extends to within a few feet of the water, because the tidal range is low and reefs protect the shore from most storm waves. Beachrock is extensively exposed both above and below present sea level along many of the beaches and is being eroded at present. The dip of the beachrock is usually somewhat less than the foreslope of the present beaches, possibly indicating that it was formed during a slightly higher stand of the sea. Beach material varies in grain size from medium sand (Wentworth scale) to gravel, but the beachrock is usually fine to medium-sand size. At Faga, Maʻefu, and a few other areas, cobbles and boulders are cemented in a matrix of medium to coarse sand.

A bench cut into the Faleasao tuff about 5 feet above high tide was not observed elsewhere on Taʻu. If this bench was formed at a higher sea level, the stand was of relatively short duration, because only the easily eroded tuff was affected. Present-day waves are destroying this bench.

Taʻu Village is built on a terrace 10 or 12 feet above sea level. A terrace at this altitude also exists at Faleasao, Paga, Sua, Tufu, Amouli, and Siʻufaʻalele. These terraces on the southern part of the island are composed of sand and coral shingle, whereas the others are entirely sand. During hurricanes, waves top the terraces—as in the hurricane of 1959 when waves destroyed a trail on the terrace more than 200 feet inland at the base of the old sea cliff near Sua. Faleasao, the village best protected from waves,
has not been demolished by storm waves during historic time, but archaeological excavations have exposed older habitations covered by sand and gravel (W. Kikuchi, personal communication, 1966).

Around the island of Ta'u there is a nearly continuous fringing coral reef. Nowhere is the reef front more than 800 feet from shore. The island of Tutuila also has a narrow fringing reef, but soundings clearly indicate that a drowned barrier reef extends more than a mile offshore (U. S. Coast and Geodetic Survey, Chart 4190, 1962). The only offshore soundings for the Manu'a Islands were completed in 1939, and are sparse except between Ta'u and Olosega islands. Moreover, their accuracy is questionable; the islands themselves are positioned 1.7 miles farther west than is shown on more recent charts. The absence of any indication of a submerged reef around Ta'u may be merely the result of sketchy data.

The reef flat contains calcareous sand, coral, and coralline algae in patches, whereas the fore-reef is composed of prolific colonies of corals and algae. At various places along the reef front there are surge channels about 15–25 feet wide and 9–15 feet deep. Corals found on Ta'u include Acropora, Pocillopora, Millepora, Madenra, Favia, Psammocora, Goniopora, Pavona, Pavites, and Goniastrea. Halimeda, Porolithon, Goniolithon, and other calcareous algae are more abundant on the reef flat than on the fore-reef.

Geologic History

There is little evidence to indicate the age of the volcanic formations. Judging from the present stage of erosion of the island, the rapid extrusion of shield-building basalts along the crest of the Samoan Ridge began during Pliocene time. Perhaps by early Pleistocene time the Lata shield had built considerably above sea level, and volcanism subsided, allowing time for erosion between some succeeding flows. The summit of the shield collapsed, and the caldera was partly filled with lavas and pyroclastic material. This collapse may have been accompanied or followed by gravity collapse of the southern portion of the shield, involving vertical dis-placement of up to 1,400 feet. Lavas from post-caldera cones mantled the shield.

After collapse of the Lata shield, possibly in middle Pleistocene time, the Tunoa shield was formed by rapid extrusion of lavas, until its summit collapsed and the resulting caldera was partly filled with lava and pyroclastic material. At about the same time, but perhaps a little later, the Luatelie shield was also built up until its summit collapsed and the crater was partly filled. Volcanism then became so infrequent during late Pleistocene time that a sea cliff approximately 200 feet high was cut around the island.

Continued volcanism from post-caldera cones such as Lepe'e, Olomatimu, and Olenunu during Recent time mantled most of the Lata shield, several of the flows spilling over the cliff into the sea. The Faleasao and To'a tuff cones and the lava flows at Fitiuta built out in front of the former sea cliff. The most recent volcanism in Manu'a was a submarine eruption about 1866 between Ta'u and Olosega islands (Friedlander, 1910).

No definite evidence was found to indicate relative changes in sea level. The 5-foot bench in the tuff complex could be explained as due to lithification resulting from proximity to sea level, and the 15-foot constructional bench could have been formed by storm waves, but the eroded beachrock, as well as the 5- and 15-foot benches, may be indications of a more recent higher stand of the sea. The narrow fringing reef may indicate submergence rapid enough to drown any former barrier reefs.

GEOL OGY OF OFU AND OLOSEGA ISLANDS

Nature and Distribution of Rock Types

GENERAL STATEMENT: Ofu and Olosega islands are a complex of volcanic cones that have been buried by lava flows from two coalescing shields. One shield is centered off the northwest coast of Olosega near Sili Village, and the other is centered at A'ofa on the northern coast of Ofu. Older cones, approximately aligned along the crest of the Samoan Ridge, include a small cinder cone at Tauga Point on northwestern Ofu, a nearby tuff cone at the western end of Samo'i beach, a composite cone exposed
in the cliff behind To'aga on southeastern Ofu, an explosion breccia cone with an associated intrusive plug at Fatuaga Point on eastern Ofu, and another tuff cone at Maga Point on the southern tip of Olosega. Rocks of the older cones comprise the Asaga Formation, and those forming the two coalescing shields belong to the Tuafanua Formation.

The subaerial part of the islands consists predominantly of lava flows of the two shields. Deeply lateritized flows on southwestern Ofu dip southwestward away from a volcanic center that lay just north of the present northern shoreline. The summit of the shield collapsed to form a caldera, the fault boundaries of which are exposed on the north coast, and the boundaries extend inland as a steep crescentic escarpment within which nearly horizontal lava flows form a gently sloping platform known as A'ofa. Extended seaward, the caldera boundaries form a crude circle with a diameter of about 1 mile. The caldera is hereinafter referred to as the A'ofa caldera, and the surrounding shield as the A'ofa shield. Vertical dikes in the sea cliff behind Samo'i parallel the boundary of the caldera and are probably related structurally to the caldera collapse.

The presence of a second shield is suggested by the dips of lava flows on Olosega, and by numerous dikes striking northeast and dipping southwestward in the high cliff behind Sili Village (Fig. 6, top and middle). The strike of the dikes gradually changes from east-northeast near the western tip of Olosega to nearly north at the northern tip. The center seems to have been beneath the ocean northwest of Sili, and the shield will be referred to as the Sili shield. Whether or not a caldera existed in this shield is uncertain, but a suggestion of one is seen in the submarine topography (Fig. 7). However, no definite evidence was found to establish the presence of two shields, either from geologic field mapping or from gravity measurements (Machesky, 1965). Because the presence of two smaller eruptive centers seems more likely, the shield-building lavas on Ofu are tentatively mapped separately from those on Olosega.

The A'ofa caldera was partly filled with thick olivine basalt, hawaiite, and ankaramite flows. Ponded lavas buried a small intra-caldera cinder cone at the mouth of Sinapoto Stream. Some of the parasitic cones on the flanks of the volcano, as well as some of the uppermost thick ankaramite flows, may be post-caldera deposits.

Local erosional unconformities stratigraphically low in the pre-caldera section at Tafalau on eastern Olosega indicate a period of decline of volcanic activity. Some of the lavas in this area lie unconformably over weathered lava flows and ash beds, dipping as steeply as 24°. A later, more extensive period of quiescence permitted the carving of deep valleys and the formation around the islands of a sea cliff about 300 feet high. Following the formation of the sea cliff, two or three thick hawaiite lavas flowed down old valleys on the southwest side of Ofu and formed Nu'upule Rock and the ridges behind Ofu Village. Nu'utele and Nu'usilaiae islets, off the west end of Ofu, are remnants of a Recent tuff cone. The Nu'u Formation consists of these post-erosional rocks, which were deposited after the formation of the sea cliff. High cliffs truncate the lava flows on southeastern Ofu and southwestern Olosega, and there may have been founding along these coasts similar to that suggested for Tu'a Island.

Thus, the rocks exposed on Ofu and Olosega islands can be placed in the following units, in approximate order of decreasing age (see legend for Ofu and Olosega islands, page 454).

1. Asaga Formation
2. Tuafanua Formation
   (a) A'ofa extra-caldera member
   (b) A'ofa intra-caldera member
   (c) Sili Member
3. Intrusive rocks, mainly dikes associated with the Tuafanua Formation and the plug associated with the Fatuaga breccia cone
4. Nu'u Formation
5. Sedimentary deposits, including alluvium, landslide debris, beaches, marshes, etc.

**ASAGA FORMATION:** Nearly all of the cones included in this formation can be seen from Asaga Strait, which separates Ofu and Olosega islands. The To'aga composite cone and the Fatuaga breccia cone, probably the oldest features exposed on Ofu and Olosega, can be seen only in the high, nearly vertical cliffs on eastern Ofu. No outcrop could be examined closely, but numerous talus blocks scattered along the shore give some indication of the rock types present.
Fig. 6. Ofu and Olosega islands. Top: Looking east toward Asaga Strait between Ofu and Olosega. Note fringing reef around the islands with numerous channels across the reef front. Ta'u Island is faintly shown in the background.

Middle: Looking northeast toward Asaga Strait. Note the curvature in the cliff (A) bounding the Sili caldera, and the intrusive plug (B) underlying the Fatuaga breccia cone.

Bottom: Boulder of feldspar-phyric basalt on the beach at Samo'i.
in the cliff above. The To'aga composite cone is formed of interbedded aa flows, pahoehoe flows, cinder, and tuff. In the cliff, the exposures are disappointingly few due to the dense vegetation, but an ash bed representing the former surface of the To'aga cone is seen to be overlain by onlapping lavas from A'otaf'a shield.

Exposed in the cliff behind Va'oto on Ofu is a bed of red ash up to 20 feet thick. It extends up the slope of the ridge to Lepe'u'a. A lower impermeable tuff bed provides a spring in the cliff behind Va'oto that is utilized for drinking water in Ofu Village. If the thick red ash bed in this area is the same as the uppermost bed of the composite cone exposed in the cliff behind To'aga, then this cone must have extended at least to Va'oto, where west-dipping beds still occur, giving a maximum diameter at sea level of 1.5 miles. The summit of the cone was probably located about 0.4 mile due east of Tumu Mountain at approximately 700 feet above sea level.

Another larger cone of at least the same height was centered offshore between Ofu and Olosega, about 1,500 feet due east of Fatuaga Point, where a related gabbroic intrusive plug is exposed. A tuff bed in the cliff on the north side of Olosega Village apparently marks the eastern surface slope of this cone, giving it a minimum diameter at sea level of 1.8 miles. The eastern portion of the cone was buried by aa flows of the Sili shield. A large percentage of the total volume of the cone is explosion breccia consisting almost entirely of fist-sized blocks of at least six distinct lithologies—vesicular pahoehoe basalt, ankaramite, dense dike rock, olivine basalt, and two types of aphanitic basalt. The matrix, comprising less than 5 per cent of the total rock, is composed of very well indurated vitric ash that contains a few fragments of olivine crystals 1–2 mm in diameter. The cone is probably the oldest feature now exposed in the Manu'a Islands.

Near Tauga Point, at the western end of Samo'i beach on Ofu, an old tuff cone has been covered by a series of about six aa flows of the A'otaf'a shield. The northern half of the tuff cone has been eroded away by wave action, and a horizontal flow of basalt that was ponded within its crater now forms a bench about 15 feet above sea level. A 10-foot-thick yellow lapilli tuff bed, dipping 20° away from the center of the cone, pinches out 500 feet to the east and overlies a 15-foot-thick unstratified, palagonitized tuff. An adjacent but slightly later small cinder cone at Tauga Point has also been buried by later aa flows from the A'otaf'a shield. Numerous ribbon and spindle bombs occur in this cone.

At Maga Point, on the southern tip of Olosega, another old tuff cone has been buried by later flows of the Sili shield. The northern slope of this cone is 34°; its summit rose at least 250 feet above the present sea level. The lower beds of this cone are lapilli tuff with horizons locally rich in basalt blocks up to 6 inches across, and the upper 50 feet is composed of cinder and red ash. A dense flow of hawaiite, 35 feet thick, was ponded within the crater of the cone. A series of thin pahoehoe flows of the Sili shield has overridden the cone and now forms Maga Point. This sequence is overlain by interbedded aa and pahoehoe flows from the Sili shield, with aa flows becoming increasingly dominant up-section.

The cones at To'aga and Fatuaga definitely pre-date the two shields. The cones at Tauga, Samo'i, and Maga are all overlain by lava flows from the shields—but they could be parasitic cones on the flanks of the shields. However, since no evidence was found to suggest that the cones were underlain by lava flows from either of the shields, they are considered to pre-date the shields and are included as part of the Asaga Formation.

Tuafanua Formation: The Tuafanua Formation comprises the two shields centered at Sili and A'otaf'a, which buried the older cones of the Asaga Formation. Tuafanua is the area on the north shore of Ofu near the intersection of the coalescing shields. The pre-caldera lavas of the A'otaf'a shield are predominantly thin-bedded pahoehoe flows with many interbedded aa flows and occasional thin beds of ash and tuff.

The Sili extra-caldera member on Olosega also consists mainly of olivine basalt. The lowermost exposure of the pre-caldera lavas from the Sili shield is found near Leaumasili Point, on the northern tip of the island. A sequence of pahoehoe flows (1–2 feet thick), with a few interbedded aa flows up to 10 feet thick, are cut by several dikes 1–4 feet thick.
that are parallel to, or dip steeply toward, the caldera boundary to the west. In other places the pre-caldera pahoehoe flows vary from 1 to 6 feet thick but are generally less than 3 feet. The flows usually dip less than 10° away from the former summit northwest of Sili Village.

Interbedded aa flows exposed in the steep cliffs behind Sili and Olosega villages generally increase up-section in number and thickness from 2 or 3 feet to more than 20 feet. As on Ta'u, some of the steeply dipping aa flows (locally up to 30°) have as much as 10 feet of clinker associated with only 1 foot of the massive central portion of the flow.

Thick aa flows comprise most of the upper 800 feet of a 2,100-foot section which extends to the summit at Piumafua Mountain. The dips of these later flows are relatively steep, ranging between 15° and 20°. A series of 3 or 4 flows of hawaiite with a total thickness of over 75 feet are the highest flows in the section that could be closely examined. The rock is quite fresh except along some joints that are partly coated with purplish-black manganese oxide. A few exposures near the summit are probably the same thick aa flows exposed in the cliff behind Sili Village, but they are too deeply weathered to be identified.

Thus, all of the upper 600 feet of the shield may be capped with flows of hawaiite. Picrite-basalts do not seem to be as abundant on Olosega as on Ofu, but a few oceanites and ankaramites are exposed along the eastern coast of Olosega. One of these ankaramite flows contains a concentration of 90 per cent augite phenocrysts up to 0.5 inch long in the frothy 1-inch thick surface crust of the flow. Table 2 is a stratigraphic section of the Sili extra-caldera member at Tafalau on eastern Olosega.

The extra-caldera lava flows of the A'ofa shield are very similar to those of the Sili Member, consisting mainly of basalt or olivine basalt except for a few flows of feldspar-phyric basalt (Fig. 6, bottom), picrite-basalt, and hawaiite. Macdonald (1944) described a hawaiite collected by Stearns from a talus block at the base of the sea cliff near Tauga Point on Ofu. This talus block must have come from the dense, thick aa flow near the top of the sea cliff, which represents the upper portion of the shield. The thick ankaramite and olivine basalt flows at

<table>
<thead>
<tr>
<th>TABLE 2</th>
<th>STRATIGRAPHIC SECTION OF THE SILI EXTRA-CALDERA MEMBER IN THE CLIFF BEHIND TAFAHU, OLOSEGA</th>
</tr>
</thead>
<tbody>
<tr>
<td>TOP</td>
<td>THICKNESS (feet)</td>
</tr>
<tr>
<td>Nonporphyritic, weathered vesicular pahoehoe flows 1-7 feet thick, dipping 12°SE</td>
<td>90</td>
</tr>
<tr>
<td>Olivine basalt, moderately vesicular aa flows 5-7 feet thick with clinker beds 3-5 feet thick, dipping 24°E</td>
<td>30</td>
</tr>
<tr>
<td>Olivine basalt with feldspar microclites forming a dense, massive flow</td>
<td>15</td>
</tr>
<tr>
<td>Nonporphyritic, vesicular aa flows 0.5-3 feet thick with clinker beds 0.5-7 feet thick, dipping 24°E</td>
<td>20</td>
</tr>
<tr>
<td>Moderately vesicular aa flows of olivine basalt 4-7 feet thick, clinker beds 3-4 feet thick, with much red cinder and ash, dipping 24°E</td>
<td>35</td>
</tr>
<tr>
<td>Brown palagonitized vitric crystal tuff with olivine and augite crystals, lying unconformably on lower flows, tuff dipping 24°E</td>
<td>5</td>
</tr>
<tr>
<td>Minor angular unconformity due to erosion</td>
<td></td>
</tr>
<tr>
<td>Nonporphyritic basalt with feldspar microclites forming dense aa flows 3-5 feet thick, clinker beds 1 foot thick, dipping 30°E</td>
<td>30</td>
</tr>
<tr>
<td>Nonporphyritic, vesicular pahoehoe flows, 0.5-4 feet thick, dipping 30°E including:</td>
<td></td>
</tr>
<tr>
<td>ankaramite gradational to olivine-augite basalt</td>
<td>40</td>
</tr>
<tr>
<td>olivine basalt with rare augite phenocrysts</td>
<td>10</td>
</tr>
<tr>
<td>basalt containing small laths of feldspar phenocrysts randomly oriented and rare olivine phenocrysts</td>
<td>10</td>
</tr>
<tr>
<td>Talus of blocks at base of cliff</td>
<td>65</td>
</tr>
<tr>
<td>Total thickness of section</td>
<td>350</td>
</tr>
</tbody>
</table>

Tumu Mountain, the summit of Ofu, are essentially horizontal and probably represent nearly the original summit of the A'ofa shield.

Pyroclastic deposits are interbedded in the A'ofa extra-caldera member. On northwestern Ofu a palagonitized yellow lapilli tuff more than 4 feet thick, an unstratified tuff more than 50 feet thick, a few thin red ash beds, and cinder in talus are present. Red cinder found in the soil 700 feet due north of Tumu Mountain is probably from an old post-caldera vent in that area, and may have been a source for the thick flows of the Nu'u Formation. A few intercalated
beds of red ash and cinder up to 10 feet thick are present in the Sili Member on southeastern Olosega.

The A'o'fa caldera has been partly filled with lava flows and pyroclastic material. At the base of the exposed section are four dense, nearly horizontal lava flows of olivine basalt, three of which are 20–25 feet thick due to ponding within the caldera. These are overlain by thinner (1–7 feet) interbedded aa and pahoehoe flows of basalt and olivine basalt. An ankaramite boulder on the beach southeast of Tafe Stream probably came from one of the thick horizontal flows exposed near the top of the 400-foot sea cliff, indicating that some of the later intra-caldera flows were picrite. Table 3 is a stratigraphic section of the A'o'fa intra-caldera member at the mouth of Sinapoto Stream.

Just west of the mouth of Sinapoto Stream the lowermost thick flows have ponded against a cinder cone, the highest point of which is now about 60 feet above sea level. More than half of the cinder cone has been eroded away by the sea, however, and its summit probably was originally about 150 feet above the present sea level. This cone must have been the source of thin (4–8 feet) aa lavas of olivine basalt that flowed down its northwestern flank to form Lelu Point.

**NU'U FORMATION:** Nu'utele and Nu'usilaelae islets, off the western coast of Ofu, are the erosional remnants of a tuff cone, which was originally about 4,000 feet in diameter at present sea level and approximately 300 feet high, and was centered off the southwestern shore of Nu'utele. The eruption occurred near sea level after an extensive period of erosion during which a sea cliff was cut around Ofu and Olosega. The cone is composed entirely of reddish-yellow palagonitized lapilli tuff with accidental blocks and lapilli of basalt, plus a few magmatic basalt lapilli. Individual beds vary from less than 1 inch to more than 5 feet in thickness. The slopes of the original cone were about 30°. No coral fragments nor any evidences of a submarine vent were found, but the eruption may have been submarine in part.

Along the western coast of Ofu at least two flows of aphanitic basalt, in places over 35 feet thick, have flowed down the slopes of the A'o'fa

---

**TABLE 3**

<table>
<thead>
<tr>
<th>Steel</th>
<th>Top (approximately 220-foot elevation)</th>
<th>Thickness (feet)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dense gray aa flow of hawaiite containing abundant microlites of feldspar and scattered microlites of olivine probably flowed over a fault scarp (dip = 25° NW)</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>Clinker</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Dense medium-gray aa flow identical with that above, but dipping only 6°N</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>Clinker</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>No outcrops; thick soil and talus cover</td>
<td>15+</td>
<td></td>
</tr>
<tr>
<td>Nonporphyritic pahoehoe flows, 1–7 feet thick</td>
<td>30</td>
<td></td>
</tr>
<tr>
<td>Olivine basalt with olivine phenocrysts 2–3 mm in diameter occurring as approximately horizontal vesicular pahoehoe flows 1–15 feet thick; a series of thin-bedded pahoehoe flows cut by a 15-foot-thick flow that apparently plunged down a small fault scarp which had truncated the thinner pahoehoe flows</td>
<td>25</td>
<td></td>
</tr>
<tr>
<td>Nonporphyritic aa flow</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Clinker</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Olivine basalt occurring as vesicular pahoehoe flows</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Clinker</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Olivine basalt occurring as a dense horizontal flow</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>Olivine basalt occurring as a dense horizontal flow</td>
<td>25</td>
<td></td>
</tr>
<tr>
<td>Clinker</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Olivine basalt forming a dense horizontal flow, a small spring issues from its lower contact</td>
<td>25</td>
<td></td>
</tr>
<tr>
<td>Olivine basalt with abundant olivine phenocrysts forming a dense horizontal flow (exposed 0.3 mile east of section)</td>
<td>20</td>
<td></td>
</tr>
<tr>
<td>Talus</td>
<td>30</td>
<td></td>
</tr>
</tbody>
</table>

Total thickness of section 221+
sea cliff around Ofu and Olosega, they are tentatively included among the Nu‘u‘u Formation.

**Intrusive Rocks:** The intrusive rocks include numerous dikes exposed in the cliffs of Ofu and Olosega, and one or possibly two plugs on eastern Ofu at Fatuaga Point. Only one dike was found intruding the A‘ofa intra-caldera member, and nearly all of the intrusive rocks are probably older than the A‘ofa intra-caldera deposits. The plug at Fatuaga Point appears to be the intruded core of the Fatuaga explosion breccia cone. There may also be a smaller, related plug about 1,500 feet to the east, where a hill has an ovoid shape suggestive of an intrusive plug. The outcrop on this small hill is aphantic basalt and is similar to the dikes which form the razorback ridge on eastern Ofu. Perhaps the fine-grained borders of a plug have not yet been eroded to reveal its coarser grained center.

The coarser grained plug (Fig. 6, middle) at Fatuaga Point is a hypabyssal intrusion of ankaramite. It was recognized and described by Daly (1924:134) as an elliptically shaped plug with a maximum diameter of 120 feet and a minimum diameter of 80 feet. Actually it is considerably larger than this, probably at least 300 by 300 feet. The highest Bouger gravity anomaly in the Manu‘a Islands (more than +310 milligals) was recorded near this plug (Machesky, 1965). There is a gradation in grain size from olivine-titanaugite gabbro in the central portion of the plug to ankaramite near the peripheries. There is also a gradation in shape from a roughly ovoid plug near sea level to a much more elongate ankaramite dike at higher elevations. The general trend of the plug’s longest diameter is approximately N 15° W and vertical.

Near sea level at Sunu‘itao, the western edge of the plug cuts beds of explosion breccia that trend approximately N 85° W and dip 13° N. Near the top of the shark’s-tooth peak at Vainu‘uula, this breccia appears to be trending N 30° E and dipping much more steeply, about 30° W. Some of the blocks included in the explosion breccia are identical with the intrusive olivine gabbro, except that they are slightly finer grained. Thus, the intrusion probably occurred nearly contemporaneously with the deposition of the breccia. Included within the plug is a pod of brecciated pahoehoe flows of vesicular basalt, which apparently was broken off from the chamber wall and carried up with the magma during the intrusion.

Near sea level the plug is cut by numerous thin dikes that strike approximately E-W and dip 55–85° N. Most of these dikes are dense and aphantic, but some of the thicker ones are vesicular. This vesicularity, along with the open miorolitic texture of the olivine gabbro, suggests proximity to the surface at the time of intrusion. These dikes parallel those of the dike complex extending from Le‘olo Ridge eastward to Olosega, as described below.

The razorback ridge of eastern Ofu is the topographic expression of a dike complex about 400 feet wide. The dikes are nearly vertical, but some may dip steeply northward. Most are dense basalt, although olivine basalt, ankaramite, and feldspar-phryic basalt also are present. Large talus blocks of diabase, which came from thick dikes at the top of the ridge, lie along the shoreline north of Vainu‘uula.

The dike complex continues across Asaga Strait to the 2,000-foot cliff behind Sili Village (Fig. 6, middle). Near Tamatupu Point, the westernmost tip of Olosega, thick dikes with dips as low as 50° N may be slightly curved concentric to the Sili caldera, but the individual dikes could not be traced far enough to confirm this. Northeast of Piumafua the number of dikes paralleling the face of the cliff behind Sili Village decreases sharply. In the cliff behind Olosega Village north-dipping and vertical dikes related to this complex decrease markedly in number both up-section and away from the caldera. A few apparently related dikes trending about E-W cut steeply across flows dipping 10–20° away from the caldera as far as 3,000 feet south of the cliff behind Sili.

A sill about 400 feet long and 30 feet thick can be seen in the cliff at Faiva near Sili Village. A low-angle dike near the extreme eastern side of the sill discordantly intrudes a series of pahoehoe flows, striking about N 5° E and dipping 15° E, and may be the feeder dike for the sill, but this relationship cannot be seen clearly because of the vegetative cover. In this portion of the cliff most of the other dikes strike about N 30° E and are vertical, whereas
the lava flows strike about N 5° E and dip eastward, indicating that the caldera boundary swings from east-west toward north in that area. A few of the thinner vertical dikes exposed in the cliffs behind Sili and Olosega villages are radial dikes which are sometimes cut by later thick dikes concentric to the caldera.

About six vertical dikes, varying from 0.5 to 6 feet in thickness are exposed in the cliff behind Samo‘i beach on Ofu, and are nearly parallel to the western boundary of A‘ofa caldera. One of these is a multiple dike approximately 1 foot thick which is intruded concordantly by several small dikes 3–6 inches thick. A piece of dike rock containing dunite xenoliths was also found on the beach there. Several other dikes occur in widely scattered places along the cliffs of northern and southeastern Ofu. Usually they are less than 4 feet thick, vertical, and approximately parallel to the cliff face. An ankaramite dike more than 40 feet thick crops out at the top of the cliff at Muli‘olo and Tumu, and is probably the source of nearly horizontal ankaramite flows on Tumu. It may be related to the collapse of the A‘ofa caldera.

**Noncalcareous sedimentary deposits:** The talus and alluvial deposits are very similar to those described on Ta‘u. Rock waste is always present at the base of the cliff encircling the islands. Several fan-shaped landslide deposits can be seen at the base of the cliff along the coast of southern Ofu, between Va‘oto and To‘aga.

Many of the streams on southwestern Ofu and southeastern Olosega cut through deeply lateritized thin-bedded pahoehoe (?) flows and have beds of reddish-brown, sticky silt. Therefore, the stream beds are of a somewhat different character than deposits along other streams in that few large boulders are found. Parts of Tala‘isina, Top‘a, Etemuli, and S‘umulaae streams on southeastern Olosega and the upper portions of Alei, Saumolia, Tufu, Matasina, and other small streams on southwestern Ofu also have silty stream beds. Large basalt boulders are much less common in the upper portions of Tafe and Sinapoto streams on northern Ofu, where they traverse the relatively level floor of the A‘ofa caldera, than in the typical boulder beds downstream.

**Calcereous sedimentary deposits:** Most of the beaches are about 50 feet wide and rarely exceed 100 feet. They have a constant foreslope of about 10° from sea level up to the vegetation along the backshore. The beaches are composed of sand, pebbles, and cobbles of coralline algae and coral. On a few beaches some volcanic fragments of basalt, ankaramite, tuff, olivine, and augite occur, but only as minor components in the predominantly calcereous sands. The median grain size, as on Ta‘u, is usually coarse sand to gravel. Samples collected at sea level from most of the beaches around the islands and offshore at Ofu and Olosega villages are well sorted (only 1 of 35 analyzed samples had $\phi > 1.3$). Beachrock is exposed in the intertidal zone of most beaches on Ofu and Olosega, and is more than 6 feet thick at Olosega Village. Usually the beachrock has approximately the same foreslope as the present beaches.

**Major Structures**

The cones of the Asaga Formation generally have slopes of 20–35° because they are composed mostly of pyroclastic material. These cones were all subsequently buried by aa and pahoehoe flows dipping 10–20° away from the two shields which were centered at A‘ofa and to the northwest of Sili Village. The nearly horizontal flows forming the highlands of Ofu must have been near the original summit of the A‘ofa shield.

A slight break in slope forms a benchlike feature at Papausi on southeastern Olosega. Lateritized thin flows exposed on the surface in this area dip 5–9° NE, somewhat less than the present ground surface. Their approximate strike (N 30–40° W) can be seen in the formation of "steps" 1–2 feet high that presumably represent different lateritized thin flows. A cross section drawn from the high cliff at Sili through Le‘ala Point (Fig. 8) shows that these beds most likely do not represent the normal slope of the Sili shield. There are no indications of any vents in this area. These lavas appear to have come from near the summit of the shield, but apparently their dips have been flattened by some kind of an obstruction. The thick aa flow of picrite-basalt that forms Le‘ala Point dips about 14° SE and probably also came from the Sili shield. It suddenly increases in thickness...
Geology of Manu'a Islands, Samoa—Stice and McCoy

Fig. 7. Geologic sketch map of Ofu and Olosega islands, showing offshore topography. Bathymetric contour interval: 600 feet.
Fig. 8. Detailed geologic map and cross section of Ofu and Olosega islands.
ALONG B—B'

CONTOUR INTERVAL 200 FEET

(For explanation of symbols see Legend on following page.)
PLEISTOCENE—RECENT

CALCAREOUS SEDIMENTS
Modern beaches (Qb) composed of unconsolidated fragments of marine organisms. Beachrock is frequently present.

NONCALCAREOUS SEDIMENTS
Alluvium (Qa), including talus, landslide debris at the base of cliffs, and stream deposits. In areas behind constructional beaches marshes (Qm) sometimes occur.

NU'U FORMATION
Palagonitized lapilli tuff (Qnt) forms Nulu'utelae and Nu'usilaiaie inlets. A few Recent (?) flows (Qnl) of hawaiite and olivine basalt may fill former deeply eroded stream valleys on western Ofu.

MAJOR EROSIONAL UNCONFORMITY

TUAFANUA FORMATION
A'ofa (Ttae) and Sili (Tts) coalescing shields comprised of olivine basalt, basalt, picrite-basalt, and hawaiite flows with a few intercalated beds of ash, tuff, and breccia. These shields and the Fatuaga breccia cone are intruded by numerous dikes. Within A'ofa caldera volcanic deposits (Ttae) consist of thick ponded flows of olivine basalt, hawaiite, and ankaramite and a buried cinder cone.

ASAGA FORMATION
Older cones approximately aligned along the regional rift zone, including a breccia cone (Tafb) with an associated plug (Tafi) at Fatuaga Point, a composite cone (Tat) at To'aga, a tuff cone (Tam) at Mags Point, a tuff cone (Tas) at the west end of Samo'i, and a cinder cone (Tac) at Tauga Point.
downslope and seems to have ponded against an obstruction, perhaps a buried cone beneath Le'ala Point or another cone offshore from there along the crest of the Samoan Ridge. Offshore soundings in that area are sparse but do suggest the presence of a cone as shown in cross section B-B' on Figure 8.

Pyroclastic deposits are concentrated on Ofu and Olosega within a zone between sea level and an altitude of about 500 feet. Phreatomagmatic explosions commonly produce pyroclastic cones near sea level; these pyroclastic deposits represent some of the oldest rocks exposed on Ofu and Olosega, suggesting little if any subsidence of these islands since their formation. If a caldera existed in the Sili shield, its floor may never have extended above sea level. The northern boundary may always have been much lower than the southern rim, leaving the southern wall exposed to wave attack. The dike complex of eastern Ofu may have been related to the collapse of the Sili shield, or it may be an expression of volcanism along the regional rift zone of the Samoan Ridge.

In the high cliff behind To'aga, occasional dikes can be seen trending approximately parallel to the cliff face. Several large normal (?) faults can be seen in this cliff, and also in the cliff along the northern coast of Ofu near Oneonelele. The bedding in the cones has suffered large displacements, but there is no surface expression of the faults, nor could the direction or amount of their displacement be measured. These faults may have been related to the collapse that formed the A'ofa caldera.

Less than one-half of the A'ofa caldera is now present above sea level. Offshore soundings (Fig. 7) have not been made in sufficient detail to determine whether the northern half has simply been eroded away or whether foun-dering occurred. Small faults downdropped to the north within the A'ofa caldera indicate that at least minor faulting has been involved.

Soundings are not complete enough to indicate the nature of the ocean bottom in the huge embayment between southeast Ofu and southwest Olosega (Fig. 6, top). As Daly (1924) suggested, some type of foun-dering probably occurred in this area, but there is no evidence for another caldera. Perhaps gravity collapse similar to that suggested for Ta'u is responsible for the formation of the high cliffs.

**Geomorphology**

**STREAMS AND VALLEYS:** The stream valleys on southwestern Ofu and southeastern Olosega extend away from the former summits of the shields in a radial drainage pattern. Streams within the A'ofa caldera drain the intra-caldera area and empty into the sea along the clifed north coast. Because these islands are both lower in elevation and smaller in area than Ta'u, there is considerably less rainfall and resultant runoff. Therefore, the streams are neither as large nor as numerous as those on Ta'u. All streams on Ofu and Olosega are intermittent, flowing only after a downpour. The stream valleys are all youthful and nowhere exceed 50 feet in depth.

**BEACHES AND COASTS:** After cessation of volcanic activity on Ofu and Olosega an extensive cliff 200–400 feet high was carved into the island by the sea. Behind Ofu Village the cliff is only about 80 feet high due to protection from wave attack afforded by the tuff cone offshore. The much higher cliffs along the northern and southern coastlines originated by faulting and/or foundering but have certainly been modified by marine erosion. The sea cliffs are usually slightly higher than those on Ta'u, perhaps because a longer period of time has elapsed since there was frequent volcanic activity, or because a larger amount of more easily eroded pyroclastic material was deposited near sea level on Ofu and Olosega.

Landsliding and subsequent removal of the talus by wave action are also important erosional processes, especially along the high cliffs of the northern and southern coasts. The numerous fan-shaped landslides and fresh scars in the cliffs above indicate that this process is operative at the present time. A landslide at Pouono, the southern part of Olosega Village, is so fresh in appearance that it probably occurred since the area was inhabited by the Samoans.

Individual blocks also work loose from the cliff face and fall, forming talus slopes that extend almost continuously around the islands at the base of these cliffs. The reef flats are lit-
tered with large talus blocks in front of areas where cliffs are high enough for falling rocks to build up sufficient momentum to roll across the reef. A Samoan legend relates how a young girl was killed by a large block that rolled across the reef at Sili, where she was fishing.

The constructional bench 12–15 feet above sea level that was found on Ta'u is also well developed on Ofu and Olosega, although here it is nearly 20 feet above sea level in some places. Sili, Olosega, and Ofu villages are all built on these sandy areas. Other examples of this constructional bench are found at Va'otō, To'aga, and Mafa'afu on Ofu and at Oge on Olosega. The bench is about 900 feet wide at Va'otō and over 1,000 feet wide at Olosega Village, but the average is about 300 feet. Usually a 9–10° foreslope rises steadily to the crest of the bench 15–20 feet above sea level; sometimes there is an intermediate bench. At Va'otō and Olosega Village, swamps have formed between the bench crest and the talus slope at the base of the cliff.

On the seaward side of Nu'utele Islet a bench is present at the same level as that in the tuff complex at Faleasao on Ta'u. The bench is 5 feet high, has a maximum width of 30 feet, and, as on Ta'u, was developed only in tuff. No evidence was found to indicate how the bench was formed, whether by a Recent higher stand of the sea—of such short duration that only the easily eroded tuff was affected—or by lithification of the tuff at sea level due to contact with sea water.

Beachrock is commonly exposed above the high tide line along beaches, indicating that it is out of equilibrium with present sea level. If beachrock forms at a shallow depth beneath the beach surface, then its exposure in Manu'a may indicate formation during a slightly higher stand of sea level.

Like Ta'u, Ofu and Olosega are completely encircled by a narrow fringing reef (Fig. 6, top). The reef front is only 0.3 mile offshore at its widest point, Ofu Village. The reef there has a more prolific coral growth than in any other area in Manu'a. Most of the coral genera recognized on Ta'u were also found on Ofu and Olosega. In addition, Orbicella and Zoaanthus were found only on Ofu. The latter is a soft Alconarian coral that is particularly abundant in the area between Ofu Village and Nu'utele Islet. A "lithothamnium ridge" occurs along the reef front near Nu'usilaeilae Islet on the south and Tauga Point on the north. Millepora tenera Baschma, a stinging coral, was found only on Ofu but, according to the natives, it is present on Ta'u also.

Both large, deep channels and shallower, narrow channels or surge channels are cut into the reef front. The large channels have sand floors, extend out to depths of about 60 feet, and are often as wide as 25 feet. Strong currents flow out through the larger channels such as those off Ofu Village between Nu'utele Islet and Tauga Point and between Nu'usilaeilae Islet and Nu'upule Rock, as well as off Olosega Village. The surge channels extend out to about 30-foot depths, have overhanging sides, and usually do not have sediment covering their floors, although a boulder-sized coral shingle sometimes occurs. Generally they do not cut completely through the reef into the reef-flat, as do the larger channels. Surge channel widths vary from 3 to 10 feet.

Geologic History

Estimating the probable lengths of time required for the various events in the formation of Ofu and Olosega islands, it seems most likely that at least five cones built during Pliocene time were buried by lavas from the A'ofa and Sili shields during Pleistocene time. After summit collapse of the shields, volcanism decreased so that a sea cliff about 300 feet high was cut around the islands. At approximately the same time, gravity collapse similar to that suggested for Ta'u may have caused the embayment of southeastern Ofu and southwestern Olosega. Faulting and further collapse also may have occurred north of the islands in the area of Sili caldera.

Recent volcanism on southwestern Ofu built the tuff cone on Nu'utele Islet. A few thick aa flows in this area may have poured down old valleys from post-caldera cinder cones. As on Ta'u, the 5-foot bench in the tuff could be explained by a consolidation due to contact with sea water, but a Recent shift in sea level is indicated by the beachrock now being eroded in many places around the islands. Hurricanes and storm waves may be responsible for the 15-
20-foot constructional bench. All sediments except the beachrock are unconsolidated and appear to be of Recent age.

ACKNOWLEDGMENTS

All of the costs for field work, thin sections, air photos, maps, and so forth, were defrayed by funds from National Science Foundation Grant No. GP-2196. Air photos and maps were obtained from the Topographic Division of the U.S. Geological Survey. G. A. Macdonald aided with many helpful comments both in the field and in the laboratory. Both Macdonald and R. Moberly, Jr., of the Hawaii Institute of Geophysics critically reviewed the manuscript.

The field work in Samoa was undertaken with the permission of High Chief Lefiti, District Governor of Manu’a. The Samoan people were extremely cooperative and their hospitality was overwhelming. Especially appreciated was the assistance of High Chief To’atolu Nua of Ta’u Village; Reverend Soloi of Fitiiuta Village; Chief Milo and Ai Fa’i of Olosega Village; and Sione Malauulu, High Talking Chief Velega, and High Chief Misa of Ofu Village. Without the help of the Samoan people the field work would have been much more difficult, if not impossible.

REFERENCES

Soil Sequences in the Hawaiian Islands

G. Donald Sherman and Haruyoshi Ikawa

The wide range of conditions under which soils have developed in the Hawaiian Islands has produced a pattern of soil geography which reflects the differential influence of the intensity and capacity factors of soil weathering.

Soil formation is the product of two actions, weathering (W) and leaching (L), on the surface and near the surface of the earth's crust. Weathering is the process of mineral decomposition, and leaching is the solution of more or less soluble constituents and their removal in the percolating waters. Both of the processes occur at different degrees of intensity but under the normal temperatures and pressures of the earth's surface. Soil is formed from its geological parent materials by decomposition of various products of volcanic action in situ or after their transportation either in their natural state or after the action of various agencies of disintegration and erosion, or after partial or complete decomposition to secondary minerals in situ or after deposition of more or less soluble constituents. In all instances soil is the product of these actions on the surface under the prevailing environment to form surface horizons which are distinct and parallel to the topographic surface rather than to the geological formations of the earth's surface.

The weathering action in soil formation (WxL) is strongly influenced by intensity factors of environment and time, and by capacity or inherent (resistance) factors of the parent material. The intensity factors are age or time of exposure (A), climate, including temperatures and rainfall (C), drainage (D), and vegetation (V), all of which govern the rate of action. The capacity factors are size of the units or texture (T), the inherent stability of mineral to decomposition (M), and the nature of the surface of mineral unit or coating (S). Thus

the rate of soil formation may be expressed by the formula:

\[ K \text{ (rate of soil formation)} = \frac{W \times L \times ACDV}{TMS} \]

Since this reaction theoretically has been in existence since the formation of the earth's surface, \( K \) is a dynamic transitory equilibrium which is proceeding toward a system having some form of static equilibrium. In reality it cannot become a static system, since, over geological time, almost imperceptible changes continue to occur causing real changes. Therefore the system is considered a dynamic static system. Thus the products of soil formation will occur as a sequence, reflecting the influence of age, climate, etc. The members of a sequence in the early dynamic stage will exhibit great variation, but with time (A) it approaches a dynamic static system as the influence of the intensity and capacity factors approach zero. During this process, then, soils in any environmental area range from great variability in early stages to a high degree of uniformity in old age.

Sequences of soils in Hawaii occur which reflect the differing degrees of dominance of one or more of the soil-forming factors during the process of soil formation from a single type of parent material—e.g., in the different areas of one lava flow. Studies are being made of the inter-relationships of the soils in these sequences as means of gaining a better understanding of soil genesis. The soils of these sequences reflect the effect of increasing intensity of the soil-forming factors, as, for example, increasing amounts of annual rainfall, age or increasing time of exposure to weathering processes, and increase in the amount of specific surface in the weathering material due to differing rock textures.

The Hawaiian Islands are a natural laboratory for the study of soil formation. The islands have a remarkably uniform subtropical climate with very little difference between the mean temperatures of winter and summer. On the other
hand, there is a wide range of annual rainfall—from 5 to over 500 inches per year, the heaviest occurring at the higher elevations of 2,000 to 4,500 feet. The distribution of rainfall varies from strongly seasonal in some areas to rather uniform distribution in others. The variable rainfall results in widely different types of vegetation—shrub, open forest, and rain forest. These vegetation types range from a high base circulating system in low rainfall areas to a very acidic system of the fern forests of the tropical rain forest areas.

The islands have developed as peaks of a mountain built up by volcanic action on the ocean floor. Progressive lava flows of basalt, andesite, and trachyite and their pyroclastic deposition of volcanic ash and cinders have built up a series of islands ranging in geological age from several million years to current depositions of lava. The oldest island is Kauai at the northwestern end of the island chain, and the most recent is Hawaii at the southeastern end of the chain. The range of geological ages represented by the different islands affords excellent facilities for a study of age on soil development on relatively similar parent rocks having a low quartz content. The mountainous character of the islands provides a great variety of drainage conditions. Thus, soil sequences are developed which reflect the effect of age, rainfall, drainage or percolating water patterns, and parent material.

SOIL SEQUENCE RELATED TO RAINFALL

Tanada (1951) pointed out the relationship between rainfall and kaolin content of soils of the Hawaiian Islands. According to his results, it was concluded that where the rainfall was more than 30 inches per year, the kaolin content of the soil decreased with increasing annual rainfall. Cline et al. (1955) and Sherman (1949) have reported a sequence of soil development which was related to both the amount of annual rainfall and its monthly distribution. The former, in an indirect manner, described and classified soils by the association of increasing content of free oxides to increasing rainfall. Sherman (1949), having the benefit of a broader knowledge of chemical composition, was able to make more specific conclusions as to the type of oxides which would be concentrated in the soil solum with the varying distribution patterns of rainfall. He found that the soils developed under a climate having alternating wet and dry seasons would show an increasing content of iron and titanium oxides and a corresponding loss of kaolin with increasing rainfall. Aluminum oxide would increase in the soils formed under a rainfall distribution which resulted in continuous moist conditions in the soil solum, and again with a loss of kaolin. In subsequent work, Sherman (1952) showed that these relationships would hold only under conditions of free internal drainage. If the internal drainage became restricted, resilication or kaolinization would occur in the soil. The data given in Table 1 show the mineral composition of a sequence of soils formed on a single basalt lava flow. As annual rainfall increases, the kaolin content decreases as long as the internal drainage of the soil is good. The Koolau soils, which have poor internal drainage, have a high content of kaolin. As rainfall increases, gibbsite increases in this soil sequence as long as internal drainage of the soils is good; again, this is shown by the Koolau soils.

A sequence of soils will develop under very low rainfall conditions which do not provide sufficient leaching for the removal of the bases. Under these conditions, the content of the montmorillonite type of clay minerals will increase with rainfall up to a point where the base removal has been sufficient to produce an acid condition resulting in an instability of the 2:1 layered aluminosilicate crystal lattice structures. At this point, kaolinization will be initiated. From this point, the kaolin content will continue to increase until base removal in the leaching nears completion, creating a very acid condition in which kaolin becomes unstable and decomposes, and further desiccation occurs. This will lead to the formation of free oxides. A sequence of soils having an increasing content of montmorillonite minerals has not been observed in the Hawaiian Islands. Soils developed on volcanic ash under an annual rainfall between 2 and 20 inches will probably show this condition. Our preliminary examination would support this possible relationship. A sequence of soils showing increasing kaolin content has been found in the soils of the Low Humic Latosols.
formed where the annual rainfall is 15 to 40 inches, with the help of some low rainfall intergrades. The intergrade soil will have decreasing amounts of 2:1 layered alumino-silicate clays with increasing kaolin clay content as rainfall increases. The peak of kaolinization will occur in soils developed under about 35 inches of rainfall. An excellent sequence of this type can be found on the island of Oahu near the West Loch area of Pearl Harbor. Beginning at this point, and following the Kunia road, one encounters, in order, soils of the Honouliuli family → Molokai family → Lahaina family developed on alluvial materials. These soils are formed under 15 inches of rainfall, in the case of the soils of the Honouliuli family, to 35 inches for soils of the Lahaina family, and show the mineral relationships described as above, from montmorillonite type of clay minerals to a completely kaolinized profile.

SOIL SEQUENCE DUE TO AGE

Mohr (1944) has pointed out that soil formation progresses through stages of development ranging from youthful to senile. Soil formation is a dynamic process which proceeds at various intensities depending on the weathering environment. The influence of time on soil formation has been studied in the Hawaiian Islands. Attempts are being made to study sites which have identical climatic conditions with comparable parent materials. Since age is the variable being studied, it is impossible to find on a single island soils showing a sequence of the effect of this soil-forming factor. Therefore, to make this study, it is necessary to select sites on different islands.

The first observed effect of age on soil formation is the disappearance of soils of two prominent great groups occurring on the geologically young islands of Hawaii and East Maui—soils of the Reddish Prairie and Latosolic Brown Forest groups. These soils are absent on the older islands with the exception of a small area on Molokai having soils of the Oli Series which belong to the Reddish Prairie group. However, the soils of these two great groups, on chemical and mineralogical examination, show evidence of strong development of Latosol features. Both soils have weak A1 horizons which grade gradually to a lighter-colored B horizon, which in
turn overlies an unweathered volcanic ash. The difference between the groups is largely in the degree of removal of bases by leaching and the increased content of free oxide. Generally, soils of the Low Humic Latosol and Ferruginous Humic Latosol occur on the older islands in areas of similar environmental conditions, but do not occur on the younger islands. The work of Tamura et al. (1955) supported the hypothesis that the soils of the Latosolic Brown Forest were the precursors of the Ferruginous Humic Latosol. This conclusion was based on similarities in mineral composition of soils of the Naiwa family of the Ferruginous Humic Latosol group of West Maui, and the soils of the Olinda family of the Latosolic Brown Forest group of East Maui. The similarities between the soils of the Reddish Prairie group and soils of the Low Humic Latosol group are even greater.

An attempt has been made to study the changes made by weathering in soils of the same type from different areas, but formed under the same climatic environment and from very similar parent materials. Field observations indicated that a Lahaina soil developed on the Waimea volcanic series of Kauai (the oldest flows of the Hawaiian Islands) showed morphological properties suggesting a greater degree of clay minerals than was normal for these soils, which are made up predominantly of kaolin clays. Chemical analyses of samples of soil of this profile were compared with the analysis of a soil belonging to the Lahaina family formed under almost identical conditions but from Molokai, a younger island. The results of these analyses are given in Table 2, for the younger Lahaina soil, and in Table 3 for the older Lahaina soil. A comparison of the data reveals that the older soil has lost more silica, calcium, and magnesium than has the younger. The higher content of titanium and iron oxides in the surface horizon of the older Lahaina soil would suggest that the process of weathering is slowly converting this soil to one having the characteristics of the Ferruginous Humic Latosol group. Further evidence of the greater desilication in the geologically older profile is shown in the molecular ratios of SiO_2 to R_2O_3, which range from 0.84 to 1.14 in the older profile to 1.36 to 1.87 in the younger profile. Likewise, the ratio of SiO_2 to Al_2O_3 was consistently lower in the older profile. The ratio of SiO_2 to Fe_2O_3 was lower in the older profile and also much lower in the surface horizon. This soil must be considered at least an intergrade to the Ferruginous Latosols.

**TABLE 2**  
**CHEMICAL COMPOSITION OF A SOIL OF THE LAHAINA FAMILY FROM THE ISLAND OF MOLOKAI; MODERATE AGE OF WEATHERING**

<table>
<thead>
<tr>
<th>CHEMICAL CONSTITUENT, PER CENT</th>
<th>0-3</th>
<th>3-15</th>
<th>15-35</th>
<th>35-46</th>
<th>46-60</th>
</tr>
</thead>
<tbody>
<tr>
<td>SiO_2</td>
<td>31.23</td>
<td>32.23</td>
<td>32.36</td>
<td>32.73</td>
<td>40.80</td>
</tr>
<tr>
<td>Al_2O_3</td>
<td>23.84</td>
<td>23.76</td>
<td>24.85</td>
<td>26.30</td>
<td>25.61</td>
</tr>
<tr>
<td>Fe_2O_3</td>
<td>23.29</td>
<td>23.96</td>
<td>23.40</td>
<td>23.46</td>
<td>17.84</td>
</tr>
<tr>
<td>TiO_2</td>
<td>4.90</td>
<td>5.78</td>
<td>5.81</td>
<td>4.67</td>
<td>3.74</td>
</tr>
<tr>
<td>MnO</td>
<td>0.30</td>
<td>0.30</td>
<td>0.22</td>
<td>0.19</td>
<td>0.28</td>
</tr>
<tr>
<td>CaO</td>
<td>0.76</td>
<td>0.58</td>
<td>0.72</td>
<td>0.43</td>
<td>0.71</td>
</tr>
<tr>
<td>MgO</td>
<td>0.51</td>
<td>0.45</td>
<td>0.43</td>
<td>0.39</td>
<td>0.62</td>
</tr>
<tr>
<td>K_2O</td>
<td>0.20</td>
<td>0.13</td>
<td>0.13</td>
<td>0.05</td>
<td>0.07</td>
</tr>
<tr>
<td>Na_2O</td>
<td>0.03</td>
<td>0.06</td>
<td>0.03</td>
<td>0.08</td>
<td>0.06</td>
</tr>
<tr>
<td>pH</td>
<td>6.2</td>
<td>6.2</td>
<td>5.2</td>
<td>4.9</td>
<td>—</td>
</tr>
<tr>
<td>K = SiO_2/R_2O_3</td>
<td>1.36</td>
<td>1.40</td>
<td>1.38</td>
<td>1.35</td>
<td>1.87</td>
</tr>
<tr>
<td>K = SiO_2/Al_2O_3</td>
<td>2.21</td>
<td>2.30</td>
<td>2.21</td>
<td>2.12</td>
<td>2.71</td>
</tr>
<tr>
<td>K = SiO_2/Fe_2O_3</td>
<td>3.57</td>
<td>3.58</td>
<td>3.70</td>
<td>3.71</td>
<td>6.07</td>
</tr>
</tbody>
</table>
TABLE 3

Chemical Composition of a Soil of the Lahaina Family of the Low Humic Latosol from Kokee Road, Kauai; Exposed to Weathering for a Long Geologic Period

<table>
<thead>
<tr>
<th>CHEMICAL CONSTITUENT, PER CENT</th>
<th>HORIZONS IN INCHES</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0-9</td>
</tr>
<tr>
<td>SiO₂</td>
<td>21.08</td>
</tr>
<tr>
<td>Al₂O₃</td>
<td>20.64</td>
</tr>
<tr>
<td>Fe₂O₃</td>
<td>34.63</td>
</tr>
<tr>
<td>TiO₂</td>
<td>10.41</td>
</tr>
<tr>
<td>MnO</td>
<td>0.24</td>
</tr>
<tr>
<td>CaO</td>
<td>0.09</td>
</tr>
<tr>
<td>MgO</td>
<td>0.96</td>
</tr>
<tr>
<td>K₂O</td>
<td>0.02</td>
</tr>
<tr>
<td>Na₂O</td>
<td>0.14</td>
</tr>
</tbody>
</table>

The chemical and mineralogical changes occurring in the profile of the older Lahaina soil support the hypothesis of sequence of soil formation presented by Sherman in 1949. In this hypothesis, it was proposed that the kaolin soils of the Low Humic Latosols would lose their bases and would slowly desilicate with geological age and gradually acquire the characteristics of soils of the Ferruginous Latosols.

SEQUENCE OF ROCK WEATHERING

A study of progressive rock weathering as it is related to the origin of the parent material

TABLE 4

Chemical Composition of Ultrabasic Basalt Rocks and the Soil Weathered from Them Under Different Rainfalls (the Soil Sample in Each Case is 2 Inches from Rock)

<table>
<thead>
<tr>
<th>SAMPLE DESCRIPTION</th>
<th>SiO₂ %</th>
<th>Al₂O₃ %</th>
<th>Fe₂O₃ %</th>
<th>TiO₂ %</th>
<th>LOSS ON IGNITION %</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. From Low Humic Latosol, Kapaa, Kauai—45 inch rainfall</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rock core</td>
<td>42.4</td>
<td>14.9</td>
<td>14.8</td>
<td>2.1</td>
<td>1.6</td>
</tr>
<tr>
<td>Weathered soil</td>
<td>25.9</td>
<td>24.5</td>
<td>30.0</td>
<td>4.7</td>
<td>10.6</td>
</tr>
<tr>
<td>B. From transition zone between Ferruginous and Low Humic Latosol groups, 2 miles west of Kapaa, Kauai—60 inch rainfall</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rock core</td>
<td>42.9</td>
<td>14.6</td>
<td>14.6</td>
<td>2.0</td>
<td>1.3</td>
</tr>
<tr>
<td>Weathered soil</td>
<td>24.8</td>
<td>29.0</td>
<td>30.0</td>
<td>4.2</td>
<td>12.1</td>
</tr>
<tr>
<td>C. From Ferruginous Latosol, Wailua Homestead, Kauai—90 inch rainfall</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rock core</td>
<td>45.8</td>
<td>16.2</td>
<td>14.9</td>
<td>2.5</td>
<td>2.5</td>
</tr>
<tr>
<td>Weathered soil</td>
<td>18.5</td>
<td>32.2</td>
<td>29.6</td>
<td>5.2</td>
<td>14.4</td>
</tr>
<tr>
<td>D. From Ferruginous-Aluminous Latosol, Wailua Game Refuge, Kauai—120 inch rainfall</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rock core</td>
<td>36.7</td>
<td>10.8</td>
<td>14.2</td>
<td>2.8</td>
<td>--</td>
</tr>
<tr>
<td>Weathered soil</td>
<td>2.4</td>
<td>39.3</td>
<td>36.5</td>
<td>6.5</td>
<td>16.7</td>
</tr>
</tbody>
</table>
of the soil is being made on the island of Kauai. Included in this study is the identification of the conditions which result in widely different first products of mineral weathering of rock. The rocks considered in this study are from along a uniform lava flow of a melilite nepheline basalt located in the Wailua Homestead area, and exposed to a range of rainfall of from 45 to 200 inches per year. The rocks immediately below the soils are weathered, most of them to kaolinitic and bauxitic saprolite. Samples of weathered saprolite can be found which have an unweathered core of the rock. In every case, the boundary between unweathered rock and the weathered clay is very sharp and abrupt. The chemical analyses and mineral identification by differential thermal analysis are given in Table 4 and Figure 1. Where the rainfall is between 40 and 60 inches, the first product of weathering is kaolin, having a silica content of 32 per cent and an alumina content of 28 per cent. Under 120 inches of rainfall, the first product of weathering is a ferruginous bauxite containing 2 per cent silica, 39 per cent alumina, and 36 per cent iron oxide. The weathered rocks between these two extreme points vary greatly, but most of them have weathered to either a kaolinitic or bauxitic saprolite. However, they show a gradation of mineral weathering in which gibbsite increases and kaolin minerals decrease, as shown in Figure 1.

The data obtained from the chemical analysis of the rock and its soil product (Table 4) show a relatively uniform composition in the rock cores. Rock D probably has lost some of its silica due to the wetness of its location. The soil analyses show the increasing influence of leaching due to increased annual rainfall. As rainfall increases, the silica content of the soils decreases (from 26 per cent to 2 per cent), the alumina content increases (from 24 to 39 per cent), and iron oxide increases slightly (from 30 to 36 per cent). The chemical and mineralogical analyses by differential thermal methods (Fig. 1) indicate that as rainfall increases, the stability of kaolin type minerals decreases and the free oxides become the stable minerals of the soil. The soil from rock A shows thermal reaction for kaolin minerals while the soil from rock D shows a trace for kaolin and a strong reaction for gibbsite.

**SUMMARY**

The soils of the Hawaiian Islands offer excellent opportunities for the study of the effects on soil formation of the differential intensity of the factors involved in soil development.

There are sequences of soils which reflect the effect of rainfall: soils rich in montmorillonite type of minerals develop in areas of low rainfall, kaolin develops where rainfall is moderate, and free oxides where the amount of rainfall...
favors complete leaching and rapid desilication of the weathering matrix.

The islands offer an excellent site also for the study of the effect of age on soil development. Examples of the transition of one type of soil group to a soil group of greater stability are described.

The interaction between the influence of parent material and of weather and rainfall is being studied. The first phase of this preliminary study is to determine why the products of rock weathering can range from kaolin to ferruginous bauxite on a single lava flow, with rainfall being the chief variable. The second phase is a study of the effect of the nature of the first product of rock weathering on subsequent soil formation. Soils of three great soil groups are developed on this parent material, namely, Aluminous Ferruginous Latosol, Ferruginous Humic Latosol, and Low Humic Latosol.

REFERENCES


The Ecology of the Replacement of *Pseudosquilla ciliata* (Fabricius) by *Gonodactylus falcatus* (Forskål) (Crustacea; Stomatopoda) Recently Introduced into the Hawaiian Islands

ROBERT A. KINZIE III

Although knowledge of the Hawaiian stomatopods was summarized by Townsley in 1953, the occurrence of a species of *Gonodactylus* not previously recorded from Hawaii (Kinzie, 1965) indicated a possible introduction and necessitated a revision of information on this group in Hawaii.

Previous workers, when discussing the Hawaiian stomatopods (Brooks, 1886; Bigelow, 1931; Edmondson, 1921; and Townsley, 1953), all indicated that *Pseudosquilla ciliata* (Fabricius) was the most common species. It was recorded as occurring on sand and mud flats as well as in coral heads. The only record of *Gonodactylus* from Hawaii before 1965 was *G. guerini* White, but this species was taken from deep water (Brooks, 1886; Edmondson, 1921; Townsley, 1953).

The stomatopod fauna of Hawaii prior to 1953 can be characterized as follows: *Pseudosquilla ciliata* was the dominant shallow water stomatopod. It was found in sand and mud flats, and was also the most common species living in dead coral heads. *P. ciliata* and occasional *P. oculata* Brullé (Townsley, 1953), were the only large (over 3 cm) stomatopods found living in coral heads.

In 1954, Townsley (personal communication) observed that a species of *Gonodactylus* was found in dead coral heads in Kaneohe Bay and on the reef at Waikiki. In 1958, Okamoto (in an unpublished class report at the University of Hawaii) reported two species of stomatopods that had not been described from the Hawaiian Islands. One was *G. hendersoni* Manning (as *G. demanii* Henderson), four specimens of which were taken in a fresh state from the stomach of one *Neotunnnus macropterus* (Yellowfin tuna) caught near Oahu. The other species was *Gonodactylus falcatus* (Forskål).

Collections on the reefs at Waikiki in 1963 yielded a number of large *G. falcatus* as well as *G. hendersoni*. Further collections at other areas (Figs. 1 and 2) indicated that *G. falcatus* was by far the most abundant stomatopod in dead coral heads and *G. hendersoni* was fairly common in some areas. On the other hand, *Pseudosquilla ciliata* was not found in dead coral heads, but it was still abundant living within burrows in sand and mud flats.

From these facts it appears that the coral head habitat, once almost exclusively occupied by *P. ciliata*, was taken over completely by *Gonodactylus falcatus* in about nine years. This paper describes some of the results obtained while investigating this hypothesis and studying the origins, possible mode of introduction, and mechanism of replacement of *Pseudosquilla ciliata* by *Gonodactylus falcatus*.

**DISTRIBUTION AND NOTES ON DESCRIPTION OF NEW HAWAIIAN SPECIES**

*Gonodactylus falcatus* (Forskål)

A synonymy of *G. falcatus* is given by Holthuis (1941).

**DISTRIBUTION:** *G. falcatus* is widely distributed through the Indo-Pacific, ranging from the Red Sea (Forskål, 1775; Ingle, 1963) through the Indian Ocean to western Australia (Stephenson, 1962), northward to the Ryukyu Islands (Fukuda, 1910), Sagami Bay (Utinomi, 1961), and Tsusima and Ogawara islands (Komai, 1927). *G. falcatus* occurs in the Pacific in Queensland (Stephenson, 1953), the Bonin...
Islands (Odhner, 1923), Saipan in the Marianas (Holthuis, 1953), Truk in the Carolines (Komai, 1927), Eniwetok in the Marshalls (University of Hawaii collections), the Gilbert Islands (Holthuis, 1953), Rotuma (Borрадайл, 1898), Fiji (Odhner, 1923), Samoa (Bigelow, 1931) and Hawaii (Kinzie, 1965).

**Morphological Variations:** As Manning (1967:3) mentioned, the qualitative aspects of the telson morphology are important as taxonomic characters in this genus. Attempts to compare statistically the Hawaiian population with populations from other areas gave no conclusive indications of affinities of the Hawaiian population. This was due to the small size of the samples from most of the areas studied and the large variance of the statistics compared.

Qualitative comparisons indicated that the Hawaiian specimens had more inflated and rounded telson carinae than comparable individuals from Samoa, Palau, the Philippines, and the Red Sea. On the other hand *G. falcatus* from Queensland has slightly more inflated carinae than comparable Hawaiian specimens.

Serène (1954) has recognized *G. falcatus*...
Pseudosquilla Replaced by Gonodactylus—Kinzie

var. ternatensis as a "dwarf race," with carinae of the telson and the sixth abdominal somite appearing more inflated, and sexual dimorphism expressed at a smaller size than in G. falcatus s.s. His descriptions and figures of this "dwarf race" show that it is similar to the Hawaiian specimens. However, Manning (1966:110) feels that until more is known the name G. falcatus should be used for specimens of this suggested race.

Fig. 2. Map of Kaneohe Bay showing plankton runs (A, B, and C), and collecting areas (1, mud flat; 2, coral reef; 3, sand flat).
Although the specimens from the Philippines that were examined had narrow carinae, individuals with more rounded carinae also occur in the same area. Kemp (1915) stated that the majority of specimens from Bantayan, Puerto Galera, and Taytay in the Philippines belongs to "form B" which corresponds to Borradaile's var. *rotundus* (probably Serène's *ternatensis*), while one specimen is the narrow keeled type "form A" (= var. *ternatensis* deMan).

**SEXUAL DIMORPHISM:** Sexual dimorphism has been noted in *G. falcatus* by Bigelow (1931) and Serène (1954). The sexes are quite distinct in Hawaiian specimens. The females (Fig. 3A) have the carinae of the sixth abdominal somite and telson narrower and more sharply defined than those of males of corresponding size (Fig. 3B). However, as Serène has noted, this inflatedness and rounding of carinae and telson teeth increases with age, so care must be taken to insure that equal-sized specimens are being compared. The dimorphism of the dactylus is also pronounced in the Hawaiian population, with the females having the swelling of the base of the dactylus making a sharp angle with the shaft (Fig. 4A), while in the males the angle is less distinct (Fig. 4B); furthermore the tip of the dactylus of the females is sharply recurved, while that of the males is not. This dimorphism is developed at a small size in the Hawaiian population. The dactylus of a 43-mm male from the Philippines were indistinguishable from those of females from the same area, while in the Hawaiian collections specimens as small as 17 mm could be sexed by inspecting the dactylus.

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**Fig. 3.** Telsons of female (A) and male (B) *Gonodactylus falcatus* from Hawaii. *sc*, Submedian carinae; *ic*, intermediate carinae; *lc*, lateral carinae; *cc*, central carinae; *lt*, lateral teeth; *it*, intermediate teeth; *at*, accessory teeth; *st*, submedian teeth.

**Fig. 4.** Dactyli of female (A) and male (B) *Gonodactylus falcatus* showing sexual dimorphism.
Although it is difficult to describe unambiguously the coloration of the two sexes, there is a definite tendency for the larger males of the Hawaiian G. falcatus to be dark with dark green to black predominating. The females are reddish shading to brown in smaller individuals. In specimens under 35 mm both males and females are tan to brown.

*Gonodactylus hendersoni* Manning

Since the completion of the work reported in this paper, the second species of *Gonodactylus* found in Hawaii has been removed from *G. demani* and named *G. hendersoni* by Manning (1967).

**DISTRIBUTION:** Burma, Indonesia, Queensland, Viet Nam, and Puerto Galera and Taytay in the Philippine Islands. On Oahu this species is most commonly found at Waikiki reef and off Diamond Head (Fig. 1). It has not been taken from Kaneohe Bay. Manning’s description (1967) is based in part on Hawaiian material.

**ORIGIN AND INTRODUCTION OF NEW HAWAIIAN SPECIES**

**Area of Origin**

The almost simultaneous appearance of these two species in Hawaii indicates that they probably came from the same area at the same time. With this consideration in mind, localities where both *Gonodactylus falcatus* and *G. hendersoni* occur will be considered as possible areas from which the founding populations might have come.

Although *G. falcatus* occurs as far north as Japan, the most northerly reports for *G. hendersoni* are from Nha Trang in Viet Nam and Taytay and Puerto Galera in the Philippines. These two species co-occur further south in Queensland and to the west through Indonesia.

**Means of Introduction**

In discussing the introduction of marine invertebrates, larval transport and introduction of adults require separate consideration.

**Larvae:** Although attempts to rear the larvae of *G. falcatus* were unsuccessful, the results indicated that the minimum pelagic life of the larvae of this species is about 22 days. This agrees with the findings of Gurney (1937) and Manning and Provenzano (1963). The great size attained by some stomatopod larvae taken at sea (Brooks, 1886:5ff.) suggests the possibility that stomatopods can prolong their larval life for an indefinite period, until proper conditions for metamorphosis are encountered. There is little concrete evidence to support this suggestion, however, and it must be considered as a tentative hypothesis until substantiating work has been done. If *G. falcatus* came to Hawaii as larvae the most likely possibility is that they were carried by the Kurashio current (Sverdrup, 1942:723). The probability seems slight that larvae of both *G. falcatus* and *G. hendersoni* were brought at the same time from as far as the northern Philippines by ocean currents.

**Adults:** Transportation of benthic adults over long distances would probably involve transport in or on ocean-going vessels. Newman (1963) suggested that the shrimp *Paelemon macrodactylus* was transported from the Orient to San Francisco Bay in the salt water system of a ship. Jones (1966) reports the introduction into Hawaii of the brackish-water copepod *Pseudodiaptomus marinus*, which had previously been recorded only in Japan. It is unlikely that this copepod was transported by ocean currents, since the time required would have covered several generations, and the species is restricted to brackish waters. Newman stated that the proper conditions for introduction by this method do not commonly occur, which would explain the infrequency of introduction of any species that cannot be transported on the exposed surface of a ship’s bottom (Matsu, Shane, and Newman, 1964). The simultaneous introduction of both species of stomatopods in the saltwater system of a ship seems unlikely.

During World War II, the United States Navy used a number of barges constructed of concrete in their operations in the south and west Pacific. At the end of the war many of these barges were towed back from the localities where they had been used. Most of them were left in Guam, but some were towed as far as the Hawaiian Islands. They are now located, submerged, in West Loch at Pearl Harbor (Fig. 1) on Oahu. These barges were frequently used
in the area of the Philippines and the South China Sea. The towed speed of these barges was about three knots, an uncommonly slow speed for sea-going vessels, but one that would not dislodge any organisms living in fissures or holes in the hull. The almost simultaneous appearance of *Gonodactylus falcatus* and *G. hendersoni*, soon after the arrival of these slow-moving barges from the area where they co-occur, is strong circumstantial evidence for their introduction by this means.

**ECOLOGY OF REPLACEMENT**

In investigating the mechanisms of replacement of *Pseudosquilla ciliata* by *Gonodactylus falcatus*, three parameters of the environment and biology of these species were compared: salinity tolerance, larval ecology, and behavior.

**Salinity Tolerance**

Both *Pseudosquilla ciliata* and *Gonodactylus falcatus* live on the shallow reef flat where fluctuations in salinity can be substantial. In an area such as Kaneohe Bay (Fig. 2) where the replacement of *Pseudosquilla ciliata* in coral heads by *Gonodactylus falcatus* is complete, the effect of differential salinity tolerance might have been important in effecting the replacement.

In May 1965, exceptionally low (0° to -0.04°) tides occurred in the mornings during the first days of the month. During the night of May 2–3 there was a very heavy rainfall. Coconut Island in Kaneohe Bay reported 10.52 inches of rain during the night and morning, and a nearby weather station reported 21.61 inches. On May 7 surface salinities in the southern part of the bay ranged from 7.8 o/oo to 30.3 o/oo with an average surface salinity of about 20 o/oo. These lowered salinities showed a gradient from the surface to about 1.5 meters. Water in the southern part of the bay showed considerable dilution for at least two weeks. On May 5 a collection was made of dead animals that had washed up on a mud flat in the bay (Fig. 2, 1). In this collection were 49 dead stomatopods of which 42 were *Pseudosquilla ciliata*, 5 were *Gonodactylus falcatus*, and 2 were *Lysiosquilla maculata*. On May 23 collections were made on a reef near Coconut Island (Fig. 2, 2). All the coral on the surface of the reef was dead, and the characteristic fauna of amphipomid and polynoid worms, alpheid shrimp, and xanthid crabs was greatly reduced or entirely absent. The only exception to this reduction in numbers was *Gonodactylus falcatus*. In 20 liters of coral, 5 *G. falcatus* were found, which is about the normal number for samples of similar size from the reef. On July 17 all the loose coral was collected from an area 25 m² on the same reef. The fauna in these coral heads appeared to be returning to normal, though it was still noticeably reduced. From this coral, however, 69 *G. falcatus* were collected. Of the 42 females in the collection, 9 were carrying eggs.

Though qualitative, these observations suggest that *Gonodactylus falcatus* has a wider range of salinity tolerance than does *Pseudosquilla ciliata*. To test this hypothesis a series of tests on the differential salinity tolerance of these two species was performed. Two procedures were used. In the first, the animal was removed from seawater of normal salinity and placed directly into the water of the test dilution. In the second series, the animal was acclimatized for specified time intervals to increasing dilutions until the maximum dilution was reached. The second method probably more closely approximated the natural conditions where the amount of runoff, and hence dilution, increases gradually.

The results of these tests are shown in Table 1. In both series of experiments *Gonodactylus falcatus* exhibited a greater degree of salinity tolerance than did *Pseudosquilla ciliata*.

**Larval Ecology**

In order to obtain information on the breeding periods of *Gonodactylus falcatus* and *Pseudosquilla ciliata*, as well as the relative reproductive activity of these two species, investigations were carried out on the planktonic larvae of both species for a period of one year. Plankton tows were made at three areas in Kaneohe Bay from October 1964 to October 1965 (Fig. 2). Run A, close behind Coconut Island, was chosen to sample water from as close as possible to a reef where both species were known to be abundant. Run B was chosen to give a sample of the more inshore water of the reef system in the bay. Run C sampled water that had less contact with the inshore reefs and was more open to the waters of the ocean.
The numbers of *Gonodactylus falcatus* and *Pseudosquilla ciliata* larvae are shown in Figure 5. The numbers of *Gonodactylus falcatus* larvae taken during the year's sampling showed two peaks—one from October to January, and one from late March to mid-April—although larvae of this species were taken throughout the year. This was especially true of run C where all but three samples contained *G. falcatus* larvae in stage IV. *G. falcatus* larvae of stages III, V, and VI were taken only occasionally.

During most of the year *Pseudosquilla ciliata* larvae were either absent from the plankton samples or were represented by small numbers, generally less than *Gonodactylus falcatus*. However, during late spring coincident with the peak of *G. falcatus*, there was a peak in numbers of *Pseudosquilla ciliata* larvae taken in all runs. If the year sampled was typical of the situation in Kaneohe Bay, *Gonodactylus falcatus* with its two periods of breeding activity would have a reproductive advantage over *Pseudosquilla ciliata* with only one. The fact that *Gonodactylus falcatus* larvae are generally more abundant might only be an indication that larger numbers of this species were present in Kaneohe Bay at the time the study was made, and might not be a measure of relative reproductive ability. However, *Pseudosquilla ciliata* was still very common on the sand and mud flats in the bay.

**Behavior**

It was observed in the field that *Gonodactylus falcatus* was apparently more aggressive than *Pseudosquilla ciliata*. Where *Gonodactylus falcatus* would snap readily with its raptorial claws when touched, *Pseudosquilla ciliata* would only occasionally strike. Whenever several *Gonodactylus falcatus* were put together in an aquarium with few places to hide, there was constant fighting and usually only the largest survived. This was found to occur even when the animals were only a little more than 2 cm long. On the other hand, *Pseudosquilla ciliata* indi-
Fig. 5. Graph of numbers of stomatopod larvae taken in Kaneohe Bay during years 1964-1965. Each group of three bars represents one day’s haul. The bars represent runs A, B, and C in that order.

Individuals fought among themselves less frequently, even when the aquarium was fairly crowded. When put together in an aquarium, the Gonodactylus falcatus killed the Pseudosquilla ciliata even when the P. ciliata were considerably larger. This suggested the hypothesis that the greater aggressiveness of Gonodactylus falcatus might have been an important factor in its replacement of Pseudosquilla ciliata in the coral head habitat.

Most of the Gonodactylus falcatus collected for these studies were taken from dead heads of the coral Porites compressa. However, this species is also found in the dead bases of living heads of Pocillopora meandrina and from clumps of the coralline alga Porolithon, and occasional individuals have also been seen in bare rock or moving about on the surfaces of coral heads.

When specimens of Gonodactylus falcatus were taken from coral heads they were consistently wedged between the branches of the coral near the base. They were usually found with the body flexed, the telson covering the anteroventral part of the body. In this position the sides of the animal are protected by the branches of the coral, the dorsal surface is covered by thick exoskeleton, and the ventral surface is within the curve formed by the animal doubling upon itself.

Pseudosquilla ciliata was taken from two types of habitat: from burrows which the animals had dug in fine muddy sand and silt, and from areas with a similar substratum but with a great deal of algal growth (Fig. 2, 3), chiefly Acanthophora, where the animals were seen moving about on the bottom in shallow water. When
Pseudosquilla ciliata was observed in burrows, only the eyes and most anterior part of the body were visible. When disturbed, an animal would rapidly retreat into the burrow, and reappear after a few minutes. Since P. ciliata can be found in burrows in muddy bottoms and walking freely on the bottom, and since, prior to 1953, it was taken from coral heads, this species seems to have a wider range of possible habitats than does Gonodactylus falcatus.

The fact that coral heads were occupied by Pseudosquilla ciliata before 1953 suggested experimental comparison of agonistic behavior in relation to a "burrow." Ten trials were made to study the behavior of P. ciliata and Gonodactylus falcatus in relation to a glass vial placed in the sand in the bottom of an aquarium to simulate a burrow. Individuals of either species would readily enter the vial. However, if Pseudosquilla ciliata had entered the vial, it was invariably driven out by Gonodactylus falcatus when the second animal was placed in the aquarium (Table 2). G. falcatus, on the other hand, was never driven from a vial by Pseudosquilla ciliata. When fighting, Gonodactylus falcatus curls its telson up under the ventral surface of the body in the same attitude as when it is in a coral head. While this is a very effective method of fighting when the animal is in a small crevice or hole, it leaves the animal unsupported when fighting in the open. When in the glass vial, G. falcatus blocks the opening with the telson, but its eyes are able to see out and the raptorial claws can be snapped out the opening. This position and method of defense is similar to that exhibited by G. falcatus living in coral heads.

Pseudosquilla ciliata, on the other hand, does not exhibit any such specialized fighting behavior, and it always fled from the vial when attacked by Gonodactylus falcatus. In their burrows in mud flats, the animals either retreated deeper inside or left the burrows if they were disturbed.

**TABLE 2**

Sizes of Gonodactylus falcatus and Pseudosquilla ciliata Used in Behavior Experiments (In All Cases G. falcatus Drove P. ciliata Out of the Vial and Went in Itself)

<table>
<thead>
<tr>
<th>EXPT. NO.</th>
<th>Pseudosquilla ciliata</th>
<th>Gonodactylus falcatus</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>5.0-cm male</td>
<td>4.5-cm male</td>
</tr>
<tr>
<td>2</td>
<td>6.3-cm female</td>
<td>4.0-cm female</td>
</tr>
<tr>
<td>3</td>
<td>5.5-cm male</td>
<td>4.5-cm female</td>
</tr>
<tr>
<td>4</td>
<td>5.5-cm male</td>
<td>4.0-cm female</td>
</tr>
<tr>
<td>5</td>
<td>5.3-cm male</td>
<td>4.3-cm female</td>
</tr>
<tr>
<td>6</td>
<td>5.5-cm male</td>
<td>4.3-cm female</td>
</tr>
<tr>
<td>7</td>
<td>6.0-cm male</td>
<td>6.0-cm female</td>
</tr>
<tr>
<td>8</td>
<td>5.5-cm male</td>
<td>5.0-cm male</td>
</tr>
<tr>
<td>9</td>
<td>7.0-cm male</td>
<td>5.0-cm male</td>
</tr>
<tr>
<td>10</td>
<td>6.8-cm male</td>
<td>5.0-cm female</td>
</tr>
</tbody>
</table>

**Discussion:** The introduction of Gonodactylus falcatus into an area where Pseudosquilla ciliata was originally the dominant stomatopod affords an opportunity to study the effects of competition and competitive exclusion in a natural situation. Gonodactylus falcatus is a species specialized for living within the spaces between the branches of coral heads and similar habitats. This is borne out by the uniformity of situations in which it was found, and by its behavioral specializations. In the terminology of MacArthur and Levins (1964) it is a "coarse-grained" species, differentiating between this type of habitat and others less suitable. Pseudosquilla ciliata would be termed a "fine-grained" species in regard to habitat selection, because it will occupy a greater variety of habitats.

Both species are generally carnivorous, capturing prey by raptorial feeding. There appears to be ample food on the reef flats for animals of this trophic level within each of the habitat areas, and competition seems to be restricted primarily to obtaining a place to live. However, it must be emphasized that this conclusion was reached on a rather intuitive level and that, until more is known about the trophic structure of coral reef systems (see Kohn, 1959, and Hiatt and Strasburg, 1960), generalizing statements should be considered suspect.

The rapid replacement of Pseudosquilla ciliata by Gonodactylus falcatus verifies the prediction that the specialized species will exclude the generalist from the habitat for which the former is specialized (MacArthur and Levins, 1964). The wider salinity tolerance and greater reproductive activity of G. falcatus may have hastened the replacement, but probably the competition was primarily for living space, and behavioral differences were the deciding factor.
It can be further predicted that the presence of *G. falcatus* in Hawaii will not affect those populations of *Pseudosquilla ciliata* utilizing habitats other than coral heads, and that *Gonodactylus falcatus* will eventually spread to the coral head habitat in other islands in the Hawaiian Archipelago.

**SUMMARY**

1. Two species of *Gonodactylus*—*G. falcatus* (Forskål) and *G. benderoni* Manning—occur on the island of Oahu in the Hawaiian Islands. The former is similar to the variety *ternatensis* using Serène's definition. *G. falcatus* is the most common species of stomatopod found in coral heads on Oahu. *G. benderoni* is abundant in coral heads in some areas.

2. *Pseudosquilla ciliata* (Fabricius), which 14 years ago was the most common stomatopod in coral heads, is now not found in coral heads on Oahu.

3. It is suggested that *Gonodactylus falcatus* and *G. benderoni* came to the Hawaiian Islands from the area of the Philippines or the South China Sea by means of concrete barges that were towed to the Hawaiian Islands at the end of World War II.

4. *G. falcatus* is more tolerant of lowered salinities than is *Pseudosquilla ciliata*. A heavy rainfall in Kaneohe Bay, which reduced surface salinities to as low as 22 per cent seawater, was more deleterious to the population of *P. ciliata* in the bay than it was to that of *Gonodactylus falcatus*.

5. Studies of the plankton of Kaneohe Bay indicate that while *G. falcatus* had two periods of breeding during the year sampled, *Pseudosquilla ciliata* had only one.

6. Comparisons of the aggressive behavior of *Gonodactylus falcatus* and *Pseudosquilla ciliata* indicate that the former is "more aggressive" and can drive the latter from a hole.

**ACKNOWLEDGMENTS**

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Relatively little information is yet available on the life histories of nereid polychaetes from the eastern Pacific. Johnson (1943) has raised some intriguing problems concerning *Nereis vexillosa*, which have not been further explored, and Smith (1950) has reported details of the life history of *Nereis limnicola* (= *Neanthes lighti*), an interesting viviparous, euryhaline species. Information is also available for a southern Californian population of *Nereis grubei*, a species which reproduces more typically. The present paper deals with a central Californian population of *N. grubei* from Pescadero Point, Monterey County. Interesting differences between these two populations with respect to physiology and breeding season have come to light during the course of an investigation of nereid metamorphosis (Schroeder, 1967).

**HABITAT**

At Pescadero Point, Monterey County, California, *Nereis grubei* occurs on an exposed coast where the surf can be quite violent, even though offshore kelp beds are well developed. The intertidal region is composed chiefly of large boulders covered with abundant alga of many species. The worms may be found here in two different situations, in which their abundance varies with the season. During the spring and summer they are most readily found in the sandy substrate beneath the common red alga *Gastroclonium coulteri*. Some specimens may be found in this situation throughout the year, but from the beginning of October until the middle of February the animals are more abundant in holdfasts of the highest specimens of the brown kelp *Egregia menziesii*. In order to collect the animals from their burrows in the kelp the holdfasts must be removed from the rock with a hammer and chisel and carefully dismembered. During the summer only a few, usually very small specimens can be recovered from these holdfasts; this was tested by allowing summer-collected holdfasts to stagnate in a pan until animals emerged from the inaccessible interstices. It seems probable that the worms move into the kelp holdfasts for the winter, when the surf is most violent. Such seasonal habitat shifts are known in other intertidal animals from this area as well (e.g., the isopod *Idothea montereyensis* [see Lee, 1966]).

The habitat reported by Reish (1954b) for the species at Point Fermin in southern California appears to be somewhat different. He found *N. grubei* in algal tufts in or between tidepools scoured from a wide, flat rock ledge. The ledge is strewn with scattered boulders and sheltered from the surf by offshore kelp beds. At Point Fermin the worm was found to be associated with a number of different species of algae, chief among which is *Cladophora trichotoma*. This alga occurs in central California as well, and a search through tufts of it near the Hopkins Marine Station, not far from Pescadero Point, failed to yield any specimens of *N. grubei*, although the worm occurs beneath *Gastroclonium* in the same area. Although Reish surveyed the algal associates of the species at Point Fermin he mentions neither *Egregia menziesii* nor *Gastroclonium coulteri*, the two major algal associates at Pescadero Point. The former is not found south of Point Conception, but the latter is recorded from as far south as San Diego (Smith, 1944). It thus appears that the more northerly population favors *Gastroclonium*, despite the presence of *Cladophora*, and that the opposite is true for the southern population.

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1 A portion of a dissertation submitted to the Graduate Division of Stanford University in partial fulfillment of the requirements for the degree of Doctor of Philosophy. Manuscript received September 26, 1967.

2 Hopkins Marine Station, Pacific Grove, California. Present address: Department of Zoology, Washington State University, Pullman, Washington 99163.
Life History of Nereis grubei—Schroeder

(although I do not know whether Gastroclonia is abundant at Point Fermin).

In an ecological study at the Hopkins Marine Station, not far from Pescadero Point, small numbers of N. grubei were found by Glynn (1965) in association with another alga, Endocladia muricata. This alga is not included in the list given by Reish for the southern California population.

Oogenesis and Metamorphosis

Nereis grubei was collected every two weeks at Pescadero Point, Monterey, California, for a period of 17 months. During the period of oogenesis the average oocyte diameter was determined for a number of specimens from each collection; the number of specimens so determined varied with experimental requirements. All diameters were measured from fresh coelomic samples with a calibrated ocular micrometer and a compound microscope. Fixation in Bouin's fluid made up with picric-acid-saturated sea water was found to cause an irregular expansion of the oocytes (Schroeder, 1966). In some animals, oocytes of considerably different diameters were present, but in most of these the recorded diameters fell into distinct size classes. In such cases only the average diameter of the largest size class was utilized in the life history study. In the few cases in which size classes were not evident, the diameters of all the oocytes from a single animal were averaged together. It is probable that such figures are lower than the value truly comparable to the others. The average oocyte diameter was used as an index to the age of female animals.

Oocytes could be found in at least a few animals throughout the year. Oogonia and tiny oocytes appear in June, when very few maturing females remain from the previous year's spawning group. The oocytes probably reach maturity (about 200µ) in 7–8 months. The young oocytes grow slowly through the fall and early winter, and the population gives rise to several swarms between mid-February and mid-June. The occasions on which nearly mature females were found in the field are indicated by the short vertical bars at the top of Figure 1. (The O in mid-March represents a day on which metamorphosing animals were expected and sought, but not found.) Such nearly mature animals probably swarmed within a couple of days of being observed, although swarming itself was never observed.

The fact that maturing animals are found on separate occasions, and not in intervening periods, implies that specimens within the population mature at different times. It should thus be possible, in midwinter population samples, to separate animals destined for different springtime spawnings.

Oocytes have been shown to grow at two different rates, both in N. grubei (Schroeder, 1966) and in N. diversicolor (Clark and Ruston, 1963). Thus in N. grubei the oocyte growth rate (rate of diameter increase) seems to accelerate when the oocytes are about 100µ in diameter, and it is at about this time that the first histological signs of metamorphosis can be detected (Schroeder, 1967). This fact is utilized in Figure 1 in an attempt to follow the development of each monthly swarm within the population as a whole. The dotted lines are projections based upon the apparent time of swarming, estimates of the growth rate during the two phases, and the recorded oocyte diameters. It is assumed that the oocyte growth rates are similar in the component animals of successive spawnings. Each month on the graph has been subdivided into 3-day periods, so that the positions of the points within a month are significant to within three days. It will be seen that during the fall animals with oocytes of a wide range of sizes are present, but that these are not separable into distinct groups until December, when most specimens can be assigned to a spawning group, even though the oocytes are still small and growing slowly. It is possible that the different spawning groups are distinct from the initial moment of oogonial differentiation, but the variability of oocyte sizes present in young animals prevents their recognition.

A number of animals was maintained in the laboratory over a period of weeks and the growth of their oocytes was checked by repeated sampling. These sampling points have also been included in Figure 1 and are connected with heavy lines. It will be seen that all but two of these animals were derived from the April spawning group, while two others metamorphosed sooner and were closer to the March
Fig. 1. Oocyte development and swarming in *Nereis grubei* at Pescadero Point, Monterey County, California. Each point in the 1966 series represents the average oocyte diameter of an animal collected on the date indicated. Dotted lines represent the postulated progress of several subgroups within the population toward their respective swarming dates. Solid lines represent growth rates from individual animals. The solid line on the left connects the largest oocyte diameters found in each collection. Days on which very mature specimens were found in the field are indicated by a *vertical line* through the delimited zone which includes the range of oocyte diameters found in swarming females. The zero represents a day on which no such animals were found; the dotted line in this group (in May) is an estimated swarming date based on laboratory observations. *Vertical stippled lines* indicate the time of the full moon through the collecting period. The 1965 collections were incomplete due to inadequate knowledge of the habitat of the species.
group. It is felt that these data provide concrete evidence in support of the projected swarming groups.

A line has also been drawn connecting the largest oocytes found in each collection before the first swarm in February. The oldest animals in each of these collections ought to be those destined to participate in the first swarm and should therefore represent a single swarming group. This line was used to estimate roughly the growth rate of the oocytes during each phase and to localize the size range during which the growth rate increases. The line suggests an oocyte growth rate of about 1.8μ/day during the second, rapid phase. Oocyte growth rates were also determined for 14 animals with oocytes over 100μ in diameter maintained in the laboratory, as mentioned above. These indicated a growth rate of 1.74±0.49μ/day. This growth rate estimate is also supported by data from a single unfed animal which was brought into the laboratory with 111-μ oocytes. It swarmed 62 days later. Assuming a final oocyte diameter of 200μ, the oocytes in this individual must have grown at a rate of about 1.4μ/day. The average growth rate, during the final period of rapid growth, is thus between 1.6 and 1.7μ/day. The growth rate may not be constant throughout the period of rapid growth in N. grubei, and a definite slowing down of growth as the maximum size is approached has been reported for N. diversicolor (Clark and Ruston, 1963).

The first swarming takes place in February, and evidence has been found for a swarm each month until June. Each swarm seems to involve fewer animals than the one preceding it, so that the bulk of the population swarms in February and March. In February virtually all the maturing animals in the Egregia holdfast habitat disappear; subsequent swarms arise from the Gastroclonium. This fact accounts for the lack of data for the spring of 1965. Collections were made during this period, but only from the holdfasts, which were almost totally devoid of maturing animals. After the discovery of N. grubei beneath Gastroclonium, both habitats were monitored during the spring of 1966. Again mature animals disappeared suddenly and almost completely from the Egregia holdfasts during February. However, a significant population remained beneath the Gastroclonium from which at least a few animals swarmed monthly until June.

One of the swarms (represented in Figure 1 by the heavy dotted line over May 1966) has been inferred from the fact that two animals taken from the field on April 26 swarmed simultaneously in the laboratory on May 19. A search of the Gastroclonium on May 22 failed to reveal any metamorphosing animals; this is what would be expected if the animals in the laboratory had swarmed simultaneously with a group in the field.

The dates of the full moon for several months of breeding activity during the winter of 1965-1966 have been indicated by vertical dotted lines bands in Figure 1, since nereid breeding activity has often been correlated with the phase of the moon (Korringa, 1947; Hauenschild, 1966). It should be recalled that the observation of metamorphosing animals in the field must antedate the swarming of these same animals, so that the swarming dates indicated in Figure 1 are all somewhat early. Furthermore, the theory of Hauenschild (1966) suggests that the moon phase might correlate at the point where the oocyte growth rate increases rather than at the time of actual swarming. It is not known whether a latent period occurs between the supposed lunar stimulus and the observed response; the figures presented, do not, in my opinion, either affirm or deny a possible phase-setting relationship with the lunar cycle. The fact that subgroups are separable within the population in early December suggests that some determination of the spawning groups has occurred before the time that the oocyte growth rate has increased within any group. This adds a third point in time for the possible intervention of environmental stimuli in determining the breeding periodicity (see discussion by Clark, 1965).

**COMPARISON WITH A SOUTHERN CALIFORNIAN POPULATION**

At the outset of this work a definite breeding season had not been expected, since Reish (1954b) reported that the population at Point Fermin showed continual reproduction throughout the year, and that specimens in some stage of metamorphosis could be taken at any time.
The two populations thus differ in the very presence of a breeding season in the population at Pescadero Point.

Constant breeding can be considered as an extremely prolonged breeding season. The average ocean temperature at Point Fermin is several degrees higher than at Pescadero Point, and a lengthening of the breeding season in the southern portion of the range of temperate zone invertebrates is known in other groups, e.g., the sea urchin Arbacia punctulata (Harvey, 1956). Additional examples are discussed by Giese (1959) and Clark (1965).

Other differences have been noted between the two populations. The heaviest female reported by Reish weighed approximately 50 mg, and smaller specimens seemed to be the rule, at least in his laboratory-raised animals. The largest female found at Pescadero Point weighed more than 1 gram, and mature females usually weighed in excess of 500 mg; the animals in the Pescadero Point population are thus an order of magnitude heavier than those in the Point Fermin population.

A further difference between the populations involves the size of origin of the oocytes. Reish (1954b) found them to originate from a solid tissue within the parapodia, from which clumps of oocytes are released upon achieving a diameter of up to 20 μ. Such a parapodial tissue has never been observed in N. grubei from Monterey County, although oogonial proliferation has been demonstrated autoradiographically in small clumps of oogonia floating free in the coelom (Schroeder, 1966). Mature oocytes from animals in the Point Fermin population were found to range in diameter from 162 μ to 380 μ. At Pescadero the size range was much narrower, 190 μ to 210 μ. Oocytes within a given mature female are very uniform in size.

Reish (1954b) raised specimens from the Point Fermin population to maturity in his laboratory and found that while they usually metamorphosed after 28 to 29 weeks, exceptional specimens metamorphosed at as early as 14 weeks of age. This variability recalls that observed by Hauenschild (1966) in Platynereis dumerilii. Although the life span of a worm from the Pescadero Point population is not known, it must be close to a year at a minimum, and is more likely to be 2 years. The period of oogenesis alone lasts 7 to 8 months, and much smaller animals than those in which gametes are found may be collected simultaneously. The development time at Pescadero Point is therefore 2 to 4 times as long as the laboratory development time for specimens from the Point Fermin population.

Whether these differences are simply expressions of latitudinal variation within a species, or whether they indicate that a deeper distinction exists between these two populations cannot be determined from the available information. The morphological identity of the two forms has been graciously confirmed by Dr. Reish, who has clarified the taxonomic position of the species in conjunction with his work on its life history (Reish, 1954a).

SUMMARY

1. The major algal associates of Nereis grubei at Pescadero Point, Monterey County, California, are Egregia menziesii and Gastroclonium coulteri. The Egregia holdfasts contain more animals during the fall and winter.

2. At Pescadero Point, Nereis grubei breeds from February to June in approximately monthly swarms.

3. Animals collected in December may be assigned to a specific swarming group by determining each animal's average oocyte diameter.

4. The average rate of oocyte growth between 100 μ and 200 μ is 1.6-1.7 μ/day. This represents more rapid growth than is shown by smaller oocytes.

5. The central Californian population differs from that in southern California in its limited breeding season, in the average size of the component individuals, and in the internal site of oogenesis.

ACKNOWLEDGMENTS

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REFERENCES


New Records of Thirteen Cottoid and Blennioid Fishes for Southeastern Alaska

JAY C. QUAST

ABSTRACT: Three categories of new records for species of fish are reported: (1) extensions of range eastward or southeastward from the Bering Sea or Gulf of Alaska—Hexagrammos octogrammus (Pallas), Artediellus pacificus Gilbert, Triglops metopias Gilbert and Burke, Anisarchus medius (Reinhardt), and Lupenurus fabricii (Valenciennes); (2) extensions of range northwestern—Ardedius harringtoni (Starks), Oligocottus snyderi Greeley, Scorpaenichthys marmoratus (Ayres), and Liparisus nanus Gilbert; and (3) "fill-ins" for species already reported to the north and south of Southeastern Alaska—Ardedius lateralis (Girard), Bothragonus swani (Steindachner), Chirolophus nugator (Jordan and Williams), and Scytalina cerdale Jordan and Gilbert.

In this paper I bring together distributional data for species that have not previously been recorded from Alaska's southeastern region. The specimens are from the fish collection of the U.S. Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska, and have been obtained principally from activities of the laboratory and the Bureau's Exploratory Fishing and Gear Research Base at Juneau.

For present purposes, Southeastern Alaska is considered to lie between the latitudes of Skagway to the north and Dixon Entrance to the south (Fig. 1). The region, an archipelago composed of marine fjords, has a roughly rectangular outline and is about 590 km long and 176 km wide.

The new records are of three types: (1) eastward range extensions from the Gulf of Alaska or Bering Sea, (2) northwestward range extensions, primarily from British Columbia but also from as far south as Monterey, California, and (3) records that fill gaps for ranges that have been established northwest and southeast of Southeastern Alaska.

Although charts of Southeastern Alaska depict the marine waters as continuous, four lines of evidence suggest that a partial faunal barrier divides the inside waters into northern and southern regions in the vicinity of Kuiu, Kupreanof, and Mitkof islands (Fig. 1). First, water temperatures are usually lower in the northern waters during all seasons than in the southern inside waters or along the outer coast of Southeastern Alaska. Second, five species of shallow-water fishes whose ranges extend into California—Squalus acanthias, Artedius harringtoni (records of Auke Bay Laboratory), Rachobolus vacca, Embiotoca lateralis, and Gymatogaster aggregata (Tarp, 1952)—have been collected in the inside waters south of the Kuiu-Mitkof region but are absent from collections from the inside waters to the north. Third, north and south of the Kuiu-Mitkof vicinity, waters deeper than 10 meters are continuous only via the outer coast. Communication east of the coast is limited to three shallow channels: Dry Strait, which usually bares at low water; Wrangell Narrows, which shallows to about 8 meters; and Keku Strait (Rocky Pass), which shallows to about 3 meters. Fourth, the net flow of surface waters in Frederick Sound, Chatham Strait, and Sumner Strait probably is seaward most of the year because rainfall in the region of the boundary and in the mountains to the eastward is heavy and occurs during all seasons. The rainfall probably creates a net surface flow away from the barrier area, thereby decreasing the opportunities for shallow-water species to reach the three restricted channels of communication.

The new eastward range extensions suggest
Fig. 1. Map of Southeastern Alaska.
that the northern inside waters of Southeastern Alaska harbor a cold-water enclave of demersal species that has affinities with faunas of the Aleutian Islands, Bering Sea, or regions even farther to the north or west. But any firm conclusion is premature because our collecting methods have not been standardized, numerous critical localities have not been sampled, and available data on distributions are not completely analyzed.

My authorities for species distributions are principally Wilimovsky (1954, 1964), Clemens and Wilby (1961), and Hubbard and Reeder (1965). Although Wilimovsky’s “Provisional Keys to the Fishes of Alaska” (1958) is extremely useful for preliminary identifications of the Alaskan fish fauna, the manuscript was given limited distribution and is no longer available (Wilimovsky, personal communication).

Collection numbers for the fish collection of the Auke Bay Laboratory are in the form of two numbers joined by a hyphen and preceded by the letters AB. All lengths are standard.

**HEXAGRAMMIIDAE**

*Hexagrammos octogrammus* (Pallas)

Two collections: two pelagic-stage juveniles, 43–45 mm, from a salmon trap near Pt. Adolphus, Icy Strait, on 21 June 1955 (AB 55-2); and three specimens, 105–182 mm, taken intertidally by divers using rotenone in the vicinity of Saming Cove, near Sitka, on 18 March 1964 (AB 64-954).

Wilimovsky (1954) gives the range as the Bering Sea to the Gulf of Alaska, including the Sea of Okhotsk. Quast (1960) gives the range as from northeastern Japan to Yakutat Bay, Alaska. An old record of Bean (1881) gives the locality of “Old Sitka” for “Hexagrammus (sic) ordinatus” (Cope) Bean,” a junior synonym of *H. octogrammus* (Quast, 1960).

Evermann and Goldsborough (1907) cite collections of this species made in 1903 from Snug Harbor and Union Bay, Alaska, but the location of these two places is uncertain. The citation suggests the localities of Snug Anchorage and Union Bay, about 65 km northwest of Ketchikan. The fact that both localities in the Ketchikan vicinity are on the cruise track of the U.S. fishery vessel “Albatross” that made collections in 1903 in Southeastern Alaska (deduced from Fassett, 1905) supports the theory that the collections originated near Ketchikan. Correspondence with Robert Kanazawa of the U.S. National Museum discloses, however, that the Snug Harbor specimen originated from the Kodiak Island–Cook Inlet vicinity and that the U.S. National Museum has no specimen of *H. octogrammus* or record of a specimen from a locality named Union Bay. Furthermore, the only locality named Union Bay visited by the “Albatross” on the 1903 cruise was in British Columbia. Very likely, therefore, no collections of this species were made in the Ketchikan vicinity. The southernmost authenticated record is for Sitka.

**COTTIDAE**

*Artediellus pacificus* Gilbert

Three collections: one 66-mm specimen taken in a shrimp trawl at 64–75 fathoms (117–137 meters) in the vicinity of the Barren Islands near the mouth of Cook Inlet on 7 August 1963 (AB 64-726); and two collections, 5 and 12 specimens, taken in a shrimp trawl net over muddy-sand bottom at 50–90 feet (15.2–27.4 meters) in Auke Bay on 25 June 1962 and 27 September 1963 (AB 62-226 and 63-182).

Distribution includes the northern Sea of Japan and Sea of Okhotsk (Schmidt, 1950); the southern Gulf of Anadyr (Andriyashev, 1937); and St. Paul Island (eastern Bering Sea) and Karluk (Kodiak Island) (Jordan and Evermann, 1898). The Auke Bay specimens represent an eastward extension of the range of about 1130 km. Differences in meristic counts between the Auke Bay specimens and those cited by Jordan and Evermann (1898), which are presumably from regions between Kamchatka and Kodiak, do not appear to be important (Table 1).

*Artedius harringtoni* (Starks)

Numerous collections from Skowl Arm, Prince of Wales Island, taken in shrimp traps fished subtidally; and 56 specimens, 23–80 mm, taken intertidally by divers using rotenone in
TABLE 1
RANGES OF COUNTS FOR Arctediellus pacificus FROM THREE REGIONS OF THE NORTH PACIFIC OCEAN

<table>
<thead>
<tr>
<th>ITEM</th>
<th>COOK INLET (AB 62-226)</th>
<th>AUKI BAY (AB 64-726)</th>
<th>TO KODIAK 1 (64-182)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of specimens</td>
<td>not given</td>
<td>1</td>
<td>17</td>
</tr>
<tr>
<td>First dorsal fin</td>
<td>VII-VIII</td>
<td>VII</td>
<td>VII</td>
</tr>
<tr>
<td>Second dorsal fin</td>
<td>12-13</td>
<td>11-122</td>
<td></td>
</tr>
<tr>
<td>Anal fin</td>
<td>11-12</td>
<td>132</td>
<td>11-122</td>
</tr>
<tr>
<td>Pectoral fin</td>
<td>22-24</td>
<td>233</td>
<td>21-244</td>
</tr>
<tr>
<td>Lateral line pores</td>
<td>22-26</td>
<td>274</td>
<td>21-284</td>
</tr>
<tr>
<td>Caudal fin divided rays</td>
<td>9 damaged</td>
<td>7-95</td>
<td></td>
</tr>
</tbody>
</table>

1 Jordan and Evermann (1898).
2 Last two rays counted as two elements.
3 Counts from both left and right fins.
4 Left side only.
5 Counts of seven were found only in the smaller specimens.

the vicinity of Samsing Cove, near Sitka, on 18 March 1964 (AB 64-954).

Distribution includes southern California to northern British Columbia (Clemens and Wilby, 1961) and Kodiak Island (Hubbard and Reeder, 1965). Judging from the distributional data, the species probably is common in the southern half of Southeastern Alaska and along nearly the entire outer coast of the region.

Arctediellus lateralis (Girard)

Common in our collections from coastal and northern and southern inside localities of South-eastern Alaska, including the southern tip of Baranof Island, Sitka, Barlow Cove, and Skowl Arm.

Clemens and Wilby (1961) give the distribution as southern California to the Queen Charlotte Islands, and Hubbard and Reeder (1965) report the species from Kodiak Island. Hubbard and Reeder also suggest that the name Arctediellus delacyi Hubbs and Schultz applies to the species described as A. lateralis. The type description of A. delacyi states that the species, based on specimens from Kodiak Island, is very closely related to A. lateralis (Hubbs and Schultz, 1941). Comparisons of critical proportions of our specimens from Sitka with those from the type description of A. delacyi Hubbs and Schultz also support the argument against the distinctiveness of A. delacyi (Table 2). The main distinguishing characteristic of A. delacyi in the type description involves thickness of the lips, a feature that probably varies according to the conditions of preservation.

Oligocottus snyderi Greeley

Three specimens, 37–57 mm, taken intertidally by divers using rotenone in the vicinity of Samsing Cove, near Sitka, on 18 March 1964 (AB 64-954).

Distribution of the species according to Clemens and Wilby (1961) is from southern California to the Queen Charlotte Islands. Our collection is the first recorded from Alaska and extends the known range northward about 340 km.

TABLE 2
CRITICAL PROPORTIONS OF Arctediellus delacyi AND A. lateralis PRESENTED BY HUBBS AND SCHULTZ (1941) AND OF SITKA SPECIMENS OF A. lateralis FROM THE AUKI BAY LABORATORY COLLECTION

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>NUMBER</th>
<th>UPPER LIP WIDTH 1 ÷ LEAST SUBORBITAL WIDTH</th>
<th>LEAST WIDTH OF LIPS 2 ÷ LEAST SUBORBITAL WIDTH</th>
<th>HEAD INTO STANDARD LENGTH</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. delacyi</td>
<td>3</td>
<td>ca. 1.0</td>
<td>ca. 1.0</td>
<td>2.75–2.85</td>
</tr>
<tr>
<td>A. lateralis</td>
<td>(3)</td>
<td>0.7-1.0</td>
<td>0.6-0.8</td>
<td>2.50–2.80</td>
</tr>
<tr>
<td>from Sitka</td>
<td>10</td>
<td>0.7-1.0</td>
<td>0.7-1.1</td>
<td>2.52–2.71</td>
</tr>
<tr>
<td>A. lateralis</td>
<td>(3)</td>
<td>0.6-0.8</td>
<td>0.6-0.8</td>
<td>2.50–2.80</td>
</tr>
</tbody>
</table>

1 Measured sagitally.
2 Least width of both lips below suborbital.
3 Not given.
Scorpaenichthys marmoratus (Ayres)

One 93-mm specimen taken intertidially by divers using rotenone in the vicinity of Samsing Cove, near Sitka, on 18 March 1964 (AB 64-954).

According to Clemens and Wilby (1961) the distribution is from southern California to northern British Colombia, and individuals are common in the Queen Charlotte Islands. Our collection is the first recorded from Alaska and extends the known range northward about 340 km.

Triglops metopias Gilbert and Burke

One 119-mm specimen taken in a shrimp try net on a silty-sand bottom at approximately 51 feet (15.5 meters) in Auke Bay, 27 September 1963 (AB 63-182). Wilimovsky (1954) gives the distribution as Bering Sea, and later (1964) reports it from Amchitka Island and the Sopochnoi Island-Petrel Bank vicinity. The Auke Bay Laboratory also has collections from near the Shumagin Islands.

The Auke Bay specimen resembles those, including the type, described from the Bering Sea by Gilbert and Burke (1912), but has counts that are one or two units, depending on the character, below the ranges cited for rays of the soft dorsal, anal, and pectoral fins and for scutes along the lateral line; it also has 21 dorsal scutes as compared with "26 or 27" in the type. The record for Auke Bay is the first for the species in the eastern Gulf of Alaska and extends the known range eastward about 2900 km.

AGONIDAE

Bothragonus swani (Steindachner)

One 51-mm specimen taken intertidally by divers using rotenone in the vicinity of Samsing Cove, near Sitka, on 18 March 1964 (AB 64-954).

Clemens and Wilby (1961) give the range as California to the Queen Charlotte Islands, and Hubbard and Reeder (1965) report the species from Kodiak Island.

LIPARIDIDAE

Lipariscus nanus Gilbert

Four specimens, 26–32 mm, taken in three collections made with an Isaac-Kidd trawl at night at 100 meters in Lynn Canal. Two collections (AB 64-63, AB 64-999) are from near Point Sherman, and one (AB 64-72) is from near Point Retreat.

Gilbert (1915) obtained five specimens, including the type, from Monterey Bay, California. The Lynn Canal collections represent a northward extension of range of about 2600 km.

STICHAEIDAE

Anisarchus medius (Reinhardt)

The species was formerly in the genus Lumpenus Reinhardt, but Makushok (1958) places it in Anisarchus Gill. The Auke Bay Laboratory has several collections from the Gulf of Alaska and the Aleutian Islands, and one collection of 54 specimens, 59–117 mm, taken in a shrimp trawl at 60–90 fathoms (32.8–49.2 meters) in Auke Bay on 25 June 1962 (AB 62-226).

Wilimovsky (1954) gives the range of the species as "Arctic Alaska-Bering Sea; North Atlantic Ocean"; Andriyashev (1954) states that the species is circumpolar and occurs in the Sea of Okhotsk and the northern Sea of Japan. The Auke Bay collection extends the known range eastward about 1400 km.

Chirolophus rugator (Jordan and Williams)

One 57-mm specimen taken intertidally by divers using rotenone in the vicinity of Samsing Cove, near Sitka, on 18 March 1964 (AB 64-954).

Clemens and Wilby (1961) give the range as from northern California to the Strait of Georgia. Hubbard and Reeder (1965) report the species from Kodiak Island.

Lumpenus fabricii (Valenciennes)

One 215-mm specimen captured by hand on a beach at low tide at Auke Bay on 1 December 1963 (AB 63-234). The Auke Bay Laboratory also has one 255-mm specimen from Kachemak Bay, Cook Inlet (AB 64-738).

Andriyashev (1954) lists the species as amphiboreal and occurring in the Chukchi Sea and the northern Sea of Japan; Wilimovsky (1954) gives the range as "Arctic Alaska-Bering Sea; North Atlantic Ocean."
Scytalina cerdale Jordan and Gilbert

Five specimens, 49–64 mm, taken by hand on a beach at low tide in the vicinity of Little Port Walter on Baranof Island on 13 May 1960 (AB 63-32).

This species has been recorded from the Bering Sea to California (Wilimovsky, 1954), and on Agattu Island in the Aleutian Chain (Wilimovsky, 1964).

REFERENCES


Egg Pouches and Other Reproductive Structures in Pelagic Chaetognatha

ANGELES ALVARINO

ABSTRACT: Some specimens of *Eukrohnia bathyantarctica* David from the collections obtained by the United States Antarctic Research Program were observed which had marsupial sacs full of eggs, and hanging from the opening of the oviducts. The eggs in the sacs, in various specimens, appeared at different stages of development, from the gastural stage up to the eclosion of the larvae.

The breeding pattern in Chaetognatha either is seldom mentioned or is hidden in the pertinent literature among other subjects related to the group. For this reason a review of the breeding characteristics merits specific attention.

Norgaard (1905) was the first to indicate the brood sacs in *Eukrohnia*, when he stated: "In samples from the Vest Fiord there were specimens with eggbags. The wider part of the fin was bent downwards, this forming a hollow in which the eggs lay tightly pressed together."

Similarly, Ritter-Zahony (1910) observed: "Die Eier waren vollständig aus den Ovarien ausgetreten und bildeten zwei pfüllenförmige, von einer gallerigen Hülle umgebene Ballen am Rücken des Tieres." He included illustrations of this sac for *E. hamata* (Möbius). However, considering the extension of the laminar part of the fin, the species probably corresponded to *E. bathypelagica* Alvarino. Ritter-Zahony (1910) also explained: "Diese Eiersäckchen lagen nebeneinander zu einem am Rumpf, drei Vierteln am Schwanzabschnitt."

Ritter-Zahony (1911), describing *E. fowleri*, stated: "Eiersäckchen, die wie bei *E. hamata* von den eigentümlich deformierten Seitenflossen umhüllt waren." He also noticed small brooding sacs in *E. hamata* from the Antarctic. These specimens probably belonged to *E. bathyantarctica* David.

Kuhl (1928) made similar observations for *Eukrohnia*.

At Point Barrow, Alaska, MacGinitie (1955) observed two mature specimens of *E. hamata* 40 mm long "carrying young in a marsupium formed by folding of the posterior lateral fins." He also explained that when the material was brought to the laboratory "some of the young, which were 3 mm long, began escaping from the marsupium."

Tchindonova (1955) stated that the majority of the specimens of *E. fowleri* were sexually mature, with ovarian sacs that had already ruptured. This probably refers to the brooding sacs.

David (1958) indicated that one specimen of *E. bathyantarctica* had "an egg-shaped opaque structure appended to the oviduct." He also suggested that in *E. bathyantarctica* and *E. fowleri* the seminal vesicles function as spermato- phores and are attached intact to the external opening of the oviducts by a fine tube which is probably the vas deferens." David (1958) was unable to find a single specimen of *E. fowleri* or *E. bathyantarctica* with mature seminal vesicles, and thus he considered the sacs observed attached to the oviducts to be remains of the seminal vesicles. These small sacs, which are also illustrated in David's figures 2a and 3c might be the brooding sacs beginning to develop.

Ghirardelli (1959a) was also able to observe specimens of *E. bathyantarctica* and explained: "Le spermatofores hanno la forma di un fiasco, limitato esternamente da una membranella anista resistente. Questa membrana forma un prolungamento (simile appunto al collo di un fiasco) che si trova infiltrato nell' orificio genitali femminile, i cui bordi si presentano assai rilevati.
In un solo esemplare la spermatofore era intera; in altri, invece, soltanto la membranella lacerata sporgeva dagli orifizi genitali. Nessuno degli esemplari esaminati ha purtroppo le vesicole seminali mature a ciò impossibile ogni supposizione sul come si formino le spermatofore.

It is unfortunate that neither David (1958) nor Ghirardelli (1959a) studied the structure of these sacs or their contents to ensure identification. Ghirardelli (1959b), commenting on the sac with mature eggs in *Eukrohnia*, stated, "le poche osa devono essere fornite di notevole quantita di materiali di reserva ed in oltre protette nella particolare tasca incubatrice."

Alvarino (1962), when first describing *E. bathypelagica*, stated, "the fins are broadest at the tail region, where they bend to the dorsal side. . . . This phenomenon is incipient in *E. hamata* and *E. fowleri*, but in *E. bathypelagica* is more conspicuous, as this part of the fin is broader." The species of *Eukrohnia* studied by Alvarino in 1962 did not include *E. bathyantarctica*. She also stated for *E. bathypelagica*, "The lamellar part of the lateral fins bends to the dorsal side, which helps drive the spermatopozoa into the oviducts, and probably also bears the newly hatched eggs."

Schilp (1941) referring to *E. hamata* observed, "The ovaries project outside the body. The cause of this abnormality is unknown to me." The iridescent membranous funnels at the openings of the oviducts which he mentioned for *E. richardi* Germain and Joubin (probably *E. fowleri*) might be remnants of the incubatory sacs.

Alvarino (1967, 1968) illustrated some pieces of a saclike remnant hanging from the oviduct of *E. fowleri*. Dawson (personal communication) observed a marsupial sac filled with eggs hanging from the oviducts of specimens of *E. bathypelagica* collected at the ice-cap region of the Arctic.

Personal observations on specimens of *E. bathyantarctica* from the antarctic and subantarctic regions, collected recently by the R. V. "Eltanin" during the United States Antarctic Research Program (U.S.A.R.P.), detected the sac containing eggs protruding from the opening of the oviducts. The brood sac (marsupial sac or brooding pouch) appeared of different sizes in various specimens, indicating various stages of development. The mature eggs in this marsupial sac were observed at different stages of development, from the formation of the blastomeres to the various phases of development of the embryos, up to the larval stage ready for eclosion. Some specimens showed remnants of the sac hanging from the oviducts. Those specimens presented one sac at each side, and the widest part of the lateral fins was bent dorsally covering more or less completely the marsupial sacs.

The brooding phases could be outlined as follows: Stage I, brood sac developing (Fig. 1A); Stage II, brood sac filled with mature eggs, up to gastrula; Stage III, brood sac with eggs containing embryos in a single coil (Fig. 1B); Stage IV, brood sac with eggs containing double coiled embryos; Stage V, brood sac broken after the eclosion of the larvae (Fig. 1C).

The illustrations were obtained using the stereomicroscope with the drawing tube attachment.

In the illustrations (Fig. 1) the seminal vesicles are clearly visible, evidence that David's observation (1958) that "the 'ruptured sacs' attached to the oviduct were seminal vesicles," was an erroneous assumption.

Tokioka (1939), when describing *Bathypterygia dellae edentata*, indicated the presence of a "capsula-like opening at the seminal receptacle"—a small bag at the opening of the oviducts. This might have been related to the brood sacs beginning to develop.

Ritter-Zahony (1910) explained that in the genus *Krohnita* brooding sacs are not present. However, Schilp (1941) noticed small membranous sacs at level with the trunk-tail septum in *K. subtilis* (Grassi).

Sanzo (1937) observed the pelagic ootheca of *Pterosagitta draco* (Krohn) containing mature eggs. The gelatinous substance of the ootheca protects both the eggs and larvae from the various physico-chemical changes until eclosion. In the Straits of Messina, this author found gelatinous colonies 6.0 to 6.4 mm in diameter, with spherical transparent eggs 0.3 to 0.4 mm in diameter.

Hertwig (1880) observed free deposition of eggs in *Sagitta bipunctata* Quoy and Gaimard and in *S. serratodentata* Krohn.
Conant (1896) witnessed the egg laying of *S. hispida* Conant at Beaufort, North Carolina. The eggs remained 20 to 30 minutes in each oviduct while a jelly coat thickened around each of them. They were pushed out by ovarian contraction and issued in two linear rows (one for each oviduct), totalling from 60 to 70 eggs.

Stevens (1910) observed the free discharging eggs in *S. elegans* Verrill. Huntsman and Reid (1921) found eggs of *S. elegans*, in various stages of development, free in the plankton of the Bay of Fundy and the Gulf of St. Lawrence.

Ghirardelli (1954) stated, "Anche le Sagitte depongono uova pelagiche spesso riunite in piccoli ammassi gelatinosi, talvolta però anche isolate."

Murakami (1959) observed in the laboratory specimens of *S. crassa* Tokioka in the process of free spawning of eggs. Elian (1960) observed eggs of *S. setosa* J. Müller and *S. euxina* Moltchanoff free in the plankton from the Black Sea.

Thorson (1936), Werenberg-Lund (1947), and MacGinitie (1955) suggested that the arctic animals show a tendency to brood their eggs or to provide some other method of protecting them until the embryos, the young larvae, or young animals develop. Ghirardelli (1959b) made similar observations for both the arctic and antarctic Chaetognatha. However, the species of *Eukrohnia* possess the brood pouch, and have world wide distribution (except *E. bathyantarctica* which is mainly restricted to the antarctic-subantarctic regions), inhabiting different depths. The temperatures in the regions inhabited by the species are in many cases similar to those encountered in the Bay of Fundy or the Gulf of St. Lawrence, where free eggs of *S. elegans* at various stages of development were observed (Huntsman and Reid, 1921).

Thus it appears that the eggs of the species of chaetognaths belonging to the genus of highest evolutionary rank are probably better equipped for survival, either by means of the chemical composition of the vitellus or by the nature of the involucrum of the egg.

Table 1 is a summary of the breeding characteristics of the Chaetognatha which may have some evolutionary significance.

I wish to express my appreciation to Professor
**TABLE 1**

**COMPARISON OF BREEDING CHARACTERISTICS OF SIX GENERA OF CHAETOGNATHA**

<table>
<thead>
<tr>
<th>Genera</th>
<th>Generic Notations</th>
<th>Breeding Characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eukrohnia</td>
<td>One pair of fins (from tail to ventral ganglion); one pair of sets of teeth</td>
<td>Brood sac or marsupium</td>
</tr>
<tr>
<td>Bathyspadella ?</td>
<td>One pair of rayed fins (from tail to near the ventral ganglion); no teeth</td>
<td>Probably as in Eukrohnia</td>
</tr>
<tr>
<td>Krohnita</td>
<td>One set of paired fins (from tail to posterior part of trunk); anterior pair of sets of teeth</td>
<td>Somewhat similar to Eukrohnia</td>
</tr>
<tr>
<td>Heterokrohnia</td>
<td>One set of paired rayed fins (from tail to level of posterior end of ventral ganglion) with a constriction about mid-length; two pairs of sets of teeth</td>
<td>Unknown</td>
</tr>
<tr>
<td>Pterosagitta</td>
<td>One set of paired fins (from tail to level of posterior septum); trunk covered by thick cuticulae (collarette); two pairs of sets of teeth</td>
<td>Pelagic jelly ootheca</td>
</tr>
<tr>
<td>Sagitta</td>
<td>Two sets of paired fins; two pairs of sets of teeth</td>
<td>Free eggs covered by thick involucrum</td>
</tr>
</tbody>
</table>

M. W. Johnson for reading the manuscript, and for his valuable advice and encouragement.

**REFERENCES**


An Additional Contribution to the Biology of the Aholehole, *Kublia sandvicensis* (Steindachner)¹

ROYDEN NAKAMURA²

Relatively little is known of the biology of the inshore fish fauna of the Hawaiian Islands, although there have been numerous publications on various aspects of the subject (Pietschmann, 1938; Gosline and Brock, 1960; Helfrich, 1959; Hiatt, 1947a, 1947b, 1951; Randall, 1955, 1958, 1961; Strasburg, 1961, 1962; Strasburg and Hiatt, 1957; Salmon, 1967; Tester, 1951, 1955; Tester and Takata, 1953; Tester and Trefz, 1954). The purpose of this paper is to present further information concerning the growth and age of a common inshore species, the aholehole (*Kublia sandvicensis*).

Materials and Methods

These data were obtained from a population of individually marked fish which were kept for over a year in a large marine pond at the Hawaii Marine Laboratory on Coconut Island, Kaneohe Bay, Oahu. All fish were initially placed into one of five arbitrarily designated size classes. The fish in size class I ranged from 80 to 100 mm fork length, class II from 101 to 120 mm, class III from 121 to 140 mm, class IV from 141 to 160 mm, and class V from 161 to 180 mm.

At approximately monthly intervals, the pond was seiend and the recaptured fish anesthetized with Quinaldine (2-methyl-quinoline). Length and weight measurements were then made and scale samples taken in conjunction with a concurrent study of scale growth. The fish were then allowed to recover from the anesthetic in holding tanks before being released into the pond. All measurements were made to the nearest 0.1 mm and 0.1 gram.

The pond in which this introduced population of fish was kept was rectangular, measuring 60 by 100 feet. The depth varied from 2 1/2 to 4 1/2 feet, depending on tidal conditions and the particular locale within the pond. The sides were constructed of stacks of large dead coral heads, and the bottom was composed mainly of sand, silt, and pieces of dead coral. Two large screened gates were provided at opposite ends of the pond to allow natural water circulation and tidal changes.

That the conditions under which the fish were maintained approximated the natural environment is evidenced by earlier observations of a small resident population of the same species in a similar, adjacent pond (Tester and Takata, 1953).

Although natural foods such as annelids and crustaceans were frequently observed in the pond, the diet of the introduced population of aholehole was supplemented by the addition of bread, commercial fish meal, and minced fish flesh.

Results

As expected, the data indicate faster growth rates for smaller fish (Table 1). Fish in size class I grew at rates of 0.120 mm and 0.073 gram per day. Fish in size classes II, III, IV grew at rates of 0.110, 0.070, 0.040 mm per day, respectively. The daily increases in weight for the same groups were 0.092, 0.071, 0.040 gram per day. Size class V, which consisted of very large fish, failed to show significant increases in length for the duration of the study. However, slight increases in weight were detected (0.004 gram per day).

Seasonal growth differences were not observed in all size classes. Sex differences in growth rates could not be studied for two reasons. First, difficulty was encountered in determining sex on the basis of external morphology. Second, throughout the entire study there was a

¹ From a thesis submitted in partial fulfillment of requirements for the degree of Master of Science at the University of Hawaii in 1965. Manuscript received September 12, 1967.

² Present address: Institute of Fisheries, University of British Columbia, Vancouver, British Columbia.
small but steady rate of escape from the enclosure which necessitated a constant replenishment of the population.

By extracting an equal number of points directly off growth curves for each of the five size classes, "Walford curves" estimating the maximum size of this species were constructed (Walford, 1946). The calculated theoretical maximum length and weight values of 198.0 mm and 109.2 grams are reasonable approximations of field observations made by the writer during this project. Recent investigators, however, have observed aholehole of greater size than these estimates (Niimi, 1967, personal communication).

Because it is difficult to determine the age of fish which live in uniformly warm waters (Lagler, Bardach, and Miller, 1962), age estimates of aholehole were made on the basis of growth rates and relative sizes. From a composite growth curve formed by the combined curves of the five size classes, it was estimated that this species requires about 1,330 days (3.6 years) to grow from 87.5 to 170.5 mm fork length. Data obtained by earlier investigators (Tester and Takata, 1953) were used for the assignment of ages to smaller fish, since this study did not include individuals less than 87.0 mm fork length. Thus it was possible to determine length-age relationships covering almost the entire size range of this species (Table 2, Fig. 1).

The length-weight relationship of the aholehole was determined from measurements of fish recaptured throughout the year in the pond. Clugston (1964), working with two subspecies of largemouth bass, used a similar format. An "individual b" value (Ricker, 1958) of 2.75 was calculated for the fish used in this study (Log Wt. = —1.51 + 2.75 Log Lt.). This is shown in Figure 2. Similar values were obtained for two groups captured during the same period from the original habitat of the introduced population.

### TABLE 1

The Growth of the Aholehole (*Kublia sandvicensis*)

<table>
<thead>
<tr>
<th>NO. FISH</th>
<th>SIZE CLASS</th>
<th>FORK LENGTH (mm)</th>
<th>GROWTH RATE (mm/day)</th>
<th>GROWTH RATE (g/day)</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>I</td>
<td>80.0–100.0</td>
<td>0.120</td>
<td>0.073</td>
</tr>
<tr>
<td>33</td>
<td>II</td>
<td>101.0–120.0</td>
<td>0.110</td>
<td>0.092</td>
</tr>
<tr>
<td>49</td>
<td>III</td>
<td>121.0–140.0</td>
<td>0.070</td>
<td>0.071</td>
</tr>
<tr>
<td>20</td>
<td>IV</td>
<td>141.0–160.0</td>
<td>0.040</td>
<td>0.040</td>
</tr>
<tr>
<td>4</td>
<td>V</td>
<td>161.0–180.0</td>
<td>0.000</td>
<td>0.004</td>
</tr>
</tbody>
</table>

### TABLE 2

Age Estimates of the Aholehole (*Kublia sandvicensis*)

<table>
<thead>
<tr>
<th>ESTIMATED AGE (years)</th>
<th>FORK LENGTH (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 or less</td>
<td>to 102.7*</td>
</tr>
<tr>
<td>2</td>
<td>102.8–142.2</td>
</tr>
<tr>
<td>3</td>
<td>142.3–158.8</td>
</tr>
<tr>
<td>4</td>
<td>158.9–170.5</td>
</tr>
<tr>
<td>5</td>
<td>170.6+</td>
</tr>
</tbody>
</table>

* Based on data from Tester and Takata (1953).

![Fig. 1](image-url). The age-length relationship of the Aholehole.
Buckley, length

I

This action was made with a theoretical frequency of

...determined with a calculated “individual b” value of 2.75.

ACKNOWLEDGMENTS

I wish to thank Lester Zuckeran and Robert Tanaka of the Hawaii Marine Laboratory, Dr. Albert Tester of the University of Hawaii, and Dr. John Magnuson of the U. S. Fish and Wildlife Service, Honolulu, Hawaii.

REFERENCES


Some Aoridae (Amphipoda: Gammaridea) Collected by the Hancock Expeditions to the Eastern Pacific, 1931–1941

A. A. Myers

ABSTRACT: New records for the Pacific are given for three species of Microdeutopus Costa, one species of Acuminodeutopus Barnard, one species of Amphideutopus Barnard, and one species of Neomegamphopus Shoemaker. Full descriptions are given of Microdeutopus hancocki sp. nov. and Microdeutopus trichopus sp. nov.

The parameters of the various families of "domicolous" Amphipoda have recently become particularly difficult to define owing to the discovery of numerous intermediate forms (Barnard, 1959, 1961b, 1962, 1964). The Aoridae can be described most conveniently as species of the aorid-photid-corophiid complex which have the male first pereaeopod (=gnathopod) more markedly developed than the second, the urosome laterally compressed, and the third uropod with two, more or less subequal rami. The present paper deals with those genera of the family Aoridae in the Hancock collections in which the first male pereaeopod has the carpopodite more bulky than the propopodite, with teeth on its posterior margin.

I am indebted to Dr. J. L. Barnard and the United States National Museum for making the material available to me, to Dr. E. Naylor for helpful discussion, and to the Natural Environment Research Council for financial support.

Microdeutopus schmitti Shoemaker

Fig. 1a, d, j, l

IDENTIFICATION: Specimens agree well with the original description (Shoemaker, 1942). Figures of the paragnaths, ventral pereon spines, and first and second pereaeopoda are given for comparison with M. hancocki sp. nov.

DISTRIBUTION: Present material came from Costa Rica, and was particularly abundant in the numerous samples from Salinas Bay. Formerly the species was recorded from Baja California and California, apparently reaching its most northerly point of distribution at Cayucos (Barnard, personal communication).

Microdeutopus hancocki sp. nov.

Figs. 1b, c, e–i, k, and 6a

IDENTIFICATION: Among M. schmitti from Salinas Bay, Costa Rica, occur a few male Microdeutopus which differ constantly from the M. schmitti males in a number of characters. Unlike M. schmitti (Fig. 1d) the first pereaeopod (Fig. 1b, c) has the basipodite greatly swollen antero-proximally, the carpopodite has a dentiform process on its anterior margin, and the propopodite has a single lobe on its posterior margin (cf. Fig. 1d). In addition, the meropodite bears very long setae which are three to four times the length of those of M. schmitti. The second pereaeopod has the carpopodite and propopodite approximately subequal in width at their junction and the propopodite is short (Fig. 1b), whereas in M. schmitti the carpopodite is distinctly broader than the propopodite at their junction and the propopodite is relatively long (Fig. 1f). Also, the spine on the ventral surface of the sixth pereaeon segment differs in the two types of male: that of M. schmitti (Fig. 1f) is well developed, though shorter than those of pereaeon segments 3–5, while in present material (Fig. 1k) it is minute. Finally, the mandibular processes of the paragnath are considerably longer in present material (Fig. 1f) than in M. schmitti (Fig. 1a).

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1 Allan Hancock Foundation Contribution No. 319.
2 Department of Zoology, University College of Swansea, Swansea, Wales. Manuscript received August 11, 1967.
Fig. 1. *Microdeutopus schmitti* Shoemaker. SALINAS BAY, COSTA RICA. δ: a, paragnaths; d, peraeopod 1; j, peraeopod 2; l, ventral surface of peraeon segments 3–6.

*Microdeutopus hancocki* sp. nov. SALINAS BAY, COSTA RICA. δ Holotype: b, peraeopod 1. δ Paratype: e, uropod 3; f, paragnaths; h, peraeopod 2; i, telson; k, ventral surface of peraeon segments 3–6. BAHIA HONDA, PANAMA. ♀ Paratype: g, peraeopod 1. SALANGO ISLAND, ECUADOR. δ: c, peraeopod 1.

In view of the magnitude of these characters, which always occur in combination, present material is designated as a new species, for which *Microdeutopus hancocki* sp. nov. is proposed. This is further justified since the form often occurs together with *M. schmitti* in the same sample in the type locality at Salinas Bay. In samples from Ecuador, Panama, and Galapagos, *M. hancocki* occurs alone, and specimens from the first two of these localities agree with the type material. Specimens from Galapagos are smaller and more delicate than the types, with the antennules and antennae relatively longer (about half the body length), and the basipodite of the first peraeopod not greatly expanded antero-proximally. In other respects, however, they agree with type specimens, and are here considered as a variant of *M. hancocki*.

Females which occur with male *M. hancocki* in Panama and Galapagos samples resemble female *M. schmitti*, but differ from the latter in having the carpopodite of the first peraeopod smoothly rounded and lacking a tooth on the posterior distal angle. In *M. schmitti* females, one or more carpal teeth develop at an early age and are clearly discernible in specimens of 3.0 mm body length, whereas, in Panama specimens considered to be *M. hancocki*, no tooth is present, even in females 4.0 mm long. Similar females occur among *M. schmitti* females from Salinas Bay, and it is assumed that these are also the females of *M. hancocki* sp. nov. For practical purposes, since separation of *M. hancocki*...
females from those of *M. schmitti* depends upon this negative character, female paratype material has been designated from the Panama collections in which *M. schmitti* has not been recorded. These can definitely be assumed to be females of the *M. bancoki* males which they accompany.

*M. bancoki* appears to tolerate a narrower range of ecological conditions than does *M. schmitti*, all the specimens of the former being obtained from sand, while the latter was collected from mud, sand, algae, shells, and coral. *M. bancoki* is apparently a shallow water form, occurring at 1½—10 fathoms; *M. schmitti* ranges slightly deeper than this, to 15 fathoms in present samples, and to 23 fathoms (J. S. Garth, personal communication).

**Formal Description**

**TYPE LOCALITY:** Salinas Bay, Costa Rica.

**MALE HOLOTYPE:** Head (Fig. 6a) lobes moderately produced, obtuse; eyes circular; paragnath (Fig. 1f) with the mandibular processes long and slender. Body length, from anterior margin of cephalosome to tip of telson, 3.7 mm (paratypes 3.2—3.8 mm); pereon segments (Fig. 1k) 3—5 each with a short, robust, anteriorly curved spine on its ventral surface, 6 with a minute spine. *Antennules* slightly more than 1/3 the body length, the first and second peduncular segments subequal, the third segment about 1/3 the length of the second; flagellum 8-segmented (paratypes 8- or 9-

<table>
<thead>
<tr>
<th>STATION</th>
<th>DATE</th>
<th>LOCALITY</th>
<th>BEARINGS</th>
<th>REMARKS</th>
</tr>
</thead>
<tbody>
<tr>
<td>113-33</td>
<td>9 Mar 1933</td>
<td>Bahia Honda, Panama</td>
<td>7°45'18&quot;N 81°32'51&quot;W</td>
<td>5—8 fa; sand</td>
</tr>
<tr>
<td>114-33</td>
<td>10 Mar 1933</td>
<td>Bahia Honda, Panama</td>
<td>7°43'46&quot;N 81°31'54&quot;W</td>
<td>shallow water; coral</td>
</tr>
<tr>
<td>116-33</td>
<td>13 Mar 1933</td>
<td>Cocos Bay, south of Port Cuelebra, Costa Rica</td>
<td>10°33'35&quot;N 85°42'30&quot;W</td>
<td>2 fa; sand, shell</td>
</tr>
<tr>
<td>125-33</td>
<td>19 Mar 1933</td>
<td>Isabel Island, Mexico</td>
<td>21°51'30&quot;N 105°53'35&quot;W</td>
<td>shallow water; Porites coral</td>
</tr>
<tr>
<td>185-34</td>
<td>25 Jan 1934</td>
<td>Off Cartago Bay, Isabela (Albemarle), Galapagos</td>
<td>0°34'57&quot;S 90°53'44&quot;W</td>
<td>32 fa; mud</td>
</tr>
<tr>
<td>187-34</td>
<td>25 Jan 1934</td>
<td>Cartago Bay, Isabela (Albemarle) I., Galapagos</td>
<td>0°36'18&quot;S 90°57'11&quot;W</td>
<td>8—10 fa; sand with rock patches</td>
</tr>
<tr>
<td>190-34</td>
<td>26 Jan 1934</td>
<td>East of south end of Isabela (Albemarle) I., Galapagos</td>
<td>0°55' S 90°30' W</td>
<td>58—60 fa; sand, nullipores</td>
</tr>
<tr>
<td>204-34</td>
<td>31 Jan 1934</td>
<td>Gardner Bay, Espanola (Hood) I., Galapagos</td>
<td>1°20'30&quot;S 18°20'56&quot;W</td>
<td>30 fa; sand</td>
</tr>
<tr>
<td>257-34</td>
<td>25 Feb 1934</td>
<td>Off South Viradores Is., Port Cuelebra, Costa Rica</td>
<td>10°35' N 85°43'15&quot;W</td>
<td>10 fa; sand, shells</td>
</tr>
<tr>
<td>398-35</td>
<td>18 Jan 1935</td>
<td>Salango I., Ecuador</td>
<td>5°35'15&quot;S 80°52'52&quot;W</td>
<td>3 fa; sand</td>
</tr>
<tr>
<td>460-35</td>
<td>8 Feb 1935</td>
<td>Playa Blanca, Costa Rica</td>
<td>10°56' N 85°52'50&quot;W</td>
<td>3—5 fa; sand, shells</td>
</tr>
<tr>
<td>461-35</td>
<td>8 Feb 1935</td>
<td>Playa Blanca, Costa Rica</td>
<td>10°56'45&quot;N 85°53'50&quot;W</td>
<td>15 fa; mud, sand, algae</td>
</tr>
<tr>
<td>475-35</td>
<td>11 Feb 1935</td>
<td>Salinas Bay, Costa Rica</td>
<td>11°04'25&quot;N 85°44'40&quot;W</td>
<td>20 fa; mud</td>
</tr>
<tr>
<td>476-35</td>
<td>11 Feb 1935</td>
<td>Salinas Bay, Costa Rica</td>
<td>11°03'33&quot;N 85°43'47&quot;W</td>
<td>8 fa; mud</td>
</tr>
<tr>
<td>477-35</td>
<td>11 Feb 1935</td>
<td>Salinas Bay, Costa Rica</td>
<td>11°03'20&quot;N 85°43'30&quot;W</td>
<td>2 fa; coarse sand</td>
</tr>
<tr>
<td>478-35</td>
<td>11 Feb 1935</td>
<td>Salinas Bay, Costa Rica</td>
<td>11°03'13&quot;N 85°43'20&quot;W</td>
<td>1½ fa; coarse sand</td>
</tr>
<tr>
<td>479-35</td>
<td>11 Feb 1935</td>
<td>Salinas Bay, Costa Rica</td>
<td>11°02'50&quot;N 85°44'10&quot;W</td>
<td>2 fa; sand</td>
</tr>
<tr>
<td>480-35</td>
<td>11 Feb 1935</td>
<td>Salinas Bay, Costa Rica</td>
<td>11°04'10&quot;N 85°44'40&quot;W</td>
<td>12 fa; shells, vegetation</td>
</tr>
<tr>
<td>481-35</td>
<td>11 Feb 1935</td>
<td>Salinas Bay, Costa Rica</td>
<td>11°03'33&quot;N 85°45'05&quot;W</td>
<td>6 fa; shells, vegetation</td>
</tr>
<tr>
<td>564-36</td>
<td>10 Mar 1936</td>
<td>Off south end of Tiburon I., Gulf of California</td>
<td>28°44'45&quot;N 112°18'20&quot;W</td>
<td>8—10 fa; kelp, coralline</td>
</tr>
</tbody>
</table>
Fig. 2. *Microdentopus trichopus* sp. nov. Isabela Island, Galapagos. ♀ Holotype: a, pereopod 1; b, telson; d, uropod 3. ♂ Paratype: e, pereopod 2; f, ventral surface of pereon segments 3-6. ♀ Paratype: c, pereopod 1; g, pereopod 2.

segmented) about equal to the peduncle; accessory flagellum 2-segmented (some paratypes 3-segmented), the first segment elongate, the second rudimentary, not extending beyond the first segment of the primary flagellum. (In a few paratypes it reaches the second segment, when the meristematic basal segment of the primary flagellum is dividing.) Antennae shorter than the antennules, the fourth and fifth peduncular segments subequal; flagellum 4-segmented, the first segment long, equal to the combined lengths of the terminal three. Peraeopod 1 (Figs. 1b, e) with the coxopodite produced anteriorly, rounded; basipodite markedly produced antero-proximally; meropodite with very long setae on the posterior border. Carpopodite oval, longer than broad, with a median dentiform process on its anterior margin, and, at the posterior distal angle, three stout teeth the most distal of which is the longest; propodite short, with a single lobe on the posterior margin; dactylopodite relatively long. Peraeopod 2 (Fig. 1b) with the basipodite concave anteriorly, carpopodite considerably longer but scarcely broader than the propodite. Peraeopods 3-7 of the usual *Microdentopus* form. Uropod 3 (Fig. 1e) with the rami subequal and longer than the peduncle; exopodite terminal margin with one very long
spine and a group of short spines, inner and outer margins each with a single spine; endopodite inner border with two widely separated spines, the most distal of which is the shorter, outer border with a solitary spine and a single group of short stout terminal spines. Telson (Fig. 17) longer than broad, the terminal crests well developed, each bearing on the dorsal surface a short stout spine and distal to it a long seta.

**FEMALE PARATYPES (Bahia Honda, Panama):** *Peraeopod 1* with the posterior margin of the carpopodite smoothly rounded and no tooth on the posterior distal angle; otherwise as female *M. schmitti*.

**TYPE MATERIAL:** 21♂♂, Station 478-35. 21♀♀, Station 113-33.

**TYPES:**
- 2♂♂ Holotype, USNM No. 112797
- 18♂♂ Paratypes, USNM No. 112798
- 2♀♀ Paratypes, BM No. 1967:7:2:3-4
- 19♀♀ Paratypes, USNM No. 112799

**DISTRIBUTION:** Costa Rica (Salinas Bay), Panama (Bahia Honda), Ecuador (Salango Island) and Galapagos (Isabela Island).

**Microdeutopus trichopus** sp. nov.

Figs. 2a–g and 6b

**IDENTIFICATION:** In the development of teeth on the posterior margin of the carpopodite and propodite of the first male peraeopod, this form resembles *Microdeutopus tridens* Schell. and *M. kraemmeri* Reid. These two species, however, have the carpopodite short and as slender as the propodite and should more correctly be attributed to the genus *Lembopsis* Pearse (see also Barnard, 1959). Present material has the carpopodite more bulky than the propodite, a feature characteristic of *Microdeutopus* Costa, and, since the specimens agree with no known *Microdeutopus* sp., they are designated as *M. trichopus* sp. nov.

**TABLE 2**

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564-36
Formal Description

TYPE LOCALITY: East of south end of Isabela Island, Galapagos.

MALE HOLOTYPE: Head (Fig. 6b) lobes moderately produced and obtuse, eyes round. Body delicate, length from anterior margin of cephalosome to tip of telson 3.8 mm (paratypes 3.0-3.8 mm). Peraeon segments 3-6 (Fig. 2f) each with a very long, slender spine on its ventral surface, those of segments 3 and 4 curved forward, and those of segments 5 and 6 slightly recurved. Antennules slightly over half the body length, the first peduncular segment slightly shorter than the second, the third about 1/3 the length of the second; flagellum slightly longer than the peduncle, 12-segmented on one side, 11-segmented on the other (paratypes with a maximum of 13 segments); accessory flagellum 3-segmented, the third segment rudimentary. Antenna about 2/3 the length of the antennule, the fourth and fifth peduncular segments subequal; flagellum 4-segmented on one side, 5-segmented on the other. Peraeopod 1 (Fig. 2a) with the coxopodite produced anteriorly, rounded; basipodite expanded anteroproximally; meropodite short; carpopodite oval, longer than broad, with a median dentiform process on the anterior margin, and at the posterior distal angle, a short stout tooth, basal to which, on the posterior margin, is another small tooth. Propopodite over half the length of the carpopodite, the palmar angle produced into a forward projecting, blunt tooth, opposable with the dactylopodite, which is of moderate length and has accessory teeth on the distal part of the inner margin. The posterior margins of the meropodite, carpopodite, and propopodite densely setose, the setae exceptionally long, being about 0.5 mm, 0.4 mm, and 0.3 mm on each podomere respectively. Peraeopod 2 (Fig. 2c) with the basipodite moderately expanded, the anterior margin slightly concave; carpopodite and propopodite subequal in length and

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Fig. 3. Acuminodentopus heteruroopus Barnard. PLAYA BLANCA, COSTA RICA. ♂: b, head and peraeopod 1; c, peraeopod 2. ♀: a, peraeopod 1; d, peraeopod 2.
breadth. *Peraeopods* 3–7 of the usual *Microdeutopus* structure. *Uropod* 3 (Fig. 2d) rami long and slender, longer than the peduncle; exopodite very slightly exceeding the length of the endopodite, with a single median spine on the outer margin and a similar one on the inner margin; endopodite with a single spine on the outer margin, and a similar, more distal spine on the inner margin. *Telson* (Fig. 2b) broader than long, the terminal crests well developed, each bearing on its dorsal surface a long seta and a short stout spine.

**FEMALE PARATYPES:** Body lengths 4.0 mm and 3.1 mm. Characters as for male, except for the structure of the first and second pereopoda. *Peraeopod* 1 (Fig. 2c) with the basipodite moderately broad; carpopodite and propopodite slender, subequal in length, the propopodite somewhat broader distally than at the junction with the carpopodite; dactylopodite longer than the palmar region of the propopodite, with accessory teeth on the posterior margin. *Peraeopod* 2 (Fig. 2g) with the basipodite moderately broad, carpopodite not greatly expanded distally, slightly shorter than the propopodite; dactylopodite short and stout.

**TYPE MATERIAL:** 35 $\delta$, 2 $\varphi$, Station 190-34.

**TYPES:**
- $\delta$ Holotype, USNM No. 112800
- $2 \delta$ Paratypes, BM No. 1967:7:2:5–6
- $32 \delta$ Paratypes, USNM No. 112802
- $2 \varphi$ Paratypes, USNM No. 112801

**DISTRIBUTION:** Galapagos (type locality and Cartago Bay, Isabela Island).

*Acuminodeutopus heteruropus* Barnard


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**Fig. 4. Acuminodeutopus heteruropus** Barnard. **Playa Blanca, Costa Rica.** $\delta$: a, uropod 3; b, paragnath; c, maxillule; d, mandible; e, telson.
IDENTIFICATION: Specimens agree well with the description of Barnard (1959), showing only a few minor points of difference. Unlike type material, the carpopodite of the first male pereaeopod has the posterior distal angle produced into a broad process which constricts about halfway along its length into a narrow, blunt-ending, inward curved tooth, which does not reach to the tip of the propodite, and in this respect resembles specimens collected in the open sea off Newport, California (Barnard, 1961). In addition, the carpopodite of the second male pereaeopod is somewhat more elongated than in type material, the propodite of the first female pereaeopod is scarcely expanded distally, and the telson in both sexes bears both spines and setae on its distal margin. The maximum size of males in the collections is 3.0 mm, that of the females, 3.5 mm.

DISTRIBUTION: Present material comes from Costa Rica (Playa Blanca and Cocos Bay), that of Barnard (1959, 1961) from Newport Bay, California.

Amphidentopus oculatus Barnard

Barnard, J. L. 1959. Contr. Allan Hancock Fdn. Occas. Paper 21, pp. 34–35, pl. 10. Fig. 5d–e

IDENTIFICATION: Specimens do not differ to any great extent from those described by Barnard (1959). The maximum size of males in the collections is 8 mm, as compared with 4.5 mm for the male holotype.

DISTRIBUTION: Present material came from the Gulf of California (Tiburon Island) and Costa Rica (Salinas Bay), that of Barnard (1959) from Newport Bay.

Fig. 5. Neomegamphopus roosevelti Shoemaker. BAHIA HONDA, PANAMA. ♀: a–c. f, pereopod 1. Amphidentopus oculatus Barnard. TIBURON ISLAND, CALIFORNIA. ♂: d, pereopod 1. SALINAS BAY, COSTA RICA. ♀: e, pereopod 2.
position of the tooth varies according to the stage of development of the animal. The propopodite also varies; in some specimens it is broad with the posterior margin convex, in others it is narrow with the posterior margin concave.

**DISTRIBUTION:** *N. roosevelti* is in this study shown to be widely distributed along the Pacific coasts of the Americas, in Mexico (Isabel Island), Costa Rica (Playa Blanca and Salinas Bay), Panama (Bahia Honda), and Galapagos (Espanola). The species reaches its most northerly point of distribution in the Pacific in the type locality (Magdalena Bay, Baja California) (Shoemaker, 1942). It is also known from the Atlantic, off the coasts of Venezuela (Myers, 1968) and Florida (unpublished observations).

**DISCUSSION**

All five genera recorded are here included in the family Aoridae, even though it is difficult to separate this family from the Photidae (Barnard, 1959). The genera *Amphideutopus* and *Neomegamphopus* are particularly difficult to allocate since they show relationships with the Photidae in the form of the head and mandible, but have the gnathopod and paragnath characteristic of the Aoridae. Following Barnard (1962) who included *Neomegamphopus* in the Aoridae, *Amphideutopus* is here also regarded as a member of that family since for practical purposes the enlarged first gnathopoda may be taken as the common feature which unites these genera within the Aoridae. Barnard has suggested that this feature probably indicates some basic difference in axial gradients between the two groups.

**REFERENCES**


The Distribution and Biogeography of *Zostera marina* (Eelgrass) in Alaska

C. Peter McRoy

Although innumerable botanists have visited Alaska to record and study its flora, most accounts terminate at the high-tide line. Consequently, the marine vegetation, especially that of the most northern coasts of Alaska, has received little attention and the distributions of many species are sketchily known. *Zostera marina* Linnaeus, the common eelgrass, has probably received more interest than most, because of its importance as a waterfowl food. In spite of this, the distribution outlined by Hultén (1941:95, 1960:69, 1964:256) and other published sources (Anderson, 1939:48; Porsild, 1952:90-94; Polunin, 1940:40-41; Setchell, 1920:563-579, 1935:560-577; Murie and Scheffer, 1939:396) is very incomplete in the light of recent surveys of the coast. By compiling the results of personal efforts and communications over the past few years, I can now document in detail the distribution of this species in Alaska.

An additional result of searching and studying the distribution of *Zostera* in Alaska has been a review of the mechanisms of dispersion that have established and maintained this distribution. These aspects of the study of *Zostera* have in turn led to considerations of the biogeography of the species which can be reconstructed from distribution records and dispersion mechanisms.

**Distribution Survey**


In Alaska, *Zostera* forms a distinct subtidal zone in protected bays, inlets, and lagoons along the coast from Bering Strait south (Hultén, 1941:95). During 1967 I was able to survey many miles of the Alaska coast to locate and examine the *Zostera* beds. These surveys included Southeast Alaska, Prince William Sound, the Cold Bay region of the Alaska Peninsula, parts of the Seward Peninsula near Nome and Teller, the coast of the Chukchi Sea between Kivalina and Cape Thompson, and the vicinity of Point Barrow. The observations from these field trips have been combined with the published records and personal observations of several people to present a detailed listing of the locations of *Zostera* beds on the coast of Alaska (Fig. 1 and Table 1).

In Southeast Alaska, the Alexander Archipelago, *Zostera* is found in most of the bays and inlets of the outer coast, but it is absent from many of these on the inside waters (Fig. 1 and Table 1). This is apparently due to the turbid effluent of glaciers. No plants were found in any of the areas receiving large amounts of glacial runoff although other environmental conditions appeared quite suitable for their growth. For example, in Doty Cove and Lime- stone Inlet in Stephens Passage (near Juneau) the absence of *Zostera* is enigmatic in winter months when ambient waters are clear; but in summer the problem is solved by the presence of very turbid water from nearby Taku Inlet. In bays and inlets receiving quantities of the turbid glacial water the subtidal zone of soft bottoms usually occupied by *Zostera* is devoid of all macrophytes.

The coast from Cross Sound to Prince William Sound is rugged and exposed to the open sea; most of the existing bays harbor glaciers or glacial streams. *Zostera* has been reported only in Yakutat Bay (Setchell, 1920:567; Fig.
Fig. 1. Chart of Alaska showing the location of records of Zostera marina on the coast. Numbers refer to locations given in Table 1.
TABLE 1

Records of *Zostera marina* in Alaska

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* Numbers refer to the geographical locations shown in Figure 1.

1 and Table 1). Isolated populations in other more inaccessible areas are of course possible. Prince William Sound contains many *Zostera* beds (Fig. 1 and Table 1), but their distribution was altered by the earthquake of March 1964. Johansen (1965:93–94) lists nine localities where he found dead *Zostera* attributable to the seismic uplift of the region. In June 1967 I revisited many of Johansen’s stations. In several of these, the most striking being the vicinity of Cordova, no new *Zostera* was seen; in other places, such as Redhead Lagoon, reduced populations were evident.

The outer coast of the Kenai Peninsula is a glaciated region where no *Zostera* has been reported, nor has any been found in Cook Inlet, which might be expected from the turbidity and currents in the Inlet. There are, however, unconfirmed reports of *Zostera* in Kachemak Bay.

Several bays on Kodiak and Afognak islands, on the Alaska Peninsula, and in the Aleutian Islands contain *Zostera* beds (Hultén, 1941:95; Beals, 1941; Fig. 1 and Table 1). The western limit of the species in North America was Vsevidof Island (Murie and Scheffer, 1959:369). This limit can now be extended to Atka and Adak islands (Jones, personal communication, 1965). The plants on Adak are evidently a result of transplantation experiments by the
U.S. Fish and Wildlife Service. No plants are known to occur in the western Aleutian Islands, probably due to the lack of protected bays. Plants are known from Kamchatka Peninsula and Bering Island on the Asian side of the Bering Sea (Hultén, 1926:75, 1960:69).

In the Bering Sea Zostera forms extensive meadows in the numerous coastal lagoons of the Alaska Peninsula (Fig. 1 and Table 1). The meadows in Izembek Lagoon on the Peninsula are the largest known single stand of the species (McRoy, 1966:103). Farther north, Zostera occurs in Nanvak and Chagvan bays and in many of the lagoons at the mouths of rivers on Nunivak Island (King, personal communication, 1963). No other Zostera beds have been found between King Salmon and St. Michael.

Porsild (1932:90–94) recorded the northern distribution of Zostera from St. Michael to Port Clarence (Fig. 1 and Table 1). Kjellman (1883:53) first observed Zostera in Port Clarence, the accepted northern limit in Alaska. Recently, Zostera has been seen beyond Bering Strait in the lagoons (Lopp and Ikpek) of the north coast of the Seward Peninsula (Burns, personal communication, 1967). I have also extended surveys to portions of the coast between Kotzebue and Barrow, but have not uncovered any other Zostera producing areas.

Mechanisms of Dispersion

The distribution of Zostera in Alaska and elsewhere in the Northern Hemisphere is the result of dispersion by several mechanisms. Oceanic currents appear to be the most effective means of long range dispersion, although there is some disagreement on this. Löve (1963:195) observes that saltwater plants are adapted to dispersal in sea water and cites as an example the seeds of Zostera with their corky appendages and buoyant vegetative parts. Sculthorpe (1967: 358), on the other hand, considers Löve's view of dispersal an "unfortunate generalization," since the seeds of Zostera and other marine angiosperms either float for only a short time or sink immediately. The seeds of Zostera have a specific gravity of 1.17 (Arasaki, 1950:70–76), a value somewhat greater than the 1.025 average of the ocean (Von Arx, 1962:118) and so would be expected to sink. In fact, however, the seeds are released attached to a reproductive stem which has several leaves and is capable of floating for long distances. Mats of Zostera and other marine angiosperms have been seen at sea several hundred miles from the coast (Menzies, Zaneveld, and Pratt, 1967: 112). There can be no doubt that dispersion on a large scale is accomplished through the seed-producing and perhaps vegetative plants that annually detach and drift with oceanic surface circulation.

The several species of waterfowl that feed on Zostera are another vehicle for dispersion. Löve and Sculthorpe concur. Arasaki (1950:70–76) demonstrated that ducks do not destroy the viability of all seeds they ingest. The coast of Alaska is a flyway for numerous species of waterfowl that annually transport seeds over at least short distances and probably farther. This is a mechanism for dispersion in a direction opposite to that of the coastal oceanic currents.

In a local area Zostera extends its cover principally by vegetative growth from rhizomes, a process quantitatively more important than the growth of new seed plants. Again, Arasaki (1950:70–76) has shown that a single plant will cover 30 cm² the first year, 1 m² the second, and 2 m² the third. At this rate, it would not take long for a population to develop in a new area once a plant has been introduced.

Biogeographical Considerations

The global distribution of this species is discontinuous circumboreal. The other species of the seagrasses, with few exceptions, are tropical or subtropical and are considered to have originated in the Indian Ocean (Setchell, 1935: 564–572). The genus Zostera, however, has no tropical representatives and apparently arose in the western Pacific Ocean, dispersing into the Northern and Southern hemispheres at a time when the tropics were less tropical. This history is supported by the present distribution of the 11 species of Zostera (Setchell, 1935:572) and the locations of fossils of Zostera ancestors in Japan (Koriba and Miki, 1930:165–204; Miki, 1932:774–778).

If the origin of Zostera marina was the western Pacific, then migration could have taken either of two routes. In the first case, dispersion could have moved in two directions from the
Zostera marina in Alaska—McRoy

origin, populating both sides of the Pacific Ocean in one direction and through the Indian Ocean and the Mediterranean Sea to both sides of the Atlantic Ocean in the other. Setchell (1935:572) suggested that a route of this sort could have occurred at a time, probably in the early Tertiary, when the Tethys Sea covered much of the Northern Hemisphere. The other possibility for dispersion is a one-way movement. This is really an argument for a one-way dispersion route through the Pacific Ocean rather than through the Indian Ocean. This path would result logically in the present distribution of the species. The theory demands that the Atlantic and its adjacent seas were populated by migration through the Arctic during a prehistoric milder climate, which should be entirely possible, for, as the distribution in Alaska illustrates, Zostera marina is a cold-tolerant species. If continuity through the Arctic once existed, relict populations would be expected along the Arctic coast. These do exist in the White Sea, the Barents Sea, the Kara Sea, and Hudson Bay (Zenkevitch, 1963:195–198; Blinova, 1962:150; Setchell, 1920:567; Porsild, 1932:91). Ekman (1953:160–164) describes similar patterns for many species of marine invertebrates and vertebrates that have discontinuous distributions in the Pacific and Atlantic oceans. Additionally, Durham and MacNeil (1967:343) report that a large number of species, more than 125, of marine invertebrates have dispersed from one ocean to the other mostly in one direction—into the Arctic-Atlantic; they consider these migrations to have occurred during the late Cenozoic.

The evidence available indicates that Z. marina originated in the western Pacific and dispersed to the north along the coast of Asia and then around to North America. Its tolerance to low temperatures permitted it not only to cross the subarctic Pacific to North America, but also to populate the Arctic and move eventually to both shores of the Atlantic. Perhaps in times of cooler climates migration continued into the north coast of the Mediterranean Sea and its adjacent seas. No other species of Zostera has this widespread distribution, nor is there another one tolerant to low temperatures. The single closely related species that has a similar, but more restrictive, temperature tolerance is Phyllospadix scouleri Hook which is endemic to the temperate Pacific Ocean. This species provides an example of the limited distribution of a less cold-tolerant species originating in the same area; it never reached the Atlantic. The opposite situation is illustrated by the distribution of Zostera nana Roth, a species less tolerant to cold water but more so to warm water; it is limited to the western Pacific, but has also been able to move through the Indian Ocean to populate parts of Africa, the Mediterranean (both north and south) and parts of the southern Atlantic coast of Europe.

SUMMARY AND CONCLUSIONS

Zostera marina, eelgrass, is a common inhabitant of the Alaska coast, occurring from the lagoons on the north coast of the Seward Peninsula to the southern limit of Alaska and beyond. New records of Zostera in Alaska are from Adak and Atka in the Aleutian Islands, Chagvan and Nanvok bays and Nunivak Island, and Lopp and Ikpek lagoons on the Seward Peninsula. In Prince William Sound the distribution of Zostera was markedly altered by uplift associated with the earthquake of March 1964.

Zostera grows in the soft sediments of shallow, protected marine bays, inlets, and lagoons. It is excluded from large river deltas, glacial fjords, and arctic environments. The distribution in Alaska is disjunct, a result of environmental restrictions rather than a lack of dispersion mechanisms. Global dispersion is a result of oceanic circulation and waterfowl migrations. Vegetative growth is the most important means of extending coverage of a restricted area. In view of the present distribution of the species and the geological structure of the Alaska coast, no extensions of the range of Zostera are expected. Populations may exist, of course, in remote places along the coast.

Alterations in the present distribution are possible only with major geological or climatic changes. Seismic uplift or depression of the south coast of Alaska could eliminate a large portion of the present populations. On the other hand, amelioration of conditions in arctic waters by a change in ice conditions could permit further extension of the present range.

The circumboreal distribution of Z. marina
is considered to be a result of dispersion from a western Pacific origin around the Pacific and through the Arctic into the Atlantic and its adjacent seas. That this was the path of migration is supported by the present distribution of the species, the location of its fossil ancestors, and similar dispersal patterns for marine invertebrates.

The migration and present distribution of *Z. marina* have resulted from the eurythermality of the plant. This feature probably also permitted survival during oscillating Pleistocene climates.

The *Zostera* communities on the Alaska coast are important contributors to all levels of production in the food web and provide refuges to innumerable species of organisms. Research is in progress on the ecology of these interesting communities.

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Zostera marina in Alaska—McRoy


Revision of the Genus *Pandanus* Stickman, Part 29

New Papuan Species in the Section *Microstigma* Collected by C. E. Carr

HAROLD ST. JOHN

The island of New Guinea has a large concentration of species of *Pandanus*, and it is evident that they have been only partly collected and studied. They occur in nearly all plant formations from sea level to 3500 meters altitude. The three species here described were collected by C. E. Carr in 1935. He attempted to cross the Owen Stanley Range, from south to north, but lost his life in the attempt.

Section *Microstigma*

*Pandanus Carrii* sp. nov. (sect. *Microstigma*)

Fig. 272

**Diagnosis Holotypi**: Arboriformis 5 m alta, radicibus trunco ramis syncarpio incognitis, foliis 1.14 (+0.02–0.05) m longis proxima basem 3.6 cm latis in medio 2.6 cm latis coriaceis supra viridibus infra pallidoribus U-sulcati 2-plicati in sectione mediali cum 49 nervis parallelis secundaribus in quaque dimidio nervis tertii nullis lamina angustia adscendente ex basi sensim in apice crasso subulato (apex deest) basi inerimi pallida, ex 11–13 cm marginibus cum aculeis 2–2.5 mm longis 6–12 mm separatis arcauis fragilibus subulatis valde ascendentibus pellidiis vel cum apicibus rubris, in sectione mediali marginibus cum aculeis 1.7–2 mm longis 5–12 mm separatis subarcauis subulatis gracilibus subadpressis ascendentibus apicibus rubris, midnervo infra inerimi, in apice subulato marginibus cum crenati-serrulis 0.2–0.3 mm longis 2–5 mm separatis rubris, syncarpio viridi, drupis 7.7–7.8 cm longis 1.4–1.6 cm latis 1.3–1.5 cm crassis prismaticis 6-angulos, pileo 14–17 mm alto deciduo laevi exulci dimidio infero late obuso 6-anguloso dimidio supero rostrato crasso, stigmat 6–7 mm longo late elliptico obiique brunneo papilloso sulcato, endocarpio subulato 4.3 cm longo subcylindrico cuneato osseo obscuro brunneo lateribus lateribus 0.7–1.5 mm crassis intra laevibus lucidis, mesocarpio extra endocarpii cum fibris et eis ad stigmatem convergentium, exocarpio et mesocarpio molliter carnoso et in fructu delapsio et in sico nigro, mesocarpio apicis extra cum fibris longitudinalibus sed intra cum membranis, mesocarpio basali carnoso et in sico valde contracto.

**Diagnosis of Holotype**: Tree-like, 5 m tall; roots, trunk, branches, and syncarp unknown; leaves 1.14 (+0.02–0.05?) m long, 3.6 cm wide near the base, 2.6 cm wide at the middle, coriaceous, above green, below paler green, U-sulcate, 2-plicated, at midsection with 49 parallel secondary veins in each half, no tertiary cross veins, blade narrowly sword-shaped, tapering gradually from near the base into the stout subulate apex (the actual tip missing), the base pale, unarmed, beginning at 11–13 cm up the margins with prickles 2–2.5 mm long, 6–12 mm apart arcuate weak subulate, strongly ascending, wholly pale or with red tips; the nearby midrib below not visible; at midsection the margins with prickles 1.7–2 mm long, 5–12 mm apart, subarcuate slender subulate, almost appressed ascending, red-tipped; the midrib below unarmed; near the apex the margins with crenate-serrulations 0.2–0.3 mm long, 2–5 mm apart, red; those of the midrib below not observed; syncarp “green”; drupes 7.7–7.8 cm long, 1.4–1.6 cm wide, 1.1–1.4 cm thick, prismatic, 6-angled; pileus 13–17 mm high, deciduous, smooth, dull, the lower half forming the broadly obtuse base, this 6-angled, bearing a thick beak; stigma 6–7 mm long, broadly elliptic, oblique, brown, papillos, sulcate; endocarp submedian, 4.3 cm long, subcylindric, tapering downward, the apex arched, bony, dark brown, the lateral walls 0.7–1.5 mm thick, within smooth, shiny; mesocarp with thick fibers up the sides of the endocarp and bending in toward the stigma; exocarp and lateral mesocarp soft fleshy, and at maturity sloughing off and drying black; apical mesocarp with fibers up the sides and within partitioned by pale membranes and filaments; basal mesocarp fleshy and at maturity much shrunked.

**Holotypus**: Papua, Koitaki (on track to Owen Stanley Mountains pass), open savannah land, 1,500 ft alt, 13. 5. 1935, C. E. Carr 12,274 (BM). Isotype (K)!

**Discussion**: *P. Carrii* is a member of the section *Microstigma*, as is its closest relative, *P. jilidanettii* Martelli, a species with drupes 9.5-
10 cm long; stigmas mostly excentric and sub-oblique; leaves 10 cm wide, and at midsection with 87 parallel secondary veins in each half, and there the margins with prickles 0.6–1 mm long, 3–7 mm apart, subulate, weak, countersunk in the margins, appressed ascending, yellowish. *P. Carrii* has the drupes 7.7–7.8 cm long; stigmas apical, oblique; leaves 3.6 cm wide, these at midsection with 49 parallel secondary veins in each half, and here the margins with prickles 1.7–2 mm long, 5–12 mm apart, subarcuate slender subulate, almost appressed ascending, red-tipped.

The species is named in honor of Cedric Eroll Carr (1892–1936) who made a notable collection in New Guinea. He crossed from Port Moresby over the Owen Stanley Range. Unfortunately, when approaching the north coast he sickened with black-water fever, and died there.

The specimen Carr 12,274 in the Arnold Arboretum herbarium is utterly different, an immature plant of the section *Pandanus*. There has been confusion in sorting and labelling it.

**Pandanus erybros** sp. nov. (sect. *Microstigma*)

Fig. 273

**Nom. vern.**: "hadoro" (Biagi language); "kerei-kerei" (Motuan language).

**Diagnosis**: Holotype: Licet arbor, radicibus truncis ignotis, foliis licet 2 m vel plus longis sed solum apice 51 cm longo preservato, eo subtiliter coriaceo supra viridi infra pallidiori V-sulcato 2-plicato in puncto 51 cm ex apice 8 cm lato et cum 65 nervis parallelis secundariis in quoque dimidio nervis tertius nullis marginibus cum aculeis 0.4–1.3 mm longis 1–3 mm separatis subulatis rectis adpresse adscendentibus pallidis, midnervo proximo infra cum aculeis 0.4–0.8 mm longis 2–4 mm separatis arcuratis crassiter subulatis apicibus brunneis, in apice acuto marginibus cum subulato-serulis 0.3–0.7 mm longis 0.5–2 mm separatis adscendentibus pallidis, midnervo infra cum aculeis 0.6–0.8 mm longis 3–5 mm separatis arcuratis subulatis adscendentibus pallidis, infructescientia cum syncarpo solitario, pedunculo 2.5 cm diametro 3-latereato bracteoso, syncarpio in 12–15 bracteis triseriatis clauso eins 9 cm latiss 22 et plus cum longis crassiter coriaceis marginibus cum aculeis 0.3–0.5 mm longis 1–2 mm separatis subulatis salientibus, midnervo infra per 15 cm inermi, syncarpio 22–27 cm longo 4.5–5 cm diametro subcilindrico obscure aurantiaco-rubro cum drupis numerosissimis eins 13–14.5 mm longis 2.5–2.8 mm latiss 2–2.5 mm crassis anguste prismaticis 5–7-angulosis parte ⅓ supera libera, pileo 3 mm alto pyramidalis, stigmatic apicalis et pellumque horizontali 1–1.2 mm lato cordato vel reniformi brun-
Fig. 273. *Pandanus erythros* St. John, from holotype. *a*, Syncarp and bracts, lateral view, × $\frac{1}{4}$; *b*, apical drupe, lateral view, × 1; *c*, apical drupe, longitudinal median section, × 1; *d*, apical drupe, apical section, × 1; *e*, apical drupe, lateral view, × 4; *f*, apical drupe, longitudinal median section, × 4; *g*, lower lateral drupe, apical view, × 4; *h*, lower lateral drupes, lateral view of apex and stigma, × 4; *i*, leaf section, 45 cm down from tip, lower side, × 1; *j*, leaf apex, upper side, × 1; *k*, leaf apex, lower side, × 1.
HOLOTYPE: Papua, Isuara, sec[ondary] forest, 3,500 ft alt, 3. 3. '36, C. E. Carr 15,922 (BM). Isotypes (K, L.)

DISCUSSION: *P. erythros* is a member of the section *Microstigma*, as is its closest relative, *P. Hollrungii* Warb. of Australian New Guinea, a species with the syncarp 35 cm long, 4-7 cm in diameter; drupes 11-13 mm long, the apex wide pyramidal; apex of the endocarp low convex; leaves at midsection with prickles of the margins 0.3-1 mm long, 1.5-3 mm apart, arcuate stout subulate, ascending. *P. erythros* has the syncarp 22-27 cm long, 4.5-5 cm in diameter; drupes 13-14.5 mm long, the apex narrowly pyramidal; apex of the endocarp conic; leaves at midsection with prickles of the margins 0.4-1.3 mm long, 1-3 mm apart, straight subulate, appressed ascending.

The new epithet is the Greek adjective *erythros*, red, and is given with reference to the orange-red fruit.

**Pandanus plicatus** sp. nov. (sect. *Microstigma*)

Fig. 274

NOM. VERN.: *'gani***.

DIAGNOSIS: Forma radiques truncus et ramiuli incogniti, basibus et mediis foliarum non conservatis, apicibus foliarum 39 cm longis preservatis 4.5 cm latis subtillator coriaces supra viridibus infra palliditer viridibus cum 48 nervis parallelis secundariis in quoque dimidio nervis tertios reticulis anguste oblongis formantibus, lamina pulvulata V-sulcate 2-plicata in apice acuto diminished in sectione inferiori visi marginibus cum aculeis 2-4 mm separatis arcuatis croxifer subulatus adscendentibus bifomatis alternantibus eis majoribus 0.7-1.3 mm longis illis minoribus 0.2-0.4 mm longis, midnervro infra angusto elevato et cum aculeis simulantes bifomatis 1.5-3 mm separatis eis majoribus 0.2-0.4 mm longis illis minoribus 0.1-0.2 mm longis, in apice marginibus et midnervro infra cum subulati-serululis 0.1-0.5 mm longis 0.5-1.5 mm separatis pallidis, infructescens cum syncarpio solitario, pedunculo 17 cm longo, 12-15 mm diametro trigono foliosi-bracteato, syncarpio in seriebus tribus foliarum inclusus, bracteis exterioribus cum basi distenta lanceolata 9-10 cm lata syncarpio aqueantibus firmo chartacea pallide lutea marginibus et midnervro infra minute spinosa apice folioso viridi ligulato, bracteis interioribus 23 cm longis lineari-lanceolatis, syncarpio 20 cm longo 6.3 cm diametro cylindrico cum drupis multis eis 20-22 mm longis 2.5-4 mm latis 2.5-3 mm crassis angustis pristmaticis 3-6-angulosis rubris et licet omnino glutinisus parte ⅔ supera libera ovoidea laevi lucida sed in sicco rugosa, stigmatic 1.5-2 mm diametro apicali horizontali subcirculares obscure brunneo papilloso, endocarpio in parte ⅕ infera osseo rubri-brunneo tubu-
liso cum seta terminali lateribus lateralibus 0.2 mm crasis intra laevisus lucidis, semine 9 mm longo, mesocarpio apicali cavernoso cylindrico cum membranis longitudinalibus bruneis paucis, mesocarpio basali fibroso et camoso.

**DIAGNOSIS OF HOLOTYPE:** Habit, roots, trunk, and branches unknown; leaf base and middle not preserved; leaf apex 39 cm long preserved, 4.5 cm wide, thin coriaceous, above green, below pale green, at the point 39 cm down with 48 parallel secondary veins in each half, the tertiary visible in outer part, forming narrow oblong meshes; blade apparently ligulate, V-sulcate, 2-pleated, narrowing to an acute apex, and at the lowest point the margins with prickles 2-4 mm apart, arcuate stout subulate, ascending, of two kinds alternating, the larger ones 0.7-1.3 mm long, the smaller ones 0.2-0.4 mm long; the nearby midrib below slender, elevated, and also with similar prickles of two types 1.5-3 mm apart, the larger ones 0.2-0.4 mm long, and the smaller ones half as long; at the apex the margins and midrib below with subulate serrations 0.1-0.5 mm long, 0.5-1.5 mm apart, pale; infructescence with a solitary syncarp; peduncle 17 cm long, 12-15 mm in diameter, trigonous, leafy bracted; syncarp completely enwrapped by numerous foliaceous bracts in 3 series; outer bracts with an expanded, lanceolate base 9-10 cm wide, as long or longer than the syncarp, firm chartaceous, cream-colored, minutely prickly on margins and midrib below, bearing a foliaceous, green, ligulate apex, probably quite long, but not preserved; innermost bracts 23 cm long, 3 cm wide, slightly exceeding the syncarp, chartaceous, colored, linear lanceolate; syncarp 20 cm long, 6.3 cm in diameter, cylindric, bearing multitudinous drupes, these 20-22 mm long, 2.5-4 mm wide, 2.5-3 mm thick, narrowly prismatic, 5-6-angled, red, apparently mucilaginous throughout, upper 1/4 free, ovoid, smooth, shiny, when dried rugose; stigma 1.5-2 mm in diameter, apical, flush, horizontal, subcircular, dark brown, papillose; endocarp in lower 3/5, bony, reddish brown, tubular, with an apical bristle bending toward the stigma, the lateral walls 0.2 mm thick, within smooth, shining; seed 9 mm long; apical mesocarp a cylindrical cavern with a few longitudinal brownish membranes; basal mesocarp fibrous and fleshy.

**HOLOTYPE:** Papua, Koitaki, wood by stream, 1,500 ft alt, 18. 6. 1935, C. E. Carr 12,590 (BM). Isotype (A)!

**DISCUSSION:** *P. plicatus* is a member of the section *Microstigma*, as is its closest relative, *P. rubriplicatus* St. John, of northeast New Guinea, a species with the drupes 14–16 mm long, 4–6 mm wide, oblance-prismatic, the upper 1/4 free; endocarp median; leaves 3.3 cm wide, and at midsection with 26 parallel secondary veins in each half. *P. plicatus* has the drupes 20–22 mm long, 2.5–4 mm wide, narrowly prismatic, the upper 1/4 free; endocarp in lower 3/5; leaves 4.5 cm wide or more, and at the point 39 cm down with 48 parallel secondary veins in each half.

The collector recorded, "Fruit red. Eaten by natives after boiling for 1 hour."

The new epithet is the Latin adjective *plicatus*, pleated, and is given with reference to the pleated leaves.

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Fig. 274. *Pandanus plicatus* St. John, from holotype. a, Syncarp and bracts, X 1/4; b, drupe, lateral view, X 1; c, drupe, longitudinal median section, X 1; d, drupe, apical view, X 1; e, drupe, lateral view, X 4; f, drupe, longitudinal median section, X 4; g, drupe, apical view, X 4; h, leaf section 39 cm from apex, lower side, X 1; i, leaf apex, lower side, X 1.
Revision of the Genus Pandanus Stickman, Part 30
The New Section Marginata from Papua

Harold St. John

Papua and its offshore islands are rich in species of Pandanus, many of which have been made known through the collections of L. J. Brass. The following is one of these, here described as a new species. It is in the affinity of the section Microstigma, but because of significant difference in the stigma, it is published below as the basis of a new section.

Section Marginata, sect. nov. (subgen. Lophostigma)

Diagnosis: Drupis 1-carpelatis, stigmatibus terminalibus elevatis horizontalibus hippocrepiformibus, sinu stigmatis late marginatis, syncarpio solitario subcylindrico, plantis masculis incognitis.

Drupe 1-celled; stigma terminal, elevated, horizontal, horseshoe-shaped owing to the broad, hard stylar band of tissue on either side of the stigmatic sinus; syncarp solitary, subcylindrical; staminate plants unknown.

Holotypus: Pandanus marginatus St. John.

To insert this in the "Key to the Sections" published in Part 1 of this series (Pacific Sci. 14(3):225), for the first C read:
C. Stigma flush, papillose,
  y. Stigmatic sinus a mere crease; stamens umbellate at apex of column ... Microstigma
  y. Stigmatic sinus with broad stylar margin on either side, forming a horseshoe-shaped stigma; staminate plants unknown ....... Marginata

Pandanus marginatus sp. nov. (sect. Marginata) Fig. 275

Diagnosis holotypi: Planta 2.5–4 m alta, "caule plerumque eramoso, radicibus fuiturosis paucis brevisibus," folis 1.9–2.26 (+0.3–0.5?) m longis in medio 4 cm latis supra basem 3.5 cm latis subtiliter coriaces supra viridibus infra palliditer viridibus et ad basem glaucis U-sulcatis 2-plicatis in sectione medio-cameris cum 42 nervis parallelis secundariis nervis tertiiis in parte ½ ultima semivisibilibus et reticulis oblongis formantibus, laminae paene ligulata sed in parte ¼ ultima ad apicem gracilem diminuienti (apex deest), basi inerni pallida ex 3–6 mm marginibus cum aculeis 1–1.8 mm longis 3–6 mm separatis rectis subulatis ad arcuati-subulatis adscendentibus pallidis vel cum apicibus minime brunnens, midnervo infra in parte ½ infera inerni, in sectione mediali marginibus cum aculeis 1.3–1.5 mm longis 4–8 mm separatis subulatis valde adscendentibus pallidis cum apicibus brunnens, midnervo infra cum aculeis 0.7–1 mm longis 4–6 mm separatis arcuati-subulatis valde adscendentibus straniis, infrafrontesia cum syncarpio solitario pendenti subcylindrico auranthaci-rubro, syncarpio 27 cm longo 7 cm diametro, drupis 17–18 mm longis 6–10 mm latis 5–7 mm crassis elliptico-oblongis 4–6-angulosis parte ½ supra libera apice obtuso, pileo 3–4 mm alto laevi lucido inter angulis contrahentis, stigmatic 2–2.5 mm longo elevato plus minusve horizontali brunneo papilloso hippocrepiformi ex lineis duobus parallelis pallidis stylaribus invaginati et sinu centrali adcenti, endocarpo centrali ellipsoideo osseo obscure rubri-brunneo lateribus 1.2 cm crassis intra laevibus lucidis, semine 6–7 mm longo, mesocarpo apicali cum fibris marginalibus fortibus eis in apice convergentibus et cum membranis transversis paucis brunnens, mesocarpo basali fibroso et carnoso.

Diagnosis of holotype: Plant 2.5–4 m tall; "stem usually unbranched; prop roots few, short"; leaves 1.9 (+0.3–0.5?) m long, 4 cm wide near the middle, 3.5 cm wide near the base, thin coriaceous, green above, pale green below and glaucous near the base, U-sulcate, 2-plaited, at midsection with 42 parallel secondary veins in each half, the tertiary cross veins faintly seen in outer half forming oblong meshes, blade almost ligulate, but in outer ½ tapering toward the slender apex (this lost in ours), base unarmed, pale; beginning at 3–6 cm up the margins with prickles 1–1.8 mm long, 3–6 mm apart, straight subulate to arcuate subulate, ascending, pale or with faint brown tips; the midrib below unarmed for the lower ½; at midsection the margins with prickles 1.3–1.5 mm long, 4–8 mm apart, subulate,
Fig. 275. *Pandanus marginatus* St. John, from the holotype. *a*, Drupe, lateral view, × 1; *b*, drupe, longitudinal median section, × 1; *c*, drupe, apical view, × 1; *d*, drupe, lateral view, × 4; *e*, drupe, longitudinal median section, × 4; *f*, drupe, apical view, × 4; *g*, leaf base, lower side, × 1; *h*, leaf middle, lower side, × 1.
strongly ascending, pale with brown tips; the nearby midrib below with prickles 0.7–1 mm long, 4–6 mm apart, arcuate subulate, strongly ascending, stramineous; infructescence with a solitary, pendent, orange-red, subcylindric syncarp, this 27 cm long, 7 cm in diameter; drupes 17–18 mm long, 6–10 mm wide, 5–7 mm thick, elliptic-oblong, 4–6-angled, upper ⅔ free, apex obtuse to the base of the stigma; pileus 3–4 mm high, smooth, shining, shrinking between the angles; stigma 2–2.5 mm long, elevated, more or less horizontal, brown, papillose, horseshoe-shaped because of the two parallel bands of hard, pale, stylar tissue that invaginate and border the central sinus; endocarp central, ellipsoid, bony, dark reddish-brown, the walls 1–1.2 mm thick, within smooth, shining; seed 6–7 mm long; apical mesocarp with strong marginal fibers converging to the apex, and within a few brown, transverse membranes; basal mesocarp fibrous and fleshy.


SPECIMENS EXAMINED: Papua, Milne Bay Dist., Dabora, Cape Vogel Peninsula, rain forest, 30–60 m alt, 8–10 April 1953, L. J. Brass 21,906 (K).

EXPANDED DESCRIPTION: Leaves over 2 m long, persisting from apex to base of stem, at midsection with 47 parallel secondary veins in each half, near the apex the pleats serrulate above; immature syncarp 6.5 cm in diameter, 3-angled, pink.

DISCUSSION: The new epithet is the Latin adjective marginatus, margined, and is given with application to the doubly margined stylar sinus.
Revision of the Genus Pandanus Stickman, Part 31
Bornean Species Collected by J. Motley

Harold St. John

Early collectors in Borneo discovered species of *Pandanus* in the native flora. Such was James Motley, and Martelli has already named *P. Motleyanus* in his honor. The writer has studied at Kew other specimens of his collecting, and has distinguished among them the three following new species.

*Pandanus apicalis* sp. nov. (sect. *Acrostigma*)

Figs. 276 and 276A

Diagnosis Holotypi: Radices caules foliisque incogniti, pedunculo 8 cm longo 13 mm diametro 3-laterato clavato cum syncarpio solitario, syncarpio 6 cm diametro (licet ovoideo et 6-7 cm longo?), drupis 29-31 mm longis 4-7.5 mm latis 2-3 mm crassis fusiformibus vel oblancoeloideis acute 5-6-angulosis partc 1/2 supera libera et proxime curvata laevi vel subpunctata eluciud, stylo 3-5 mm longo crassiter subulato proxime curvato osseo luteo lucido basi late angulosa, stigmat 3-5 mm longo lineari brunneo papilloso ad apicem exsudatio, syncarpio in parte 1/4 infera obovatum truncatum albo chartaceo tenuissimo, semine 4 mm longo, mesocarpio apicali cavermosto elongato cum fibris longitudinalibus et membranis albis, mesocarpio basali fibroso et carnoso.

Diagnosis of Holotype: Vegetative parts unknown; peduncle 8 cm long, 13 mm in diameter, 3-sided, clavate, bearing a single syncarp, this 6 cm in diameter (apparently ovoid and 6-7 cm long?); drupes 29-31 mm long, 4-7.5 mm wide, 2-3 mm thick, fusiform to oblancoeloide, sharply 5-6-angled, upper 1/2 free and proximally inclined, smooth or slightly punctate, dull; style 3-5 mm long, thick subulate, proximally curved, bony, greenish, shining, the base broadly angled; stigma 3-5 mm long, linear, brown, papillose, extending to the apex; endocarp in lower 1/4, ovobovoid, truncate, white, papery, very thin; seed 4 mm long; apical mesocarp an elongate cavern with longitudinal fibers and white membranes; basal mesocarp fibrous and fleshy.

Expanded description: Plant acaulescent; leaves 2-3 mm long, at about the middle 37 mm wide, near the base 28 mm wide, coriaceous, V-sulcate and sharply 2-pleated, dark shiny green above, pale somewhat shiny green below, near the midsection with 34 parallel secondary veins in each half, the tertiary cross veins seen below toward the tip, forming short rhombic meshes; blade ligulate, tapering into the 8 cm trigonous subulate apex, this at the point 10 cm down 7 mm wide, the base apparently pale and unarmed, beginning more than 5 cm from the base the margins with prickles 1.5-2.3 mm long, 6-14 mm apart, oblique deltoid, compressed, ascending, stramineous; the midrib below unarmed for more than the 40 cm; near the midsection the margins with prickles 0.4-0.6 mm long, 8-13 mm apart, broad subulate to subarboeous lanceolate, compressed, strongly ascending, stramineous; the nearby midrib below unarmed; on the subulate apex the margins and midrib below with serrations 0.2-0.4 mm long, 1-2 mm apart, stramineous; syncarp 9.3 cm long, 7.2 cm in diameter, ovoid; drupes 29-38 mm long, greenish yellow, upper 1/2-3/4 free; endocarp in lower 1/4-1/2; endocarp walls 0.1 mm thick, within smooth.

Holotypus: Borneo, grows in damp woods, James Motley XXXVI, 1,247 (K Mus.).


Discussion: *P. apicalis* is a member of the section *Acrostigma*, as is its closest relative, *P. septentrionalis* St. John, of Mount Kinabalu, North Borneo, a species with the drupes 26-28 mm long; pileus 4-6 mm high, pyramidal-hemispheric; style 2-3 mm long; stigma 1-2 mm long; and the endocarp apex convex. *P.
**Fig. 276.** *Pandanus apicalis* St. John, from holotype. *a*, Peduncle and base of syncarp, × 1; *b*, drupe, lateral view, × 1; *c*, drupe, longitudinal median section, × 1; *d*, drupe, apical view, × 1; *e*, drupe, lateral view, × 4; *f*, drupe, longitudinal median section, × 4; *g*, drupe, style, and stigma, apical view, × 4.

*Pandanus* apicalis has the drupes 29–31 mm long; pileus 15 mm high, lanceoloid, sharply 5–6-angled; style 3–5 mm long; stigma 3–5 mm long; and the endocarp apex retuse.

Up to now there is no evidence as to in what part of Borneo Mr. Motley found the specimen. He lived and worked on two sides of the island, and may well have travelled widely while there. He collected several other species of *Pandanus* in Borneo, one of which bears his name. The only other known collection was made by Brunig in the lowland forests near Kuching, Sarawak.

The new epithet is the Latin adjective *apicalis*, apical, and is given with reference to the fact that the stigma extends to the apex of the style.

**Pandanus bracteosus** sp. nov. (sect. *Microstigma*)

Figs. 277 and 277A

**Diagnosis.** Holotypi: Radicibus caulibusque incognitis, folio 1.05 m longo 4 cm lato circa basem 2.8 cm lato coriaceo supra viridi infra pallidiori V-sulcato 2-plicato in sectione mediola cum 40 nervis parallaeis secundaris in quoque dimidio nervis tertii transversis infra evidentis plerumque obliquis et reticulis rhombicos brevioribus quam laetioribus forman-}

**Fig. 276A.** *Pandanus apicalis* St. John, from Brunig 9,975. *b*, Leaf base, lower side, × 1; *i*, leaf middle, lower side, × 1; *j*, leaf apex, lower side, × 1; *k*, leaf apex, upper side, × 1.
culo 3 cm longo in toto clauso a bracteis congregatis viridibus, bractea infera 3 cm longa 1.8 cm lata lanceolata cum marginibus superioribus serratis, bractea ultima 6.5 cm longa 2 cm lata oblongo-lanceolata marginibus et midnervo infra in parte ½ ultima subulato-serratis, bracteis syncarpiorum 2.5 cm longis 2.3 cm latis elliptici concavis, syncarpio apicali 2 cm diametro globoso, syncarpiis lateralibus 1.5 cm diametro simulantibus, drupis submaturis videtur sed endocarpio et semine non maturato deinde immaturis, drupis inaequalibus eis apicalibus paene duplo latioribus et crassioribus quam illis medialibus et lateralibus inferioribus, drupis 6.5–7 mm longis 3.3–5 mm latis 2.5–3.5 mm crassis anguste elliptici-obovoideis

Fig. 277. *Pandanus bracteosus* St. John, from holotype. a, Fruiting spike, lateral view, × 1; b, drupe, lateral view, × 1; c, drupe, longitudinal median section, × 1; d, drupe, apical view, × 1; e, drupe, lateral view, × 4; f, drupe, longitudinal median section, × 4; g, drupe and stigma, apical view, × 4; h, leaf, × ½; i, leaf base, lower side, × 1; j, leaf middle, lower side, × 1; k, leaf apex, upper side, × 1; l, leaf apex, lower side, × 1.

Fig. 277A. *Pandanus bracteosus* St. John, staminate plant (*Motley* 1,247). a, Inflorescence, lateral view, × 1; b, fascicle of stamens, lateral view, × 10.
subcompressis parte \( \frac{1}{2} \) supera libera, pileo sub-hemispheric 2-2.5 mm alto laevi lucido, stigmati 1.5-2 mm lato vadose reniformi prostrato brunneo papilloso, sinnibus proximalibus latis et conspicuis et ex sinu stigmatici projectentibus basi fructu per 1.7-2 mm carnosa, semine incognito, parte supero (mesocarpio apicali) 5-5.5 mm longo in lateribus cum fibris fortissimis longitudinalibus arcuatis.

**DIAGNOSIS OF HOLOTYPE:** Roots unknown; stem "2.5-3.3 m tall"; leaf 1.05 m long, 4 cm wide \( \frac{3}{4} \) way out, 2.8 cm wide near the base, coriaceous, green above, paler green below, V-sulcate, 2-pleated, at midsection with 40 parallel secondary veins in each half; tertiary cross veins evident below throughout, mostly oblique, forming rhombic meshes shorter than broad; blade almost ligulate, widest at \( \frac{1}{2} \) from apex and scarcely tapering before the contraction to the acute tip, at the point 10 cm down 36 mm wide, the base unarm, pale; beginning at 2.5 cm up the margins with prickles 1-2 mm long, 1-4 mm apart, the first few subulate serrar, the subsequent ones subsigmoid thick subulate, compressed, ascending, pale with brown tips; the midrib below beginning at 11 cm up with prickles 3-3.5 mm long, 13-24 mm apart, arcuate subulate strongly reflexed, stramineous with dark brown tips; at midsection the margins with prickles 2.2-3 mm long, 7-11 mm apart, straight or subarcuate stout subulate, strongly ascending, pale with brown tips; throughout the central third the midrib unarm; near the apex the margins and midrib below with arcuate subulate prickles 0.6-1.5 mm long, 0.5-2.5 mm apart, strongly ascending, pale with dark brown tips; toward apex the pleats above with prickles 0.5-1.3 mm long, 2-11 mm apart, arcuate subulate, rigid, strongly ascending, pale; pistillate inflorescence 7 cm long, many-bracted, cernuous, and the 3 syncarps mostly concealed; peduncle 3 cm long, completely concealed by the crowded green bracts; lowest peduncular bract 3 cm long, 1.8 cm wide, lanceolate, only the upper margins serrar; uppermost peduncular bract 6.5 cm long, 2 cm wide, oblong lanceolate, the margins subulate-serrate nearly throughout as is the midrib below in outer half; bracts subtending the syncarps 2.5 cm long, 2.3 cm wide, elliptic, concave; apical syncarp 2 cm in diameter, globose; lateral syncarps 1.3 cm in diameter, similar; drupes appearing nearly mature, but as they lack endocarp and seed they are immature; drupes unequal, those near the apex being nearly twice as wide and thick as the median and lower lateral ones; drupes (immature) 6.5-7 mm long, 3.3-5 mm wide, 2.5-3.5 mm thick, narrowly elliptic-obovoid, slightly compressed, upper \( \frac{1}{2} \) free; pileus almost hemispheric, 2-2.5 mm high, smooth, shining; stigma 1.5-2 mm wide, widely shallow reniform, flush, chocolate brown, papillose; proximal sinus wide and prominent, slightly exceeding the cleft of the stigma; fruit body with lower 1.7-2 mm fleshy; endocarp in lower \( \frac{1}{2} \), becoming bony, with an apical bristle; seed not seen; upper part 5-5.5 mm long (apparently the upper mesocarp) bounded by numerous heavy, arching, longitudinal fibers.

**Stamine Plant** (Motley 1,247): Habit and herbage unknown; staminate inflorescence an 8 cm rhachis with thick, rigid bracts subtending the spikes; lowest bract 10.5 cm long, 4 cm wide, lanceolate, navicular, the margins and midrib below toward the apex minutely serrate; uppermost bract 15 mm long; spikes 1.5-3 cm long, 10 cm in diameter, cylindric, dense; stamens clustered together, mostly in pairs; column 0.8 mm long, bearing at its tip the free filament tips, these 0.4-0.5 mm long; anthers 7 mm long, linear, bearing at the tip a 0.5 mm subulate prolongation of the connective.

**HOLOYPUS:** [Indonesian] Borneo, Bangarmassing (= Bandjarmassin), 1857-8, J. Motley (CGE). Isotype (K)!

**SPECIMENS EXAMINED:** [Indonesian] Borneo: Bangarmassing, J. Motley 1,247 (K).

**DISCUSSION:** *P. bracteosus* is a member of the section *Microstigma*, as is its closest relative, *P. palaensis* Elmer, of Mindanao, Philippines, a species with bracts of the fruiting spike caduous; stigma 0.5-0.8 mm wide, transversely elliptic; leaves 24-28 mm wide, at midsection with 24 parallel secondary veins in each half; at midsection the margins with prickles 0.8-1.2 mm long, 3-10 mm apart, arcuate subulate, compressed, ascending. *P. bracteosus* has the bracts of the peduncle and fruiting rhachis persistent, almost concealing the syncarps; stigmas 1.5-2 mm wide, shallow reniform;
leaves 40 mm wide, at midsection with 40 parallel secondary veins in each half, and with the margins with prickles 2.2–3 mm long, 7–11 mm apart, straight or subarcuate stout subulate, strongly ascending.

P. bracteosus is placed in the section Microstigma, although the staminate flowers are unusual. This section has the several stamens united in clumps and with the free filament tips umbellate at the apex of the united filament lower parts, the column, which is typically longer than the anthers and their free filament tips. In P. bracteosus the stamens of a clump are few, mostly two, and the column is only \( \frac{1}{4} \) the length of the anthers and their free filament tips. One other known species, *P. polycephalus* Lam., also has the column much shorter than the free parts. In both of these species the free parts are truly umbellate on the apex of the column. Despite its shortness the grouping and connation of the stamens seems to follow the same basic plan. Consequently *P. bracteosus* seems to be correctly placed in the section Microstigma.

The new epithet is the Latin adjective *bracteosus*, with bracts, and is given with reference to the persistent bracts hidng the syncarps.

**Pandanus sulcatus** sp. nov. (sect. Rykia)

Fig. 278

**Diagnosis Holotypi:** Licet frutex, ramulis in apice 12 mm diametro, foliis 16 mm latis coriaceis profunde U-sulcatis 2-platis licet ligulata in puncto 8–11.5 cm ex basi cum 20–21 nervis paralllelis secundariis in quoque diamidio, nervis tertiiis reticulati breviter oblongiis formantibus, basi inermi pallida, ex 3–4 cm marginibus cum aculeis 0.8–1.5 mm longis 3–7 mm separatis subulati-serrulatis ad arcuato-subulatis crassis compressis asclendentibus stramineis, midnervio proximo infra inermi, sectione mediali non visi, in apice subulato marginibus et midnervio infra cum aculeis 0.5–0.8 mm longis 1–2 mm separatis arcuati-subulatis asclendentibus stramineis, infrascissentia spicata cum 3 syncarpiis, pedunculo 9.5 cm longo 7 mm diametro 3-laterato subclavato, syncarpio apicali 6 cm longo 3.8 cm diametro cylindrico obtuso cum 90 drupis, syncarpiis lateralius 4–4.3 cm longis 3.5 cm diametro ellipsoido cum 80 drupis, etis 19–21 mm longis 7–12 mm latis 6–11 mm crassis ex basi ad apicem drupis sensim majoribus late cuneatis 5–6-angulosis in apice latissimo, apice obtuso videtur sed vere vados retuso parte \( \frac{1}{6}–\frac{1}{2} \) supera libera laevi lucido, pileo 2–3 mm alto, stylo 3 mm longo \( \frac{1}{2} \) bifido osseo, stigmate 1.5 mm longo lanceolato bifido bruneo papilloso, endocarpio centrali obpyramidali osseo obscure bruneo apice concavo lateralius lateralius 1–1.5 mm crassius intra lucido sublaevi sed in spiris striatis, semine 4 mm longo anguste obconico, mesocarpio apicale valde oblate suborbiculari cavernoso cum membranis latis bruneis paucis, mesocarpi basali fibroso et carnoso.

**Diagnosis of Holotype:** Apparently a shrub; branches 12 mm in diameter at apex; leaves of unknown length, all cut off at 8–11.5 cm from the base, 16 mm wide, thick, coriaceous, deeply U-sulcate, 2-pleated, blade apparently ligulate, at 8–11.5 cm from the base with 20–21 parallel secondary veins in each half, the tertiary veins seen near the base, especially above, forming short oblong meshes, the base unarmed, pale, beginning at 3–4 cm up the margins with prickles 0.8–1.5 mm long, 3–7 mm apart, subulate-serrulate to arcuate stout subulate, compressed, ascending stramineous; the nearby midrib below unarmed; on the subulate apex the margins and midrib below with prickles 0.5–0.8 mm long, 1–2 mm apart, arcuate subulate, ascending, stramineous; instructescence a spike with 3 syncarps; peduncle 9.5 cm long, 7 mm in diameter, 3-sided, slightly clavate; apical syncarp 6 cm long, 3.8 cm in diameter, cylindric, the ends obtuse, bearing 90 drupes; the lateral syncarps 4–4.3 cm long, 3.5 cm in diameter, ellipsoid, bearing 80 drupes; drupes 19–21 mm long, 7–12 mm wide, 6–11 mm thick, progressively larger from base to apex of syncarp, broad cuneate, 5–6-angled, the apex the broadest part, appearing obtuse but actually shallow retuse, upper \( \frac{1}{6}–\frac{1}{2} \) free, the surface smooth, shining; pileus 2–3 mm high; style 3 mm long, bifid \( \frac{1}{2} \) way, bony; stigma 1.5 mm long, lanceolate, bifid, brown, papilllose; endocarp central, obpyramidal, bony, dark brown, the apex concave, the lateral walls 1–1.5 mm thick, within shining, smoothish, but somewhat peripherally striate; seed 4 mm long, narrowly obconic; apical mesocarp strongly oblate suborbicular, a cavern with a few broad brownish membranes; basal mesocarp fibrous and fleshy.

**Expanded Description:** Stout shrub 6 m tall; branchlets 1.2–2.2 cm in diameter, white, ringed by dark brown leaf scars; prop roots 1.3 m long; leaves 98 (+ 50–70 ?) cm long, 28 mm wide near the middle, 16–24 mm wide near the base, near the middle with 20–26 parallel secondary veins in each half and there the
Fig. 278. *Pandanus sulcatus* St. John, from holotype. a, Fruiting spike, $\times$ 1; b, drupe, lateral view, $\times$ 1; c, drupe, longitudinal median section, $\times$ 1; d, drupe, apical view, $\times$ 1; e, drupe, lateral view, $\times$ 4; f, drupe, longitudinal median section, $\times$ 4; g, drupe, apical view, $\times$ 4.
margins with prickles 0.4-0.8 mm long, 4-10 mm apart, subulate with a long lower side, compressed, almost appressed ascending, stramineous with red tips, alternately large and small, the nearby midrib unarmed; infructescence a spike of 3-4 syncarps; peduncle 9-14 cm long; apical syncarp the largest, 6-6.5 cm long, 3.8-5 cm in diameter, the lateral syncarps 4-5.5 cm long, 3.5-5 cm in diameter; drupes 19-26 mm long; pileus 2-4 mm high; style erect, 3-4 mm long.

**Holotypus:** Borneo, James Motley 38 (K MUS.).

**Specimens examined:** Sarawak, Ulu Begrih, Bawan, Balingian, ridge top, leached yellow sandy soil, mixed Dipterocarp forest, low altitude, 20-10-63, Paul Chai S.19,455 (SAR).

Indonesian Borneo: West Kutei, Mt. Palimanan, on Belajan R., near Tabang, foothills along Meu R., 100 m alt., 6 Sept. 1956, A. Kostermans 12,726 (L).

**Discussion:** *P. sulcatus* is a member of the section *Rykia*, as is its closest relative, *P. angustus* St. John, of Hayoep, southeast Borneo, a species with the drupes 15-19.5 mm long, 6.5-8 mm wide, the upper 1/3 free; pileus 3-4.5 mm high; endocarp in lower 1/3; seed 6 mm long; leaf margins beginning at 5-6 cm from the base with serrae 1-1.6 mm long, 5-8 mm apart, yellowish. *P. sulcatus* has the drupes 19-26 mm long, 7-12 mm wide, the upper 1/6-1/4 free; pileus 2-4 mm high; endocarp central; seed 4 mm long; leaf margins beginning 3-4 cm from the base with prickles 0.8-1.5 mm long, 3-7 mm apart, subulate-serrulations to arcuate stout subulate prickles, ascending, stramineous.

The collector, James Motley, was an engineer who developed a coal mine near Kalangan, but eventually was murdered by the natives. He collected a good many plants, and already has one *Pandanus* species named for him.

The new epithet is the Latin adjective *sulcatus*, furrowed, and is given with reference to the deep central furrow of the leaves.
Revision of the Genus Pandanus Stickman, Part 32
The New Section Involuta from Papua

Harold St. John

The flora of New Guinea is rich in both the number of the species and the sections of Pandanus. In the present paper are described an additional species and section from that large tropical island.

Section Involuta sect. nov.
(subgen. Lophostigma)

Carpelis separatis 1-loculatis ellipsoideis, stylo breviter cylindrico et infra stigmatem bojaris formanti deinde involuta prolongato et 2–6 lobis cordatis vel flabellatis centralibus supra stigmatem circularem formanti.

Carpels distinct, 1-celled, ellipsoid; style apical, short cylindrical, forming a collar below the stigma and at one edge upward produced, involute, with 2–6 cordinate or flabellate horizontal lobes, central and above the irregular ring-like stigma; staminate plants unknown.

Holotypus: Pandanus involutus St. John.
Discussion: The section also contains P. leiophyllus Martelli, of Indonesian New Guinea. The name is from the Latin participle, involutus, infolded, and refers to the structure of the style apex.

Pandanus involutus sp. nov. (sect. Involuta)
Figs. 279 and 279A

Diagnosis of Holotype: Arbor gracilis ad 12 m alta, trunco brevi ex radicibus fulturosis paucissimis longioribus salientibus sustentis, foliis 1.19 (+ 0.04 ?) m longis proxima basem 3 cm latis in medio 2.8 cm latis coriaceis supra viridibus lucidisque infra pallidioribus et glaucis U-sulcatis 2-plicatis in sectione

1 B. P. Bishop Museum, Honolulu, Hawaii 96819, U. S. A. Manuscript received September 7, 1964.
2 This can be inserted in the author’s key in Part 1 of this series (Pacific Sci. 14(3):225), after the second I. “Stigma terminal,” insert:
a. Stigma an irregular ring, partly covered by involute central cordinate or flabellate lobes of the style ......................... Involuta
b. Stigma not so, mediai cum 48 nervis parallelis secundariis in quoque dimidio nervis tertius nullis lamina ligulata sed in parte ¼ ultima in apice gracili trigono subulato sensim diminuente (sed apice perdit) eo in puncto circa 10 cm ex apice 3 mm lato basi inermi pallida vel rosacea, ex 2.5 cm marginibus cum aculeis 0.3–0.7 mm longis 1.5–3 mm separatis infinis deltoides salientibus tum alteris lancea-deltoides distali con-cavis sed in toto adscendentibus pallidis, midnervio infra ulterius inermi, in sectione mediai margini cum serrulis 0.2–0.4 mm longis 1–3 mm separatis brunneis, in apice subulato marginibus et midnervio infra cum crenelis 0.1–0.2 mm longis 0.3–1 mm separatis, sincarpico licet 13–14 cm longis 10–15 cm diametro licet ovoideis in bracteis siccis clausis, nucleo ovoideo in centro molle in margine membranoso et cum fibris paucis superficie cum foramenbus favicis 3–4 mm profundi membranos pallidis, drupis 18–20 mm longis 7–9 mm latiss 6–8 mm crassis oblanei-ellipsoideis parte ½ suprema libera obtusa, pileo 7–9 mm alto latovert ovoideo 6-angulosu laevi lucido cum vicinis adnatis et in laminis caducis, stylo osseo lucido apicali cylindrico 1–1.5 mm alto deinde in 2–6 lobis involutus elevatis productis parte ½–¾ supera horizontali irregulariter cordinate vel flabellatae, stigmatic solitario suborbiculari intra bojaris inferis et lobis centralibus superis styli, endocarpio in parte ½ infera truncato osseo obscure brunneo vel nigro lateribus lateralis 1.5–1.8 mm crassis intra laevibus lucidis, semine 9–10 mm longo, mesocarpio apicali 3 mm longo oblatori-orbiculari cavernoso cum membranis brunnise paucis, mesocarpio basali parvo fibroso et carnosso.

Diagnosis of Holotype: Slender tree up to 12 m tall, trunk short, supported on unusually few, very long, wide-fung prop roots; leaves 0.93–1.19 (+ 0.04 ?) m in length, near the base 3 cm wide, at the middle 2.8 cm wide, coriaceous, green and shiny above, pale green and glaucous below, U-sulcate, 2-pleated, at midsection with 48 parallel secondary veins in each half, no tertiary veins; blade ligulate but in outer ¼ gradually tapering into the slender trigonous subulate apex (but the small tip lost in ours), this at about 10 cm down 3 mm wide, the base unarmed, pale or pinkish, beginning at 2.5 cm up the margins with prickles 0.3–0.7 mm long, 1.5–3 mm apart, the lowest few deltoid, salient,
Fig. 279. *Pandanus involutus* St. John, from holotype.  

- **a**, Syncarp, lateral view, × 1;  
- **b**, drupe, lateral view, × 1;  
- **c**, drupe, longitudinal median section, × 1;  
- **d**, drupe, apical view, × 1;  
- **e**, stigmas, apical and oblique views, × 4;  
- **f**, leaf base, lower side, × 1;  
- **g**, leaf middle, lower side, × 1;  
- **h**, leaf apex, lower side, × 1.
then the succeeding ones lance-deltoid, the outer edge concave, but the whole ascending, pale; the midrib below unarmed to well beyond the middle; at midsection the margins with serrations 0.2–0.4 mm long, 1–3 mm apart, brown; on the subulate apex the margins and midrib below with crenulations 0.1–0.2 mm long, 0.3–1 mm apart; infructescence with a solitary syn
carp, erect among the leaves; peduncle 18 mm in diameter at apex, more than 7 cm long, clavate, 3-sided, with crowded, deciduous bracts; syn
carp apparently about 12.5 cm long, it is 10–10.5 cm in diameter, ellipsoid, enclosed in dry, brown bracts, these in 3 ascending tiers, each of 4–6 imbricate bracts, the outermost one with the body 21 cm long, 8 cm wide, lanceolate, the linear tip lost; the 3–4 inner bracts in each tier subequal, 14–15 cm long, 10–12 cm wide, ovate, acute, the upper margins and midrib minutely prickly; core ovoid, the whole center of soft, evanescent tissue, the margin of membranes and a few fibers, the outer surface pocked by honeycomb-like sockets (for the
drupe bases), 3–4 mm deep, of pale membranous tissue; drupes 18–20 mm long, 7–9 mm wide, 6–8 mm thick, oblong-ellipsoid, 6-angled, upper ½ free, obtuse; pileus 7–9 mm high, broadly ovoid, 6-angled, smooth, shining, the adjacent ones adnate and dehiscing in sheets; style bony, shining, apical, forming a stout cylinder 1–1.5 mm high which then is pro
duced into 2–6 involute raised lobes, their upper portions horizontal, irregularly cordate or flabellate and occupying ½–2½ of the truncate stigmatic apparatus; stigma solitary, but occurring as the marginal part of the apical disk, 3–4.5 mm in diameter, more or less circular, but of irregular shape, filling the interval between the collar of the lower part of the style and its involuted expanded central lobes; endocarp in lower 2½, obovoid, truncate, bony, dark brown to black, the lateral walls 1.3–1.8 mm thick, within smooth, shining; seed 9–10 mm long; apical mesocarp 3 mm long, very oblate orbic
cular, a cavern with a few brownish membranes; basal mesocarp scant, fibrous and fleshy.


DISCUSSION: The only close relative of this species is P. leiophyllus Martelli, from Windesi, Geelvink Bay, Indonesian New Guinea, a species with the drupes with the upper ½ free; pileus 4–5 mm high, rounded convex, broadly retuse, and many with hornlike, lateral ascending processes; stigma with one broad invagination at the sinus and slight hints of others around the margin; endocarp walls 0.7–0.8 mm thick; leaves 3.4–3.5 cm wide, the secondary parallel veins 42–46 in each half at midsection, the tertiary cross veins seen below in outer ⅓, oblique, forming narrow rhombic meshes. P. involutus has the drupes with the upper ½ free; pileus 7–9 mm high, broadly ovoid, not horned; stigma with 2–6 prominent stylar invaginations; endocarp walls 1.3–1.8 mm thick; leaves 3 cm wide, at midsection with 48 parallel secondary veins in each half, the tertiary veins none.

In 1913–1914, in the same book, Martelli
published his binomial three times as *P. lejo-phyllus* and twice as *P. leiophyllus*. He apparently considered the *i* and the *j* as identical and interchangeable. Now, it is settled by the 1966 International Code, Art. 73, Note 6, that when used as a vowel, it must be *i*, so his epithet is *P. leiophyllus*.

The new epithet is the Latin participle, *involutes*, infolded, and is given with reference to the involute style.
An Account of the Species of the Red Alga Herposiphonia Occurring in the Central and Western Tropical Pacific Ocean

George J. Hollenberg

ABSTRACT: Fourteen species of the genus Herposiphonia are described. The following species and varieties are new: H. arcuata, H. crassa, H. delicatula, H. dendroida, H. dendroida var. minor, H. dubia, H. nuda, H. obscura, H. parca var. interrupta, H. pacifica, H. trichia, H. variabilis. The distributional range is extended for H. parca, H. subdisticha, and H. tenella. H. secunda is reduced to a form of H. tenella.

Emphasis is given to the nature and arrangement of trichoblasts and of sexual reproductive structures as features of taxonomic importance.

The genus Herposiphonia was established by Nägeli (1846). H. tenella is generally considered the type species, although no binomials are cited by Nägeli. The name Herposiphonia was also used by Kuetzing (1843:417) for a group of species of Polysiphonia, including P. tenella (Hutchinsia tenella of C. Agardh 1828: 105). Hence, Herposiphonia (Kuetzing) Nägeli appears to be the basis for lectotypification of the genus by Schmitz (1889), with H. tenella as the type species.

The basic features of the genus have been described in considerable detail by Falkenberg (1901) and by Boergesen (1918). Approximately 30 species have been previously described.

The most distinctive features of the genus are the dorsiventral construction and the more or less regular sequence of exogenous determinate branches and indeterminate branches. In the basic pattern of branching, indeterminate branches arise on alternate sides of the axes at intervals of four nodes, with determinate branches alternating on either flank at the intervening nodes, and with the most distal determinate branch on the same side as the next indeterminate branch distally. In most species the indeterminate branches usually remain small or rudimentary. The determinate branches are simple in most species, but are branched in a few species. The apex of indeterminate branches is usually rolled away from the substratum, the determinate branches commonly arching toward the apex of the related indeterminate branch. The branches are never corticated. In certain species the chromatophores are commonly arranged in transverse bands in the pericentral cells on the side toward the central cell. Rhizoids always arise from the distal end of ventral pericentral cells, most commonly one per segment. They are cut off from the pericentral cell by a curving wall.

Trichoblasts and reproductive structures arise exclusively on the determinate branches. The sequence of determinate and indeterminate branches, commonly considered a dependable taxonomic feature, seems to be reliable for most species, but not for certain species. The relative number and nature of the trichoblasts, and the number of segments in determinate branches, as well as the number of pericentral cells, are features usually characteristic for a given species, although there is often considerable variation, especially in the number of segments in the determinate branches and the degree of development of the trichoblasts. The nature and position of fully mature trichoblasts is, in the opinion of the writer, a fairly dependable taxonomic feature. Also, the number of segments developing in determinate branches beyond the first formed trichoblast is usually significant.

Probably one of the most important taxonomic features is the nature and position of the reproductive structures, especially the sexual reproductive structures, although, unfortunately, the latter are infrequently found. Tetrasporangia always arise one per segment in normally

1 University of Redlands, Redlands, California. Manuscript received September 26, 1967.
straight series on the side of the branches away from the apex of the axis bearing the branch.

The following symbols indicate the chief collectors of the materials studied: D., Maxwell S. Doty, University of Hawaii; G., Malvern Gilmartin, Jr., at the time at the University of Hawaii; H., G. J. Hollenberg; Ha., H. E. Hackett of Duke University; H., T., and B., G. J. Hollenberg, Roy Tsuda, and Richard Buggeln; L., C. R. Long, a graduate student at the University of Hawaii, and T., Roy Tsuda, a graduate student at the time at the University of Hawaii, along with Richard Buggeln. All "D" collections were made by Maxwell S. Doty unless otherwise indicated. The notation "(N.Y.)" indicates collections examined at the New York Botanical Garden.

The areas represented in the study are mostly those represented in a previous report on species of *Polysiphonia* from the central and western tropical Pacific Ocean (Hollenberg, 1968). The areas are treated in the same order as in that report. Although they are not within the main areas represented by the study, it seemed best to include certain collections from the western Atlantic Ocean. Also included are collections by H. E. Hackett (Ha.) in the Maldives Islands (6°55'N to 0°41'S, 72°73°34'E), on cruise 8 of the TE VEGA International Indian Ocean Expedition, 1964. The geographic location of the main collection areas is given in the report on *Polysiphonia*.

Type material will be deposited in the Smithsonian Institution, Washington, D.C. Isotypes

**KEY TO THE SPECIES OF *Herposiphonia***

1. Determinate branches subdistichous ........................................... *H. subdisticha* .......................... 2
2. Mostly with a determinate or an indeterminate branch or branch primordium on every segment ............ 3
3. Mostly with one or more segments between successive indeterminate branches without a branch of either type ................................................................. 11
4. Trichoblasts and scar-cells lacking, except for scar-cells at the former point of attachment of spermangial branches ................................................................. *H. nuda* .......................... 4
5. Trichoblasts or scar-cells present, the trichoblasts sometimes very rudimentary ................................ 5
6. Trichoblasts infrequent and very rudimentary .......... *H. dubia* .......................... 5
7. Trichoblasts and/or scar-cells frequent to abundant, mostly well developed .................................. *H. trichia* .......................... 5
8. Trichoblasts unbranched ................................................................. 6
9. Trichoblasts branched ........................................................................ 6
10. Trichoblasts and/or scar-cells not more than 2 per branchlet, strictly terminal, with a percurrent axis and 7 or more laterals; scar-cells large ................................................................. *H. dendroides* .......................... 7
11. Determinate branches composed of 40-55 segments; trichoblasts 6 or more, one per segment on the branch tips ................................................................. *H. filifera* .......................... 8
12. Determinate branches composed mostly of fewer than 30 segments; trichoblasts mostly 2-3 at branch tips ................................................................. *H. crassa* .......................... 8
13. Diameter of mature determinate branches mostly less than 80μ, pericentral cells mostly 12 or fewer .......... 9
14. Procarps and spermangial stichidia strictly terminal; trichoblasts 2-3, terminal .................................... *H. parca* .......................... 9
15. Cystocarps and spermangial stichidia not terminal ........................................................................ 10
16. Sexual reproductive structures borne 3-10 segments from the branch apex at maturity ........................................ *H. tenella* .......................... 10
17. Sexual reproductive structures borne mostly on the lower half of the determinate branch ................................................................. *H. delicata* .......................... 10
18. Most of the indeterminate branch primordia arrested at the few-celled stage ....................................... *H. obscura* .......................... 11
19. All indeterminate branches developing to obvious, although often small branchlets ........................................ *H. arcuata* .......................... 12
20. Most of the indeterminate branches developing into conspicuously branched laterals; main axes commonly growing free from the substratum in terminal parts ................................................................. *H. variabilis* .......................... 12
21. Central cells of determinate branches conspicuously larger than the pericentral cells ............................ *H. filifera* .......................... 13
22. Central cells of determinate branches not conspicuously larger than the pericentral cells .................. *H. arcuata* .......................... 13
23. Determinate branches mostly less than 1 mm high and composed of fewer than 30 segments ........................ *H. variabilis* .......................... 15
24. Determinate branches commonly 10-15 mm high and composed of 50-70-(90) segments ................ *H. pacifica* .......................... 15
25. Determinate branches mostly 35-50μ in diameter, composed of 12-14 segments; procarps and spermangial stichidia arising mostly on the basal half of the determinate branches ........................ *H. delicata* .......................... 15
26. Determinate branches mostly 60-100μ in diameter, composed of 16-18-(30) segments; procarps and spermangial stichidia arising terminally or in the upper half of the branches; spermangial stichidia with a short sterile tip ........................................................................ *H. tenella* form *secura* .......................... 15

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or syntypes and many glucose slide mounts of various species will be stored at the University of Hawaii.

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The material collected by C. R. Long was collected under the auspices of the Pacific Ocean Biological Survey Program conducted by the Division of Birds, Smithsonian Institution.

Herposiphonia arcuata sp. nov.

Fig. 5

Densely branched algae, forming extensive patches mostly on other algae; main axes commonly growing free from the substratum, and most of the indeterminate branches developing into laterals of varying lengths; indeterminate branches 140–190μ in diameter, with segments 1.0–1.5 diameters long; determinate branches morphologically erect, arising mostly at intervals of 3 segments, alternately on either flank, followed by an indeterminate branch on the same side, but more lateral in position; mostly 1 but frequently 2 or more nodes without a branch occurring between an indeterminate branch and the next distal determinate branch; determinate branches composed of 10–12–(20) segments, 1.0–2.0 diameters long, strongly arched distally, and mostly remaining slightly arched when mature; pericentral cells mostly 10, slightly smaller than the central cells; chromatophores nonzonate; walls brownish, relatively firm; trichoblasts usually 2–3 per determinate branch, usually poorly developed, but sometimes up to 1.7 mm long, with 4–6 dichotomies; tetrasporangia 60–75μ in diameter, in series of 4–6 in the middle or terminal parts of the branches; cystocarps ovate to globular, to 300μ in diameter, arising terminally on the 6th to 9th segment, the branch growing beyond the developing cystocarp 8–9–(15) segments and bearing in succession 5 or more trichoblasts spirally arranged; spermatangial stichidia 160–175μ long, 50–65μ broad, mostly one per segment in spiral sequence on 8–12 short terminal segments, each arising as a primary fork of a trichoblast, and terminating in a sterile tip of 1–2 short cells, quickly deciduous.

Algae ramosissimae, maculas amras in saxis et in algis aliis formantes; partes distales ramorum principalium a substrato puerque discreetae crescentes; plerique ramuli indeterminati in ramulis laterales longitudine variantes evolventes; ordinatis ramificationis unum nudum sine ramis et unicum ramum determinatum dorsilateralem inter ramos indeterminatos puerque praebens; rami determinati e 10–12 segmentis 1.0–1.5 plo longioribus quam latis, versus extremitatem distale rami fertillis valde arcuatius plerumque compositis; cellulae pericentrales plerumque 10; chromatophora non zonata; trichoblastae puerumque duae, usque ad 1.5 mm long., 4–5 dichotomias habentes; tetrasporangia 60–75μ diam., 4–6 continus; cystocarpi ovati ad fere globulares, ad 300μ diam., terminaliter orientes, ramo 8–10 segmenta ultra cystocarpum evolventem formante; stichidia spermatangialia 160–175μ × 50–65μ, acumen sterile, ex una ad duas cellularas breves constans, habentia, saepissime unum spermatangium in omni segmento in spira in 8–10 segmentis terminalibus brevibus, omne spermatangium ut furca primaria trichoblastae orientis, max, autem, deciduum.

Type collection: D. 19611, tetrasporic, cystocarpic, spermatangial, awash at Ka‘ula, Oahu, Hawaii, legit M. S. Doty and H. B. S. Womersley, Jan. 21, 1962. It is represented by two glucose slide mounts and considerable fluid-preserved material.

Additional collections examined: Hawaiian Islands:—D. 13019, on reef, Koloa, Oahu, Oct. 30, 1955; D. 13039A, cystocarpic, on Griffithia sp., and D. 13051, on Sargassum sp., both awash, Kailua Beach Park, Oahu, Nov. 27, 1955; D. 17110, cystocarpic, on Sargassum sp., near the Natatorium, Waikiki, Oahu, Nov. 20, 1958; D. 20050.1, tetrasporic, spermatangial, on other algae, wave-battered shore, Laie, Oahu, legit R. Tsuda, R. Buggeln, and G. Trono, May 5, 1963; D. 20224, tetrasporic, awash, Kailua Beach Park, Oahu, Nov. 14, 1965; an unnumbered collection by M. Kajimura, tetrasporic, on Sargassum sp., Sans Souci
Herposiphonia of Tropical Pacific—Hollenberg


This species seems closest to H. pecten-veneris Harvey (1853) as described by Taylor (1960), especially in the freely-growing branches, with most of the indeterminate branches developing as lateral axes. It differs from Taylor’s description in several respects: (1) somewhat more densely branched with less extensive free branches, and mostly shorter segments in the indeterminate branches; (2) mostly with one or more bare nodes between successive branches, seemingly not a feature of H. pecten-veneris; (3) mostly more numerous and longer segments in the determinate branches, especially branches bearing mature cystocarps; (4) the apices of indeterminate branches strongly curved as in H. pecten-veneris, but the convex side morphologically ventral rather than dorsal as described by Taylor.

Herposiphonia crassa sp. nov.

Figs. 12, 13

Relatively coarse, densely branched algae, attached by numerous unicellular rhizoids, mostly with digitate tips, with 3 erect determinate branches between successive indeterminate branches and with no bare nodes; prostrate branches 240–300 μ in diameter, with about 12 pericentral cells and with segments mostly shorter than broad; indeterminate lateral branches mostly remaining very short; determinate branches simple. Diameter, 100–140–(200) μ at the base and mostly narrower above, with a blunt apex, with 14–18 pericentral cells and composed of 8–9 segments, mostly about 1 diameter long; chromatophores not zonate; trichoblasts 2–3, the first one formed mostly one segment from the apex, followed by 1 or often 2, on reduced terminal segments, which are displaced slightly toward the distal end of the related indeterminate branch; trichoblasts coarse, up to 1.7–(2.4) mm long and 60μ in diameter at the base, with 6–7 forks and rounded apices 10–11μ in diameter; young trichoblasts with an evident percurrent axis composed of 6–7 spherical cells, with laterals in two longitudinal rows on the distal side relative to the related indeterminate branch, the percurrent axis of the trichoblast not evident at maturity; tetrhapangia about 65μ in diameter, in straight series of 4–6 in the middle portion of determinate branches. Sexual plants unknown.

Algae praecipue caespiticiae, tres ramos determinatos erectos inter ramos indeterminatos successivos habentes; rami prostrati 240–300μ diam.; rami determinati 140–200μ diam. ad basim, manifeste angustiores supra, ex 8–9 segmentis plerumque aequo longis ac latissimis compositi; trichoblastae 2–3, grossae, prima in segmento infra apicum, deinde una duease in segmento terminali reducto, ad latus versus apicum rami fertilis summoto, orientibus; trichoblastae ad 2.4 mm long.; 6–7 furcas habentes; tetrhapangia 4–6 continua in parte media ramorum nata.

TYPE COLLECTION: D. 22538, tetrasporic, abundant on boulders, Kahakuloa Bay, Maui, Hawaii, legit H., T., and B., April 21, 1965. This collection is represented by 3 glucose slide mounts and fluid-preserved material.


This species is close to H. parae, from which it differs chiefly in being much coarser, with more numerous pericentral cells, mostly shorter segments, tapering determinate branches, and coarser trichoblasts. It is also characteristically saxicolous, whereas H. parae is usually epiphytic.

Herposiphonia delicatula sp. nov.
Figs. 1A, 1B, 2H, 3

Epiphytic algae, with indeterminate prostrate branches mostly 35–40µ in diameter, composed of segments 1–2 diameters long, with 7–8 pericentral cells, attached by rhizoids with digitate and frequently multicellular tips; determinate branches erect, in alternating series of three between successive alternating, indeterminate branches, which mostly remain short; erect branches 30–40µ in diameter, composed of 12–14–(30) segments 1.0–1.5 diameters long or occasionally longer, with 6–8 pericentral cells; chromatophores commonly zonate; trichoblasts 3–4, terminal, with 1–3 dichotomies, mostly poorly represented, but occasionally as much as 700µ long, with a basal cell up to 250µ long and 20µ in diameter; tetrasporangia in series of 5–8 in the lower or middle part of the branches; procarps arising on the 4th to 6th segment from the base of the branches; cystocarps not observed; spermatangial stichidia lanceolate, about 80µ long, and 25µ in diameter, arising on the convex side of the branches 3–5 segments from the base or sometimes nearer the apex, without a sterile tip.

Algae epiphyticae ramos prostratos plerumque 55–40µ diam. habentes, cellulis pericentralibus 7–8; rami determinati erecti, tribus in positionibus alternantibus inter ramos indeterminatos successivos sitis, 30–40µ diam., et plerumque 12–14 segmentis 1.0–1.5 plo longioribus quam latis compositis, cellulis pericentralibus 6–8; trichoblastae 3–4, terminales, 1–3 dichotomias habentes, plerumque parum evolutae, interdum, autem, usque ad 700µ long., cellula basali usque ad 250µ long.; tetrasporangia 5–8 continuæ, in partibus inferioribus medìsive ramarum nata; procarpi in segmento quarto vel sexto a basi ramarum orienses; cystocarpi non observati; stichidia spermatangialia lanceolata, 80 × 25µ, uno vel duobus in late ren convexo ramarum in segmento terto ad quinto a basi natis, sine cacumine sterile.

TYPE COLLECTION: D. 21876.1, tetrasporic, cystocarpic, spermatangial, on Amphiroa sp., on a reef at Falas Island, Truk group (7° 32’ N, 151° 45’ E), Caroline Islands, legit E. Meñež, Aug. 1960. This collection is represented by three glucose slide mounts.

ADDITIONAL COLLECTIONS EXAMINED: HAWAIIAN ISLANDS—D. 19135Z3, tetrasporic, dredged at 26 fa in front of the river mouth, Waialua, Oahu, Aug. 2, 1959; MARSHALL ISLANDS—H. 48–1213.71, Amen I., Bikini Atoll, July 7, 1948; CAROLINE ISLANDS—all legit E. Meñež, D. 15126.1, on Amphiroa sp., on a reef at Tafansak Village, Kusiae I., July 16, 1960; D. 23261.2, on Halimeda sp., Falas I., D. 23438.2, tetrasporic, cystocarpic, on Amphiroa sp., Moen I., D. 23444.1, tetrasporic, on Amphiroa sp., from a reef at Falas I., July 1960; D. 23471.2, tetrasporic, on a jointed coralline, on a reef at Yap I., Aug. 18, 1960; PHILIPPINE ISLANDS—D. 18099C, tetrasporic, on Sargassum sp., Davao, Mindanao, June 22, 1958; MARIANA ISLANDS—D. 20129, spermatangial, 20130, on Sargassum sp., Guam, legit E. Meñež, Oct. 12, 1960; MALAYSIA—D. 18179, on Thalassia, floating in a channel between Tandjung, Penang and Singapore, Oct. 29, 1957; MALDIVE ISLANDS—Ha. 9–2E–121–33B, on Dictyota sp., is doubtfully referred to this species. It was collected from the channel between Maro and Malefufi, Faddifolu Atoll, Mar. 24, 1964; WESTERN ATLANTIC OCEAN—a collection by Louis G. Williams, No. 247, on Codium sp., from Shark Shoal Jetty, Beaufort, North Carolina, July 25, 1949, identifies readily with H. delicatula, differing chiefly in the number of segments in the determinate branches, as many as 40 segments being counted. The material is cystocarpic, with procarps arising in the lower center of the branches, and with mature cystocarps ovoid and about 200µ in diameter. The number and position of the trichoblasts could not be determined with the material at hand.

This species is closest to H. tenella, and like that species exhibits considerable variability of branching pattern, some specimens having no
nodes devoid of branches, others having 1–4 bare nodes between successive branches. From H. tenella it differs in being more slender, usually with fewer pericentral cells, but differing especially in the position of the sexual structures, which arise mostly in the lower part of the branches rather than in the upper part as in H. tenella. Frequently the branching pattern changes in a given branch, so that no bare nodes occur in one portion of a branch, but one to several in another part, a feature reported to occur in H. tenella also.

*Herposiphonia dendroidea* sp. nov.

Figs. 1C, 1D, 1E, 9

Epiphytic or saxicolous algae with prostrate indeterminate branches 95–120 μ in diameter, composed of segments mostly about 1 diameter long, attached by numerous rhizoids with digitate and frequently multicellular tips; 3 determine erect branches 50–70 μ in diameter in alternating positions between successive alternating indeterminate branches, with usually no bare nodes; pericentral cells 8–10; central cell at least twice the diameter of the pericentral cells; mostly 7–9 segments in determinate branches, with segments mostly less than 1 diameter long; chromatophores zonate; 2 trichoblasts on the determinate branches, one a short terminal one on the much reduced terminal segment, which is slightly deflected in the direction of the apex of the related indeterminate branch, and a much larger one, apparently terminal but in fact subterminal on the second segment from the branch apex; young trichoblasts with a prominent percurrent axis, the larger one 90–100–(800) μ long with 5–6 laterals alternately inserted on the axis, not distichously, but directed, at least in early stages, toward the smaller trichoblast; basal cell of the larger trichoblast up to 240 μ long and 60 μ in diameter at maturity, the percurrent axis becoming obscure; tetrasporangia in straight series in the upper parts of determinate branches; sexual reproductive structures not observed.

Algae epiphytice aut saxicola, ramos indeterminatos prostratos 95–120 μ diam., segmentis aequis longis ac latis, habentes; rami determinati tres, nodi nudi inter ramos indeterminatos successivos plerumque nulli; cellulas pericentrales 8–10; plerumque 7–9 segmenta in ramos determinatis, saepissime breviora quam lata; chromatophora zonata; duae trichoblastae in ramis determinatis, una terminali brevi in segmento terminali multum reducto qui ad apicem rami fertilis indeterminati paululum deflectit, et una multo maior, ut videtur, terminali, subterminali, vere, autem, in segmento penultimo sita; trichoblastae juvenes axem percurrentem perspicuum habentes, trichoblasta maior 90–100–(800) μ long., 5–6 ramulis lateribus praeditae; tetrasporangia in serie recta, in partibus superioribus ramorum determinatorum nata; structurae reproductivae sexuales non observatae.

**TYPE COLLECTION:** D. 11125.1, tetrasporic, abundant on dead coral beyond the reef ridge, transect area, Ngaruamaa I., Raroia Atoll, Tuamotu Archipelago, legit M. S. Doty and Jan Newhouse, July 8, 1952. This collection is represented by two glucose slide mounts and fluid-preserved material.

**ADDITIONAL COLLECTIONS EXAMINED:** PHOENIX ISLANDS—L. 2335.5, on *Dictyosphaeria* sp., Howland I., Oct. 10, 1964; L. 2532.4, in algal turf, north shore of Gardner I., Oct. 23, 1964; L. 2644.4, on *Halimeda* sp., Birnie I., Nov. 8, 1964; L. 2685.4, in algal turf at a depth of 3 ft, northeast reef, Enderbury I., Nov. 11, 1964; TUAMOTU ARCHIPELAGO—legit M. S. Doty and Jan Newhouse, Raroia Atoll (16° S, 142° 26' W), 1952; D. 11160.4, on dead coral, reef near lagoon pass, July 9; D. 11508B, on other algae, Onorea, near Pakakota, Aug. 5.; MARSHALL ISLANDS—H. 48–1213.18, Amen I., Bikini Atoll, July 7, 1948. Plants of the last named collection had mostly 1–2 bare nodes between successive indeterminate branches.

A variant form of this species is represented by D. 11858.8 in which only a single, strictly terminal trichoblast occurs on the determinate branches. These specimens were collected by M. S. Doty and Jan Newhouse near Ottetou, Raroia Atoll, Tuamotu Archipelago, July 21, 1952.

*Herposiphonia dendroidea* var. *minor* var. nov.

Figs. 7, 24

Epiphytic algae with the general features of the species, especially as regards trichoblasts, but much smaller, having determinate branches mostly 80–100 μ high and 25–35 μ in diameter, with 6–7 pericentral cells; determinate branches usually 3, between successive indeterminate
Figs. 3-11. (Scale = 150μ)

4. *Herposiphonia pacifica*. Tip of determinate branch, with spermatangial stichidia.
5. *Herposiphonia arcurata*. Apical portion of free part of indeterminate branch, with determinate and indeterminate branches.
8. *Herposiphonia nuda*. Terminal portion of an indeterminate branch, with determinate branches.
9. *Herposiphonia dendroidea*, showing densely branched trichoblasts on the determinate branches.
10. *Herposiphonia filifera*. Terminal portion of a young determinate branch, with numerous short segments and immature trichoblasts.
11. *Herposiphonia subdisticha*, showing rudimentary trichoblasts at the apex of one or two determinate branches on the left.
branches, but frequently at alternate nodes, with indeterminate branches on the intervening nodes; trichoblasts mostly much shorter than in var. *dendroidea*; cystocarps terminal, prominently urceolate, 200µ in diameter, 300µ long; spermatangial branches unknown.

Algae epiphyticas proprietates speciei, praecipue trichoblastis, habentes, multo minores, autem, rami determinatis plerumque 80–175µ alt., 25–35µ diam., cellulis pericentralibus 6–7; rami determinati plerumque in nodis alternatis orientes, rami indeterminati in nodis interjacentibus, aut interdum, tres rami determinati inter ramos indeterminatos successivos sibi.

**TYPE COLLECTION:** D. 11533.2, tetrasporic, cystocarpic, on *Caulerpa* sp., under reef ledge, in front of Oneroa Village, Akau, Raroia Atoll, Tuamotu Archipelago, legitim M. S. Doty and Jan Newhouse, Aug. 5, 1952. This collection is represented by a glucose slide mount and fluid-preserved material.

**ADDITIONAL COLLECTIONS EXAMINED:** Tuamotu Archipelago—all legit M. S. Doty and Jan Newhouse, 1952; D. 11368B1, D. 11477B, on *Microdictyon* sp., lagoon reef, Mataiva, Raroia Atoll, July 29; D. 11514, on *Lagora* sp., in channels, just north of Oneroa, Raroia Atoll, Aug. 5; D. 11538.1, on dead coral, and D. 11542B, on *Microdictyon* sp., along with the type collection; Marshall Islands—H. 48–0914.6, outer reef, Uku I., Bikini Atoll, July 9, 1948; H. 48–1091A, on *Porockiella* sp., outer reef, Arji I., Bikini Atoll, July 12, 1948; H. 48–1213.168, Amen I., Bikini Atoll, July 7, 1948; H. 48–1609A, on reef several miles north of Bikini I., Bikini Atoll, July 5, 1948; Caroline Islands—all legit Ermani Mezñ, 1960; D. 23032.3A, on *Microdictyon* sp., reef between Ifalik and Falalap islands (7° 14’ N, 144° 27’ E), Aug. 10; D. 23112.6, abundant on *Microdictyon* sp., reef, eastern side of Ifalik and Falalap islands, Aug. 10; D. 23207.2, abundant in algal turf on other algae, southern tip of Sorol I., Aug. 13; D. 23756.3, in algal turf on reef, Quoi I., Truk group, Aug. 2; Maldives Islands—Ha. 30–2Q–17B, probably to be referred to this variety, was collected on Bushy I., Addu Atoll, May 10, 1964.

This variety is most commonly found growing on species of *Microdictyon*.

**Herposiphonia dubia** sp. nov.

Fig. 15

Saxicolous algae forming extensive mats to 12 mm high; indeterminate prostrate branches to 150µ in diameter, of segments 0.6–1.0 diameters long, with about 12 pericentral cells, and with 1–2 unicellular rhizoids per segment; apex of indeterminate branches and young determine branches strongly inrolled; each determine branch followed distally by an indeterminate branch and the latter followed by 1–2 bare nodes; determine branches 100–120µ in diameter, composed of 45–75 segments 1.0–1.5 diameters long, with 12–16 pericentral cells and a central cell distinctly larger to twice the diameter of the pericentral cells; apex of determine branches blunt or rounded, often remaining inrolled or arched at or near maturity; secondary indeterminate branches frequently developing from the apical parts of determine branches; walls relatively thick and brownish; chromatophores not zonate; trichoblasts mostly lacking but 1–2 very rudimentary ones occasionally present; tetrasporangia 40–50µ in diameter in straight series of 15–25 in the upper parts of the determine branches; sexual reproductive structures not observed.

Algae saxicolae, tegetes amplus usque ad 12 mm alt. formantes; rami indeterminati prostrati ad 150µ diam., e segmentis 0.6–1.0 longioribus quam latis, c. 12 cellulæ pericentralæ atque 1–2 rhizoidea in omnì segmenti habentibus, compositi; 1–2 nodi nudi inter ramos indeterminatos successivos unum ramum distaliter consequentes; rami determinati 100–120µ diam., e 45–75 segmentis 1.0–1.5 po longioribus quam latis, 12–16 cellulæ pericentralæ habentibus, compositi; cellula centralis multo maior quam cellulæ pericentralæ; parietes crassiores; chromatophora non zonata; trichoblastae plerumque nullæ, 1–2, autem, maxime rudimentariae interdum visae; tetrasporangia 40–50µ diam., 15–25 in serie recta in partibus superioribus ramorum determinatorum; structurae reproductiveæ sexuæ non observatae.

**TYPE COLLECTION:** D. 22472.1, tetrasporic, reef flat, Kahana, Maui, Hawaii, legit H., and B., Apr. 20, 1965. This collection is represented by several glucose slide mounts and fluid-preserved material.

**ONE ADDITIONAL COLLECTION,** D. 22349.1 was from rocks, mid-littoral, intertidal basalt east of Maalaea, Maui, legit H. T., and B., Apr. 19, 1965.
12, 13. Herposiphonia crassa. Terminal portion of an indeterminate branch.
15. Herposiphonia dubia. Terminal portion of an indeterminate branch and portions of determinate branches.
16. Herposiphonia parca, showing immature terminal cystocarps.
18. Herposiphonia variabilis, with terminal spermatangial stichidia.
In the branching pattern and the numerous segments in the determinate branches this species is similar to *H. pacifica*. From that species it differs in the relatively stiff determinate branches, with mostly shorter segments, but chiefly in the almost complete absence of trichoblasts. The tendency of the determinate branches to remain slightly arcuate at maturity and the bluntly rounded apices of the determinate branches are additional features distinguishing *H. dubia*.

*Herposiphonia filifera* sp. nov.

Figs. 2D, 10

Saxicolous algae with prostrate indeterminate branches 60–80μ in diameter, composed of segments about 1 diameter long and attached by frequent unicellular rhizoids; determinate branches erect, unbranched, up to 6 mm high and 45–65μ in diameter, with up to 57 segments, mostly 1.5–2.0 diameters long in median parts of mature branches; pericentral cells 12–14, central cells considerably larger, somewhat barrel-shaped, and with nearly as many chromatophores as the pericentral; 3 determinate branches in alternating positions between successive indeterminate branches, with no bare nodes; chromatophores frequently zonate; trichoblasts one per segment on the terminal 10–14 segments, alternately to pseudodichotomously branched 4–5 times, ultimately up to 500μ long, arising in spiral sequence, with 1/5 to 1/6 divergence, somewhat tardily deciduous, leaving relatively small scar-cells on the branches, which are ultimately frayed at the attenuate apices; tetrasporangia 45–55μ in diameter, tetrahedrally divided, in straight series of 15 or more toward the branch apices, not much distending the segments; cystocarps terminal, ovoid-globular, 240–373μ in diameter; spermatangial stichidia in terminal, spiral series of 4 or more, wholly replacing trichoblasts, each lanceolate, and slightly to markedly arched toward the apex of the bearing branch, at maturity about 115μ long and 16μ in diameter at the base.

Algae tres ramos determinatos erectos inter ramos indeterminatos successivos habentes; rami determinati usque ad 6 mm alt., plurumque 45–65μ diam., c. 12 cellulas pericentrals habentes, et e segments usque ad 57, 1.5–2.0 plo longioribus quam laitis in paribus mediis, compositi; chromatophorae vulgo zonatae; trichoblastae in 10–14 segmentis terminalibus, plurumque una in omni segmento, sitae; pseudodichotome 4–5 ramosae, postremo usque ad 500μ long., in spira orientes, tarde deciduntae; tetrasporangia 15 vel plurum in serie versus apices ramorum, segmenta parum distendentia; cystocarpi terminales, ovoido-globulares, ad 375μ diam.; stichidia spermatangialia multa, pro trichoblasicis omnino substituta, lanceolata, paululum arcuata, ad 115μ long.

**TYPE COLLECTION:** T. 779.5, cystocarpic, in basalt tidepools, near Onenoa, Tutuala I., American Samoa, legit R. Buggeln, Aug. 13, 1964. Represented by a glucose slide mount and fluid-preserved material.


All of the Atlantic specimens cited above seemed clearly referable to *H. filifera*, having the same branching pattern, approximately the same number of segments in the determinate branches, a similar number of pericentral cells and length of segments in mature determinate branches, a more or less simultaneous elongation of the segments of determinate branches, and numerous, relatively persistent trichoblasts of similar aspect, as well as other minor features.
Numerous tetrasporangia arise in series near the branch tips and the tips of older branches tend to become frayed.

*H. filifera* resembles *H. caespitosa*, described by Tseng (1944) from Hong Kong, in the branching pattern, in the numerous well developed, spirally disposed, branched trichoblasts, in the terminal cystocarps on shortened branches, and the numerous, terminal, spermatangial stichidia. From the description given by Tseng, *H. filifera* differs in being considerably more slender, in having nearly twice as many segments in the determinate branches, in the tapering rather than "obtuse-rounded" apices of the determinate branches, in tetrasporangia more numerous and more terminal in position, and in considerably smaller and arcuate spermatangial stichidia without the large sterile terminal cell described for *H. caespitosa*. Efforts to obtain specimens of *H. caespitosa* for comparison have been unsuccessful.

In the number of pericentral cells and the number of segments in the erect branches, as well as in the numerous tetrasporangia in the upper parts of the determinate branches, *H. filifera* resembles *H. pacifica*. It differs from *H. pacifica* in the lack of bare nodes on the indeterminate branches, in the more or less simultaneous elongation of the numerous segments of young determinate branches, and in the relatively persistent trichoblasts, which likewise develop more or less simultaneously, 8 or more being commonly present at one time, rather than mostly 1–2 being present at a given time as in *H. pacifica*. Furthermore, scar-cells are relatively small in *H. filifera*, but large in *H. pacifica*.

*Herposiphonia nuda* sp. nov.

Figs. 2E, 2F, 2I, 8

Epiphytic algae, with prostrate, indeterminate axes attached to the host by frequent unicellular rhizoids, with a branch on every node, and with 3 erect determinate branches in alternate positions on either flank between successive indeterminate branches, as is characteristic of the genus in general; prostrate branches 80–105 µ in diameter, with mostly 7–8 pericentral cells and slightly smaller central cells, and with segments 1–2 diameters long; determinate branches very slender, 2–3–(3.5) mm high, 40–60(80) µ in diameter, composed of 25–30–(44) segments 1.5–3.5 diameters long, with 4–5 pericentral cells slightly flattened periclinally and a much more slender central cell, the branches terminating in a conical or rounded cell, and occasionally bearing a lateral branch; chromatophores seemingly not zonate; trichoblasts and scar-cells totally lacking in vegetative branches; spermatangial stichidia 2–3 per ramulus, arising from the entire trichoblast primordium on the concave side of the young branches well above the median point, lanceolate, about 275 µ long and 70 µ in diameter at maturity and bearing a sterile tip of 2–3 cells; procarps arising in similar positions; mature cystocarps and tetrasporangia not observed.

Algae epiphyticae, rami prostrati tres ramos determinatos erectos inter ramos indeterminatos successivos ferentes; rami prostrati 80–105 µ diam., cellulis pericentralibus plerunque 7–8; rami determinati 2–3–(3.5) mm alt., 40–60–(80) µ diam., e 25–30–(44) segmentis 1.5–3.5 plo longioribus quam laxis compositi, cellulae pericentrales segmentorum 4–5, cellula centralis longe tenuiores; rami in cellulam conicum rotundatum desinentes, ramum lateralem interdum ferentes; chromatophora non zonata; trichoblastae et cellulae-cicatrices in ramis vegetativis nullae; stichidia spermatangialis 2–3 in omni ramulo, et primordio trichoblastae toto in latere concavo ramorum ivuvenem longe supra partem median orientia, lanceolata, matura c. 275 × 70 µ, cacumen sterile e 2–3 cellulis constans ferentia; procarpi similiter positi; cystocarpi maturi atque tetrasporangia non observata.

**TYPE COLLECTION:** D. 19137J1, cystocarpic and spermatangial, on Padina sp., dredged at 15–20 ft, Iiio Point, Molokai, Hawaii, Sept. 7, 1959. This collection is represented by one glucose slide mount and fluid-preserved material.

**ADDITIONAL COLLECTIONS EXAMINED:**

**HAWAIIAN ISLANDS—**D. 19135J1, spermatangial, D. 19135K2, cystocarpic, and D. 19135Z2, on Hypnea sp., all epiphytic and dredged at 26 ft, in front of the river mouth, Waialua, Oahu, Aug. 2, 1959; D. 19137N1, sterile, dredged along with the type; MARSHALL ISLANDS—**G. 760.3, on Halimeda sp. in the lagoon at a depth of 9 m, Eniwetok Atoll, Sept. 7, 1955; MALDIVE ISLANDS—**Ha. 15–1F–124–26, on a foliose red alga, dredged at 36 ft, in the lagoon near Bomasdu I., Miladummadula Atoll, Mar. 29, 1964; Ha. 26–2N–23A, at a depth of 2 ft, Wilingili, Addu Atoll, Apr. 30, 1964.
This species is similar to *H. tenella* in its slender form and pattern of branching. It differs from that species in having fewer pericentral cells and considerably longer and more slender segments in the determinate branches, but more especially in the lack of trichoblasts and in the point of origin of sexual reproductive structures.

**Herposiphonia obscura** sp. nov.

Fig. 25

Epiphytic algae with prostrate indeterminate branches about 100μ in diameter, with 8–10 pericentral cells and composed of segments mostly about 1 diameter long, attached by frequent unicellular rhizoids arising singly at the nodes; apex of indeterminate branches only moderately inrolled; erect determinate branches with 8–10 pericentral cells and composed of mostly 7–20 segments, very variable in number in determinate branches on a given indeterminate branch, rarely by renewed apical growth with up to 85 segments; segments in determinate branches 0.5–1.5 diameters long, with a diameter similar to that of the indeterminate branches; each determinate branch followed distally by an indeterminate branch and 1–5 (5) bare nodes; indeterminate branch primordia mostly remaining very rudimentary, consisting of about 5 or 6 cells representing the first very short segment of the branch; chromatophores not zonate; walls thin, usually brownish, dispersions opaque; trichoblasts 1–2, terminal, mostly absent or very rudimentary, rarely up to 300μ long, with 3–4 dichotomies; reproduction unknown.

Algae epiphyticae, ramos prostratos indeterminatos c. 100μ diam., cellulis pericentralibus 8–10, apice modicis involuto, habentes; rami erecti determinati similis, cellulas pericentralas 10–12 habentes, et e 7–18 (40) segmentis 80–90μ diam., 0.5–1.5 pllo longioribus quam latis compositis; ramus indeterminatus aut primordium rami et unus ad tres nodi nudi omnis ramum determinatum distintam consequentes; primordia ramorum indeterminatorum maxima ex parte semper magnopere elementaria, e c. 5–6 cellulis, segmentum primum rami brevissimun experimentibus, constantis; chromatophora non zonata, membranis tenuibus, subbraneis, dispersions opaci; trichoblastae nullae aut rarae elementarsae, reproductio ignota.

**TYPE COLLECTION:** D. 19645J1, epiphytic, dredged off Ewa Beach, Oahu, Hawaii, Feb. 22, 1962. This collection is represented by a glucose slide mount and fluid-preserved material.

**ADDITIONAL COLLECTIONS EXAMINED:** HAWAIIAN ISLANDS—D. 19117B1, epiphytic, dredged at 25 fa, Pokai Bay, Oahu, July 30, 1959; D. 19136K2, epiphytic, dredged at 16 fa, Waialua, Oahu, Aug. 2, 1959; D. 19645A1, D. 19645L2, dredged off Ewa Beach, Oahu, along with the type collection; LINE ISLANDS—D. 18995.1, on *Halimeda* sp., seaward reef flats, Christmas I., (1° 55' N, 157° 20' W), May 16, 1962; D. 20022.1, on *Halimeda* sp., June 3, D. 20040, on coral, seaward reef flats, Christmas I., May 16, 1962 (all of the Christmas Island collections were made by Ralph F. Palumbo); GILBERT ISLANDS—D. 18937.5, epiphytic, coral reef, Marakai I., legit Jane Cooper, July, 1962, identified by R. Tsuda (1964) as *Polysiphonia fragilis* Suringar; MALDIVES ISLANDS—Ha. 11–1D–122B–16, dredged at 25–35 fa, near Maduvari I., southwest boundary of Fadifolu Atoll, Mar. 25, 1964.

A collection by Leonard Horwitz, no. 9598a, from the lagoon side of Ine I., Arno Atoll, June–Aug. 1951, identified by E. Y. Dawson (1956:59) as *Lophosiphonia bernudensis* Collins and Hervey, is certainly a *Herposiphonia* and probably *H. obscura*, judging by Dawson's Fig. 65, in which the determinate branches are followed by the very rudimentary indeterminate branch primordia and then two bare nodes. The rhizoids arise from the morphologically distal end of the pericentral cells as seen by the relative positions of determinate and indeterminate branches.

Due apparently to the thinness of the walls, plasmolysis of the cells of this species readily occurs in the dilute glucose mounting medium used. The central cells in this species are about the same diameter as the pericentral cells. The very rudimentary indeterminate branches constitute perhaps the most distinctive feature of this species.

**Herposiphonia pacifica** sp. nov.

Figs. 2A, 2B, 4, 19

Chiefly saxicolous algae, forming extensive turf or tufts up to 1.5 cm high; prostrate branches 100–170–(200)μ in diameter, with
Fig. 19-25. (Scale = 150μ)


20. *Herposiphonia parca* form *dispar*, showing the comparative size of determinate and indeterminate branches.

21. *Herposiphonia variabilis*, showing a variant branching pattern.

22. *Herposiphonia parca*, with young terminal cystocarps.

23. *Herposiphonia parca*, with young terminal spermatangial stichidia.


8–10–(12) pericentral cells and composed of segments about 1 diameter long, attached by unicellular rhizoids arising at irregular intervals, mostly one per segment and having mostly digitate tips; indeterminate branches arising on alternate sides of prostrate axes at intervals of 3–5 segments, with a single determinate branch between successive indeterminate branches, and with the latter always one node distal to the former; determinate branches normally simple, 60–90–(140)μ in diameter, composed of (30)–60–80–(100) segments, which are mostly about 1.5 diameters long in median parts, and which have mostly 12–14 pericentral cells, but may have as few as 8 or as many as 16; central cell at least twice as wide as the pericentral cells; determinate branches usually gradually narrowed at the base and gradually or abruptly narrowed at the apex; chromatophores usually not zonate; trichoblasts 3–5–(8), up to 2 mm long, with about 7 forks, arising somewhat distichously, at decreasing intervals of 8 segments to 1 segment, mostly 1–2 being present at one time; scar-cells relatively large; tetrasporangia in long series of 20–30 in the terminal parts of the branches, slightly distending the segments; spermatangial stichidia lanceolate-arcuate, 400–560μ long, 50–80μ broad at the base; with a sterile tip of 1–2 short cells, up to 6 or more stichidia arising in acroptelar succession at intervals of 6–1 segments at the apices of the branches; procarps and cystocarps not observed.

Algae praesertim saxicola, caespites penicillosae amplus usque ad 1.5 cm alt. formantes; rami prostrati 100–170–(200)μ diam., cellulas pericentrales plerumque c. 10 habentes, et e segmentis circa aequo longis ac latis compositi; rami indeterminati in latibus alternis ramorum prostratorum, intervallis 3–4–(5) segmentis, orientes, unico ramo determinato inter ramos indeterminatos successivum sito, ramos determinato in nodo qui distillator ramum indeterminatum admodum praecedit semper sito; rami determinati normaliter simplices, 60–90–(140)μ diam., e 60–80–(100) segmentis compositi, segmentis c. 1.5 plo longioribus quam latis, et plerumque 12–14 cellulas pericentrales diametro c. ditida pars cellulae centralis habentibus; chromatophora non zonata; trichoblastae 3–5–(8), usque ad 2 mm long., 7–(9) furcas habentes, et intervallis decrecentibus 8 ad 1 segmenta, saepissime 1–3 semel subdistichae orientes; cellulaeaeaticrates magnekiae; tetrasporangia in partibus terminalibus ramorum determinatorum 20–30 seriatis disposita, segmenta paululum distentia; stichidia spermatangialia lanceolato-arcuata, 400–560 × 50–80μ, cuseum sterile ex 1–2 cellulis brevibus constantis habentia; usque ad 6 stichidia in successionem acroptelai, intervallis 6–1 segmentis ad apices ramosorum determinatorum, orientia; cystocarpi ignoti.

**TYPE COLLECTION:** D. 22396, tetrasporic, on basalt shore, intertidal, near Maalaea, Maui, leg. H., T., and B., April 19, 1965. This collection is represented by a glucose slide mount and fluid-preserved material.


Indeterminate branches were observed in several instances to develop from the upper parts of determinate branches in the case of L. 2708.2 listed above. On account of the reduced number of pericentral cells in the plants of this collection there is some question concerning their identity.

This widely distributed and fairly common species exhibits considerable variability in size. Specimens collected in more isolated areas such as Johnston Island and the Marshall Islands are usually smaller than those on larger land masses such as the Hawaiian Islands and the Asiatic mainland. However, more slender forms occur also in the Hawaiian Islands. One such collection, D. 17197A2, has determinate branches mostly less than 100 μ in diameter, with segments mostly not over 1 diameter long. It was collected from Kalapana Beach, Kaimu Bay, island of Hawaii, Feb. 27, 1953. Of special interest in this collection is the occurrence of a mature cystocarp attached at about the 8th segment from the base of the determinate branch. The cystocarp is distinctly urceolate and is about 300 μ in diameter. In view of the terminal position of the spermatangial stichidia of H. pacifica, the position of this cystocarp would seem to make questionable the identity of this collection.

_Herposiphonia parca_ Setchell. Setchell 1926:103
_H. terminalis_ Segi 1954:365, nomen nudum
Figs. 2C, 16, 20, 22, 23

Epiphytic algae, with prostrate indeterminate branches typically 100–150 μ in diameter, composed of segments 1.0–1.5–(2.0) diameters long, with 8–10 pericentral cells and attached by numerous rhizoids, often with digitate or multicellular apices; 3 determinate erect branches in regular sequence between successive indeterminate branches, typically without bare nodes; determinate branches strongly arched when young, composed of 8–12–(20) segments, mostly about 1 diameter long but often shorter or up to 2.5 diameters long, (40)–50–75–(90) μ in diameter, with mostly 8–10 pericentral cells; chromatophores often zonate; trichoblasts 2–(3), terminal, the shorter one on the side toward the apex of the bearing branch; trichoblasts with 3–5 unequal forks and tapering to delicate tips, often rudimentary but frequently to 400 μ long and occasionally up to 1.2 mm long; tetrasporangia in straight series of mostly 5–6 in the middle or lower segments of determinate branches; procarps and cystocarps strictly terminal, the cystocarps globular to slightly urceolate, up to 400 μ in diameter; spermatangial stichidia 2–(3), terminal, oblong at maturity, up to 190 × 80 μ with a sterile tip of 1–2–(5) cells.

**TYPE LOCALITY:** Tahiti. This is one of the most common species found in the central tropical Pacific Ocean. Examination of the type collection, represented by four slide mounts, kindly loaned by the University of California at Berkeley, confirmed the writer’s opinion that the
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numerous collections listed herewith are readily referable to H. parca, although more segments commonly occur in the determinate branches than are present in the type material.

Considerable variability occurs among the various collections. Frequently encountered are more slender forms with up to 20 segments in the determinate branches and with the segments 2 or more diameters long. These variants are indicated in the following account with an asterisk. In some of these there are only 6 pericentral cells in the segments of the determinate branches. Another variant has indeterminate branches up to 3 times the diameter of the determinate branches. These are marked with a dagger (†) and are designated as form dispar.

COLLECTIONS EXAMINED: HAWAIIAN ISLANDS—D. 19144LA4†, dredged 6–12 fa, Port Allen, Kauai, Sept. 12, 1959; a collection by Gary Collins, tetrasporic, on Galaxaura sp., Haena Beach, Kauai, Apr. 16, 1965; D. 8904†, 8905.1†, in connecting channel of holding ponds, Coconut I., Kaneohe Bay, Oahu, Oct. 7, 1955; D. 19135AA1†, D. 19136Fl†, dredged at 15 fa, in front of river mouth, Waialua, Oahu, Aug. 2, 1959; D. 19706.1, awash at Kaihau Beach, Oahu, Sept. 20, 1962; D. 20047.1, on rocks, Laie, Oahu, legit R. Tsuda, G. Trono, and R. Buggeln, May 5, 1963; H. 65–65, spermatangial, on Codium sp., bottom of large tide pool, Wawamalu Beach, Oahu, May 1, 1965; a collection by Gary Collins, tetrasporic, dredged at 2–3 fa, Kaneohe Bay, Oahu, Mar. 20, 1965; D. 22301.2, in a tidepool, northeast bench, Hanuma Bay, Oahu, legit R. Tsuda, Feb. 17, 1965; D. 19137A1*, spermatangial, dredged at 15–20 fa, Iilo Point, Molokai, Sept. 7, 1959; D. 22384, D. 22389, D. 22390.1, on other algae, basalt shore, near Maalaea, Maui, legit H., T., and B., Apr. 19, 1963; D. 17063.1, on Amansia, on wave-dashed basalt, Pohoiki, Puna, island of Hawaii, Jan. 27, 1953; D. 20193.9, in algal turf, Kaena ponds, Kaena, Puna, island of Hawaii, Mar. 19, 1965; a collection by John Fitzsimons, on other algae, Kapoho, island of Hawaii, Mar. 1, 1965; JOHNSTON ISLAND—H. 65–118A, tetrasporic, H. 65–136, tetrasporic, spermatangial, on dead coral at a depth of 1–2 m, 20 m shoreward from the outer reef margin, north of North Island, legit R. S. Jones, Apr. 22, 1965; LINE ISLANDS—L. 2703.6*, on Laurencia sp., exposed coral heads, Jarvis I., Nov. 16, 1964; SOCIETY ISLANDS—D. 12095.1, D. 12099.1, on other algae, under coral boulder, lagoon shore, Arue Pt., Tahiti, Sept. 15, 1952; FIJI ISLANDS—D. 12123.1*, in algal turf, Nanvevu Cuvu, Singtoka, Viti Levu, Sept. 22, 1952; GILBERT ISLANDS—D. 18904.1†, tetrasporic, Abemannama I., legit M. J. Cooper, July, 1962; MARSHALL ISLANDS—D. 12723.1, on other algae, seaward reef, Parry I., Eniwetok Atoll, July 24, 1954; G. 749.1, at a depth of 9 m, lagoon reef, Eniwetok Atoll, Sept. 7, 1955; H. 48–Y58.21, on other algae, Runit I., Eniwetok Atoll, July 27, 1948; CAROLINE ISLANDS—all legit Ernani Meñex, 1960; D. 21838.2, on other algae, reef flat at Epwelkapw, Fonape (6°59'N, 158°11'E), June 16; D. 15071.1, on Amphiroa sp., on reef, eastern side of Manatepait I. (7°15'N, 158°18'E), June 20; D. 21046†, tetrasporic, on sea grass, south end of Moen I., Truk group, Aug. 1; D. 23656.2, on Padina sp., reef at Falas I., Truk group (7°52’N, 151°45’E), D. 23804.1, on branching coralline, Falas I., D. 23811, on branching coralline, Falas I., all July 30; D. 23648.1, on dead coral, Dublon I., Truk group, July 31; D. 23253.2, on dead coral, southern tip of Sorol I. (8°8’N, 140°4’E), Aug. 13; D. 23559.1, D. 23471.3, D. 21857.3*, on other algae, reef at Yap I. (9°29’N, 138°8’E), Aug. 13; D. 15586.2*, tetrasporic, D. 15556.2, spermatangial, on Sarzassum sp., on reef, Koror I., Palau group, Sept. 5; D. 15981.1*, tetrasporic, on Padina sp., on reef at Iwayama Bay, Palao I. (7°20’N, 134°31’E), Aug. 22; D. 15576.2, on Padina sp., D. 15654.1, tetrasporic, on other algae, D. 21721, on other algae, all from reef flat, Pulo Anna I., Sept. 3; D. 15398A1, on Turbinaria, south end of Helen Reef (2°48’N, 131°45’E), Aug. 28; PHILIPPINE ISLANDS—D. 18103B, 18103C, on other algae at a depth of 3–6 ft, near Davao, Mindanao, June 22, 1958; three collections by D. P. Abbott, 1957, a tetrasporic specimen from sand flats east of Laminusa I., Siasi, Sulu Sea, Jan. 29, sterile specimens on a reef flat west of Cagayan, Sulu Sea, Feb. 28, and spermatangial and cystocarpic specimens from Gnat Reef, Balabac I., Mar. 4; GUAM—D. 20135, D. 20136, on
corallines, legit Ermani Meñez, June 10–12, 1960; Indonesia—a collection by A. Weber-van Bosse (as Herposiphonia tenella), on Gelidiella sp., from Maumeri I., Flores, kindly loaned from the Rijksjournal, Leiden; an unnumbered collection, slender form, on a sea grass, Tandjung Gul, Singapore, Jan. 1965; MALDIVE ISLANDS—

A collection by E. Y. Dawson, no. 7360C, cystocarpic, Summerland Keys, Florida, May 28, 1949, seems readily referable to H. parca. These specimens bear several strictly terminal cystocarps, which are strongly urceolate at maturity, measuring 480μ in diameter and 640μ in length.

*Herposiphonia parca* var. *interrupta* var. nov. Fig. 6

With the features of the species but with a bare node generally occurring between the first and second determinate branches in a distal direction from a given indeterminate branch.

Algae proprietates speciei praeententis,pleramque, autem, nudum nudum inter ramos determinatos primos secundosque habentes, un ramo indeterminato distaliter positum.

**TYPE COLLECTION:** D. 22369, tetrasporic, in algal turf and on Gracilaria, Maalaea Jetty, Maui, legit H. T., and B., Apr. 19, 1965. The type collection is represented by a glucose slide mount and fluid-preserved material. This variety is known only from collections in the Hawaiian Islands, where it is common. Mature reproductive structures were not observed.


*Herposiphonia subdisticha* Okamura. Okamura (1899:11) Fig. 11

Decumbent algae 2 cm or more long, attached by frequent unicellular rhizoids, with dichotous or nearly dichotous branches, with a determinate or an indeterminate branch on every node and with 3 alternating determinate branches between 2 successive alternating indeterminate branches; determinate branches 500–600μ long, 70–100μ in diameter, with mostly blunt apices and narrowed at the base, slightly to strongly curved toward the tip of the bearing branch, and often slightly curved toward the substratum, composed of 10–12 segments mostly shorter than broad,
pericentral cells 10–12, around a central cell at least twice as broad, the pericentral cells somewhat obliquely oriented; trichoblasts terminal, infrequent, mostly very rudimentary, with 1–3 forks, occasionally as much as 1 mm long, soon deciduous; tetrasporangia about 65 µ in diameter, in straight series of 3–4 or more in swollen segments of determinate branches borne on short indeterminate laterals, not in the determinate branches of main axes; sexual plants not observed.

TYPE LOCALITY: Enoshima, Boshu, Japan.

A single collection, D. 12122 T, tetrasporic, abundant on a branching coralline alga, was taken at Navuevu Cuvu, Singtoka, Viti Levu, Fiji Islands, Sept. 22, 1952. The specimens conform in general to Okamura's description, including the presence of the usually very rudimentary trichoblasts. From Okamura's description the Fijian specimens differ in several respects: (1) they are probably more strictly distichous, with the determinate branches curving slightly toward the substratum; (2) the apices of indeterminate branches are slightly inrolled; (3) the tetrasporangia seem to be borne in the determinate branches of short lateral indeterminate branches, a feature not reported for H. subdisticha. Information concerning the sexual reproductive structures may be necessary to determine whether or not the Fijian alga is to be identified with the Japanese species.

Dawson (1963:434) concluded that H. rigida Gardner (1927:100), H. rigida var. laxa Setchell and Gardner (1930:164), and H. parva Hollenberg (1943:575) (H. pygmaea Hollenberg, in Smith 1944:369) are all to be identified with H. subdisticha. Apparently Dawson failed to note that Okamura described the determinate branches of H. subdisticha as bearing "in its young state very short and minute deciduous fibrillae at the apex." Examination of many specimens of distichous Herposiphonia from the coast of California has failed to reveal a single instance of trichoblasts on the determinate branches. Furthermore, the California specimens are strictly distichous rather than subdistichous, and the determinate branches are not narrowed at the base as in the case of the Fijian specimens. The position of the sexual reproductive structures, when known, may provide further distinctions. Cystocarps of distichous specimens of Herposiphonia from California are borne toward the base of the determinate branches.

It seems necessary to conclude that distichous Herposiphonia plants from California should not be referred to H. subdisticha.

Herposiphonia tenella (C. Ag.) Schmitz 1889: 449

Hutchinsia tenella C. Agardh 1828:105

Fig. 14

Epiphytic algae, with prostrate indeterminate branches 80–90 µ in diameter, with about 8 pericentral cells, and composed of segments mostly 1.0–1.5 mm long, bearing 3 erect determinate branches in alternating positions between successive indeterminate branches, with mostly no bare nodes; determinate branches up to 1.5 mm high, 50–60 µ in diameter, composed of 16–18 segments, mostly about 1.5 mm long, with 8–9 pericentral cells; chromatophores zonate; trichoblasts 2–5, in spiral sequence on the branches, the first one arising 2–8 segments from the ultimate apex, with 3–4 forks, mostly short, but occasionally up to 1.5 mm long; spermatangial stichidia (only one observed) 190 µ long, 35 µ broad, cylindrical, with a one-celled short sterile tip, borne on the third segment from the branch apex; procarps, cystocarps, and tetrasporangia not observed.

TYPE LOCALITY: On the coast of Sicily.


Algae of the above collections are structurally in close agreement with the description of H. tenella given by Falkenberg (1901) in most respects. Falkenberg reports 20–50 segments in the determinate branches. The writer was privi-
leged to examine a portion of a specimen from the Agardhian herbarium in Lund, which the Keeper, Dr. Sven Snogerup, concluded was the type of *H. tenella*, since it was annotated by J. G. Agardh as "Hutch tenella C. Ag. sp. orig." Examination of this material showed that the determinate branches were composed of about 15 segments. In other respects the material corresponds closely with Falkenberg’s description.

*H. tenella* form *secunda* (C. Ag.) comb. nov.

*Herposiphonia secunda* (C. Ag.) Falkenberg (1901:307)

*Hutchinsia secunda* C. Agardh 1824:149


In some of the specimens listed above the determinate branches are somewhat larger, up to 80μ in diameter, with 40 or more segments 1.5-2.0 diameters long, whereas Falkenberg (1901) states that in *H. secunda* the determinate branches are relatively plump, with 14-20 segments, which are mostly shorter than broad. Through the kindness of Dr. Sven Snogerup, Keeper of the herbarium, Lund University Museum, the writer was privileged to examine a specimen from the Agardhian herbarium, which Dr. Snogerup considers an isotype specimen of *H. secunda*. It is a glass slide mount, no. 39158, with the following notation on the original packet: "Hutchinsia unilateralae, Aug. 6, 1825, Tingi, Schousboe." This specimen exhibits the chief features described by Falkenberg (1901), with mostly 1 determinate branch and 2 bare nodes between successive indeterminate branches. The determinate branches are composed of 10-12 segments, with about 10 pericentals. The specimen is tetrasporic, with fruiting segments about 1 diameter long. The tetrasporangia are in series of 7-8 in the upper part of the branches. The lower sterile segments are 1.5-2.0 diameters long. The chromatophores do not seem to be zonate. There are about 3 terminal trichoblasts, with 6-8 dichotomies. They are about as long as the branch bearing them.

Fluid-preserved material from the type locality, northern Africa, would prove helpful in determining the correctness of the above identification.

Prof. J. Feldmann of Paris kindly sent the writer a collection of *Herposiphonia* from le Troc, Banyuls, France. He identified this alga as *H. secunda*. The specimens were fluid-preserved and in excellent fruiting condition, with an abundance of procarps and cystocarps. In most respects the plants of this collection matched the description of *H. secunda* given by Falkenberg. However, the segments of determinate branches of Feldmann’s plants are mostly 1.5-(2) diameters long, as they are in a number of the collections from the Pacific listed above. The procarps arise apically or subapically, 2-3 per branch, but the branch continues to grow beyond the developing cystocarp for 8-10 segments.

Falkenberg (1901) and Boergesen (1918) both reported instances in which the branching pattern for *H. tenella* and that for *H. secunda* occurred on the same branch. The writer has observed similar instances not only in plants of the *H. tenella* type, but in other species as well. Hence it has seemed necessary to conclude, as did Boergesen at first, with some reservations, that *H. secunda* should be considered merely a form of *H. tenella*. The branching pattern seems
to be a good key feature for distinguishing between certain species, but it is an unreliable feature in this instance.

_Herposiphonia trichia_ sp. nov.

Fig. 1G

Epiphytic algae, with prostrate branches about 45μ in diameter, attached by frequent rhizoids, and bearing 3 erect, slightly more slender, determinate branches 1–2 mm high, and composed of 10–16 segments, arising in alternating positions between successive indeterminate branches or branch rudiments, with no bare nodes, or sometimes with determinate and minute indeterminate branches at alternate nodes; pericentral cells 6–8 in indeterminate branches and lower parts of determinate branches, but occasionally reduced to 4 in the slender terminal parts of the latter; chromatophores not zonate; trichoblasts unbranched or occasionally with 1 or 2 laterals, up to 700μ long and about 8μ in diameter at the base, composed of 8–9 cells, gradually tapering to a rounded or conical tip, arising one per segment in 1/4 spiral sequence in the terminal parts of the determinate branches, mostly soon deciduous, leaving relatively large scar-cells; tetrasporangia relatively large, 60–70μ in diameter, in straight series of 10–12–16 in the much-distended lower half of the determinate branches; spermangial stichidia arising from the entire trichoblast primordium, without a sterile tip, 1 or 2 per branch on short unicellular pedicels, on the convex side of the branch, 3–5 nodes from the base; procarps borne singly in similar positions; cystocarps not observed.

Algae epiphyticae, tres ramos determinatos inter ramos indeterminatos successivos habentes, nodis nudis nullis; cellulae pericentrales plerunque 6 in ramos indeterminatis atque in partibus inferioribus ramorum determinatorum, in partibus terminalibus tenuibus, autem, ramorum determinatorum ad 4 rudentes; trichoblastae non ramosae aut interdum unum duobusve ramis lateralis praeditae, ad 700μ long., et c. 8μ diam. ad basim, ex 8–9 cellulis compositae, ad camenum rotundatum gradatim attenuatae; una in unoquaque segmento spirali in partibus ramorum terminalibus orientes, plerunque mox decidueae, cellulas-iacitores maiores reliquentes; tetrasporangia 60–70μ diam., 10–12 in serie recta in ramorum dimidio inferiore sita; stichidia spermangialia e toto trichoblastae primordio, unum vel duo in unoquaque rame determinato in latere convexo in nodo secundo ad quinimum a basi posita, sine camumino sterilib; pro- carpi similiter orientes; cystocarpi non observati.

**Type collection:** D. 23461.1, tetrasporic, on _Amphiroa_ sp., on a reef, Yap I., Caroline Islands, leg. Ernani Meñez, Aug. 18, 1960. This collection is represented by two glucose slide mounts.

**Additional collections examined:** D. 23466.1, spermangial, on _Amphiroa_ sp., along with the type collection; D. 23471.1, with procarps, on _Amphiroa_ sp., from the same locality as the two preceding collections. This species resembles _H. hollenbergii_ described by Dawson (1963:430) from the Pacific coast of Mexico. From that species it differs in the following respects: (1) decreasing size and number of pericentral cells in the upper parts of determinate branches, rather than increasing to 60–80μ and to 10–12 pericentral cells in the upper parts of determinate branches as in the Mexican plants; (2) the pattern of development of secondary indeterminate branches; and (3) the much longer unbranched trichoblasts, which are described by Dawson for _H. hollenbergii_ as “short, sparse or absent.” From _H. delicatula_ the present species differs chiefly in the mostly unbranched trichoblasts.

_Herposiphonia variabilis_ sp. nov.

Figs. 1F, 2G, 17, 18, 21

Saxicolous algae with prostrate branches 70–100μ in diameter, with segments 0.7–1.0–(2.0) diameters long, with about 10 pericentral cells and with slightly inrolled apex, attached by frequent unicellular rhizoids; erect determinate branches 0.3–1.0–(2.0) mm high at maturity, 70–80μ in diameter, composed of 10–16–(50) or more segments 0.6–1.5 diameters long, with 8–10 pericentral cells and a central cell up to twice as large as the pericentral cells; only 1 determinate branch between successive indeterminate branches, each indeterminate branch being followed distally by (0)–1–6 bare nodes; indeterminate branches usually not extensive; chromatophores commonly zonate; trichoblasts 3–4–(9) per erect branch, with only 2–3 present at one time, the first-formed one as much as 10 segments from the ultimate branch apex; trichoblasts up to 2.5 mm long, with 4–6 dichotomies and gradually narrowed to delicate tips, the basal cell frequently 200–350–(730)μ long and 40–45–(58)μ in diameter at maturity;
trichoblasts with about \( \frac{1}{2} \) spiral divergence, at intervals of 1–5 segments, soon deciduous, leaving large scar-cells and commonly prominent wall-scars; tetrasporangia 40–50\( \mu \) in diameter, in straight series of (6)–13–24, in terminal parts of the branches; cystocarps subterminal, 350\( \mu \) in diameter, ovate, with a prominent ostiolar beak; spermatangial stichidia slightly lanceolate, 160–200\( \mu \) long and 60–65\( \mu \) in diameter, on a short 1-celled pedicel, and with the short 1-celled sterile apex, arising terminally from the entire trichoblast primordium.

Algae saxicolaee ramos prostratos ad 100\( \mu \) diam. qui ramos determinatos erectos 0.5–1.0–(2.0) mm alt. et 70–80\( \mu \) in diam., e 7–15–(30) segmentis 0.6–1.5 plo longioribus quam latis compositos, ferunt, cellulis pericentralibus 8–10, habentes; 1–5 nodi nudi inter ramos indeterminatos successivosplerumque semper breves, unicum ramum consequentes; chromatophora vulgo zonata; trichoblastae 3–4–(9) in unoquoque ramo erecto, 2–3 semel, trichoblasta primum formata usque ad segmentum decimum ab apice rami sita; trichoblastae usque ad 2.5 mm long., 4–6 dichotomias habentes, ad caulina tenuia gradatim attenuatae, intervallis 1–3 segmentis spiraliter ordinatae, mox deciduae, magnas cellulas-cicatrices reliquentes; tetrasporangia 40–50\( \mu \) diam., in partibus terminalibus sita; cystocarpi subterminales, c. 350\( \mu \) diam., ovati, rostro ostiolarri conspicuo praeediti; stichidia spermatangialia sublanceolata, 160–200\( \mu \) long., 60–65\( \mu \) diam., apicem sterilem unicellulararem brevemque habentia, in parte extrema ramorum determinatorum orientia, et primordio toto trichoblastae formata.

**TYPE COLLECTION:** H. 65–113, tetrasporic, cystocarpic, spermatangial, on dead coral at a depth of 1–2 m and 20 m shoreward from the outer reef margin north of North I., Johnston Island, legit R. S. Jones, April 22, 1965. This collection is represented by 7 glucose slide mounts and additional fluid-preserved material.


This is a very variable species as to number of bare nodes, degree of development and number of trichoblasts, and the number of segments in the determinate branches. As many as 75 were counted in L. 2705.3. In some instances the large number of segments seems to be due to renewed growth of the branch. Determinate branches occasionally develop one or more laterals which may be either determinate or indeterminate. Although procarps arise subterminally, mature cystocarps may be as much as 10 segments from the branch apex, as a result of continued growth of the branch.

**H. variabilis** is probably closest to *H. tenella* forma *secunda*, from which it differs chiefly in the following respects: (1) the greater variability in the number of segments in the determinate branches (Falkenberg [1901] reports 14–20 segments for the European specimens examined); (2) the great length of the trichoblasts in some specimens; and (3) the more numerous tetrasporangia in many cases.

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Herposiphonia of Tropical Pacific—HOLLENBERG


CORRECTION

Acknowledgments in: Steele, C. W., 1967, Fungus populations in marine waters and coastal sands of the Hawaiian, Line, and Phoenix Islands, Pacific Sci. 21(3):317–331, should be emended as follows:

1. Of the 67 sand samples studied, 38 were collected under the auspices of the Pacific Ocean Biological Survey Program, Smithsonian Institution, Washington, D. C. 20560. Specifically, these included 8 samples from Kure, collected by C. H. Lamoureux; 14 samples from the other Leeward Islands, 11 samples from the Phoenix Islands, and 5 samples from the Line Islands, all collected by C. R. Long.

2. Of the 59 water samples studied, 10 were collected under the auspices of the Pacific Ocean Biological Survey Program, Smithsonian Institution, Washington, D. C. 20560. Specifically, these were: 1 sample from Midway, collected by C. R. Long, and 9 samples from Johnston Island, collected by A. Young.

3. The data obtained from these samples and incorporated with the data obtained from the 29 independently collected sand samples and 49 independently collected water samples constitute Paper No. 39, Pacific Ocean Biological Survey Program, Smithsonian Institution, Washington, D. C. 20560. In addition the author acknowledges the Pacific Ocean Biological Survey Program as the source of the map included as Figure 1 in this publication.

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