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Some Pearlfishes from Guam, with Notes on Their Ecology. C. Lavett Smith

Notes on the Life History of Two Californian Pomacentrids: Garibalis, Hypsypops rubicunda (Girard), and Blacksmiths, Chromis punctipinnis (Cooper). Conrad Limbaugh

Further Notes on the Identification and Biology of Echeneid Fishes. Donald W. Strasburg

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The Correct Name for the Hawaiian Gossypium. Robert L. Wilbur

Chromosome Homology in the Ceratobium, Phalaenanthe, and Latourea Sections of the Genus Dendrobium. H. Kamemoto, K. Shindo, and K. Kosaki

NEWS NOTE:

Tenth Pacific Science Congress Papers

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JENS W. KNUDSEN

It was the aim of this research project to study the growth and reproductive cycles of the Puget Sound Brachyura and Anomura as they are related to oceanographic and environmental conditions. These goals were designed to answer many of the basic questions concerning the local crab population and to serve as a basis for more restricted physiological experimentation dealing with behavior and reproductive cycles. A continuous survey of the intertidal and near-shore crab fauna was made to determine the seasonal change in gonad development, egg production, the time of fertilization, deposition of eggs, and other related features. As many species of Anomura and Brachyura as could be accommodated were captured and maintained in running sea water aquaria for additional studies of food and feeding habits, ecdysis, copulation, and other phenomena linked to maturity and reproduction. The aim to survey all Brachyura and Anomura in the southern Puget Sound area had to be modified to exclude the hermit crabs due to the extreme amount of time required for field observation of this group. It has been our goal to correlate reproductive activity of all of these species with annual environmental changes so far as possible and to determine trigger mechanisms involved in the reproductive cycles. Considerable experimentation was attempted along these lines as is discussed herein.

ACKNOWLEDGMENTS

A research project of this nature has required the help and support of many institutions and individuals. To the Division of Biological Sciences of the National Science Foundation that has generously granted Pacific Lutheran University funds for this research,1 the principal investigator and those students who received research experience and financial aid wish to express their thanks. The Metropolitan Park Board of Tacoma has rendered a tremendous service in providing research space at the Point Defiance Aquarium; we wish to thank them, and especially Cecil Brosseau, for their help with space, equipment, and invaluable information. We wish to acknowledge the special laboratory space and facility donated by Dr. S. C. Eastvold and the Pacific Lutheran University. The writer wishes to express his indebtedness to biology majors who have served on this project. Especially helpful have been the efforts of Bert Freeman and Lloyd Dillingham; in addition, other student assistants served one or more semesters on the grant: Ron Barbour, Ray Herbig, Gary Vestal, Ruth Olsen, Pat Lingelbach, and Ron Heyer. The art work was done by Ron Heyer. Of invaluable aid have been the suggestions and help rendered by other carcinologists, especially Dr. Josephine F. L. Hart Carl of the Provincial Museum, Victoria, British Columbia, and Dr. John S. Garth of the Allan Hancock Foundation, University of Southern California, Los Angeles.

FIELD COLLECTING AND STUDY AREAS

Three main sites were used within the area of Tacoma for year-long study of the southern Puget Sound crabs. These sites are somewhat variable in nature and thus offer a good cross-section of the different types of habitat within Puget Sound. Collecting was confined to the intertidal area because adequate dredging facility was not available. The most frequently visited site was that of Titlow Beach. This is a curved beach situated at the southern end of the Tacoma Narrows where the bay is fairly broad and is protected by pilings

1 Department of Biology, Pacific Lutheran University, Tacoma 44, Washington. Manuscript received June 5, 1962.

2 N. S. F. grant G-9066.
and ferry dock facilities at one end and a somewhat rocky prominence at the other end. Thus relatively calm water free from strong currents exists. The substrate grades from rocky rubble to almost pure mud. In one area a small stream drains into the Titlow Beach habitat and has formed an underwater delta consisting of mud and coarse sand. Along the upper margin of the beach large boulders have been placed as a retaining wall, thus affording a site where spray zone animals and plants may live. This beach is typical of most Puget Sound intertidal areas.

The second site studied was at the Point Defiance boathouse. Situated on the north side of Point Defiance, it opens to the Dalco Passage. The immediate area associated with the boathouse is similar to that of Titlow Beach, for rock rubble covers much of the shell-fragment and coarse sand substrate. Adjacent to the boathouse, however, a long expanse of beach extends toward the north and west and affords a heavy growth of Zostera marina. At this site those species that dwell typically on pilings or under rock rubble or within the Zostera beds were studied.

The third site frequently visited was under the Narrows Bridge in that confined stretch of water known as the Tacoma Narrows. This is the only drainage site for the extremely large southern arm of Puget Sound and hence the currents "boil" through the Narrows at a high velocity during the changing of the tide. On the east side of the Narrows very large boulders have been placed by the railroad company to retain the banks. A limited number of very narrow beaches extend out from these boulders. From the low low-water mark the substrate frequently drops off abruptly to depths that appear to be 15 ft or more. This habitat is so heavily washed by swift currents that sediments not protected by rocks are swept away. Those animal and plant species that fully require a protected outer rocky coast with fairly strong oceanic waves often exist here because the high velocity of the current serves as a substitute for waves. This site was visited whenever the tides were sufficiently low to insure good collecting.

Three other sites were visited on occasion. Gig Harbor, just north of Tacoma, is a well-protected area with a muddy bottom and a large number of piers and floating boat docks. This site was examined occasionally for the large number of spider crabs that could be found there. Quartermaster Harbor across from the Point Defiance Aquarium offered a large number of piers for collecting. Another site visited three or four times annually was near the lighthouse in the Port Orchard channel just north of Port Orchard, about 1 mile southwest of Point Glover and across the channel from White Point. The prominence at the lighthouse is a natural headland composed of very large boulders that project out into the waterway. Like the Narrows, this site has extremely heavy currents; unlike the Narrows, however, the rocks project straight out into the current rather than simply forming a margin along the current. This site was well provided with invertebrates, some of which are found almost exclusively in the outer reaches of Puget Sound or in the protected open oceanic coastline. Likewise the flora was more reminiscent of that of the protected rocky coastline. Here many of the species of crabs that had been encountered in southern Puget Sound were also present, but in addition such genera as Pachycheles were found.

METHODS AND MATERIALS

FIELD COLLECTING: The tide in the eastern Pacific is a mixed tide, thus giving unequal lows or highs during any given day. About every 14 days a period of low tides occurred but only once out of each month would the tide be sufficiently low to enable the collection of specimens which live at the extreme lower limits of the intertidal zone. Several collecting trips were made during each series of low tides. During the transitional periods of tidal change (January–March and September–October) bimonthly collecting was continued and an endeavor was made to obtain all of those species under study, even though the depth of the tides was not adequate. However, it was necessary to use laboratory animals in part to fill in where field records were not obtainable. In many instances it was felt that the laboratory data were not obtained under natural conditions and thus these have been disregarded in the final analysis. Collecting was always carried out by hand or by hand-operated nets and dredges.
LABORATORY FACILITIES: The Pacific Lutheran University facility consisted of a very large walk-in cooler with a system that maintained room temperature isothermally with Puget Sound water. Aerated glass aquaria filled with sea water were set up in this cold room. The room was partitioned off with a completely light-proof curtain, and independent lighting systems with time clock controls were set up on either side of the room. Aquarium heaters were employed when higher than room temperatures were desired. Thus it was possible to control the length of "daylight" and the tank temperature so that many environmental factors could be altered within each aquarium.

The Point Defiance facility consisted of nine

<table>
<thead>
<tr>
<th>Species</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Brachyura-Grapsidae</strong></td>
<td></td>
</tr>
<tr>
<td><em>Hemigrapsus nudus</em> (Dana)</td>
<td>Very common.</td>
</tr>
<tr>
<td><em>Hemigrapsus oregonensis</em> (Dana)</td>
<td>Very common.</td>
</tr>
<tr>
<td><strong>Xanthidae</strong></td>
<td></td>
</tr>
<tr>
<td><em>Lophopanopeus bellus bellus</em> (Stimpson)</td>
<td>Common.</td>
</tr>
<tr>
<td><strong>Cancridae</strong></td>
<td></td>
</tr>
<tr>
<td><em>Cancer productus</em> Randall</td>
<td>Common.</td>
</tr>
<tr>
<td><em>Cancer magister</em> Dana</td>
<td></td>
</tr>
<tr>
<td><em>Cancer gracilis</em> Dana</td>
<td></td>
</tr>
<tr>
<td><em>Cancer oregonensis</em> (Dana)</td>
<td>Common.</td>
</tr>
<tr>
<td><em>Telmessus cheiragonus</em> (Tilesius)</td>
<td>At Titlow Beach, rare.</td>
</tr>
<tr>
<td><strong>Majidae</strong></td>
<td></td>
</tr>
<tr>
<td><em>Chionetes Baird</em> Rathbun</td>
<td>University of Puget Sound, dredged 18 fathoms.</td>
</tr>
<tr>
<td><em>Hyas lyratus</em> Dana</td>
<td>University of Puget Sound collection, dredged.</td>
</tr>
<tr>
<td><em>Oregonia gracilis</em> Dana</td>
<td>Not numerous.</td>
</tr>
<tr>
<td><em>Pugettia gracilis</em> Dana</td>
<td>Common, but not numerous.</td>
</tr>
<tr>
<td><em>Pugettia producta</em> (Randall)</td>
<td>Common, but not numerous.</td>
</tr>
<tr>
<td><em>Scyra acutifrons</em> Dana</td>
<td>Common, but not numerous.</td>
</tr>
<tr>
<td><strong>Anomura-Porcellanidae</strong></td>
<td></td>
</tr>
<tr>
<td><em>Petrolithodes eriomerus</em> Stimpson</td>
<td>Abundant in restricted localities.</td>
</tr>
<tr>
<td><em>Pachycheles rudis</em> Stimpson</td>
<td>Not abundant.</td>
</tr>
<tr>
<td><em>Pachycheles pubescens</em></td>
<td>Not abundant.</td>
</tr>
<tr>
<td><strong>Lithodidae</strong></td>
<td></td>
</tr>
<tr>
<td><em>Cryptolithodes typicus</em> Brandt</td>
<td>One specimen, Tacoma Narrows.</td>
</tr>
<tr>
<td><em>Haplogaster mertensii</em> Brandt</td>
<td>Not common, restricted.</td>
</tr>
<tr>
<td><em>Lopholithodes foraminatus</em> (Stimpson)</td>
<td>Dredged by Point Defiance Aquarium.</td>
</tr>
<tr>
<td><em>Phyllolithodes papillosus</em> Brandy</td>
<td>Very rare.</td>
</tr>
</tbody>
</table>
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30-gal aquaria of a plywood construction, one 150-gal tank, and numerous smaller aquaria. All of these were supplied with running sea water and furnished with both barnacle-encrusted rocks and marine algae as required by the different species of crabs. A time switch controlled the lighting so that the length of "daylight" could be regulated. Different species of crabs were seldom mixed within the various tanks, to avoid competition and fighting. The cleaning of the tanks and feeding of the crabs twice weekly demanded the full-time attention of one student throughout the entire project.

REPRODUCTIVE CYCLE: Almost all of the data collected concerning the annual reproductive cycle of the various species studied were obtained by field collecting, and only where an indication is made to the contrary are the data obtained by laboratory observation. By selecting and preserving samples of the crabs collected, the development of ova within the ovaries could be watched and measured. Ovaries were studied by dissecting these and placing them on a temporary wet-mount microscope slide. They were then placed on a micro-slide projector and the projected ovary with its developing ova was measured by a predetermined metric scale. Size and color data were recorded in each case.

Observations of crab copulation were made by chance. With the numerous field trips and continuous laboratory observation, many fine records were obtained. The crabs were at no time conditioned by hormones or isolated for copulation studies, and all records are considered to be normal and valid.

The time of egg deposition was obtained from the field record. As many females as possible or practical were collected bimonthly, and counts of the total number of females with eggs and studies of the egg condition were made. Incubation period is determined mainly from the total field record as plotted, or, from the literature. In few cases are the data obtained in the laboratory. In most instances it was felt that laboratory results may be altered somewhat due to some abnormal condition and therefore field records were used whenever possible. In some cases the actual mechanics of hatching were observed for various species of crabs. The number of broods per year was determined by field observations, laboratory observations, and by

the dissection of females carrying developing eggs on the pleopods. These dissections determined the nature and degree of development within the ovaries. All three means were used whenever possible to give an accurate picture of the number of broods per year. Some attempts were made to study the larval development by actually rearing larvae in the laboratory. By far the largest proportion of crabs in Puget Sound have already been studied and the description of the larvae of these crabs is now being prepared for publication. Those species yet unstudied remain so because of difficulty in rearing them in the laboratory. Many species already known were run through the life cycles in part at least to compare both the morphology and ecology with the literature.

FAMILY Grapsidae

Hemigrapsus HABITAT: The two species of Hemigrapsus, nudus and oregonensis, will be treated together for the sake of comparison. The habitat of H. nudus is listed by Way (1917: 358), as being a situation where rocks and stones cover a sandy substrate. MacKay (1931: 189; 1943:151), Rathbun (1918:268), and others simply list the habitat as being among rocks near shore. Schmitt (1921:274) describes H. nudus as being strictly a littoral species. Hiatt (1948:141) encountered H. nudus and H. oregonensis in what he calls "the second and less common biotope" of Pachygrapsus crassipes. This biotope is found most commonly in estuaries and bays, and consists of a gradation of very large boulders giving way to rock and stone and finally gravely rubble as one proceeds from the offshore area towards the higher reaches of the intertidal zone. Hiatt mentions that Pachygrapsus crassipes is quite abundant around the larger boulders but is replaced by H. nudus and finally by H. oregonensis as one moves progressively toward the fine sandy or muddy substrate.

Hemigrapsus oregonensis is thought of as living on muddy portions of the coast line (Way, 1917:359; MacKay, 1943:152; and others). Hiatt (1948:142) lists this species as being common in the third biotope of P. crassipes, along muddy shores of bays and estuaries. He describes the hiding places of this species as
small holes formed along mud banks, from which the crab will venture out to foray along the entire expanse of the muddy beach. Schmitt (1921:275) suggests that *H. oregonensis* is quite common in dredge hauls ranging from 1½ to 3½ fathoms. The substrate from which these hauls were made consisted of shelly bottoms or mud bottoms.

Within the southern Puget Sound system of waterways one will encounter a variety of substrates beginning with large coarse boulders where the current is rather swift, such as the Port Orchard area or the Tacoma Narrows. Adjacent to this the substrate gives way to rock over sand where the boulder size may become progressively smaller, until finally one encounters in the numerous small bays and inlets a pure mud or fine sand substrate intermingled here and there with gravel in areas where seepage is quite common.

The substrate of coarse to fine sand overlain with a fair supply of rocks and boulders makes up the greatest expanse of the intertidal area. To a collector first visiting this type of a habitat it would appear as if the two species of *Hemigrapsus* share the identical habitat, for both abound in very large numbers. However, *H. nudus* prefers the upper reaches of the intertidal zone and is found abundantly during periods of low tide under large boulders situated over a coarse sand or broken shell substrate. Rickerts and Calvin (1952:208) note that *H. nudus* is found in a "middle zone" in California, where temperatures are cooler than in the upper zones, while it is found in the upper zone in Puget Sound. The temperatures in these two zones may approach being isothermal and thus explain the pattern of distribution. *H. oregonensis* is most common in the lower reaches of the intertidal zone. A careful check of the substrate will show that this crab is found where there is a very fine silty sand or mud present beneath the rocks, and that frequently coarse gravels make up a substrate between the rocks. This species seems to prefer shallow depressions where the gravel or mud is saturated with water, a sharp contrast to the very well-drained substrate on which *H. nudus* is often found. There are numerous invertebrate burrows in this habitat and these are frequently occupied by *H. oregonensis*. *H. nudus* also visits this lower zone from time to time, especially during the colder parts of the winter months when both sexes move down in the intertidal zone, or in the spring when females carrying eggs will occasionally be found hiding there. There are no data, however, which suggest that females move to this zone in order to keep the eggs moist, for equally large numbers are found at low tide in the very high and extremely dry parts of the intertidal area. When *H. oregonensis* is found in the uppermost reaches of the intertidal area, it is in situations which are kept moist by surface run-off or in depressions where very shallow tide pools form. Thus, the preference seems to be that *H. nudus* will select larger boulders with relatively good drainage beneath and that *H. oregonensis* will select any situation in which the body may be bathed almost continuously with water.

As one moves from this typical habitat to the more rocky headlands, he finds that *H. oregonensis* begins to drop out in population counts but that *H. nudus* remains a dominant member of the fauna. Conversely, as one moves from the rock and sand situation towards that of a fine mud and gravel, he finds that *H. nudus* drops from the population count but *H. oregonensis* becomes extremely abundant. This habitat is perhaps more suitable for *H. oregonensis* since, because of its diminutive size, this crab can hide even between pieces of gravel. The fine sand grains or mud tend to hold more water, thus meeting another requirement of this species. Where the water is extremely swift and the substrate is composed exclusively of large boulders, the only member of the genus likely to be found is *H. nudus*.

Associated with the habitat of this genus is the growth of various phyla of microscopic algae upon the rocks. Such a micro-turf may consist of diatoms, desmids, very young growths of the green algae, some of the finer species of the brown algae, etc. Such a turf is essential, being the chief food of members of this genus. Like *Pachygrapsus* species, crabs of this genus spend a tremendous amount of time gleaning the micro-algae from the rocks by means of their large chelae. At night or when the crabs appear to be undisturbed, they may be seen in large numbers foraging along the tops of rocks. It is interesting to note that the males frequently
will be found highest up on the rocks while the females are more timid and remain along the lower sides of the rocks where they can reach a hiding place in case of an emergency. As the tide comes in and covers the zone, these crabs move about in large numbers, yet become quite secretive if the presence of the collector is obvious. The behavior of the males as compared with the females was especially noteworthy in *H. nudus*. When females of this species were captured upon the rocks at night they quickly autotomized appendages in order to escape. Males, on the other hand, were quite reluctant to autotomize an appendage but rather would resort to bluffing or actual pinching with the chelae.

**Hemigrapsus nudus**

**FOOD AND FEEDING HABITS:** Thirty-four specimens were collected in the Titlow Beach area for stomach analysis. The animals were preserved with a 5% formalin solution to insure a quick and complete saturation of the stomach contents. In the laboratory the stomachs were removed and the contents examined under dissecting and compound microscopes. Of the 34 animals examined, 4 had completely empty stomachs while 3 had only partially full stomachs. The largest portion of the gut contents was made up of marine algae, while the second largest portion consisted of inorganic material such as sand grains. The least abundant material found in the gut content consisted of animal tissue. Amongst the algae, diatoms and desmids made up the greatest portion of material. Some species of green algae (*Ulva* sp. and *Enteromorpha* sp.) were frequently found. To determine the source of the diatoms and desmids, scrapings were made along the sides and tops of rocks within the habitat of this species. A microscopic analysis of these scrapings demonstrated that the algae present were identical with those found in stomachs of *H. nudus*. Furthermore, diatoms taken in sea water samples did not match those found in the stomachs. Examination of the rocks showed that young fronds of the above-named green algae were frequently present. Our observations have shown that this species gleams from the surface of the rock using the large chelae. The feeding method is primarily the same as that described by Hiatt (1948:178) for *Pachygrapsus crassipes*. Crustacean exoskeletons made up the most notable portion of the distinguishable animal tissue within the gut contents. Amphipods could be recognized and fragments of other similar arthropods, were present. No attempt was made to determine the exact species of either the animal or plant material, for the source of this material seemed to be the most important thing in this instance. Abundant small arthropods exist wherever *Hemigrapsus* feed and thus these animal fragments are probably accidental in their appearance. Hiatt (1948:178) describes *Pachygrapsus* as being an active predator which will frequently attempt to capture living animals. The present writer has seen *Pachygrapsus* on numerous occasions in California in the act of eating freshly killed animals, even large individuals of newly-molted *Cycloxyznths*. No such observations have been made for *H. nudus* in the field, though there is little doubt that this species will capture and eat animal material when it is available. On occasion this species was seen feeding on dead animal tissue. However, the food supplied by scavenging probably contributes very little to the total volume consumed by this species. Feeding activities are most readily observed at night. When in total darkness crabs will migrate from their hiding places and feed along the sides and tops of rocks. *Hemigrapsus* may confine much of its feeding to periods of low tide to prevent the tiny diatoms from being washed from the chelae, although this species does feed while under water. *H. nudus* is definitely a herbivore, but obtains a small portion of its food as a predator and scavenger.

**SYNOPSIS OF REPRODUCTIVE ACTIVITY:** Figure 1 shows that oogenesis in *H. nudus* begins in the fall and continues into the first weeks of January. Numerous observations of copulation were made during the later weeks of December and into the first weeks of January. Egg deposition begins very early in January and the rate of deposition increases swiftly until over 70% of the females are ovigerous at the end of that month. The number of females bearing fertilized eggs on the pleopods increases very slowly from this point on, until a peak of 98.6% is reached in the early weeks of April. Hatching very
noticeably begins at about the first week in May and continues, somewhat slowly at first but then increasing in rate, until about the middle of June. Less than 1% of the females examined were found to carry a second brood of eggs. At this time a period of quiescence occurs until oogenesis begins again in the fall. After the middle of July no trace of egg-bearing females could be found at the Titlow Beach collecting site, even though several hundred females were examined at each bimonthly collecting trip.

OÖGENESIS: The process of oogenesis probably begins while the female is carrying eggs of the previous brood attached to the pleopods. Of 20 females dissected in the middle of June, 4 showed no visible development (using the technique described above), while the remainder showed some slightly detectable development of ova within the ovaries. In most cases these ovaries were predominantly hyaline or whitish in color, but faint orange or reddish ova could be observed. These, however, were too small to be measured. By the end of September an average measurement of 0.25 mm diameter showed that considerable ova development had occurred. From this point on, development proceeded at a regular but slow pace, and by the end of November ova averaged 0.36 × 0.39 mm in size. From this time on until the time of egg deposition there was only a slight increase in ova size. There was a gradual change in color as the ova developed. In September most of the ova were yellow or yellow-orange in color. The orange color prevailed until November but then showed a gradual change to a deep brown prior to egg deposition.

SEASON OF COPULATION: Many records of copulation were made at the Point Defiance laboratory from December 18 to the end of the month. Copulation occurred both during lighted periods and at night. Field records, which are few, suggest that copulation occurs under large stones which afford suitable room and ample protection. Only one period of copulation is necessary as this species, unlike H. oregonensis, is single-brooded.

COURTSHIP AND COPULATION: The process of courtship or copulation has not been described for the genus Hemigrapsus. One complete account is recorded by Hiatt (1948:199)
for a near relative, *Pachygrapsus crassipes*. Hiatt's description, the first for the Grapsidae, clearly shows that this species is strikingly different from other members of the Brachyura in its method of copulation, in that the male assumes an inferior position to the female. Our research attempted to learn the time of copulation in the total reproductive cycle of *Hemigrapsus*, and also to determine if the account given by Hiatt applied to *Hemigrapsus* as well. The discovery that both *H. nudus* and *H. oregonensis* are similar to *Pachygrapsus* in this respect suggests that the Grapsidae in general may differ from most other families of Brachyura.

In December, soon after the shortest day of the year, *H. nudus* was seen on numerous occasions in the act of copulation. Hiatt's notation of the extreme speed with which a pair of *Pachygrapsus* will begin copulation applies also to *Hemigrapsus*, as frequently pairs of the latter genus would be found *in copulo* with no observation of the onset of this act.

*H. nudus* does not precede copulation with a period of courtship, as is the case with many Cancroid crabs as cited by Williamson (1903: 101), Hay (1904: 405), Churchill (1918: 105), Knudsen (1960: 7), and in this paper under the genus *Cancer*. A male initiates copulation by approaching the female and grasping her by the chelae or carapace. After a few seconds to a minute of "wrestling" with variable gestures and shifts in position, the male begins to position the female. The first uniform act occurs when the male lifts the female by her chelae and places her in a vertical position with her anterior end upward and the posterior part of the carapace down on the substrate. Simultaneously the male tilts his body upward in a similar manner so that both male and female come to rest upon their last two pairs of walking legs with their ventral thoracic surfaces in contact (Fig. 2). From this position the male rolls over on his dorsal side with the female held firmly above him. The female is held with her dorsal side upward and her ventral thorax in contact with that of the male (Fig. 3). The male uses the chelae to hold the female by the carapace and uses pereiopod pairs two and three, and on occasion four, to maintain his grasp. The act of penetration of the vulvae by the male's pleopods could not be seen due to our vantage point.

However, by carefully capturing a pair *in copulo* in such a way as to hold the two firmly in the mating position, the relationship of the male and female abdomens was observed. Such observation, together with accounts in the literature (Hiatt, 1948: 199; Knudsen, 1960: 7), suggests that the following activity occurred. As the male proceeded to roll from a vertical position to its "back," he simultaneously raised his abdomen in such a way as to hook the abdomen of the female. With a posterior thrust of his abdomen the male then forced the female's abdomen down and thus exposed the vulvae. Mechanically, as the male's abdomen is moved backward, the pleopods or intromittent organs are brought into position for penetration and sperm transfer. When interrupted, or when cop-
ulation is completed, the female generally scrambles off backwards while the male attempts to right himself.

Hiatt (1948:199) suggests that *Pachygrapsus crassipes* copulates mainly at night, as his total observations were few in relation to the amount of observation time. In our work, however, we have noted that *H. nudus* was seen most often in copulation during the day under lighted conditions (12 records) rather than at night (2 records). Our observation time during the breeding season was, by far, greater in the daytime and thus we have no firm conclusion as to the preferred time, or light condition, for copulation. Probably this species will copulate at any time that the female is receptive and there is no outside disturbance.

**Fertilization and Egg Deposition:** Bi-monthly counts of up to several hundred females allowed us to trace the onset of egg deposition through two entire seasons. The date at which egg deposition began and the rate of deposition during the second year was remarkably close to that of the first year for both species, and differed only by about 5 days in either direction. Thus, on or shortly before New Year’s Day, egg deposition begins and continues extremely rapidly. Rickerts and Calvin (1952:31) note that this species produces eggs as early as November in Monterey Bay, California, in contrast to Puget Sound specimens. Perhaps water temperature may have some influence, although in both areas temperatures are declining at the time of deposition. Fertilization occurs as the eggs are discharged through the vulvae, at which time they are attached to the pleopods. A remarkable 98.66% of all females examined were found to have eggs early in April. Nonovigerous specimens examined at this time showed no development within the ovary and probably were unhealthy or beyond a reproductive age. Figure 1 shows that hatching begins rapidly early in May and reaches a peak toward the end of that month. By the first weeks in June all of the eggs have hatched. At this time less than 1% of all of the females examined showed the production of a second brood or a new brood.

**Productivity:** Fifty-one females of all size classes of *H. nudus* were selected for egg counts. The sizes ranged from 11.9 mm in carapace width up to 34.0 mm in carapace width, and the number of eggs varied from 441 up to 36,456 eggs for the two extremes of sizes. The average number for all 51 specimens was 13,000 per brood. Since only one brood is produced per year this figure probably can be used as the average annual production for this species.

**Larval Development:** *H. nudus* has been studied and completely described in its larval development by Hart (1935:424–430). There are five zoea stages and one megalops stage.

**Hemigrapsus oregonensis**

**Food and Feeding Habits:** Throughout the year 12 specimens were preserved for stomach content studies. Of the 12, 2 had totally empty stomachs and 2 had only partially full stomachs. Like *H. nudus*, members of this species had been feeding upon diatoms and other algal forms obtained by scraping the upper surfaces of rocks within the intertidal zone. The diatoms were the same sessile forms as described for *H. nudus*. However, most of the individuals had some green algae, probably *Ulva* and *Enteromorpha*, but none had any fragments of animal tissue within the stomach. *H. oregonensis* lives somewhat lower in the intertidal zone than does *H. nudus*, and at this level a large quantity of *Ulva* is found attached to the rocks. Thus, it seems quite natural that this green alga should be used as a source of food. In the laboratory *H. oregonensis* will consume animal tissue such as fish or cut clam or even fragments of crab muscle tissue, and thus must be considered a scavenger when dead animal tissue is available. This species is predominantly a herbivore, however, and is considered to obtain most of its food from plant sources. *Hemigrapsus oregonensis* feeds in the same manner as *H. nudus*, but is more timid in its behavior.

Both *H. oregonensis* and *H. nudus* use the tactile, visual, and chemical senses in their feeding. While gleaning from the rocks at night the tactile senses are presumably used almost exclusively, for the eyes would be of little value in this situation. Chemoreceptors on the tips of the walking legs could possibly be used to determine the presence of marine algae. In the experimental aquarium these species can locate bits of meat by means of chemoreceptors and
thus are motivated in their feeding in a manner like that described by Hiatt for Pachygrapsus crassipes.

On March 1, 1960, the water temperature in the tanks at the Point Defiance laboratories reached the seasonal low of 6.9 C. This low temperature was maintained for several days running and during this period almost all of the food offered to all species of crabs, including Hemigrapsus nudus and oregonensis, all three species of Cancer, and two species of Pugettia, was ignored. Probably this temperature marks a point at which the crab metabolism is retarded and little feeding is required or is possible.

SYNOPSIS OF REPRODUCTIVE ACTIVITY: Figure 4 shows that oogenesis within the ovaries begins sometime during the month of October and continues until the time of ovulation, fertilization, and egg deposition. Egg deposition begins about the middle of February and at about March 10 starts to increase rapidly. Egg deposition is completed at the end of April. In the early weeks of May hatching begins and continues until the end of July. The second brood appears very shortly after the hatching of the first brood begins, showing that there is a very short duration when the females are without eggs on the pleopods. Those females producing a second brood complete egg deposition by the first week of August and hatching is completed by September 24. At this time there is no sign of activity within the ovaries of the female and it is assumed that a period of quiescence is resumed until oogenesis commences once again.

OÖGENESIS: Each month 10 to 12 females of this species were dissected and the ovaries were studied for signs of oogenesis. During October only one individual showed enough development that the ova could be measured (approximately 0.23 mm). In November the specimens showed considerable size increment in that most of the ova were recognizable and measured slightly under 0.20 mm, though 2 of 14 individuals showed ova slightly larger than 0.20 mm. In January the ova averaged about 0.35 × 0.29 mm. One individual out of 8 in this group showed ova only slightly larger than 0.20 mm diameter. The February sample again showed a considerable increase in over-all size, with ova as large as 0.47 × 0.42 mm, but

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FIG. 4. The reproductive cycle of Hemigrapsus oregonensis.
averaging closer to about 0.40 × 0.38 mm. In 10 specimens sacrificed in February, 3 had ova about 0.20 mm in diameter.

The ova begin to take on pigmentation as development occurs. During October most of the ovaries were hyaline, while the one individual showing some development had ova of a rusty brown color. Generally the transition in color is from a light yellow to an orange, to a purplish-brown, and finally to a very dark purplish or orange-brown color.

Oogenesis occurs a second time during the reproductive season in about 70% of the females. The progression of ova development is simultaneous with the embryonic development of those zygotes attached to the pleopods. Very shortly after the hatching of the first brood has occurred, copulation probably takes place and a second brood is brought forth. Inasmuch as histological sections were not made of the ovaries, it was impossible to detect accurately the exact time of the onset of oogenesis. By our technique it would appear that early October is the time when activity can first be recognized with any certainty.

PERIODS OF COPULATION: Very few observations of copulation were made for this species either in the laboratory or in the field. Perhaps the small size of the individual and its drab coloration would account for this in part. Those records obtained were gotten around March 20 and April 15. Using H. nudus and its total reproductive cycle as a partial guide, it is suggested that copulation in H. oregonensis may begin as early as the first of February and probably continues until about April 20. In any event, it would seem that copulation occurs just shortly before egg deposition. Whether or not a second period of copulation is required is not known. Dissections of the spermatheca of those animals bearing ova have not been completed. Thus, knowledge of whether or not sufficient sperm is stored is lacking. Probably a second period of copulation is required, as in the case of Pachygrapsus crassipes (Hiatt, 1948:200).

ACT OF COPULATION: The act of copulation of H. oregonensis is similar to that of H. nudus and P. crassipes although this species, being smaller, may need even less time. The position is typical of that of H. nudus, as the male rolls over on his back and positions the female with her ventral thoracic surface against his. The chelae of the male are folded over the carapace of the female, extending in a posterior-median direction, thus forming a V. The walking legs are also used to hold the female or to alter her position. Our observations show that the male generally lifts the female and rolls over, simultaneously positioning her after he is resting on his carapace. Thus, a minor difference between this species and H. nudus may exist in that the latter often positions the female before rolling backwards. A somewhat imperfect view of the act showed that the male H. oregonensis lowers the abdomen of the female in the manner described for H. nudus.

An interesting observation made in an experimental tank may shed some light on the initiation of copulation and thus is given almost in full as it appears in our laboratory notes. A pair was found in copulation and records were taken of the activity. For 25 min the pair remained in copulation with only slight abdominal movements and an occasional leg movement observed. At the end of this period, the female broke away and rushed across the tank where a second male abruptly caught her, rolled over and began copulation. The first male broke up this pair by shaking the new male loose. At this time the female darted under a rock. The male in pursuit, unable to reach her with his thick chelae, backed under the rock and pulled the female out by means of his last walking legs. The male then held the female without copulating, for over 40 min, attempting to position her from time to time. At the end of the period the male successfully copulated with the female until she again broke away. A new male caught the female and, in a fluid movement, rolled over and began copulation. The original male returned and succeeded in freeing the female in order to copulate with her again before she finally escaped to the safety of a rock crevice.

It is of interest, first of all, that at least three of the five males in the aquarium were ready to copulate with the female whenever she was free, while one was even successful in dislodging other males in order to copulate. Second, there were nine other females of this species in the same tank, most of which later produced a batch of eggs, thus proving maturity and fertility.
Moreover, this activity occurred in the middle of the copulatory season when one would expect mating to occur. Thus it would seem that, like many mammals and other well-known animals, the males of this species of crab (if no others) become physiologically ready to copulate early in the season but are not aggressive until the female is ready. Such readiness is probably signaled to the male by some hormone which is released into the water as the last act of readiness prior to copulation. Thus, it is suggested that a hormone or some such chemical stimulus is secreted by the female which excites the male into action. This would answer the question of why the “eager” males did not simply grasp other females which were ever-present in the aquarium. Such a signal or trigger for copulation is not the same as that which begins oogenesis or spermatogenesis, but would only affect a male which had completed the maturation process.

**Egg Deposition and Fertilization Period:** As with other crabs, fertilization occurs in this species at the time of ovulation and egg deposition. As the eggs pass down the oviducts, they become fertilized in the region of the spermatheca and then pass through the vulvae and are caught within the “egg basket.” The abdomen and the exopodites of the pleopods form the baskets and hold the eggs until they are firmly attached to the endopodites of the pleopods. Bimonthly counts of up to 300 females of this species were made to determine the pattern of egg deposition and hatching. A few individuals begin egg deposition as early as February 18, but the percent of individuals (4.66–5.83) remains very low until about March 10. At this time (see Fig. 4) there is an abrupt increase in the rate of egg deposition for all individuals. Egg deposition continues until about the first week in May, when over 90% of the individuals have eggs attached to the pleopods. According to Figure 4 it would appear that hatching begins very shortly after this peak is reached, for a gradual fall-off in the percent of individuals with eggs is noticed. It is quite possible that those individuals which produced eggs early in February may have begun the hatching process even prior to the peak of egg deposition. This may account for the fact that only 90% of the females are seen with eggs at any one time. When these data are compared with H. nudus, it will be seen that nearly 99% of the females may have eggs at one given time. As early as May 20 the second brood of eggs begins to appear for some individuals. Figure 4 shows a sharp increase in the number of females with new eggs, suggesting that only a short lag between broods occurs. A careful check of the condition of the developing embryos continues to show an increasingly large number of new eggs and a correspondingly smaller number of prehatch specimens. A climax of hatching for brood number one is reached shortly before the peak of egg deposition for brood number two, which is around August 6. The percentage of females producing two broods drops to about 70% and shortly after the peak is reached hatching again occurs and continues until September 24, when less than 1% of the individuals still have eggs in the prehatch condition.

To demonstrate more fully that a second brood is produced 38 females were dissected on June 13, shortly after brood number two had begun to appear. Of the 38, 22 had no eggs attached to the pleopods, while 16 had new eggs attached to the pleopods. Of the 22 specimens without eggs all but 6 had well-developed oocytes that were visible through the membranous wall of the abdomen and upon dissection showed fully developed ova. Five of these 6 showed little or no development of ova within the ovaries while the sixth specimen proved to be immature and thus not ready for reproduction. Of the 16 individuals bearing new eggs none had well-developed ova in the ovaries, showing that these had now been spent on a second brood. Three of this latter group showed some very slight development in the ovaries in the way of pigmented eggs. It is suggested that these eggs simply were not ovulated at the time of deposition and hence remained to give the appearance of slight development.

On May 15 the number of females bearing their first brood of eggs reached 59% of all of the females observed. A special measurement of the 326 females collected was made to determine the relationship between size classes of those females with and without eggs. Gradations of 2 mm from 8 mm to 20 mm were used so that crabs closely approaching one gradation or
another were simply grouped into that size class. Figure 5 shows the distribution of those females with and without eggs. It will be noted that the 12 and 13 mm size range contained the largest number of reproductive and nonreproductive females, and that the total number of individuals drastically drops off on either end of the curve. It will be noted that the two curves are amazingly similar, indicating that egg deposition does not necessarily occur earlier in larger or smaller size classes, but that the period of deposition is irrespective of size class and is determined solely by the season itself.

PRODUCTIVITY: Egg counts were made for 42 specimens of *H. oregonensis*. The number of eggs ranged from around 800 to over 11,000 per brood. The average for the 42 specimens was 4,500 eggs per brood. When the number of eggs is plotted against the width of the carapace, it can be seen that the number of eggs increases in almost a straight line until a size class of 12.5 mm is reached. At this time the line breaks, indicating that the number of eggs produced actually increases above the expected rate of production for the smaller animals, as the carapace size increases. As many as 22,000 eggs could be produced in a single year by some of the largest females which produce two broods. For those females that have two broods a year the average production would be about 9,000. However, since only about 70% actually produce the second brood, on the basis of 100 individuals a yearly average of 7,650 would be obtained. This latter figure is probably more accurate for the population as a whole and is used to denote annual production.

LARVAL DEVELOPMENT: The larval development of this species has been worked out by Hart (1935:430–432), using specimens taken from Vancouver Island, British Columbia, which is close to the latitude of our own studies. She lists the time required for development to the first crab stage in two individuals as being 4 and 5 weeks. If the southern Puget Sound specimens develop at a similar rate, the first crab stages could reach the beach in the early weeks of June and continue to arrive into October. Hart has completely illustrated the larval stages of *H. nudus* and has given sufficient data on *H. oregonensis*, so that those extremely similar larvae may be separated when taken in plankton.

POSSIBLE TRIGGER MECHANISMS

In a study of trigger mechanisms which may initiate the reproductive processes, several possibilities must be considered: is the reproductive life cycle triggered at its very beginning, in the species being studied, and then do all subsequent events simply follow suit as in a chain reaction? Or does each individual event such as oögenesis, copulation, egg deposition, etc., have its own individual triggering device? A review of the literature has shown that most generally photo-period, temperature, or a combination of both serve as triggering mechanisms for reproductive activity amongst the invertebrates and many of the vertebrates. Since a parallel, though sometimes lagging, physiological cycle progresses almost concurrently with the annual cycle of external stimuli, a study of trigger mechanisms must eventually include a careful study of hormone and other physiological activities. Although many experiments were attempted in our research, none produced results of sufficient magnitude to warrant in this paper a review of the literature concerning trigger mechanisms, or an exhaustive description of experimentation. Experiments were set up during several parts of the year where temperature and photo-period were either increased, decreased, or maintained at a steady state, either simultaneously or independently, and the species.

![Fig. 5. Distribution of female Hemigrapsus oregonensis, with or without eggs attached to the pleopods, when plotted by size class.](image-url)
of *Hemigrapsus*, *Lophopanopeus*, and *Petrolis-*

the were subjected to these artificial environmental changes. In comparing the life histories of *Hemigrapsus oregonensis* and *H. nudus* several events notably occur just after significant changes in photo-period or temperature have occurred. Namely, in *H. nudus* (Fig. 1) copulation begins at about the shortest day in the year and progresses steadily as the photo-period lengths. However, in this cycle there is no correlation with temperature, as the temperature has slowly been decreasing prior to the onset of copulation and after the period of copulation. At the end of this reproductive cycle the temperature is still somewhat on the rise, but the photo-period has again reached its peak and the days begin a shortening trend at the time when the last of the larvae hatch. It is conjecture to do more than suggest that there may be some correlation between the life cycle and this trend from the shortest photo-period to the longest photo-period. On the other hand, the life cycle of *H. oregonensis* (Fig. 4) seems to parallel the trend of temperature with reference to egg deposition and the maintenance of the first and second broods. That is, egg deposition of the first brood begins rapidly after temperatures start to rise in March, and the second brood does not complete hatching until temperature has reached its peak and has begun a downward trend. The exact time at which copulation is most prevalent for this latter species is not well known and hence this event cannot be paralleled with photo-period or temperature. In both species the seeming correlation between environmental factors and reproductive activity failed to account for the onset of spermatogenesis or oogenesis. It is quite possible that the original triggering stimulus was received during the summer or fall prior to oogenesis and spermatogenesis, and that subsequent reproductive behavior simply followed as a chain reaction probably triggered by hormone activity. That hormones are important is clearly seen in the data given for *H. oregonensis*, where it is noted that some probable chemical stimulus caused males to mate only with certain females and to ignore all others. The striking difference between the two species of *Hemigrapsus* suggests, however, that different external stimuli may be influencing the onset of reproduction in these two species. Because of original mistiming of experimentation, which was based on reproductive activity as recorded in the literature, and a series of mechanical difficulties in cooling and lighting devices, our data are incomplete and inconclusive in this aspect of research. Thus, we will reserve this problem for later research and publication.

**FAMILY XANTHIDAE**

*Lophopanopeus bellus bellus*

**HABITAT:** The pebble crab, *Lophopanopeus bellus bellus*, is replaced in the south by its counterpart, *L. bellus diegensis*. As shown by Knudsen (1960:171) this species differs from the *Lophopanopeus* complex of *leucomanus* in that it prefers the more quiet water of bays or estuaries to the open ocean shores. The writer finds *L. b. bellus* occupying a micro-habitat identical to that of *L. b. diegensis* in the south. The former subspecies is found in Puget Sound at the lower extremes of the intertidal zone and seems to prefer a situation where a single layer of rock covers fine sand or mud. Rocks which do not fit closely to the substrate, but leave a slight gap underneath, are less frequently occupied by this crab. On the other hand, this species burrows well back under large rocks that hold so firmly to the substrate that hydrogen-sulfide mud is produced. Like the southern subspecies, the Puget Sound form often "plays dead" for a few minutes when disturbed in its hiding place. Way (1917:367) states that this crab is always found with *Cancer oregonensis* buried in sand and mud under rocks on rocky shores. Around Titlow Beach and Point Defiance the two species often occur together but *Cancer oregonensis* is also found higher up in the intertidal zone. Our collecting records indicate that not all rocky shores are suitable for *Lopho- panopeus*. In all cases where this crab is found there is a noticeable water current, though often not strong, during the ebb and flow of the tide. The presence of a tidal current is the only factor that the present writer finds to separate the *Lophopanopeus* habitat from almost identical, adjacent stretches of beach where *Lophopanopeus* is not present.

**FEEDING HABITS:** Stomach analyses were made for seven individuals. The nature of the ma-
material in the stomachs made identification of the fragments quite difficult, as compared with fragments obtained from herbivorous species such as *Hemigrapsus*. Within the various stomachs were found fragments of brown algae (sp. ?) and some form of green plant which resembled *Zostera*. Diatoms similar to those found in the stomachs of *Hemigrapsus* were also present in a few of the specimens. A peculiar whitish material, more or less well broken up, and resembling coralline algae was also found. As recorded by Knudsen (1959:114) this genus feeds to a large extent on coralline algae of the species *Corallina gracilis*, *C. vancouverensis*, *Boszia orbigniana*, and *B. gardneri*. Encrusting and free-living coralline algae are found in limited quantities in the Puget Sound habitat of *Lophopanopeus* and thus may be used as a food source by this species. Some animal tissue (crustacean, mussel, and barnacle fragments, and nematode worms) was also found. The nematode worms are believed to be stomach parasites, however, and not a food source.

SYNOPSIS OF REPRODUCTIVE ACTIVITY: Figure 6 shows that oogenesis begins in the autumn and continues until the time of egg deposition. The ova reach a near maximum size in December and then increase in size very slowly until the time of deposition. Fertilization and deposition begin in the early weeks of January and continue very rapidly throughout the month of February. Early in March a leveling-out is reached, with a high of 92.3% of the females bearing eggs. Our observations and those of Hart (1935:414) show that hatching begins in May but the appearance of brood number two tends to offset hatching as far as the percentage of females bearing eggs is concerned. Thus, Figure 6 shows a slow increase until the first week of June, at which time the hatching of brood number one sharply increases and offsets the rising curve of brood number two. About 60–70% of the females produce a second brood which matures rapidly and hatches, probably, throughout the month of September. A solid line on Figure 6 indicates that accurate field measurements have been made to substantiate the curve, but a broken line indicates that field data are few, or lacking. A brief period of quiescence follows the second brood and then oogenesis begins again in the fall.

**FIG. 6.** The reproductive cycle of *Lophopanopeus bellus bellus.*
COPULATION: Many records of copulation in _L. bellus bellus_ were obtained in the laboratory but none were obtained in the field. The season of copulation is just prior to egg deposition. This would suggest that only a brief period of a few days or weeks separates copulation and egg deposition. On June 9, seven females were dissected which had just hatched their first brood. Six showed ovaries in a highly developed and ovigerous condition, while one had ovaries showing no development. Of the seven, four had the spermatheca completely empty while two had a small amount of sperm present, and one had a large quantity of sperm. These data suggest that copulation is necessary prior to the second brood. The process of copulation in this subspecies is identical with that of _L. bellus diegensis_ as described by Knudsen (1960:7).

PRODUCTIVITY: The eggs in egg masses taken from 20 females of various size classes were counted and the average was determined. The number of eggs per brood ranged from 36,000 down to 6,000, with an average for the 20 animals of 15,640. Thus, an average for all females having two broods in a year could be 31,000 eggs per year, but with only about 90% of the females producing a first brood and only about 70% producing a second brood, a more accurate average for all females with or without eggs would be about 25,000 eggs per year. The average egg count given here is extremely high as compared with _L. leucomanus leucomanus_ (Knudsen, 1960:9) but the size range of the northern _L. b. bellus_ is much larger than in those specimens counted for _L. l. leucomanus_.

LARVAL DEVELOPMENT: The larval development of _L. bellus_ was studied and fully illustrated and described by Hart (1935: 414-420). Since that time Menzies (1946:1-45) made a revision of the genus _Lophopanopeus_ and has placed _L. diegensis_ Rathbun in the _L. bellus_ complex, making _bellus_ and _diegensis_ subspecies of the species _bellus_. After Menzies’ revision, the larval development of _L. bellus diegensis_ was described by Knudsen (1959:57-64) and the larval development of _L. leucomanus leucomanus_ was also studied (Knudsen, 1958:51-59).

POSSIBLE TRIGGER MECHANISMS: The early part of the visible life cycle of this species is similar to that of _Hemigrapsus nudus_ in that copulation occurs during and after the shortest days of the year and egg deposition begins about the same time as in _H. nudus_ and continues as the photo-period lengthens. When daylight has reached its maximum length in June the second brood (which is lacking in _H. nudus_) begins and continues to follow the rise in water temperature. While there seems to be some correlation between photo-period, temperature, and the timing of brood number one and brood number two, data to support such correlations are lacking.

**Family CANCRIDAE**

_Cancer oregonensis_

HABITAT: Of the Puget Sound cancroid crabs, _Cancer oregonensis_ is somewhat unique in that not all of the individuals migrate during the reproductive season, but rather many remain in a consistent area within the overall habitat. This species is consistently found with _Lophopanopeus bellus bellus_ and slightly above the latter species within the intertidal zone. The habitat requirements seem to be almost identical with those of _Lophopanopeus_. It is also common to find this species high up on pilings which are heavily encrusted with barnacles and mussels. In this situation _C. oregonensis_ selects a small cavity between the encrusting organisms and uses this for its home site. It feeds on barnacles and other marine organisms within and around this home site.

FEEDING HABITS: While a large number of _C. oregonensis_ stomachs were dissected during the routine of counting eggs and measuring ovary development, only a few animals had food within the stomachs. The rest, apparently, were not feeding during periods of reproductive activity. Prasad and Tampi (1951:675) report that females of the cancroid crab _Neptunus pelagicus_ do not eat while carrying eggs on the pleopods, as is suggested here. The gut contents of eight individuals, five females and three males, were analyzed. In some, partially digested material resembling polychaete worms with numerous bristles was found. In others, fragments of crustacea such as amphipods, small shrimp, or crabs were found. One animal had the stomach completely filled with red eggs identical to those carried on her own pleopods. There is little doubt but that this crab had been eating
its own eggs. Whether these were fertile or not is difficult to say as the eggs were extremely new. One male specimen contained algae fragments which resembled Ulva. While this species is all but impossible to observe in the field, many observations of feeding and other activities have been made in the Point Defiance aquarium. Whenever barnacles are available this crab will feed almost exclusively on them, to the extent that it will ignore fresh-cut fish placed in the aquarium. In the public display rooms this crab often becomes a nuisance by continuously crushing barnacles and littering up the tanks with fragments of barnacle shells.

**REPRODUCTIVE ACTIVITY:** Courtship and copulation in this species is concurrent with the molting process of the female. The months of April, May, and June mark the peak of female molting and probably of copulation. On April 14, 43 females were located at the Tacoma Narrows and many of these were in the process of courting or copulation. Again upon June 8, 11 females of 69 encountered were in the process of courting. Six of the 11 females showed that the epimeral line was broken, indicating that ec dysis was soon to occur. In August, 10 females were collected at random and dissected to determine if sperm was in the spermatheca. Of the 10, 4 had full spermatheca, 2 had some sperm, and 4 had empty spermatheca. These few data suggest that copulation may occur any time during the late spring or summer, and that sperm is stored until the time of egg deposition in the late fall. Ovaries that were studied in May showed no evidence of oogenesis, though some were milky white in color. Dissections made in June showed 3 out of 5 specimens with ovaries whitish to clear, 1 with the ovary whitish in color and showing some development of the follicles, and 1 showing large yellow follicles. Of the 10 specimens dissected in August, 3 showed considerable development of the ovaries, while 7 were underdeveloped. All specimens with developed ovaries had some sperm in the spermatheca, but not all animals with stored sperm showed ovary development.

Fewer females were found in the field during the time of egg deposition and incubation than at other times in the year. Females with eggs were encountered during the last weeks of November. All females collected through the middle of February had eggs attached to the pleopods. However, the numbers of individuals of this species encountered were so small (the highest being 18 females with eggs out of 18 encountered on January 26) that no graph will be presented. In April and in June an occasional female with eggs was encountered. These latter records were considered to be second-brood individuals.

In conclusion, it would seem that oogenesis occurs in the summer and fall; that egg deposition begins in the last weeks of November, that eggs are carried until the middle of February when hatching is completed, and that hatching is followed by a period of quiescence, molting, and finally copulation, in that order.

**COPULATION:** Our field observations of Cancer oregonensis show that this species tends to court as other cancroid crabs do, and that the male carries the female about for several days prior to molting, then copulates with the female after she has completed the molting process. The male will continue to court or protect the female until her shell is hard enough for her to resume normal activity. This species may be more secretive than the larger species, Cancer productus, and hence observations of courting pairs moving freely about under water were not made. During periods of low tide, however, numerous courting pairs were found buried deep under rocks in little pockets surrounded by fine grained sand. The male assumes the normal superior position over the female and remains hidden during the courtship period. By carefully grasping the courting pair, it was possible to see the male with the pleopods inserted in the vulvae of the female. The very secretive behavior of courting and copulating pairs, in contrast to C. productus, suggests that this species is unique in its courtship. Courting pairs found in barnacle masses high up on pilings remain well hidden between barnacles during courtship. In the laboratory courting pairs had less chance to hide themselves, but nevertheless burrowed down into the gravel substrate and remained as concealed as possible.

**PRODUCTIVITY:** The eggs within the egg masses of 17 C. oregonensis females were counted to determine their seasonal productivity. Sizes of the females varied from a carapace width of 17 mm to 26 mm, and the number of eggs
ranged from 10,000 to 33,000. For 17 individuals counted, the average productivity per brood was 20,540 eggs per female. Usually there is only one brood per year and those females producing a second brood or, perhaps more correctly, a late brood, are rare. Thus, the average of 20,540 represents the seasonal productivity for this species.

_Cancer productus_

**HABITAT:** Geographically, _C. productus_ is found from Alaska to Magdalena Bay, Baja California, in two major types of habitats. Primarily it is found in bays and estuaries, such as Puget Sound, Grays Harbor, Willapa Bay, and other similar areas in the state of Washington and up and down the coast. The second type of habitat is that classified as a "protected rocky coast," which could be characterized by any of the small rocky bays or inlets along the open ocean front where rocky headlands or other rocky obstructions cause wave refraction and thus create a zone of less violent action. This second type of habitat is perhaps a minor one. _C. productus_ is found under these conditions at the Tacoma Narrows in Puget Sound.

The writer considers the primary habitat of this species to be that of the large bay or sound. Schmitt (1921:222) notes that _C. productus_ is remarkably absent from fine sand and mud substrates in San Francisco Bay. Rather, he lists this species as being found largely upon sand, gravel, or rock substrates. Cleaver (1949:70) mentions that _C. magister_ remains generally in areas with sand or mud bottoms in the bays along the Washington coast. He states that while this species may occasionally be found on rock or gravel, it is, as a rule, replaced by _C. productus_, which is predominant in such situations. Weymouth (1914:124) suggests that _C. productus_ lacks a straining apparatus to prevent fine particles of mud and sand from entering the gill chamber. Thus, this species is restricted to those zones which will allow it to bury itself in the substrate without clogging the gill chambers. Our own observations in Puget Sound coincide with those of Schmitt and other workers, for this species is frequently found around the Point Defiance boathouse, under the dock at Titlow Beach, and in many similar areas in which the substrate consists of hard packed sand, gravel, or broken shell fragments.

Our observations suggest that this species is equally active at night or in the daytime. Due to its large size _C. productus_ has few enemies within the zone of its normal activity. While many of the very large rock fishes, octopi, or other marine animals will prey upon this species, and other crabs as well, these predators are normally absent in the most favored micro-habitat of _C. productus_. When inactive this species may be found hiding at the base of pilings, where it buries itself beneath gravel or shell fragments, or else hides beneath sunken logs or rocks which loosely cover the substrate. Extremely rarely does one find this species hiding in hydrogen-sulfide mud.

The time and place of activity or inactivity of _C. productus_ seems to be governed mainly by the "choice" of the individual, its age or sex, or the particular phase of reproductive activity or molting activity carried on. A survey of our bimonthly reports for 2 years of collecting shows that from January through May males are predominant in the intertidal zone, while females are almost totally lacking. Those few females encountered during this time were, with one exception, without eggs. From the end of May on into June the sexes are almost equally distributed in numbers, while the females predominate throughout the summer months up into early October. Then the males and females are almost proportional in numbers throughout November and December. Males were never totally wanting in our field collecting at any time of the year, as were female specimens. As will be noted under Reproduction, presence or absence coincides well with the period of egg development, molting of the males, and the times of copulation. Juvenile specimens were abundant only in areas adjacent to those occupied by the adult individuals. These observations suggest that males and females may have a horizontal migration to the deeper water during periods of the year, or they may become inactive and extremely secretive and thus remain carefully hidden within the habitat area. Cleaver (1949:70) reports for _C. magister_ that:

An interesting feature of this species is the tendency to aggregate by size and sex. Until a width of two or three inches is reached, crabs of both sexes are found
together in approximately equal numbers. With the onset of sexual maturity, a definite segregation occurs. Adult females are comparatively rare in Grays and Willapa Harbors, although in some areas of the ocean they are overwhelmingly abundant, particularly in the late winter and early spring months.

Cleaver further notes (1949:67) that some data suggest an offshore migration for this species and confirm a coastwise migration. It is quite possible that C. productus may be similar to C. magister in having an offshore or vertical pattern in migration. Prasad and Tampi (1951:676) show that other members of the family Cancridae, in particular Neptunus pelagicus, segregate according to size and sex in a manner similar to that described above.

It was interesting to note that this species displays a negative rheotaxis in response to the lowering of the tide. It was frequently observed that this species continuously moved ahead of the receding tide, without being “pushed” by the edge of the water or the reduction of the water level. In experimentation, crabs were released into a 3 × 8 ft aquarium and allowed to become tank-adapted. It was noted that they moved about at random in the aquarium. At this time a stream of salt water was introduced at one end of the aquarium, so that a current was created along the bottom of the tank. The crabs oriented themselves and began moving in the direction of the current. The rate of crab movement roughly corresponded to the rate of current created in the tank. It is suggested that this species responds to weak currents created as the water recedes in the intertidal zone, and may govern its tidal migration mainly by these currents.

FOOD AND FEEDING HABITS: C. productus is not secretive in its feeding but, rather, is often bold in its attempt to obtain food. It was regularly observed feeding on barnacles attached to pilings, or on dead fishes or other animal matter available in the habitat. Discounting the food supplied by fishermen in the form of cast-away fishes, barnacles seem to be the most consistent source of food. C. productus will feed around the base of pilings, or will climb up on the pilings in order to obtain this food. The large chela is used in breaking barnacles, while the smaller chela serves to transfer the barnacle to the mouth parts. Crabs of this species main-
tained at the Point Defiance aquarium frequently captured and are smaller crabs of the same species or other species. At such times C. productus merely waited motionless until the smaller crabs approached within striking distance, then lunged forward to capture the smaller crab, crushing the carapace with the large chela. In feeding experiments where crabs were secretly fed small pieces of fish with no light available for their vision (they were observed under red light), C. productus was able to locate pieces of food in a brief time. If water was circulated through the tanks at the time of feeding, so as to distribute the meat juices more readily, the time required for locating food was greatly decreased. Probably this species uses tactile receptors, chemoreceptors, and eyes, either individually or in combination, in its feeding.

REPRODUCTIVE ACTIVITY: Because of the secretive nature and/or disappearance of females during part of the reproductive season, field data are almost wanting concerning some phases of reproduction in C. productus. Many animals were maintained in the laboratory in order to augment our field observations. Copulating pairs could be found at almost any time of the year though they were numerous only in the summer and fall months. Beginning in June and continuing on through July and August mating pairs are encountered regularly and in large numbers. Only one or two pairs were observed as late as the first of November. This species, like the other cancroid crabs, copulated just after the molting of the female. Egg deposition begins for a few individuals as early as October, and individuals may be found carrying eggs on the pleopods as late as the early weeks in June. Our records would tend to indicate that most of the females extrude eggs by December or January, and that most eggs hatch by late March or early April. In the laboratory three females which extruded eggs prior to December 20 had completed the hatching process by March 6. Two of these females then extruded new, but small, clutches of eggs without first molting or copulating. However, it was impossible to maintain these females until the time of hatching, though the eggs appeared viable and in the process of development. Thus, it is not known if the female has sufficient stored sperm to fertilize a second brood, nor whether this is
typically carried out by females of this species. Ovaries removed from ovigerous females in March most frequently showed no development, though a few had some eggs apparently left from the previous brood. Cleaver (1949:79–80) states that May and June are the peak months for copulation in *C. magister* and that the majority of the females carry eggs between the first of November and the last of February. A check of this latter species by Cleaver on February 19, 1947, showed that 86.5% of the females had or were carrying eggs. Thus, there is a similarity in the timing and the procedure of the reproductive cycle of *C. magister* and *C. productus*. Both show a considerable lapse of time between copulation and egg deposition. The eggs of *C. productus* are bright orange when first deposited. These gradually become more brownish in color and become hyaline and gray by hatching time. Egg masses were not counted for this species.

**COPULATION**: Copulation of *C. productus* is similar to that described in this paper for *C. oregonensis* and by others (Churchill, 1918:105; MacKay, 1942:18; Cleaver, 1949:79–80; Knudsen, 1960:7), in that a courtship period precedes the molting of the female and copulation follows the process of molting. As discussed for *Hemigrapsus oregonensis* in this paper, there seems to be some attraction, such as the release of molting-hormones by the female, so that males may identify females that are about to molt. Unlike *Cancer magister* (Cleaver, 1949:80), pairs of *C. productus* do not separate following the act of copulation; rather, the male continues to protect the female for several days. A check of the female exuvium shows that the spermathecae are removed at the time of molting, as recorded by Cleaver. Unlike *C. oregonensis*, this species does not go into seclusion during the time of courting, but moves freely about at this time. Courting pairs are frequently seen up on pilings where the male may feed, or running across the sandy substrate. In the aquarium captive males tend to be polygamous, as is suggested by Cleaver for *C. magister*.

*Cancer gracilis*

**HABITAT**: For a discussion of the habitat of *C. gracilis* see *C. productus*. This species was encountered only in sympathy with *C. productus* when the former species was present in the intertidal zone. However, the habitats in which both species occur are quite sandy, and approach the extreme in sandiness for *C. productus*.

**FEEDING HABITS**: No analysis of stomach content was made for *C. gracilis*. This species was seen feeding in the identical situation with *C. productus*. Crabs were common both on the pilings, feeding on barnacles, and at common mess with *C. productus* feeding on fish detritus. From general appearances it would seem that this crab uses approximately the same food as *C. productus*.

**REPRODUCTIVE ACTIVITY**: Field records for *C. gracilis*, other than those of copulation and courtship, are almost totally wanting. Our laboratory records suggest that the reproductive cycle is about identical with that of *C. productus*. Females in the laboratory produced egg masses between the months of December and April. Whether or not a second brood is produced in nature is unknown, as only a few laboratory animals produced a second brood. However, the known second broods produced in the laboratory consisted of very few eggs as compared with the normal brood. The time of courtship and copulation coincides with that of *C. productus*.

**COPULATION**: During the summer months numerous pairs of *C. gracilis* were seen feeding under the pilings at Point Defiance. However, during the reproductive periods of the year pairs or individuals became less abundant and soon became absent from the intertidal fauna of those areas observed. From a few pairs isolated in the Point Defiance aquarium and from some field observations we have noted that the process of copulation and courtship is identical with that of *C. productus*. Courting pairs of *C. gracilis* were found amongst other noncourting individuals and would move about the substrate very freely. The larger size of this species may account for the fact that it needs little protection, as does *C. oregonensis*. Males were discovered carrying both hard-shelled and soft-shelled females. When the female of the pair was soft-shelled, most frequently the pair was in the act of copulation. Unlike *C. magister*, the males of this species protect the females after copulation.
FAMILY MAJIDAE

MOLTING: It has been suggested by Drach (1939:106-377) that the spider crab Maia squinado reaches what is known as a puberty molt, at which time no further molting occurs. At the time of the puberty molt crabs of the Majidae become sexually mature and then begin egg production. This is contrary to the other brachyuran families found in Puget Sound, for which molting continues after maturity.

In order to test Drach's theory for the Puget Sound majids a number of experiments and field observations were attempted. Animals were maintained in the laboratory for up to 9 months without any molting. Such experiments became unsatisfactory in time as feeding and overcrowding became problems in the aquaria. A female Pugettia producta was encountered on November 14, just after having completed molting, but the exuvium became lost before it was noted whether or not this was immature or mature. Several additional molts of this species and of other species of Puget Sound spider crabs were recorded, but in all cases these were either prepuberty molts or puberty molts and none demonstrated that molting occurs after the puberty molt. Likewise, no exuvia of mature females were ever located on the beaches, as were those for other families of crabs.

If there is a puberty molt and the female spider crab autotomizes a leg either prior to or following the puberty molt, then regeneration (or at least complete regeneration) would be impossible. With this thesis in mind, a series of experiments and field observations was begun where mature animals with partially regenerated limbs were collected and maintained in the laboratory, and additional specimens were brought into the laboratory and were forced to autotomize limbs. In no case did any of the partially regenerated limbs continue to develop when additional molts were lacking, and no other method of regeneration was used. Freshly autotomized appendages of mature individuals showed the primary stages of regeneration which consist of scabbing, but no papillae or subsequent growth occurred. Thus, one must conclude that adults with partially regenerated limbs completed this regeneration prior to the puberty molt, at which time the growth ceased.

Some inconclusive light was shed on this problem when specimens of P. producta were dissected. On one occasion a female which had recently completed hatching a brood of eggs died in the aquarium. This animal was dissected and it was noted that the spermatheca was completely empty but that the ovaries were extremely well developed and laden with "ripe" eggs. This demonstrated that a new reproductive cycle was in the making and suggested that a molt could occur at this time, as would be true for other families of crabs. However, no new integument was formed beneath the exoskeleton as can be seen in crabs about to molt. The old integument, moreover, was firmly attached to the exoskeleton, suggesting that no pre-molt metabolic activity was occurring. Numerous field dissections gave the same data.

A size differential found in sexually mature females of P. producta suggests either that the number of molts prior to the puberty molt is not consistent in all specimens, or that molting may continue after sexual maturity is reached. Another somewhat negative point is found in the encrusting organisms living as commensals on the carapace of Pugettia. The majority of the specimens bearing eggs have no encrusting organisms such as barnacles on the carapace, which suggests that these animals have recently molted. Whether or not this molt was the puberty molt is unknown. Some individuals, on the other hand, have barnacles which appear to be far larger than one-year old animals and suggest that they have been growing on the carapace for more than a year. This tends to rule out the fact that these individuals have molted in the recent past. Although all of these data are somewhat negative and could readily be ruled out by one positive datum, they strongly support the theory that spider crabs cease molting following sexual maturity.

Pugettia gracilis

HABITAT: The graceful kelp crab, Pugettia gracilis, ranges from the western extremity of the Aleutian Islands eastward and southward to Monterey Bay (Garth, 1958:196-197), and from the intertidal zone down to about 40 fathoms (Way, 1917:371). Way records it as being abundant everywhere in the Friday Har-
bor region in eel grass (Zostera marina), while Hart (1950:106) records it from kelp ribbons at Parry Bay. In the southern Puget Sound region the majority of our specimens are found attached to those pilings which were very heavily encrusted with barnacles and other fouling organisms, or clinging to similarly encrusted rocks under the Narrows Bridge. Less frequently were specimens taken from Zostera beds. Those individuals taken from Zostera were frequently smaller, immature animals. The requisites for the habitat of this animal seem to be an area where there is, first, abundant food, and second, some situation where the crab may get up off the bottom and thus be exposed to continuous currents. Probably the currents are necessary for the crab’s survival. It is interesting to note that Garth (1958:199) lists the specimens from the Hopkins Marine Station at Monterey Bay, California, as not being from the intertidal zone. The fact that this species occurs below the intertidal zone in the south, where temperatures closely approximate those temperatures of the northern intertidal zone, would indicate that temperature may be a southern limiting factor. For at levels below the intertidal zone in the south this species could find a suitable habitat and source of food and still enjoy a much colder range of temperatures. Like Pugettia producta this species also has the dactylae somewhat modified for holding on to kelp. This species may be more abundant in kelp than our records indicate, as our collecting in kelp was very limited.

**REPRODUCTIVE ACTIVITY:** P. gracilis was often encountered at the Tacoma Narrows and was occasionally found at Point Defiance, but seldom were more than just a few of these animals seen at any time. Thus, the total number of records for this species is too small to be of great significance. Garth (1958:199) cites collecting ovigerous females at Coos Bay, Oregon, when 14 of 16 specimens were with ova in late June, and in mid-July at Bodega Bay, California, in March and at Stewarts Point in November. In Puget Sound we have collected ovigerous females almost every other month throughout the entire year. During 4 of the 6 months in which no ovigerous females were encountered, only immature specimens were collected, and during 2 months, July and October, mature but nonovigerous specimens were observed. Specimens with very new dark purple eggs, intermediate reddish-brown eggs, or grayish-brown prehatch eggs could be found during almost any month of the year. Hatching was most frequently observed in May and June both in the laboratory and in the field. On the other hand, five out of eight specimens collected during the first week of August had very new dark purple eggs. It is not known whether one or two broods of eggs are produced annually.

**PRODUCTIVITY:** The eggs within the egg masses of five specimens were counted. The hepatic carapace width of these specimens ranged from 20 mm to 25 mm, and the number of eggs per brood range from 6,200 to 13,300, with the average being 10,500 per brood.

**COPULATION:** Accounts of copulation in the family Majidae seem to be absent in the literature. The secretive nature of the spider crabs would probably cause such a vital process to go unobserved in the field or laboratory. Probably copulation occurs while the crabs are on pilings and thus the chance for observation may be poor. Detailed observation of P. gracilis in copulation was possible on only three occasions.

The remarkable fact seems to be position assumed by the male and female, in that the male is oriented under the female with his ventral side upward. The only record of such a position is that of Hiatt (1948:199) for a grapsoid crab, Pachygrapsus crassipes, and accounts given in this paper for the two species of Hemigrapsus. It is quite possible that the Majidae may resemble the Grapsidae in respect to posture, and that the female-over-male position is more common in the Brachyura than the literature would suggest. The many descriptions for the cancroid crabs (Williamson, 1903:101; Hay, 1905:405; Churchill, 1918:105; and others), have fostered the general opinions that (1) crabs copulate in a male-over-female position, and (2) many species copulate in a soft-shell condition. With the more recent literature on crab natural history the general pattern of brachyuran copulation is becoming more well known.

P. gracilis was observed *in copulo* both in the Point Defiance laboratory and in the field. All of our observations were made in December and February, but the period of mating is probably not limited to those months for reasons discussed below. In the laboratory pairs were
observed under both lighted and darkened conditions. Our records indicate that time of day has no effect on time of copulation, but there is no clear proof of this. Field records were made only at night, while laboratory animals copulating in the day time may have been conditioned to artificial lighting.

In every case the pairs observed in the laboratory were on a level substrate, as the few rocks available to the crabs did not permit them to cling to a vertical surface. In nature all of the animals observed were either on vertical pilings or on vertical rock surfaces. This suggests that either a vertical or horizontal substrate is adequate, but that the vertical is probably used more often. In either case, the body position of copulating pairs is always horizontal. The process of the initiation of copulation was not seen. Pairs observed in nature used the last two pairs of walking legs to hold onto the vertical surface of the substrate, and the chela and first two pairs of walking legs to hold the opposite sex. In one case copulation continued for over an hour after observation began. A pair carefully removed in copulo from a piling, in such a way that they could not separate, revealed that the male abdomen is positioned under that of the female and that sperm is transferred by means of the first and second pleopods.

**Pugettia producta**

**HABITAT:** The kelp crab, *Pugettia producta*, is shown to have a range from British Columbia to Baja California by Garth (1958:188–189). I have seen this species in a multitude of different habitats ranging from open kelp beds off California to unprotected rocky coast, protected rocky coast, and into bays or estuaries. Baker (1912:100) states that at Laguna Beach, California, the young of the kelp crab are very common in tide pools clinging to "Fucus" and other brown algae, but mature specimens are only to be found in the kelp beds. Way (1917:370) found this crab abundant everywhere in the Friday Harbor region in eel grass, on kelp, and on the piles under docks, common to at least 40 fathoms. Other workers generally cite this species as living on kelp, on pilings, or in similar situations. In my experience this species not only uses a broad range of habitats but is seasonal in the micro-habitat that it occupies. On the open coast of California it was commonly found among the rocks or in the shorter species of kelp, such as *Egregia*, during the extreme winter period. In summer the adults migrated to the large floating kelp, leaving only the juveniles in the immediate intertidal zone, as described by Baker. In the Puget Sound area a similar phenomenon is observed in that this species becomes extremely abundant on pilings during the cold parts of winter. The kelp crab is absent from pilings during summer months when the floating kelp, *Nereocystis*, is fully grown and abundant. This crab is also found in summertime feeding amongst drifts of *Sargassum* on a smooth sandy substrate. Whether or not the kelp crab feeds in this manner during wintertime is not known. It is noteworthy, though, that the crabs disappear from pilings during summer months; where one will find a few specimens in summertime, he may find ten to fifteen in wintertime. The chief requirements for the habitat of this species seem to be abundant supplies of fresh water and of food. Being primarily a herbivore, it devours tremendous quantities of brown algae. Juveniles are most frequently found in *Zostera* beds, as cited by Way. Adults are occasionally found there also, but the marine grass does not support the weight of the adult and thus the animals seldom stay within this zone. *P. producta* shows a distinct preference for some type of structure which will enable it to climb up above the substrate, and pilings or the floating kelp are most frequently inhabited.

**FOOD AND FEEDING HABITS:** About 15 specimens of *P. producta* were examined to determine their food content. The material in the stomach consisted principally of plant tissue. Members of the brown algae are the primary source of food. Among the most common species of algae are *Fucus, Sargassum, Nereocystis*, and, on occasion, *Ectocarpus*. Small amounts of red algae resembling *Gigartina* spp. and some species of filamentous red algae were also noted. During the extremes of winter, when most of the specimens are found on pilings, the diet of this crab seems to change markedly. In the field large specimens of *Pugettia producta* were engaged in breaking barnacle shells and consuming the tissue inside
of the shell. Stomachs examined during this period contained large quantities of barnacle fragments, fragments of the common mussel, *Mytilus edulis*, and also small quantities of hydroids and bryozoans. Apparently this crab becomes quite carnivorous during periods when the large brown algae are absent from its typical habitat.

During feeding operations this species uses the walking legs to hold on to the algae and the chelaped s to cut bits of algae and transfer them to the mouth parts. Large fragments are swallowed whole and are later ground up by the gastric mill within the stomach. When feeding on barnacles the chelaped s are again used. The movable finger is inserted into the open edge of the barnacle and the shell is pried outward, thus breaking the side of the barnacle's case. The shell then becomes dislodged from the piling and the tissue is devoured. Presumably small mussels are broken in a similar manner. In the laboratory one could not help but notice the keen visual awareness of this species as food was placed in the aquarium. Algae and cut fish alike were caught in mid-water as they sank past the crabs. The slightest movement of food seemed to attract the attention of crabs quite some distance away in the tanks. Cut fish that was secretly placed in the tank, however, would go unnoticed for some time. This suggests that sight and the tactile senses are most highly developed for feeding, and that the chemical sense is not very extensively used.

**Reproductive activity:** Garth (1958:192), in his discussion of breeding of *P. producta*, states that gravid females were commonly found at Coos Bay, Oregon, in June and July; in Sonoma County, northern California, from October to February; and at Dillon Beach, Marin County, in August and November. In southern California females with ova have been taken from November to February and in lower California in January, March, and June. In our own collecting, field encounter of this species ranged from a few up to about 18 females each month, except during May, September, and October, when we were unable to locate any females of this species. Females carrying eggs were found during every month of the year with the exceptions noted above. Moreover, except in November and December, all females examined each month had eggs. This species seems to be omni-seasonal in its egg production, but there is a trend of egg deposition beginning in November and December and becoming more apparent in the month of January. This is followed by an embryonic development during March, April, and May. Some extremely new eggs are found again in April, July, and August with hatching in August, February, and April. Since none of the field animals observed from month to month were tagged, it would be conjecture to say whether two broods of eggs are produced annually. Laboratory data seem to indicate that the development of a single brood requires the greater part of the year.

**Productivity:** Eggs within the egg masses of 11 individuals were counted to determine the size of an average brood. The hepatic carapace width of these specimens ranged from 41 mm to 56 mm; and the number of eggs per mass varied from 34,000 to 84,000, with an average of 61,000 eggs per brood. New eggs are bright orange and progress to a very deep red before part of the embryo becomes hyaline and deep purple. At this time the eyes begin to show and there is a reduction in the amount of purple material within the egg case. The egg mass appears somewhat grayish-purple at time of hatching, due to the hyaline interior, eye spots, and purple pigmentation.

**Copulation:** At no time was the process of courtship and/or copulation observed for *P. producta*. The process is probably similar to that as described for *P. gracilis*. On several occasions in the field we observed what appeared to be the onset of copulation: pairs of *Pugettia producta* were seen on pilings, going through a wrestling motion which resembled the beginning of copulation. The animals were situated with one individual above the other, each facing the other. Repeatedly, as we continued to observe this process, the lowering tide would interrupt the activity. The pair would then move farther down on the piling and resume this "grappling" motion, but before copulation could begin the tide would again interrupt. The pair was finally forced to leave the piling and move out on the sandy substrate. These animals probably copulate either on pilings or on the large bladder kelp at night, but are probably more secretive about it than other species.
Oregonia gracilis  

**HABITAT:** The decorator crab, *Oregonia gracilis*, ranges from Bristol Bay, Alaska, to Monterey Bay, California, and from the intertidal zone down to depths of 212 fathoms (collected by the Albatross, recorded by Rathbun, 1894: 59). Way (1917:369) records that this animal is quite abundant at all depths down to 55 fathoms, or possibly greater, at Friday Harbor. She cites such areas as the pilings at the Friday Harbor dock, eel grass off Browns Island, and along various beaches in the San Juan Island chain. While the general nature of the habitat in southern Puget Sound seems to be similar to that recorded by Way, the crabs can not be considered as abundant. Adult forms were scarce indeed, and considerable effort was required to find even one or two individuals during the winter season on the pilings. The fact that these crabs are so highly decorated and that they choose to live amongst algae and invertebrate-encrusted pilings may mean that their presence was simply less noticeable. Adults were found chiefly on pilings or on sea walls, while juveniles were more frequently found on Zostera. Due to the lack of individuals our records are extremely weak for this species and we have made no all-out attempt to study its reproductive cycle. We will present those data that are available to make the record as complete as possible.

**REPRODUCTIVE ACTIVITY:** Data concerning reproductive activity for *O. gracilis* seem to be scarce and incomplete. Rathbun (1925:73-78) records ovigerous females from St. George Island, Pribilof Islands, in May and September; from Attu Island and Petral Bank, Aleutian Islands, in June; for Cordova and Yes Bay, south-eastern Alaska, in June and August, respectively; and from Comox, Vancouver Island, British Columbia, in July. Garth (1958:139) records as gravid 25 of 40 females taken in late July, and 20 of 40 females taken in early August in the San Juan Strait—Puget Sound region. One specimen collected at Point Defiance in October, three collected there in December, and one collected in February were ovigerous. The eggs for these months were of a new, bright red nature. The summertime records of both Rathbun and Garth should not be interpreted as meaning that females are most frequently ovigerous during that season for, by consulting Rathbun's many station records, one may see that all occurred during the late spring and summer months and none were made between October and April. Those few specimens of *O. gracilis* maintained at the Point Defiance aquarium behaved like the other species of spider crabs cited above: that is, eggs were carried over the major part of the year and development was quite slow, with hatching occurring after irregular intervals.

**PRODUCTIVITY:** Three specimens, sacrificed for ova counts, ranged in carapace width from 17 mm up to 25 mm. The number of eggs ranged from 2,800 up to 17,400, with an average of 9,200 eggs per brood. Data are too few to suggest that only one brood is produced per year, although this, is probably the case. Observations of other reproductive activity such as courtship, copulation, and egg deposition are wanting.

Scyra acutifrons  

**HABITAT:** The sharp-nosed crab, *Scyra acutifrons*, is recorded from Kodiak Island, Alaska, to San Diego, California, and from the intertidal zone down to 40 fathoms (Rathbun, 1910: 175; 1925:196), and down to 55 fathoms by Way (1917:371). The writer recalls having taken this species north of the published range in the Cook Inlet area in Katchemac Bay, while doing king crab research in the summers of 1957 and 1958.

This species was taken only in two situations in southern Puget Sound: first, on pilings where barnacles were extremely numerous, and, second, on rocks in areas where strong currents prevailed during changing of the tide. Way suggests that this species is not abundant, and this was surely our own experience. We did not find it within *Zostera* beds, and only on one occasion was it found moving across an open sandy substrate. The crabs are often decorated with bits of sponge, hydroids or other invertebrates, or bits of algae, and generally match the surroundings of pilings or rocks very closely. Like the other species of spider crabs, *Scyra* attains a position with the anterior end pointing downward and thus is very inconspicuous when hiding amongst barnacles on a piling. Frequently the only sign that would allow one to detect
the crab was the tiny amount of coloring between the pinching fingers of the chelae. From our collecting and our field impressions we would say that this species is definitely more abundant in December and January than in the spring and summer months. However, it is also true that during these cold-water months the algae are practically absent from the pilings. Thus this crab is probably more readily observed in the absence of algae or other invertebrates.

**REPRODUCTIVE ACTIVITY:** The nature of the hidden places used by *S. acutifrons* has made observation of reproductive activity, other than the possession of eggs by females, difficult to observe. Garth (1958:253) records collecting ovigerous females off southern California in every month but March, July, and September; and Way (1917:371) records taking two ovigerous females in July at Friday Harbor, Washington. Ovigerous females were collected or observed during every month except April and May and September and October, when no specimens of *Scyra* were collected at all. There is no doubt that ovigerous females do occur during these “barren” months, since females with very new eggs were found just prior to these times. Moreover, females with extremely new eggs were collected during all of those months cited above and hatching was witnessed in the months of December and January, and June, July, and August. Results of 2 months of collecting will give an idea of the egg development encountered during different months of the year. During July, 12 of 17 females were ovigerous and, of the 12, 8 had extremely new eggs, one was of intermediate development showing eyes, and 3 were in the hatching stage. In December, 29 of 53 were ovigerous, with 25 having extremely new eggs, 3 well-advanced eggs, and one being in the hatching condition. Apparently there is no well-defined season of reproduction that governs periods of quiescence and periods of reproduction, although there is some suggestion that hatching may be confined to June through August and December and January.

**PRODUCTIVITY:** Eggs in egg masses of 12 specimens of *Scyra* were counted. These specimens ranged from 19.5 mm to 30 mm in carapace width, and the egg mass size ranged from 2,700 eggs to 16,300 eggs, with an average of 8,600 eggs per female per brood. Dissections show that oogenesis occurs while the female has ova attached to the pleopods and thus a second brood may be produced very shortly after the current brood has hatched.

**FAMILY PORCELLANIDAE**

*Petrolisthes eriomerus*

**HABITAT:** *Petrolisthes eriomerus* may be found in abundance in certain localities within the southern Puget Sound area. It was collected in large numbers in the Tacoma Narrows and at the Port Orchard collecting site. Smaller numbers were collected and observed at the eastern end of Titlow Beach and few specimens were observed at Point Defiance. Workers who have described the habitat of this animal consistently mention that they are found under rocks in the intertidal zone (Way, 1917:350; Hart, 1930:105). Haig (1960:76) states that this crab occurs under stones in the lower part of the intertidal zone in the northern part of the range, south to San Luis Obispo County, California. Both Way and Haig cite some deep collecting records for this species, but these records are predominantly for the southern extreme of the range, suggesting that isothermic temperature may be a partial key to the habitat of this crab.

One habitat characteristic must always be present when these animals are to be found: there must be some current, however strong, which will bathe the habitat and will supply it with fresh plankton which is the chief source of food for this species. In all cases the number of specimens seemed proportional to the swiftness of the current. The effect of a swift current on the habitat may be manifold: water is removed, food is carried into the habitat, and excessive debris is removed from the undersides of rocks. *P. eriomerus* is commonly seen clinging to the underside of rocks with its ventral side up towards the rock surface. When rocks are turned over numerous specimens are found clinging to the bottom. This species typically lives and feeds in this inverted position, using the tarsal hooks for holding onto rocks, or for locomotion. Without the protection of rocks these crabs right themselves and walk about on a sandy substrate in a normal manner. When these animals are dislodged and dropped into water they use the abdomen for locomotion.
They swim by trailing their front chelae and flapping their abdomens, thus propelling themselves backward through the water.

FEEDING HABITS: More than 20 specimens of *P. eriomerus* were examined microscopically to determine the nature of the stomach content. As all of the contents seemed quite similar, detailed notes were kept only for 10 individuals. The majority of stomachs contained almost pure masses of diatoms. Only one contained sessile diatoms found growing on the rocks within the *Petrolistes* habitat. The others contained diatoms of a pelagic form. Two or three had extremely large fragments (up to 1 mm long) of some species of green algae. From the gut content alone it seems that this animal is predominantly a filter feeder, though evidence shows that some cropping of sessile algae is carried out also. Observations in the field and in the aquarium show that this species spends most of its time with its ventral surface held against the bottom side of a rock and with the face showing at the edge of the rock where water currents are continuously being sampled. The movement of the mouth parts suggests that this animal filters its food from the water. Laboratory animals, for the most part, refused meat fragments offered to them. This species, then, is thought to stay within the confines of the rock under which it is hiding, and to feed at the periphery of this rock by filtering or by cropping algae growing within chelae reach.

SYNOPSIS OF REPRODUCTIVE ACTIVITY: Figure 7 shows that oogenesis probably begins in the month of October and continues until the time of ovulation, fertilization, and egg deposition. We assume that copulation probably takes place in January. Egg deposition begins in the early part of February and increases rapidly until the early weeks of April, when the majority of females have produced their first brood of eggs. Hatching probably begins around the first of May for the first brood and continues into the first week of August. Egg deposition for brood number two begins about the middle of May and reaches its peak about the early part of August. At this time hatching of brood number two begins and continues into early October. Referring to the physical conditions represented on Figure 7, one could make the suppositions that copulation begins shortly after the shift
from decreasing photo-periods to that of increasing photo-periods; and that there is some correlation between deposition of brood number one and increase in water surface temperature. However, these suppositions need a considerable amount of research to test their validity.

**COPULATION:** No data as to the time, method, or frequency of copulation were obtained.

**OÖGENESIS AND EGG DEPOSITION:** The exact time at which oögenesis begins is not known, but a projected curve suggests that it begins in October. By early November some of the ovas show considerable development of the ova, while others have ova ranging around 0.015 mm in size. However, by the end of November those few specimens examined had ova averaging about 0.35 mm in diameter and bearing a yellow-orange pigment. By the end of January most of the ova measured about $0.68 \times 0.60$ mm. Throughout February there is a very slight increase in size until deposition occurs. Figure 7 shows the season of egg deposition for both the first and second broods as far as our data will permit. From the latter part of February until mid-April egg deposition occurs rapidly but then begins to taper off until the middle of May, when over 97% of the females have eggs. Hatching begins toward the end of May and continues until the first week of August, when the last of brood number one hatches. Brood number two begins before the first of June and egg deposition is rapid until the early part of August, when from 74 to 80% of the females carry new eggs. From here a theoretical curve would show that hatching follows very quickly and that brood number two probably is completed by the end of September or the early part of October. It is possible, therefore, that oögenesis may begin again while brood number two is still carried on the pleopods.

**PRODUCTIVITY:** The number of eggs carried by 37 different females was determined. Carapace length ranged from 6.9 mm to 13.6 mm. Broods ranged from only 10 eggs in the smallest individual to 1,580 in the largest specimen. The average count for 37 individuals was 621 per brood. If each female produced two broods per year, a total of about 1,250 would be produced. Considering that only up to 80% of the females produce a second brood, a more accurate annual production for all females would be about 1,100 eggs per year. The extremely large size of the egg of this species (about 0.75–0.80 mm) demonstrates that a larger larval form is produced, which theoretically could better fend for itself and thus lessen the danger of predation and starvation.

**Pachycheles rudis**

**HABITAT:** The habitat of *Pachycheles rudis* is below the minus-zero tide level where water currents are strong, in such places as are listed by Haig (1960:172): under stones, the holdfasts of kelp, in sponge cavities, among rock oysters and mussels, in tunicate beds, and in the discarded burrows of dead burrowing clams. MacGinitie (1935:712) states that males and females live together in pairs. This species was taken on occasion under rocks with *Petrolisthes eriomerus* at the Tacoma Narrows. It was found in great abundance, however, at Port Orchard, in the situations cited by Haig. Most frequently pairs were found within the empty burrows of rock-burrowing clams (*Petricola*). The size of the animals within the burrows often seemed much greater than the outer aperture of the burrow. When the burrows were opened with a geological pick larger specimens seemed unable to escape by means of the normal aperture, or else were reluctant to do so. It is suggested that young pairs occupy these burrows, feed on plankton and grow, reproduce, and continue their existence until they have reached a size much greater than the tapered burrow opening. Specimens brought to the Point Defiance laboratory would occupy any small cavity provided, such as small vials, cones made out of screen wire, and empty shells. Animals removed from these artificial chambers again proved to be in pairs. In the laboratory this species was extremely sensitive to the oxygen content of the water. If the running sea water was shut off within the 30-gal tanks for a period of several hours, death occurred, and increased as time progressed. This species was more sensitive in this respect than the other crab-like Anomura we worked with, and the Anomura in turn proved to be more sensitive than the Brachyura.

**REPRODUCTIVE ACTIVITY:** Our field records for *P. rudis* from the middle of December through August show that between 75 and 100%
of the females were reproductively active. Egg deposition begins in the middle of December and continues into the spring and early summer. Without a doubt, developing embryos are carried long after the middle of August, although we have no observations for this species from that time on. Data suggest that two or three broods of eggs may be produced each season. The peak of hatching of the first brood is evident in April and May, though it may begin in the last week of March in some individuals. Females carry new, orange-colored eggs or "prehatch" eggs (gray and showing eyes) throughout April and May. A study of these animals in the first week of May shows that: (1) almost 100% of the females with prehatch eggs have ovaries swollen with large, bright orange ova which will produce the second brood of offspring; (2) about 50% of the females with new orange eggs attached to the pleopods have ovaries still engorged with bright orange ova which may represent brood two or three; and (3) about 50% of the females with new eggs attached to the pleopods have ovaries holding a few to about a half the normal number of ova in the bright orange, prefertilized state. These data may mean that either some females produce a first or late winter-to-spring brood, a second or spring brood, and a third or summer brood for a total of three broods (usually), or that females produce two broods. In the latter case, some of them would begin with a winter–spring brood and others would begin in the spring, thus giving a staggered timing and a seeming third brood. Our data show all of the females to be ovigerous in late December, thus suggesting three broods, but these data are too few to be more than suggestive. Eight of 16 females encountered during the first week of August had eggs which were classified "almost prehatch," but belonging to the second or new brood, while the remainder of the specimens had extremely new eggs attached to the pleopods. One field datum is of interest here. A single female bearing extremely new eggs was found to have a very soft exoskeleton and had obviously just molted. This suggests that the females may molt prior to extruding the new brood.

PRODUCTIVITY: Fourteen females were preserved and the eggs counted. The carapace width ranged from 12.0 to 16.8 mm, and the number of eggs ranged from 210 to 2,130. The average was 928 eggs per brood. This latter figure is misleading, in one sense, as to the reproductive capacity of P. rudis. Of the females representing all size classes, 43% had large clutches of eggs (from 1,175 to 2,130), with an average of 1,555 eggs per female. The remaining 57% had small clutches of eggs (from 210 to 625), with an average of 410 eggs per female. Of the large-brood females, half were with new eggs and half with prehatch eggs attached to the pleopods, while all had ovaries completely swollen with bright orange ova. Of the small brood females (87% with new eggs on the pleopods), 63% had ovaries with some large orange ova, while 37% had ovaries filled with large orange ova. These data support the idea that three broods may be produced by this species each year, but suggest that not all broods are equally large that is, roughly proportional to carapace size, as is true for the Grapsidae and Xanthidae, etc. Rather, any one of the possible three broods may be small or large.

**FAMILY LITHODIDAE**

*Haplogaster mertensii*

**HABITAT:** *Haplogaster* is not considered to be at all common in the southern Puget Sound area. It was collected only at one locality, the Tacoma Narrows. There, in the swift moving currents, this crab is located under rocks which afford good protection, but provide considerably more room for moving about than would be required by *Petrolisthes eriomerus*. Although in its ecological make-up the Port Orchard collecting site seems to be similar to the Tacoma Narrows, this crab is not found there. These animals were never collected in abundance, eight or nine being a large number for any one trip. With very few exceptions all of the specimens were released at the time of collecting to insure a continuous population for study. It is possible that currents are necessary in this habitat to clean debris from under rocks and thus insure ample space, and to bring food and oxygen to this crab. Experimentation has not been made as to oxygen requirements of this animal, but it seems possible that its restricted distribution may be governed by any of the above factors, not least of all oxygen.
FEEDING HABITS: Whenever it was necessary to sacrifice a specimen of *Haplogaster*, the stomach contents were analyzed (this crab is sufficiently rare in the southern Puget Sound area to justify an extremely conservative use of specimens). Three animals were examined. In the stomach contents fragments of some species of brown algae were fairly common, along with some monofilamentous red algae, and fragments of what appeared to be *Ulva* or some other green algae. One animal contained a large quantity of single diatoms, most of these being extremely small. However, in the laboratory when animals were introduced into the tanks they immediately attacked barnacles attached to the rocks and fed on these by twisting the shell of the barnacle with the chelae and eventually crushing the barnacle. Apparently this species is omnivorous and feeds both by filtering, by gleaning algae attached to rocks, and by breaking barnacle shells to obtain animal tissue. It is not known whether or not this species captures motile forms.

REPRODUCTIVE ACTIVITY: The reproductive activity of *H. mertensii* remains a mystery for the most part, because of its scarcity in southern Puget Sound waters and the difficulty of feeding and maintaining it under proper environmental conditions over long periods of time in the laboratory. The few data obtained are of value, however. With only one exception, every female encountered in the field during the latter part of November, December, January, and April had developing embryos attached to the pleopods (tides during February and March were unsuitable for obtaining *Haplogaster*). Eyes within the egg shell became evident during the month of January, and hatching occurred in the laboratory and in the field during the middle part of April. Females observed during June and July were without eggs attached to the pleopods, and no further observations were made until the latter part of November and early part of December, when females again carried eggs.

PRODUCTIVITY: Three females were preserved and their eggs were counted. The carapace width and the number of eggs borne by these specimens are as follows: (1) carapace 15.6 mm, 600 eggs; (2) carapace 18.0 mm, 2,076 eggs; (3) carapace 19.1 mm, 2,070 eggs.

REFERENCES


Some Pearlﬁshes from Guam, with Notes on Their Ecology

C. Lavett Smith

ABSTRACT: From October, 1960, to July, 1961, 230 specimens of pearlﬁshes were collected on the fringing reefs of Guam. Four forms are represented and their distinguishing features are discussed. These specimens were taken from four species of holothurians and from the armless starﬁsh, Culcita novaguineae. Carapus mourlani was found only in Culcita; the other three occurred in two or more hosts. Thelenota ananas, Stichopus chloronotus, and an unidentified Holothuria contained only one species each, but Holothuria argus served as host of three pearlﬁsh species. Sea cucumbers that produce adhesive threads as well as those that do not were utilized as hosts. Over 100 specimens of Holothuria atra were opened without ﬁnding a single pearlﬁsh. Although this species has been reported as a host, it is probably not a preferred one.

The most common species is Carapus homei, its usual host is Stichopus chloronotus. Tenuis larvae were collected from October through February. Repeated collections in the same area of Tumon Bay indicated that there was a decrease in the infestation rate after February. C. homei probably spawns in late summer, and the larvae assume the inquiline habit during the fall and winter months. Small samples from other parts of the island indicate that infestation rates vary with the locality.

It is unusual to ﬁnd more than one pearlﬁsh in a single host, and the ﬁsh are not conﬁned to the respiratory trees but are often found free in the body cavity. During the period when the tenuis larvae are present C. homei often feeds on the larvae of its own species, perhaps indicating that there is competition for hosts. This could account for the infrequent occurrence of more than one ﬁsh per host. Carapus homei also eats shrimp. Encheliophis gracilis, however, seems to feed on the gonads of its host. C. homei leaves the host at night and on four occasions was seen some distance from any probable hosts.

The form called Carapus mourlani is structurally very similar to C. homei but differs in having superficial melanophores. Since mourlani occurs only in Culcita and homei never does, there is a possibility that the observed differences are due to the effects of the host. Until this can be demonstrated experimentally it seems desirable to retain the name mourlani.

IT IS WELL KNOWN that some pearlﬁshes (family Carapidae) dwell within the bodies of echinoderms and other invertebrates, although few of the recognized species have been studied in detail. Arnold (1956) revised the family and thoroughly surveyed the literature but some nomenclatural problems remain, owing to the unavailability of the types of certain nominal forms. Schultz (1960:393) has emphasized the need for studies of series of specimens from various hosts “... in order to furnish sufficient
information on habits and characters for proper identification of species.”

Much of the difficulty in identifying pearlfishes lies in the fact that they undergo dramatic metamorphoses during their life history. Although the life histories of most pearlfishes are unknown, it is generally assumed that they are similar to that of Carapus acus (Brunnich), which has been studied in detail by Emery (1880) and others. The floating eggs hatch into pelagic larvae characterized by a caudal filament (Parr, 1927:133) and a remarkable dorsal appendage, the vexillum. At the end of the first (vexillifer) stage, these appendages are lost and the larva, now called a tenuis, assumes the inquiline habit. The tenuis is elongate with short rounded pectoral fins and has the anus at the rear of the body cavity. As the pearlfish transforms into its definitive form, here called the adult, the pectoral becomes longer, the anus moves forward, and there are marked changes in body proportions accompanied by a drastic reduction in total length. Thus, at some sizes, a given fish may be in the vexillifer or early tenuis stage, the late tenuis, or the adult stage. (See Arnold, 1956: fig. 1, and Fig. 2 of the present discussion.) Several specimens collected in Guam that seemed at first to represent a distinct species were found to be the late tenuis stages of Carapus homei.

In October, 1960, I found pearlfishes inhabiting the holothurian Stichopus chloronotus Brandt in certain areas of the fringing reefs of Guam. Periodic collections of this and other echinoderms until July, 1961, yielded 250 specimens from 567 possible hosts. Four species of carapids were represented as follows (numbers and sizes in parentheses):

**Encheliophis gracilis**
(Bleeker) 
(15, 167–220 mm)

**Carapus homei**
(Richardson) 
(208, 68–197 mm)

**Carapus mourlani** (Petit) 
(5, 74–94 mm)

**Carapus parvipinnis**
(Kaup) 
(2, 63–238 mm)

Schultz (1960:392) reported *Encheliophis vermiculatus* Müller from Guam, but since I have not collected it, it will be omitted in the following discussion.

**NOMENCLATURE**

The form referred to here as *Carapus mourlani* was considered by Arnold (1956:274) to be the same as *C. homei*. In structural features it seems to be nearly identical with *homei*, but it differs in having superficial melanophores on the head and body and it lives in the starfish *Calcita novaguineae* Müller and Troschel instead of in holothurians. If the differences are due to the effects of the different hosts these forms may be the same species, although there is still the possibility that they are reproductively isolated through active host selection. It is perhaps significant that only the *mourlani* form seems to occur in Hawaiian waters; however this could be due to the scarcity of suitable holothurian hosts. For the moment it seems preferable to follow Schultz (1960:393) in recognizing two species, although he used the name *mourlani* with some hesitation since he did not see the type which came from Madagascar. The nomenclature of other species is that of Arnold (1956).

It is usually stated that carapids have no pelvic girdles, but alizarin staining reveals the presence of small rodlike bones between the lower ends of the cleithra. These resemble the pelvic bones of *Dinematicithys* (Gosline, 1960: fig. 3b) except that there are no pelvic fins. Alizarin staining also reveals a row of deeply imbedded plaques along the lateral line. These seem to be vestigial scales and are found in *Encheliophis gracilis*, *Carapus mourlani*, *C. homei*, and in a slightly different form in *C. parvipinnis*.

The five species reported from Guam can be distinguished by means of the following key and the features summarized in Table 1.

**HOSTS**

Pearlfishes were found in four species of holothurians and in the pillow starfish, *Calcita novaguineae*. Occasional sampling of nine other species of holothurians revealed no inquilines but the numbers sampled (except *Holothuria atra*, see below) were small and low incidences could have been missed. The numbers of hosts examined and inquilines found are summarized in Table 2.
KEY TO THE PEARLFISHES OF GUAM

A. Maxilla adnate to the suborbital................................. *Encheliophis* B
   Maxilla not adnate to the suborbital; separated from it by a deep groove...............Carapus C

B. Pectoral fins absent..............................................*Encheliophis* vermicularis
   Pectoral fins present............................................*Encheliophis* gracilis

C. Body everywhere covered with fine punctuations, each a single melanophore. These are
   in several layers and are present in the skin covering the eye. Pectoral fins reduced,
   almost vestigial, less than 1/3 head length........................................Carapus parvipinnis
   Melanophores not as above. Pectoral well-developed, more than 1/2 the head length.........D

D. Body without superficial melanophores, although the meninges and peritoneum are pig-
   mented and there is a row of deep melanophores along the base of the anal fin and on
   the back of the skull, the nasal capsule, the lower and upper jaws. There are usually
   one or two conspicuous melanophores near the upper end of the ceratohyal........Carapus homei
   
Body with definite but sparse superficial melanophores in addition to those of the meninges
   and the peritoneum. Melanophores of the head not as above.......................Carapus mourlani

TABLE 1
DISTINGUISHING CHARACTERISTICS OF FOUR SPECIES OF PEARLFISHES FROM GUAM

<table>
<thead>
<tr>
<th>CHARACTER</th>
<th><em>Encheliophis</em> gracilis</th>
<th><em>Carapus</em> parvipinnis</th>
<th><em>Carapus</em> homei</th>
<th><em>Carapus</em> mourlani</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maxillary bone</td>
<td>adnate</td>
<td>free</td>
<td>free</td>
<td>free</td>
</tr>
<tr>
<td>Eye</td>
<td>large</td>
<td>tiny</td>
<td>moderate</td>
<td>moderate</td>
</tr>
<tr>
<td>Pectoral fins</td>
<td>large, 1/3 head</td>
<td>tiny, 1/4-1/3 head</td>
<td>large, 1/2 head</td>
<td>large, about 1/2 head</td>
</tr>
<tr>
<td>Reverted lower lip</td>
<td>absent</td>
<td>present</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>Gill membranes</td>
<td>broadly united</td>
<td>slightly united</td>
<td>slightly united</td>
<td>slightly united</td>
</tr>
<tr>
<td>Gill opening extends</td>
<td>no</td>
<td>yes</td>
<td>yes</td>
<td>yes</td>
</tr>
<tr>
<td>above pectoral base</td>
<td></td>
<td>terete</td>
<td>compressed</td>
<td>compressed</td>
</tr>
<tr>
<td>Body shape</td>
<td></td>
<td>present, several layers</td>
<td>present, 1 layer</td>
<td>present, 1 layer</td>
</tr>
<tr>
<td>Superficial melanophores</td>
<td>no</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td>Countershading</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Head pigmentation:</td>
<td></td>
<td></td>
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<tr>
<td>cornea</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>nasal capsule</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>occiput</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>lower jaw</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ceratohyal</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Teeth on jaws</td>
<td>1 row</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Host</td>
<td>Holothurians</td>
<td>Holothurians</td>
<td>Holothurians</td>
<td>Holothurians</td>
</tr>
</tbody>
</table>

It is of interest that only *Carapus mourlani* enjoyed an exclusive relationship with its host. All
of the other three species occurred in two or more hosts. Perhaps this indicates that the
utilization of a starfish as a host is a recent development and only this form has been able
to make the necessary physiological adjustments. Other aspects of this relationship will be dis-
cussed later.

*Stichopus chloronotus* Brandt probably serves normally as host of only *Carapus homei*. The
single specimen of *Encheliophis* found in this species could have come from a *Holothuria argus* Jaeger that had been placed in the same container with the *Stichopus*. There is no doubt,
however, that *H. argus* serves as host to three species (*E. gracilis*, *C. homei*, and *C. parvipinnis*) since some of the collections contained only this host.

Holothuria sp. (a stout-bodied, thread produ-
cing, burrowing form, whitish in color with
two broad brownish transverse bands on the
Pearlfishes from Guam—Smith

TABLE 2
HOST SPECIFICITY IN SOME GUAM PEARLFISHES

<table>
<thead>
<tr>
<th>INQUILINE</th>
<th>N</th>
<th>Stichopus chloronotus</th>
<th>Thelenota ananas</th>
<th>Hol. argus</th>
<th>Hol. species</th>
<th>Calcita novaguineae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Encheliophis gracilis</td>
<td>15</td>
<td>1</td>
<td>—</td>
<td>12</td>
<td>2</td>
<td>—</td>
</tr>
<tr>
<td>Carapus parvipinnis</td>
<td>2</td>
<td>—</td>
<td>1</td>
<td>1</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Carapus homei</td>
<td>208</td>
<td>187</td>
<td>—</td>
<td>21</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Carapus moulani</td>
<td>5</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>5</td>
<td>—</td>
</tr>
<tr>
<td>None</td>
<td>—</td>
<td>196</td>
<td>0</td>
<td>17</td>
<td>17</td>
<td>9</td>
</tr>
<tr>
<td>Total</td>
<td>230</td>
<td>384</td>
<td>1</td>
<td>51</td>
<td>19</td>
<td>14</td>
</tr>
</tbody>
</table>

dorsal surface) harbored only *Encheliophis gracilis*. *Thelenota ananas* (Jaeger) contained only *Carapus parvipinnis*, although in the latter case only one specimen was examined. Both of these hosts have habits that may impose limits on the species of inquilines inhabiting them; *Thelenota* lives in deeper water off the edge of the reef and the *Holothuria* burrows in sandy areas of the moat.

*Holothuria atra* has been reported as a pearlfish host but it seems to be, at best, a second choice. In Tumon Bay, Guam, I examined 107 *atra* without finding any pearlfishes, although more than 80% of the *Stichopus chloronotus* from the same part of the bay contained *Carapus homei*. There is some difference in the habitats of these two holothurians; *atra* is most abundant in quiet, shallow, sandy parts of the moat, whereas *Stichopus* lives on harder bottom near the edge of the reef where there is a good flow of fresh sea water. The ranges of the two overlap, however, and I have observed *C. homei* at night in places where *atra* was more common than *Stichopus*. The suggestion that *H. atra* is not a preferred host is supported by Bonham's statement (1960:255) that no pearlfishes were found in several hundred *atra* from the Marshall Islands, although there was a *Carapus homei* in the single *Stichopus* he examined. Strasburg (1961:479) also reported a low incidence of *Encheliophis gracilis* in *H. atra* from Hawaii (one pearlfish in 114 *atra* examined).

The ability of some holothurians to produce adhesive threads when molested might be pos-
finding as many as five *Carapus (bermudensis)* in a single holothurian host in the Bahamas, but I have never seen more than two in an individual host. Moreover, the total number of inquilines never exceeded the total number of hosts in any one collection. It is possible, then, that some of the few "twins" observed may have been postcapture transfers.

**SEASONAL VARIATIONS**

Repeated collections in Tumon Bay indicate that there is a decrease in rate of infestation from November to June (Table 3). It is suggested that this is not due to sampling error alone, because only the collections made from November to February contained tenuis larvae. This would seem to indicate that the tenuis enter the host during the late fall and winter months and at that time there is a high rate of infestation. As the season progresses there is loss through mortality and the incidence decreases. It would be of interest to follow this through several complete cycles to obtain data on recruitment and mortality rates.

There are also different rates of infestation in different areas of the reefs (Table 4). This variation is not correlated with the abundance of the hosts because all areas have approximately the same density of hosts except Asan. The Asan area is peculiar in that there is a very strong flow of water over the edge of the reef and a dense population of *Stichopus chloronotus*. Aronson and Mosher (1951:489) also reported different levels of pearlfish infestation in different parts of the Bimini harbour.

**ACTIVITY OUTSIDE OF THE HOST**

It has been suggested that some pearlfishes never leave the host unless it eviscerates, but this is certainly not true of *Carapus homei* or *Encheliophis gracilis*. *C. homei* seems to leave the host regularly during the night and on four occasions I observed free swimming individuals between 9 and 11 P.M. One of these was taken in a commercial fisherman's beach seine; the others were seen hovering about 18 inches above the bottom in water 3 or 4 ft deep. The fish, observed as I swam along with an underwater flashlight and a face mask, remained motionless until I came within a foot or two of them. I was able to catch one in a hand net; the others escaped. In neither of the latter cases was there a *Stichopus* host nearby and my efforts to chase one into a host were unsuccessful.
TABLE 3
Seasonal Variation in Rates of Infestation of Tumon Bay Stichopus chloronotus
(All hosts were collected in the same part of the bay.)

<table>
<thead>
<tr>
<th>MONTH</th>
<th>NUMBER OF Stichopus</th>
<th>% WITH Carapus homei</th>
</tr>
</thead>
<tbody>
<tr>
<td>November 1960</td>
<td>24</td>
<td>88</td>
</tr>
<tr>
<td>December 1960</td>
<td>102</td>
<td>84</td>
</tr>
<tr>
<td>January 1961</td>
<td>14</td>
<td>71</td>
</tr>
<tr>
<td>February 1961</td>
<td>37</td>
<td>76</td>
</tr>
<tr>
<td>March 1961</td>
<td>10</td>
<td>80</td>
</tr>
<tr>
<td>April 1961</td>
<td>4</td>
<td>—</td>
</tr>
<tr>
<td>May 1961</td>
<td>25</td>
<td>16</td>
</tr>
<tr>
<td>June 1961</td>
<td>16</td>
<td>31</td>
</tr>
</tbody>
</table>

An individual removed from its host during daylight hours attempted to re-enter the slit and eviscerated body of the holothurian. It was easily captured by hand and made no effort to escape from my closed fist. The observations of pearlfish out of the hosts at night did not seem to be related to any unusual conditions, and the scarcity of such observations is probably due to the limited time spent on the reefs at night.

On one occasion I was told of an *Encheliophis gracilis* observed entering an unidentified sea cucumber about three o’clock in the afternoon. The host was opened and the fish was recovered.

LIFE HISTORY

Arnold (1956) has summarized the life history of *Carapus acus* and the observations recorded here only serve to indicate that the life history of *C. homei* is generally similar. Tenuis larvae of *homei* were found in *Stichopus chloronotus* from October to February, and posttenuis stages were collected until May. None of the *homei* taken during this study (October to July) had maturing gonads, indicating that spawning takes place during the summer months as in the case of *C. acus*.

Transformation from the tenuis to the adult form is accompanied by a considerable reduction in total length. The longest tenuis was 197 mm, the shortest adult 69 mm, suggesting that they may lose as much as 65% of their length during transformation. Figure 5 shows the changes in head length–body length ratio accompanying the transformation from tenuis to adult.

Two female *Encheliophis gracilis* with nearly ripe ovaries were collected February 23 and May 26. The February specimen, 217 mm long, had a single developed ovary 16 × 11 × 6.5 mm. A rough count places the number of oocytes of the largest class at approximately 14,000. Several other size classes are distinguishable. The May specimen is 186 mm long, its ovary is 11.6 × 7.5 × 3.6 mm. In view of the structural distinction of *Encheliophis* it is unfortunate that its life history remains unknown.

FOOD HABITS

Stomachs of 185 pearlfishes were examined with the following results:

<table>
<thead>
<tr>
<th><em>Encheliophis gracilis</em></th>
<th>11 examined</th>
</tr>
</thead>
<tbody>
<tr>
<td>empty</td>
<td>6</td>
</tr>
<tr>
<td>holothurian viscera</td>
<td>4</td>
</tr>
<tr>
<td>unidentified remains</td>
<td>1</td>
</tr>
<tr>
<td><em>Carapus parvipinnis</em></td>
<td>1 examined</td>
</tr>
<tr>
<td>empty</td>
<td>1</td>
</tr>
<tr>
<td><em>Carapus mortiani</em></td>
<td>5 examined</td>
</tr>
<tr>
<td>empty</td>
<td>5</td>
</tr>
<tr>
<td><em>Carapus homei</em></td>
<td>168 examined</td>
</tr>
<tr>
<td>empty</td>
<td>127 (75.6%)</td>
</tr>
<tr>
<td><em>C. homei</em> tenuis</td>
<td>19 (11.3%)</td>
</tr>
<tr>
<td>shrimp</td>
<td>12 (7.2%)</td>
</tr>
<tr>
<td>unidentified fish</td>
<td>5 (3.0%)</td>
</tr>
<tr>
<td><em>C. homei</em> adult</td>
<td>1 (0.6%)</td>
</tr>
<tr>
<td>shrimp and fish</td>
<td>2 (1.2%)</td>
</tr>
<tr>
<td>unidentified remains</td>
<td>2 (1.2%)</td>
</tr>
</tbody>
</table>

The stomachs of *Encheliophis gracilis* that contained what appeared to be holothurian viscera were very full and considerably distended. This threadlike material has been identified from histological sections as testis tissue. Stras-
burg (1961:479) found similar material in the stomachs of Hawaiian specimens.

Neither Strasburg nor I found any food in the stomachs of the *Carapus* recovered from the pillow starfish. The specimens from Guam all appeared emaciated, leading one to wonder if *Culcita* could be an abnormal host which is frequently though accidentally invaded and from which there is no escape. If this is so, perhaps the distinctive melanophore pattern of *C. moullani* is merely part of a starvation syndrome and the "species" *moullani* is nothing more than those individuals of *C. homei* that chance to enter the wrong host. The simple experiments necessary to confirm or reject this hypothesis have yet to be performed.

All of the *Carapus homei* with tenuis larvae in their stomachs were collected from November through February, when the larvae are assuming the inquiline habit. Eight out of 15 specimens collected November 25 had fed on tenuis larvae. Apparently there is intense competition for hosts at that time and any larva that enters an occupied host may be eaten. The presence of an adult in another's stomach indicates that even the later stages are subject to this hazard.

Since the larva is longer than the adult, stomachs containing larvae were greatly distended. The head usually appeared to be in a more advanced stage of digestion, indicating that consumption of the larva requires a considerable period of time. One specimen had 29 mm of the tail of the larva still protruding from its mouth.

The presence of shrimp in the stomachs of *C. homei* is further evidence that this species leaves the host to feed.

**ACKNOWLEDGMENTS**

I deeply appreciate the aid received from students at the College of Guam and from Mr. Bert Bronson, who first introduced me to nocturnal studies of the reefs. Mr. George Arita, of the University of Hawaii, kindly prepared the histological sections of the material from the stomach of *Encheliopis*. Mrs. Elizabeth Jennings typed the manuscript, and Dr. Barry Muir critically reviewed the paper and made numerous helpful suggestions.

**REFERENCES**


Notes on the Life History of Two Californian Pomacentrids: Garibaldis, *Hypsypops rubicunda* (Girard), and Blacksmiths, *Chromis punctipinnis* (Cooper)¹

CONRAD LIMBAUGH

**ABSTRACT:** The range, life history, food, competitors, predators, and ectoparasitic cleaners of *Hypsypops rubicunda* and *Chromis punctipinnis* are considered. Both species exhibit elaborate prespawning and spawning behavior. Nest preparation and nest behavior of the garibaldis are discussed in detail.

*THE POMACENTRIDS* are well represented in tropical waters; de Beaufort (1940) listed 88 species divided into 11 genera for the Indo-Australian Archipelago, and Smith (1953) gave 24 species for the South African area. The literature concerning New World species badly needs revising, but there seem to be approximately 20 species, divisible into 8 genera, in the eastern Pacific. One of these genera, *Azurina*, appears to be endemic to the eastern Pacific.

Most of the species are small and often vividly colored. Most exhibit distinct habitat preferences, varying widely from species to species. Such forms as *Hypsypops, Microspathodon,* and *Pomacentrus* are bottom-dwelling and generally take cover in holes in reefs, while *Chromis punctipinnis* and *C. atriolobatus* tend to form schools well off the bottom. The schooling habit is most marked in the slender, graceful *Azurina eupalama* and *A. birundo*. Members of this family exhibit elaborate prespawning and spawning behavior. Males establish nesting sites which they zealously protect from all intruders both before and after egg-laying activities (Limbaugh, 1955; Longley and Longley, in Longley and Hildebrand, 1941).

Only two pomacentrids are represented in southern California waters: the bright orange garibaldi, *Hypsypops rubicunda*, and the more somber blacksmith, *Chromis punctipinnis*.

**GARIBALDI**

**Brief Description**

A garibaldi is a deep-bodied fish with coarse scales. It has a single dorsal fin with about 12 spines and 16 rays. The large male garibaldi has a lump on the forehead. The adults are uniformly bright orange, but the young bear many iridescent blue spots on their orange bodies (Figs. 1, 2) and gradually pass through numerous color phases before assuming adult coloration. The color pattern of the young was first described by Smith (1883). Developmental color phases and their biological significance as well as the biochemical aspects of the pigmentation of young and adults have been discussed by Fox (1936), Hubbs (1947), and Kritzler et al. (1950).

1 This paper, based on research notes maintained by the author prior to his death, has been organized by Howard M. Feder, Hartnell College, Salinas, California. Conrad Limbaugh, chief diving officer at Scripps Institution of Oceanography and one of the world's foremost underwater naturalists, had been working on numerous and diverse research projects before he met his untimely death in a diving accident in the Mediterranean, in March 1960. Many of his projects, including this one, were left unfinished. Because of the extensive field notes and photographic records he maintained, it is anticipated that eventually the results of most of his studies can be assembled and published so the vast wealth of his accumulated knowledge will not be lost.

Preparation of this manuscript was aided by the Conrad Limbaugh Memorial Fund and by a grant from the Permanent Science Fund of the American Academy of Arts and Sciences. Manuscript received June 15, 1962.
Fig. 1. An adult male (above) and two juveniles (below) *Hypsypops rubicunda*. The adult is bright orange while the young bear iridescent blue spots.

**Recorded Range**

They have been reported from Monterey, California (Girard, 1858), to Santa Maria Bay, Baja California (Fitch, 1953). The Monterey specimen was regarded as a product of a warming cycle in our coastal waters (Hubbs, 1948); the species typically does not range much north of Point Conception. Extensive diving off the California and Baja California coasts as well as the offshore islands permits listing numerous specific areas in which adult and juvenile garibaldis have been observed (Table 1). I noted adults from Naples, California, to Punta San Rosarita, Baja California, and from Santa Cruz Island to San Martin Island; while juveniles were seen from Malibu Beach, California, to Ensenada, Baja California, and from Santa Catalina Island to the Coronado Islands.

**Length**

The maximum length recorded for a garibaldi is 35.6 cm, or 14 inches (Barnhart, 1936; Roedel, 1953). The largest specimen I collected was 29.3 cm, or 11.5 inches; it was taken in the northern portion of their range. They attain sexual maturity at about 20 cm, or 8 inches.

**Habitat**

Garibaldis prefer living over rocky bottoms on exposed or semiprotected coasts where the water is clear. They frequent rocky reefs having plenty of crevices and small caves for cover. On rare occasions individuals have been observed high on a column of the giant kelp, *Macrocystis pyrifera*, apparently searching for food.

Adults have been observed in tide pools and
at depths of 90 ft, depending upon the clarity of the water and the depth of the thermocline. They generally remain above the thermocline, where most of the population is concentrated between 4 and 42 ft. When the water is dirty they remain closer to their rocky retreats.

Juveniles may be found in tide pools and to depths of 40 ft.

**Life History**

They were present throughout the year in all regions noted in Table 1, and individuals probably remain in a restricted territory during most of their lives. Each fish roams a rather large territory, but there are definite concentrations of individuals in certain areas, possibly depending upon whether or not the environment is favorable. In some cases, these groups may use the same crevices for cover. The individuals in a group were never observed fighting, but tagged fish introduced from other regions were quickly driven away.

Garibaldis defend their territories vigorously, reluctantly retreating from a diver to their rock holes only when directly approached. They generally wait at the entrance if they are not pursued (Fig. 3). If they are further molested, they will enter the hole and either leave by another opening or wedge themselves into a crevice. They may be taken by hand at this time but at the risk of lacerated hands and arms. Disturbed garibaldis generally emit thumping sounds easily heard by a diver.

The breeding season seems to be continuous throughout the spring and summer. It may begin as early as March and persist through July, lasting longer in warm years and in the southern portions of their range. There may be no spawning season in the northern part of the adult distribution.

All signs of blue are lost in mature adults; the faintest trace of blue is an indication of immaturity. There are slight color and size differences between sexes: males tend to be more reddish (red-orange) and are slightly larger than the females in a given area. No evidence is available to determine if the color difference is seasonal.

The male prepares a nest by cleaning a rocky surface of all but the strongly adherent calcareous organisms. In the center of the cleared area he cultivates an elliptical patch of velvety red algae. Plant material taken from nests off La Jolla,
several challenges, in which the male may bite her, she arrives inside an area where he ceases to challenge her. This area is about a foot in diameter.

Once inside the protected area the female moves slowly back and forth over the garden maintaining her genital area against the plants. The male usually joins her unless he is disturbed by the presence of other fishes. During spawning he is in a highly excited state, characterized by rapid darting motions, frequent challenges of other fishes, and quick returns to the nest. If he joins the female he may keep his genital area next to hers. At this time, quivering vio-

California, contained three principal kinds of algae. The most abundant was Ophidoclados californicus; the other two species were Pierosiphonia dendroides Falk. and Spermothamnion snyderea Farlow. A nest from 35 ft of water off Point Loma, California, was composed of algal material not previously described, and may represent a new genus (E. Yale Dawson, personal communication). I could not determine whether the algae grew on the nest site or were placed there by the male. The patch is usually 10 to 12 inches along its major axis. The nest site is always shaded and generally on a vertical surface in shallow water; in deeper water, it is in the open in a horizontal plane. These differences in nest orientation are undoubtedly related to the light requirement of the red algae. The "garden nest" is kept clean and cropped to about ½ inch, while the surrounding rocks for a distance of 10 to 35 cm are kept completely bare by the male's continual activity. The nest is guarded constantly and other fishes, including male garibaldis, are driven off.

Spawning begins shortly after a female from a nearby area wanders into the general vicinity of the nest. The male challenges her when she approaches within 4 to 15 ft of the nest by making very loud thumping sounds and rushing toward her. Unlike the invading males, she does not swim swiftly away; instead she evades the male by darting past him toward the nest. After

Fig. 3. An adult male Hypsypops rubicunda at the mouth of a crevice, where he has retreated upon the approach of the diver.
lently, he releases sperm on the eggs as they are laid. After the female departs he may go over the eggs again, still in a state of high excitement.

One end of the capsule-shaped egg (Fig. 4) is attached to the red seaweed by short threads. The eggs measure approximately 1 by 2 mm and are orange-yellow in color immediately after they have been spawned. They gradually turn greenish-gray as development proceeds.

The eggs hatch in 2 to 3 weeks in laboratory aquaria maintained at 60–70 F (15.6–21.1 C). However, they do not keep well in laboratory tanks. They hatch only if they are agitated and those that do hatch can be maintained only until their yolk supply is depleted. A few newly hatched young were fed on brine shrimp larvae and some of them survived in the aquaria up to 6 days. In the field the eggs hatch in several weeks and larvae may be collected in near-shore plankton hauls.

The male continues to guard the nest as long as it contains developing eggs. He is very pugnacious, challenging fishes up to 3½ times his own length, biting them and making thumping noises which ultimately drive them away. A nest left unguarded is quickly attacked by other male garibaldis and the eggs are devoured. The resident male on returning will make the encroaching male beat a hasty retreat.

Foreign objects such as shells, stones, crabs, and starfish (Figs. 5, 6) are removed if they settle or are placed on the nest. If the summer waves raise the sand level until it endangers the nest, the male will clean the sand away. Some dig holes as deep as 8 inches around the nests.

Half-inch young appear from July through November. They are brilliantly colored with iridescent butterfly-blue markings over an otherwise translucent orange body, and the heads are striped with blue. As they grow older, the orange color deepens and they gradually lose their blue markings (Figs. 1, 2, 7). These brightly-colored young seek shelter within the tiny crevices of their habitat. As they enter the shade of a crevice the bright blue turns black (because it is a reflected color), and the fish disappears from sight. Young garibaldis are frequently associated with the large red urchin, Strongylocentrotus franciscanus. I have collected these young by using SCUBA, a small dip net, and a glass bottle.

The half-grown fish pass through a dull orange stage, when they are much less conspicuous than either the young or the adults. As they

![Fig. 5. An adult male Hypsypops rubicunda removing a starfish of the genus Pisaster that has been placed on the nest by the diver.](image)

![Fig. 6. An adult male Hypsypops rubicunda carrying a starfish (shown in Fig. 4) away from the nest area.](image)
reach maturity the last of the bright blue markings, those on the edges of their fins, disappear. Studies of aquarium-grown fish and of size groups in nature indicate that they mature at about 3 years.

Food

Garibaldis probably prefer the bryozoan *Membranipora serrilamella* to all other organisms; most of the stomachs examined contained this species. Some fishery workers feel that in the course of feeding on algae they incidentally take in bryozoan material. Further study is needed to clarify this situation. Other material in their stomachs besides bryozoans and algae included sea anemones, worms, small crabs, amphipods, gooseneck barnacles, clams, snail eggs, and their own eggs.

Competitors and Predators

Spearfishermen represent a potential predator of considerable importance, but garibaldis are now protected by law from this danger. No other predator or competitor has been observed.

Parasites and Cleaning Symbiosis

External parasitic organisms such as bacteria, fungi, copepods, and isopods are removed from garibaldis by senoritas, *Oxyjulis californica*, and kelp perch, *Brachyistius frenatus*. This peculiar habit, which is shared by fishes in many other families in different oceans, has modified the behavior of the parasitized species so that they will seek out cleaner fishes to remove particular parasites. A garibaldi will often hold its operculum open so that a senorita can remove gill parasites. In addition to these two fishes the red and white shrimp, *Hippolyssma californica*, has been observed removing parasites from garibaldis (Limbaugh, 1955; 1961 a, b).

Garibaldis' Future

These fish are quite common, although they are less abundant than before spearfishing started. They are now partially protected by law, and wisely so, because they are very easy to spear or capture and might stand a real danger of extermination. Although they are still taken in quantity for aquarium use, especially the
juveniles, by collectors having commercial licenses, the population will probably regain its former abundance, and their beauty will continue to afford pleasure to underwater observers.

BLACKSMITHS

Brief Description

Blacksmiths are oblong fishes with heavy scales and rather blunt heads. The single dorsal fin has 13 spines and usually 12 rays, and there are two spines located at the front of the anal fin. They are blue-gray in color with small black dots on their backs, the soft portion of the dorsal fin, and on the caudal fin. The young-of-the-year are gray-blue anteriorly and yellow-orange posteriorly and have an iridescent blue margin around their dorsal, caudal, and anal fins. Kritzler et al. (1950) briefly described their color patterns.

Recorded Range

The blacksmith extends from Monterey Bay (Radvich, 1961) to central Baja California (Roedel, 1955). I have observed them while diving at Point Dume, Rocky Cove, Long Point, Newport Beach, La Jolla, and Point Loma along the mainland coast, and around the islands of Santa Cruz, Santa Catalina, San Clemente, Los Coronados, and Guadalupe.

Size

The 11-inch specimen reported by Radvich (1961) appears to be the largest known. The largest adults I observed while diving were about 25 cm long. Blacksmiths mature in the La Jolla area when they are about 14 cm long (5.5 inches) and 2 years old. Observations suggest that they are somewhat larger at maturity in the northern part of their range.

Habitat

They live over steep rocky banks and among tall seaweeds as well as around rocks; they generally face the incoming currents. Adults have been found from the surface to 150 ft, and they probably visit depths of 300 ft or more; however, the average depth of adult occurrence is 30 ft. The young are found from the surface to about 50 ft.

Life History

They are extremely abundant throughout the year in southern California waters. Young and adult blacksmiths school or aggregate in definite size groups. In general, the smaller fish are found in shallower water, although large adults live in shallow water in the northern portion of their range. They may be found in loosely-oriented schools, or, when molested or pursued, in large, well-oriented, compact schools.

In the northern and central portion of their range adults are ripe in June and July. Eggs obtained by stripping were cherry red and relatively large, approximately 1.5 mm in diameter. Turner and Ebert (1963) observed the blacksmiths breeding and nesting at Santa Catalina Island, California, in the summer of 1961. The blacksmiths laid their eggs back in holes and small caverns that were made by 15 to 30 pound rocks that formed a tumbled slide running offshore. They were nesting from 12 to 80 feet beneath the surface and probably deeper. The male first cleared an area and then herded a female into his “den” by biting and otherwise harassing her. From the egg counts and varying states of development probably more than one female laid eggs in a single nest. The masses of eggs were salmon pink when laid, oblong and adhered by means of filaments (up to 7) at one end of the egg. The male guarded the nest very pugnaciously during brooding. Actual egg-laying could not be observed because the nesting holes were too small at the entrance to permit peeking in. Whenever a guarding male was driven off a whole horde of fishes would swarm in to eat eggs.

The juveniles appear in large, semipelagic schools in August, September, and October; they are 1/2 to 1 inch long at this time. By November only a few 1-inch-long specimens can be found in the central portion of their range. To the south, however, (Guadalupe Island) they occur as 1/2-inch young into November. By June of the following year they are between 2 and 3 inches long.

The blue-and-yellow juveniles school densely in the open ocean, sometimes entering kelp beds. As they grow larger they settle in shallow sandy
areas protected by large rocks. Yearling blacksmiths are somewhat more solitary, seeking refuge in small caves and crevices.

Food

When larval fishes, small crustaceans, and young squid are abundant in the plankton, large schools of blacksmith, señoritas, and kelp top-smelt, Atherinops affinis cedroscensis, often intercept the inflowing current moving into a kelp bed. Screens of these fishes filter the tiny organisms from these currents; their activities probably materially affect the amount of plankton entering the kelp beds.

Blacksmiths, as well as most of the other fishes of the kelp canopy, utilize the extremely abundant opossum shrimp, Mysidopsis californica, for food. Hyale frequens and other small amphipods also serve as their food.

Predators

A number of animals have been observed preying on blacksmiths: moray eels, Gymnothorax mordax, kelp bass, Paralabrax clathratus, ling cod, Ophiodon elongatus, and Brandt’s cormorants, Phalacrocorax penicillatus. Their great abundance indicates that blacksmiths are probably important forage fish.

Parasites and Cleaning Symbiosis

Juvenile pile perch, Damalichthys vacca, and señoritas have been observed cleaning parasites from them (Limbaugh, 1955; 1961 a, b).

Fig. 8. A señorita (Oxyjulis californica) cleaning a Chromis punctipinnis. Other individuals are waiting to be cleaned. Note the awkward position assumed by the one being cleaned. (Photograph by Charles H. Turner, State of California Department of Fish and Game.)
Two Californian Pomacentrids—Limbaugh

Subadults seek out cleaning fishes and aggressively place themselves in positions that make it almost mandatory for the cleaners to feed on their external parasites (Fig. 8). Groups of blacksmiths completely hiding a cleaning fish are a common sight over shallow rocky reefs (Fig. 9). While having their parasites removed they will assume almost any position: on their sides, heads up, heads down, or even upside down. If the cleaner should try to leave, they will follow and crowd in front of it preventing its escape.

Use as Food

They are sometimes found in the fresh fish markets (Barnhart, 1936), and they form a very small proportion of the southern California "perch" catch (Roedel, 1953). The quality of their flesh is excellent but they are seldom caught on hook-and-line because of their small mouths and general feeding habits.

The blacksmith population remains at a high level.

ACKNOWLEDGMENTS

John E. Fitch, California Department of Fish and Game, and Carl L. Hubbs and Richard Rosenblatt, Scripps Institution of Oceanography, assisted in the preparation of the final draft. E. Yale Dawson, Beaudette Foundation, Solvang, California, identified the algal material in the garibaldi nest. Suggestions made by James Stew-
art, Scripps Institution of Oceanography, Ron Church, Scientific Diving Consultants, La Jolla, California, and Dan Ryan are deeply appreciated.

REFERENCES


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Further Notes on the Identification and Biology of Echeneid Fishes

DONALD W. STRASBURG

Attempts to identify several small echeneid fishes revealed that some of the more useful adult characters are not present in the young. Specifically, disk length, pectoral fin rigidity, body and fin morphology, and scale size and number are features which change with growth. Certain meristic characters were found to be constant over the 14 to 640-mm length range considered, and were usable in identifying small specimens. This paper presents a key to the Echeneidae with further observations on their biology.

The methods employed require only brief description. The leathery membranes were removed from the fins of all but the smallest individuals in order for the rays to be counted. This was particularly necessary for the dorsal fin, the anterior rays of which are recumbent and would otherwise escape detection. The uppermost pectoral ray, a short bony splint, was counted as a ray. Scale examination involved removing a small square of skin from the side below the rear edge of the disk, staining this square with alizarin, and removing the rubbery epidermis. Both lateral line and ordinary scales were then visible in this piece of tissue. No type material was examined, nor was it possible to see specimens of all species. The names used are in accordance with Maul (1956).

Table 1 presents the meristic data obtained from specimens in the collection of the Bureau of Commercial Fisheries Biological Laboratory in Honolulu. These data are the main basis for the following key, although supplementary information was used for the species not seen and to broaden the range of some characters. This information was obtained from the following reports: Bigelow and Schroeder (1953:485–487), Breder (1936:43), Cadenat (1950:265; 1953:674–680), Clemens and Wilby (1949:329), Clothier (1950:51), Follett and Dempster (1960:172–176), Fowler (1941:269–275), Hildebrand (1946:479), Jordan and Evermann (1898:2268–2273), Krefft (1953:278), Maul (1956), Meek and Hildebrand (1928:896–899), Munro (1955:268), Schultz (1943:258–260), Smith (1950:341–342; 1958:319), and Szidat and Nani (1951:399–407).

The two species of Remoropsis recognized by Maul (1956) do not differ meristically, nor are they clearly distinguishable by other means. In general, the body scales of brachyperterus are large, closely spaced, and superficial, while those of pallidus are small, scattered, and embedded. In large brachyperterus, however, the scales are partially embedded, and, in addition, some pallidus have large scales. The shape and spacing of the lateral line scales varies from point to point along the lateral line, and Strasburg (1959:244) found specimens with the coloration of pallidus but the lateral line of brachyperterus. These facts suggest that pallidus and brachyperterus are very closely related, if not synonymous. In the absence of a definitive monograph, they are retained as distinct species characterized solely by color pattern.

The length of the sucking disk has sometimes been used as a taxonomic character in the Echeneidae (cf Maul, 1956:18). Rhombobatus has been distinguished from the other genera, exclusive of Remigia, by the fact that its disk reaches to or past the pectoral tips. The posterior extent of the disk and pectoral fins of echeneids of various lengths is shown in Figure 1. Below 65 mm standard length the pectorals of Rhombobatus extend farther posteriorly than the disk, as is always the case with Remora, Remoropsis, and Phtheirichthys. While this character may be used for large individuals, it

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1 U. S. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii. Manuscript received September 26, 1962.
<table>
<thead>
<tr>
<th>CHARACTERS</th>
<th>NO. OF LAMINAES OR FIN RAYS</th>
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</thead>
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<tr>
<td></td>
<td>9  10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40</td>
</tr>
<tr>
<td>disk laminae, <em>P. lineatus</em></td>
<td></td>
</tr>
<tr>
<td><em>R. osteochir</em></td>
<td></td>
</tr>
<tr>
<td><em>R. remora</em></td>
<td></td>
</tr>
<tr>
<td><em>R. pallidus</em></td>
<td></td>
</tr>
<tr>
<td><em>R. brachypterus</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1  7 3 8 36 9 1</td>
</tr>
<tr>
<td></td>
<td>13 15 1</td>
</tr>
<tr>
<td></td>
<td>4  7 7 1</td>
</tr>
<tr>
<td></td>
<td>3  3</td>
</tr>
<tr>
<td>dorsal rays, <em>P. lineatus</em></td>
<td></td>
</tr>
<tr>
<td><em>R. osteochir</em></td>
<td></td>
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<tr>
<td><em>R. remora</em></td>
<td></td>
</tr>
<tr>
<td><em>R. pallidus</em></td>
<td></td>
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<tr>
<td><em>R. brachypterus</em></td>
<td></td>
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<tr>
<td></td>
<td>2  5 13 17 10 6 1</td>
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<tr>
<td></td>
<td>2  4 12 8 3</td>
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<td>2  3 4 7 3</td>
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<td>1</td>
</tr>
<tr>
<td>anal rays, <em>P. lineatus</em></td>
<td></td>
</tr>
<tr>
<td><em>R. osteochir</em></td>
<td></td>
</tr>
<tr>
<td><em>R. remora</em></td>
<td></td>
</tr>
<tr>
<td><em>R. pallidus</em></td>
<td></td>
</tr>
<tr>
<td><em>R. brachypterus</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1  13 18 15 5 2</td>
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<td>3  19 7</td>
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</tr>
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<td></td>
<td>2  2</td>
</tr>
<tr>
<td>pectoral rays, <em>P. lineatus</em></td>
<td></td>
</tr>
<tr>
<td><em>R. osteochir</em></td>
<td></td>
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<tr>
<td><em>R. remora</em></td>
<td></td>
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<tr>
<td><em>R. pallidus</em></td>
<td></td>
</tr>
<tr>
<td><em>R. brachypterus</em></td>
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<td>1  19 27 7</td>
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<td>8  16 4 1</td>
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<td></td>
<td>3  15 1</td>
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<tr>
<td></td>
<td>2  2</td>
</tr>
</tbody>
</table>
KEY TO THE ECHENEIDAE

1a. Disk laminae 13 or fewer
   2a. Laminae 9–11, dorsal 30–40, anal 29–38..............Phtheirichthys lineatus (Menzies)
   2b. Laminae 12–13, dorsal 16–22, anal 20–26..............Remorina albescens (Schlegel)

1b. Disk laminae 14 or more
   3a. Laminae 20–28, usually 21–27
      4a. Dorsal 31–42, anal 30–38...............................Echeneis naucrates Linnaeus
      4b. Dorsal 20–26, anal 20–26...............................Remilegia australis (Bennett)
   3b. Laminae 14–20, usually 15–19
      5a. Dorsal 21–27 (usually 22–26), laminae 17–20
         6a. Pectoral 20–23........................................Rhombochirus osteochir (Cuvier)
         6b. Pectoral 26–29........................................Remora remora (Linnaeus)
      5b. Dorsal 28–33, laminae 14–18 (usually 15–17)
         7a. Caudal black with white corners in specimens 27–164 mm standard length; dorsal and anal black with white edges, white becoming obsolescent with growth..............................Remoropsis brachypterus (Lowe)
         7b. All fins uniformly pale colored......................Remoropsis pallidus (Schlegel)

TABLE 2
HOSTS OR HABITS OF ECHENEID FISHES

<table>
<thead>
<tr>
<th>ECHENEID</th>
<th>NO. EXAMINED</th>
<th>STANDARD LENGTH (mm)</th>
<th>HOST OR HABIT</th>
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<tr>
<td>Phtheirichthys lineatus</td>
<td>3</td>
<td>32.8–300</td>
<td>free-living</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>44.0–55.8</td>
<td>long-line buoy or bait</td>
</tr>
<tr>
<td>Rhombochirus osteochir</td>
<td>4</td>
<td>14.3–45.7</td>
<td>free-living</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>51.2</td>
<td>long-line buoy</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>48.4</td>
<td>Acanthocybium solandri</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>66.7–85.0</td>
<td>Tetrapturus angustirostris</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>49.8–230</td>
<td>Makaira audax</td>
</tr>
<tr>
<td></td>
<td>27</td>
<td>38.5–313</td>
<td>Makaira ampla</td>
</tr>
<tr>
<td>Remora remora</td>
<td>7</td>
<td>31.3–77.4</td>
<td>free-living</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>49.3–87.6</td>
<td>Carcarbinus melanopterus</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>50.9–154</td>
<td>Pterolamiops longimanus</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>222</td>
<td>Prionace glauca</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>640</td>
<td>Rhincodon typus</td>
</tr>
<tr>
<td>Remoropsis brachypterus</td>
<td>1</td>
<td>27.1</td>
<td>free-living</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>80.0</td>
<td>Makaira audax</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>83.7–112</td>
<td>Makaira ampla</td>
</tr>
<tr>
<td>Remoropsis pallidus</td>
<td>1</td>
<td>118</td>
<td>free-living</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>79–83</td>
<td>Istiophorus orientalis</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>116–184</td>
<td>Makaira audax</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>128–152</td>
<td>Makaira ampla</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>128–194</td>
<td>Istiompax marlina</td>
</tr>
<tr>
<td>Echeneis naucrates</td>
<td>2</td>
<td>50–57 (est.)</td>
<td>Ostracion lentiginosus and the author</td>
</tr>
</tbody>
</table>
is clear that *Rhombochirus* shorter than about 65 mm cannot be distinguished from the other genera by the disk length/pectoral length relationship.

Table 2 summarizes the length and host data for the specimens listed in Table 1. Where the host was identified only as "marlin" or "shark" no listing was made in Table 2. Also excluded are three echeneids removed from fish stomachs: a 46-mm *P. lineatus* and a 118-mm *R. pallidus* from *Neothunnus macropterus*, and a 56-mm *R. osteochir* from a "swordfish." The term "free-living" denotes echeneids captured by plankton net, midwater trawl, or dipnet beneath a light.

An aspect of echeneid biology which merits some discussion is the change in habit or host with growth. As shown by Strasburg (1959), attachment tends to be specific with respect to host and attachment site. For example, *Phtheirichthys* is either free-swimming or attached

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**Fig. 1.** Relative posterior extent of sucking disk and depressed pectoral fin for various echeneids.
to immotile objects, Remora is found externally on sharks, and Remoropsis pallidus takes refuge beneath the opercula of marlins. Although it is known that the early stages are planktonic, there has hitherto been no information on the size at which attachment first occurs, or whether there are trial hosts.

The material at hand indicates that the transition from the free-swimming to the attached state occurs at about 40–80 mm standard length. Phtheirichthys then attaches to immotile objects, as occasionally do some of the others. Rhombochirus selects a variety of marlin-like fishes for its attachment, while Remora attaches to sharks. One of the Echeneis studied was attached to a 49-mm trunkfish, Ostracion lentiginosus (Fig. 2), collected on the reef at Waikiki, Oahu, Hawaii. Except for a few brief excursions to the host’s belly, it remained inverted as shown. Unfortunately, neither the echeneid nor the trunkfish was preserved, and their lengths are only estimates derived from the relative proportions shown in the photograph. The second Echeneis could not be captured but was also about 50 mm in length. It joined me while swimming in 10-ft deep water at Beaufort, North Carolina. Its black and white pattern made it conspicuous, and it was sighted at a distance of 15 ft, swimming directly toward me. The fish made numerous attempts to attach to my black swim fins, touching them but not actually attaching because of my continuous movements. It eluded all attempts to capture it.

It would seem that attachment becomes obligatory somewhere in the 40 to 80-mm length range. Alternate hosts, such as Acanthocybium, Tetrapurus, and Carcharhinus melanopterus, may then be selected in the absence of the definitive host species. These small hosts may be regarded as trial vehicles because they bear only small echeneids. The size of the echeneids carried by them would be restricted by the relatively fewer ectoparasites available as food or, as in the case of the Ostracion–Echeneis association, by problems of list and drag resulting from a bulky adherent.
As a corollary, one would expect large echeneids to select large hosts or, in their absence, to revert to free swimming. The latter appears to be the case with *Echeneis naucrates*, 39-inch individuals of which are free-living around piers at Eniwetok, Marshall Islands (Strasburg, 1957: 60). The 640-mm *R. remora* listed in Table 2 confirms the first part of the hypothesis, for it was one of about three dozen individuals of similar size accompanying a 50 to 60-ft whale shark, *Rhincodon typus*, at Maro Reef (northwest of the main Hawaiian Islands). Attempts to lure this shark to the fishing vessel were unsuccessful because the chopped fish bait was intercepted by the darting remoras. Twelve remoras were caught by pole and line using tuna flesh as bait, but only a single specimen was preserved. Its stomach was empty, unfortunately, so that no light can be shed on its diet. It is doubtful that such a large fish could subsist mainly on its host’s ectoparasites (cf Strasburg, 1959:246).

Some of the smaller specimens listed in Table 2 are the smallest reported representatives of their species. The 27.1-mm *brachypterus* is considerably shorter than Gudger’s (1928) 77-mm fish, and my 14.3-mm *osteochir* is smaller than his 36-mm specimen. Gudger presents few descriptive data, however, and his specimens seem to differ from what are here called *brachypterus* and *osteochir*. On the basis of pectoral counts, Beebe’s (1932) 15-mm “*Remora remora*” is *Rhombochirus osteochir*, while his 88-mm specimen is correctly identified as *R. remora*.

Beebe (ibid.) also misinterpreted certain morphological peculiarities of the lips and jaws of his small *osteochir*. These were stalked cup-like structures which he termed “suckers,” and which he postulated were used for host attachment prior to the development of the cephalic disk. Actually the “suckers” on the mandible are the enlarged fleshy sockets which normally bear the fangs, while those on the upper lip are merely large pores. The fangs are easily extracted with forceps, imparting a sucker-like appearance to the supporting tissues. My 14.3-mm *osteochir* has seven outer and two inner fangs on each side of the mandible, making a total of 18 sockets. This is a reasonable approximation of the 20 “suckers” and four fangs which Beebe found in his 15-mm fish.

The young echeneid’s need for its relatively enormous fangs is presently inexplicable. These teeth are not deciduous but instead become inconspicuous through overgrowth of the gums and the appearance of other teeth between them.

Its intimate association with another species could impose serious reproductive restrictions on an echeneid. Unless both sexes attached to the same host individual, spawning would be limited to times when the host species aggregated. Echeneids attached to hosts which schooled or congregated to feed would have many opportunities for mating, but those accompanying solitary hosts would have to spawn simultaneously with them.

The material at hand was examined for gonad maturity and the presence of both sexes on the same host individual. Unfortunately, the specimens were not always so segregated that the latter could be determined. Thus, although mature *Remora remora* and *Remoropsis pallidus* were found, it was not certain whether both sexes had been attached to the same shark or marlin. The available *Remoropsis brachypterus* and *Phtheirichthys lineatus* were few and sexually immature.

In contrast to the above, the *Rhombochirus osteochir* data present a relatively clear picture of the physical distribution of the sexes. Thirteen marlin and spearfish bore 2 *Rhombochirus* apiece. In 10 cases the 2 were a male and female of the same size and degree of maturity (7 pairs were judged to be ripe, based on abdominal distension of the female). The 11th pair was a small female and a fish half her size whose sex could not be determined. The remaining 2 couples consisted of young fish of undetermined sex. A 14th host was accompanied by 3 *Rhombochirus*, a ripe male and female and a small individual, one-fourth the length of the others, whose sex could not be ascertained.

With 11 out of 14 pairs bisexual and in the same maturity stage, it would seem that *Rhombochirus* can reproduce quite independently of its host’s aggregating habits. This does not mean that it always does so, for mature single *Rhombochirus* were also collected. In such cases, however, there is a possibility that these fish were remnants of pairs the other members of which had detached during the capture of the host.
Echeneid Fishes—Strasburg

REFERENCES


Morphogenesis of *Tedania gurjanovae* Koltun (Porifera)

Gerald J. Bakus

**DURING THE COURSE** of a study of the marine sponges of the San Juan Archipelago, Washington, the discovery of several specimens of *Tedania gurjanovae* Koltun (Koltun, 1958:65, fig. 20) was of special interest because of the opportunity provided to observe its larval metamorphosis. This species had been known previously only from the eastern part of the Tatar Strait, off Sakhalin, USSR, at depths of 60 to 100 m (Koltun, 1958, 1959). The present specimens (No. 30, 58, 90, 112, lot 163) were dredged in depths of 73 to 198 m in President Channel and San Juan Channel, San Juan Archipelago, Washington, and now reside in this writer’s personal collection. An account of the morphology, larval metamorphosis, ecology, and taxonomy of the Washington population is given here.

The suggestions and criticisms offered by Dr. Dixy L. Ray, Dr. Paul Illg, Dr. Melville Hatch, Dr. Standish Mallory, and Dr. Willard Hartman are appreciated. Many others contributed to this study. Support was given by the National Science Foundation during the summers of 1958, 1959, and 1961, and the facilities at the University of Washington Friday Harbor Laboratories were used. Translations from Russian to English of both sponge distribution records and a description of *Tedania gurjanovae* Koltun were made by Dr. Gordon Orians.

**ADULT MORPHOLOGY**

*Tedania gurjanovae* is an amorphous encrusting sponge that shows a tendency to macerate after being dissected or upon being collected in broken pieces and preserved. It commonly measures up to 12 mm thick but broken pieces of No. 163 attained a size of up to 4 cm by 3 cm by 2 cm. These fragments probably represented portions of a larger specimen. Specimen No. 90 is an encrusting form that intermittently covers plates of *Balanus* and measures up to 1 mm thick.

The color in life ranges from very light cinnamon to Lido (Maerz and Paul, 1950: pl. 12, D-4, F-5; pl. 13, C-3). In alcohol it is beige to nearly white. The species is odorless so far as is known.

The sponge surface may be smooth but often is gently to roughly undulated (Fig. 1). It is felt like to the touch. The consistency is moderately soft and spongy. The surface may be slippery because of detritus and production of mucus. The dermal anatomy is considerably obscured in some preserved specimens and observations on living material are useful. Oscules may be absent but, if present, are usually numerous, irregularly distributed, open at the body surface, and measure up to 1 mm in diameter. Some oscules have an accumulation of hastate tornotes around their periphery. Pores are abundant and range from 21 to 68 μ in greatest diameter. In No. 163 they were no longer observed after about one hour in the preservative, indicating that they had closed.

The dermal membrane measures from 20 to 25 μ thick. Hastate tornotes (Fig. 2b), arranged more or less perpendicular to the body surface, occur immediately below the dermal membrane. They are loosely distributed and often simulate short wisps of commercial glass wool. Groups of about 10 perpendicular tornotes occasionally occur. In a few regions tornotes are almost parallel to the sponge surface. Hastate tornotes and styles (Fig. 2a) sometimes penetrate up to 50 μ beyond the dermal membrane.

The endosomal mesenchyme ranges from being loose and fluffy to cotton-like. Style tracts extend toward and sometimes penetrate the body surface. The tracts measure from 34 to 55 μ in diameter and the styles are united by small amounts of spongin. Numerous hastate tornotes and some styles are found irregularly distributed

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1 Allan Hancock Foundation, University of Southern California, Los Angeles, California. Manuscript received July 2, 1962.
Tedania gurjanovae—Baku

Fig. 1. Tedania gurjanovae Koltun \((X \frac{2}{3})\). Small sample, Specimen No. 58. Large sample, Specimen No. 112, encrusting on Modiolus.

Throughout the endosome, Onychaetes (Fig. 2c–e) occur both scattered and in trichodragmata. Excurrent canals measure up to 500 \(\mu\) in diameter, whereas smaller canals range down to 83 \(\mu\) in diameter. Canals are moderately numerous.

The spicules and their dimensions are listed in Table 1. The mean dimensions of each spicule category of specimen No. 30 and 112 are based on 10 measurements, and each size range is represented by 1 minimum and 1 maximum measurement.

The styles are often curved. Occasional juvenile styles were observed. Hastate tornioes sometimes have very slightly inflated ends. Onychaetes are straight or slightly curved and occur in two size ranges. The smaller forms (I) tend to be prominently roughened, whereas the larger sizes (II) are only slightly rugose (Fig. 2c–e). Juvenile onychaetes also occur. One measurement is \(81 \times 1 \mu\). Onchaetes are often found in trichodragmata measuring from 60 to 100 \(\mu\) thick.

**ECOLOGICAL NOTES**

Tedania gurjanovae is collected chiefly from a biotic community of lamellibranchs (mussels) and barnacles. In some specimens the endosome is contaminated by a few sand grains.

Biological associates include: No. 30, T. gurjanovae partly encrusting on barnacles (Bal anus) with another sponge (Halichondria), all of which are encrusting on the carapace of a crab; No. 58, T. gurjanovae encrusting around a barnacle (Balanus) with attached polychaete tubes (Fig. 1); No. 90, T. gurjanovae encrusting on barnacles (Balanus); No. 112, a few foraminifera on the sponge surface, T. gurjanovae encrusting on a mussel (Modiolus modiolus Linnaeus) and surrounding a barnacle (Balanus) and several large polychaete tubes (Fig. 1); No. 163, one large endosomal polychaete tube. Koltun (1959:156) reported that Tedania gurjanovae is frequently found encrusting on the valves of scallops (Chlamis).
TABLE 1

Spicule Measurement (in μ) of Tedania gurjanovae Koltun

<table>
<thead>
<tr>
<th>Author</th>
<th>Specimen No.</th>
<th>Depth and Habitat</th>
<th>Bakus</th>
<th>Bakus</th>
<th>Koltun, 1958</th>
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<tbody>
<tr>
<td>Bakus</td>
<td>30</td>
<td>192 m rock-shell bottom</td>
<td>112</td>
<td>110-128 m rock-shell bottom</td>
<td>2974</td>
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**LARVAL METAMORPHOSIS**

The dissection of a specimen of a sponge (lot No. 163) on 26 July 1959 revealed living embryos attached by the posterior end to the parental mesenchyme (Fig. 3a). Motile cilia were distributed over the entire surface except for the posterior pole. A minute region at the anterior end was very slightly pigmented. Both embryos and subsequently released larvae were cream colored. The larvae were typical parenchymulae, roughly oblong in shape, and measured from 500 μ long by 332 μ in mid-length diameter to 576 μ by 433 μ. In released larvae the anterior pole had very short cilia; cilia were lacking on the posterior end (Fig. 3b). Elsewhere the cilia were longer and of approximately equal dimensions. Several larvae contained one or two visible parental (?) spicules passing through their mesenchyme. This had no apparent effect on their swimming behavior. The presence of spicules in larvae of Demospongiae is common. Ali (1956:558-559), in a study on the development of Lissodendoryx similis Thiele, found that the larvae contained both microscopic and macroscopic spicules and in greater density than found in the adult.

Larval spiculation was studied in preserved embryos. A mature embryo, ready to leave the parent sponge, contains several hundred onychaetes of both adult size groups, but the majority are of the smaller category (I). Moreover, there are about 25 to 35 conspicuously tapering and mildly echinated acanthostyles that measure about 120 μ in length by 10 μ in basal shaft diameter or 5 μ in mid-shaft diameter. Both onychaetes and acanthostyles are concentrated into a dense packet near one pole, though many onychaetes occur elsewhere throughout the larva. Since the larval acanthostyles apparently do not occur in the adult they may undergo further change to the stylote configuration. The late embryonic spicule distribution of Tedania gurjanovae looks something like that of the T. charcoti embryo as figured by Burton (1932:362, fig. 47L). Burton (1932:361) reported that acanthostyles are the first spicules to appear in embryos of T. charcoti Topsent and that they become converted into smooth styles as development progresses. Further growth is indicated by a segregation of styles in a near bundle at the "aboral pole of the embryo" and a rapid increase in numbers of raphides. Burton believes that raphides are probably the prototypes of adult onychaetes.

The larvae swam with the anterior end directed forward and completed spiral gyrations.
One larva was observed swimming with the posterior pole directed forward. It was not unusual for natatory parenchymulae to pause for several minutes on the bottom of the glass bowl.

There appeared to be no obvious negative or positive phototaxis. Lévi (1956:119) noted that the larvae of Haliclonia indistincta (Bowerbank) showed no particular taxis. Larvae of Lissodendoryx similis (Ali, 1956:557) and Mycale syrinx (O. Schmidt) (Wilson, 1935:287) have shown negative phototaxis. Whether or not sensory cells are associated with this behavior is unknown at the present time (Jones, 1962:13–14). Further observations on larval behavior are discussed by Jones (1962:13–14, 49–50). Ali (loc. cit.) and Wilson (loc. cit.) both reported that some sponge larvae swim upwards then adhere to the water surface film and eventually die or disperse into scattered fragments and disintegrate.

Four larvae were removed from their attachment to the parent and placed in a finger bowl of sea water to observe settling behavior. Two of the larvae were fixed to the bottom of the finger bowl 6 hr later; of the remaining larvae one appeared to be caught in the water surface film, the other attached to the bottom of the finger bowl after about the 7th hr. A few larvae appeared to have a slightly invaginated posterior pole just prior to fixation on the glass substratum (Fig. 3c).

Larvae of Lissodendoryx similis (Ali, 1956:575) commence attachment to a substratum after about 40 hr; almost 24 hr of this period is spent swimming near the water surface. Sexual larvae of Esperella sordida (Bowerbank) (Delage, 1892:370) swim for about 20 hr, whereas those of Mycale syrinx remain motile for 1 to 3 days (Wilson, 1935:295). Some larvae of Mycale syrinx rotate on a substratum for as long as 10 days before fixation. The duration of the larval period of Halisarca metschnikovi Lévi is 2 days, and that of Halisarca dujardini Johnston, less than 1 day (Lévi, 1956:79). Asexual larvae of Esperella fibresilis Wilson (Wilson, 1894:298) swim freely for 1 to 2 days, whereas, those of Callyspongia diffusa (Ridley) (Sivaramakrishnan, 1951:287) show natatory activities for only 6 to 8 hr. It is known that within a single species of marine animal the planktonic period varies considerably with temperature, the availability of food, and the proper substratum (Thorson, 1957:482; Moore, 1958:314). Tedania gurjanovae apparently has a brief swimming period, at least under laboratory conditions.

In the present study, as a parenchymula larva attached to the glass substratum by the anterior end, the ciliary beat slackened in frequency and within 10 to 15 min all cilia appeared to be motionless. Approximately 30 min after fixation the typical larval habitus became completely disorganized. The mesenchymal cells collapsed from their original position and spread into a flat light-yellow circular plate measuring about 600 μ in diameter (Fig. 3d). Segregation and spreading of cells continued. At 3 hr of age the

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**Fig. 2.** Spiculation of *Tedania gurjanovae* Koltun. a. Style, × 375; b. tornote, × 375; c. onychaete I, × 560; d. end of onychaete I, × 1260, note the echinations; e. onychaete II, × 375, note the comparatively finer echinations.
disc measured 1065 μ in diameter and consisted of an internal subspherical light-yellow mass 800 μ in diameter surrounded by a transparent band of protoplasm containing no observable cell boundaries (Fig. 3e). The rate of development in *Tedania gurjanovae* during the early stages of metamorphosis seems to be considerably more rapid than that described for *Lissodendoryx similis* (Ali, 1956). The length of time necessary for *Tedania gurjanovae* to reach histological maturity was not determined in the present study. Wilson (1935:295) reported that the formation of choanoocyte chambers and canals in some cultures of *Mycale syrinx* occurred within 3 to 4 days after discharge of the larva from the parent, and Lévi (1956:81) noted that the histogenesis of *Halisarca dujardini* into a functional rhagon took about 2 days after larval fixation.

At 1 day of age the juvenile encrustation revealed several small styles that were irregularly scattered in the mesenchyme. These may still have been the embryonic acanthostyles, but with the 112.5 X magnification of a dissecting microscope echinations were not apparent. At 7 days of age the styles were showing some evidence of orientation perpendicular to the substratum. After 13 days most of the styles, especially in the center of the disc, were oriented perpendicular to the substratum. Hastate tori notes were observed for the first time. A very thin dermal membrane with scattered mesenchymal cells constituted the sponge surface. The endosome was translucent and archeocytes were concentrated at the sponge base and around perpendicular megascleres. The sponge had almost doubled in thickness since the seventh day of attachment. No oscules were observed. At 19 days of age the colonies were almost unchanged except for increased thickness. One specimen had formed a fistule about 1.5 mm high.

The colonies were last observed on 28 August 1959 (at an age of 33 days). They had remained relatively minute. The largest two sponges measured roughly 1.5 mm by 0.75 mm and 2.0 mm by 0.75 mm in diameter. Their thickness did not exceed 2 mm. None of the specimens showed evidence of oscule formation. Perhaps in culture these sponges remained in a diminutive condition because their environmental conditions present in the laboratory differed from their natural deeper water habitat.

**TAXONOMIC DISCUSSION**

The holotype of *Tedania gurjanovae* Koltun is specimen No. 2974, Zoological Institut, Akademija Nauk, Leningrad, USSR. The habitus, habitus, and natural color of this species as reported by Koltun (1958:65) closely resemble that of local San Juan representatives. The spicule morphology and size are also very similar to local forms except that the onychae and are longer and more rugose in the Russian specimen. The endosomal anatomy is too briefly described to make a useful comparison. Koltun (1959:156) states: "The main skeleton is in appearance like an irregular net of organized bundles of spines."
Burton (1932:345) recognized the Vancouver Island specimen of *Tedania fragilis* Lambe (see Lambe, 1895:136) as 1 of the 24 valid species of its genus. De Laubenfels (1961:197) collected *Tedania fragilis* from a depth of 50 to 60 m, northeast of Blakeley Island (San Juan Archipelago). I examined the holotype (USNM No. 7401) of *Tedania fragilis* Lambe and found that it differs from specimens discussed in this paper in the following features: the spiculation is larger and onychaetes are often erratically curved. The short-size category of onychaetes is lacking. The hastate torrones often have slightly inflated ends that may be micropined. Some torrones have one end hastate and the other rounded or subtrigone. Style tracts are more abundant and interstitial styles are irregularly distributed, although some meshes do occur. The holotype is dry and exceptionally fragile. The specimens from the San Juan Archipelago described in this paper are placed tentatively in *Tedania gurjanovae* Koltun.

**SUMMARY**

The adult morphology, larval metamorphosis, biological associates, taxonomic status, and distribution of *Tedania gurjanovae* Koltun are described. This species has been dredged from a rock-shell substratum on the continental shelf and apparently ranges from the San Juan Archipelago in the northeast Pacific to Tatar Strait in the northwest Pacific. The larval natatory period is 6 to 7 hr. Metamorphosis involves a complete collapse of the larva into an amorphous mass somewhat platelike in over-all shape, within which many cells can be seen. Segregation occurs; this results in a core of inner cells (archeocytes) and an outer transparent layer of protoplasm not shown definitely to be cellular. Development continues to a miniature adult-like habitus which is reached after about 2 to 3 weeks.

**REFERENCES**


KOLTUN, V. M. 1958. Siliceous sponges (Corncuspiginda) from the southern region of the Kurile Islands and waters, washed up on southern Sakhalin. Issledovania Dalnevos-tochnyh Morei SSSR 5:42–77. [In Russian.]

——— 1959. Silicospongin sponges of the Northern and Far Eastern Seas of the USSR—Keys to the fauna of the USSR. Opredeliare Po Faune SSSR 67:1–227. [In Russian.]


Bathymetric Distribution of Chaetognaths

ANGELES ALVARÍNO

The present report on the vertical distribution of the Chaetognatha is based on a study of the collections of plankton made by the Scripps Institution of Oceanography expeditions in the Pacific (Fig. 1) and Indian oceans. Therefore, all the data included and discussed in this paper have been obtained by the author from studies and analysis of thousands of plankton samples from those oceans; and, when other sources of information are used in the discussion, the name and date of the corresponding authority and publication are given. The samples studied here that cover the Pacific and Indian oceans were taken at 140 m depth (oblique hauls), and at other various depths: 270, 300, 363, 600, 700 or 868 m (closing nets or vertical tows), down to 3000 m deep (mid-water trawls). The results obtained from these expeditions and from the material examined while studying the seasonal distribution of chaetognaths in the California waters, and also from previous work in the Atlantic, has made it possible to group the species of this phylum into several categories based on their distribution in depth.

The correlation between the distribution in depth of the species and the conditions affecting this distribution can only be reached through a knowledge of the two-dimensional distribution of each of the species, the factors involved in their distributional fluctuations, and the extent to which changes in those factors may affect the distributional pattern.

It was found, from these observations, that each individual species of chaetognaths occurs generally at about the same levels throughout the oceans, with the particular exception of Eukrohnia hamata (Möbius), as will be shown later in this paper. Therefore, these species can be grouped in three categories according to the strata they populate:

- Epipelagtonic (upper 150–200 m)
- Mesoplanktonic (200–1000 m)
- Bathypelagtonic (below 1000 m level)

In each of these categories several series of stratification, or zonations, can be established. In the upper layers there is more zonation of the species than in the levels below 200 m. Because of the large number of species involved and the great variability of the conditions in the upper layers, the picture is a complex one. Migrations related to food, light, and seasonal changes may take place in the upper strata. In these upper layers competition is more active than in the deeper strata, and this is conditioned by the large number of species involved.

In general, the Chaetognatha decrease in number of species and in number of individuals per species with increase in depth, that is, the number of individuals per volumetric unit of water is larger in the upper layers than in deep waters. The species typical of waters below the 200 m level are one-fifth of the total of the phylum. Differences are found regarding this point, depending on the geographical localities under study. Thiel (1938) found more species and greater biomass of chaetognaths in the upper 50 m. Hida (1957) stated: "regardless of time of day of hauling, oblique hauls between the surface and 40 m. yield larger numbers of chaetognaths and pteropods for m³ of water strained than deeper hauls between the surface and 140 m." A similar relation was found in the tropical Pacific (Hida and King, 1955). However, in both north and south high latitudes the layers below 200 m sustain a larger number of species of chaetognaths than do the upper strata. Whereas, as noted above, in other oceanic

1 Contributions from Scripps Institution of Oceanography, New Series. Manuscript received July 5, 1962.
regions the number of species in the upper 200 m exceeds the number of those in the deeper levels.

DISCUSSION

The Chaetognatha have six pelagic genera: Bathyspadella (recorded once, Tokioka, 1939), Heterokrohnia, Eukrohnia, Krohnitta, Pterosagitta, and Sagitta. The first two inhabit waters below the 1000 m level, Eukrohnia is mainly bathypelagic, with the exception of *E. hamata*, which changes its distribution in depth with latitude. Pterosagitta and Krohnitta populate the upper strata. The genus Sagitta is the most successful of the group: it appears to have the highest evolutionary level in the phylum, is the most abundant in species, and inhabits the greatest variety of environments throughout the oceans. Consequently, its species appear in each of the oceanic levels.

The species of Chaetognatha observed by the author in the samples studied from the Pacific and Indian oceans can be grouped as follows:

Epipelagtonic:
- *Krohnitta subtilis* (Grassi) 1881
- *K. pacifica* (Aida) 1897
- *Pterosagitta draco* (Krohn) 1853
- *Sagitta bedoti* Béraneck 1895

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**Fig. 1.** Plan of the stations of the various expeditions in the Pacific.
S. bierii Alvariño 1961
S. bipunctata Quoy and Gaimard 1827
S. elegans Verrill 1873
S. euneritica Alvariño 1961
S. eugenioides Doncaster 1903
S. hexaptera d’Orbigny 1834
S. hydroides Alvariño 1853
S. minima Grassi 1881
S. pacifica Tokioka 1940
S. pseudoserratodecens Tokioka 1939
S. pulchrna Doncaster 1903
S. regularis Aida 1897
S. serippsae Alvariño 1962
S. tasmanica Thomson 1947

Mesoplanktonic:
Sagitta decipiens Fowler 1905
S. macrocephala Fowler 1905
S. marri David 1956
S. planctonis Steinhaus 1896
S. zereios Fowler 1905
S. maxima (Conant) 1896

Bathyplanktonic:
Eukrohnia bathyantarctica David 1958
E. bathypelagica Alvariño 1962
E. fowleri Ritter-Zahony 1909
E. hamata (Möbius) 1875 (in low latitudes)

Heterokrohnia mirabilis Ritter-Zahony 1911 (recorded in the Pacific by Bieri, 1959; Tchindonova, 1955)

The species present below 200 m are cosmopolitan in distribution (inhabiting the Atlantic, Indian, and Pacific oceans), with the exception of E. bathyantarctica and S. marri, which were recorded circumpolarly in Antarctic waters; E. bathypelagica which appears to be restricted to the depths of the Pacific and Indian oceans, according to the present data (Alvariño, 1962, 196-196), and Bathyspadella edentata, represented by one specimen from the Pacific (Tokioka, 1939).

Sagitta elegans and S. gazellae typify the arctic-subarctic and the antarctic-subantarctic waters respectively (Fig. 2). The arctic constitutes an ecological individuality because of its uniform conditions. S. elegans is the typical chaetognath of the upper 100–150 m of this region, extending into the northern part of both the Pacific and the Atlantic. The extension of the distribution of S. elegans appears to be controlled by the concentration of oxygen in the water. S. elegans extends in the Pacific to 38°N. Here 297 plankton samples were studied from 182 stations distributed along this northern Pacific region. S. elegans was found in only 128 localities, and in each case it was concurrent.

Fig. 2. World distribution of S. elegans and S. gazellae. Location of the profiles that appear in this paper.
TABLE 1

Species Observed at Different Depths in Various Pacific Water Masses

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<th>DEPTH OF HAUL&lt;sup&gt;1&lt;/sup&gt; (meters)</th>
<th>SPECIES (author's data)</th>
<th>DEPTH OF HAUL&lt;sup&gt;1&lt;/sup&gt; (meters)</th>
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<sup>1</sup> It is obvious that the species recorded at the various depth-hauls may be listed in more than one place in these strata. For instance, <i>S. hexaptera</i> in California waters appears in both the upper 150 m and in hauls from 300 to 150 m. Similarly, <i>K. pacifica</i> in the northwest central Pacific waters appeared in samples from 150–326 m, etc. It should be understood that, broadly speaking, the species of chaetognaths belong to either the epi-, meso-, or bathyplanktonic domain, and that only in the particular cases previously explained, their bathymetric distribution appears to be altered because of currents (sinking of the waters, upwelling, etc.).
<table>
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<tr>
<th>REGION</th>
<th>DEPTH OF HAUL(^1) (meters)</th>
<th>SPECIES (author’s data)</th>
<th>REGION</th>
<th>DEPTH OF HAUL(^1) (meters)</th>
<th>SPECIES (author’s data)</th>
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</table>
| northwest Pacific central waters | upper 150                     | *K. pacifica*  
*K. subtilis*  
P. draco  
S. bedoti  
*S. bipunctata*  
*S. enflata*  
S. ferox  
S. hexaptera  
S. minima  
S. pacifica* | southeast central Pacific waters | upper 140  
|                               |                               |                                                                            |                               | *K. subtilis*  
P. draco  
*S. bipunctata*  
*S. enflata*  
S. ferox  
S. hexaptera  
S. minima  
S. pacifica* |                               |
|                               | 325–150                       | *K. pacifica*  
S. decipiens* |                               | 500–140                       | *S. decipiens*  
S. gazellae  
S. zetesios* |
|                               | below 500                     | *E. bathypelagica*  
E. fowleri  
E. hamata  
*H. mirabilis\(^2\)*  
*S. macrocephala*  
S. maxima  
S. zetesios* |
| Pacific equatorial waters     | upper 150                     | *K. pacifica*  
*K. subtilis*  
P. draco  
S. bedoti  
*S. bipunctata*  
*S. enflata*  
S. ferox  
S. hexaptera  
S. neglecta  
S. minima  
S. pacifica  
*S. pseudoserratodentata*  
S. pulchra  
S. regularis  
S. robusta*  
S. decipiens  
S. zetesios* |
|                               | 283–140                       | *E. hamata*  
*S. hexaptera*  
S. zetesios* |
|                               | 600–300                       | *E. hamata*  
S. decipiens  
S. planctonis* |
|                               | below 600                     | *E. bathypelagica*  
E. fowleri  
S. macrocephala  
S. maxima* |
| subantarctic waters           | upper 150                     | *E. hamata*  
S. gazellae  
S. taimanica* |
|                               | 283–140                       | *E. hamata*  
*S. hexaptera* |
|                               | 600–300                       | *E. hamata*  
S. decipiens  
S. planctonis* |
|                               | below 600                     | *E. bathypelagica*  
E. fowleri  
S. macrocephala  
S. maxima* |
| antarctic waters              | upper 150                     | *E. hamata*  
S. gazellae* |
|                               | 283–140                       | *E. hamata*  
*S. hexaptera* |
|                               | 600–150                       | *S. marri*  
S. maxima  
S. planctonis* |
|                               | below 2000                    | *E. bathyantarctica* |

\(^{1}\) Tchindonova and Tokioka records.  
\(^{2}\) Bieri’s records.
with oxygen values of more than 6 ml/L. The presence of *S. elegans* was expected in the rest of the localities of this region (because of the characteristics of the waters); however, it was noteworthy that every negative station and sample for *S. elegans* corresponded to oxygen values below 6 ml/liter. Consequently it was found in these studies that *S. elegans* does not occur in the Pacific in waters with less concentration of oxygen than the amount stated above; and this could also be the limiting factor in the spreading of this chaetognath to deeper levels. *S. elegans* is present in the Oyashio waters, but when these waters collide with the Kuroshio, its southern distribution is abruptly interrupted, even at deep levels, in the region where the two bodies of water meet.

The conditions are also more or less uniform in antarctic waters in the west–east direction (Baker, 1954), while the gradients change from south to north. It is well known that the plankton (and this is true for the Chaetognatha population according to our data) follows a rather homogeneous circumpolar distribution in the antarctic belt. *S. gazellae* is the typical chaetognath in the upper layers of these waters. It extends along the antarctic and subantarctic regions spreading northward from the subtropical convergence in deep waters.

*S. gazellae* was observed in the present study at MacMurdo Sound (samples were kindly sent by Mr. J. L. Littlepage), in a current from ice-water interface to 7, 10, and 72 m depth; extending along the upper 200 m in the south Pacific to 30° S, and to 21° S at about 400 m depth. *S. gazellae* was also observed in the upper 200 m, in the samples taken by the Drake Expedition (material kindly sent from Argentina by Dr. E. Balech) at 55° S to 60° S and 60° W to 62° W to 63° 33' W.

The typical mesoplanktonic Chaetognatha occupy different layers. Thus *S. decipiens* inhabits the upper part of the mesoplanktonic region, while *S. zetesios* and *S. planctonis* occupy the core, and *S. macrocephala* and *S. marri* extend from the lower levels of the mesoplankton to the upper part of the bathyplanktonic domain, and *S. maxima* changes its depth distribution with latitude. The fact that David (1956), Moore (1949), and Thomson (1947) reported *S. planctonis* in surface waters could be due to upwelling processes. *S. planckonis* Steinhaus and *S. zetesios* Fowler are easily distinguished (although many authors failed to separate them), by using morphological characteristics that are constant, instead of the meristic characteristics related to hooks, teeth, etc. For example, reliable morphological characteristics for this identification are: length of tail segment in relation to the total length, and the shape and position of the lateral fins. In *S. planctonis* the tail segment is shorter than in *S. zetesios*. The posterior fins in *S. planctonis* are triangular in shape, while those in *S. zetesios* are roundish. In *S. planctonis* the anterior end of the anterior fins reach up to the level of the ventral ganglion, whereas in *S. zetesios* they reach only to the level of the posterior end of the ventral ganglion. In order to verify this, here are the quotations from the respective species' authors. Steinhaus (1896): "Vorderflossen sehr sehrmal bis zur Mitte des Bauchganglion"; and Fowler (1905): "anterior fin well separated from the posterior, longer and narrower than posterior, wider behind than in front, not quite or only reaching the hinder end of the ventral ganglion."

In the samples studied here, *S. marri* was found only at levels below 200 m, south of parallel 50° S, in 59% of the samples from stations located between 50° S and 65° S, in the south Australian waters and the south Pacific.

*S. planctonis* was observed in the present studies distributed along the subantarctic waters, in a region limited by the subtropical convergence and the antarctic convergence.

*S. hexaperta, S. regularis*, and *K. pacifica* are also found very often extending (present data) to the lowest strata of the epipelagial and even to the upper strata of the mesoplankton.

*S. bipunctata* is an oceanic cosmopolitan species, which inhabits the epipelagionic region, extending in the Pacific from the 40° N to the 35° S (Alvariños, in press a). Bieri (1959) suggested it is an antequatorial species, as he did not find it within 5° to 10° on either side of the Equator. *S. bipunctata* was observed in the present studies in the upper 150 m in 46 stations along the Pacific equatorial belt, in a band of a width extending from 10° N to 15° S. (The stations correspond to the following expeditions: Equapac Horizon, Equapac Stranger,
The bathypelagic domain is populated by E. fowleri, E. bathyantarctica, E. bathypelagica, H. mirabilis, and B. edentata.

Some species, such as E. hamata, E. fowleri, E. bathypelagica, H. mirabilis, S. maxima, and S. macrocephala, are common to both the arctic-subarctic and antarctic-subantarctic waters. They are cosmopolitan in the most complete sense, with the exception of E. bathypelagica, connecting both polar or subpolar regions along the depths of the oceans. Thus, the isolation of the arctic and antarctic is relative (Barnes, 1957). E. hamata populates the Atlantic, Pacific, and Indian oceans at different depths, and the upper layers of the arctic and antarctic (various authors and personal unpublished data). E. fowleri also inhabits the three oceans, extending in the Pacific from 53° 57' N to 46° S (several authors, and personal unpublished notes). E. bathypelagica (personal studies) extends in the Pacific from 53° 56' N to 46° S. H. mirabilis, reported by Bieri (1959), David (1958b), Ritter-Zahony (1911), and Tchindonova (1955), was observed in samples taken respectively from 2300 m, 3000-2000 m, 2000-3423 m, and 5000 m. S. macrocephala (personal records) appeared in the Pacific from 40° N to 46° S. S. maxima was observed in the present material from 45° N to 46° S. However, observations obtained up to the present show that the antarctic and subantarctic waters have three indigenous chaetognaths: S. gazellae in the upper layers, and E. bathyantarctica and S. marri in deep waters. The antarctic belt also has indigenous siphonophores: Diphyes antarctica, Marrus antarcticus, and Pyrostegophos vanboeffenii, and one species, Dimophyes arctica, which is common to the arctic and antarctic waters, extending to deep levels at low latitudes (author, unpublished data). The arctic-subarctic region has S. elegans as a chaetognath of its own, and no siphonophore restricted exclusively to this region.

In the Pacific from 40° N to 40° S at least 20 species of oceanic Chaetognatha are present in the upper 200 m. In this same span, two other species of Sagitta are found at depths below the 200 m level: S. decipiens, extending from 200 or 600 m deep; and S. zeteticus, from 300 to 800 m, besides the other species that cover the same span but extend both northward and southward. This zonation in depth is also observed for both species in the Atlantic and Indian oceans (author, unpublished data).

The mesopelagic domain can be subdivided into three zones: upper, median, and low, each having its characteristic species. The indications are that each species may have its own vertical range, a region in which to find optimal conditions. The zonation in the strata varies, not only for the different species but also for the respective individuals at different stages of maturity. The type of distribution for some species may vary with latitude, season, etc. Thus it is necessary to emphasize that the above established classification must be further subdivided into other types of vertical stratification or zonations. These are:

1. Vertical distribution related to latitude.
2. Vertical distribution affected by the circulation in the oceans.
3. Ontogenic vertical distribution.
4. Seasonal and diurnal vertical distribution.

With the exception of zonation in relation to seasonal or diurnal migration, a problem that merits special attention in another study, these points will now be discussed.


The sampling at different depths unfortunately does not cover the Pacific conveniently. Although in most of the cases the plankton samples were taken at different depths in each of the stations distributed throughout the Pacific (Fig. 1), in only half of the cases were the stratified samples taken with closing nets. However, with the data at hand it could be observed that the distribution in depth varies for some species with the geographical location. Species that appear only in deep layers in one region, are found in shallower depths or in surface waters in other areas.

E. hamata is unique in this respect; it covers the epil-, meso-, or bathypelagic categories in relation to latitude. It lives at great depths in the tropical and subtropical regions of the oceans, but in the subarctic and subantarctic regions it gradually rises near the surface toward
both poles (Fig. 3). This diagram is very similar to that of Thiel (1938) for the same species, covering from 60° S to 20° N in the Atlantic. This schematic diagram showing the distribution of *E. hamata* in the Pacific from arctic to antarctic waters was made by combining the data obtained from the study of more than 4,000 samples taken by the Scripps Expeditions in the Pacific from 1952 to 1962 (Fig. 1), and the monthly CalCOFI cruises for 1954 and 1958. It is important to notice in the present diagram the incipient emergence of *E. hamata* in the equatorial region. This emergence was also found for *E. fowleri* and *S. maxima*; while *S. bipunctata* occasionally submerged slightly in some locations of this region. For example, at station 49 of the Transpacific Expedition (47° 35.7' N—167° 44.8' E), the maximum number of individuals of *E. hamata* was found at about 225 m depth (Figs. 4, 5). In this locality the number of specimens or the volume of chaetognaths will be larger at this depth than at any other layer in this column of water, although the chaetognath population is represented by only one species. However, if these data were combined with the data from several other localities, the large amount of specimens at this layer will be shown in the results. This may be the case in Leavitt’s (1947) surprising results.

*S. maxima* follows a pattern rather similar to *E. hamata* in its respective vertical distribution in the Pacific; it was observed in the present studies from 45° N to 46° S, although it reaches levels below those occupied by *E. hamata* in both high latitudes. *S. maxima* was observed 20 times in California waters, at about 140 m depth, in regions where upwelling was evident. However, it is found in these waters normally at depths below 140 m (author, unpublished data).

The adjacent seas isolated from the depths of the ocean by shallow regions do not have representatives of the bathyplanktonic species. *E. hamata* is recorded along the narrow Aleutian passes that connect the Bering Sea with the Pacific, as this species extends into the surface layers in that region. However, in other areas, where the population of *E. hamata* does not inhabit the upper strata and the connecting sill with neighboring waters is above its vertical distribution level, it does not pass to adjacent seas. This could be the case in the Mediterranean, where the Gibraltar sill at a depth of 320 m and the outward undercurrent make a barrier to the inward migration of the chaetognaths which inhabit layers below the threshold. A similar picture was found for the Siphonophorae (Bigelow and Sears, 1936); for the deep water Medusae (Kram, 1924), and for the euphausiids (Ruud, 1936). Germain and Joubin (1916) reported *E. hamata* and *S. planctonis* from six and four localities respectively in the Mediterranean. Germain (1930–1932) includes *E. hamata* in the fauna list of the Mediterranean and explains that *S. macro-
cephala does not enter these waters. I examined the literature on the Chaetognatha of the Mediterranean and the following authors did not find either of these species in the Mediterranean: Alvariño (1957a), Baldasseroni (1913, 1914), Furnestin (1953a, b, 1955, 1956, 1957, 1958a, b), Ghirardelli (1950, 1952), Hamon (1952), Ramul and Rose (1945), Rose and Hamon (1953), Scaccini and Ghirardelli (1941), Trégouboff (1958a, b). Ghirardelli (1950) says: "Il prof. Trégouboff mi segnala di aver pescato una sola volta un unico esemplare di E. hamata che disgraziatamente è andato perduto." Rose (in Trégouboff and Rose 1957:482) says: "E. hamata est rarissime, elle n'a été vue qu'une fois à Villefranche par M. Trégouboff..." and that "S. planctonis est très rare et vit à grande profondeur. Nous ne l'avons jamais recoltée." Furnestin (1953a) says that certain species of chaetognaths (S. hexaptera, S. setosa, S. planctonis, P. draco, Spadella cephaloptera, and Spadella profunda) were not found in the samples she analyzed, although they were reported by other authors, and she considers some of those species "extrêmement rares et d'autres demanderaient même confirmation de leur présence, comme c'est le cas pour S. planctonis, Spadella profunda, E. hamata."

All this information suggests that either only a few individuals of S. planctonis and E. hamata enter the Mediterranean occasionally, which might happen when the outflow slows down and the Atlantic inflow conveys into the Mediterranean stray members of the respective chaetognath populations from regions in the Atlantic where these chaetognaths appear in the epipelagtonic layers; or the positive records reported are erroneous due to contamination, or mislabeling of the samples, or other error. E. hamata has been observed (Alvariño, 1957b) over the Iberian Atlantic continental shelf, at depths from 5 to 10 m, in regions of upwelling (author, unpublished notes), and at less than 50 m at 46° and 47° N in the Bay of Biscay (author, unpublished data).

No E. fouleri, S. macrocephala, or S. zetesios have been observed in the Mediterranean, and perhaps, according to the references above, also E. hamata and S. planctonis could be included in this group.

The Gulf of California connects with the Pacific along the deep open sea, and E. hamata was observed there in samples taken from 700 m depth.

The restriction of E. bathyantarctica and S. marii to antarctic waters could be due to the fact that they inhabit the belt of great depths occurring in those waters (Baker, 1954), in a region well defined by the antarctic West Wind Drift. Their distribution pattern is probably related to the circulation systems of theantarctic regions; thus they appear to be confined to the waters of the subantarctic West Wind Drift.

2. Vertical distribution affected by the oceanic circulation.

Each of the species of chaetognaths occupies different zones in the corresponding epipelagtonic, mesopelagtonic, or bathyplanktonic domains. The levels each species occupies change somewhat under the effects of the geographical location, and there is evidence of stratification associated with size and maturity of the individuals, which will be discussed later.

Sometimes a given species does not follow the normal distribution pattern, and it appears to assume a stratification dependent upon the prevailing currents and turbulence. In certain localities, species typical of the upper layers are recorded at deeper levels than usual, apparently due to the sinking of the water masses they populate, or deep water species may appear in the upper layers because of upwelling. These phenomena are detected throughout the examination of the chaetognath population and are correlated with hydrographic data (Alvariño, 1962, in press a).
Figure 5 is a quantitative profile of the distribution of the chaetognaths in the northwest Pacific, off the Kurile Trench. This diagram shows that the number of specimens, mainly of *E. hamata* (see also Fig. 4) is highest at about 200-300 m. The pattern formed at stations 52 and 54 (Fig. 6) is probably due to the turbulence and piling up of the central Pacific waters against the northern waters. At stations 52 and 54 (Fig. 6) eight species of chaetognaths were observed in the upper 200 m, six were observed from 510 m to 200 m, and four species below 510 m; whereas at stations 44–50 *S. elegans* and *E. hamata* were the only chaetognaths recorded in the upper 200 m and the latter in the strata below these levels. At stations 52 and 54 in the upper 200 m converge *S. elegans* (arctic-subarctic); *S. scrippsae* (transition); *S. minima*, *S. hexaptera*, *P. draco*, *K. subsilis* (central Pacific), and *S. bedoti* (typical in those longitudes of Kuroshio waters). Between 510 m and 300 m *S. scrippsae*, *S. minima* and *K. subsilis* are still found, with *S. decipiens*, *S. zetesios* and *E. hamata*. Below 510 m occur *S. decipiens*, *S. zetesios*, *S. macrocephala* and *E. hamata*. In these stations (52 and 54) more species are found in the upper 200 m and mid-levels than in the deep layers.

The southern boundary of *S. elegans*’ distribution in the eastern Pacific and the northern boundary of *S. scrippsae* overlap (Fig. 7). *S. scrippsae*, an epipelagtonic and typical chaetognath of the Transition Area (between central Pacific and subarctic waters), the Alaska gyral, and the California Current (Alvariño, 1962, in press a), modifies its distribution in depth with the geographical region and with the age of the individuals. *S. scrippsae* extends along the upper 200 m in its main distributional region; but in the southernmost boundaries of the California Current, where these waters meet the warm inflow from the south and southwest, the population of *S. scrippsae* sinks with the cold waters (Fig. 8), reaching a depth of 600 m in the outermost edges of the distributional region. This means that, although *S. scrippsae*
has in general an epiplanktonic distribution, it sinks to deeper levels in the southernmost part of the California Current and disappears in these sinking waters. In this case, the distribution of *S. scrippsae* in the lowest levels of the epiplanktonic domain or in upper layers of the mesoplanktonic region is due to the geographical location that is related to the oceanic circulation.

From station 25 southward (53° 32.5' N—163° 20.8' W to 35° 46.8' N—130° 02.5' W) the waters in the upper 200 m are inhabited by several species of *Sagitta* (Fig. 7): *S. elegans* from 41° N northward (station 13), and *S. scrippsae* (outstanding as an "indicator" of the California Current) from 46° N southward; and, from 40° N southward, also were present *S. bierii*, *S. pacifica*, *S. pseudoserratodentata*, *S. bipunctata*, *S. hexaperta*, *S. enslata*, *K. subtilis*, plus 10 other species that populate the low latitudinal regions of the California waters. In this section (Fig. 7) can be observed the progressive sinking of *E. hamata* toward the low latitudes, and the stratification of *S. decipiens*, *S. zetesios*, and *S. macrocephala* (see also Fig. 9).

*S. decipiens* extends in the Pacific from the southern boundary of the subarctic waters to the subtropical convergence in the southern hemisphere. It populates the mesoplanktonic layers, and occasionally is found in the upper 140 m hauls, in which case its occurrence is an evidence of upwelling in that particular location, confirmed in every case by the hydrographic data (Alvarino, in press a).

*S. zetesios* extends in the Pacific from 46° N to 36° S, and *S. planctonis* from about 30° S southward. It appears from the author's data that the first species is more abundant than the latter.

*S. macrocephala* was observed from the Aleutian Trench region to 46° S in the Pacific (personal data).

The record of a particular species at greater depths than usual may be due to different factors, as already explained. Therefore, the difference is clear between truly deep water species like *E. fowleri*, midwater *S. decipiens*, *S. macrocephala*, and *E. hamata* (epiplanktonic in high latitudes, bathypelagic in low latitudes), or *S.*

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**Fig. 6.** Profile Stations 44–54 of the Transpac Expedition (53° 40.8’ N, 161° 55.5’ E to 40° 34.5’ N, 170° 02.3’ E).
**Bathymetric Distribution of Chaetognaths—Alvariño**

Fig. 7. Profile of the Transpac Expedition, Stations 4–24 (35° 46.8' N, 130° 02.5' W and 53° 15.0' N, 161° 55.0' W).

*scrippseae* (epiplanktonic, although at the southermmost part of its distribution region this species sinks with the waters it populates).

Epiplanktonic species appearing at deeper layers than usual may indicate a convergence. An illustration of this point was found by the author in a region in the south central Pacific, where the respective northern and southern boundaries of distribution of *S. gazellae* and *S. pacifica* coincide at depths below 200 m. This overlapping in the distribution of *S. gazellae* and *S. pacifica* was obtained from the examination of samples from the Downwind and Monsoon expeditions. The stations of the Downwind Expedition used in this case extended from 23° 30' N—125° 05' W to 46° 25' S—123° 38' W and 125° 03' W (October 1957 to December 1957), and from 10° 01.5' N—118° 58' W to

Fig. 8. Profile Stations 94–106 of the NORPAC CalCOFI Expedition (31° 01' N, 118° 07' W to 27° 25' N, 150° 00' W). The distribution of *S. scrippseae* has been disclosed from the other species that occur in the same region.
S. decipiens

Fig. 9. Profile Stations 33-43 of the NORPAC CalCOFI Expedition (41° 45' N, 124° 29' W to 38° 35' N, 149° 59' W); with the distribution in depth of the mesoplanktonic species in the California waters. Notice the offshore sinking of E. hamata.

46° 44' S—113° 09' W (December 1957 to February 1958). The data from Monsoon Expedition covered from 64° 11' S—165° 56' W and 63° 05' S—178° 31' E to 11° 03' N—142° 28' W (February 1961 to April 1961). The data for S. gazellae at latitudes higher than 64° S are from MacMurdo Sound. The bathymetric distribution of S. pacifica northward from 20° N was obtained by studying records from the Capricorn, NorthPac, Equapac, Transpac, Shellback, and Tethys expeditions.

There is no doubt of the proper identification of both species. S. gazellae can be well separated from its close relatives (see Alvarino, 1962, and references. For S. pacifica see Alvariño, 1961, and references).

S. gazellae extends from the antarctic waters to 29° S in the Pacific, spreading farther north at mid-depths at stations where S. pacifica was also recorded in deeper layers than usual. S. pacifica, an inhabitant of the upper 100 m in the tropical and equatorial Pacific, extending from 40° N to 20° S, and from here to 35° S, was observed at levels below 200 m down to 400 m. These two species, one recruited from the tropical Pacific (S. pacifica), and other from the antarctic-subantarctic waters (S. gazellae), populate the upper 100 m in their respective dis-

Fig. 10. Latitudinal bathymetric distribution of S. pacifica and S. gazellae.
tributational region, and their corresponding southernmost and northernmost edges of their respective domains overlap in deep waters (Fig. 10), indicating a region of convergence in the respective distribution of the species—a convergence that partially coincides with the region of the hydrological convergence. *S. hexaplera*, *S. bipunctata*, *S. enflata*, *K. subtilis*, and *P. draco* (cosmopolitan species inhabiting the Pacific central waters) were recorded in the upper layers of that region of convergence, whereas at levels below 300 m *S. gazellea*, *S. pacifica*, *S. decipiens*, *S. macrocephala*, *E. fowleri*, *E. bathypelagica*, *E. hamata*, and *S. zetitesios* were recorded. The specimens of *S. gazellea* recorded in this region were less than 20 mm long, at early Stage I of maturity. The boundary of the subtropical convergence also marks the northern limit of the distribution of *S. tasmanica* and *S. planctonis*.

In other instances, when two masses of water pass one above the other, then the typical cold water species sink with the waters while the warm water species extend throughout the upper layers.

*S. tasmanica* inhabits the upper 150 m in the Atlantic and in the southernmost part of the Indian Ocean (author, unpublished data). It enters the Pacific along with the subantarctic West Wind Drift, and its northward spread into the south Pacific stops at the region of the subtropical convergence. It extends westward, turning northward off the southern part of South America. This is demonstrated by the records of this species off Chile and at the southern part of Peru. It does not progress in the main Peru Current. The author’s data on the distribution of *S. tasmanica* in the Indian and Pacific oceans were obtained from samples collected by the Scripps Expeditions in both oceans (paper in preparation). Unfortunately, David (1958, 1959) did not explain if the *serratodentata* he recorded is *S. serratodentata* Krohn or *S. tasmanica* Thomson; although the locations of the records correspond to the distributional region of the latter.

*S. planctonis* extends along the mid-depths of the Atlantic and Indian oceans, and enters the south Pacific with the subantarctic West Wind Drift, spreading to the subtropical convergence (personal data).

The greatest number of specimens for the
smallest number of species per unit volume of water filtered was found in the arctic-subarctic and antarctic-subantarctic regions and in some localities of the transition and neritic areas (personal data). The greatest specific diversity with a small number of specimens was found in the subtropical, tropical, and equatorial waters, and in regions of mixing of waters from the above extreme geographical regions.

To emphasize the importance of the ocean's circulation with respect to zonation in depth of chaetognath species, diagrams from the different geographical localities and zones of dynamic disturbances have been prepared (Fig. 11). These diagrams show in general the quantitative specific distribution in depth of the Chaetognatha in the different water masses of the Pacific. The results obtained do not preclude the possibility that in the future, with more detailed studies, some slight variations may be observed. The California region includes the species recorded there from latitude 42° N to the southernmost tip of Baja California. This region appears to have the greatest number of species of chaetognaths in the upper 200 m, and the study of those species indicates the various origins of the inflows into the region. In Figure

TABLE 2

<table>
<thead>
<tr>
<th>LATITUDE N</th>
<th>DEPTH (meters)</th>
<th>MAXIMUM SIZE (millimeters)</th>
</tr>
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<td></td>
<td>300</td>
<td>50</td>
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<tr>
<td></td>
<td>below 300</td>
<td>60</td>
</tr>
<tr>
<td>39°</td>
<td>170</td>
<td>&lt;30</td>
</tr>
<tr>
<td></td>
<td>340</td>
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<tr>
<td></td>
<td>510</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td>680</td>
<td>60</td>
</tr>
</tbody>
</table>

Fig. 12. Ontogenic vertical and latitudinal distribution of *S. gazellae.*
Ontogenic Vertical Distribution of *S. gazellae*

<table>
<thead>
<tr>
<th>LATITUDE S</th>
<th>DEPTH (meters)</th>
<th>MAXIMUM SIZE (millimeters)</th>
</tr>
</thead>
</table>
| MacMurdo Sound (77°) 46°  
42°          | 7, 10, 72       | 90                        |
|            | 140            | 40                        |
|            | 283            | 50                        |
|            | 346            | 60                        |
|            | 283            | 40                        |
|            | 400            | 45                        |

11 the southern part of the subarctic waters is called the transition area.  
*S. pseudoserradentata* and *S. bierii* are typical of the northeast Pacific central waters; and *S. lyra* of the northwest central waters, mainly the Kuroshio. Probably there are species typical of either southeast central and southwest central Pacific waters. Here are included our data from only the southeast central Pacific waters, because of the few data at hand from the southwest central Pacific region.

3. Ontogenic distribution of the chaetognaths with depth

Bigelow (1926), Huntsman (1919), and Russell (1931) found that the young of *S. elegans* appear in more superficial waters than do the adults. Fowler (1905) reported similar behavior for *E. hamata*. These records agree with my personal observations for the above species.

Ontogenic Latitudinal Distribution of *S. scirppae*

<table>
<thead>
<tr>
<th>LATITUDE N</th>
<th>MAXIMUM SIZE RANGE RECORDED (millimeters)</th>
</tr>
</thead>
<tbody>
<tr>
<td>46°</td>
<td>60</td>
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<tr>
<td>44°</td>
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</tr>
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<td>42°</td>
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<td>40°</td>
<td>60</td>
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<tr>
<td>38°</td>
<td>46–50</td>
</tr>
<tr>
<td>36°</td>
<td>40–45</td>
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<tr>
<td>34°</td>
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<tr>
<td>32°</td>
<td>32–45</td>
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<tr>
<td>30°</td>
<td>28–45</td>
</tr>
<tr>
<td>28°</td>
<td>24–40</td>
</tr>
<tr>
<td>26°</td>
<td>15–36</td>
</tr>
<tr>
<td>24°</td>
<td>10–34</td>
</tr>
</tbody>
</table>

and for *S. scirppae*, *S. gazellae*, *S. zetesi*, *E. fowleri*, *S. minima*, *S. planctonis*, and *S. macrocephala*.

The life history of these species might possibly reflect the history of the phylum. It appears that the older genera and species have been relegated to the deep strata. The young genera and the young of each of the species are represented by a large number of species and individuals respectively per volumetric unit of water; while the old genera and species have fewer species and individuals respectively, in those parameters.

The movement of the adults to deep layers could also be related to increased in weight of the individuals, associated with ripening of the sexual products. Further observations on this type of behavior might show if the Chaetognatha respond to a change in density like *Daphnia pulex* (Eyden, 1923), which decreases in specific gravity when emptying its brood pouch. A similar regulation in pelagic fishes has been observed by several authors.

A size stratification is usually found; sometimes the mature specimens do not invade the deep strata. Mature *S. scirppae*, 50–60 mm in length were found in the upper 140 m collections, at 43° 46.5' N—125° 08.5' W to 43° 26.5' N—125° 08.5' W.
Personal observations on the ontogenic distribution of *S. gazellae* are shown in Figure 12. This agrees with David’s (1955) ontogenic distribution of this species.

Adults as well as young *S. scrippsi* were found in the transition region and in the main part of the California Current, while only the young were recorded at the outer edges and southernmost boundaries of these water masses. The structure of the population of *S. scrippsi* shifts with latitude along with the extension of the inflow of the respective water mass (Alvariño, in press).

It was observed that only the young of *S. gazellae* (present data) and *S. scrippsi* spread to the outer edge of their distributional region.

The young of *S. zetesios* appeared in the northeast Pacific at about 300 m, whereas the adults were found only at depths below 500 m.

In station 46 of the NORPAC CalCOFI (38° 20’ N—127° 05’ W) specimens of *S. minima* of a size larger than usual were found from 700 to 280 m depth.

Studies of the life history of the species, mainly those of particular interest as “indicators,” will give some understanding of their ecological needs, and of their relation to oceanographic concepts.

ACKNOWLEDGMENTS

This work was carried out under the Marine Life Research Program, the Scripps Institution of Oceanography’s component of the CalCOFI, and also was supported in part by a grant from the National Science Foundation (NSF G19417).

I wish to express my grateful appreciation to Dr. M. W. Johnson, Dr. E. W. Fager, and Dr. Mary Sears for their kind advice and helpful suggestions.

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Contributions to the Knowledge of the Alpheid Shrimp of the Pacific Ocean, IX
Collections from the Phoenix and Line Islands

Albert H. and Dora May Banner

This paper initiates a series of three studies in the continuing series on the alpheids from the central Pacific that are based primarily upon collections made under the auspices of the Bernice P. Bishop Museum. In 1954 the senior author received a travel grant from the Bernice P. Bishop Museum and Yale University that permitted him to collect alpheids from wide areas in the central Pacific. The grant was made as part of the tri-institution program (TRIPP) of those two institutions and the University of Hawaii for the increase of scientific knowledge of the Pacific.

While collecting under the grant the Phoenix, Fiji, Tonga, Samoa, Cook, and Society archipelagos were visited. In each group of islands the marine environment was sampled as thoroughly as possible, with windward and lee reefs, lagoon, and ocean habitats being examined. Wherever possible a rough transect was taken across the reef to the depths that could be reached by effective skin diving. Often, however, difficulties in transportation interfered with the collecting scheme. For example, it was impossible in the time available to reach the low islands in the Fijian Archipelago, or the Tuamotus. Moreover, strong winds and surf at times rendered collecting on the outer side of the ocean reef too dangerous. This occurred, for example, at Canton in the Phoenix Archipelago and at Tongarabu in Tonga.

Specimens from other collections have supplemented the collections made under the grant.

In addition to the Bishop Museum—Yale University grant mentioned above, this study was supported in part by a series of grants from the National Science Foundation (NSF-G-1754, 3863, and 9937).

As reported in Part VIII of this series, the specimens upon which this study is based were lost in a fire at the Hawaii Marine Laboratory. This paper is the one referred to as being held at the Bishop Museum at the time of the fire.

Environment Data

Canton Island is an atoll in the Phoenix Group that lies at 2° 50' S and 171° 43' W; it is about 9 miles long by 4 miles wide, with an extensive and deep lagoon opening to the ocean only through a narrow passage on the western side. Rainfall is slight and there is no apparent runoff, even by seepage, unless during rare periods of torrential rains. All collections were made in the period from 27 February to 5 March 1954.

Description of Stations

Stations 1–9 were taken on the sandy edge of the western side of the lagoon near a deserted military pier where living and dead coral heads were scattered.

BC 1. Solid head of coral; 3 ft deep.
BC 2. Partially dead head of Pocillopora sp.; 3 ft deep.
BC 3. Solid but unattached head of dead coral; 3 ft deep.
BC 4. Massive head of dead coral covered with a thick algal mat; 3 ft deep. Some of the shrimp were in holes in coral under the mat, but more were living in the mat.
BC 5. Almost dead head of Pocillopora sp.; 3 ft deep.
BC 6. Massive and solid head; 3 ft deep.
BC 7. Heads of ramulose Acropora sp., with dead bases containing many openings and
spaces; 6 ft deep. All shrimp collected were from the dead bases, none from the living Acropora.

BC 8. A dead, coherent head of coral; 6 ft deep.

BC 9. A dead head of encrusting coral with numerous large cavities and passages; 14 ft deep.

BC 10. From several solid coral fragments; 2–6 ft deep.

Stations 11–18 were along the ocean reef on the leeward (southwest) side of the atoll. Here the reef varied from about 140 to over 200 yards wide. The uppermost edge was a boulder rampart, with a sand beach below; below the sand zone there was a zone of consolidated beach rock, some wave-polished and some erosion-pitted. The reef flat proper was flat and without salient features except for occasional scattered boulders; its surface was covered with a dense algal mat about 1 inch thick. The seaward side of the reef was broken into surge channels without any coralline algal ridge.

BC 11, 12, 13. Coral blocks covered with algal mat found at end of surge channels.

BC 14. Heads of growing Porites sp. shaped like inverted wash pans; fourth head of similar shape, 15 inches in diameter and 4 inches thick, but dead and covered with a thick mat of algae; all from the middle reef flat at about 0 ft tidal level. On living heads and bases only about six alpheids were collected; but on the dead head specimens were numerous, most being found between the head and the algal mat, but with some occupying superficial holes and fissures in the head proper.

BC 15. Loosely consolidated masses of coralline algae, with many openings and passages; from head of surge channel, outermost reef.

BC 16. Consolidated coralline rock (apparently largely coralline algae); about 10 ft shoreward from head of surge channel.

BC 17. Pocillopora meandrina Verrill; from head of surge channel. All specimens except A. lottini Guérin and Synalpheus charon (Heller) from dead coral at base of head.

BC 18. Dead and overgrown head of Pocillopora; from middle reef flat, 40 ft from beach limestone margin.

Stations 19 and 20 were located on the flourishing coral growths immediately within the lagoon from the sole pass from the ocean. Here at both incoming and outflowing tides the current was so strong that slower boats could not breast it; collecting was possible only during periods of slack water. While all pieces of coral, living and dead, examined had a minimal alpheid population (only 24 specimens were collected in about 5 hr of work), the snapping of the shrimp was audible and indicated a much

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**Fig. 1.** Islands from which collections are reported upon in this study.

**Fig. 2.** Canton Atoll, Phoenix Islands, showing collecting stations. The dotted line indicates the 10-fathom depth. (Taken from U. S. Hydrographic Office Chart #5740.)
larger population; presumably the shrimp were deeper in the coral mass, impossible to collect with the equipment available.

BC 19. Dead coral heads in the −1-ft tidal level, few shrimp.

BC 20. Various corals, mostly dead massive heads; 6–20 ft deep.

Stations 21 and 22 were located on the broad intertidal beach of fine sand at the most southwesterly portion of the lagoon. Most of the beach was devoid of traces of alpheids (unless they were deep sand-burrowing species as those of the Brevirostris group). The specimens collected were found associated with scattered coral heads and boulders, living and dead, especially under coral and beachrock boulders resting in slight pools on the sand flat.

BC 21. Under scattered boulders, resting on sand; depths ranging from 0 to +1-ft tide level.

BC 22. Coral heads, mostly dead, from outer beach edge; at 0-ft tidal level or slightly below.

Stations 23–25 were from near the ocean side of the lagoon pass and within the pass. The ocean reef here was solid and flat, with few loose heads or boulders that could provide holes for alpheids; the pass proper was the result of blasting during World War II and had much dead coral.

BC 23. Specimens collected under flat coraline rocks in a shallow tide pool, where they were buried in tunnels and excavations in a thin sand layer; depth about +0.5-ft tide level.

BC 24. Attached, overgrown head of dead coral; depth about −1-ft tide level.

BC 25. Overgrown head of Porites, mostly dead, seaward portion of lagoon pass; about 6 ft deep.

Another small group of specimens came from Christmas Island, an atoll in the Line Islands lying at 1° 55' N and 157° 20' W. It has a land area of 234 sq miles. Areas plainly identifiable as being part of an extensive lagoon are now filled in, bridged across, and cut off, so the area within the outer ring of the island is a series of lagoons separated from the sea by land. Most of the isolated lagoons have high salinity and are apparently devoid of higher plant or animal life. As the main lagoon is approached from the filled portion of the old lagoon bed there are a series of sublagoons, separated from the main lagoon by broad shallow sills; the inner of these, too, are lacking snapping shrimp at least. The main lagoon and the reefs around the island are usual for tropical atolls and have the usual fauna. Some of the collections reported from this island were made in 1959 by the senior author, incidental to procuring poisonous fish, and some were made by members of the British Royal Air Force stationed on the island. Most of the collection is lacking in environmental data, but where possible notes on the environment are given under the species concerned.

Palmyra Island, like Christmas Island, lies in the Line Islands at 5° 52' N and 162° 06' W. The few specimens from this island were collected by the senior author in 1959 while studying poisonous fish there.

Johnston Island, lying at 16° 45' N and 169° 30' W, is represented in the collections by a few specimens loaned by the Bernice P. Bishop Museum and the U. S. National Museum.

J-1 to J-8 were collected in 1947 on the outer reef edge on the northwest side of the island by F. Bayer.


24-9 Bishop Museum. Collected on Tanager Expedition in 1923. No further data.

1799 Bishop Museum. Same data as above.

10980 Johnston Island. Collected by Maxwell Doty. No further data.

AUTOMATE de Man

Automate gardineri Coutière


LOCALITY: 2 specimens from BC 21.

ATHANAS Leach

Athanas indicus (Coutière)

For synonymy, see Banner and Banner, 1960.

LOCALITY: 3 specimens from BC 11.

DISCUSSION: In the field notes on the collection from BC 11 it was remarked that "the small black alpheid of the lower genus probably Arete" was found in apparent commensal as-
sociation with a black ophiuroid in the holes in the coral. Unfortunately, lack of facilities prevented further identification of the species in the field, and upon return to Hawaii it was found that three species of Athanas were collected from BC 11. Which of the species was associated with the brittle star is not known for certain, but the fact that the three specimens, somewhat fragmentary, of A. indicus were aberrant might indicate this species was the one. When an opportunity presents itself a series of the athenids associated with ophiuroids should be collected and contrasted with the Echinometra-associated A. indicus.

*Athanas rhothionaster* Banner and Banner 1960

**LOCALITIES:** 1 specimen from BC 11; 8, BC 13; 3, BC 24.

*Athanas djiboutensis* Coutière

**LOCALITIES:** 1 specimen from BC 5; 5, BC 13; 7, BC 14; 4, BC 20; 1, BC 22; 2, BC 23.

*Athanas dorsalis* (Stimpson)
For synonymy see Banner and Banner, 1960.

**LOCALITY:** 24 specimens from BC 11.

**SALMONEUS** Holthuis

*Salmoneus sibogae* (de Man)

**LOCALITY:** 1 small fragmentary specimen from BC 14.

**DISCUSSION:** While this specimen is lacking in most of its legs, the form of the rostrum and telson is similar to intact specimens of this species that will be reported upon in a later paper.

The name of this genus was changed by Holthuis in 1955:88.

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**ALPHEOPSIS** Coutière

*Alpheopsis equalis* Coutière


**LOCALITIES:** 1 specimen from BC 20; 1, BC 22; 1, BC 23; 2, BC 25. 1 specimen from Christmas Island.

*Alpheopsis diabolus* Banner
*Alpheopsis diabolus* Banner, 1956. Pacific Sci. 10(3):325, fig. 3.

**LOCALITY:** 1 specimen from BC 23.

**NEOALPHEOPSIS** Banner

*Neoalpheopsis biatti* Banner
*Neoalpheopsis biatti* Banner, 1953. Pacific Sci. 7(1):21, fig. 6 a–l.

**LOCALITY:** 4 specimens from Christmas Island.

**DISCUSSION:** This is the second time Neoalpheopsis biatti has been reported. Banner reported 4 specimens from Hawaii in the original description.

**SYNALPHEUS** Bate

*Synalpheus paraneomeris* Coutière


3 In the original description there is a typographical error in the name in the text; the name used on the plate, *Alpheopsis diabolus* is correct; moreover, the legs referred to in the bottom paragraph, left column, p. 327, are the third, not second, legs.
Synalpheus paraneomeris Edmondson, 1923.
B. P. Bishop Mus., Bull. 5:30. (2 specimens from Christmas Island).


Discussion: Our specimens display the variation as discussed by Banner (1953:41; 1956:351) and Coutière (1905:872). However, among the large number of specimens at hand there are 4 in which the rostrum and orbital hoods are greatly reduced. These specimens include 1 from BC 17, part of a collection of 8; 1 from Tahiti (BD 2) from a collection of 104 specimens; 1 from Tonga (BT 17) from 2 specimens; 1 from Kapingamarangi #174 from a collection of 2 specimens. Since these strongly resemble the other specimens of the same species in their individual collections, we feel this reduction is simply malformation.

S. sluiteri was described by de Man as “closely related to Synalpheus paraneomeris.” However, de Man listed a number of characteristics in which the two species differed. Most of these differences, such as the proportions of the antennular peduncle, and the articles and dactyls of the third legs, are easily within the range of variation previously reported. Two possible differences remain: First, de Man stated that the “upper angle of basicerite subacute, a little prominent, though not spinform.” This description, without plates, could apply to the maximal development found in the specimens in these collections, or it may be markedly different. Second, the size of the ova, being 1.2–1.5 mm long as opposed to about 1.0 mm for near-mature eggs of our specimens. As egg diameters are influenced by the maturity of the embryo, and as poecilology is known among the synalpheids, not much reliability should be placed on this difference. Therefore we have tentatively made S. sluiteri a synonym of Synalpheus paraneomeris.

Synalpheus kusaiensis Kubo (Journ. Imp. Fish. Inst. Tokyo, 34(1):87, fig. 10, 1940) is quite close to S. paraneomeris in its general form, its appendages, and other characteristics. However, the development of the squamous portion of the scaphocerite is markedly different from any specimens in these collections. In Kubo’s figures the squamous portion reaches only to the end of the second antennular article and is only slightly more than half as long as the lateral spine, while the square in S. paraneomeris is variable. It usually reaches to near the end of the third article and is about two-thirds of the length of its lateral spine. In none of the specimens did the square approach the condition depicted for S. kusaiensis.

Synalpheus charon (Heller)

Localities: 1 specimen from BC 17; 3, BC 25.

Synalpheus streptodactylus Coutière
Synalpheus neomeris streptodactylus Coutière, 1905. Fauna and Geog. Mald. and Laccad. 2(4):870, pl. 10, fig. 11.
Synalpheus streptodactylus de Man, 1911. Siboga Exped. 39a1(2):226, pl. 7, fig. 29.

Locality: Canton Island: 2 specimens from BC 8.

Synalpheus tumidomanus (Paulson)

Localities: 1 specimen from BC 9; 2, BC 10; 2, BC 25.

Synalpheus coutieri Banner

Locality: Canton Island: 1 specimen from BC 8.
Synalpheus beroni Coutière

ALPHEUS Fabricius
MEGACHELES GROUP

Alpheus callumianus inermis Banner
Alpheus callumianus inermis Banner, 1956. Pacific Sci. 10(3):342, fig. 12 a–i.
LOCALITIES: Canton Island: 1 specimen from BC 15; 1, BC 24.

Alpheus callumianus medius Banner
Alpheus callumianus medius Banner, 1956. Pacific Sci. 10(3):340, fig. 11 a–h.
LOCALITY: Christmas Island: 1 specimen.

Alpheus oahuensis Banner
Alpheus oahuensis Banner, 1953. Pacific Sci. 7(1):64, fig. 20 a–l.
LOCALITY: Christmas Island: 1 specimen.

Alpheus deuteropus Hildendorf
LOCALITY: Christmas Island: 5 specimens.

DISCUSSION: These specimens were collected from fissures in a head of Astreopora myriophthalma found about the low-low tide zone on the ocean reef on the lee side of the island (near the old village site called Paris). Upon return to Hawaii several heads of Porites lobata Vaughn showing fissures were collected from about 6-fathom water in Kaneohe Bay, Oahu. Each fissure had a pair of cohabiting A. deuteropus.

The fissures are usually up to about 10 cm long, but may be considerably longer; the width is 5 mm or less, and the depth usually about 2 or 3 cm. The fissures are in the living coral and their tops are at times flush with the head and at times depressed at the base of a "valley" between the lobes. They are usually sinuate and often have blind side branches 1 or 2 cm long.

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The shrimp appear to live at the base of the fissure, and when frightened they will withdraw into round blind tubes penetrating directly into the head of coral. In one head, the only one examined that cracked so as to permit the following of the tube, the tube penetrated about 2 cm and then bifurcated, with the branches lying at an angle of about 90° to each other and penetrating about 4 cm beyond the bifurcation; at the end of the branches were hidden alpheids, the male in one branch and the female in the other.

MACROCHIRUS GROUP

Alpheus lottini Guérin
Crangon ventrosa Banner, 1953. Pacific Sci. 7(1):84, fig. 28.
Crangon latipes Banner, 1953. Pacific Sci. 7(1):52, fig. 27.

LOCALITIES: Canton Island: 2 specimens from BC 2; 2, BC 17. Johnston Island: 1 specimen from J-1; 2, J-5; 2, J-6; 2, J-16; 2, J-17.

DISCUSSION: In the heads of Pocillopora meandrina examined at Canton Island it was noted that this species and Synalpheus charon (Heller) live in different zones in the live coral. Alpheus ventrosus, together with crabs of the genus Trapexia, lived in the portions more distal from the base, and S. charon lived in the most basal branches of the live coral.

It is with regrets that we follow Holthuis (1958:22) in changing the name of this species from the well-known A. ventrosus H. Milne-Edwards to the seldom-used A. lottini Guérin (in Guérin's description lottini is spelled lottini but on the plates it is spelled lottini. The latter spelling takes precedence). Guérin's name does take precedence, but had Kingsley (1883) not
published on a re-examination of the type in a long over-looked paper, the specimen name would have been a nomen dubium, for Guérin’s figure and description were both inaccurate and non-specific (cf Banner, 1958:164). As a consequence Guérin’s name was not used, and the two other names for the species, A. ventrosus and A. laevis, were used almost 80 times in the literature, and by such authorities as de Man and Coutière. However, A. lotti was used in 1893 (Sharp), 1915 (Stebbing), 1919 (Stebbing), 1950 (Barnard). So appeal cannot be made to the Internation Commission on Zoological Nomenclature for, according to the Article 23, Section (b), the name must be unused for at least 50 years before an appeal can be made to place it as a nomen oblivium.

**Alpheus amirantei** Coutière


**LOCALITY:** Johnston Island: 4 specimens collected by M. Dory, Sta. #10980. **DISCUSSION:** This species, which is inadequately represented here, will be discussed in a subsequent paper.

**Alpheus gracilis** Heller


**LOCALITIES:** Canton Island: 1 specimen each from BC 9, 10, 18; 2, BC 11. Christmas Island: 2 specimens.

**Alpheus clippertoni** (Schmitt) new combination


*Crangon nanus* Banner, 1953. Pacific Sci. 7 (1): 90, fig. 30 a-m.


*Alpheus huikau* Banner, 1959. Pacific Sci. 13 (2): 139-140, fig. 5 a-e.

Nec *Crangon nanus* Krøyer, Naturhist. Tidskr. 4 (3): 231.

\*While this paper was in press Chace published on this new combination and indicated the same synonymy in U. S. Natl. Mus. Proc. 113 (3466): 609, 1962.

**LOCALITIES:** Canton Island: 4 specimens from BC 11; 4, BC 12; 6, BC 16; 1, BC 24. Christmas Island: 1 specimen.

**DISCUSSION:** Dr. Fenner A. Chace, Jr., of the U. S. National Museum examined the type specimens of *A. hawaiensis clippertoni* (Schmitt) and other specimens of *A. nanus* (Banner) and found them to be identical; the grooves on the large chela that Dr. Schmitt had indicated as barely perceptible were found to be prominent (Chace, in a personal correspondence). Therefore the name *huikau*, as the name *nanus* before it, must be cancelled, and the subspecific name applied by Schmitt must be raised to specific rank.

In 1937 Chace erected a new genus, *Pomognathus*, for a new species of alpheid (*P. coralinus*) from the waters of Baja California (1937: 124, fig. 5). The new genus was separated from *Alpheus* by the lack of epipods on the thoracic legs, and from *Synalpheus* by “the larger chela of the first pair of legs and the opercular third maxillipeds.”

Yet *Alpheus paragracilis* Coutière and *A. clippertoni* (Schmitt) show very close relationship to this genus and species. In the three species, the form of the orbital hoods, the development of the rostrum, the general proportion of the antennular and antennal peduncles, the development of the thoracic legs and telson show what appears to be a modification at the specific level of the same fundamental plan.

In the Indo-Pacific species the mouthparts protrude in a conspicuous fashion, from an over-development of the anterior labrum and a hemispherical expansion of the incisor process of the mandible. The outer mouthparts are quite normal for the genus except for the third maxillipeds, the base articles of which are broad, flattened, and curved to enclose the more anterior appendages. In *A. paragracilis* this article is not expanded, but in *A. clippertoni* the article is expanded slightly, but not as much as in *P. coralinus* (Fig. 3).

Fundamental to this consideration is the branchial formula of the species involved. According to definition, all members of *Alpheus* have five pleurobranches, one arthrobranch, and eight epipodites, with the last mastigobranch on the fourth walking legs, and the last setobranch on the
fifth walking legs. In *Pomognathus* there are "no epipods on any thoracic legs."

A group of 60 specimens of *A. paragracilis* from much of the range represented in the collections (Society, Cook, Samoa, Tonga, Hawaii, and Marshall islands) were examined; of these 58 lacked the last mastigobranch and setobranch normal for *Alpheus*, with the final epipodites occurring on the third and fourth walking legs. One had a rudimentary mastigobranch on the fourth, with no setobranch on the fifth, therefore approaching the condition normal to *Alpheus*; and the last lacked the mastigobranch on the third leg, approaching the condition of *Pomognathus*. In 30 specimens of *A. clippertoni* from a similar geographic range all specimens were like the normal *A. paragracilis*, with the last mastigobranch on the third and the last setothebranch on the fourth. The question is, how much reliance should be placed on the branchial formula as an absolute generic criterion? Certainly the formula is not fixed in *A. paragracilis*, nor is it constant in other genera (see Banner and Banner, 1960:134).

To us it appears that *Pomognathus corallinus* is an extension of the line of modification found in *A. paragracilis* and *A. clippertoni*, both in structure of the mouthparts and in branchial formula. *Pomognathus* does not show close relationship, in our opinion, to *Synalpheus*, and the reductions of the epipodites in *Pomognathus* is merely parallel to that of *Synalpheus*. It is possible that additional species may be found intermediate between *A. paragracilis* and *P. corallinus*; if they are found, the whole series should be reconsidered. However, for the present we believe that the *A. paragracilis* and *A. clippertoni* should be retained in *Alpheus*, and *Pomognathus* should be considered as a distinct genus.

*Alpheus macrochirus* Richters

*Alpheus macrochirus* Richters, 1880. Meeresfauna der Insel Mauritius und der Seychellen, Decapoda, p. 164, pl. 17, figs. 31–33.


**LOCALITIES:** Canton Island: 1 specimen from BC 14; 1, BC 16. Christmas Island: 5 specimens.
Alpheus edmondsoni Banner


**LOCALITIES:** Christmas Island: 5 specimens.

**DISCUSSION:** Dr. Dory, one of the collectors of this species cited in our 1959 paper (*Pacific Sci.* 13:141), has corrected what was an apparent misinterpretation of the label of the specimen. The citation should read "Onorea Island, Raroia Atoll, Tuamotu Archipelago . . . collected by Morrison, Dory, and Herre . . .”

**OBBSOMANUS SUBGROUP**

*Alpheus obesomanus* Dana

*Alpheus obesomanus* Dana, 1852. *U. S. Explor. Exped.* p. 547, pl. 34, fig. 7.

**LOCALITY:** Canton Island: 1 specimen from BC 24.

*Alpheus malleodigitus* (Bate)

*Betaeus malleodigitus* Bate, 1888. *Challenger Rps.* 24:565, pl. 101, fig. 5.


**LOCALITIES:** Canton Island: 1 specimen from BC 8; 3, BC 11; 3, BC 13; 2, BC 24.

**DISCUSSION:** The characteristics, name, and synonymy of this species will be discussed in a future paper.

The one specimen, a male, in BC 8 is apparently malformed. In all characteristics except the antennules and antennae it is like the usual specimens of this species, but the antennules, while symmetrical, are very short, so that the typically reduced scaphocerite reaches to the middle of the third article, and one carpopodite reaches to the end of the antennular peduncle while the other exceeds it by about one-fourth its length. This appears to be the result of an accident of inheritance or of environment.

**CRINITUS GROUP**

*Alpheus ovaliceps* Coutière

*Alpheus ovaliceps* Coutière, 1905. *Fauna and Geog. Mald. and Laccad.* 2 (4): 888, pl. 77, fig. 27.

**LOCALITY:** Canton Island: 1 specimen from BC 14; 1, BC 16; 3, BC 24.

*Alpheus bucephalus* Coutière

For synonymy see Banner and Banner, 1957.

**LOCALITIES:** Canton Island: 1 specimen from BC 1; 4, BC 4; 2, BC 6; 4, BC 8; 4, BC 9; 4, BC 10; 1, BC 22.

*Alpheus bradypus* Coutière


**LOCALITIES:** Canton Island: 2 specimens from BC 4; 8, BC 6; 1, BC 8; 1, BC 11; 7, BC 16; 1, BC 24.

*Alpheus brevipes* Stimpson


**LOCALITIES:** Canton Island: 2 specimens from BC 11; 4, BC 17. Johnston Island: 2 specimens from J–8. Christmas Island: 8 specimens.

*Alpheus clypeatus* Coutière


**LOCALITY:** Johnston Island: 1 specimen from J–4.

**DIADEMA GROUP**

*Alpheus ehlersii* de Man


*Nec. A. macrochirus* Richters, 1880, and other references.

**LOCALITY:** Canton Island: 1 specimen from BC 12.

*Alpheus diadema* Dana

For synonymy see Banner, 1956.

**LOCALITIES:** Canton Island: 1 specimen each from BC 1 and 18; 10, BC 14; 3, BC 22.
Alpheus pararcrinitus Miers


Crangon pararcrinitus Edmondson, 1923. B. P. Bishop Mus., Bull. 5:29. (Four specimens from Palmyra Island).

LOCALITIES: Canton Island: 5 specimens from BC 1; 2, BC 2; 1, BC 4; 2, BC 5; 1, BC 6; 2, BC 9; 3, BC 20; 5, BC 25. Christmas Island: 15 specimens.

The separation by Holthuis (1958:25) of A. pararcrinitus into two species, and the examination by Chace (1962:609) of West African specimens of A. pararcrinitus will be discussed in a future paper; it is sufficient here to state that we recognize the Indo-Pacific species as A. pararcrinitus Miers.

Alpheus gracilipes Stimpson


LOCALITIES: Canton Island: 3 specimens from BC 5; 2, BC 22.

EDWARDSII GROUP

Alpheus levinsculus Dana

Figure 4

Alpheus edwardsii levinsculus Dana, 1852. U. S. Explor. Exped. 13:543, pl. 34, fig. 3 a-f.

Alpheus levinsculus de Man, 1911. Siboga Exped. 39a(2):411, pl. 23, fig. 98 a-b.


Nec Alpheus levinsculus Bate, 1888. Challenger Rpts. 24:549, pl. 93, fig. 1.


Nec Alpheus bouvieri hululensis Coutière, 1905. Fauna and Geog. Mald. and Laccad. 2(4):908, pl. 85, fig. 46.

LOCALITIES: Canton Island: 1 specimen from BC 18. Wake Island: 5 specimens including the 9.8-mm male described below. Johnston Island: 7 specimens.

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DESCRIPTION: Specimen described with anterior body displaced from under carapace.

Rostrum triangular, short, not reaching to middle of first antennular article, lateral margins slightly concave with curve continuous with orbito-rostral front; in lateral view, tip somewhat depressed (that of female shown in drawing is crushed downward). Orbito-rostral grooves shallow and broad, interorbital crest slight and rounded, merging with the carapace near posterior margin of eyes. Orbital hood slightly inflated, hemispherical, frontal margin only slightly arcuate.

Second antennular article slightly longer than broad, longer than the third article, shorter than visible portion of first article (some of the length visible of first article may be from displacement of body). Stylocerites short, acute, slightly exceeding end of first article. Basicerite with strong lateral tooth, slightly shorter than stylocerite. Lateral margin of schaphocerite almost straight; lateral spines slightly exceeding length of antennular peduncle. Carpcerite exceeding length of antennular peduncle by length of last article.

Third maxilliped with first and last article equal in length, about twice length of middle article; tip of third article abruptly truncate and bearing numerous heavy setae, some of which equal article in length.

Large cheliped with merus twice as long as broad, bearing two weak spines and a seta on inferior internal margin; superior margin rounded distally, inferior internal margin terminated by small tooth. Chela almost three times as long as broad, with outer palmar face bearing triangular depressed area arising from transverse groove and continuing proximally to linea impressa; lower shoulders pronounced, but not continuing more than one-fifth width of face. Inner face of palm without marked depressions. Dactylus heavy, one third length of entire chela, tip rounded.

Small cheliped with merus similar to that of large chela in armature, but with face 2.5 times as long as broad. Palm without sculpture, 1.7

This description and these figures were to be of specimens to be designated as neotype and neocotype; however, the specimens were lost in the Hawaii Marine Laboratory fire.
Fig. 4. *Alpheus leviusculus* Dana, male and female, from Wake Island. *a* and *b*, Anterior region, female, dorsal and lateral aspects (note that rostral tip is crushed downward, and body is displaced anteriorly); *c*, anterior carapace male, showing normal rostrum; *d* and *e*, large cheliped male; *f*, small cheliped, male; *g*, small cheliped female; *h*, third maxilliped of male, exterior or lower view; *i*, third maxilliped tip (not all setae of back side shown); *j*, second leg, male; *k*, third leg, male; *l*, telson, male.
times as long as broad, terminating in small but distinct tooth above dactylar articulation. Fingers not *balaeniceps*-shaped, bearing, however, slightly broadened opposing faces with slight row of setae on the margin; fingers equal in length to palm. Small chela of female is of similar form and armature, but about four-fifths as long as that of male.

Carpus of second leg with ratio of secondary articles as 10:5.1:2.8:2.8:5.4.

Third leg with small movable spine on ischium. Merus unarmed, 3.7 times as long as broad, with distal end about 0.6 as broad as middle. Carpus 0.5 times as long as merus, 3.0 times as long as broad, with relatively small teeth terminating superior and inferior margins. Propodus 0.7 as long as merus, about 6.0 times as long as broad, bearing 9 movable spines on inferior margin, scattered setae on superior margin. Dactyulus 0.21 as long as merus, slightly curved, acute, and with slight thickening at point where secondary unguis might occur. Fourth legs similar to third.

Telson 1.6 times as long as broad anteriorly, with posterior margin 0.6 times as broad as anterior; lateral margins slightly arcuate, with uniform curve; distal margin broadly arcuate; superior and distal spines usual.

**DISCUSSION:** In the collection loaned to us from the Bishop Museum there was a group of five specimens from Wake Island, the type locality for Dana's species. Unfortunately, three of the specimens were small and the other two, which had been selected to be the neotype and allotype, were somewhat broken. However, the group of specimens from Johnston Island, which lies about the same latitude and only 1,600 miles away were almost identical with the Wake Island specimens and were in good condition. Both groups were used in preparing this description.

Dana's description of *A. levisculus* is general enough to cover several species in the Edwardsii group. However, his figures are clear and do agree with our specimens except in two characteristics. First, there extends down the inner face of the large chela from the groove on the top margin a well-demarked U-shaped depression, while in Dana's figure no depression is shown on the inner face of the chela. This difference is likely to be the result of faulty delineation. Second, the spine above the mov-

able dactylus of the small chela is not shown. However, this character may be variable, as in *A. paracrininus* Miers, or the chela as drawn by Dana could have been so rotated that the spine was not visible.

*Alpheus levisculus* Bate definitely does not belong to this species, being easily distinguished by the awl-like shape of the rostrum, the extended flattened areas between the orbital hoods and rostral base, and the relatively smooth large chela. It should also be noted that *A. levisculus* is found on the reef flat while Bate's sole specimen came from 20 fathoms. His specimen does not appear to be similar to any other species within the group or the genus, so we propose, therefore, to apply to it the name of *Alpheus batesi*.

Our specimens also agree well with those of de Man (1911:fig. 98) except in the third leg. In de Man's specimen the merus of the third leg was five times as long as broad, while the maximum length-breath ratio found in these 45 specimens is 4.4 times as long as broad.

*Alpheus levisculus* was considered by de Man to be closely related to *A. bastardii* Coutière and *A. bouvieri* A. Milne-Edwards. The points of difference between these nominal species in relation to the variations of the 45 specimens in this collection are discussed herewith:

**Rostrum length.** The rostrum of *A. levisculus* in Dana's figures and in these specimens is roughly triangular and reaches only slightly beyond the middle of the first antennular article. The grooves beside the rostrum are shallow. The rostrum of *A. bouvieri* is reported to be similar. However for *A. bastardii*, Coutière (1898) states that the rostrum is "Très faible et très obtuse, large, conique . . ." and that it is not separated from the orbital hoods by grooves, yet in the figures of both the 1898 and 1905 works he indicated slight grooves. In these specimens the length of the rostrum, when compared to the first antennular article, appears to be influenced by the displacement of the carapace in capture (the carapace appears to be easily displaced, as it is in *A. clippertonii* [see under *C. nanus* Banner, 1953, fig. 30]). The grooves flanking the rostrum exhibit the expected variation; some are very shallow, approaching the condition that Coutière indicated in fig. 1a (1898) and fig. 45 (1905) for *A.

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A. bastardi, the others are deeper but still shallow in relation to other species. In other words, the orbito-rostral area varies from an almost flat condition to a condition with shallow, ill-defined grooves.

**Ratio of antennular articles.** In *A. leviusculus* Dana shows the antennular articles to be almost equal. de Man (1911) pictures the second article slightly longer than the first, and the third a little shorter than the first, with the second article less than 2 times as long as broad. The type specimen is reported by Coutière 1898 (text and fig. 1) to have the second antennular article 1.5 times as long as the first and twice as long as broad, with the third article slightly shorter than the first. *A. bastardi* (loc. cit., fig. 1a) has all the articles of the antennular peduncle almost the same length and the second article as long as broad. However, Coutière in his 1905 plates (pl. 85, figs. 44, 45) shows specimens of *A. bouvieri* and *A. bastardi* to be almost exactly the reverse of the differential proportions of his 1898 figure. Obviously Coutière himself did not put much reliance upon this criterion for the species.

In our specimens the ratio of the lengths of the antennular articles range from 1:1.1:1 to 1:1.5:1 and the length-breath ratio of the second articles ranged from 1 to 1.5 times as long as broad. These figures seem to bridge the differences among the three species in question, especially in view of the confusion of Coutière in the proportions of his species.

**Antennular squame and spine.** *A. leviusculus* as figured by Dana (fig. 3a) had a narrow squame, with the external spine about half the length of the third antennular article. The outer margin was slightly curved. *A. bouvieri* is similar. *A. bastardi* carries a slightly broader squame with a straight margin, and a spine which reaches only slightly beyond the end of the squame. The range of the relative proportions of the squame and spine in our specimens encompasses the differences reported for the three species.

**Large cheliped.** The chelae for the three species in question are without distinguishing characters and have similar length-breath ratios. However, no writer has mentioned the slight spines that are almost always to be found on the inferior-internal margin of their meri, nor the blunt terminal tooth on this edge. These differences may be individual variation.

**Small cheliped.** There are two minor differences reported in the small cheliped. First, de Man (1911:412) describes a small spine above the movable dactylus which Coutière does not mention for either *A. bouvieri* or *A. bastardi*. This tooth appears in all of these specimens. Second, in 1905, Coutière described and figured a moderately well-developed setiferous crest on the dactylus of the males of *A. bouvieri* which he uses as a criterion to separate the species from *A. bastardi*, where it is lacking. Neither Dana nor de Man mentioned this character for *A. leviusculus*. In our series most specimens were without the crest, yet in two males a crest of poor development was found along the inner side of the movable dactylus.

**Third leg.** The only other point of difference is the merus of the third leg. In 1905 Coutière stated that the length-breath ratio of the third leg of *A. bouvieri* is 3.5 and in *A. bastardi*, 4.5. Dana pictures the third leg merus of *A. leviusculus* to be 3.5 times as long as broad. de Man's sole specimen had a ratio of 5. The merus in our series ranges from 3.1 to 4.4 times as long as broad.

It is apparent that the subtle differences separating *A. leviusculus*, *A. bouvieri*, and *A. bastardi* are either within the range of variation found in the specimens of this collection, or represents only slight extensions of the range. We have, therefore, placed the two latter species in synonymy.

Three other species are related to this complex: *A. bouvieri halulensis* Coutière (1905:908, pl. 85), *A. coutieri* de Man (1911:409, fig. 97), and *A. ladronis* Banner (1956:360, fig. 20).

The description of *A. bouvieri halulensis* is so inadequate that without the re-examination of the type specimen, or, better, of a toptotypic series, it is impossible to ascertain its true relationship. While we believe that it may be found to be within the range of variation of *A. leviusculus*, yet on the basis of specimens described its rostrum appears to be specifically distinct. Therefore, we suggest that this described form be retained under the name of *A. halulensis* until additional specimens are examined.
A. contierei is obviously closely related to A. bowvieri bululensis. Like A. bululensis it can be distinguished from A. leviacus by the base of the rostrum and the long rostral carina. It will be discussed more fully in a later paper.

A. ladronis Banner, while related, can be readily separated from A. leviacus by the large chela. The top groove of the large chela in A. ladronis is shaped almost exactly like that of A. crassimanus, with the proximal margin of the groove gradually rounded instead of abrupt, as in A. leviacus. Further the spine on the inferior internal margin of the large chela is large and subterminal in A. ladronis, while in A. leviacus it is small and terminal. In many of the males of A. ladronis one finds a balaeniceps condition, while in A. leviacus, when a fringe of hairs is found it is thin and does not pass over the top of the dactylus. The merus of the small chela also bears a large subterminal spine on its inferior internal border. The rostral carina is sharper and can be plainly seen from above, whereas in A. leviacus the animal must be rotated to make the slight carina visible.

Finally, although the proportions of the merus of the third leg are variable in both species, that of A. ladronis (20 specimens) averages 4.6 times as long as broad, while that of A. leviacus averages about 4.0 times; the extremes of the ranges of the two species overlap.

Alpheus crassimanus Heller

Alpheus crassimanus Heller, 1865. Reise der Novara, Crust. p. 107, pl. 10, fig. 2.

LOCALITIES: Canton Island: 4 specimens from BC 18; 1, BC 19.

Alpheus pacificus Dana


Alpheus strenuus Dana


LOCALITIES: Canton Island: 2 specimens from BC 14; 14, BC 23. Christmas Island: 2 specimens.

Alpheus funafutensis Borradaile


LOCALITIES: Canton Island: 11 specimens from BC 14; 3, BC 18.

DISCUSSION: These specimens agree well with Borradaile's original pictures and description and de Man's (1911) further notes. Some minor variations were noted. The rostrum varied from one-half to three-fourths the length of the first antennular article. The rostral keel always extended back to the bases of the orbital hoods but was less broad than that pictured by Borradaile (fig. 10a). Some of the keels were quite sharp while others were slight. The tips of carpocerite and scaphocerite reached variously from slightly beyond the end of the antennular peduncle to a distance equal to the length of the third article beyond that article. The square, which was narrow, sometimes reached to the end of the second antennular article or to the end of the third, and in all cases the spine extended well past the end of the antennular peduncle. Borradaile in his original description remarked that the fingers of the small chela were elongate, yet he pictured them as stubby and shorter than the palm; our specimens agree with the figure. The small chela resembles very closely that of A. parvirosstris Dana. The most distinctive characteristics of this species are the granulation and hairiness on the inside of both the large and small chela.

Alpheus parvirosstris Dana


LOCALITIES: Canton Island: 7 specimens from BC 1; 2, BC 2; 3, BC 3; 4, BC 4; 6, BC 5; 4, BC 7; 6, BC 8; 7, BC 9; 25, BC 10; 2, BC 19; 10, BC 20; 3, BC 22; 2, BC 25.
THUNOR Armstrong

*Thunor microscaphis* Banner

Figure 5


**LOCALITY:** 1 ovigerous female from BC 13, carapace length 4.9 mm.

This specimen has a slightly longer scaphocerite than the type specimen, a male from the Marshall Islands, and the female from Saipan, but the article is shorter than that of the male from Saipan. Except for the telson there is almost perfect agreement in other parts.

In the three specimens previously described the tendency to develop dorsolateral ridges on the telson, leaving a median groove, was noted; on this specimen these ridges are pronounced and actually rise above and curl over the median groove. Because of the inward rolling of the posterior portion the terminal truncation of the telson, when seen in dorsal view, appears to be almost a point. Unlike telsons previously reported for the family, both the lateral and the terminal setae extend beyond the posterior lateral spines, which are very poorly developed, and lie along the dorsal ridges projecting over the medial groove. Only one of the four dorsal spinules normally found could be seen. The outer uropod, without a trace of the transverse articulation, also has its outer margin rolled upward, and the sutural spines seem to be lacking; the distal margin of this uropod bears a series of short movable spines. Both the outer and inner uropod bear many long setae; on the latter they are along the middle of the superior surface.

This development of the telson may be found to be a characteristic adequate to separate this specimen as a new species; however, until more mature female *T. microscaphis* are studied, it seems more logical to consider this specimen as merely a more mature stage of the species already described.

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**Fig. 5.** *Thunor microscaphis* Banner. Female from Canton Atoll. Telson and uropods: a, dorsal view; b, lateral view (at a slight angle).
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The Correct Name for the Hawaiian Gossypium

ROBERT L. WILBUR

For almost a century the endemic Hawaiian Gossypium has been known as G. tomentosum. This species has received much attention especially in recent years since it has been thought by some to form together with the two American cultivated cottons, G. hirsutum L. and G. barbadense L., a small section of closely related species with a similar distinctive origin. The section is unique within the genus in that its three related species, as interpreted by Hutchinson, Silow, and Stephens (1947), are allotetraploids reputedly having derived one genome from the diploid American complex and another from the group to which the Asiatic and African cultivated cottons belong. Naturally species with apparently as bizarre an origin as these three have been frequently discussed in the cytological, genetic, and phytogeographical literature. As a result the name G. tomentosum has become very well known indeed for the Hawaiian plant. Unfortunately for the sake of stability, this application of the name does not appear to withstand scrutiny.

Although the native Hawaiian Gossypium was collected by the naturalists on both the expeditions of Cook, who discovered the Islands in 1778, and of Vancouver, who visited in 1792 and 1793, it was apparently first considered as a distinct and undescribed species by Nuttall who wintered in Hawaii from January–March 1835 and perhaps again the following winter. However, he failed to publish the results of his study. Seemann encountered Nuttall’s Hawaiian collections in the British Museum while preparing his account of the genus as it occurred in Fiji. He concluded that the Hawaiian specimens were conspecific with plants representing what he presumed to be an undescribed cotton introduced into Fiji. He adopted Nuttall’s unpublished herbarium name, provided a description, and cited specimens of his own and, in addition, of Pritchard and of Smythe from Fiji and also collections of Nelson, Menzies, Nuttall, and Diell from the Hawaiian Islands.

Seemann’s instructions from the British Colonial Office directed him to pay particular attention to Fiji as a possibly important cotton producing area. These islands had been provisionally ceded to Great Britain in 1859 and a small party including Seemann was sent to evaluate the state of this Melanesian kingdom before formally accepting its responsibility. Seemann’s investigation during his 8 months residence resulted in his enthusiastic conviction that ”the Fijis seem as if made” for the cultivation of cotton. It is therefore quite certain that Seemann paid particular attention to the genus as represented in Fiji. Four species were recognized, all of which were thought by him to be introduced. Because of the rarity of Seemann’s ”Flora Vitiensis,” it seems desirable to include here both the description and the comments made by him concerning the species in question.

1 Department of Botany, Duke University, Durham, North Carolina. Grateful acknowledgment is made to the National Science Foundation for a grant of research funds to Duke University (NSF-Grant 18799) which has made the present study possible. I should also like to thank Dr. F. R. Fosberg for his most helpful advice, but this of course in no way implies that he is necessarily in agreement with the conclusion reached in this paper. Manuscript received May 7, 1962.

2 This name is used in its traditional sense and no attempt is made here to evaluate the conclusion by Prokhanov (1959) that G. barbadense is merely a broad-leaved variety of G. arboreum L. and hence that the proper name for the species which includes the sea island cotton is G. peruvianum Cav.

4 G. tomentosum, Nutt. mss.; fruticosum; ramulus foliiis bracteisque cano-tomentosis folii 3–5 lobis, lobis ovatis acuminatis v. acutis integerrimis obscure v. distincte punctatis; stipulis cordatis v. ovatis acuminatis; pedunculis 1–2-floris; bracteis ova-to-oblongis, basi cordatis, apice laciniatis, lacinii ovato-lanceolatiss integerrimis; calyce subtruncato distincte nigro-punctato; petalis (flavis) obovatis, extus in parte exteriori tomentosis, in parte inclusa latiore tenuiore glabris; capsulis 3-valvis, valvis apiculatis; seminibus liberis
dense croceo-velutinis, lana (3/4 unc. long.) crocea.—
G. religiosum, Roxb. Fl. Ind. vol. iii, p. 185, non Linn. 
G. parvifolium, Nutt. Herb.—Viti Levu, on the Raki-
raki coast (Smythe!), Kadavu (Pritchard! Seemann! 
n. 28). Also collected in Oahu, Atooi, Hawaii (Diell! 
Nuttall!), Maui, Sandwich Islands (D. Nelson! Men-
zie!).

This is the plant which A. Gray (Bot. Wilkes, p. 
179) calls G. religiosum, but it is not that of Cavanil-
les, which is more glabrous, has a deeper-crested calyx, 
white flowers, and the seeds quite glabrous, after the 
removal of the wool. The Sandwich Islands plant is 
apparently identical with that described by Roxburgh 
I. c. under the name G. religiosum, which, he says, 
has "seeds free, clothed with firmly-adhering, short, 
tawny down, and long wool of the same colour." 
There is a specimen of "Yellow Cotton" from Joy-
negau (Trovel!) at the British Museum, which has 
very small leaves,—the smallest I have seen in this 
genus,—agreeing as far as it goes with the above 
species; and there is a starved specimen of G. tomen-
tosum from Hawaii (Diell!) which has the leaves 
amost small, and which Nuttall had provisionally 
named G. parvifolium. But generally the leaves and 
flowers of G. tomentosum are those of the size usual 
in this genus.4

A considerable number of the features men-
tioned in the quoted description are definitely 
not diagnostic for they are to be found in many 
species of Gossypium. More important, many of 
these described features are to be found in both 
the Hawaiian endemic and the Fijian cotton which 
Seemann, Pritchard, and Smythe all col-
lected 100 years ago. Certain of the features 
described in the original publication, however, 
clearly exclude either the Hawaiian endemic or the 
Fijian introduction and these features will 
be discussed briefly below.

The stipules of the Hawaiian species are de-
scribed as "minute" by Watt (1907) and "subu-
late" by Degener (1933). The stipules of the 
variant of G. hirsutum to which Seemann's No. 
28 belongs are described by Watt as "broad, 
oblique, ovate lanceolate . . . subcordate." Ob-
vously Seemann's description of the stipules of 
G. tomentosum in his original description were 
not from the Hawaiian plant to which the name 
has been applied but from the Fijian cotton.

4 This footnote quoted Solander's manuscript de-
scription of the cotton found in the Society Islands, 
which is apparently what has been called G. taitense 
Parl.—R.L.W.

4 This footnote provided the original description of 
Gossypium drynarioides Seem. = Kokia drynarioides 
(Seem.) Lewton.—R.L.W.

PACIFIC SCIENCE, Vol. XVIII, January 1964

The involucral bracts of the Hawaiian species 
possess small triangular teeth, each at most two 
or three times longer than their width and not 
deeply laciniate as they are in the cotton from 
Fiji collected by Seemann. Again, it is obvious 
from Seemann's account that this described fea-
ture of G. tomentosum was taken from the in-
troduced Fijian plant.

Seemann's key to the species of Gossypium 
found in Fiji states that the seeds of his G. 
tomentosum retain tawny "moss" after the re-
moval of the wool. All authors are agreed that 
the seed-hairs of the Hawaiian species are not 
separable into "fuzz" and "floss." Seemann's 
description states that the trichomes of G. to-
mentosum are about 3/4 inch long (= c. 1.9 cm), 
while those of the Hawaiian endemic are stated 
seldom to exceed 1 cm in length.

In contrast to all of the above described 
features, which could never have been observed 
on the Hawaiian plant, the subtruncate calyx 
could scarcely have been observed except on 
the Hawaiian specimens, inasmuch as the Fijian 
plants would be expected to possess the pro-
nounced calycine teeth characteristic of almost 
of the hirsutum cottons.

Watt (1907:69–71) first pointed out that 
Seemann was in error in associating specimens 
from Fiji with collections made by Nuttall in 
Hawaii. Watt then in effect proposed to typify 
the name G. tomentosum by the Hawaiian ele-
ment included in the original description and in 
this interpretation he has been followed by all 
subsequent authors. However, it is readily ap-
parent that the greater portion of Seemann's 
original diagnosis can apply only to the Fijian 
cotton and clearly excludes the Hawaiian en-
demic. The typification of such taxa which, when 
originally published, contained two or more 
elements has often proven itself to be a most 
difficult problem. In an effort to provide broad 
principles for the solution of such problems a 
guide for the determination of types has been 
added to the International Code (Lanjouw, 1961: 
65) and includes the following instruction as 
to proper procedure:

d. In choosing a lectotype, any indication of intent 
by the author of a name should be given preference 
unless such indication is contrary to the protologue,...

e. In cases when two or more elements were in-
cluded in or cited with the original description, the
reviewer should use his best judgment in the selection of a lectotype, but if another author has already segregated one or two elements as other taxa, the residue or part of it should be designated as the lectotype if its essential characters correspond with the original description. If it can be shown that the element best fitting the protologue has been removed, it should be restored and treated as the lectotype. Whenever the original material of a taxon is heterogeneous, the lectotype should be selected so as to preserve current usage unless another element agrees better with the protologue (Rec 7B).

f. The first choice of a lectotype must be followed by subsequent workers (Art. 8) unless the original material is rediscovered, or unless it can be shown that the choice was based upon a misinterpretation of the protologue.

The protologue is defined in the Code as everything associated with a name at its first publication.

It therefore seems certain that the name *G. tomentosum* must be typified by the plants principally characterized by the publishing author who studied them with considerable care in the field. The original account certainly better fits the Fijian introduced cotton than it does the Hawaiian endemic. It is an error to typify the name by the element which Seemann mistakenly considered as conspecific on the basis of rather fragmentary herbarium specimens, even if the name suggested by Nuttall was adopted by Seemann for the proposed species. A photograph of Nuttall’s specimen in the British Museum was kindly provided by J. E. Dandy, who also wrote that he could find no manuscript notes by Nuttall that Seemann might have used. The secondary position of the Hawaiian element in Seemann’s concept may perhaps even be indicated by his appending their localities and collectors after the citation of the Fijian specimens with the preface “Also collected in Oahu . . .”. The authority for the name *G. tomentosum* has been variously cited as “Nutt.” or “Nuttall,” “Nuttall in Seem.” or “Nutt; Seem.” The last of these citations of authority is given sanction in the modernized version by the substitution of “ex” for the semeicon by the International Code as an example for Recommendation 46C. Although Seemann attributed the name to “Nutt. mss.”, an examination of the description indicates that Seemann based his description almost entirely upon the plants studied by him in Fiji. In this case there are more compelling reasons than the desire to shorten the citation for attributing the name solely to Seemann rather than to “Nutt. ex Seem.”

The year following Seemann’s publication of *G. tomentosum*, Parlatore (1866) published a good description and an illustration of the Hawaiian endemic, naming it *G. sandwicense*—not *G. sandvicense* as cited by Hillebrand (1888), Watt (1907), Degener (1933), or Hutchinson, Silow, and Stephens (1947). Parlatore questioningly placed Nuttall’s herbarium name in synonymy. The name *G. indicum* Lam. employed by Menzies, in naming his collection made while accompanying Vancouver, was also cited in synonymy along with “*G. religiosum Forst.*,” the name under which David Nelson’s collection, made during Cook’s voyage of discovery, was to be found in the British Museum.

The more pertinent synonymy for the Hawaiian endemic *Gossypium* appears, then, to be as follows:


*G. tomentosum* Seem., Fl. Vit. 22. 1865 in small part.


REFERENCES


PARLATORE, FILIPPO. 1866. Le Specie dei Cotoni. Firenze. 64 pp.


Chromosome Homology in the Ceratobium, Phalaenanthe, and Latourea Sections of the Genus *Dendrobium*

H. Kamemoto, K. Shindo, and K. Kosaki

The *Dendrobium* genus comprises over 1,000 species of epiphytic orchids distributed over a vast triangular area connecting India, New Zealand, and Japan, and including most of the tropical and subtropical land areas between 60 and 180 east longitude. This large genus has been subdivided into numerous sections on the basis of morphological characteristics (Holttum, 1957). Members of the Ceratobium, Phalaenanthe, and Latourea sections are distributed in New Guinea and surrounding areas. Both Ceratobium and Latourea are represented by at least 30 species each, while Phalaenanthe includes a relatively few species. Several species in these sections have been widely cultivated and extensively hybridized to produce the improved and popular horticultural varieties of today.

Cytological investigations to date have revealed $2n = 38$ for all species in Ceratobium, Phalaenanthe, and Latourea sections, and both $2n = 38$ and 40 in other sections but with 38 predominating (Ito and Mutsuura, 1957; Kosaki, 1958; Vajrabhaya and Randolph, 1961; Kosaki and Kamemoto, 1962). Thus divergence of species in the genus appears to have been accompanied by little or no change in chromosome number.

During the past 2 decades, numerous intraspecific and interspecific species hybrids in *Dendrobium* have been produced by various orchid hybridizers. Since cytological studies, particularly observations on chromosome homology, are very useful in elucidating taxonomic and phylogenetic relationships, as well as in aiding the breeding of orchids, the present investigation was initiated to examine the meiotic behavior of all available species and hybrids involving the Ceratobium, Phalaenanthe, and Latourea sections, and to establish the relationships of species of these groups.

**MATERIALS AND METHODS**

The species involved in this study are listed in Table 1 along with their geographical distribution, while the hybrids with their registered names are found in Table 2. Plants were obtained from the Foster Botanical Garden and orchid nurseries in Honolulu. Young pollinia were sliced and fixed in 1:1:2 mixture of chloroform, 95% ethyl alcohol, and glacial acetic acid for 20-30 min at room temperature. They were then transferred to 45% acetic acid for 20-30 min to soften the tissue and promote the stainability of chromosomes. They were then squashed and stained in 1% aceto-orcein.

**OBSERVATIONS**

*Meiosis in Species*

Meiosis in 11 species representing the sections, Ceratobium, Phalaenanthe, and Latourea (Figs. 1-12) showed consistently 19 bivalent chromosomes at metaphase I (Table 3). The products of meiosis were normal tetrads with 19 chromosomes distributed in each microspore.

The bivalents were either rod or ring shape with terminalized chiasmata (Figs. 24-26). The size of bivalents differed markedly within a complement. This difference was more conspicuous in species of Ceratobium and Phalaenanthe than in Latourea. There were also distinguishable differences in the genomes of different species within the same section.

Metaphase I configurations of *D. undulatum* were characterized by the presence of conspicuously large and heteropysnotic bivalent chromosomes (Fig. 24) which were readily discernible at late prophase and metaphase of either meiosis or microspore division. These chromosomes

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might well serve as "markers" for the genome of D. undulatum.

*D. strebloceras* possessed two pairs of chromosomes which were larger in size than the rest of the complement and were strongly heteropycnotic at prophase of meiosis. *D. striatotes* showed similar characteristics, but with additional pairs of large bivalents. *D. veratrichium, D. phalaenopsis* (Fig. 25) and others also possessed several large bivalents but of graded size and heteropycnos.

**Meiosis in Within-Section Diploid Hybrids of Ceratobium**

The 10 intrasectional diploid hybrids of Ceratobium (Figs. 13, 14) investigated showed regular pairing at meiosis (Table 4). However, some of the bivalents were conspicuously heteromorphic. This might be expected on the basis of the morphological variations of chromosomes of the different genomes.

The number and form of heteromorphic pairs varied from one hybrid to another depending on the parentage. The two hybrids of *D. undulatum—D. veratrifolium* x *D. undulatum* and *D. undulatum* x *D. gouldii*—showed a markedly heteromorphic bivalent involving the large "marker" chromosome of *D. undulatum*. Highly heteromorphic bivalents were also observed in *D. striatotes* hybrids. Four such bivalents were observed for *D. striatotes* x *D. tokai*, and four to five in *D. veratrifolium* x *D. striatotes* (Fig. 27). The smaller of the bivalent chromosomes often appeared as a chromatid thread pulled out from the darkly stained larger chromosome. These bivalents characteristically separated precociously.

**Meiosis in Between-Section Diploid Hybrids of Phalaenanthe and Ceratobium**

In addition to the natural hybrid, *D. superbiens* (Figs. 17, 18), six diploid intersectional hybrids involving Phalaenanthe and Ceratobium (Figs. 15, 16) exhibited similarly irregular meiotic behavior (Tables 5, 9, Figs. 28, 29). Both bivalents and univalents were observed, and occasionally some trivalents probably resulting from the chance association of sticky chromosomes were also seen.

The bivalents in PMCs varied in number from 19 to 13 and the univalents from 2 to 12. Most of the PMCs formed 19-16 bivalents and 0-6 univalents. As indicated in Table 5, the mean number of bivalents was highest (18.9)
A second plant of the same cross also produced a relatively low number of bivalents (17.1). Other hybrids averaged from 17.7 to 17.8 bivalents. Excepting D. superbiens, all hybrids exhibited two or more extremely heteromorphic bivalents.

### TABLE 3

**Mean Chromosome Configurations at Metaphase I of Meiosis in PMCs of Species, \(2n = 38\)**

<table>
<thead>
<tr>
<th>SECTION</th>
<th>SPECIES</th>
<th>MEAN CONFIGURATION PER PMC</th>
<th>NUMBER OF PMCS OBSERVED</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ceratobium</td>
<td>D. gouldii</td>
<td>19.0 II</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>D. grantii</td>
<td>19.0 II</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>D. stratiotes</td>
<td>19.0 II</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>D. strebloceras</td>
<td>19.0 II</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>D. tokai</td>
<td>19.0 II</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>D. undulatum</td>
<td>19.0 II</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>D. veratrifolium</td>
<td>19.0 II</td>
<td>25</td>
</tr>
<tr>
<td>Phalaenanthe</td>
<td>D. bigibbum</td>
<td>19.0 II</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>D. phalaenopsis</td>
<td>19.0 II</td>
<td>25</td>
</tr>
<tr>
<td>Latourea</td>
<td>D. macrophyllum</td>
<td>19.0 II</td>
<td>25</td>
</tr>
</tbody>
</table>
(Fig. 29) which often separated precociously. The synaptic force of the heteromorphic bivalents was weak as evidenced by the precocious separation and the frequent close proximity of large and small univalents in a metaphase figure.

*D. superbiens* has been considered a natural hybrid between species of the sections Phalaenante and Ceratobium (Holtrum, 1957). Its hybrid nature can be confirmed through the meiotic irregularity which is comparable to that of other intersectional hybrids.

The products of meiosis were predominately tetrads (Table 9). These reflect the relatively high degree of chromosome pairing at meiosis. The percentage of spore tetrads was 90 or higher for all hybrids except *D. phalaenopsis × D. gouldii (#2)*, which produced about 30% dyads and dyads with microcytes.

**Meiosis in Tetraploid Hybrids**

A within-section tetraploid, *D. stratiotes × D. undulatum* and a between-section tetraploid, *D. phalaenopsis × D. gouldii*, exhibited considerable difference in meiotic behavior (Table 6, Figs. 30, 31). Metaphase I configurations of the within-section tetraploid were various combinations of univalents, bivalents, and quadrivalents. The bivalents varied in number from 38 to 32, and the quadrivalents and univalents from 2 to 0. Common configurations were 1

<table>
<thead>
<tr>
<th>HYBRID</th>
<th>MEAN CONFIGURATION PER PMC</th>
<th>NUMBER OF PMCs OBSERVED</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>D. veratrifolium × D. undulatum, #1</em></td>
<td>19.0 II</td>
<td>25</td>
</tr>
<tr>
<td><em>D. veratrifolium × D. undulatum, #2</em></td>
<td>19.0 II</td>
<td>25</td>
</tr>
<tr>
<td><em>D. veratrifolium × D. stratiotes</em></td>
<td>19.0 II</td>
<td>25</td>
</tr>
<tr>
<td><em>D. veratrifolium × D. tokai</em></td>
<td>19.0 II</td>
<td>25</td>
</tr>
<tr>
<td><em>D. veratrifolium × D. schulleri</em></td>
<td>19.0 II</td>
<td>25</td>
</tr>
<tr>
<td><em>D. veratrifolium × D. Taurus</em></td>
<td>19.0 II</td>
<td>25</td>
</tr>
<tr>
<td><em>D. stratiotes × D. tokai</em></td>
<td>19.0 II</td>
<td>25</td>
</tr>
<tr>
<td><em>D. undulatum × D. gouldii</em></td>
<td>19.0 II</td>
<td>25</td>
</tr>
<tr>
<td><em>D. taurinum × D. gouldii</em></td>
<td>19.0 II</td>
<td>25</td>
</tr>
<tr>
<td><em>D. mirbelianum × D. johannis</em></td>
<td>19.0 II</td>
<td>25</td>
</tr>
</tbody>
</table>

* D. Taurus = *D. taurinum × D. undulatum.*
TABLE 5
MEAN CHROMOSOME CONFIGURATIONS AT METAPHASE I OF MEIOSIS IN PMCs OF BETWEEN-SECTION HYBRIDS OF PHALAENANTHE AND CERATOBium, 2n = 38

<table>
<thead>
<tr>
<th>HYBRID</th>
<th>MEAN CONFIGURATION PER PMC</th>
<th>NUMBER OF PMCs OBSERVED</th>
</tr>
</thead>
<tbody>
<tr>
<td>D. superbiens (natural hybrid)</td>
<td>2.04&lt;sub&gt;i&lt;/sub&gt;+17.80&lt;sub&gt;j&lt;/sub&gt;+0.12&lt;sub&gt;j&lt;/sub&gt;</td>
<td>25</td>
</tr>
<tr>
<td>D. phalaenopsis x D. undulatum</td>
<td>2.34&lt;sub&gt;i&lt;/sub&gt;+17.76&lt;sub&gt;j&lt;/sub&gt;</td>
<td>29</td>
</tr>
<tr>
<td>D. phalaenopsis x D. gouldii, #1</td>
<td>3.87&lt;sub&gt;i&lt;/sub&gt;+17.07&lt;sub&gt;j&lt;/sub&gt;</td>
<td>23</td>
</tr>
<tr>
<td>D. phalaenopsis x D. gouldii, #2</td>
<td>6.48&lt;sub&gt;i&lt;/sub&gt;+15.76&lt;sub&gt;j&lt;/sub&gt;</td>
<td>25</td>
</tr>
<tr>
<td>D. phalaenopsis x D. tokai</td>
<td>2.42&lt;sub&gt;i&lt;/sub&gt;+17.73&lt;sub&gt;j&lt;/sub&gt;+0.04&lt;sub&gt;j&lt;/sub&gt;</td>
<td>26</td>
</tr>
<tr>
<td>D. phalaenopsis x D. latourea</td>
<td>1.00&lt;sub&gt;i&lt;/sub&gt;+18.50&lt;sub&gt;j&lt;/sub&gt;</td>
<td>24</td>
</tr>
<tr>
<td>D. phalaenopsis x D. tokai</td>
<td>0.16&lt;sub&gt;i&lt;/sub&gt;+18.92&lt;sub&gt;j&lt;/sub&gt;</td>
<td>100</td>
</tr>
<tr>
<td>D. phalaenopsis x D. veratrifolium</td>
<td>2.50&lt;sub&gt;i&lt;/sub&gt;+17.70&lt;sub&gt;j&lt;/sub&gt;+0.03&lt;sub&gt;j&lt;/sub&gt;</td>
<td>30</td>
</tr>
</tbody>
</table>

Meiosis in Within-Section Hybrid of Latourea

The single plant of D. atrovioiaceum x D. macrophyllum (Figs. 19, 20) was a rare and unexpected hypodiploid with 2n = 37. Meiotic behavior was comparable to that often encountered in trisomics (Tables 7, 9, Fig. 32). Twenty-four out of 25 PMCs examined showed one trivalent plus 17 bivalents and only 1 PMC showed 18 bivalents plus a univalent.

A few bivalents were more or less heteromorphic. Trivalents were either V-shape or, as can be seen in Figure 32, a chain of three. At anaphase I, the chromosomes of the bivalents separated regularly to both poles, while the trivalent usually separated two for one. The products of meiosis were tetrads.

Meiosis in Between-Section Hybrid of Ceratobium and Latourea

The irregular meiosis in D. lasianthera x D. macrophyllum (Fig. 21) revealed variations in number of bivalents from 14 to 7 with a mean of 10.8 and univalents from 10 to 26 with a mean of 16.3 (Table 8, Fig. 33). Nearly all bivalents were heteromorphic. Univalents were of variable size, and scattered in and around the loose metaphase plate.

At anaphase I, the bivalents separated toward both poles, while the univalents often lagged between the two anaphase groups, and ultimately the entire group was reconstituted into restitution nuclei. Dyads and dyads with microcytes were, therefore, common products of meiosis. A few triads, tetrads, and tetrads with microcytes were also observed (Table 9). The relatively high frequency of triad formation suggests that restitution also occurred at the second division.

Meiosis in Between-Section Hybrid of Phalaenanthex and Latourea

Meiosis in D. phalaenopsis x D. New Guinea (Figs. 22, 23) was highly irregular. The number

TABLE 6
CHROMOSOME CONFIGURATIONS AT METAPHASE I OF MEIOSIS IN PMCs OF TETRAPLOID HYBRIDS, 2n = 76

<table>
<thead>
<tr>
<th>SECTIONS INVOLVED</th>
<th>HYBRID</th>
<th>CHROMOSOME CONFIGURATIONS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1&lt;sub&gt;j&lt;/sub&gt; 1&lt;sub&gt;j&lt;/sub&gt; 2&lt;sub&gt;j&lt;/sub&gt; 2&lt;sub&gt;j&lt;/sub&gt; 2&lt;sub&gt;j&lt;/sub&gt;</td>
</tr>
<tr>
<td>Ceratobium x Ceratobium</td>
<td>D. stratiotes x D. undulatum</td>
<td>38&lt;sub&gt;j&lt;/sub&gt; 37&lt;sub&gt;j&lt;/sub&gt; 36&lt;sub&gt;j&lt;/sub&gt; 35&lt;sub&gt;j&lt;/sub&gt; 34&lt;sub&gt;j&lt;/sub&gt; 33&lt;sub&gt;j&lt;/sub&gt; 32&lt;sub&gt;j&lt;/sub&gt; 2&lt;sub&gt;j&lt;/sub&gt; 2&lt;sub&gt;j&lt;/sub&gt; 2&lt;sub&gt;j&lt;/sub&gt;</td>
</tr>
<tr>
<td>Phalaenanthex x Ceratobium</td>
<td>D. phalaenopsis x D. gouldii</td>
<td>12 2 15 3 4 1 2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
of bivalents ranged from 7–0 with a mean of 1.8, and that of univalents from 23–38 (Table 8). PMCs with no bivalents and 38 univalents were common. No definite metaphase plates were formed at metaphase I (Fig. 34). The movement of chromosomes to either pole at anaphase I was not orderly enough to produce the usual daughter nuclei, and consequently restitution was common for the majority of PMCs. The products of meiosis were mostly dyads with or without microcytes, but tetrads, monads, and triads were also observed (Table 9).

**DISCUSSION**

Meiosis in 11 species investigated was, as one might expect, regular. Also the within-section hybrids of Ceratobium exhibited 19 bivalents regularly indicating a strong homology of species genomes within this section (Fig. 35). However, some morphological variation of chromosomes was evidenced through the formation of heteromorphic bivalents in the species hybrids. The relatively high fertility that breeders encounter in these within-section hybrids reflects the strong homology of the parental genomes.

The between-section diploid hybrids involving the Ceratobium and Phalaenanthe sections indicated a greater divergence of parental genomes, for bivalents per PMC averaged from 18.9 to 15.8. The fertility of these hybrids is generally impaired by the irregularity in metaphase pairing.

Meiosis in intra- and intersectional tetraploid hybrids throw additional light on the genome homology in Ceratobium and Phalaenanthe. The within-section tetraploid hybrid of Ceratobium, *D. stratiotes x D. undulatum* formed quadri-valents, bivalents, and univalents which is a characteristic chromosomal behavior of autotetraploids, while the between-section tetraploid hybrid of Ceratobium and Phalaenanthe, *D. phalaenopsis x D. gouldii*, behaved as a typical amphidiploid with the exclusive formation of bivalents. It might be noted that the diploid counterpart of the within-section tetraploid showed good pairing at meiosis, while the diploid counterpart of the between-section tetraploid was irregular in meiosis. The intersectional diploid hybrids are generally low in fertility due to the poor chromosome pairing at metaphase, but doubling results in regularity in meiosis and the consequent restoration of

**TABLE 7**

<table>
<thead>
<tr>
<th>HYBRID</th>
<th>CHROMOSOME CONFIGURATIONS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>17x+1s</td>
</tr>
<tr>
<td></td>
<td>2x+16s+1s</td>
</tr>
<tr>
<td></td>
<td>1x+18s</td>
</tr>
<tr>
<td><em>D. atrovioleum x D. macrophyllum</em></td>
<td>22</td>
</tr>
</tbody>
</table>

**TABLE 8**

<table>
<thead>
<tr>
<th>SECTION</th>
<th>SPECIES CROSSED</th>
<th>MEAN CONFIGURATION PER PMC</th>
<th>NUMBER OF PMCs OBSERVED</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ceratobium x Latourea</td>
<td><em>D. laianthera x D. macrophyllum</em></td>
<td>16.31x+10.83s</td>
<td>30</td>
</tr>
<tr>
<td>Phalaenanthe x Latourea</td>
<td><em>D. phalaenopsis x D. New Guinea</em></td>
<td>34.28x+1.81s+0.32s</td>
<td>31</td>
</tr>
</tbody>
</table>

* D. New Guinea is *D. atrovioleum x D. macrophyllum.*
fertility. On the other hand, tetraploidy in intrasectional hybrids results in reduced fertility due to the homologous parental genomes forming multivalents.

*Fig. 35. Diagrammatic representation of chromosome homology in hybrids of *Dendrobium*. The hybrid investigated was a monosomic.*

*H. superbiens* was originally given species status but now it is generally recognized as a natural hybrid between species from the sections *Phalaenante* and *Ceratobium* (Holttum, 1957). The intersectional hybrid, *D. phalaenopsis x D. undulatum* most closely resemble *D. superbiens* in external morphology, but the large "marker" chromosome of *D. undulatum* was conspicuously absent in the particular plant examined. Further studies involving several individual plants collected from their natural habitat should clarify the cytological aspects of this natural hybrid.

It appears that the taxonomic gap between Ceratobium and Latourea is much wider than that between Ceratobium and Phalaenante (*Fig. 35*), for the Ceratobium-Latourea hybrid exhibited an average of 10.8 bivalents per PMC, while the Ceratobium-Phalaenante hybrids averaged between 18.9 to 15.8. The gap between Phalaenante and Latourea is still greater as indicated by the very weak homology of parental genomes forming an average of only 1.8 bivalents per PMC.

The separation of species into the three groups, Ceratobium, Phalaenante, and Latourea appears to be valid on the basis of external morphology, cytology, or crossability. Ceratobium and Phalaenante are phylogenetically much more closely related to each other than they are to Latourea. Also, it might be concluded that Latourea is more closely related to Ceratobium than to Phalaenante. If evolution of these groups occurred in a sequential manner, then it is logical to assume that divergence proceeded from Latourea to Ceratobium to Phalaenante.

Considerable differences in taxonomy and phylogy might be noted for the *Dendrobium* genus and the *Vanda* alliance. Holttum (1957) has pointed out that:

The flower-form throughout the tribe (Dendrobium) is remarkably constant; there is much greater variation in vegetative characters. This is an interesting contrast to the *Vanda*-*Arachnis* tribe, in which floral form is very varied and vegetative form much less so.
Botanists always consider flower-characters more important than vegetative ones when deciding on the limits of genera, for which reason the Vanda tribe has many genera and the Dendrobium tribe few. But it is fairly clear that some sections of Dendrobium are no more nearly related than some genera of the Vanda tribe; species of one section will often not cross with species of another, though intergeneric crosses in the Vanda tribe are common.

Cytological evidences support Holtum's views (Tanaka and Kamemoto, 1960, 1961; Kamemoto and Shindo, 1962; Shindo and Kamemoto, in press). The divergence between sections of Dendrobium as measured by the degree of chromosomal homology is often much greater than that between some genera of the Vanda alliance. For example, chromosome homology among strap-leaved Vanda, Neofinetia, and Asco centrum or between terete-leaved Vanda and Luisia is much stronger than that among some sections of the Dendrobium genus. From the cytological standpoint, the entire Dendrobium genus with its 30 or more sections is somewhat comparable to the entire Vanda alliance comprising numerous genera and therefore, if taxonomy of these groups were to be based on chromosome homology, the merger of several genera in the Vanda alliance and the elevation of several sections of the Dendrobium genus to generic rank are indicated.

Dressler and Dodson (1960) have concluded that there are no infallible "key characters" universally applicable for orchid classification. Emphasis on a single or limited number of taxonomic characters will inevitably lead to over-splitting or over-lumping, since different groups of orchids may have different rates of divergence of certain characters. It appears that for both Dendrobium and Vanda alliances, major revisions in classification based on an intensive study of morphological characters coupled with the accumulated knowledge on crossability and chromosome homology is highly desirable.

**SUMMARY**

Meiotic chromosome behavior was observed for species and intra- and intersectional hybrids involving Ceratobium, Phalaenanthe, and Latourea of the genus Dendrobium. Meiosis was regular in all species, showing 19 bivalents at metaphase I. The within-section diploid hybrids of Ceratobium formed 19 bivalents as in the

**TABLE 9**

**SPORAD FORMATION IN BETWEEN-SECTION HYBRIDS**

<table>
<thead>
<tr>
<th>SECTION</th>
<th>HYBRID</th>
<th>SPORAD</th>
<th>TOTAL</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Tetrad</td>
<td>Tetrad+ms*</td>
</tr>
<tr>
<td>Phalaenanthe</td>
<td>D. phalaenopsis x D.</td>
<td>95</td>
<td>1</td>
</tr>
<tr>
<td>x Ceratobium</td>
<td>undulatum</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>D. phalaenopsis x D.</td>
<td>64</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>gouldii, #2</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>D. phalaenopsis x D.</td>
<td>94</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>tokai</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>D. phalaenopsis x D.</td>
<td>95</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>taurinum</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>D. phalaenopsis x D.</td>
<td>92</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Johnnii</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>D. phalaenopsis x D.</td>
<td>87</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>veratrifolium</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phalaenanthe</td>
<td>D. phalaenopsis x D.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>x Latourea</td>
<td>undulatum</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ceratobium</td>
<td>D. lasianthera</td>
<td></td>
<td></td>
</tr>
<tr>
<td>x Latourea</td>
<td>D. macrophyllum</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* ms = microcytes.
species, but a few heteromorphic pairs were observed in some of the hybrids, which suggested morphological changes in certain homologous chromosomes of the parental species involved.

Including the natural hybrid, *D. superbiens*, the between-section diploid hybrids of Phalaenathe and Ceratobium exhibited irregularities in meiosis with the number of bivalents in each hybrid averaging from 15.7 to 18.9.

A within-Ceratobium tetraploid hybrid, *D. stratiotes* × *D. undulatum* formed 1 or 2 quadrivalents and behaved somewhat like an autotetraploid, while a tetraploid hybrid between Ceratobium and Phalaenathe, *D. phalaenopsis* × *D. gouldii* formed only bivalents, similar to an amphidiploid.

A Ceratobium-Latourea hybrid formed an average of 10.8 bivalents per PMC, while a Phalaenathe-Latourea hybrid formed only 1.8 bivalents. It can be concluded that Ceratobium and Phalaenathe are relatively closely related, while Latourea is more distantly related to Ceratobium and Phalaenathe, and that if sequential divergence occurred in these groups, the order appears to be Latourea to Ceratobium to Phalaenathe.

REFERENCES


NEWS NOTE

Tenth Pacific Science Congress Papers

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A Symposium and Panel Discussion

J. C. Christ, convener and chairman

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- The Use of Soil Surveys in Conservation Planning
- Watershed Management
- Economics of Conservation Programs
- Soil and Water Conservation in Relation to Wildlife Habitat
- Forestry Potential in Hawaii
- Plant Selection for Conservation Purposes

Participating in the panel discussion—"Who is Responsible?"—were the following:

- Marcos M. Alicante (Philippines)
- R. G. Downes (Australia)
- Edward H. Graham (United States)
- Ching Po Liu (Taiwan)
- Arthur T. Semple (Central America and Mexico)

Mr. Christ was formerly state conservationist, U. S. Department of Agriculture, Soil Conservation Service, Honolulu, Hawaii.

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Origin and Affinity of Kodiak Island Biota

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ALAN SOLEM
Nonmarine Mollusks of New Caledonia

CHARLES E. FORD, JR.
Reproduction in the Aggregating Sea Anemone

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NEWS NOTE:

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The Origin and Affinity of the Biota of the Kodiak Island Group, Alaska

ROBERT E. VINCENT

KODIAK ISLAND occupies an important biogeographical position. Situated along the northwestern border of the Gulf of Alaska, this island and its neighboring lesser islands have biogeographic relationships that radiate in three directions: westward along the Aleutian Islands, northward toward interior Alaska, and southeastern toward the temperate Pacific Coastal and Rocky Mountain regions of North America. The Aleutian and Bering Strait migration routes tend to funnel through this strategic area. Furthermore, the Island Group was probably severely glaciated during at least the later part of the Pleistocene. Karlstrom (1960) found geological evidence of a small late Pleistocene refuge on southwestern Kodiak Island. Nearly all subsequent biota, besides that which may have persisted on the refuge or on nunataks, would have had to originate as reinvaders from adjacent land or sea areas. A third peculiar feature in addition to location and glacial history is the possible significance of major habitat change caused by an encroaching timber line across the northeastern part of Kodiak Island.

A working hypothesis based solely upon geographic consideration could be proposed: that the biota of Kodiak Island is fashioned from elements of the three diverse regions with which it has geographic relationships. The purpose of this paper is to consider the relationship of the Kodiak Island Group biota to that of mainland Alaska. This should suggest what areas contribute heavily to the fauna and flora and indicate if geographic location is supported biogeographically.

A study of postglacial immigration of the Kodiak biota can be enlightening to the processes of intercontinental migrations, reinvasion following extirmination, and centers of postglacial dispersion. The Bering land connection and the Aleutian chain of islands have been

migration routes from Asia. After Pleistocene glaciation, northwestern Alaska was a major reservoir of plants and animals to reoccupy nearly barren areas, as Kodiak Island is presumed to have been.

METHODS

Because the indigenous mammal and freshwater fish fauna is sparse, it is necessary to place major emphasis upon plants. Hulten's Flora of Alaska and Yukon (1941) was used as the source for vascular plant distribution records. It is realized that Hulten's comprehensive work does not include all Alaskan species, nor are ranges as completely known as would be desirable. There are many areas within this vast state where few botanical collections have been made; range extensions and adjustments are being recorded annually. Yet, even within the limitation of knowledge concerning the flora of Alaska, the general trends and salient features should be little affected by addition of a few species or minor range adjustments.

Alaska can be divided into five subregions (exclusive of Kodiak Island) for purposes of grouping plant distribution records. These subregions are:

Southeastern Alaska (northwestward to Yukon)
Kenai Peninsula—Cook Inlet area
Alaska Peninsula (Iliamna to Cold Bay)
Aleutian Islands
Interior Alaska (all Alaska north and east of Bristol Bay and the Alaska Range)

Each of these subdivisions is a fairly well naturally defined unit, except for the large interior region. This area encompasses nearly all of the true arctic and much of the boreal zone in Alaska. Those species recorded by Hulten from southwestern Yukon were included in the interior subregion, for this area is the geographic connection between interior and southeastern Alaska.

In this study species that have been recorded
from Kodiak Island were tabulated along with each of the other subregions in which the species have also been recorded. This resulted in determining the total number of plant species on the Kodiak Island Group and in what other parts of Alaska the same species occurred. Interpretation of these data needs qualification in order to allow for a discontinuous distribution or for a hiatus in distributional records. A situation of this nature arises because only intra-Alaska distribution was considered. To illustrate: if a species was not recorded from the southeastern region but was found in the remainder of Alaska, it would appear that the species in question was a northern form, but this species could range along the British Columbia or Washington coasts. Thus, an erroneous conclusion could result from considering only intra-Alaskan ranges. However, for consistency, distribution outside of Alaska and the southwestern part of Yukon was not considered in the compilation of the subregional plant lists.

PHYSICAL FEATURES

Geologically, the Kodiak Archipelago is a continuation of the Kenai Peninsula 40 miles to the northeast. Separating the islands from the Alaska Peninsula on the northwest is the 20-30-mile wide and 600-plus-ft-deep Shelikof Strait. Fourteen islands larger than 7 sq miles make up the 4,900 sq miles of land in the archipelago. Kodiak is much the largest with 3,588 sq miles, and Afognak, with 700 sq miles, is second. This Island Group extends for approximately 180 miles in a northeast-southwest direction (Fig. 1).

The oldest rocks are Triassic and Jurassic, but overlying these are thick series of slate, graywacke, and conglomerates of late Mesozoic Age. More recent are deposits of sandstones and shales (Capps, 1937). The area was a center of extreme glaciation as local glaciers pushed seaward from all directions and as extremities of Peninsular and Kenai glaciers reached the Island Group. An intricate fjord coastline resulted from this glaciation.

Relief is irregular, with peaks rising to 4,000 ft on Kodiak Island and 2,200 ft on Afognak Island.

The temperate climate is uniformly cool, with a well-distributed annual precipitation of approximately 60 inches. Maximum air temperatures are in the low 80's and minimums seldom go below 0° F (Capps, 1937).

A layer of volcanic ash from the 1912 eruption of Mount Katmai covered much of the Island Group with up to several inches of pumice. Griggs (1915, 1918) and Wilcox (1959) discussed the influence of this and subsequent volcanic ash falls on vegetation.

VEGETATION

The Pacific Coastal Forest reaches its most northwesterly extension on Kodiak Island. Shuyak and Afognak islands are discontinuously forested at elevations below 700 ft. Outliers of this coastal forest extend north and south across Kodiak Island from Ugak Bay to Ugak Bay. To the immediate northward, along the base of the Alaska Peninsula, there are also small sections of coastal forest.

Dominating the forest is Picea sitchensis (Bong.) Carr., the only conifer on the archipelago. The open understory consists of Vaccinium ovalifolium Smith, Oplopanax horridus (Sm.) Mig., and Rubus spectabilis Pursh.

There seems to be little doubt but that Picea
FIG. 2. The number of plant species on Kodiak Island that are also found in other regions of Alaska.

forest is extending its range. Pollen analysis, historical records, tree growth, and tree age all indicate the recent advance of the forest border in the area near the village of Kodiak (Bowman, 1934; Griggs, 1934a, 1946; Heusser, 1960). No evidence has been reported that showed a more northward or westward conifer treeline during the hypsithermal. As Aleksandrova (1960) found on Novaya Zemlya, coniferous trees probably had not yet reached the Kodiak Island Group by the period of thermal maximum.

Calamagrostis canadensis (Michx.) Beauv. and Alnus crispa (Ait.) Pursh. that appear in the Picea forest openings become the characteristic plant cover for the southwestern part of Kodiak Island. Nearly all well-drained sites are occupied by this plant combination, which Griggs (1936) classified as subclimax in the nearby Katmai district. Hulten (1960) described this Alnus-Calamagrostis-Streptopus vegetation of western coastal Alaska as similar to that of some sections of Kamchatka. Superimposed on this vegetation along stream valleys is Populus trichocarpa Torr. and Gray. Other shrubs which commonly appear are Betula nana L., Vaccinium vitis-idea L., and Empetrum nigrum L. Abundant grasses are Hordeum brachyantherum Nevski., Elymus mollis Trin., Eriophorum angustifolium Roth, and Hierochloe alpina (Sw.) Roem. and Schult. Twenty-six species of Carex are found
on the Island Group. Mosses and lichens which are important in many tundra areas are of minor importance on western Kodiak Island, but eastward mosses form a prominent ground cover under the spruce forest.

Although the Kodiak tundra-like area has many affinities with the more northern tundras, it should not be considered a true tundra. As is characteristic of many northern vegetation types, it is not the species present that are characteristic but the relative abundance of each. Griggs (1934b, 1936) discussed this problem in regard to the Katmai district of the Alaska Peninsula. Kodiak Island is the only place in North America where the Arctic Zone is not bordered on the south by the boreal forest. In this area arctic or quasi-arctic vegetation makes direct contact with the temperate coastal forest.

THE FLORA AND ITS RELATIONSHIP TO OTHER REGIONS

Hulten recorded 377 species of vascular plants from the Kodiak Island Group. Of these same plants 329 are also found in southeastern Alaska; 314 in the Kenai–Cook Inlet area; 311 in the Alaska Peninsula; 243 in the Aleutians; and 266 in interior Alaska (Fig. 2). These total figures strongly indicate that all sections of Alaska have contributed to the flora of Kodiak. Of the total Kodiak flora, 156 species are found in all of the five designated subregions; and 132 more species are in all of Alaska except one subregion. As with most northern floras (Porsild [1951] stated that one-third of the North American arctic plants are circumpolar), that of Kodiak is dominated by holarctic or at least neoarctic species. The sharpest break in the flora is with the Aleutians; 62 species which are found on Kodiak Island are also in all Alaska except the Aleutians. Phytogeographically, much of the Aleutians belongs to Kamchatka (Hulten, 1960), but the remainder of Alaska is North American.

Following the previous division, the Alaska distribution of the Kodiak flora can be grouped into eight types of distributions. These are listed along with a few representative examples.

2. All Alaska except Kenai-Cook Inlet (13 species): *Agrostis borealis* Hartm., *Carex stylosa* C. A. Mey., *Renunculus repens* L.

If we examine the latter three of the above groups (the others have too wide a distribution to denote an affinity pattern), further indication may be apparent as to the relationship of the flora of Kodiak Island to the remainder of Alaska.

There are three general directions from which plants could reach the Kodiak Island Group: (1) from the west via the Aleutians and through the Alaska Peninsula, (2) from the northern interior by way of the Alaska Peninsula and the Kenai Peninsula, and (3) from the southeast out of southern Alaska, again by way of the Kenai Peninsula and the Alaska Peninsula. Ocean currents could also be a factor, as the Gulf of Alaska Current runs in an arcuate path from southeastern Alaska past Kodiak Island (Fig. 3).

Of the species whose ranges in Alaska are applicable, 50 came from the east and 13 each from the north and west. The diversity of possible elements from the southeast should not be overlooked. There are montane, coastal, boreal, and some arctic elements available from this direction.

Seven species are listed by Hulten with an Alaskan range of only Kodiak Island. This apparent endemism is probably due to a lack of data, for Anderson (1959) listed several of
these same species as being fairly widespread throughout coastal Alaska.

Further insight regarding affinity of the Kodiak flora may be found by examining some of the characteristic species and the elements with which they are commonly associated.

Three species are found that are typical of both Asiatic and American sectors of the North Pacific. They are *Fritillaria camtschatica* (L.) Ker., *Oplopanax horridus* (Sm.) Mig., and *Casiope lycopodioides* (Pall.) D. Don.


Petran tundra has such characteristic species present as *Carex pyrenaica* Wahl., *C. nigricans* C. A. Mey., *Androsace chamaejasme* Host., and *Thalictrum alpinum* L. There are eight species of *Poa*, four species each of both *Agrostis* and *Luzula*, as well as representatives of *Festuca*, *Phleum*, and *Trisetum*.

The widespread arctic-montane species: *Polygnum viviparum* L., *Oxyria digyna* (L.) Hill, and *Saxifraga oppositifolia* L. are also present.

The boreal forest element consists of such species as *Vaccinium uliginosum* L., *V. vitis-
idaea L., Viburnum edule (Michx.) Raf., Pedicularis labradorica Panzer., Cornus canadensis L., and Calamagrostis sp.

Coastal forest species are: Picea sitchensis (Bong.) Carr, Vaccinium ovalifolium Smith, Oplopanax horridus (Sm.) Mig., and Rubus spectabilis, Pursh.

Conspicuous by their absence from Kodiak, yet present in adjoining regions or throughout Alaska are: Poa arctica R. Br., Arctagrostis latifolia (R. Br.) Griseb., Draba nivalis Lilj., Sagina intermedia Fenzl., Picea glauca (Moench) Voss., and Astragalus alpinus L.

ANIMAL DISTRIBUTION

An interesting zoogeographical situation arises in regard to the land mammals. Only six species are known to be native to the Island Group (Myotis lucifugus, Microtus oeconomus, Vulpes fulva, Ursus middendorffi, Mustela erminea, and Lutra canadensis). At least 12 introduced mammals have become established. Many of these introduced mammals as well as others not present are common on the nearby mainland but have not become naturally established on the islands.

The indigenous mammals have affinities with several regions. U. middendorffi is closely related to the Asiatic bears. M. lucifugus is a widely-distributed more southerly form. M. oeconomus is typically a northern meadow mouse. The remaining three native species have a general circumpolar distribution or else a closely related palaearctic counterpart. Many of the introduced species are either more southern forms or boreal species. The near absence of the expected boreal mammals is conspicuous. All native mammals could have easily moved from the mainland to the islands either by flight or swimming, or were small enough to be transported by drift.

Thus, mammals show much the same affinity pattern as plants: a dominance of holarctic forms, with the remainder of the fauna having strong relationships to Asia, the Arctic, and more southerly regions. Introduced species from the boreal and coastal forests thrive. As in plants, mammals not expected to have been found in Beringia appear to have been late in arriving on the Island Group or have invaded the islands only with man's help.

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The avifauna appears to be drawing its members from four areas: Asiatic immigrants, such as Branta nigricans and Larus hyperboreus; Bering Sea immigrants, as Aethio cristatella and Fratercula corniculata; northern immigrants, as Gavia stellata and Lagopus lagopus; southeastern immigrants, as Megaceryle alcyon and Ixoreus naevius; and numerous widespread holarctic species. Williamson and Peyton (1962) found five species of birds in the nearby Iliamna area that possessed characteristics intermediate between interior and coastal populations. However, the avifauna of this region differs from the biota of Kodiak Island in that an Hudsonian avifauna dominates.

All freshwater fishes on the Island Group are euryhaline. Members of each species move readily back and forth between fresh and salt-water. The wide-ranging north temperate Gas- terosternus acuticeps, the five species of the North Pacific genus Oncorhynchus, the more southerly Salmo gairdneri, Cottus aleuticus with its range centered in the Aleutians, and two charrs (Sal- velinus malma, a southern species, and S. alpinus, an arctic species), whose range overlap on Ko- diak Island, collectively present an affinity pattern similar to that of the plants.

DISCUSSION

Climatic similarity is encouraging the expression of southeastern elements. The atypical arctic element may be due to this same maritime temperate climate and proximity of the Island Group to the large unglaciated portion of north-western Alaska. Re-immigration has not proceeded as rapidly as climatic change; thus, a gap exists between current and seemingly po- tential distribution. In the case of mammals, this gap is being closed rapidly by introduction. The Kodiak region is characterized by the north- ward advancement of the temperate coastal elements into an area now occupied by a hetero- geneous biota. Boreal elements, both plant and animal, that normally occupy this region are much reduced.

Although Kodiak latitudinally belongs in the Boreal Zone, boreal elements are not as well represented as arctic, montane, or coastal ele- ments. Poor boreal expression may stem from the barrier formed by the Rocky Mountain complex between the boreal areas. The effective-
ness of this barrier is suggested by the number of plant species (13) found in all regions of Alaska (including Kodiak) except the Kenai-Cook Inlet area and the marked individuality of the coastal forest. In the absence of boreal expression, coastal forests elements extend farther north into arctic situations in order to occupy this habitat. In addition, approximately 20 common boreal mammals that have not made their way by natural means to the Islands are found on the nearby Alaska mainland. This again indicates late arrival of this group of mammals in southwestern Alaska.

Abundance of arctic plant elements may be the result of the archipelago being closer to the Beringian refuge than it was to the more continental boreal region. A reservoir of arctic plant species was available to invade the denuded temperate islands (Hulten [1937] said that nearly all plants west of Prince William Sound originated in Beringia), whereas many boreal plant and animal species had to migrate from southern refuges, occupying much of the present Boreal Zone before reaching Kodiak. In place of a mountain barrier to surmount, arctic species could follow the Bering Sea coastal plain. This same mountain complex, which is a barrier to boreal species, probably accounts for the prevalence of Petran tundra species. Coastal forest species, on the other hand, could utilize the exposed coastal plain as a migration route from the Washington-Oregon refuge area.

The information presented in this paper establishes that the Kodiak Archipelago is drawing members for its youthful biota from several sources, namely, Asia via the Aleutians and Bering Strait, interior and arctic Alaska, and southeastern Alaska. Boreal biota is largely lacking due to mountain barriers and distance to late Pleistocene refuges utilized by boreal species. Favoring the prevailing climate, coastal forest elements are expanding over the archipelago. There is little evidence to suggest that the refuge area on southwestern Kodiak Island was an important center of dispersal.

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Nonmarine Mollusks of Rongelap Atoll, Marshall Islands

NORMAN J. REIGLE

It has long been realized that the coral atolls and low islands of the Pacific possess a meager, limited, and characteristic snail fauna which are of little zoogeographical value (Pilsbry; 1900, 1916, Cooke; 1926). Cooke (1934) has described the terrestrial molluscan fauna of one of the typical lower islands; and recently Solem (1959) has listed the major molluscan elements of the atoll fauna.

In recent years the Marshall Islands served as a center for United States atomic testing. This large operation brought about many changes in the life of certain islands, including mass shiftings of human populations. In view of the possible influence of population movements and of testing on the fauna of an area, it might be helpful to record the available distribution records, not only to learn what is happening to the mollusks in the course of the nuclear tests but also to obtain a better knowledge of the fauna in this area.

Published records of nonmarine mollusks in the Marshall Islands are very scarce. Although this group is composed of 32 islands and 867 reefs (Robson, 1946), the nonmarine mollusks of only 2 of the islands have been reported. The Marshalls are a homogenous series of islands, with the highest elevation about 33 ft (Osborn, 1944). Consequently, these islands lack the more interesting and diverse land snails which are found on the higher islands, and it is not surprising that little has been written about this vast area.

Pease (1860) described six new species from Ebon which have since been reduced to two (see Cooke and Kondo, 1960: 180–191; H. B. Baker, 1940: 150; Pilsbry, 1917:151–152). Schnee (1904) listed three land snails and one oncidiid slug from Jaluit. His paper was concerned primarily with vertebrates and only a few mollusks were collected. Since the paper of Pease from which most of the published Marshall Island records have been derived contains only descriptions of new species, and the Schnee records are only incidental, it is apparent that these records are incomplete. Recently Omphalotropis fragilis Pease has been recorded on two of the atolls (Marshall, 1950); and Abbott (1958) described a new subspecies from Eniwetok and also recorded it from two neighboring atolls, including Rongelap. Cooke and Kondo (1960), in their revision of the Tornatellinidae and Achatinellidae, supplied additional records for the area. Several records from the “Marshall Islands” which really refer to Nauru, stem from a paper by O. Boeteger (1904). Prior to 1914 this island was part of the German Marshall Islands Protectorate, but is not generally considered geographically a part of the Marshall Islands.

Rongelap Atoll, also known under the names of Rimski-Korsakoff I., Rongelab, Rongorappu To, and Pescadore, is located in the northeastern portion of the Marshall Islands at 11° 20' N, 166° 50' E (Fig. 1). A general description and more complete maps of Rongelap and neighboring atolls, of Bikini, Eniwetok, and Rongerik, were published by Taylor (1950).

The land snail fauna of Rongelap is typical of a Pacific atoll. As one would suspect, all of the species have a wide range of distribution in the Pacific. The only exception is one subspecies, thus far recorded only from the Marshall Islands (Abbott, 1958). The various species recorded were unequally distributed on the islands. Of the 10 species mentioned here, 6 represent new records for the Marshall Islands.

MATERIAL STUDIED

This study was based upon a collection made in September 1959 by Dr. I. Eugene Wallen, aquatic biologist with the Atomic Energy Commission. Collections were made on five islands in the atoll, and most were made within 150 ft from shore. Of the 450 specimens collected,
two-thirds were found alive. This collection was presented to Dr. Henry van der Schalie, who was working on Eniwetok at that time. The Rongelap collection was later given to the author for study. In addition one lot of shells containing two species was collected by Dr. van der Schalie on the island of Japtaq, Eniwetok Atoll. Four lots of Marshall Island nonmarine snails were contained in the University of Michigan Museum of Zoology collection. One of these is a new locality record.

The material examined has been deposited in the University of Michigan Museum of Zoology, and representative Truncatellidae were placed with the Museum of Comparative Zoology, Harvard University.

Acknowledgments: I wish to thank Dr. Henry van der Schalie for helpful suggestions and the use of facilities; Dr. William J. Clench for kindly determining Truncatella granum; Mrs. Annie Gismann for reviewing the manuscript; and Lee Lonsdale for preparing the illustration.

SYSTEMATIC LIST

The nonmarine snail fauna collected by Dr. Wallen on Rongelap Atoll comprised the following species:

Family Ellobiidae

Melampus luteus Quoy and Gaimard
Marshall Islands records: none.
Distribution on Rongelap: Mellu; only 2 living specimens.

Melampus fasciatus Deshayes
Marshall Island records: none.
Distribution on Rongelap: Mellu; 18 living specimens.
Family Pupillidae

*Gastrocopta (Sinalbinula) pediculus* (Schuttleworth)


Distribution on Rongelap: Arbar, Gogan, Burok, and Mellu.

This snail was the most abundant on the atoll and comprised nearly 50% of the shells collected. Live specimens were taken at each of the stations listed. It was found commonly on and around dead coconut leaves. One specimen was collected by Dr. van der Schalie on the island of Japtan, Eniwetok Atoll.

Family Tornatellinidae

*Lamellidea pusilla* (Gould)


Distribution on Rongelap: Arbar, Gogan, and Mellu.

Although *Lamellidea* was not abundant at any of the stations, the series (including a number of juveniles) was large enough to make a satisfactory determination. Pease's *Tornatellina nitida* and *Lamellidea serrata* belong with this species (Cooke and Kondo, 1960:190).

Family Helicarionidae

*Liardetia (Liardetia) samoensis* (Mousson)

(= *striolata* Pease)

Marshall Island records: Ebon (Pease, 1860).

Distribution on Rongelap: Gogan; only 10 dead specimens were found.

Family Subulinidae

* Lamellaxis (Allopeas) gracilis* (Hutton)

Marshall Island records: none.

Distribution on Rongelap: Arbar, Gogan, Burok, and Mellu.

Although this widely distributed snail was found on four of the five islands, visited, it was not abundant on any of the islands and represented only 6% of the whole collection. Living specimens were taken from Gogan and Mellu. Dr. van der Schalie also collected a series of live *L. gracilis* on the island of Japtan, Eniwetok Atoll.

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Family Truncatellidae

*Truncatella (Truncatella) guerini* A. and J. B. Villa (= *valida* Pfeiffer)

Marshall Island records: none.

Distribution on Rongelap: Mellu and Keishi-echi.

*T. guerini* was very commonly collected on two of the islands and comprised one quarter of the collection. It was found living at both stations.

*Truncatella (Truncatella) granum* Garrett

Marshall Islands records: none.

Distribution on Rongelap: Arbar; 5 specimens, 2 living, were found.

Family Assimineidae

*Assiminea nitida marshallensis* Abbott


This species was collected commonly on Arbar. Of the 56 specimens examined only 1 had attained the maximum growth that is characteristic of this subspecies.

*Assiminea cf. hidalgoi* Gassies

Marshall Island records: none.

Distribution on Rongelap: Arbar.

Eight specimens of *Assiminea*, which closely resemble New Caledonian specimens of *A. hidalgoi*, were found with *A. nitida marshallensis*. *A. hidalgoi* is a part of a widespread but, as yet, unclarified complex of species (Abbott, 1960). Since the systematics of the species outside the Philippines are in a confused state, it seems best not to assign a definite identification to the species in question. The radula formula observed in these specimens is: centrals $4-1-4$ to $5-1-5$; laterals $6-1-7$; inner marginals 9-10; outer marginals 15+.

ADDITIONAL RECORDS

The following nine species have been reported from the Marshall group but were not
collected on Rongelap. Some of these records may not be valid.

Oncidium "(verruculatum Cuvier?)." Jaluit (Schnee, 1904). This record probably refers to O. peronii Cuvier, a species Hoffman (1929) mapped as occurring in the Marshall Islands, while he excluded the former species.

Pupina complanata (Pease). Ebon (Pease, 1860).


Subulina octona (Bruguieres). Jaluit (Schnee, 1904).

Omphalotropis fragilis Pease. Ebon (Pease, 1860), Likiep and Arno (Marshall, 1950). There are also three specimens from Jaluit in the Museum of Zoology, University of Michigan collection.

Tornatellides simplex Pease. Ebon. This isolated record outside of the general distribution is discussed by Cooke and Kondo (1960:26).

Tornatellinops sp. Included in a map by Cooke and Kondo (1960, Figs. 6 and 78).

Elasmias "(apertum Pease)." Arno and Majuro (Cooke and Kondo, 1960).

Elasmias manilense (Dohrn). Jaluit (Schnee, 1904). The specific identity of the Marshall Island Elasmias is apparently not yet definitely established; hence this record is questionable.

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New Records of New Caledonian Nonmarine Mollusks and an Analysis of the Introduced Mollusks

ALAN SOLEM

THE ILLUSTRATED HANDBOOK of New Caledonian nonmarine mollusks issued by Franc (1957) has been supplemented by an annotated check list (Solem, 1961). Additional records are given by Solem (1960), and material collected by Borys Malkin between July and October 1958 is reported on here. A few notes on specimens from other sources are included, particularly on two very puzzling shells omitted from Solem's discussion (1960) to allow more critical examination. The location of cited materials is indicated by the following symbols: ANSP (Academy of Natural Sciences, Philadelphia), BPBM (Bernice P. Bishop Museum, Honolulu), CNHM (Chicago Natural History Museum). In each case the catalog number of the set is indicated to facilitate later efforts to consult the cited specimens.

Many of the Loyalty Island records are new, but the most important data are the addition of six species to the New Caledonian fauna, all of them introduced from other areas. Elasmias apertum (Pease), Lamellaxis micra (Orbigny), Opeas oparanum (Pfeiffer), Varicella sp., Diastole cornula (Pease), and Lacteoluma sp. were not previously known from New Caledonia.

1. RECORDS OF NONMARINE MOLLUSKS

The following locality records were thought worthy of publishing. With minor alterations, the sequence of species follows Solem (1961). References to previous literature can be located in Solem (1961) and are not repeated here.

Family HELICINIDAE

Pleuropoma primeana (Gassies, 1863)
Tadine, Mare, Loyalty Islands (CNHM 109456)

Pleuropoma mediana (Gassies, 1870)
Tadine, Mare, Loyalty Islands (CNHM 109457)

Family POTERIIDAE

Gassiesia conderti (Fischer and Bernardi, 1856)
Kuro, Ile des Pins, New Caledonia (CNHM 109427)

Family PLANORBIDAE

Physastra nasuta (Morelet, 1857)
Wabawo, Mare, Loyalty Islands (CNHM 109389)

Ouro, Ile des Pins, New Caledonia, in a rapid stream (CNHM 109445)

Muine, Ile des Pins, New Caledonia, in a small, shaded pond (CNHM 109446)

Vao, Ile des Pins, New Caledonia, on leaf debris in a rapid stream (CNHM 109447)

Gyransus (G.) r os s i ter i (Crosse, 1871)
Vao, Ile des Pins, New Caledonia (CNHM 109416)

Family TORNATELLINIDAE

Elasmias mariei (Crosse, 1874)
Tadine, Mare, Loyalty Islands, on vegetation (CNHM 109489)

Elasmias apertum (Pease, 1864)

1 Curator of Lower Invertebrates, Chicago Natural History Museum. Manuscript received February 27, 1963.
Elasmias apertum (Pease), Cooke and Kondo, 1960, Bull. B. P. Bishop Mus. 221:222-224, fig. 97 a–d
Tadine, Mare, Loyalty Islands, on vegetation (CNHM 109490)
La Roche, Mare, Loyalty Islands, on vegetation (CNHM 109385)
Cengeite, Mare, Loyalty Islands, on vegetation (CNHM 109386)

The numerous examples obtained show that this is a well-established species on Mare.

Tornatellinops nouseensis (Crosse, 1870)
Tadine, Mare, Loyalty Islands (CNHM 109491)

Family PUPILLIDAE

Gastrocopta (G.) servilis (Gould, 1843)
Tadine, Mare, Loyalty Islands (CNHM 109352, CNHM 109488)

Family ENIDAE

Subfamily PACHNODINAE

Rhachistia bistrio (Pfeiffer, 1855)
La Roche, Mare, Loyalty Islands, on foliage (CNHM 109435)
Tadine, Mare, Loyalty Islands, on foliage (CNHM 109492)
Cengeite, Mare, Loyalty Islands, under logs (CNHM 109437)

Verdcour (1961) has confirmed my earlier suggestion (Solem, 1959:60–62) that the New Caledonian–New Hebridean populations are conspecific with the East African R. braunsii. Undoubtedly, the Pacific Ocean populations represent a very early accidental introduction by European commerce.

Subfamily DRAPARNAUDEINAE

Draparnaudia lifuana Pilsbry, 1901
Tadine, Mare, Loyalty Islands, on dead foliage (CNHM 109411)

Solem (1962: 219–223, figs. 1–7) studied the anatomy of this material to determine the systematic position of Draparnaudia. Previously, the genus was associated with the sigmurethrous Cameniidae or Bulimulidae and was reluctantly kept in the Cameniidae (Solem, 1961:483–484).

Family SUBULINIDAE

"Opeas" oparanum (Pfeiffer, 1846)
Tadine, Mare, Loyalty Islands (CNHM 109391)

Subulina octona (Bruguière, 1792)
Kuro, Ile des Pins, New Caledonia (CNHM 109429)

Lamellaxis (Allopeas) micra (Orbigny, 1835)
Helix micra Orbigny, 1835, Magazin de Zool., 1835: 9, Santa Cruz de la Sierra, Bolivia
Kuro, Ile des Pins, New Caledonia (CNHM 109397)

Material reported by Solem (1960) as O. pumilum consists of juveniles of this species.

Family OLEACINIDAE

Varicella sp.
River drift at sea coast a few miles from Bourail, New Caledonia (ANSP 281661)

The single worn shell cannot be identified to specific level but is unquestionably a member of this genus (sensu lato). This is the first Pacific Ocean record for this Greater Antillean taxon.

Family ENDODONTIDAE

Andrefrancia vincentina (Crosse, 1870)
Forer de Thi Hanna at 800 m elevation, New Caledonia, under bark (CNHM 109353)

Family HELICARIONIDAE

Liardetia (L.) samoensis (Mousson, 1865)
Dge, Ouen Island, New Caledonia (BPBM 92282)
Tadine, Mare, Loyalty Islands (CNHM 109487)
Muine, Ile des Pins, New Caledonia (CNHM 109375)
Cengeite, Mare, Loyalty Islands (CNHM 109374)
Diastole (D.) conula (Pease, 1861)

Diastole (D.) conula (Pease), H. B. Baker, 1938, Bull. B. P. Bishop Museum, 158: 46–47, pl. 17, fig. 3, pl. 5, figs. 9, 10

Tadine, Mare, Loyalty Islands (CNHM 109380)

A single, slightly subadult specimen provides the first New Caledonian record for this Polynesian species. D. conula is widely distributed in the Society and Cook islands and has been reported from Rurutu in the Austral Islands.

Coneuplecta (Durgellina) calculosa (Gould, 1852)

Tadine, Mare, Loyalty Islands (CNHM 109486)
Vao, Isle des Pins, New Caledonia (CNHM 109366)
Wabawo, Mare, Loyalty Islands (CNHM 109379)

Bourail, New Caledonia (BPBM 212153)

Family ZONITIDAE

Hawaiiia minuscula (Binney, 1841)
Kuto, Ile des Pins, New Caledonia (CNHM 109378)

Family EULOTIDAE

Bradybaena similis (Ferussac, 1821)
Cengeite, Mare, Loyalty Islands (CNHM 109438)
Tadine, Mare, Loyalty Islands (CNHM 109440, CNHM 109443)
La Roche, Mare, Loyalty Islands (CNHM 109442)
Kuto, Ile de Pins, Loyalty Islands (CNHM 109441)

Family PARYPHANTIDAE

Rhytida (Ptychorhytida) inaequalis (Pfeiffer, 1854)
Kuto, Ile des Pins, New Caledonia, under logs in forest (CNHM 109413)

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Rhytida (Ptychorhytida) inaequalis (Pfeiffer, 1846)

Foret de Thi Hanna at 800 m elevation, New Caledonia (CNHM 109387)

Family SAGDIDAE

Lacteoluna sp.

River drift at sea coast a few miles from Bourail, New Caledonia (ANSP 151005)

Two worn specimens (ANSP 151005) are easily recognizable as thysanophorine. They may be the young of Lacteoluna selenina (Gould). As in the case of Varicella, this is the first Pacific record of a West Indian group.

II. NONMARINE MOLLUSCA INTRODUCED INTO NEW CALEDONIA

The New Caledonian land snail fauna contains a number of species that are obvious introductions from other parts of the world, several species that were spread through the Pacific by primitive man, and a few disharmonic elements that, although not yet equated with foreign taxa, are probably human imports. Collecting in the islands was very extensive from 1850 to 1880; thereafter only casual collections were made until 1911, when Sarasin and Roux assembled the materials reported on by Dautzenberg (1923) and Grimpe and Hoffmann (1925). In 1928 T. D. A. Cockerell gathered the specimens listed in Solem (1960), and in 1958 Borys Malkin collected the specimens reported on above. Each collection revealed new additions to the introduced fauna, but the widely separated periods of collecting make information as to the time of arrival impossible to establish for the majority of the imports. Some records exist for introduction of ornamental and food plants (Guillaumin, 1942), but no notice was taken of snails that might have been hidden in the soil-matted roots or sealed to the underside of a leaf. In nearly every case, all we can say is that a particular snail was established prior to a certain date. Despite the limited evidence as to time of introduction, the areas of origin of the introductions form a coherent pattern worth recording.
The following list contains species suspected of being imported, as well as those that were unquestionably brought in by commerce.

Family ANCYLIDAE

_Ancylius reticulatus_ Gassies, 1865, has not been found by subsequent collectors. The original description and figures fail to provide any characteristics by which this species can be separated from the European _A. fluvialis_. I have not seen material of this species.

_Ancyulus noumeensis_ Crosse, 1871, is equally little known. The inclination of the apex to the right precludes the possibility of this being the European _Aeroloxus lacustris_, but does not differ from some of the West Indian ancylics. The type locality "Noumea" is in itself suspect, since the city environs were substantially altered even at this early date.

Family VERONICELLIDAE

_Laevicaulus altie_ (Ferussac, 1825) is a Central African species that has been widely dispersed by man into India, Indonesia, and Madagascar (see Forcărt, 1953:63–68, 97–98). Much of its African distribution is caused by human agency, so that its original range is unknown. It was not reported from New Caledonia by early workers and was first collected by Sarasin and Roux in 1911.

_Angustipes (Sarasinula) plebeius_ (Fischer, 1868) was described from material collected in New Caledonia about 1863 (see Gassies, 1871:12). Common in New Caledonia, it has been reported in Tahiti, Upolu, and several of the Fijian Islands. Its native range is apparently Brazil and the West Indies, where it was long known as _Angustipes dubius_ (Semper) (see H. B. Baker, 1931:134–136).

Family TORNATELLINIDAE

The classification of this family has been put on a magnificent footing by Cooke and Kondo (1960), who also have covered the speciation patterns of the Polynesian, Micronesian, and Hawaiian species in exhaustive detail. Lack of material, however, prevented their giving full consideration to the affinities of extralimital species. Procurement of adequate samples will undoubtedly prove that many of the peripheral "species" are based on introduced populations of Polynesian species.

_Elasmia maries_ (Crosse, 1874) is one of the 21 "species" listed by Cooke and Kondo (1960). Unquestionably endemic species are found on Rapa, Rurutu, Raiyavae, Guam, and possibly the Caroline Islands. Possibly the remaining species are based upon introduced populations, although their status cannot be satisfactorily evaluated at this time.

_Elasmia apertura_ (Pease, 1864) is widely dispersed in Polynesia. Many localities are known for the Marquesas, Tuamotu, Australis, Society Islands, and Cook Islands, with additional records from Tongatapu, Rotuma, and Sunday Island in the Kermadec Group (see Cooke and Kondo, 1960:223). The New Caledonian introduction, at some time prior to 1958, was probably achieved through commerce with French Polynesia.

_Tornatellinaeus noumeensis_ (Crosse, 1870) belongs to a very widely distributed genus of 25 "species," at least one of which, _T. variabilis_ (Odhner), has been widely dispersed by man. The status of the New Caledonian morph is uncertain, but accidental introduction from Polynesia is a distinct possibility.

Family PUPILLIDAE

_Gastrocopta (Sinalbinula) pediculus_ (Shuttleworth, 1852) is almost universally distributed on both high and low islands of the Pacific Ocean. Pilsbry (1916–1918:141) considered that it might have been native to Indonesia or Melanesia, being carried there subsequently both by primitive man and modern commerce. It was well established in New Caledonia prior to 1859, when it was described as _Pupa artensis_ Montrouzier. Probably it was brought in from Polynesia.

_Gastrocopta (G.) servilis_ (Gould, 1843) is widely spread in the West Indies, Central America, and Brazil (var. oblonga) (see Pilsbry, 1916–1918:70–72, 141–144). It was introduced into Hawaii before 1892 and into the Philippines before 1895. The first New Caledonian
collection was made in 1928 (see Solem, 1960).  
Papisoma (Psychopatula) dioscoricola (C. B. Adams, 1845) ranges from South Carolina to southern Florida, and then from southern Texas to Brazil. The equivalent Old World species, P. orcula (Benson, 1850), is known from Africa, India, Indonesia, the Philippines, Australia, and some Pacific islands. Quite possibly orcula and dioscoricola are synonymous. This species was introduced to New Caledonia before 1874.  

Family ENIDAE  

Rhachistia bistrio (Pfeiffer, 1855) is an East African snail introduced into New Caledonia before 1855 (see above).  

Family FERUSSACIIDAE  

Cecilioides (Geostilbia) aperta (Swainson, 1840) is a strictly West Indian species, although it was found in the gardens of Noumea before 1867.  

Family SUBULINIDAE  

Subulina octona (Bruguère, 1792) is a tropical American species that long has been dispersed throughout the tropic and warm temperate regions of the world. The first New Caledonian record (Layard, 1889), however, was on plants imported from Reunion Island off Madagascar.  

Lamellaxis (Allopes) gracile (Hutton, 1834) was probably originally from the Neotropical region, but for almost a century has been pantropical in distribution. It was first reported from New Caledonia in 1859.  

Lamellaxis (Leptopeas) micra (Orbigny, 1835) is a native of Central and South America and the West Indies. It was first collected in New Caledonia in 1928.  

Pseudopeas tuckeri (Pfeiffer, 1846) is an Australian species reported from New Caledonia by Pilsbry in 1906. It has not been dissected and its position in the family is uncertain.  

"Opeas" oparanum (Pfeiffer, 1846) is a puzzling form of uncertain affinity widely distributed in the Pacific islands. It has not been dissected and we have no knowledge of its place in the family. Possibly it is a mutant of a West Indian or South American species. It was not reported from New Caledonia prior to 1958.

Family HELICARIONIDAE  

Conuspecta (Durgellina) calicina (Gould, 1852) is widely distributed in the Society, Cook, and Marquesas islands and evidently has been introduced into the Bismarck Archipelago (see H. B. Baker, 1941:234-235). The New Caledonian introduction was prior to 1868.

Liartetia (L.) samoensis (Mousson, 1865) was recorded from Samoa, Fiji, the Cook, Society, Ellice, Marquesas islands, and New Hebrides prior to 1870. In New Caledonia the earliest collection was prior to 1866. A strongly differentiated group of Liartetia (subgenera Dasyconus, Oceanesia, and Nesoreus) is endemic in the Society Islands, while the majority of the species will probably be found to be southeast Asian and Indonesian when the helicarianid faunas of these areas are adequately studied.

Diasstole (D.) conula (Pease, 1861) is found on several of the Society and Cook islands, and also on Ruuru in the Austral Islands. The New Caledonian introduction, undoubtedly from French Polynesia, was prior to 1958.

Family ZONITIDAE  

Hawaiiina minuscula (Binney, 1841) has been recorded from Hawaii before 1850, and from Pitcairn and Tahiti in the 1930's. It was found on Lord Howe Island in 1887, was collected on Norfolk Island before 1913, and has been reported several times from European greenhouses. The first New Caledonian record was in 1888.

Family LIMACIDAE  

Deroceras laeve (Müller, 1774) is a Holarctic species introduced into many different parts of the world. It was widespread in New Caledonia by 1911 and probably was introduced before 1871.

Family OLEACINIDAE  

Varicella sp. is a member of a West Indian group. The not yet identified species was introduced before 1928.
Nonmarine Mollusks of New Caledonia—SOLEM

Family SAGDIDAE

Lacteolana sp. belongs to a West Indian complex. It was introduced prior to 1928.

Family EULOTIDAE

Bradybaena similis (Ferussac, 1821) was probably native to southeast Asia and Indonesia, but is now pantropical and often present in subtropical areas. It reached New Caledonia before 1911 and has long been established in such Pacific island groups as the New Hebrides, Fiji, Society, and Hawaiian islands.

Family HELICIDAE

Helix (Cryptomphalus) aspersa (Müller, 1774) is a European species widely used for food that has been introduced into nearly all portions of the Pacific world, from California and Juan Fernandez to Tahiti and New Zealand. Its importation to New Caledonia can be traced to a visit by a French man-of-war to Lifu in 1879, with a local Frenchman thoughtfully putting the young in his garden to keep a supply of escargot (see Kew, 1893:205–206).

DISCUSSION

It is quite possible that many of the species listed as established comparatively recently were overlooked by earlier collectors, and undoubtedly some of the pantropical species were introduced into New Caledonia from secondary centers (i.e., the West Indian Subulina octona being brought in from Reunion Island). Multiple introductions almost certainly happened. Despite these limitations, a chronological listing of introductions shows a reasonable correlation with the patterns of settlement and commerce, and provides an instructive example of the faunal homogenization occurring in land-snail faunas today.

Data on the history have been taken from O’Reilly (1953).

In the early 1840’s sandalwood traders were visiting New Caledonia and by 1850 several attempts had been made at establishing missions. During the 1850’s considerable colonization took place and in 1860 there were 432 European residents. The following introduced snails had been found:

Rhachistia bistrio from Africa
Lamellaxis (Allopes) gracile from West Indies or Africa
Gastrocopta pediculus from Polynesia (?)

In this period Madagascar and the islands of Mauritius and Reunion were provisioning stops for ships from France to the Pacific. It is thus quite possible that the Rhachistia and Lamellaxis (presumably well established by this time in the Malagasy region) were brought in on ornamental plants. Possibly the Gastrocopta had been introduced by primitive man.

During the 1860’s regular service was instituted between French Polynesia and New Caledonia, and ship passage to Europe was reduced to 94 days. Commercial contacts with Australia were moderately frequent. Some ships came via the French West Indies. The following introductions were discovered:

Ancylus reticulatus possibly from Europe
Angustipes plebeius from the West Indies
Ceciliodes aperta from the West Indies
Conenuplecta calcusola from Polynesia
Liardetia samoensis from Polynesia
Tornatellino ps nounmeensis possibly from Polynesia

All the above can readily be derived through accidental introduction on land plants or on water cress (Ancylus).

In the 1870’s several colonization schemes suffered varying degrees of success, regular mail service was established with Sydney, and the growing of sugar cane became extensive. Newly discovered imports were:

Deroceras laeve probably direct from Europe
Helix aspersa from a French man-of-war Elasmias mariee possibly from Polynesia
Pupisoma dioscorica from the West Indies
Ancylus nounmeensis from an unknown locality

The growth in importance of the nickel mines, increasing colonization, and better com-
munications between 1880 and 1911 produced the following set of introductions:

- *Laeviculaeus alte* from Africa
- *Subulina octona* from Reunion (originally West Indies)
- *Pseudopeas tuckeri* from Australia
- *Hawaiiia minuscula* originally North American, but direct source unknown
- *Bradybaena similaris* most probably on sugar cane, source unknown

With most of the molluscan "tropical tramps" well established by 1911, the rate of additions decreased, probably reflecting growing stringency of quarantine regulations as well as a decrease in the number of candidates for introduction. New records are all of West Indian taxa:

- *Gastrocopta servilis* from West Indies
- *Lamellaxis mira* from West Indies
- *Varicella* sp. from West Indies
- *Lacteolina* sp. from West Indies

The effects of the depression of the 1930's and isolation from normal commerce caused by World War II may have been the reasons behind restricted introductions from 1928 to 1958. Only three more species were added:

- *Elasmias apertum* from Polynesia
- "Opeas" *oparanum* from Polynesia
- *Diastole conula* from Polynesia

As would be expected, the centers of commercial contact, particularly in regard to interchange of plant products, have provided by far the largest portion of the introduced taxa. French Polynesia, the West Indies, and the former French possessions of the Malagasy region each contributed heavily, with a much smaller number coming from Europe and, possibly, only one from Australia. *Hawaiiia minuscula* and *Bradybaena similaris* had attained such a wide dispersal prior to their discovery in New Caledonia that no guess can be hazarded as to the source of the New Caledonian populations.

So far, New Caledonia has not received the Giant African Snail, *Achatina fulica*, that is such a nuisance in many parts of the Pacific. It does, however, have its full share of the land snail "tropical tramps," those species found, for example, in the port towns of the southeastern United States, Central American coastal cities, Mauritius, Singapore, and nearly every Pacific island regularly served by commerce. Hawaii, Tahiti, Viti Levu, Guam, and countless other islands have their cultivated and otherwise ecologically altered areas taken over by this pantropical snail fauna. The famed endemic land snails of the Pacific islands are restricted to the rapidly shrinking patches of native forest. In all too short a time the land snail fauna of the Pacific islands will consist solely of a homogeneous blend of the introduced forms listed above. It is with a real sense of sadness that I have attempted to chronicle for the terrestrial malacologist of 2020 the places where the living land snails of Polynesia and Micronesia originated!

**REFERENCES**


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Nonmarine Mollusks of New Caledonia—Solem


Reproduction in the Aggregating Sea Anemone, *Anthopleura elegantissima*

CHARLES E. FORD, JR. ¹

ABSTRACT: From a sample of 240 specimens of the aggregating sea anemone, *Anthopleura elegantissima*, collected a few miles north of the Golden Gate, males and females were shown to be distributed as unisexual aggregations on the rocks.

The degree of gonadal development was measured by taking the gonad index (the ratio of volume of gonads to wet weight of anemone) every month for nearly 2 years (1959 and 1960). This showed an annual reproductive cycle, beginning in late fall or winter, and culminating in complete spawning of the population in late September.

Measurements of ovarian egg size during 1959 and 1960 corresponded well with the cycle as expressed by the gonad index.

Male and female cycles were not directly comparable on the basis of the gonad index, but identifiable males were observed over nearly the same periods as females, producing tailed sperm during the time when ovarian eggs were near their maximum size, and spawning at the same time.

The aggregating sea anemone, *Anthopleura elegantissima* (Brandt, 1835), is one of the most conspicuous and abundant intertidal animals of the Pacific coast of North America, ranging from Alaska to southern California. It is a member of the largest and most widely distributed family of anemones, the Actiniidae. Other members of the family in other parts of the world occupy very similar habitats in the same gregarious fashion. It is found firmly attached to rocks in the midtidal range from approximately 0–4.5 ft above mean lower low water level, and to higher levels where wave action is extreme (Hand, 1955). On the rocky outer coast, where it is most abundant, it occurs as single individuals or, most commonly, as aggregations of a few animals to many thousands, some of which seem interrupted only by the discontinuities of the substrate. It also occurs in bays, usually as larger, isolated individuals. The receding tide leaves these animals contracted into little mounds covered with bits of rock, shells, sand grains, and other debris held by adhesive papillae on the body column.

Although abundant and conspicuous, *Anthopleura elegantissima* has only recently been critically described (Hand, 1955), and nothing has been published on its reproductive history. In fact, the only published detailed descriptions of annual gonad cycles in any coelenterates are those of Marshall and Stephenson (1933) on several reef-building corals, and Stephenson (1934) on the hydroid, *Myrionema*. For information on the structure and biology of sea anemones in general, see especially Stephenson (1928), and also Hyman (1940), and for a discussion of reproductive cycles in marine invertebrates, see the recent review by Giese (1959).

The following study of reproduction in *A. elegantissima* includes (1) evidence concerning the distribution of males and females on the rocks, and (2) the annual gonad cycle.

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his gratitude to Dr. Cadet Hand, under whose guidance this work was carried out, and to acknowledge with appreciation his generous help with arrangement and discussion of the data.

**MATERIALS AND METHODS**

All living material used in this study was collected from an approximately 100-yd length of coastline about 4 miles by road south of Stinson Beach, Marin County, California (latitude 37° 52' N), and studies were carried out in the Department of Zoology of the University of California, Berkeley.

For the study of the gonad cycle, a population of *Anthopleura elegantissima* was sampled at approximately 4-week intervals, except when prohibited on two occasions by inclement weather or poor tides, for a period of 21 months, from February, 1959, to October, 1960. Several individuals were taken from each of several rocks, assuring the inclusion of nearly the range of sizes to be found.

The animals were anaesthetized for several hours in a 50-50 solution of sea water and magnesium chloride isotonic with sea water. They were then injected with and preserved in Bouin's picric-formol solution.

The reproductive state was assayed by determining the ratio of the estimated volume (in milliliters) of gonadal tissue to the wet weight (in grams) of the preserved sea anemone. This ratio is referred to as the gonad index, after Bennett and Giese (1955).

Before being weighed, the preserved animals were cleaned of debris adhering to the column, cut in half longitudinally, and squeezed gently and blotted on damp paper towelling for about ½ minute to remove surplus fluid from within the coelenteron.

The gonads, of which there may be a few to more than 100 per individual, develop as thickened folds of the mesentery between the longitudinal retractors muscles and the mesenterial filaments, and basal to the level of the pharynx. To estimate the total gonad volume, each animal was dissected to count the total number of gonads, which was multiplied by the average volume of a sample of 5 gonads. The volume of each of the 5 gonads was determined by multiplying together the length, width, and thickness as measured by a calibrated ocular micrometer in a binocular dissecting microscope. Bits of each of the 5 sampled gonads were teased apart and squashed gently in water and examined microscopically. In all but the most immature, the gonads from each animal are identified either as ovaries by the presence of ova (18 to about 200 microns in greatest diameter) with prominent nuclei, or as testes by the presence of vesicles filled with small round spermatocytes (3 to 4 microns), or with tailed sperm. Even in the field maturing females can be distinguished by the presence of the light chocolate-brown ovaries when the animal is torn open. However, even nearly mature males (with tailed sperm in the testes) must be preserved and dissected to distinguish the milky-white testes from the tangled masses of mesenterial filaments.

To further characterize the reproductive state of the females, the greatest diameter of the largest ovum found in each of the squashed bits of ovary was measured by means of a calibrated ocular micrometer in a compound microscope and the average was recorded.

For the study of the distribution of males and females on the rocks, a sample of 240 individuals was taken on July 1, 1961. From each of 12 rocks 2 samples of 10 animals each were taken from closely packed aggregations on extreme sides of the rock, noting the approximate distance between the 2 samples of 10, and whether they were part of the same or of separate aggregations. In the laboratory the animals were relaxed, preserved, and subsequently weighed and dissected; and the sex of those with gonads was determined.

**DISTRIBUTION OF SEXES**

While processing the animals collected in 1959 for the study of the gonad cycle, it was observed that all but a few individuals with gonads were unquestionably females, giving a sex ratio of approximately 7.5 females to 1 male. So on October 5, 1960, 100 animals were collected from the population, 2 groups of 10 from each of 5 rocks, as a larger sample for determining the sex ratio in the population. However the population had apparently entirely spawned out, as no individuals were found to bear gonads (2 weeks earlier, many animals sampled had
TABLE 1

**Distribution of Males and Females in 24 Groups of 10 Animals**
**Each Collected on 1 July 1961**

<table>
<thead>
<tr>
<th>ROCK NO.</th>
<th>SAMPLE</th>
<th>FREQUENCY</th>
<th>NO. GONADS</th>
<th>MEAN WT. OF SAMPLE IN GRAMS</th>
<th>DISTANCE A TO B IN FEET</th>
<th>CONTINUOUS OR DISCONTINUOUS</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>a</td>
<td>10</td>
<td>-</td>
<td>1.09</td>
<td>7</td>
<td>Disc.</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td>-</td>
<td>6</td>
<td>0.73</td>
<td></td>
<td>Disc.</td>
</tr>
<tr>
<td>2</td>
<td>a</td>
<td>10</td>
<td>-</td>
<td>1.33</td>
<td>3</td>
<td>Disc.</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td>-</td>
<td>-</td>
<td>0.91</td>
<td></td>
<td>Disc.</td>
</tr>
<tr>
<td>3</td>
<td>a</td>
<td>6</td>
<td>4</td>
<td>0.92</td>
<td>2.5</td>
<td>Disc.</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td>-</td>
<td>9</td>
<td>0.80</td>
<td></td>
<td>Disc.</td>
</tr>
<tr>
<td>4</td>
<td>a</td>
<td>10</td>
<td>-</td>
<td>0.77</td>
<td>3</td>
<td>Disc.</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td>-</td>
<td>3</td>
<td>0.72</td>
<td></td>
<td>Disc.</td>
</tr>
<tr>
<td>5</td>
<td>a</td>
<td>-</td>
<td>10</td>
<td>0.44</td>
<td>12</td>
<td>Disc.</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td>3</td>
<td>7</td>
<td>1.53</td>
<td></td>
<td>Disc.</td>
</tr>
<tr>
<td>6</td>
<td>a</td>
<td>10</td>
<td>-</td>
<td>1.18</td>
<td>4</td>
<td>Cont.</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td>-</td>
<td>10</td>
<td>0.61</td>
<td></td>
<td>Disc.</td>
</tr>
<tr>
<td>7</td>
<td>a</td>
<td>5</td>
<td>5</td>
<td>3.11</td>
<td>6</td>
<td>Disc.</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td>-</td>
<td>1</td>
<td>0.47</td>
<td></td>
<td>Disc.</td>
</tr>
<tr>
<td>8</td>
<td>a</td>
<td>5</td>
<td>5</td>
<td>2.10</td>
<td>4</td>
<td>Disc.</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td>-</td>
<td>7</td>
<td>2.06</td>
<td></td>
<td>Disc.</td>
</tr>
<tr>
<td>9</td>
<td>a</td>
<td>4</td>
<td>6</td>
<td>0.91</td>
<td>2</td>
<td>Cont.</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td>-</td>
<td>4</td>
<td>1.25</td>
<td></td>
<td>Disc.</td>
</tr>
<tr>
<td>10</td>
<td>a</td>
<td>-</td>
<td>10</td>
<td>0.89</td>
<td>1.3</td>
<td>Disc.</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td>9</td>
<td>-</td>
<td>3.19</td>
<td></td>
<td>Disc.</td>
</tr>
<tr>
<td>11</td>
<td>a</td>
<td>-</td>
<td>3</td>
<td>2.37</td>
<td>4</td>
<td>Disc.</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td>4</td>
<td>-</td>
<td>0.77</td>
<td></td>
<td>Disc.</td>
</tr>
<tr>
<td>12</td>
<td>a</td>
<td>-</td>
<td>2</td>
<td>2.89</td>
<td>12</td>
<td>Cont.</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td>5</td>
<td>-</td>
<td>2.81</td>
<td></td>
<td>Disc.</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Total of Individuals</th>
<th>38</th>
<th>102</th>
<th>100</th>
</tr>
</thead>
<tbody>
<tr>
<td>Per cent of Individuals</td>
<td>15.8</td>
<td>42.5</td>
<td>41.7</td>
</tr>
<tr>
<td>Number of Samples of 10</td>
<td>7</td>
<td>15</td>
<td>2</td>
</tr>
<tr>
<td>Per cent of Samples</td>
<td>29.2</td>
<td>62.5</td>
<td>8.3</td>
</tr>
</tbody>
</table>

very large gonads), thus delaying this study until the following summer. When the animals collected in 1960 for the study of the gonad cycle were all dissected, the observed sex ratio was 1.8 females to 1 male. Thus it was suggested not only that the sex ratio might be other than 1:1, but that males and females might not be distributed at random within the aggregations, or in the population as a whole.

The data from the collection of the 240 animals taken on July 1, 1961, shown in Table 1, suggest the reason for the observed sex ratios. The rocks, numbered 1 to 12, were selected in a generally north to south sequence over the area from which animals had previously been collected for the study of the gonad cycle, thus including many of the same aggregations previously sampled.
The most important fact realized from the data in Table 1 is that in no case were both an identifiable male and an identifiable female found in the same sample of 10 animals. In fact, in 25% of the samples, every individual was identified as a female. Assuming a random distribution of males and females, the probability of a single sample of 10 animals being all of one sex is \( \frac{1}{2} \) to the 10th power, and of 5 samples of 10 being all of one sex is \( \frac{1}{2} \) to the 50th power. Thus it is apparent that the sexes are not randomly distributed, but aggregated into separate or perhaps contiguous groups of males and females.

What is not evident from the data presented is the size of the unisexual aggregations, as they were not sampled randomly but in patches about 8 to 12 cm across. What is needed to estimate the size of the unisexual aggregations and even to show whether all continuous masses of anemones are of but one sex, is a series of random samples of say, 10 animals each, from a number of continuous aggregations. It should be noted that the 3 pairs of samples taken from continuous masses (on rocks 6, 9, and 12) yielded but one sex in each case, and that in the 2 cases in which both sexes were found on the same rock (Nos. 1 and 3), the pairs of samples were taken from separate aggregations.

To estimate the sex ratio, there are two ways to manipulate the data in Table 1. If the data are considered to comprise a sample of 240 individuals, the sex ratio is 102 identifiable as females to 38 males, or about 2.7:1, which for this sample size (140), deviates very significantly from a 1:1 ratio. However, if each group of 10 animals is considered to be a part of a separate asexually produced clone, and is treated as but a single individual, the sex ratio of identifiable animals is 15 females to 7 males, which for this sample size (22) does not deviate significantly from a 1:1 ratio, and suggests a need for sampling a larger number of aggregations, perhaps at other locations.

Thus the clumped distribution of the sexes, and the apparent predominance of females in the population, explain in part the sex ratios observed in samples of animals collected in 1959 and 1960 for the study of the gonad cycle. The marked increase in the frequency of males observed in 1960 over 1959 (indicated in Fig. 3) might well be explained by the unfortunate fact that the same rocks were not sampled in both years. Until mid-July, 1959, animals were taken from rocks in the area of rocks 1 through 6 of Table 1, which are in the northern half of the collecting area and adjacent to a small sandy beach to the north. In July, 1959, the sand level rose to cover most of the rocks from which animals had been collected. It should be noted that samples from rocks 1 through 6 consisted of mostly females and but a few males. Animals taken during the remainder of 1959 were taken in the area of rocks 5 through 9, samples from which yielded only females. The sand level did not rise to cover the anemones in the southern half of the collecting area, so in 1960 animals were collected from the area of rocks 6 through 12, from which a much larger proportion of males were taken. Thus the unfortunate circumstances of sampling from a population in which the sexes are not randomly distributed are offered as the most probable explanation for the dearth of males in 1959 collections, and their sporadic occurrence in 1960.

It is interesting to speculate about the significance of the clumped distribution of the sexes with regard to the origin of the aggregations in the population. It could be argued that, as is suggested above, unisexual aggregations are actually asexually produced clones, arising by binary fission from a single individual. In fact, throughout the year a few scattered individuals are observed to be pulling apart in the process of fission, and there are usually a few individuals in each sample collected showing a light-colored vertical scar on the column indicating a recent division. Hand (1955) and others (personal communication) have reported seeing populations of *A. elegansima* in which almost every anemone is dividing or has just divided, during the months of January to March.

One might also suggest that the animals are in unisexual aggregations as the result of an active process of movement of individuals. However, when a solidly packed aggregation is removed from the substrate except for a small patch of individuals in the center, and the patch is observed over a period of weeks, the tendency is for the animals to quickly spread out, separating most of the individuals. Also, animals placed closely together in tanks in the laboratory sepa-
SURFACE WATER TEMPERATURES
AT FORT POINT, GOLDEN GATE.
rate from one another and cease to wander further within a few days. This would tend to suggest that individuals are aggregated into large masses only as a result of growth and asexual reproduction within the limitations of space.

A third explanation might suggest some factor influencing larval settling, such as some substance released by larvae which first settled, which attracted larvae of the same sex and repelled those of the opposite sex. However, considering the relatively great distances involved, and the large volumes of moving sea water through which these substances would have to pass, this seems to be the most improbable explanation.

ANNUAL GONAD CYCLE OF *A. elegantissima*

The data for the gonad index of the aggregating sea anemone for 1959 and 1960 are given in Figure 1. It is evident that only a single breeding cycle occurred during each year, with gonads small during the winter months, and increasing during spring and summer to a peak before spawning out completely in September. Overlap of 95% confidence bands about the sample means indicates a generally good correlation between the cycles of the 2 years, except that the maximum gonad index may have been reached 2 months earlier in 1960 than in 1959.

The maximum ovum diameters for each sample for the two years are presented in Figure 2, which shows an almost continuous increase in ovarian egg size, from very small during the winter months to a maximum size just before spawning in September.

In both 1959 and 1960, tailed sperm were observed in July in smears of the testicular tissue of one or two males, and by mid-August all testes were filled with tailed sperm.

There seems to be some slight correlation between size and sexual reproduction, as shown in Table 1 and observed throughout the year, in that a greater proportion of the smaller individuals (weighing 0.3 to 3.0 g) are found to be without gonads than are larger individuals (3 to 10 g). However, even the smallest animals may be fertile and the largest animals may be without gonads.

If any correlation may be safely drawn between the events of the gonad cycle and ocean temperatures, as shown in Figure 1, it is that gonad size and ovarian egg size increase with the rising temperatures of the summer months, and spawning occurs shortly after temperatures have reached a peak in early fall and begun to decrease. It must be noted, however, that the temperature data were taken at the Golden Gate, several miles south of the collecting area. Most importantly, due to their position in the intertidal zone, these animals spend nearly half the time out of water, exposed to much greater temperature extremes and fluctuations than are indicated in Figure 1.

The data for male and female reproductive cycles for 1959 and 1960 are given in Figure 3. However, no attempt is made here to compare male and female cycles on the basis of these data, because of the circumstances of sampling as explained above under the topic of the distribution of the sexes.

DISCUSSION

The present account reports a single gonad cycle per year for the aggregating sea anemone, *Anthopleura elegantissima*, with the gonad index and ovarian egg size increasing gradually from a low in the fall after spawning, to a high the following September, when spawning again occurs. Spawning was not observed by the author, nor are there any published accounts of spawning in this species, but reports of such observations have been received by personal communication. These reports place the time of spawning near the end of summer, which agrees with the present findings, and state that the majority of individuals in the population were shedding.

**Figure 1.** Gonad cycle of *Anthopleura elegantissima* in 1959 and 1960, and corresponding ocean temperatures. Temperature data were obtained from the U. S. Dept. of Commerce, Coast and Geodetic Survey, Bureau of Marine Data. Each sample is plotted in a frequency histogram, with heavy lines joining the means and 95% confidence limits computed for a "t" distribution for small samples (Wilks, 1948). Below, the 95% confidence bands for the two years are compared.
Fig. 2. Average maximum ovum diameters measured in 1959 and 1960. Samples of 25 animals each, taken on February 3 and March 3, 1959, and October 5, 1960, and a sample of 100 individuals taken on September 30, 1959, had no gonads and hence no ova.

Fig. 3. Male and female gonad cycles of *A. elegantissima* for 1959 and 1960 (not strictly comparable due to circumstances of sampling).
either brownish mucous masses of eggs or milky-white masses of sperm.

There were no indications of hermaphroditism. Neither were there any suggestions that this species broods its young internally, as reported by Atoda (1954) for a Japanese Anthopleura. Further work needs to be done to determine the origin of the aggregations of anemones on the rocks, and to determine the relative importance of sexual and asexual reproduction in maintaining a population in a given location. The distribution of the sexes into groups of males and females should prove to be a useful tool and point of reference for such study.

REFERENCES


**Polydora** and Related Genera (Annelida, Polychaeta) from Eniwetok, Majuro, and Bikini Atolls, Marshall Islands

KEITH H. WOODWICK

ABSTRACT: In a study of more than 250 specimens of spionid polychaetes collected at Eniwetok, Majuro, and Bikini atolls, Marshall Islands (1956 and 1957) five new and two known species were found.

One of the species (**T. spinosa**) is the type for a new genus, **Tripolydora**, which is closely related to **Polydora**, **Pseudopolydora**, and **Boccardia** by virtue of its modified fifth segment. It is unusual in having branchiae on the fifth segment, and the hooded hooks are trifid and begin on Segment 9. The other new species are **Pseudopolydora corallicola**, **Pseudopolydora pigmentata**, and **Polydora tridenticulata** from coral material, and **Pseudopolydora reisbi** from areas of pollution. The known forms, **Pseudopolydora antennata** Claparède and **Polydora armata** Langerhans, are considered in reference to the literature.

The ecologic and systematic positions of the seven species are discussed.

In a study of a group of spionid polychaetes collected at Eniwetok, Majuro, and Bikini atolls, Marshall Islands, in 1956 and 1957, five polydorids new to science were found and are described herein. In addition, information is provided concerning the natural history and distribution of two known species present. The material was collected by Dr. Donald J. Reish, Department of Biological Sciences, Long Beach State College, Long Beach, California. The field work was made possible by the U. S. Atomic Energy Commission through its Eniwetok Marine Biological Laboratory.

More than 250 specimens were collected, including five new species and **Polydora armata** Langerhans and **Pseudopolydora antennata** (Claparède). The new species belong to **Polydora** Bosc, **Pseudopolydora** Czerniavsky, and a closely related new genus, **Tripolydora**. The new forms include **Polydora tridenticulata**, **Pseudopolydora corallicola**, **Pseudopolydora pigmentata**, **Pseudopolydora reisbi**, and **Tripolydora spinosa**.

Among papers providing information concerning polydorid forms from the Marshall Islands area or related ecological regions are those of Hartman (1954) and Okuda (1937). Hartman reported **Polydora** spp. from various parts of Eniwetok Atoll. She noted that one of these resembled **P. armata**. Okuda reported **P. armata** and **Ps. antennata** from coral and related habitats of southern Honshu, Japan.

Collections from the three atolls include material from such diverse habitats as sandy mud to algal materials (including coralline algae), but mainly from coral rocks. Both the ocean and lagoon sides of the atolls were sampled, as were the near, middle, and far sides of the various islands (Fig. 1 and Table 1). The collection periods were from August 22, 1956, to September 7, 1956, and from June 30, 1957, to July 15, 1957 (collections during 1957 at Eniwetok Atoll only). Ecological factors of the collecting areas will be presented in the discussion of the respective species.

The holotypes are in the U. S. National Museum and the remainder of the specimens are at the Eniwetok Marine Biological Laboratory.
DESCRIPTION AND SYSTEMATICS

*Polydora armata* Langerhans 1880

Fig. 2(1-6)

This species was found at nine stations and was represented at both Eniwetok and Bikini atolls. The specimens had the characteristic spines of the fifth and the diagnostic specialized posterior notopodial setae. A 27-segment specimen measuring about 2.5 mm had small branchiae on Segment 7 and well-developed branchiae on Segments 8–12. On all specimens it was difficult to distinguish the branchiae from the dorsal post-setal lobes. Hartman (1954) noted...
that certain polydorids found in her study were like *P. armata* but had branchiae on more segments than the originally described form. The specimens in this collection generally agree with Langerhans (1880)—gills from 7th to 12th; Fauvel (1927)—gills begin on 7th, 5 to 7 pairs only; and Hartman (1941)—gills begin on 7th, 5 to 6 pairs.

Figure 2 includes a series of drawings of the spines of the fifth segment of *P. armata* which illustrates the appearance of the structure as seen from different angles and at different stages of wear (2, 4, 6). These drawings are paired with comparable figures (1) from Fauvel (1927), (3) from Okuda (1937), and (5) from Ehlers (1905). The third pair of drawings support the synonymy of *Polydora monilis* Ehlers with *P. armata* (Day, 1954).

*Polydora armata* occurred at Eniwetok Atoll on the following islands: Aniyai, Japant, Rigili, Aaraanbiru, and Engebi. It was found at Bikini on Enyu.

*P. armata* at Eniwetok occurred on both the lagoon and ocean sides of the island. It also was collected on the close, far, and middle parts of the island. It was found in coral rocks from reef flats (at one station near the surge zone), on the undersurface of rocks, in old coral heads, and in rocks in reef flat tide pools; at both Eniwetok and Bikini it was collected from coralline algae identified by Reish as *Porolithon*.

Table 1

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>ENIWETOK</th>
<th>MAJURO</th>
<th>BIKINI</th>
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<td>1956</td>
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<td>0</td>
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<tr>
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<td>3</td>
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<td>3</td>
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<td>0</td>
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<td>0</td>
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<td>2</td>
<td>0</td>
</tr>
<tr>
<td><em>Tripolydora spinosa</em></td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
</tbody>
</table>

*Pseudopolydora antennata* (Claparède) 1870

Fig. 2(7, 8)

This species was found at 15 stations, 12 on Eniwetok and 3 on Majuro Atoll. By number of specimens it is the dominant form in the collections.

The individuals are attenuated posteriorly, as was noted by Fauvel (1927). A species which measured 0.7 mm wide anteriorly was about one half this width at the posterior end. The prostomium is deeply bifurcated, with the lateral lobes long enough in some specimens to be turned to the side like frontal horns. The caruncle extends to the anterior margin of the modified fifth segment on some specimens, to the posterior margin of the sixth in some, and to intermediate positions in other specimens. With limitations, it can be generalized that longer specimens have a more posterior extension of
the caruncle. The median nuchal tentacle is located at the level of Segment 1. There are two pairs of eye spots; the anterior eyes are about twice the size of and are farther apart than the posterior pair. On preservation the specimens failed to retain their palps.

In Segment 1 the notopodia and neuropodia are present but not well developed; the former are located in a more dorsal median position than the notopodia of other segments. There are no notosetae.

Segments 2, 3, and 4 have well-developed post-seal lobes with two rows of numerous setae.

Segment 5 from a dorsal view is distinguishable from the preceding and succeeding segments, but it is less modified in this form than in members of the genera Polydora and Boccardia. The fifth segment is slightly larger than the other segments. It has reduced notopodial and neuropodial lobes. The setae are oriented in two U-shaped or horseshoe-shaped rows, as is typical for the genus. The setae of the fifth have a second tooth (8) not figured by other workers (7); if it is a special characteristic for the Marshall Island forms it seems not significant enough to suggest further taxonomic breakdown.

Segment 7 has the first and a fully-developed pair of branchiae. A complete specimen of 46 segments had 6 abranchiate, 25 branchiate, and 15 abranchiate segments in that succession; a complete specimen of 66 segments had numbers of 6, 24, and 36, respectively. The last branchiae are less developed than the largest on the specimen but they are not reduced to small papillae.

Segment 8 has the first neuropodial hooded hooks. They are bidentate and typical for the group.

The pygidium is cuplike, having a heavy cuff with dorsal and ventral clefts. It is larger in diameter than the posterior-most body segments. It is opaque, somewhat refractile, with a general whitish coloration.

Calcareous particles were found in the gut of many of the worms. Their tubes were heavy-walled, formed of mucus and coral-like material. One specimen from Uliga (Majuro) was expanded dorsally in each segment from 13 through 26; the material within was a pale pink-orange in color and is suggested to be reproductive in nature.

Table 2 provides a comparison of Pseudopolydora antennata as described by several workers. In most characteristics the forms described are alike. The table emphasizes the areas of difference.

P. antennata was collected at Eniwetok on the islands of Eniwetok and Parry (11 stations). It was also taken at Uliga of Majuro Atoll. This species was found on both the ocean and lagoon sides but, unlike most of the forms in this collection, its habitat is mud, sandy mud, and coarse sand. It is able to survive in polluted areas for it was present in black odoriferous mud 5 ft from a sewer outfall on Parry. Claparède (1870) described it from galleries of wood inhabited by Teredo (ship worm). Okuda (1937) collected it from a muddy substratum between crevices of shore rock.

Associated polychaetes at separate stations included Opisthosyllis brunnea Langerhans, Lysidice collaris Grube, and Mesochaetopterus

### TABLE 2

**Comparison of Characteristics of Pseudopolydora antennata**

<table>
<thead>
<tr>
<th>CHARACTERISTICS</th>
<th>FAUVEL (1927)</th>
<th>ENIWETOK</th>
<th>OKUDA (1937)</th>
<th>FAUVEL (1932)</th>
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<td>extension of caruncle...</td>
<td>to 2nd or 3rd</td>
<td>ant. 5th to post 6th</td>
<td>post 6th</td>
<td>not stated</td>
</tr>
<tr>
<td>branchiae...</td>
<td>begin 7th to 40–50th</td>
<td>begin 7th to 32 (46)</td>
<td>begin 7th to 90–100th (104)</td>
<td>begin 7th not stated</td>
</tr>
<tr>
<td>size</td>
<td>20–30 mm</td>
<td>17 mm</td>
<td>30 mm</td>
<td>20–30 mm</td>
</tr>
<tr>
<td></td>
<td>65–100 segm.</td>
<td>74 segm.</td>
<td>104 segm.</td>
<td></td>
</tr>
<tr>
<td>second tooth, setae of 5th</td>
<td>not indicated</td>
<td>present</td>
<td>not indicated</td>
<td></td>
</tr>
</tbody>
</table>
Polydora from Eniwetok, Majuro, and Bikini—Woodwick

minuta Potts. There was no consistent relationship with any one species. (Information on related species was supplied by Dr. Donald J. Reish.)

Pseudopolydora coralicola n. sp.

Fig. 2 (9–12)

A complete specimen had 36 segments; it was 5.0 mm long and less than 1.0 mm wide. Unlike most polydorids it is somewhat square in appearance from the 5th segment anteriorly. The body is widest at the anterior end near the 5th segment and is attenuated in the posterior third.

The prostomium is damaged but its appearance suggests bifurcation (9). The caruncle extends to the posterior end of Segment 6. A nuchal tentacle is present in the dorsal median line at the level of Segments 1 and 2. There is an anterior pair of eyes present and the usual posterior pair of eyes is represented by a single enlarged eye spot just to the right of the median line. Possibly the left member of the posterior pair has been displaced to the right and the two fused.

Segment 1 is about half as wide as Segment 5. The neuropodium is displaced dorsally to a position comparable to that of the notopodia of segments posterior to Segment 2. The neurosetae project anteriorly. The neuropodium is also displaced towards the median dorsal line near the caruncle. There are no notosetae and the post-septal lobes are more ciliate than lobate.

In Segment 2 both the noto- and neuropodia are slightly displaced towards the dorsal midline. Setal lobes and setae are present in both the noto- and neuropodia. Notosetae include long dorsal capillaries and two rows of shorter setae, the most anterior of which are the shortest and have a heavy-winged shape; those of the posterior row, slightly winged but more capillary in nature, are widened in the distal portion.

In Segments 3 and 4 the setal arrangement shows intergradations leading to the typical U-shaped double bundle of setae in Segment 5. Dorsal to these two rows are the well-developed groups of capillary setae.

Segment 5 is the widest part of the body. As previously noted, the setal arrangement is a culmination of the pattern established in succession through Segments 2–4. The anterior dorsal capillaries are well developed and in general are instrumental in producing a homogeneity of appearance in the anterior segments—typical of Pseudopolydora but not of Polydora and Boccardia. The lower two rows of setae are turned back (the ventral-most setae are displaced to the posterior and then turned dorsally so that the original setae at the dorsal and ventral extremities of a row are now the apical setae in the unjoined or dorsal part of the U-shape); as the two rows orient into the U-shape they produce an inner and an outer row of separate types of setae. The latter are spoon-shaped and, if unworn, the spoon has a sharp basal point. The inner row (posterior row) is made up of heavier stalked setae having an angled distal end terminating in a rounded tip (11). The latter are like the typical modified hooks or spines found in the fifth segment of Polydora and Boccardia species. There is a neuropodial lobe with associated setae.

Segments 6 and 7 contain large paired internal glands in the same location as glands which the author has seen in stained-sectioned material of Polydora nuchalis Woodwick. In the latter species the stain reaction suggested a function related to mucous secretion for the glands.

Segment 7 has full-sized branchiae, which are large in size on succeeding segments through Segment 13; they decrease in size posteriorly but are still present in Segment 21.

Segment 8 has the first neuropodial hooded hooks, as is typical for members of the genus. The hooks are bidentate, with the larger tooth having about a 90° angle with the main setal shaft. The accessory tooth is smaller and closely applied to the main tooth. This relationship occurs in other Pseudopolydora, for example Ps. kempf Southern (1921). An unusual feature of the hooded hooks is the fenestration of the ends of the teeth (10).

The pygidium is 0.3 mm wide, flared in shape but not broadly, being no greater in diameter than the pre-pygidial segments. It has a definite dorsal notch and a less well-developed ventral notch (12).

 Bundles of posterior notopodial spines are found in the posterior third of the body. These
straight, heavy capillary spines extend about 0.3 mm out from the body wall. Individually they are distally attenuated, and as a group they converge to produce a fairly sharp over-all terminal point. Cellular units or glands, columnar in shape, are clustered at the base of the notopodial spines. The bundles of notopodial spines are a dominant feature of the external morphology of this form and are therefore diagnostic in nature. Species of both Polydora and Boccardia have these posterior notopodial spines, but this is the first of the well-known species of Pseudopolydora to have this characteristic.

*Pseudopolydora corallicola* occurred in coral rock on the ocean side of Engebi Island of Eniwetok. It was associated with *Eurythoe complanata* (Pallas).

**Pseudopolydora reishi** n. sp.

Fig. 5 (1–3)

*Pseudopolydora reishi* n. sp. was collected at three stations, all on Eniwetok. Two complete specimens measuring 1.2 mm and 2.0 mm had 26 and 30 segments respectively. The prostomium is bifurcated anteriorly; the caruncle extends to the posterior margin of Segment 1 (1). The palpi are short. Eye spots were not present on these specimens. There is no nuchal tentacle.

Segments 1 through 4 are similar in notopodial and neuropodial morphology; however, there is a successional increase in size of the segments from Segments 1 to 4.

Segment 5 is greatly enlarged and is immediately separable morphologically from preceding and succeeding segments. This is an atypical characteristic for members of the genus *Pseudopolydora*. The enlarged 5th has a poorly developed bundle of dorsal capillary setae, with no definite post-setal lobe present. The usual U-shaped double row of setae has been flattened out so that the inner row becomes the dorsal row of setae made up of heavy spines with a modified falcate distal end lacking a sharp point. The ventral row consists of setae with an expanded distal end tipped by a fenestrated or hairy region (2).

Setae are reminiscent of those found in other forms, including *Boccardia columbiana* Berkeley (1927) and *B. probosidea* Hartman (1940), but not those of any other *Pseudopolydora* species. The neuropodium of the 5th includes a few, well-developed capillary setae which project some distance from the body wall.

Segment 7 has the first gills which are also present on Segments 8–11. Segment 8 has the first neuropodial hooded hooks. The appearance of the hooded hooks in Segment 8 is characteristic for the indicated genus, although that of Segment 5 and its setal arrangement are not. The hooded hooks are bidentate, with the main tooth large in comparison to the accessory tooth. The main tooth forms an angle of about 90° with the main shaft.

The pygidium is funnel-shaped, having heavy walls made up of cells or cells and their products oriented to give a striated appearance, with the striations forming parallel, straight lines from the proximal base of the pygidium to the distal edge of the cuff. The dorsal pygidial notch is deeper than the ventral notch (3).

*Pseudopolydora reishi* was found on Eniwetok Atoll at Engebi and Parry islands on the lagoon and ocean sides, respectively. On Parry Island this species was associated with areas of pollution in marine waters, being found at stations located 20 and 150 ft from sewer outfalls; however, on Engebi the collecting area was a region of hard coral rocks in sand not indicated as odoriferous. *Pseudopolydora reishi* was associated with *Phyllochaetopterus ramous Willey* and *Pseudopolydora antennata* at the 150-ft sewer outfall station, and with *Dodecaceria laddi* Hartman and *Pseudopolydora pigmentata* in the hard coral rocks.

In recognition of his endeavors in collecting the materials discussed in this paper, and because his field of research has included studies of marine pollution and indicator organisms, this form has been named for Dr. Donald J. Reish.

**Pseudopolydora pigmentata** n. sp.

Fig. 5 (4–6)

*Pseudopolydora pigmentata* n. sp. was found at two stations on Eniwetok. Only incomplete specimens were available. One specimen with 16 segments measured 1.6 mm. The peristomium of the specimen was slightly damaged but the anteriorly rounded prostomium was intact (4).

The caruncle reaches to the anterior margin of Segment 2; however, the segmental furrow be-
between Segment 1 and 2 is displaced posteriorly (on the dorsal median line), so that the caruncle terminates on the level of the middle of Segment 2. There is no nuchal tentacle and only one pair of eyes; the latter are suggested to be the posterior median pair of the two pairs usually present in polydorids.

Segment 1 is small in size compared to Segment 2. There are no notopodial setae; neuropodial setae are present but the entire parapodial relationship is shifted towards the mid-dorsal line.

Segments 2 and 3 are well developed and typical.

Segment 4 is unusual in its structure and will be discussed with reference to Segment 5.

Segment 5 is modified although in over-all appearance it resembles the preceding and succeeding segments, as is typical for the genus. There is a bundle of dorsal anterior capillary setae, but there is no well-developed post-septal lobe. The modified setae are strong, falcate hooks with a characteristic lined appearance (5). There are four on each side. The accessory setae are limbate. There is a well-developed neuropodium. Segment 4 shows an intergradation between the setae of Segments 3 and 5. In Segment 4 these setae are falcate, but have a thinner shaft and sharper point than those of Segment 5: they show the characteristic lined appearance. There are three on the right side of the segment and four on the left. These setae are comparable to the posterior row of winged setae of Segment 3. This is the most marked development of modified setae in Segment 4 of known polydorids.

Segment 6 has a pair of small branchiae; the branchiae increase in size on Segment 7, and are full sized on Segment 8. They are present on all the other segments of the 16 segment specimen.

The neuropodial hooded hooks first appear on Segment 8. They are bidentate; the free point of the accessory tooth is very small compared to that of the main tooth (6).

The specimen is named for the well-developed dorsal pigmentation. It has paired brown pigment stripes on the dorsal surface of each segment from Segments 2–13. In some of the anterior segments there are two pairs of stripes.

Pseudopolydora pigmentata occurred in hard coral rocks from the lagoon side of Eniwetok and Engebi islands of Eniwetok Atoll. At Eniwetok it was associated with Opisthosyllis brunnea Langerhans, and at Engebi with Dodecaceria laddi Hartman and Pseudopolydora reishi.

Polydora tridenticulata n. sp.

Fig. 4(1–5)

Polydora tridenticulata n. sp. was collected at five stations, all on Eniwetok Atoll. A complete specimen of 64 segments measured 9.0 mm in length and 0.7 mm at the widest part. In general shape the worm tapers toward the posterior end.

The prostomium is bifid and continues posteriorly as a well-developed caruncle to the posterior margin of Segment 3. There is no nuchal tentacle and the eyes are absent (1).

Segment 1 has well-developed notopodial lobes and notosetae moved towards the dorsal median line.

Segment 5 is well-developed and has a definite indentation separating it from Segment 6. It projects anteriorly ventral to Segment 4 and posteriorly dorsal to Segment 6. The dorsal anterior capillary setae project noticebly from the lateral surface of the segment. The large spines of the modified 5th have a heavy main falcate stalk with two lateral teeth placed subterminally on opposite sides of the stalk (2). They provide different images as one views the setae from different angles. At respective angles the lateral teeth (a) are not visible, (b) resemble a rimming flange (3), (c) suggest a single lateral tooth (4), and (d) show the true situation of two lateral teeth on opposite sides subterminal to the main point. On some specimens the lateral teeth are worn off the anterior (first) spine(s), but succeeding spines and the developing posterior embedded spines have sharp lateral teeth. Often in study of polydorids the true appearance of the modified spines of the 5th can be seen only by freeing the developing embedded posterior spines in which all teeth, fibers, and points are unworn. The accessory setae are plumose with a broad terminal end. There is a small bundle of neuropodial setae.

Segment 7 has the first neuropodial hooded hooks. They are bidentate with a well-developed lower tooth.

The branchiae are first present as well-developed structures on Segment 11; however, very small branchiae may be present on Segment 10.
Branchiae are present only as far as Segment 26 on a complete 64-segment specimen.

Posterior notopodial spines are lacking, but a few long thin capillary setae are present in each notopodium.

The pygidium is slightly wider than the last segment. It is not of the flared-disc shape, but has a heavy cuff of refractile tissue. The cuff is as long as 2 1/2 pre-pygidial segments. The pygidium has a dorsal notch (5).

*Polydora tridenticulata* was found at stations on the lagoon and ocean sides of Japam, and from the lagoon side of Rigili and Engebi islands of Eniwetok Atoll. This form is an inhabitant of coral rock and by setal structure is likely a boring form. It was associated with *Pseudonereis anomala* Gravier at two stations, and at separate stations with *Palola sicilisensis* (Grube) and *Haplosyllis spongicola* (Grube).

*Polydora tridenticulata* is similar to *Polydora anoculata*, *P. giardi*, *P. flava*, and *P. caeca*. It is like the first two in gill arrangement, and similar to the others in appearance of the setae of the fifth. However, unlike the last two, *P. tridenticulata* lacks posterior notopodial spines.

**Tripolydora**, new genus  
**Type T. spinosa**, new species

The fifth segment is modified as in *Polydora*, *Pseudopolydora*, and *Boccardia*. The general appearance of the worm and of the fifth segment indicates closer affinities with *Pseudopolydora* than with the other two genera. It differs from all three in that the neuropodial hooded hooks begin on Segment 9 and are tridentate. Branchiae are present on segments.

**Tripolydora spinosa**, n. sp.  
**Fig. 4 (6–9)**

*Tripolydora spinosa* n. sp. was found at two stations, both on Eniwetok. Complete specimens of 25, 25, and 40 segments measured 1.5, 1.6, and 3.0 mm respectively. The body is tapered slightly in the posterior one-third. The rounded prostomium continues posteriorly as a heavy caruncle reaching to the posterior margin of the third segment (6). The palps are retained on some specimens; on a 25 segment individual they extend to the middle of the body. No eyes are visible.

Segment 1 is poorly developed, lacking noto- setae and post-setal lobes. The neuropodium has shifted towards the dorsal midline, and the entire segment is but a vestige compared to Segment 2 and succeeding segments.

Segment 2 has the first branchiae, which are present also on Segments 3, 4, and 5 in a reduced size. Fully-developed branchiae begin on Segment 6. The branchiae are present posteriorly on all but a few pre-pygidial segments.

Segment 5 is a modified segment but resembles that of members of *Pseudopolydora* as, in general, it is not quickly separable from the preceding and succeeding segments on the basis of shape, branchiae, and setal components. It does, however, have two or three modified spines on each side. The spines are heavy-shafted, having a semifalcate tooth at one side surrounded by a subterminal flange with a central indentation (7). The neuropodium is well developed, having both setae and a post-setal lobe.

The neuropodial hooded hooks are important diagnostic characteristics with respect to their structure and location. They are tridentate (8); other forms with a modified fifth segment have unidentate or bidentate hooks. These hooks appear first in Segment 9, in a posterior row accompanied by an anterior row of winged setae; the latter are present anteriorly as far as Segment 4 and posteriorly to Segment 10. At the anterior and posterior limits they intergrade with capillary setae.

Posterior notopodial setae are present as a heavy bundle of fine needles in the last 4 segments of a 30-segment specimen (9). The preceding four segments intergrade with the general setal arrangement.

The pygidium is smaller in diameter than the pre-pygidial segment; it has two ventral lappets and two less distinct dorsal lappets. Its shape is not like the flaring cup typical of most
forms having modified spines in the fifth segment (9).

Tripolydora spinosa was found at Eniwetok Atoll on the lagoon side of Rigili in coarse sandlike rock, and on the lagoon side of Bogombo in beach rock from a high intertidal region. It was associated with Lysidice collaris Grube in both areas.

**DISCUSSION**

**Geographic and Ecologic**

Hartman (1954:619) said of the Marshall Islands polychaetes, "The annelid fauna of this area clearly has an affinity with fauna from other parts of the Indo-Pacific." Of the known forms in the present collection, Pseudopolydora antennata and Polydora armata, the following can be said. *Pseudopolydora antennata* has been reported from many parts of the world, including South Africa, the Mediterranean region, the English Channel, and, for the Indo-Pacific, from Krusadai Island, Gulf of Manaar, Indian Ocean, and Japan. *Polydora armata* has been found in all these areas with the exception of Krusadai Island and with the addition of Ceylon. The two species are thus widely and similarly distributed geographically, indicating that they are both cosmopolitan forms in a general pattern; however, they are restricted in ecological distribution. *Pseudopolydora antennata* has been found in sand and mud, in some cases from polluted regions. *Polydora armata* has been found as a boring form closely associated with calcareous materials. These two are representative of the Indo-Pacific fauna but in no way are restricted to that general region. Determination of the endemity of the new species must await further data.

Reish (1959), in a study of marine pollution in the Los Angeles-Long Beach Harbor area, included *Pseudopolydora paucibranchiata* (Okuda) as one of the indicator organisms. *Pseudopolydora antennata*, as a close relative of the above species and because of its niche, should receive consideration as a possible indicator organism in any future pollution surveys in areas in which it is endemic.

The bulk of the forms in the present collections were closely associated with calcareous materials. Hartman (1954) stated, "Most of the annelids may be regarded as having a destructive effect on the reef building processes of corals or coralline algae. . . . Polydora . . . may perform the same function rasping with the aid of modified setae." In addition to these modified setae of the fifth many polydorids described from calcareous materials have heavy posterior notopodial spines which should be considered as instrumental in any process of mechanical boring. Known forms having these notopodial spines include Polydora hamata, P. caulleryi, P. armata, P. caeca, and P. hoplura. Additional species described in this paper include *Pseudopolydora corallicola* and *Tripolydora spinosa*.

Hartman (1954) presented a short review of the effect of annelids on coral atolls, in which polychaetes were suggested by one worker to be the most important boring animals in coral rock. In this regard it would be extremely valuable to supplement the past qualitative studies on coral-boring forms with future quantitative studies to better characterize the roles of respective agents in coral destruction and the over-all significance of each.

**Systematic**

The generic breakdown of the polydorid forms has been unstable since the late 1800's and at the present time no one arrangement is accepted by all workers.

Bosc (1802) established the genus *Polydora*; in later works Carazzi (1895) introduced the subgenus *Boccardia*, and Mesnil (1896) the separate but closely related genus *Carazzia*. Many subsequent workers accepted an arrangement of subgenera *Polydora* (*Polydora*) and *Polydora* (*Carazzia*) but retained *Boccardia* as a separate genus. Fauvel (1927) treats all three groups as subgenera, as do Okuda (1957) and Berkeley and Berkeley (1952).

Hartman (1959), in her catalog of the poly-

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**Fig. 4.** 1–5, *Polydora tridenticulata*, n. sp. 1, Anterior end, X200; 2–4, setae of fifth (different views), X2000; 5, pygidium, X200. 6–9, *Tripolydora spinosa*, n. gen., n. sp. 6, Anterior end, X150; 7, setae of fifth, X750; 8, trifid hooded hooks, X1800; 9, posterior notopodial spines and pygidium, X150.
chaetous annelids of the world (Part II), employs separate genera for Polydora, Boccardia, and Pseudopolydora. The latter, from Czerniavsky in 1881, is given priority over Carazia of Mesnil in 1896.

In this paper the arrangement follows that of Hartman. The author is of the opinion that the tendency to accept Boccardia as a separate genus on the basis of branchial arrangement and to retain Pseudopolydora [= Carazia] as a subgenus is not supportable, for the latter have a specialized 5th segment less modified than that in members of the other two groups; and, quite significantly, the hooded hooks begin not on Segment 7 but on Segment 8. If the separation of one genus is accepted, then both should be accepted. Thus, it would seem that, according to an individual's taxonomic approach, there should be three separate genera or one genus with three subgenera.

The appearance in these collections of members of a new but closely related genus has not helped to clarify the relationships between the respective genera, as Table 3 illustrates.

Polydora and Boccardia are similar in general appearance and in extreme modification of the 5th segment; however, they vary in branchial arrangement. Pseudopolydora and Tripolydora are similar in general appearance and modification of the fifth, but vary in general branchial arrangement, setal arrangement in the fifth segment, and segmental appearance of hooded hooks. Both Boccardia and Tripolydora have branchiae anterior to the 5th, but vary in hooded hooks (segmental appearance and shape); and the latter is the only genus whose members have branchiae on the 5th segment.

With the acceptance of these four genera (or subgenera) the position of two other species becomes problematical.

In Polydora commensalis Andrews (1891) the hooded hooks do not appear until Segments 12–14. This form was placed in Polydora because the branchiae begin posterior to the modified fifth; however, they begin on Segment 6 and in most fully described members of this genus the branchiae are first present on Segment 7. Polydora commensalis has a highly modified anterior end, an unusual pygidium, and may be sexually dimorphic. The hooded hooks of Polydora citrana Hartman (1941) begin on Segment 10 and its prostomium and pygidium are unusual. If one separates the genera (or subgenera) of Polydora and Pseudopolydora on the basis of appearance of hooded hooks on Segments 7 and 8 respectively, the taxonomic position of P. commensalis and P. citrana must be re-examined.

**REFERENCES**


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**TABLE 3**

CHARACTERISTICS OF POLYDORIDS

<table>
<thead>
<tr>
<th>GENUS</th>
<th>BRANCHIAE</th>
<th>HOODED HOOKS</th>
<th>MODIFIED 5TH SEGMENT</th>
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<tr>
<td></td>
<td></td>
<td>Begin</td>
<td>Shape</td>
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<td>Polydora</td>
<td>post. 5th—absent 5th</td>
<td>7</td>
<td>bifid</td>
</tr>
<tr>
<td>Boccardia</td>
<td>ant. 5th—absent 5th</td>
<td>7</td>
<td>bifid</td>
</tr>
<tr>
<td>Pseudopolydora</td>
<td>post. 5th—absent 5th</td>
<td>8</td>
<td>bifid</td>
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<tr>
<td>Tripolydora</td>
<td>ant. 5th—present 5th</td>
<td>9</td>
<td>trifid</td>
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Redescription of *Bolbella californica* Allgen, 1951 (Enchelidiidae: Nematoda), with Notes on its Ecology off Southern California

GILBERT F. JONES

ABSTRACT: *Bolbella californica* Allgen, 1951 (Enchelidiidae: Nematoda), the southern California species of the genus, is redescribed. A limited analysis based on 79 specimens is made of its intraspecific variation. As redescribed, *B. californica* may be distinguished from all other species of this genus by the number of esophageal bulbi, 9 to 10; no previously described species has more than 8 bulbi.

*B. californica* was collected from 18 locations on the southern California mainland shelf, in the depth range of 5.5 to 9.1 m. Bottom sediments at these locations were variable.

A MULTIBULBATE ESOPHAGUS is characteristic of two genera, *Bolbella* and *Polygastrophora*, of the nematode family Enchelidiidae. Although superficially similar in appearance these two genera belong to two separate and distinct subfamilies, *Bolbella* to the Eurystominae and *Polygastrophora* to the Enchelidiinae. Males of the Enchelidiinae have reduced buccal cavities while those of Eurystominae are well developed, the females being well developed in both genera (Wieser, 1953).

To date 14 species have been assigned to the genus *Bolbella*. Nine of these, including 1 from California, have been synonymized with species of *Polygastrophora*, transferred to the genus *Polygastrophora*, or placed in synonymy with other species of *Bolbella*. The species *B. californica* Allgen, 1951 has been referred to *Bolbella tenuidens* Micoletzky and Kreis, 1930. Wieser (1953:133) states "I have no doubt that *B. californica* Allgen, 1951 is identical with *B. tenuidens*, though this assumption has been based on the incomplete figures and description given by the author." It is difficult to evaluate this conclusion on the evidence presented in the original description of *B. californica*.

Of *Bolbella*, 79 specimens have been collected off southern California during a benthic sampling program of the Allan Hancock Foundation using the R/V "Velero IV." Based on these collections a redescription of *B. californica* Allgen is presented. In addition some notes are given regarding its ecology on the southern California mainland shelf.

GENUS Bolbella Cobb, 1920

TYPE: *Bolbella tenuidens* Cobb, 1920

*Bolbella californica* Allgen, 1951, Figures 1a–j.

COLLECTIONS: Redescriptions of the male and female are based upon a representative specimen of each collected at "Velero IV" Station 6373-59, off Huntington Beach, California, 33° 39' 25" N, 119° 01' 00" W, in 9.3 m of water. The bottom was fine gray sand with some rocks and shells. Specimens were also collected at 17 other stations on the southern California mainland shelf; these results are summarized in Table 1.

REDESCRIPTION OF THE MALE (Fig. 1a–f):

Length = 2.72 mm; ratios, a = 31.6, b = 4.1, c = 16.0. Head (Fig. 1b): labial papillae six, more distinct than in female; cephalic setae 10, length to 12⁄μ; buccal cavity well developed, 13μ × 12μ, and separated into two chambers by two chitinous bands, anterior chamber 5μ × 7μ, posterior chamber 7μ × 6μ; armature of three teeth, large right subventral tooth more slender than in female, length 7μ, equipped with accessory piece at tip and surrounding tip; two

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1 Allan Hancock Foundation, University of Southern California, Los Angeles. Manuscript received March 14, 1963.
Redescription of *Bolbella californica*—JONES

FIG. 1. *Bolbella californica* Allgen, 1951.  

a, Male, entire; b, male, head; c, male, multibulbate esophagus with nine distinct bulbi; d, male, precloacal supplement; e, male, spicules and gubernaculum; f, male, tail; g, female, head; h, female, vulva; i, female, multibulbate esophagus with ten distinct bulbi; j, female, tail.
small teeth, one left subventral in position, one dorsal in position; amphids not observed.

Body: cuticle without striations; cervical setae more numerous and longer than in female, length to 22 µ; maximum body diameter 85 µ at 1400 µ from the anterior end.

Esophagus (Fig. 1c): nerve ring surrounds esophagus 291 µ from the anterior end, body diameter at nerve ring 58 µ; esophagus with nine distinct bulbs, posterior end of esophagus 666 µ from anterior end, corresponding body diameter 79 µ.

Reproductive structures: two pre-cloacal supplements present (Fig. 1d), located 390 µ and 260 µ anterior to the cloaca; spicules (Fig. 1e) curved, 68 µ in length; gubernaculum complex, with central element from which lateral pieces project on the outer sides of the spicules, length 21 µ.

Tail (Fig. 1f): cloacal opening 2550 µ from anterior end, corresponding body diameter 44 µ; tail with three subterminal setae, with caudal gland orifice; tail length 170 µ.

**DESCRIPTION OF THE FEMALE (Figs. 1g–j):**

Length = 3.22 mm, ratios, a = 33.9, b = 4.1, c = 17.2, V = 45.6%. Head (Fig. 1g): labial papillae six, indistinct; cephalic setae 10, length to 9 µ; buccal cavity 15 µ × 15 µ, separated into two chambers by three chitinous bands, anterior chamber 6 µ × 10 µ, posterior chamber 9 µ × 9 µ; armature of three teeth, large right subventral tooth, length 9 µ, equipped with an accessory piece at tip and surrounding it; two small teeth, one left subventral in position, one dorsal in position; amphids 4 µ in diameter.

Body: cuticle without striations; cervical setae scant, length to 12 µ; vulva (Fig. 1b) situated 1480 µ from anterior end, corresponding body diameter 95 µ.

Esophagus (Fig. 1i): nerve ring surrounds esophagus 317 µ from anterior end, corresponding body diameter 49 µ; esophagus with 10 distinct bulbs; posterior end of the esophagus 780 µ from anterior end, corresponding body diameter 73 µ.

Tail (Fig. 1j): anus 3033 µ from anterior

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**TABLE 1**

**Station Data**

<table>
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<th>STATION</th>
<th>DATE</th>
<th>N LAT.</th>
<th>W LONG.</th>
<th>GENERAL LOCATION</th>
<th>DEPTH (m)</th>
<th>SEDIMENT</th>
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<th>♂ ♂</th>
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<td>34-23-10</td>
<td>119-30-40</td>
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<td>v f sd</td>
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<td>-</td>
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<td>118-29-30</td>
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<td>1</td>
<td>-</td>
<td>-</td>
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</table>

* Abbreviations: blk = black, br = brown, f = fine, gr = gray, m = medium, sd = sand, sh = shells, sty = silty. v = very.
end, corresponding body diameter 44\(\mu\); tail with a single subterminal seta, with caudal gland orifice, length 187\(\mu\).

**INTRASPECIFIC VARIATION:** A limited number of measurements were made on 62 of the 79 available specimens of *B. californica*. Based on these measurements mean ratios and corresponding ranges of body length/body width (\(= a\), body length/esophagus length \(= b\), body length/tail length \(= c\), and vulva position as percent of body length \(= \text{Vu}\)) were calculated. A summary of these results appears in Table 2.

A variation exists in the number of bulbi in the esophagus of females. Either 9 or 10 are present; but some specimens with 10 bulbi possess an indistinct anterior bulbus. Each of the two males examined has 9 bulbi. Allgen describes *B. californica* as possessing 7 to 9 esophageal bulbii; his figure (figure 50) shows 8. It is probable that he failed to note the indistinct anterior bulbii.

All other species of *Bolbella* possess 8 bulbi (Inglis, 1961) or less (7 in *B. heptabulba* Timm, 1961).

**ECOLOGICAL NOTES**

The offshore area of southern California is a complex assemblage of islands, banks, ridges, basins, and troughs designated as a “continental borderland” by Shepard and Emery (1941). The narrow strip of bottom immediately adjacent to the continent forms only 6.2\% of the continental borderland and is designated the mainland shelf (Emery, 1960).

Samples were collected along the inner margin of the shelf from off Santa Barbara to off San Diego, California, in 2.4 to 10.1 m. *B. californica* occurred at 18 of 100 sampling locations. The mean depth of water was 7.6 m (range, 5.5 to 9.1) at these 18 locations. This agrees closely with the depth given by Allgen (1951:368), 3.6 to 9.1 m, for the type locality in San Diego Bay.

Bottom sediment at the type locality is described as “sandy” (Allgen, 1951:368). In the present study, sediments where *B. californica* were collected are variable, as the following values indicate: % gravel, 0.0 to 29.0 (mean, 1.7); % sand, 40.6 to 93.8 (mean, 67.1); % silt-clay, 2.7 to 59.4 (mean, 31.1). Median diameters have a somewhat more limited range of 56 to 163\(\mu\) (mean, 78\(\mu\)), in part due to the lack of clays in all but one sample. All sediments were well sorted, 1.15 to 1.41 (mean, 1.25).

Major elements of the macrobenthos associated with *B. californica* are summarized in Table 3. The most important of these are the polychaetes *Nephys caecoides* and *Pronospio malmreni*; the amphipod *Paraphoxus epitomus*; the cumacean *Diastylipsis tenuis*; and the mollusks *Tellina buttoni* and *Olivella baetica*.

**METHODS**

The nearshore portion of the shelf, in water depths from 2.4 to 10.1 m, was sampled from the motor launch of the research vessel “Velero IV,” using a modified 1/10 sq m Van Veen grab. The methods utilized in the shipboard handling and the laboratory analysis of these samples are described by Hartman, Barnard, and Jones (1960). The animals collected were limited by the size of the mesh, 0.495 mm, through which the sediment was screened aboard ship before preservation and sorting.

**TABLE 2**

**INTRASPECIFIC VARIATION IN LENGTH MEASUREMENTS**

<table>
<thead>
<tr>
<th></th>
<th>(\phi) (\phi) (\text{ RANGE (MEAN)})</th>
<th>(\delta) (\delta) (\text{ RANGE (MEAN)})</th>
<th>JUV. (\delta) (\text{ RANGE (MEAN)})</th>
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<tr>
<td>(L)</td>
<td>2.29 — 3.35 (2.78)</td>
<td>2.20 — 2.72 (2.46)</td>
<td>1.98 — 2.44 (2.20)</td>
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<tr>
<td>(a)</td>
<td>25.4 — 43.3 (33.2)</td>
<td>26.9 — 31.6 (29.3)</td>
<td>33.0 — 47.8 (39.5)</td>
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<tr>
<td>(b)</td>
<td>3.1 — 4.6 (4.0)</td>
<td>4.1 — 4.3 (4.2)</td>
<td>3.5 — 4.3 (4.0)</td>
</tr>
<tr>
<td>(c)</td>
<td>11.7 — 20.4 (16.8)</td>
<td>14.8 — 16.0 (15.4)</td>
<td>14.4 — 19.6 (15.8)</td>
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<tr>
<td>(Vu)</td>
<td>38.3 — 47.2 (43.2)</td>
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<td></td>
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</tbody>
</table>

* Abbreviations: \(L\) = length in millimeters, \(a\) = body length/body width, \(b\) = body length/esophagus length, \(c\) = body length/tail length, \(Vu\) = vulva position as percent of body length.
TABLE 3
MAJOR MACROFAUNAL ASSOCIATES OF Bolbella californica

<table>
<thead>
<tr>
<th>ORGANISMS BY PHYLOGENETIC GROUPS</th>
<th>MEAN NUMBER/0.1 m² (RANGE)</th>
<th>PERCENT OCCURRENCE WITH Bolbella</th>
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<td>Polychaeta:</td>
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<tr>
<td>Aricidia lopezi</td>
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<td>Chaetozone nr. spinosa</td>
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<tr>
<td>Diopatra ornata</td>
<td>1.0 (0 – 6)</td>
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<tr>
<td>Goniada littorea</td>
<td>14.6 (1 – 35)</td>
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<td>6.1 (0 – 34)</td>
<td>54</td>
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<tr>
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<td>5.3 (0 – 25)</td>
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<td>5.7 (0 – 13)</td>
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<td>Prionospio malmgreni</td>
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<td>Prionospio pinnata</td>
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<td>84</td>
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<td>Thalenessa spinosa</td>
<td>0.8 (0 – 2)</td>
<td>61</td>
</tr>
<tr>
<td>Tbaryx spp.</td>
<td>19.1 (0 – 185)</td>
<td>54</td>
</tr>
<tr>
<td>Amphipoda:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paraphoxus epitomus</td>
<td>4.5 (0 – 17)</td>
<td>78</td>
</tr>
<tr>
<td>Cumacea:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diastylopsis tenuis</td>
<td>17.1 (0 – 144)</td>
<td>72</td>
</tr>
<tr>
<td>Mollusca:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Olivella baetica</td>
<td>4.6 (0 – 30)</td>
<td>67</td>
</tr>
<tr>
<td>Tellina buttoni</td>
<td>7.9 (0 – 60)</td>
<td>72</td>
</tr>
<tr>
<td>Nemertea:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>unidentified species</td>
<td>9.2 (2 – 53)</td>
<td>100</td>
</tr>
</tbody>
</table>

Specific determinations of the faunal components of the samples were made by the scientists of the Allan Hancock Foundation and the Beaudette Foundation mentioned in the acknowledgments and by the author (for Nematoda and Mollusca). Sedimentary analyses were made by the geologists of the Offshore Research Project.

ACKNOWLEDGMENTS

The writer is indebted to the National Science Foundation (NSF Grant G-15369) and to the California State Water Pollution Control Board for support of this work, to the Allan Hancock Foundation for providing facilities, and to the many scientists and crew members who have served aboard the R/V “Velero IV.” Special thanks go to Dr. Olga Hartman, under whose direction the biological research was conducted, for identification of the polychaetes and for her critical reading of the manuscript; to Dr. Robert E. Stevenson and Dr. Richard Tibby, directors of the Offshore Research Project for supplying the physical data; to Dr. J. Laurens Barnard of the Institute of Marine BioResearch of the Beaudette Foundation, Santa Ynez, California, for identifying the amphipods; to Mr. Robert R. Given for identifying the cumaceans; and to Captain Fred C. Ziesenhenne for the identification of the echinoderms.

REFERENCES


Redescription of *Bolbella californica*—JONES


Occurrence of Two Species of Young Threadfin, *Polydactylus opercularis* and *P. approximans*, in the Offshore Waters of the Eastern Tropical Pacific Ocean

W. L. Klawe and F. G. Alverson

Two species of threadfin,\(^2\) (*Polydactylus*, Polyenidae), occur along the Pacific coast of the Americas. *P. opercularis* ranges from the upper portion of the Gulf of California to northern Peru; *P. approximans* is found from southern California to northern Peru (Hildebrand, 1946; Berdegué, 1956). The two are known collectively as “bobo” by U. S. West Coast tuna fishermen who capture them for bait from Santa Maria Bay, Mexico, to the Gulf of Guayaquil, Ecuador (Alverson and Shimada, 1957). Adults of both species commonly occur in inshore waters, where they are utilized for food by the indigenous human population. The juveniles, however, have often been found at a considerable distance offshore, where they are, on occasion, found in quantity.

Information concerning the offshore occurrence of young *Polydactylus* was obtained from two sources: (1) logbooks kept by the masters of tuna clippers, in which a record of navigational and fishing activities, including the procurement of bait, is kept; and (2) collections made by scientists from the Scripps Institution of Oceanography, Bureau of Commercial Fisheries, Inter-American Tropical Tuna Commission, and other institutions. The bobo taken by the tuna fishermen were captured with either a lampara net or a crowder, a small net used to concentrate bait in the wells (Godsil, 1938; Alverson and Shimada, 1957). Listed in Table 1, by date of capture, are the locations and amounts of bobo taken for use as bait. The locations of capture have been plotted in Figure 1. Practically all the collections taken by scientists were made with the aid of a night light, an electric light suspended outboard of a drifting vessel so that the organisms attracted may be dipped out with a fine-mesh net. Listed in Table 2, for each threadfin collection made by scientific personnel, is the date and location of capture, number, size-range, and species. The locations of capture have been plotted in Figure 2.

In our collections the young of both species were not taken beyond 100 miles offshore, north of the Gulf of Tehuantepec, and 250 miles offshore south of the Gulf, the only exception being the occurrence of *P. approximans* in the vicinity of the Galapagos Islands, some 600 miles offshore (Figure 2). These limits are probably fairly accurate descriptions of the offshore distribution as numerous collections to the westward (Klawe, 1963) did not yield any young.

*P. approximans* has been recorded from 27:38 N and 114:50 W (off Turtle Bay, Baja California) in the north to 5:52 S and 81:28 W (off Point Aguja, Peru) in the south. *P. opercularis* has been recorded from 23:55 N and 108:00 W (Gulf of California) in the north to 5:52 S and 81:28 W in the south. The north-south offshore distribution of the young, of both species, is similar to the north-south inshore distribution of the adults.

The specimens of *P. opercularis* collected by night lighting and other methods, excepting the bait fishery, had a size-range of 7–87 mm, the vast majority being less than 50 mm in fork-length (Table 2). Three samples of *P. opercularis* which were given to the Commission by tuna fishermen had size-ranges of 46–67 mm, 58–72 mm, and 63–89 mm, respectively (Table 1). The length-frequency distribution of two of these samples has been plotted in Figure 3. Specimens of *P. approximans* collected by methods other than the bait fishery ranged in size

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1 Inter-American Tropical Tuna Commission, La Jolla, California. Manuscript received December 20, 1962.

2 The following names are used for threadfin in some of the Latin American countries: ratón, aleta de hebra in Mexico, amarillo in Ecuador, and barbudo in Peru.
from 7–140 mm (Table 2). The larger specimens, over 100 mm, were captured in the vicinity of Chame Point, Panama, and San Blas, Mexico, and we believe that they are not representative of the sizes to be found in the open sea. We have no specimens of this species from the tuna bait fishery.

The bait fishery for threadfin is mostly accidental. The threadfin are encountered by chance on the tuna grounds and, if weather, bait supply, time available, etc. are favorable, the clippers will attempt to catch them. For example, one of us (W.L.K.) in early April 1957 was aboard the clipper M/V "Mary Lou," Captain S. Parmigiani commanding, which at the time was fishing approximately 50 miles off San José, Guatemala. Numerous schools of threadfin were observed and at times scattered schools were observed as far as the eye could see. In one attempt 100 scoops\(^3\) of \textit{P. opercularis} were captured from one of these schools.

\(^3\) One scoop is equal to about 8 lb of fish.
<table>
<thead>
<tr>
<th>DATE</th>
<th>LOCATION</th>
<th>SCOOPS OF BAIT</th>
<th>REMARKS</th>
</tr>
</thead>
<tbody>
<tr>
<td>29 Mar. 1953</td>
<td>12° 30' N 88° 47' W</td>
<td>60</td>
<td>187 specimens 46–67 mm returned, identified as P. opercularis</td>
</tr>
<tr>
<td>30 Nov. 1953</td>
<td>40–50° SW Cape Corrientes, Mexico</td>
<td>700</td>
<td></td>
</tr>
<tr>
<td>1 Apr. 1955</td>
<td>12° 05' N 88° 23' W</td>
<td>200</td>
<td></td>
</tr>
<tr>
<td>5 Mar. 1956</td>
<td>12° 17' N 90° 33' W</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td>27 Aug. 1956</td>
<td>30–40° WSW Cape Corrientes, Mexico</td>
<td>150</td>
<td></td>
</tr>
<tr>
<td>2 Feb. 1957</td>
<td>60–70° SW San Benito, Mexico</td>
<td></td>
<td>amount not logged</td>
</tr>
<tr>
<td></td>
<td>13° 32' N 92° 54' W</td>
<td>60</td>
<td>19 specimens 58–72 mm returned, identified as P. opercularis</td>
</tr>
<tr>
<td></td>
<td>13° 58' N 93° 53' W</td>
<td>85</td>
<td>with &quot;crowder&quot;</td>
</tr>
<tr>
<td></td>
<td>13° 13' N 92° 29' W</td>
<td>300</td>
<td></td>
</tr>
<tr>
<td></td>
<td>13° 43' N 93° 10' W</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td></td>
<td>13° 17' N 92° 26' W</td>
<td>410</td>
<td></td>
</tr>
<tr>
<td>4 Feb. 1957</td>
<td>SW San Jose, Guatemala</td>
<td>250</td>
<td></td>
</tr>
<tr>
<td>2 Mar. 1957</td>
<td>12° 02' N 89° 08' W</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td>4 Mar. 1957</td>
<td>22° 09' N 106° 30' W</td>
<td>30</td>
<td></td>
</tr>
<tr>
<td>5 Mar. 1957</td>
<td>22° 09' N 106° 30' W</td>
<td>48</td>
<td></td>
</tr>
<tr>
<td>5 Mar. 1957</td>
<td>22° 09' N 106° 30' W</td>
<td>115</td>
<td></td>
</tr>
<tr>
<td>9 Mar. 1957</td>
<td>22° 30' N 106° 07' W</td>
<td>250</td>
<td></td>
</tr>
<tr>
<td>9 Mar. 1957</td>
<td>22° 09' N 106° 30' W</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td>10 Mar. 1957</td>
<td>22° 09' N 106° 30' W</td>
<td>175</td>
<td></td>
</tr>
<tr>
<td>11 Mar. 1957</td>
<td>22° 09' N 106° 30' W</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td>11 Mar. 1957</td>
<td>22° 09' N 106° 30' W</td>
<td>65</td>
<td></td>
</tr>
<tr>
<td>3 Apr. 1957</td>
<td>12° 30' N 91° 07' W</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td>3 Apr. 1957</td>
<td>13° 05' N 91° 48' W</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td>4 Apr. 1957</td>
<td>off Acajutla, El Salvador</td>
<td>some bait</td>
<td>Commission personnel sampled</td>
</tr>
<tr>
<td></td>
<td></td>
<td>bobo</td>
<td>103 specimens 63–89 mm, P. opercularis</td>
</tr>
<tr>
<td>9 Apr. 1957</td>
<td>17° 38' N 104° 47' W</td>
<td>90</td>
<td></td>
</tr>
<tr>
<td>20 Apr. 1957</td>
<td>17° 29' N 104° 23' W</td>
<td>130</td>
<td></td>
</tr>
</tbody>
</table>

As may be seen from Figure 1 and Table 1, the catches have been centered around Cape Corrientes, Mexico, in the north and off Guatemala and El Salvador in the south. Approximately equal amounts have been taken from each locality. The only species identified has been P. opercularis from three samples taken off Guatemala—El Salvador. We have, therefore, definite proof of only one species that schools in large aggregations offshore. We believe, however, that P. approximans also schools in large aggregations as its occurrence offshore is well documented (Table 2) and threadfin in other localities, i.e., the Gulf of Mexico, are known to school offshore (Bullis, 1961).

Although the bobo is used occasionally for bait by tuna fishermen, offshore catches of this bait fish are on the whole negligible when compared with the total bait catch. In 1957 slightly more than 2,500 scoops of threadfin were taken on the high seas as compared with the total bait catch of all bait species in the eastern Pacific of 3,700,000 scoops.

It is interesting to note that the coloration of P. opercularis collected off San José, Guatemala (see above), showed adaptation to the pelagic habitat from which these fish were removed. The fish were bluish-gray dorsally and whitish-silver ventrally. We were told by some of the tuna fishermen that when the young threadfin with the bluish coloration are kept for a few days aboard the vessel in the baitwells, they assume the adult coloration, i.e., inshore coloration, which is a greenish-brown color with some
**Table 2**

**LOCATION, NUMBER, SIZE-RANGE, AND DATE OF CAPTURE OF *P. opercularis* AND *P. approximans* BY SCIENTIFIC PERSONNEL**

<table>
<thead>
<tr>
<th>DATE</th>
<th>LOCATION</th>
<th>NO. OF SPECIMENS</th>
<th>SIZE-RANGE (mm) *</th>
<th>COLLECTOR OR REFERENCE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Lat. N</td>
<td>Long. W</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1946</td>
<td>?</td>
<td></td>
<td>5° 52.3' S  81° 28.3'</td>
<td>1</td>
</tr>
<tr>
<td>18-III-51</td>
<td>13° 49'</td>
<td>91° 01'</td>
<td>1</td>
<td>87.0</td>
</tr>
<tr>
<td>24-III-54</td>
<td>Galapagos Is., Ecuador</td>
<td>1</td>
<td>25.0</td>
<td>USNM No. 181258</td>
</tr>
<tr>
<td>14-IV-54</td>
<td>11° 43'</td>
<td>87° 12'</td>
<td>3</td>
<td>5.0-29.0</td>
</tr>
<tr>
<td>1-IX-55</td>
<td>9° 35'</td>
<td>86° 17'</td>
<td>4</td>
<td>30.0-49.0</td>
</tr>
<tr>
<td>6-IX-55</td>
<td>9° 12'</td>
<td>87° 06'</td>
<td>7</td>
<td>3.0-25.5</td>
</tr>
<tr>
<td>2-XII-55</td>
<td>11° 48'</td>
<td>88° 25'</td>
<td>7</td>
<td>3.0-25.5</td>
</tr>
<tr>
<td>16-I-56</td>
<td>5° 27'</td>
<td>81° 27'</td>
<td>7</td>
<td>27.0</td>
</tr>
<tr>
<td>4-II-56</td>
<td>18° 02'</td>
<td>104° 02'</td>
<td>1</td>
<td>87.0</td>
</tr>
<tr>
<td>11-III-56</td>
<td>21° 05'</td>
<td>106° 43'</td>
<td>4</td>
<td>28.0-39.0</td>
</tr>
<tr>
<td>11-III-56</td>
<td>21° 05'</td>
<td>106° 43'</td>
<td>10</td>
<td>28.0-39.0</td>
</tr>
<tr>
<td>25-IV-56</td>
<td>12° 08'</td>
<td>88° 12'</td>
<td>5</td>
<td>25.0-65.0</td>
</tr>
<tr>
<td>9-V-56</td>
<td>16° 16'</td>
<td>100° 19'</td>
<td>2</td>
<td>18.0-28.0</td>
</tr>
<tr>
<td>11-VI-56</td>
<td>SE Is. Cleopha, Tres Marias</td>
<td>1</td>
<td>18.0-24.0</td>
<td>?</td>
</tr>
<tr>
<td>4-XI-56</td>
<td>20° 53'</td>
<td>106° 28'</td>
<td>1</td>
<td>44.0</td>
</tr>
<tr>
<td>4-II-57</td>
<td>18° 02'</td>
<td>104° 02'</td>
<td>1</td>
<td>57.0</td>
</tr>
<tr>
<td>13-II-57</td>
<td>22° 26'</td>
<td>106° 06'</td>
<td>48</td>
<td>21.0-53.0</td>
</tr>
<tr>
<td>9-IV-57</td>
<td>12° 22'</td>
<td>87° 39'</td>
<td>7</td>
<td>18.5-39.5</td>
</tr>
<tr>
<td>17-IV-57</td>
<td>12° 57'</td>
<td>89° 25'</td>
<td>3</td>
<td>38.0-40.0</td>
</tr>
<tr>
<td>18-IV-57</td>
<td>3° 03'</td>
<td>89° 52'</td>
<td>40</td>
<td>21.0-51.5</td>
</tr>
<tr>
<td>23-IV-57</td>
<td>6° 36'</td>
<td>78° 14'</td>
<td>4</td>
<td>17.0-23.0</td>
</tr>
<tr>
<td>16-VI-57</td>
<td>6° 18'</td>
<td>77° 47'</td>
<td>3</td>
<td>26.5-42.5</td>
</tr>
<tr>
<td>10-VI-58</td>
<td>0° 22'</td>
<td>80° 50'</td>
<td>4</td>
<td>15.0-19.1</td>
</tr>
<tr>
<td>11-VI-58</td>
<td>17° 36.5'</td>
<td>102° 23'</td>
<td>1</td>
<td>32.0</td>
</tr>
<tr>
<td>15-VI-58</td>
<td>21° 37'</td>
<td>106° 31.5'</td>
<td>4</td>
<td>7.0-21.0</td>
</tr>
<tr>
<td>22-VI-58</td>
<td>0° 22'</td>
<td>80° 50'</td>
<td>4</td>
<td>16.0-29.0</td>
</tr>
<tr>
<td>2-VII-58</td>
<td>2° 01'</td>
<td>81° 01'</td>
<td>2</td>
<td>21.0, 22.0</td>
</tr>
<tr>
<td>7-VI-58</td>
<td>12° 41'</td>
<td>91° 35'</td>
<td>1</td>
<td>30.0</td>
</tr>
<tr>
<td>14-II-59</td>
<td>15° 00'</td>
<td>93° 00'</td>
<td>3</td>
<td>44.0, 45.0, 46.0</td>
</tr>
<tr>
<td>19-III-59</td>
<td>23° 55'</td>
<td>108° 00'</td>
<td>9</td>
<td>24.5-27.5</td>
</tr>
<tr>
<td>10-IV-59</td>
<td>18° 56'</td>
<td>104° 10'</td>
<td>1</td>
<td>43.0</td>
</tr>
<tr>
<td>22-III-60</td>
<td>20° 34'</td>
<td>105° 54'</td>
<td>6</td>
<td>16.5-32.5</td>
</tr>
<tr>
<td>20-VII-60</td>
<td>9° 21'</td>
<td>85° 07'</td>
<td>1</td>
<td>22.0</td>
</tr>
<tr>
<td>21-VII-60</td>
<td>9° 21'</td>
<td>85° 07'</td>
<td>1</td>
<td>10.0</td>
</tr>
<tr>
<td>14-IV-61</td>
<td>19° 06'</td>
<td>103° 19'</td>
<td>9</td>
<td>20.5-31.5</td>
</tr>
<tr>
<td>25-26-III-62</td>
<td>11° 34.4'</td>
<td>87° 00'</td>
<td>1</td>
<td>19.0</td>
</tr>
<tr>
<td>27-III-62</td>
<td>10° 24'</td>
<td>85° 53'</td>
<td>1</td>
<td>28.0</td>
</tr>
<tr>
<td>1946</td>
<td>6° 46'</td>
<td>78° 00'</td>
<td>1</td>
<td>34.0</td>
</tr>
</tbody>
</table>

---

**Polydactylus approximans**

<table>
<thead>
<tr>
<th>DATE</th>
<th>LOCATION</th>
<th>NO. OF SPECIMENS</th>
<th>SIZE-RANGE (mm) *</th>
<th>COLLECTOR OR REFERENCE</th>
</tr>
</thead>
<tbody>
<tr>
<td>VIII-07</td>
<td>Taboga Is., Panama</td>
<td>1</td>
<td>27.0</td>
<td>USNM No. 62925</td>
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<tr>
<td>VII-12</td>
<td>Chame Pt., Panama</td>
<td>2</td>
<td>30.0, 32.0</td>
<td>USNM No. 82027</td>
</tr>
<tr>
<td>8-III-13</td>
<td>Chame Pt., Panama</td>
<td>3</td>
<td>20.0-37.0</td>
<td>USNM No. 82195</td>
</tr>
<tr>
<td>26-VII-13</td>
<td>Chame Pt., Panama</td>
<td>20+</td>
<td>22.0-110.0</td>
<td>USNM No. 82193</td>
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<tr>
<td>? 1913</td>
<td>Chame Pt., Panama</td>
<td>1</td>
<td>55.0</td>
<td>USNM No. 82194</td>
</tr>
<tr>
<td>1946</td>
<td>5° 52.3' S  81° 28.3'</td>
<td>1</td>
<td>?</td>
<td>Hildebrand (1946)</td>
</tr>
</tbody>
</table>

* Fish measured from tip to snout to the shortest median ray in caudal fin.
<table>
<thead>
<tr>
<th>DATE</th>
<th>LOCATION</th>
<th>NO. OF SPECIMENS</th>
<th>SIZE-RANGE (mm) *</th>
<th>COLLECTOR OR REFERENCE</th>
</tr>
</thead>
<tbody>
<tr>
<td>31-III-50</td>
<td>Near Tres Marias</td>
<td>1</td>
<td>35.0</td>
<td>W. Richards</td>
</tr>
<tr>
<td>30-VII-52</td>
<td></td>
<td>7</td>
<td>55.0-62.0</td>
<td>USNM No. 181276</td>
</tr>
<tr>
<td>27-IX-52</td>
<td></td>
<td>11</td>
<td>41.0-63.0</td>
<td>Fish &amp; Wildlife Service</td>
</tr>
<tr>
<td>28-IX-54</td>
<td></td>
<td>20</td>
<td>12.0-41.0</td>
<td>?</td>
</tr>
<tr>
<td>1-XI-55</td>
<td></td>
<td>16</td>
<td>18.0-23.0</td>
<td>M. B. Schaefer &amp; B. M. Shimada</td>
</tr>
<tr>
<td>6-XI-55</td>
<td></td>
<td>14</td>
<td>20.0-33.0</td>
<td>A. Ebiling</td>
</tr>
<tr>
<td>11-XI-55</td>
<td></td>
<td>2</td>
<td>31.0, 33.0</td>
<td>A. Ebiling</td>
</tr>
<tr>
<td>13-XI-55</td>
<td></td>
<td>1</td>
<td>13.0</td>
<td>A. Ebiling</td>
</tr>
<tr>
<td>13-XI-55</td>
<td></td>
<td>1</td>
<td>32.0</td>
<td>A. Ebiling</td>
</tr>
<tr>
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<td></td>
<td>21</td>
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<td>A. Ebiling</td>
</tr>
<tr>
<td>2-XII-55</td>
<td></td>
<td>21</td>
<td>19.0-39.5</td>
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yellow in the ventral and in the entire caudal region.

In still another respect young threadfin caught in the pelagic situation exhibit marks of that habitat. Young *P. opercularis* collected off the Tres Marias Islands, Mexico, were infested with juvenile stages of the parasitic copepod *Caligus coryphaene* (Shiino, 1959). The regular hosts of this parasite are usually such pelagic fishes as the dolphin, various tunas, and the bonito, to mention a few.

Numerous predators, besides man, take advantage of the aggregations of threadfin found offshore. Skipjack (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus macropterus*), sailfish, sharks, and oceanic birds were observed (by W.L.K.) feeding on the threadfin some 50 miles off San José, Guatemala, in April 1957. We have been informed that the crew of the clipper M/V "Commander" observed whales feeding on schools of threadfin 40 miles WSW of Cape Corrientes, Mexico, in August 1957.

![Fig. 2. Locations of capture of bobo by scientific personnel.](image-url)
It would be reasonable to assume that the presence of young of small size (for our purposes less than 40 mm) is an indication of recent spawning. We have arbitrarily divided the eastern Pacific into three geographical areas, north of the Gulf of Tehuantepec, Central America, and South America, and plotted the occurrence of small fish for each species, by month, regardless of the year of collection.

It appears that *P. approximans* spawns throughout the year in all three areas. Most likely the same applies to *P. opercularis*, although the evidence is not as strong as that for *approximans*. It should be noted, however, that the number of *P. opercularis* in our collection is smaller than that of *P. approximans*. The fact that one of the species definitely and the other most likely spawns throughout the year is of no surprise, as *P. indicus* in the region of Bombay, India, has a spawning season extending through the entire year (Karekar and Bal, 1960).

### REFERENCES


**Klawe, W. L. 1963.** Observations on the spawning of four species of tuna (*Neothunnus maccopterus*, *Katsuwonus pelamis*, *Auxis thazard* and *Euthynnus lineatus*) in the eastern Pacific Ocean, based on the distribution of their larvae and juveniles. Inter-Amer. Trop. Tuna Comm., Bull. 6(9):447–514.


### Table: Spawning Season of Tuna

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### Table: Geographic Distribution of Tuna

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Exclusive of the mackerels and tunas, whose commercial importance has caused them to be studied extensively, the early life history of scombroid fishes is poorly known. This is particularly true of the families Gempylidae and Trichiuridae, even though they are the bases for fisheries in Australia, South Africa, Madeira, and parts of Asia. There is also a paucity of life-history information about the non-schooling Scombrids. This paper describes young stages of the scombroid Acanthocybium solandri (Cuvier and Valenciennes), the gempylid Nealotus tripes Johnson, and the trichiurid Diplospinus multistratiatus Maul, all three belonging to monotypic genera. The first has a slight commercial importance (Iversen and Yoshida, 1957:370), the others may be considered rare species of no commercial value.

The three families are taxonomically well known, the Scombrids having been reviewed by Fraser-Brunner (1950), the Gempylidae by Matsubara and Iwai (1952) and Grey (1953), and the Trichiuridae by Tucker (1956). All of these authors dealt essentially with adult fish. Postlarval Acanthocybium are hitherto unrecorded, the smallest specimen mentioned in the literature measuring 27 cm (Kishinouye, 1923: 387). Similarly, the smallest Diplospinus is 125 mm (Maul, 1948:45), although there is a possibility that a 69 mm Lepidopus may in reality be a Diplospinus (Tucker, 1956:81). Small Nealotus have been recorded by Lütken (1880:458), Günther (1887:35), Norman (1930:351), and Voss (1957:304). Lütken figured his specimens but regarded their identity as dubious. His larger specimen (about 13 mm standard length) has 20 spines in the first dorsal and is probably Nealotus. His smaller fish measures only about 8 mm in standard length and cannot be identified with certainty.

All material reported upon here was collected by "British Columbia" trawl during cruise 47 of the Bureau of Commercial Fisheries research vessel "Hugh M. Smith." This cruise took place in October—November 1958, in the central Pacific southeast of Hawaii. A description of the collection method is included in Matsumoro's report (in press) on the young tunas taken on this cruise. Figure 1 locates the trawling stations and capture sites of the species under consideration. Additional data may be found in Table 1 and in the species diagnoses.

Following capture, the fish were preserved in formalin and subsequently transferred to 65% ethyl alcohol. This particular concentration produced less wrinkling, hardening, and distortion than the customarily used 70% solution. Most specimens were stained with alizarin, but clearing the tissues, as with glycerin, was not done.

Thanks are due Messrs. G. Palmer, N. B. Marshall (British Museum), and G. E. Maul (Museu Municipal do Funchal) for supplementary information on Diplospinus, and Mrs. Nancy A. Voss (University of Miami Marine Laboratory) for data on Nealotus. The Inter-American Tropical Tuna Commission (La Jolla, California) loaned young Scomberomorus. I am also indebted to Tamotsu Nakata, Bureau of Commercial Fisheries Biological Laboratory, Honolulu, for preparing the figures.

Acanthocybium solandri (Cuvier and Valenciennes)

Station 60 1 specimen: 23.7 mm

The single Acanthocybium captured is rather easily recognizable in spite of the fact that its

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1 Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii. Manuscript received November 13, 1962.
TABLE 1
STATION DATA, "HUGH M. SMITH" CRUISE 47

<table>
<thead>
<tr>
<th>STATION NO.</th>
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<td>149° 32' W</td>
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</tr>
<tr>
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<td>0843-1027</td>
<td>02° 09' S</td>
<td>149° 47' W</td>
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<tr>
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<td>2015-2148</td>
<td>12° 13' N</td>
<td>149° 36' W</td>
<td>96</td>
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</tbody>
</table>

finlets have not yet differentiated. The fin formulae are D XXVII, 24 and A 22 as a consequence of persistent membranes between the fins and presumptive finlets. The anal formula is additionally misleading in that spines and rays cannot be distinguished. As is apparent from Figure 2, the spacing between the rays of the future finlets is greater than between the rays of the soft dorsal and anal fins. Further demarcating the finlets is the dusky pigment of their membranes. Following finlet formation this fish would presumably have had fin formulae of D XXVII, 14 + 10 and A 12 + 10.

Other characters of this specimen are 23 pectoral rays, 1, 5 pelvic rays, 7 branchiostegal rays, and 17 principal caudal rays. All caudal rays, except the 5 mesial ones, have their bases covering the hypurals, tending to conceal the latter. The gill filaments are J-shaped but as yet show no tendency to fuse into the adult gill reticulum. Tooth size and spacing are irregular, in contrast to the homodont adult dentition, with about 28 teeth on each dentary and 25 on each premaxillary. The anterior teeth in both jaws are curved and fanglike. The anterior margin of the preopercle bears a short spine at the angle and another on the lower limb. The posterior margin has two short spines on the upper limb, a long spine at the angle, and five irregular spines on the lower limb. There are two tiny spines on the posterior tip of the pterotic, but these are too small to appear in the drawing. The body is dusted with tiny melanophores, giving a uniform tan color, except on the dorsal part of the snout, which is dark brown.

An unusual feature of this specimen is a conical cartilaginous projection surmounting the mandibular symphysis. This projection has been noted in the adult, but not commented upon (Conrad, 1938:10). A similar structure has phylogenetic significance in relating the Gempylidae and Trichiuridae (Tucker, 1956:123), as well as taxonomic importance within the Gempylidae (Grey, 1953:138). Because its presence in Acanthocybium was thought to indicate hitherto unsuspected relationships between the Scombridae and the Gempylidae-Trichiuridae, a search was made for the structure in other scambroids. There is no indication of it in the young of any of the tunas (Auxis, Euthynnus, Geru, Katsuwonus, Neothunnus, Parathunnus, and Thunnus) according to W. M. Matsumoto (personal communication), but a prominent mandibular protuberance was found in juvenile Scomberomorus maculatus, 11.5-19.2 mm in standard length. Scomberomorus is regarded as phylogenetically basal to Acanthocybium (Fraser-Brunner, 1950:135), and the presence of this jaw projection confirms a close relationship. That there is a tie between these genera and the Gempylidae-Trichiuridae is further indicated by their mutual low-crested crania, elongate compressed bodies, and reduced squamation. In all scambroids examined, including a 565-mm
Gempylus serpens, the jaw protuberance is flexible (and sometimes decurved in Nesiarchus nasutus), precluding its use as a spear, and instead suggesting a hydrodynamic function (cf Wisner, 1958: 68).

Nealotus tripes Johnson

Station 2 1 specimen: 176 mm
Station 32 10 specimens: 16.4–41.5 mm
Station 49 8 specimens: 19.6–25.8 mm
Station 51 59 specimens: 10.0–20.2 mm
Station 53 3 specimens: 10.0–22.0 mm
Station 56 4 specimens: 9.0–24.0 mm
Station 58 6 specimens: 21.2–25.0 mm
Station 60 2 specimens: 21.4–28.0 mm
Station 70 1 specimen: 37.0 mm

When first examined, the smaller specimens listed above were thought to be Nesiarchus nasutus Johnson, to which they bear a strong superficial resemblance (cf Voss, 1954). Subsequent staining revealed their salient taxonomic feature, a reduction in the number of pelvic rays, showing that they belonged in a different branch of the Gempylidae, the Rexea-Prometrichthyso-Nealotus group. According to Grey (1953:139), these genera are characterized by a reduction of the pelvic fins to a pair of spines, or by the total absence of these fins. Only the largest of the above specimens, a fish 176 mm in length, has the pelvics reduced to mere spines and thus is referable to Nealotus tripes. The remainder range from 9.0–41.5 mm, and have pelvic formulae of 1,2 or occasionally 1,1 (Table 2). In this length range, as is shown in the following paragraphs, the pelvic rays gradually become overgrown by abdominal tissues, within which they are clearly visible after alizarin staining. At larger sizes the rays presumably are too deep to be seen without dissection or staining. Norman (1930:351) failed to find them in N. tripes specimens 53 and 88 mm long. Dissection of the pelvic region of my 176-mm fish revealed fragments of raylike material in the musculature ventral to the pelvic bones. These fragments were fused to the pelvis anteriorly, and appeared to serve as anchoring struts.

In young Nealotus individuals there are two prominent spines preceding the anal fin, whereas adults are generally regarded as having only one. My 176-mm specimen conforms to the adult concept externally, but when dissected its perianal region contained a small, flat spine, triangular in outline, embedded behind the first. Matsubara and Iwai (1952:207) also noted a second anal spine, but in their 199-mm fish it is shown as being externally visible.

With an ontogenetic loss of pelvic rays and anal spines, the genus Nealotus (and perhaps others) becomes more difficult to define. Characteristic counts are given in Table 2, along with data for Nesiarchus nasutus, a species of similar appearance.

Figure 3 depicts the smallest Nealotus examined, a fish 9.0 mm in standard length. At this size the vertical fin rays have not all differentiated, the dorsal being XX-I,18 and the anal
II-I,15, with both fins showing rudimentary raylike structures in the membranes posterior to the fins. The principal caudal rays number 9 + 8, the pectorals 13, and the pelvics I,2. Each pelvic spine is long, triradiate in cross-section, and spinigerous on all three edges. The inner pelvic ray is not only much shorter than the outer, but is also membranously bound to the belly anteriorly, whereas the outer ray is free. Like the pelvics, the dorsal spines are triradiate and spinigerous, with the degree of spinulation decreasing posteriorly. The first two dorsal spines bear spinules on all three edges while the rest bear them only laterally; in addition, the number of spinules per spine decreases toward the rear of the fin. The anal spines are like two spiny-edged, short-handed spoons, attached by the bowls with the convex side forward, and the second nesting into the first.

The preopercle bears two strong denticulate spines at its angle and two short smooth spines on its lower limb. The pterotic has two slender spines almost perpendicular to the body surface. A row of 10 denticulations above the eye completes the head armament.

The mandible is prognathous and its tip is surmounted by a small cartilaginous pad. The mandibular symphysis is edentulous, but there are two retrorse fangs on either side of it. About seven short upright teeth are borne on the dentary. There is a large fang on each side of the premaxillary symphysis and a larger one posterior and mesial to the first. About 13 other teeth, some little more than denticulations, occur on the premaxillary. The palatines lack teeth, while the vomer bears a single prominent tooth at each posterior tip.

Pigmentation consists of a brown streak from the top of the head to the rear dorsal base, plus diffuse brown color around the dorso-anterior orbit and along the premaxillary. There is some inconsistency between specimens, probably reflecting differences in chromatophore contraction at death rather than the presence of more than one species.

The 15.6-mm fish shown in Figure 4 differs from the 9-mm one principally in having achieved the adult fin complement (D XX-I, 19 + 2; A II-I, 16 + 2). The two dorsal and anal finlets are connected to each other and to the preceding fins, being detectable only by a variation in spacing. The pelvic spines are as before, but the rays are now adnate to the belly for about half their length. The anal spines have developed a keel on their previously smooth anterior surfaces.

The head armament consists of the two spines at the angle of the preopercle (these now having lost their denticulations), two short spines on the lower limb of the preopercle, a single perpendicular spine on the pterotic, and two pos-
terior spinelike extensions of the strengthening ribs of the opercle. The supraorbital denticulations have been reduced to one or two.

Both the mandible and the upper jaw now bear small cartilaginous symphysial pads, and the dentition is much advanced. Besides the anterior pair of fangs, each dentary has 11 slightly retrorse teeth, and 12 similar teeth are found along the edge of each premaxillary. Anteriorly the premaxillary has 3 or 4 large curved fangs, the posterior ones longest, and all larger than the fangs on the dentary. The vomer has a posterior tooth on each side, and there are about 4 slender teeth located on or near each palatine. Those which are merely near the palatines lack ossified bases. There are as yet no gill-rakers on the first arch.

Pigmentation is again inconsistent between specimens, except for a pronounced dark spot between the first two dorsal spines. Well-marked individuals are colored as is the 9-mm fish; others lack the dark pigmentation of the head and dorsal fin base.

At 31.0 mm (Fig. 5) many of the larval features have been replaced by juvenile characters. The dorsal finlets are still interconnected

<table>
<thead>
<tr>
<th>TABLE 2</th>
</tr>
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<tbody>
<tr>
<td><strong>Counts Made on Nealotus tripes and Nesiarchus nasutus</strong></td>
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<table>
<thead>
<tr>
<th>PART</th>
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<th>Nesiarchus nasutus (No. specs.)</th>
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<td></td>
<td>1</td>
</tr>
<tr>
<td>Second dorsal</td>
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<td>23</td>
</tr>
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<td>23</td>
</tr>
<tr>
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<tr>
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<td></td>
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</table>

* Standard length range: Nealotus, 10.0-176 mm; Nesiarchus, 11.7-105 mm. Finlets listed as such even if attached to fins by persistent membranes.
but are free from the last dorsal ray. The same is true of the anal finlets, except that there is a persistent basal membrane between the last anal ray and the first finlet. The dorsal spines have lost the spinules from their anterior edges, and the lateral spinules are less prominent on all fin spines, the space between the spinules having become filled with bony material. The pelvic rays are both buried in epidermal tissues, with the short mesial ray lying deeper than the long lateral one.

The upper spine at the preopercular angle is prominent, but the lower is broad and scarcely noticeable. The lower preopercular limb is smooth, and the opercular spinules are reduced in size. The cartilaginous protuberance at the tip of each jaw is conical and well developed. The dentary has 2 anterior fangs and 13 variably smaller teeth; the premaxillary bears 3 anterior fangs and about 16 smaller teeth. The vomer has 2 teeth on each posterior tip, and there are about 6 teeth on or near each palatine. As before, some of the latter are attached to unossified material on the roof of the mouth. There are \( 3 + 1 + 8 \) gill-rakers on the first arch, the one at the angle being much larger than the others.

A new feature is the lateral line, a few scales of which are visible on the 31-mm fish. These lie in the skin and are better developed and more numerous anteriorly. In a 35-mm specimen (not shown) the lateral line is nearly completely developed. It is a tubelike structure containing 78 scales and extending from the head to the caudal peduncle. Scale spacing is occasionally irregular, suggesting incomplete development or loss through damage.

Pigmentation consists of rows of tiny, close-set, dark dots, giving an over-all tan color. This is intensified on top of the head, at the jaw tips, along the dorsal base, on the sides of the caudal peduncle, and around the anal spines. The fins lack pigment except for a distal dark spot between the first three dorsal spines.

A 41.5-mm fish (Fig. 6) is essentially a juvenile. Persistent larval features include the slightly denticulate fin spines, the absence of scales except in the lateral line, and basal membranes between the finlets. The pelvic rays are embedded, the two preopercular and two opercular spines are reduced in size, and the symphysial jaw pads are less prominent (and now curved in the case of the upper jaw). The teeth have increased slightly in number, there now being 5 anterior fangs and 19 lateral teeth on the premaxillary, 2 fangs and 16 lateral teeth on the dentary, 8 or 9 teeth on each palatine (all firmly ankylosed to the palatine and none free on the roof of the mouth), and 1 or 2 elongate teeth posteriorly on each side of the vomer. There are 94 scales in the lateral line but none elsewhere. There are \( 3 + 1 + 8 \) slender gill-rakers on the first arch. Pigmentation is as in the 31-mm fish, except that there are now indications of distal dark spots between the first four dorsal spines.
It is unnecessary to figure my 176-mm fish, for it has essentially the same features as the 199-mm specimen shown by Matsubara and Iwai (1952:208). As noted earlier, it differs in having the second anal spine embedded. Other data from my specimen are as follows. The lower jaw has a rudimentary symphysis pad. 1 or 2 anterior fangs on each side, and a row of 17 lateral teeth set closely together like the teeth of a saw. On the premaxillary are 3 large anterior fangs and a row of 21 closely-spaced lateral teeth. The symphysis pad of the premaxillary is blunt, decurved, and scarcely noticeable. The roof of the mouth is overgrown by membranes which, when removed, reveal an edentulous vomer. There are 8 short, blunt denticles on each palatine. The gill-rakers consist of numerous spinules so variable in size, position, and spacing that they cannot be enumerated (cf Matsubara and Iwai, 1952:209). The specimen is partially skinned and the lateral line scales cannot be counted.

*Diplospinus multistriatus* Maul

Station 66 2 specimens: 103 and 166 mm
Station 68 10 specimens: 10.0–17.4 mm
Station 70 1 specimen: 156 mm

The genus *Diplospinus* is known from Madeira, the West Indies, and the Philippine–East Indian region (Tucker, 1956:79). The above specimens are the first from the central Pacific Ocean. Postlarvae are hitherto unknown, although they and earlier stages have been found for other trichiurids (Delsman, 1927; Padoa, 1956:508–513; Regan, 1916:144–145). The following descriptions and figures illustrate development in which a short, high-bodied postlarva becomes an increasingly attenuate juvenile.

As pointed out by Tucker (1956:81), there is a possibility that *Diplospinus multistriatus* Maul is a synonym of *Lepidopus gracilis* Brauer. The latter was described from a specimen 69 mm in length (Brauer, 1906:291), which differs from *multistriatus* chiefly in characters which change with growth. Although it was impossible to examine the type of *gracilis*, a brief study was made of a feature thought to distinguish it from *multistriatus*, the ratio of standard length to head length. This ratio is plotted against standard length in Figure 7. The data represent the present specimens, the type series of *multistriatus* as described by Maul (1948:45), a recently collected 65-mm *multistriatus* with a SL/HL ratio of 5.5 (Maul, in litt.), and the type of *gracilis*. The curve was derived from the regression of head length on standard length, $\bar{Y} = 3.397 + 0.1350X$, calculated from the above *multistriatus*.

From Figure 7 it would seem that *multistriatus* and *gracilis* are separate species. This is confirmed by the fiducial limits of the head length of *multistriatus* 69 mm in standard length (the length of Brauer's *gracilis*). At this size one can expect a head-length range of 12.3–13.1 mm, using $P_{.01}$ values of $t$ and the formula

$$\bar{Y} = \sqrt{\frac{1}{n} + \frac{x^2}{Sx^2}}$$

(Snedecor, 1946:120). The 14.25-mm head

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**Fig. 4.** *Nealotus tripe* 15.6 mm in standard length.
Porstlarval Scombroids from the Central Pacific—STRASBURG

length of gracilis lies significantly distant from this range, and the two forms are therefore considered distinct species.

Because not all postlarvae in the 10.0–17.4 mm length range have acquired the adult fin ray complement, it is necessary to list meristic and length data conjointly in Table 3. The number of dorsal and anal fin rays increases irregularly with size. The pectoral, pelvic, and caudal fins and the branchiostegal rays show little or no meristic variation. Except for one specimen with 13 rays on one side and 12 on the other, the pectoral was constant at 12 rays. There were 7 branchiostegal rays and 9 + 8 principal caudal rays, the latter being difficult to count because of damage or nonattainment of definitive shape. In all 13 specimens the pelvic fins are represented by a pair of stout denticulated spines, in agreement with Maul’s findings (1948:42) but not with Tucker’s (1956: 79–81). The latter, working with a “completely skinned” paratype, observed “Ventral fin I–I; a narrow scale-like spine and an external split ray twice as long.” Palmer and Marshall (in litt.) have re-examined this paratype but failed to find the external split ray, observing only the scale-like spine and the pelvic bones. I suggest that Tucker’s “ray” was in reality the splintlike pelvis, perhaps loosened in its muscular bed by the force which skinned the fish. In my specimens the attenuate pelvis bears a marked resemblance to a soft ray and is, coincidentally, just twice as long as the pelvic spine.

The most distinctive feature of the 10.0-mm postlarval Diplospinus is its relatively great depth at mid-length. As shown in Figure 8, this is caused by a ventral distension of the belly by the elongate pelvic bones, a condition reminiscent of the Balistidae and Monacanthidae, except that in Diplospinus the pelvis extends posteriorly. The great depth of Diplospinus is quite different from the narrow belly of Lepidopus at

Fig. 5. Nealtus tripes 31.0 mm in standard length.

Fig. 6. Nealtus tripes 41.5 mm in standard length. The eyes are lacking in this specimen, but have been drawn as they appear in another of about the same size.
Fig. 7. Standard length/head-length ratio of Diplospinus multistriatus and Lepidopus gracilis.

this size (Regan, 1916: fig. 7). The abdominal walls of Diplospinus are braced laterally by the very long, slender postcleithra.

Attached to each pelvic bone is a hypertrophied pelvic spine, V-shaped or nearly tri-radiate (through attenuation of the V's apex) in cross-section, with about 20 spinules along each of its three edges. The two detached anal spines and the anterior four or five dorsal spines are similar to the pelvics in shape and armament, while the others are smooth and less obviously tri-radiate. The low number of soft dorsal rays (Table 3) is probably attributable to damage rather than youth, for a 10.4-mm specimen has 10 more rays in this fin.

The head is armed with a long slightly serrated spine at the preopercular angle, a shorter spine just above it, and two other short spines below, the last three spines being smooth. The three strengthening ribs of the upper opercle project from the opercular edge as slender spines. Dorsal to these projections are two spines at right angles to the body surface: a stout serrated spine on what is probably the pterotic, and a slender smooth one on the post-temporal. Two short spines occur above each eye.

A pair of stout anterolaterally directed tusks lies at each side of the symphysis of the prognathous mandible, these being ventral to the jaw edge, horizontal in position, and unopposed by other teeth. Behind them are three or four retrorse denticles in the anterior half of each dentary, with no teeth posteriorly. The premaxillary has an enlarged tooth at either side of the symphysis, one or two retrorse denticles lateral to this, and six or seven tiny denticles scattered along the rest of its length. The vomer and palatines are ossified but edentulous. There is no trace of a cartilaginous jaw protuberance.

Pigment is restricted to a brown spot distally in the membrane between the first three dorsal spines.

At 13.2 mm (Fig. 9) the postlarva has become more elongate and less high-bodied. There is a variable increase in the number of dorsal and anal rays, and the spinigerous condition has spread posteriorly to include three-fourths of the dorsal spines. The caudal fin is beginning to fork. The preopercular spines are as before, while the post-temporal and pterotic spines are equal in size and both are smooth. The suprarobital spines are short and inconspicuous. A peculiarity of this specimen is its possession of only two opercular-strengthening ribs, each with a spine-like projection. The normal number of ribs, and spines, is three.

Just posterior to its nearly horizontal tusks each dentary bears an upright, unopposed tooth, and behind this is a row of eight emergent teeth extending to the rictus. The premaxillary has a pair of curved fangs on each side of the symphysis, followed by about six teeth of varying size extending to the rictus. The vomer has two prominent teeth on each posterior tip, while the palatines lack teeth. A cartilaginous pad has not yet appeared at either jaw tip. The nasal capsule is visible as a yellowish sub-epidermal sac which lacks external ducts.

**TABLE 3**

<table>
<thead>
<tr>
<th>STANDARD LENGTH (mm)</th>
<th>DORSAL FIN</th>
<th>ANAL FIN</th>
</tr>
</thead>
<tbody>
<tr>
<td>10.0</td>
<td>XXX, I, 16*</td>
<td>II–I, 19</td>
</tr>
<tr>
<td>10.4</td>
<td>XXX, I, 26</td>
<td>II–I, 20</td>
</tr>
<tr>
<td>11.1</td>
<td>XXXI, I, 25</td>
<td>II–I, 19</td>
</tr>
<tr>
<td>11.2</td>
<td>XXXII, I, 29</td>
<td>II–I, 22</td>
</tr>
<tr>
<td>12.0</td>
<td>XXX, I, 27</td>
<td>II–I, 23</td>
</tr>
<tr>
<td>12.1</td>
<td>XXXII, I, 27</td>
<td>II–I, 20</td>
</tr>
<tr>
<td>12.6</td>
<td>XXX, I, 30</td>
<td>II–I, 29</td>
</tr>
<tr>
<td>13.2</td>
<td>XXXI, I, 30</td>
<td>II–I, 23</td>
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<tr>
<td>16.5</td>
<td>XXXI, I, 33</td>
<td>II–I, 27</td>
</tr>
<tr>
<td>17.4</td>
<td>XXXII, I, 35</td>
<td>II–I, 28</td>
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<tr>
<td>103</td>
<td>XXX, I, 37*</td>
<td>II–I, 31</td>
</tr>
<tr>
<td>156</td>
<td>XXXII, I, 35</td>
<td>II–I, 28</td>
</tr>
<tr>
<td>166</td>
<td>XXXII–I, 38</td>
<td>II–I, 30</td>
</tr>
</tbody>
</table>

* Damaged (?)
Pigment consists of the distal brown spot in the spinous dorsal, large melanophores on top of the head and occiput, and diffuse brown color anterior to the eye, posteriorly on the maxillary, in front of the pelvic bases, and on the branchiosteal membranes.

Definite indications of the forthcoming ribbon shape are seen in the 17.4-mm postlarva (Fig. 10). There is little trace of the earlier abdominal distension and the head is relatively short. The adult fin ray complement has been attained, although the fins are immature in that their spines still bear spinules. The pelvics are still excessively large and the caudal is well forked.

On the head, the preopercular spines are as before except that those on the lower limb are shorter and stouter. The opercular ribs and
spines and the post-temporal and pterotic spines are likewise little changed. A single low spine, actually little more than a crest, occurs above each eye. The upper of the two tusks on the dentary is much the larger, and the upright tooth posterior to the tusks equals it in size. About 15 curved teeth, some occurring as pairs, occupy the length of the dentary. Anteriorly the pre-maxillary has 3 or 4 greatly enlarged fangs, the anterior 1 or 2 about half the size of the others. Behind the fangs is a row of about 10 short teeth similar to those of the dentary. The vomer still has 2 teeth near each posterior tip, and these are attached on the inner surface of the bone rather than to its crown. Each palatine bears 6–8 short denticles. There are \( 3 + 1 + 11 \) long, slender gill-rakers on the first arch. The nasal capsule has 2 openings, an oval anterior nostril and an irregular posterior one. The nostrils must form suddenly, for they are not present in a 16.5-mm specimen. Small patches of cartilage surmount the tips of both jaws, where they appear to do nothing more than smooth over irregularities in the bones.

Large melanophores occur on top of the head, but give way to smaller ones which extend in a narrow line from the occiput along the entire base of the spinous dorsal. Dark pigment overlies the nasal capsule and occurs as a ring around the orbit. The maxillary, posterior dentary, and pre-pelvic and branchiostegal regions are also dusky, and there is a dark spot in the spinous dorsal fin membranes. (These membranes are damaged in the 17.4-mm fish and the spot is drawn as it appears in a 16.5-mm specimen.)

REFERENCES


Identification of *Leptocephalus acuticeps* Regan as the Larva of the Eel Genus *Avocettina*

**GRACE L. ORTON**

Regan (1916:140, pl. 7, fig. 5) based the description of a distinctive new eel larva, *Leptocephalus acuticeps*, on a single 47-mm specimen from the South Atlantic. He did not attempt to allocate this larva within the eel classification, but D'Ancona (1928:109) and Bertin (1936:7) assigned it to the Congridae. Although no additional specimens of *L. acuticeps* appear to have been reported since the brief original description, Bertin re-examined the original larva and gave important supplementary information on it, and an additional illustration.

Recent accessions of eel larvae from the eastern tropical Pacific in the Scripps Institution of Oceanography fish collection include two specimens that closely match the major known characters of *Leptocephalus acuticeps*. The present paper describes these larvae and assigns them to *L. acuticeps*. Comparative study indicates that *L. acuticeps* belongs to the *Avocettina* section of the family Nemichthyidae, and suggests that it is best interpreted as the general kind of larva that characterizes all of the *Avocettina* as a group.

**DESCRIPTION OF NEW SPECIMENS**

*Collection data.* The two larvae of *Leptocephalus acuticeps* from localities in the eastern tropical Pacific have the following collection data:

1. SIO62–639–26A; from "Scot" expedition, Scripps Tuna Oceanography Program, Station No. 36; 6° 30′ N, 95° 54.8′ W; May 9, 1958; total length 124 mm. (2) SIO62–387–26A; same expedition, Station No. 59; 5° 34′ N, 81° 28.5′ W; May 18, 1958; total length 107 mm.

*Morphology.* These are moderately slender larvae, with a long, straight gut, and a short tail (Fig. 1). The smaller specimen has a total length of 107 mm; snout to anus, 97 mm; tail, 10 mm. The larger has a total length of 124 mm; snout to anus, 111 mm; tail, 13 mm. The maximum height is about 8% of the total length on the 107-mm larva, about 7% on the 124-mm larva. The head proportions are quite generalized, neither markedly elongated nor unusually shortened, compared with other leptocephali in general (Fig. 2). The rounded eyes lack the thick white supporting pad ("iridochoroid process") that sheaths the eyeball of certain other leptocephali (notably, most congrids). The snout profile is moderately concave. The jaws are moderately long and their tips are approximately even. The larval dentition, presenting no unusual features, consists of 12 or 13 lanciform teeth on each side of the upper jaw, and 11 or 12 on each side of the lower jaw. The rather small first upper tooth on each side is attached to one of the pair of sliver-like rudimentary premaxillary bones that are close together on the upper tip of the ethmoid cartilage. The other upper teeth border the maxillary and comprise 6 or 7 large ones followed by 5 or 6 distinctly smaller ones. These size classes are more sharply defined in the 107-mm larva. The teeth on the lower jaw decrease in size more evenly. The small, subtriangular nasal capsule lies directly adjacent to the upper anterior quarter of the eye margin. The rounded anterior nostril is smaller than the vertically ovoid posterior one; both are well defined, though small. The moderately large tongue rises well upward from the floor of the mouth, but neither its tip nor its sides project freely. The moderately large gill arches bear well-defined margi-
nal flaps but no definite respiratory filaments. Both larvae have well-developed pseudobranchs. The pectoral fins are moderately small. On the 107-mm larva the fin base is on the fourth somite, and the adpressed edge of the fin membrane reaches about halfway across the sixth somite. On the 124-mm larva the pectoral is one somite farther forward; its base is on the third somite and its free edge reaches the fifth. The caudal fin (Fig. 3) is well defined but the narrow hypurals are not very heavily chondri- fied, and their combined vertical diameter is only slightly greater than that of the notochord and spinal cord together. The three or four caudal rays quite fully occupy the available space, and hence few if any additional rays are likely to form on older larvae. The last basal elements of the dorsal and anal fins are in contact with the hypurals. The dorsal fin begins as a barely perceptible thickening at about the 149th somite on the 107-mm larva, and at about the 153rd somite on the 124-mm larva. (Position of a structure or color-pattern element in relation to a numbered somite is determined by extending a vertical line from the feature in question and counting the somite that forms its midlateral angle where this vertical line meets the body axis.) The somites total 182–187, of which 158–161 (about 86% of the total) are preanal and 24–26 are postanal. A major vertical artery extends down from the aorta to the viscera at the 16th or 17th somite, and another one (or two very close together) at the 26th or 27th somite. The narrow liver is moderately long, very thinly tapered anteriorty and slightly thicker toward its more bluntly pointed posterior end. It begins at the 13th somite in the 107-mm larva and at the 8th somite in the 124-mm larva; in each it ends at about the 27th somite. Since the pylorus is at the 25th somite in each larva, the liver subends about 12 and 17 prepyloric somites, respectively. The gut is a simple straight tube, with no undulations or regional enlarge- ments. The slightly thickened kidney parallels the top of the gut for about 36 or 37 somites behind the pylorus, to somite 61 or 62 (Fig. 4). There is a conspicuous vertical artery at somites 50–51 (damaged on the 124-mm larva). The major renal artery leaves the body axis at somite 58 or 60, and the renal portal vein at somite 63 or 64. The artery is vertical, but the vein slants forward. Behind its junction with the renal portal vein, the kidney narrows abruptly to form the thin, scarcely visible duct that continues along the top of the gut for an additional 97–99 somites and terminates directly behind the anus, between somites 158 and 161.

**Pigmentation.** The pigmentation is unusual, compared with that of other leptocephali in general, both in the complexity of its pattern
and in the small size and dense spacing of its melanophores (see Figs. 2–4). The uppermost element in the pattern is a middorsal band of melanophores in the skin. It begins at the third somite on the 107-mm larva but is not visible until the 15th somite on the 124-mm larva. In each the row extends to the tail tip. For most of its length, this stripe has an irregularly varying width of from one to several cells. When it meets the anterior end of the dorsal fin (about somites 149–153), the row narrows to a single file, which extends along the tops of the basal elements within the fin. Thus, the pigment cells come to lie progressively deeper inward from the surface as the thin edge of new fin tissue grows upward above the basals. An internal supraspinal row of small, densely spaced melanophores runs along the top of the spinal cord from the hindbrain to the tail tip, where the row ends just ahead of the hypurals. The cells are evenly spaced and of uniform size. Another internal row of melanophores, between the kidney and the top of the gut, extends from about the 16th somite to the anus. Anteriorly, it comprises a single line of cells, but at about the 50th somite the row begins to double, and thence continues more or less regularly doubled for the rest of its course. An external midventral row of tiny melanophores extends from the anterior end of the pericardium to the anus. This row shows strong zonation in cell abundance (compare Figs. 2 and 4). The melanophores form a wide, densely crowded patch below the pericardium, and a single densely spaced row from there to about the 27th somite (below the posterior end of the liver). Beyond the liver, the row thins out rapidly and its cells are widely spaced and inconspicuous until they again crowd together a short distance anterior to the anus. Although this ventral row underlies the gut very closely, it is in the skin rather than on internal surfaces. There are no melanophores along the midlateral surfaces of the somites, where many other kinds of eel larvae bear a conspicuous longitudinal row of black cells. Three rather inconspicuous patches of internal pigment (Fig. 1) lie between the midlateral axes and the lower edges of the somites, in approximately the anterior half (about 50 to 56%) of the total length. They are situated in the vertical connec-

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**Fig. 2. Leptocephalus acuticeps.** Morphology and pigmentation of head and anterior end of body of the 107-mm larva, through somite 16. Somite 4 includes base of pectoral fin; somite 13 marks origin of liver; somite 16 includes origin of a major vertical artery.
Comprehensive tissue between the right and left muscle layers, and each patch or spot consists of an oblique or more or less vertical cluster of small, contracted, and rather widely spaced melanophores. On each specimen the first spot is at somites 25–26, the second at somites 50–52, and the third at somites 85–86. Each of the first two spots is close to a vertical blood vessel (Fig. 4). In addition to these three aggregations of melanophores, the median connective-tissue zone bears occasional very small, inconspicuous, separate melanophores scattered irregularly at wide intervals. Most of these cells are below the level of the notochord, but a very few are above it. The predominant pattern on the short tail (Fig. 3) consists of continuations of the supraspinal and middorsal rows. A midventral row, symmetrical with the latter, is developing along the outer edges of the posterior anal-fin basals. There are occasional melanophores along the inner edges of the anal basals, and scattered melanophores in the median connective-tissue zone (both above and below the midlateral axis), especially in the posterior half of the tail. The caudal fin is liberally dotted with very minute melanophores. The head is sparingly pigmented, except for the solidly dark eyes. There are a few tiny melanophores in the tip of each jaw, and a few along the lower-inner edge of the lower jaw. The heavy midventral band of pigment below the pericardium begins sufficiently far forward (Fig. 2) that it might also be regarded as a part of the head pattern.

Comparisons

A. Leptocephalus acuticeps

The specimen on which Regan based the larval name Leptocephalus acuticeps was collected in the South Atlantic (21° S, 37° 50' W) by the "Terra Nova" expedition. The data and illustrations in Regan (1916) and Bertin (1936), when combined, characterize L. acuticeps unusually completely, and show it to be very distinctive and more confidently identifiable than are most other described leptocephali. The given data on somite counts are even sufficiently complete to reveal several useful proportional characters that both authors had overlooked. In the following discussion of this specimen, the characters that pertain to somite numbers and positions are calculated from Regan's original counts. Bertin omitted the first two somites, which appeared to be incomplete ventrally. My own counts on specimens examined include all discernible anterior somites regardless of
whether they seem to extend completely to the ventral margin of the musculature.

The total length of the original specimen of *L. acuticeps* was 47 mm. The maximum height was about 8.5% of the total length. The dorsal profile of the head was markedly concave; the jaws bore about seven upper and six lower teeth on each side; Regan's illustration shows sufficient space behind these for the addition of more, perhaps smaller, teeth during larval growth. The tip of the lower jaw protruded slightly. The somites totalled 207, of which 174 (84%) were preanal and 33 were postanal. The gut was a long, straight, simple tube, with no apparent specializations. An enlargement of the liver occurred at about the 30th somite (hence, the 30th somite can be considered the approximate location of the pylorus). There were major vertical blood vessels anteriorly at somites 16 and 27, and farther back at somites 61, 71, and 76. The kidney terminated at about the 76th somite, and there were therefore about 46 somites between the pylorus and the posterior end of the kidney, and about 100 between the latter position and the anus. Although Regan did not describe the tail, his illustration shows that the fleshy part was obtusely rounded, with a distinctly rayed tip. Bertin mentioned that the hyurals were scarcely visible and that the caudal was pointed. The vague definition of these characters certainly stems at least partly from the relatively young stage of the specimen. The known pigmentation of this original specimen included an internal row of minute, densely spaced melanophores along the top of the spinal cord, a similar row along the top of the gut beginning at about the 30th somite (probably at or near the pylorus) and extending to the anus, and another row (probably external) along the ventral surface from the heart region to at least the pyloric region. The sides of the tail bore a few small scattered melanophores, both above and below the level of the notochord. There were three internal spots visible through the lower halves of the somites, each spot composed of a loosely clustered, roughly linear group of small melanophores. The first spot was at somites 27–30, the second at somites 61–62, and the third at somites 104–107. The first and second spots were each near a major vertical blood vessel.

The two eastern Pacific larvae described in the present paper match the determinable characters of Regan's Atlantic larva of *L. acuticeps* so closely that there is no doubt of their close relationship to it, and therefore I have assigned them to *acuticeps*. So far as known, they differ from the Atlantic specimen only in details of the sort that are readily subject to variation among very closely related larvae or between growth stages of a single form. The Scripps specimens share the general format and visceral characters of *acuticeps*, but they are much larger and have about twice as many teeth, the head profile is straighter, and the tips of the jaws are even. The Scripps larvae have somewhat lower somite counts and the preanal somites constitute a slightly higher percentage of the total number. In addition, the pylorus is about five somites farther forward in the Scripps larvae than its estimated position in the original *acuticeps*, the posterior end of the kidney and the main renal blood vessels are about 12–14 somites farther forward, and there are about 10 or 11 fewer

**Fig. 4. Leptocephalus acuticeps.** Section between somites 50 and 63 of the 107-mm larva. Numbers designate somites. Somite 50 includes origin of vertical artery at anterior limit of the cluster of melanophores that comprises the second of the three internal spots; somite 58 includes origin of main renal artery; somite 61 marks posterior limit of kidney; somite 63 includes origin of renal portal vein.
somites between the pylorus and the posterior end of the kidney. There is close agreement in the number of somites between the posterior end of the kidney and the anus. The differences in visceral proportions are consistent with the lower total somite count and the consequently shorter gut in the Scripps specimens.

The pigmentation of the eastern Pacific larvae closely matches the known pattern of the Atlantic specimen. The internal suprarectal row of melanophores has essentially the same extent; the internal suprarectal row apparently extends farther forward (Regan did not show any prepyloric pigmen in this row); and the external midventral row is apparently more complete (Regan showed no postpyloric pigment here). The original references did not indicate any middorsal pigment on the Atlantic larva. In the Scripps larvae the three internal spots are placed somewhat farther forward in relation to somite numbers, but (as will be discussed in a later section) they have essentially the same position in relation to the viscera and to certain blood vessels. Regan did not mention these spots in the original description, but Bertin discovered them, described them in detail, and figured one of them. These markings comprise an unusual pattern element which, so far as I can determine, is known elsewhere only in the larvae of Nemichthys (see discussion below). The descriptions did not mention scattered internal melanophores anterior to the anus in addition to the three aggregate spots, but they did indicate that the tail bore small melanophores both above and below the median axis, and in Regan's illustration this speckling forms essentially the same pattern as it does on the Scripps specimens.

Although the maximum sizes that the Atlantic and Pacific larvae attain are still unknown, simple individual or growth-stage variation could account for most of the evident differences between the available Pacific larvae and the described Atlantic specimen. The smaller number of teeth, more concave head profile, slightly protruding lower jaw, slightly deeper body, and poorly defined hypurals of the original specimen of acuticeps are developmental features that are commonly seen in young stages of leptcephali. Whether the minor color pattern differences represent growth-stage characters will remain uncertain until more complete developmental series are available. The difference in somite counts is the principal feature which suggests that the populations in the two regions may differ at the species level, but more data are needed before this difference can be evaluated.

It is now pertinent to discuss the place of L. acuticeps in the eel classification. Apparently only two authors have compared acuticeps with other larvae (L. oxycephalus Pappenheim and L. magnaghi D'Ancona), and only two have attempted to assign it to a category in the eel classification (both to the same family, the Congridae). Elsewhere, however, one can find clues that clearly point to the proper taxonomic position of acuticeps.

B. Leptocephalus oxycephalus

Pappenheim (1914:190, pl. 9, figs. 3, 5) based his brief description of L. oxycephalus on seven Atlantic larvae that measured 177–193 mm in total length, and he placed about 40 additional smaller and less well-preserved specimens from the Atlantic and Indian oceans in oxycephalus with less certainty. He credited this larval form with total somite counts of 220–230, of which 180–190 were preanal. At about the 30th somite, he noted a structure that he tentatively identified as the liver anlage. He listed only two other characters, both rather uninformative: the head was low and the caudal fin was normal. Pappenheim did not mention pigmentation, and none is definitely apparent in his photographs of L. oxycephalus, but this does not necessarily mean that pigment cells actually were totally absent. It is quite possible that pigment had faded before he received the collection, or that the individual melanophores were too small to show on the photographs. In his descriptions of other leptcephali in the same paper, he tended to omit pigment characters or to treat them very superficially. Hence he may have considered the color pattern too insignificant to require detailed description. In Pappenheim's illustrations the general format of L. oxycephalus rather closely resembles that of the Scripps specimens of L. acuticeps, but it also looks much like a very generalized congrid larva, and the characters discernible in the photographs are insufficient to permit definite discrimination. Regan (1916) considered his new L. acuticeps to be very simi-
lar to *L. oxycephalus*, and he mentioned no differences other than the somewhat lower somite count of *acuticeps*. D'Ancona (1928) rejected affinity of *oxycephalus* to *acuticeps* because of the ostensible lack of pigment in *oxycephalus*. Bertin (1936) doubted that they are related, but he gave no reasons. On present knowledge, I consider *L. oxycephalus* too incompletely known to be identified with certainty.

C. *Leptocephalus magnaghii*

D'Ancona (1928:109) rejected Regan's view that *L. acuticeps* resembles *L. oxycephalus*, and suggested instead that *acuticeps* should be compared with his own newly described leptocephalus from the Red Sea, *L. magnaghii* (op. cit.: 44; pl. 3, figs. 4, 5). He stated that the somite counts of *acuticeps* and *magnaghii* show no essential difference (*acuticeps*, total 207, preanal 174; *magnaghii*, total 205–219, preanal 157–161, excluding a metamorphosing larva with shortened gut). He suggested that *acuticeps* might even be considered a younger stage of *magnaghii*, but he decided to recognize both forms because of a difference in lateral pigmentation that he did not think could be explained by either individual or growth-stage variation; i.e., the presence of a midlateral longitudinal row of melanophores along each side in *magnaghii* and the absence of such rows in *acuticeps*.

*L. acuticeps* and *L. magnaghii* differ more widely than D'Ancona realized. *L. magnaghii* does resemble *acuticeps* in total somite count, in its long straight gut, and in the low number of caudal rays, but it differs in virtually all other significant features of morphology and pigmentation that can be compared. D'Ancona was unaware that *acuticeps* has the unusual pattern of three internal blotches, for Regan did not mention or figure these spots and Bertin's comments on them had not yet been published. The Scripps fish collection includes extensive series of *magnaghii*-like larvae from the eastern tropical Pacific. These leptocephali are identifiable as heterocongrid eels on the basis of compared somite and vertebral counts, congrid characters of metamorphosing specimens, and remnants of the larval color pattern that are retained by juveniles of *Taenioconger* sp. in the Scripps collection. The close agreement of the Scripps larvae with D'Ancona's detailed description and excellent illustrations of *magnaghii* (including a metamorphosing specimen) suggests that this larval name was based on heterocongrid larvae, possibly of two species.

The relatively greater importance of characters other than the somite count, in the critical comparison of *L. magnaghii* and *L. acuticeps*, exemplifies the paradox that data on somite counts can be both essential and misleading. The eels comprise such a large and complex group that totally unrelated forms may independently have the same, or broadly overlapping, ranges of variation in vertebral counts. For example, at least ten families are already known to contain species with vertebral counts that fall within the range of about 145–155. Thus, an unidentified leptocephalus that has a somite count within this range might belong to any one of at least ten families. The successful identification of eel larvae requires the use of many additional characters. The visceral anatomy supplies more informative clues to the family affinities of a leptocephalus than does the somite count.

D. Congrid Larvae

*Characters of congrid larvae.* So far as I can find, only D'Ancona and Bertin have tried to assign *Leptocephalus acuticeps* to a family in the eel classification. Each author considered it to be a congrid, but neither stated his reasons. A detailed comparison of *acuticeps* with congrid larvae should reveal whether it properly belongs with them, but two formidable difficulties hamper this comparison: the wide disagreement among taxonomists as to the composition of the family Congridae, and the resultant uncertainty over the criteria for defining congrid vs. non-congrid larvae. The present paper is hardly the place for an attempt to settle the natural boundaries of this family, yet some sort of limits must be indicated in order to permit useful larval comparisons.

The type genus, *Conger*, is the base line for comparison of larval stages as well as of adults.

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8 Heterenchelidae, Muranidae, Synaphobranchidae, Ilyophididae, Nessorhamphidae, Echelidae, Ophichthidae, Congridae, Muraenocidae, Serrivomeridae.
in this heterogeneous group. Fortunately, the larvae of its type species, C. conger (Linnaeus), and of two closely related eels from the Atlantic and Mediterranean are known. The latter two species have had (and are still having) a confused nomenclatorial history, but they are identifiable under the commonly used names Ariosa balearica (de la Roche) and Congermuraena mystax (de la Roche). The similarities among the definitely identified leptocephali of these three nominal genera provide a basic standard for defining true congrid larvae, and their differences indicate some of the kinds of variational trends that one can expect to find in related larvae. I have examined Pacific larvae of the Ariosa balearica and Congermuraena mystax groups, but have not yet seen Conger larvae. The larvae of this central group of indisputable congenids share essentially the same basic form. Its conspicuous features include the long, straight, simple gut (without regional enlargements or other specializations), and the short tail with a well-defined caudal fin that typically comprises 6–10 caudal rays. These larvae differ among themselves in size, proportional details, somite counts, and in anatomical characters of the sort that I have used above in the description of Leptocephalus acuticeps (position of the pylorus, length of the kidney, etc.).

The quite different color patterns of these three kinds of larvae indicate that the true congenids have undergone considerable evolutionary diversification in larval pattern. Conger conger has a pair of ventrolateral rows of melanophores, apparently external, paralleling the gut; a midlateral row, also apparently external, on each side of the body axis; and several large melanophores on each side of the pericardium. Congermuraena mystax has the ventrolateral and pericardial pigment, but lacks the midlateral row. In both of these larvae, the melanophores are relatively large and conspicuous. Ariosa balearica differs sharply, both in the pattern itself and in the very small size and dense spacing of the melanophores. This pattern includes densely crowded rows of tiny melanophores externally along the middorsal and anterior midventral surfaces, and internally along the top of the gut. In place of the simple longitudinal row of large melanophores along the midlateral surface, A. balearica has an elaborate lateral surface pattern composed of a uniform series of short, oblique, parallel black lines just below the midlateral axis along nearly the full length of the larva. Each of these short black lines consists of a dense row of minute melanophores placed lateral to the myocomma between two contiguous somites. Since the row of cells marks the section of the myocomma that lies just below the midlateral axis, the row therefore conforms to the oblique ventrocaudal orientation of this part of the myocomma. The diagrammatically repetitive composition of the pattern results from the regular presence of a row of cells on almost every myocomma.

A typical congrid larva is readily identified as such, for it has morphological and color-pattern characters that are consistent with the trends indicated in this basic group of known larvae. For example, the Scripps collection includes many eastern Pacific leptocephali that are easily allocated to the Congridae, and it is evident that they include at least a dozen different kinds though few of these can yet be identified with named adults. The color patterns of most of these kinds of larvae are simple modifications of the Conger conger type.

It is not known whether larvae of all true congenids conform strictly to the format of this basic group of identified larvae, or how widely a larva may depart from this type in morphological and pattern characters and still retain recognizable evidence of congrid affinity. However, some idea of the limits within which congrid larvae might evolve (and, thus, whether Leptocephalus acuticeps might belong here) can come from study of the problem groups that have been interpreted variously by different authors. The heterocongrid eels are an instructive example. Whether the heterocongrids (the garden eels, or tube eels) are best retained in the Congridae or interpreted as a separate but closely related family is still under debate in the literature. Known heterocongrid larvae (Leptocephalus magnagibis from the Red Sea, and closely similar larvae from the eastern tropical Pacific) differ from larvae of the Conger-Congermuraena-Ariosa complex in some respects (e.g., higher somite counts, relatively shorter gut, and more anterior origin of the
dorsal fin), yet they retain an unmistakable structural similarity to these basic congrid larvae and their pigmentation is a simple variant of the *Conger conger* type of larval pattern. The heterocongrids probably should be considered genetically close to the typical congrids, no matter how one may choose to juggle their nomenclature. The nettastomid eels, which are still sometimes included in the Congridae (e.g., Ginsburg, 1951), exemplify the opposite extreme. Their known larvae differ strikingly from the typical congrid larvae in both morphology and pigmentation. The head and jaws are usually very elongated, the viscera are exceptionally short and complexly specialized, and the color patterns are unusual. These and other specializations indicate that these larvae have evolved along distinctive lines and suggest that the nearest relationships of the nettastomids are to stocks that are remote from the congrids. Several groups of genera in addition to the nettastomids seem far too discordant with the type genus, *Conger*, in both adult and larval characters, to be retained within the same family. These include the dysommids, especially if the larva that Grassi (1913:170, pl. 10, figs. 1, 5) assigned to *Todarus brevirostre* was correctly identified, and the muraenesocids. I agree with authors who have elevated each of these groups to family rank. It seems to me that certain other genera (e.g., *Hoplunnis, Oxyconger*, and *Gavialiceps*) that are sometimes placed in the Congridae should also be excluded, but their larvae are still unknown and their adult stages are too incompletely described to support effective discussion of affinities. Some of these forms may prove to be muraenesocids, when the limits of that family are better understood, but others (notably, *Gavialiceps toeniola* Alcock) perhaps represent phyletic lines that are distinctive enough to justify family rank.

These examples help to establish criteria for the probable limits within which the larvae of true congrids have evolved, but a more precise understanding must await the specific identification of many more larvae, particularly in the less well-known genera that are of questionable status. Although present knowledge precludes a more authoritative discussion, this summary at least provides some basis for evaluating the possible affinity of *Leptocephalus acuticeps* to the typical Congridae.

**Comparison of Leptocephalus acuticeps with congrid larvae.** Neither D’Ancona nor Bertin gave his reasons for considering *Leptocephalus acuticeps* to be a congrid, but they probably noticed the characters of long, unspecialized gut and short tail that it shares with the congrids and with certain other leptocephali. It is also likely that they noticed the partial similarity of its pigmentations to that of the *Ariosoma balearica* larva, for both of them have reported on larvae of the *balearica* group. However, comparative study indicates that *acuticeps* does not belong here, even though the limited present knowledge reveals few absolute distinctions that firmly exclude it from the Congridae. There are some rather subtle morphological differences between *L. acuticeps* and typical congrid larvae. In *L. acuticeps* the nasal capsule is conspicuously smaller, the eyeball lacks the white (or partly pigmented) supporting sheath that most but not all known congrid larvae have, and the tongue is fully adherent, in contrast to its usually free tip and edges in congrid larvae. The hypurals are narrow and rather weakly chondrified, and there are only 3 or 4 caudal rays compared with the 6–10 generally reported for congrid eels. The somite counts of *L. acuticeps* exceed the vertebral counts of the better known congrids, most of which fall between 130–160, but this is not an excluding character, for a few congrids are known to have counts that overlap or even exceed the known somite counts of *L. acuticeps*. For example, Asano (1962) listed vertebral counts of 173–181 for *Congrina retro- tincta* (Jordan and Snyder), and 203–206 for *Uroconger lepturus* (Richardson). The Scripps collection contains unidentified Indo-Pacific congrid leptocephali with somite counts as high as 230. The similarities in pigmentation between *L. acuticeps* and the larva of *Ariosoma balearica* include the very small size and dense spacing of the melanophores, and the presence of middorsal and anterior midventral surface rows and an internal row along the top of the gut. There are important differences in the rest of the pattern. *L. acuticeps* has a complete row of internal supraspinal melanophores and the distinctive three oblique internal spots, and lacks lateral
surface pigment. Few congrid larvae are known to have any trace of internal supraspinal pigment. The internal three-spot pattern of *Acu-cticeps* has no known counterpart in congrid larvae. Numerous differences in morphological characters indicate that *Acu-cticeps* is not related to *Ariosoma bairdii*.

At present, the best evidence that supports the exclusion of *L. acu-cticeps* from the Congridae is its close resemblance to the definitely identified larvae of a different family, the Nemichthyidae.

**E. Nemichthys Larvae**

**Characters of Nemichthys larvae.** The distinctive larvae of *Nemichthys* (family Nemichthyidae) have been described and illustrated under several leptocephalus names, for their various size-groups and stages in metamorphosis have repeatedly been considered new kinds of larvae. Data on metamorphosis enabled Roule and Bertin (1929:61) and Beebe and Crane (1937:357) to assign all of these varying larvae to *Nemichthys*. It is possible that the extensive described material may also include larvae of *Nematoprora* or *Ce-rcomitus*, for these genera are closely related to *Nemichthys* and probably closely accord with it in larval characters. A complete review of the literature on the *Nemichthys* group is not essential to the present paper, however, for the two references cited above give adequate surveys of the literature on the larvae up to 1937, and very little that is pertinent to this paper has been published since then. The discussion that follows is based both on the literature and on Nemichthys larvae from the eastern Pacific in the Scripps collection.

Larvae of the *Nemichthys* group may attain a total length of at least 359 mm before metamorphosis (Roule and Bertin, op. cit.), and they are therefore among the largest known leptocephali. Total length is a rather deceptive measure of their size, however, for they are also among the slenderest of the known leptocephali (except during their more conventionally proportioned earliest stages), and hence they look smaller than the length indicates. The general form of the well-grown *Nemichthys* larva is a long narrow ribbon that has a nearly uniform width along much of its length and ends in a very thin, pointed tip without a well-defined caudal fin. The slenderess of the larva becomes more exaggerated as the total length increases. The gut is a straight, simple tube that extends exceptionally far back, and the preanal somite count is therefore unusually high. The bulging cranium, strongly concave snout profile, and slender jaws give the head distinctive and somewhat birdlike contours. The forms of *Nemichthys* have the highest vertebral counts known in the eels, and both of the references cited above suggested that additional somites and vertebrae probably continue to form at the tail tip throughout life, in contrast to the definitive growth pattern known in other eels. The narrowness and dense spacing of the terminal segments make a precise count difficult, especially on the smaller larvae. A 147-mm larva in the Scripps collection (SIO62–640–26A) has 225 preanal somites and about 50 postanal somites, making an approximate total of 275. Beebe and Crane (1937:363) reported that the total number may reach 450 before metamorphosis, and the same authors (op. cit., p. 351) recorded a vertebral count of 660 in an adult *Nemichthys*.

Roule and Bertin (1929:61) and Beebe and Crane (1937:357) had two kinds of nemichthyid larvae, which they termed "A" and "B." These probably represent different species, and possibly different genera, but the nomenclatural details need not be explored in this paper. Roule and Bertin found that the "Dana" collections contained 664 larvae of type A and only 26 of type B, and included a sufficient range of growth stages of each type to demonstrate that the two kinds do differ and are not themselves stages in a continuous series. The type B larva reaches a greater total length (to 359 mm) than type A, and has a higher number of preanal somites (maximum known, 320). An internal row of very small melanophores along the top of the spinal cord and a similar row along the top of the gut both begin at about the 10th somite. The smaller type A larva (maximum length before metamorphosis, about 255 mm) has fewer preanal somites (maximum known, 248), and its internal rows of minute supraspinal and supraintestinal melanophores begin farther back, at about the 25th somite. Type A has an important color-pattern character that the authors did not find in type B. This
The combination of excessively attenuated form and extremely high somite count tends to isolate larvae of Nemichthys from other leptocephali and to mask any similarity to them, but a critical examination of details reveals characters that link Nemichthys closely with Leptocephalus acuticeps. Direct comparison of these larvae shows that their most conspicuous differences correlate rather simply with their greatly different somite counts and tail-tip structure. In Nemichthys the visceral anatomy borders a greater number of somites, so that the various organs are associated with more posterior somites than is true of their counterparts in L. acuticeps, but the visceral proportions are much the same as in acuticeps. The two kinds of larvae differ markedly in tail-tip structure. L. acuticeps has a bluntly rounded tail tip with a well-defined caudal fin; the Nemichthys larva has a thin filament-like tail tip with little or no apparent definition of fin elements. The Nemichthys larva and L. acuticeps both have internal rows of supraspinal and suprainterstitial melanophores (which are relatively uncommon in eel larvae), and they agree in the small size and dense spacing of the cells in these rows. The most significant shared pigment character is the presence and similar placement of the unique pattern of three internal spots. It seems surprising that when Bertin (1936) redescribed the original larva of L. acuticeps he did not mention the resemblance of its internal three-spot pattern to that of Nemichthys, which he (with Roule) had described in detail only a few years before. Apparently, however, Bertin considered the extreme elongation and high somite counts of the Nemichthys larva to be primary characters of sufficient importance to outweigh any resemblances to other leptocephali. Perhaps, also, he had not yet studied a sufficiently wide variety of larval color patterns to realize the uniqueness of this one. L. acuticeps differs from Nemichthys in having melanophores along the middorsal surface and in having more extensive pigment midventrally from the pericardium to the anus. Nemichthys appears to lack the scattered, isolated melanophores in the median connective-tissue zone which, in L. acuticeps, supplement the three aggregate spots.

In respect to somite numbers, the three internal spots are somewhat farther forward in L. acuticeps than in Nemichthys, but in relation to the total length the reverse condition eventually occurs because of the differences in the nature of the proportional changes during growth. Both kinds of larvae are subject to lengthening through enlargement of somites, but in addition Nemichthys lengthens through the continued formation of new somites posteriorly. Thus, in Nemichthys the posterior end literally grows away from the spot pattern. A superficial examination of the spot positions reveals only that the two kinds of larvae differ, but a comparison of the spot positions with visceral "landmarks" instead of simply with somites reveals a striking agreement. Although the first spot averages about 10–14 somites farther back in Nemichthys than in the Scripps larvae of acuticeps, in both forms the spot occurs above or just behind the pylorus, close to or overlapping the position of a median vertical artery that extends down from the aorta to the viscera. The second spot averages about 20–23 somites farther back in Nemichthys than in acuticeps, but in both kinds the spot occupies the same morphological position about 10–12 somites ahead of the posterior end of the kidney, near or overlapping the
vertical artery that precedes the main renal artery (Fig. 4). The location of the third spot averages about 30 somites farther back in Nemichthys, but in both kinds of larvae it is situated in the same region about 24–31 somites behind the posterior end of the kidney. The internal morphological affinities of the third spot are not clear from the present data, but may be determinable from histological examination or from study of the anatomical changes that occur in this region during metamorphosis. From Bertin’s data one can diagram the positions of the spots and of the major blood vessels in the holotype larva of L. acuticeps, and the result is essentially the same as in the Scripps larvae of acuticeps and in Nemichthys: the first spot coincides with the position of a median vertical artery in the pyloric region, and the second coincides with a similar vessel about 10 somites anterior to the main renal artery. Bertin’s illustration (his fig. 4) includes this spot and artery.

It might seem reasonable to suppose that color-pattern elements that are directly beside the somites are associated primarily with these immediately neighboring somites rather than with some other structure. The contrary explanation in the present example traces to the fact that the spots in question are internal rather than external to the somite surfaces. In eel larvae, the visceral complex is displaced far downward, usually completely below the lower edges of the somites. The essential links between the body axis and the viscera (blood vessels, supporting connective tissue, etc.) are greatly attenuated and occupy a thin median vertical plane sandwiched between the laterally compressed right and left halves of the somites. The available evidence indicates that position of the diagnostic internal three-spot pattern in this group of larvae is primarily a function of the visceral and arterial positions and therefore only indirectly dependent on somite number. Evolutionary changes that have shifted the critical internal landmarks farther forward or backward along the body have also shifted these characteristic spots correspondingly, and thus the markings have maintained their predictably constant relationship to the specific blood vessels and visceral organs. The more conspicuous positional association is with the pylorus and the end of the kidney, but experimental studies (if such work is ever feasible on deep-sea leptcephali) might show that the specific vertical blood vessels are the more direct determinants.

This problem demonstrates graphically the importance of noting precisely whether a color-pattern element that is “on the somites” actually occurs outside or inside of the transparent muscle layer. The morphological affiliations, and hence the evolutionary potentialities, of these two locations are quite different.

Once it is established that L. acuticeps and the Nemichthys larva share a uniquely integrated structural and color-pattern character in the predictable detail that hints genetic relationship, then the probable significance of the similarities and differences that they show in other characters becomes clear. The Nemichthys larva is, essentially, an exaggerated acuticeps that has specialized in extremely attenuated shape, very high somite count, and the probably continuous addition of new somites in its filament-like tail tip. These chief larval differences involve the same characters as do the differences that separate the adults of Nemichthys from those of certain related genera, and these characters suggest the probable correct generic placement for Leptocephalus acuticeps.

ASSIGNMENT OF Leptocephalus acuticeps TO Avocettina

Opinions on the generic composition and best nomenclatural treatment of the Nemichthys group differ greatly. Some authors divide the presumed relatives of Nemichthys into several families, and set the entire group apart from all other eels at the subordinal level. Others reduce the number of families, chiefly by lumping rather than by deletion from the group, and either accept or omit the subordinal category. Roule and Bertin (1929) proposed subordinal rank for these eels and, on the basis of small differences, divided them into six families: Nemichthyidae, Avocettinidae, Avocettinopsidae, Gavialicipidae, Cyematidae, and Serrivomeridae. Trewavas (1932) reduced this assemblage to three families: Serrivomeridae (including Gavialiceps in part; she placed G. toemiola in the nettastomid genus Saurenchelys), Cyematidae, and
Nemichthysidae. Böhlke and Cliff (1956), representing the trend toward more extreme lumping, recognized only the Nemichthysidae (including Avocettina, Avocettinops, and Cyema) and the Serrivomeridae (including Gavialiceps). The larvae of Serrivomer and Cyema are quite well known, particularly from the studies by Beebe and Crane (1936) and Bauchot (1959) on the former, and by Bertin (1937) on the latter. These larvae clearly have differentiated along quite different evolutionary lines than have Nemichthys and Leptocephalus acuticeps, and are outside the scope of the immediate larval problems discussed in the present paper. Thus, regardless of which way one thinks it best to delimit the family Nemichthysidae (a very inclusive, or a narrowly limited version), it is apparent that the adult stage of L. acuticeps can be sought in the more restricted group of forms that are thought to be phyletically the closest to Nemichthys. The forms in this limited group center around two principal genera, Nemichthys and Avocettina. Although the several pertinent genera are usually keyed out primarily on the basis of their lateral-line characters, a different grouping is more practical for the purposes of the present discussion, for it utilizes characters that can be determined on larvae as well as on adults. The widely distributed Nemichthys and the less well-known genera Nematoprora and Cercomitus comprise the more extremely attenuated of the snake eels, with excessively high vertebral counts that may continue to increase throughout life, and a thinner and more whiplike tail that has little or no trace of a defined caudal fin. Reported vertebral counts of Nematoprora exceed 259 (Trewavas, 1932:649, for a specimen with an incomplete tail), and of Nemichthys range from 300 to as high as 660 (Beebe and Crane, 1937). The eels that may be grouped with Avocettina include Labichthys and, tentatively, the incompletely known Avocettinops. These eels are less extremely attenuated, have a better differentiated caudal fin, have much lower vertebral counts, and apparently develop a fixed number of vertebrae rather than adding new units indefinitely. The known vertebral counts of the Avocettina group are only moderately high, compared with other eels in general. Beebe and Crane (1937:366, 375) reported a range of variation from about 170 to 198 in Avocettina, and from about 175 to 180 in Labichthys. Bertin (1942:106) reported a count of about 192 vertebrae in Avocettinops. The known caudal-ray counts are low, compared with eels as a whole: five rays in Avocettina (Beebe and Crane, 1937:371), and four in Avocettinops (Bertin, 1942:107).

The somite counts of 182 and 187 on the two eastern Pacific larvae of Leptocephalus acuticeps fall within the known range of variation in vertebral counts of Avocettina. The count of 207 on the Atlantic larva of acuticeps is a little higher than the known maximum adult vertebral count. If the questionable Leptocephalus oxycephalus Pappenheim should prove to belong to this group, its somite counts of 220 to 230 would indicate the existence of related populations that have vertebral counts substantially higher than the presently known maximum among the Avocettina-like eels. L. acuticeps resembles Avocettina also in its low caudal-ray count.

Although metamorphosing specimens are still lacking, the available data warrant the tentative identification of Leptocephalus acuticeps as a larval stage of the Avocettina group. The ostensibly extreme differences between the Nemichthys larva and L. acuticeps seem inevitable consequences of the basic differences between Nemichthys and Avocettina. From the known vertebral and caudal-fin characters of the adults of these two genera, one can predict that their larvae must differ in somite and tail-tip characters in precisely the way that L. acuticeps does differ from known larvae of Nemichthys.

The available evidence suggests that acuticeps is probably significant above the species level. Similar problems on other leptocephali indicate that eel larvae in general tend to show strong group resemblances and relatively small or obscure species differences. For example, Anguilla larvae conform to a distinctive and easily recognized generic format wherever they occur, but in the Indo-Pacific Jespersen (1942) found that they are difficult to separate into species to match the approximate dozen named species that are currently recognized for adults in that region. Similarly, Bauchot (1959) found that two named larvae, Leptocephalus lanceolatus
Strömman and *L. lanceolatoides* Schmidt, encompass larval populations that represent several species of *Serrivomer*. The available data suggest that *L. acuticeps* is probably also an indicator of group relationships. The many basic morphological and color-pattern characters that *acuticeps* and larval *Nemichtys* share have been sufficiently stable to withstand the amount of evolutionary divergence that now separates the genera *Avocettina* and *Nemichtys*. Hence the existing intrageneric variation in these characters undoubtedly has even narrower limits. Since all species in the *Avocettina* group (including *Labichthys* and, tentatively, *Avocettinops*) thus probably have very similar larvae, I have elected to treat *L. acuticeps* in a practical sense as a larval group category that designates, comprehensively, the general kind of larva that is characteristic of the avocettinas as a whole. This avoids the needless redundancy of establishing a new formal (but temporary) leptocephalus name for each ostensibly different minor population within the *Avocettina* group.

A more detailed understanding of larval differentiation within this group of eels awaits not only the study of more extensive larval collections but also additional taxonomic work on the adults. The number of valid species and genera of avocettinas is uncertain, and a worldwide revision of the group is needed. Problems that await study include the status of the genus *Avocettinops*. Is its single recognized species, *Avocettinops schmidtii* Roule and Bertin, a distinct entity, or is it based on spawned-out, senile individuals of *Avocettina* spp. with regressive skeletal characters?

Much remains to be learned about the color-pattern characters of nemichthyid larvae, particularly with respect to developmental changes and population differences. The known larvae of the avocettinas (*Leptocephalus acuticeps*) are more heavily pigmented than are larvae of *Nemichtys*, both in the density of the markings that they share and in the presence of additional pattern elements. Since the evidence of evolutionary trends in color patterns commonly consists of simple modifications of a recurring basic pattern, the characters of these known nemichthyid larvae suggest some pattern variants that might reasonably be watched for among other closely related but still undiscovered larval populations. In such larvae, certain parts of the pattern might be less fully developed than they are in known larvae of *Nemichtys*, or the pattern might be still more complex than it is in the known specimens of *L. acuticeps*. The characteristic internal-spot pattern might be modified, or it might be totally absent, as has been reported for type “B” larvae of *Nemichtys* (Roule and Bertin, op. cit.). The scattered, inconspicuous internal melanophores that supplement these spots in the Scripps larvae of *L. acuticeps* might be more heavily developed in some related larval populations.

The assignment of *Leptocephalus acuticeps* to the *Avocettina* group provides information that is useful for various evolutionary studies. Since *L. acuticeps* has a more generalized format than do the extremely attenuated larvae of *Nemichtys*, *L. acuticeps* probably more nearly represents the basic nemichthyid larva and it is, consequently, the more important larva to treat in comparative studies on the evolutionary affinities of the nemichthyids to other eels. The ostensible morphological similarity between nemichthyid and congrid larvae is one of the problems that needs inquiry. Both *L. acuticeps* and the larva of *Nemichtys* show sufficient resemblance to congrid larvae, especially in the various proportional characters that are associated with the gut length, to suggest the need for a renewed study of the relationships of these two families, which are usually placed far apart in the classification. Although the available evidence does not warrant any assumption that these two families are more closely related than hitherto suspected, it does suggest that future work on leptocephali may profitably emphasize a more intensive comparative study of their basic anatomy so that the phyletic significance of their obviously diversified characters can be evaluated and used more effectively in eel systematics.

**SUMMARY AND CONCLUSIONS**

Regan (1916) based the South Atlantic eel larva, *Leptocephalus acuticeps*, on a single 47-mm specimen, which Bertin (1936) later re-examined and discussed in greater detail. The relatively complete published data and the unusual nature of certain of the characters set
acuticeps well apart and make it more confidently identifiable than are most other described leptocephali.

Two larvae from the eastern tropical Pacific in the Scripps Institution fish collection appear to be the first new material on L. acuticeps to be reported since the original specimen. They share the general format and the determinable visceral and pigmentation characters of the original specimen, and differ in details that apparently represent growth-stage differences and individual or population variation.

For unspecified reasons, D’Ancona (1928) and Bertin (1936) assigned L. acuticeps to the Congridae, but the studies reported in the present paper show that in both morphological and color-pattern characters acuticeps most closely resembles the larvae of Nemichthys, the type genus of the Nemichthyidae. The larva of Nemichthys differs from more conventional leptocephali in its greatly attenuated shape, very high somite count, and apparent continuous, life-long addition of new somites in its thin, filament-like tail tip. However, a detailed comparison of the Nemichthys larva with Leptocephalus acuticeps shows that these outwardly conspicuous differences mask fundamental resemblances in both morphological and color-pattern characters, and that the larva of Nemichthys is, essentially, an exaggerated acuticeps. The most significant of the pigment characters that they share is an internal three-spot pattern (visible through the transparent somites) that is not known to occur in any other leptocephali. These spots are in the anterior half of the body, occupying the level between the midlateral axis and the lower edge of the somites. Each spot consists of several small melanophores loosely grouped together in a more or less linear cluster, situated on the median connective tissue that is compressed between the right and left muscle layers. The spots are substantially farther back in Nemichthys larvae than in L. acuticeps, in relation to somite numbers. In both kinds of larvae, however, the first spot is above or slightly behind the pylorus, near or overlapping a vertical artery; the second spot is about 10–12 somites ahead of the posterior end of the kidney, adjacent to or overlapping the last vertical artery anterior to the main renal artery; and the third spot is about 24–31 somites behind the posterior end of the kidney. The anatomical significance of this third location is not clear from the present data. The predictable relationship between the internal three-spot pattern and the visceral anatomy suggests that these color-pattern and structural characters have operated as a very stable unit during phyletic changes.

Although metamorphosing specimens are still lacking, the available evidence places Leptocephalus acuticeps in the Avocettina section of the family Nemichthyidae. From the known adult characters of Nemichthys and Avocettina, one can predict that their larvae must differ in somite and tail-tip characters in precisely the way that L. acuticeps differs from larvae of Nemichthys. On present knowledge, acuticeps cannot be restricted to any single species, and it is probable that all species in the Avocettina group (including Labichthys and, tentatively, Avocettinops) have larvae of this general type. Thus, it seems best to treat acuticeps comprehensively as an informal group category that designates the kind of larva that characterizes the avocettinas as a whole. A more detailed understanding of differentiation in larval populations within the acuticeps complex must await not only the study of larger series of larvae but also a world-wide revisionary study of the adult avocettinas.

REFERENCES


Leptocephalus acuticeps—Orton


Some Aquatic Fungi Imperfecti from Hawaii

C. J. Anastasiou

Fresh-water hyphomycetes from tropical locations have been reported by Ingold (1956, 1958, 1959, 1960), Dixon (1959), Greathead (1961), Hudson (1961), Hudson and Ingold (1960), and Nilsson (1962). Reports from the Pacific area include California (Ranzoni, 1953), and Japan (Tubaki, 1957, 1960; Suzuki and Nimura, 1960a, b; and Nimura, 1960).

The Fungi Imperfecti reported in this paper were collected from streams in the Na Pali Kona Reserve on the island of Kauai, Hawaii, during August 1961. Collections were taken from the Kokee, Waineki, Elekiniki, Kauaikanina, and Kawaiok streams, and from roadside ditches. At that time the streams were full and foam and scum were abundant.

Most of the species reported here were identified from spores collected in foam and scum. Colonies developing on rotting leaves, collected from the same group of streams, confirmed the identification of many of these fungi. The extremely rich flora of Fungi Imperfecti included the following species:

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- Alatospora acuminata Ingold
- Anguillospora crassa Ingold
- Anguillospora flagellifera Ingold
- Articulospora tetracladia Ingold
- Articulospora inflata Ingold
- Campylospora chaetocladia Ranzoni
- Chaetospermum chaetosporum (Pat.) A. L. Smith and Ramsb.
- Clavariopsis aquatica De Wild.
- Lemnoniera aquatica De Wild.
- Lanulospora curvula Ingold
- Tetrachaetum elegans Ingold
- Tricladium angulatum Ingold
- Tricladium anomalum Ingold
- Tricladium gracile Ingold
- Tricladium splendens Ingold
- Triscelophorus monosporus Ingold
- Varicosporium elodeae Kegel

In addition to the above, vermiform spores similar to those of Anguillospora gigantea Ranzoni, A. pseudolongissima Ranzoni, Flagellospora curvula Ingold, and F. penicilliodes Ingold were common in scum and foam. However, these could not be identified with any degree of certainty since they did not develop on the leaf material observed. Monochaetia and Pestaloia spores were also very common in foam.

Several unidentified spore types were observed, but the most common one closely resembled spores of a possible species of Articulospora illustrated by Ingold (1958:111). At least 50 spores of this type were observed on two slides made from foam collected from Kokee Stream. Spore size, septation, and manner of articulation are as described by Ingold.

Leaves collected from the streams were plated out in about 1/4 inch of distilled water. After about 6 weeks, tetraradiate spores developed abundantly above the water surface. This fungus produced aleuriospores consisting of an elongate, septic main axis continuous with the aleurophore and with elongate secondary branches arising from the lower part of the main axis. Superficially they resemble spores produced by species of Triscelophorus (Petersen, 1962:131-134). However, on the basis of the type of conidiophore, the morphology of the main axis of the spore, the manner in which the appendages are produced, and the fact that there are always a few spores produced which lack appendages, I have decided to consider it a species of Dactylella.

Dactylella appendiculata sp. nov.

Fungus aquaticus; mycelium septatum, hyalini, ramosum; cellulae 8-65 × 1.5-4 μ; aleuriophori 50-400 × 1.5-4 μ, septati, hyalinii, simplices, summerti vel ex aqua emergentes; aleuriospori, apicati, hyalinii, plerumque e quatuor bracthiis, singillatiim producti; axis principalis 57-108 (r = 84) × 9.3-14.5 μ, ex 5-8 cellulis; brachia divergentia septata, orientia e secunda cellula axis principalis, 10-136 (r =
Aquatic Fungi Imperfecti from Hawaii—ANASTASIOU

Fig. 1. Dactylella appendiculata. a–b, Stages in the development of aleuriospores from curved spore primordia. i, Mature aleuriospore which developed from a curved spore primordium. j, Mature aleuriospore which developed from a straight spore primordium. k, Resting cells from agar culture.
PACIFIC
produced
with
agar.
Sporulation
mass
dominant
to
Fig.
form
ever,
of
riospores
main
distinctly
cell
the
CMI,
to
this
point
arising
August
204
submerged
10-136
87)
armed,
four
Dactylella
production
2
2-3.5
8
x
8-65
50-400
15-4
mu,
septate,
hyaline,
unbranched,
submerged
or
emerging
from
the
water;
aleuriospores
apical,
hyaline,
produced
singly,
usually
4-armed,
main
axis
57-108
(x = 84)
9.3-
14.5
mu,
of
5-8
cells;
divergent
arms
septate,
arising
from
the
second
cell
of
the
main
axis,
10-136
(x = 87)
2-3.5
mu,
constricted
at
the
point
of
origin;
resting
cells
in
branching
chains,
5-25
mu
diam.

HOLOTYPE:
Hawaii.
On
leaves
in
water
from
Kokoe
stream,
Na
Pali
Kona
Reserve,
Kauai,
August
30,
1961,
Anastasia
H47.
Transfers
of
this
holotype
have
been
deposited
at
ATCC,
CMI,
CBS,
and
DAOM.

Dactylella
appendiculata
is
characterized
by
the
production
of
aleuriospores
developing
one
to
four
determinate,
lateral
arms
from
the
second
cell
of
the
main
axis
(Fig. 1g-i,
Fig. 2c-f).
These
arms
are
formed
consecutively
from
the
apical
portion
of
the
second
cell.
In
other
species
of
Dactylella
(Drechsler,
1937:489,
493,
501)
germ
tubes
usually
arise
from
the
apical
portion
of
this
cell.
In
D. appendiculata
the
arms
are
distinctly
constricted
at
the
base
but
a
wall
does
not
appear
to
be
laid
down
at
this
point.
However,
septation
occurs
distally
in
the
arms.
The
main
axis
of
the
aleuriospore
develops
into
a
form
(Fig. 1j,
Fig. 2c)
characteristic
of
many
species
of
Dactylella
if
the
spore
primordium
is
initially
straight.
If
the
spore
primordium
is
curved,
the
main
axis
appears
as
in
Fig. 1i
and
Fig.
2d-f.
Fig. 1a-i
and
Fig.
2a
are
stages
in
the
development
of
spores
of
the
second
and
predominant
type.
Fig.
2b
is
a
stage
in
the
development
of
a
spore
of
the
first
type.

In
the
original
collection
conidiophores
were
produced
from
submerged
hyphae
and
emerged
to
about
200
mu
above
the
water
surface.
At
maturity,
the
spores
dropped
to
form
a
dense
mass
floating
on
the
surface
tension
membrane.
Sporulation
did
not
occur
in
pure
culture
on
agar.
However,
when
a
portion
of
the
colony
on
agar
is
submerged
in
water,
very
weak
sporulation
occurs
after
3
to
5
weeks'
icubation
at
room
temperature.
Increased
sporulation,
though
still
sparsely,
occur
when
a
rotting
leaf
is
sterilized
with
the
water
before
incubation.

Since
this
species
resembles
certain
predaceous
species
of
Dactylella,
it
was
cultured
in
water
containing
nematodes
and
rotifers.
No
predaceous
apparatus
was
formed,
whether
or
not
these
organisms
were
present.
No
improvement
in
sporulation
occurred
after
addition
of
nematodes,
but
when
water
containing
rotifers
and
other
microorganisms
was
added
spores
were
abundantly
produced
on
the
surface
of
leaves
in
the
culture.
Almost
all
spores
developed
on
short
aleuriospores
(up
to
150
mu)
and
were
completely
submerged
at
maturity.
All
of
these
developed
from
curved
spore
primordia.
Some
of
the
spores
produced
above
the
surface
of
the
water
developed
from
straight
spore
primordia.

Germination
of
aleuriospores
occurred
mainly
by
germ
tubes
from
the
apical
and
basal
cells
of
the
main
axis
as
well
as
from
any
cell
of
the
divergent
arms.
Germ
tubes
arising
from
the
main
axis
are
only
slightly
constricted
at
their
point
of
origin,
where
a
distinct
septum
was
usually
observed.
Germination
from
the
divergent
arms
is
normally
by
branching
rather
than
elongation
of
the
arms.

The
colony
on
MeYe
agar
(Benjamin,
1959:
322)
was
slimy
and
dull
white
in
color,
with
very
little
aerial
mycelium.
In
age,
branched
chains
of
yeastlike
resting
cells
were
produced
(Fig. 1k;
Fig. 2g).
Similar
resting
cells
developed
in
the
water
of
the
original
isolate
and
subsequent
transfers.

The
relationship
between
Dactylella
appendiculata
and
other
species
of
Dactylella
is
comparable
to
that
between
Campylospora
chaeto-
cladia
and
Tripopseudum.
In
spore
morphology,
C.
chaetocladia
differs
from
Tripopseudum
by
the
production
of
filiform
appendages
at
the
apex
of
the
arms.
Some
justification
for
placing
C.
chaetocladia
in
a
separate
genus
is
to
be
found
in
differences
in
conidiophores
and
spore
color
(Ingold
and
Cox,
1957:320;
Hughes,
1951:
22).
Such
differences
between
D. appendiculata
and
Dactylella
do
not
exist.
In
my
opinion
differences
in
habitat
and
modification
of
germ
tubes
to
form
spore
branches
do
not
constitute
sufficient
reason
for
placing
this
organism
in
a
genus
which
does
not
show
its
true
relationship.

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in
this
project
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by
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Committee
of
the
Faculty
of
Graduate
Studies
at
the
University
of
British
Columbia.
Fig. 2. *Dactylella appendiculata*. a–d: Stages in the development of aleuriospores from curved spore primordia. b, Two-celled stage in the development of an aleuriospore from a straight spore primordium. c, Mature aleuriospore from a straight spore primordium. e, f, Mature spores from curved spore primordia. g, Resting cells from water culture. X556.
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The Taxonomy of *Polysiphonia* in Hawaii

ERNANI G. MEÑEZ

ABSTRACT: An investigation of *Polysiphonia* collections from Oahu, Hawaii, Molokai, and Maui of the Hawaiian Islands has revealed the presence of seven species: *Polysiphonia mollis* Hook. & Harv., *Polysiphonia pulvinata* (Roth) J. Ag., *Polysiphonia subtilissima* Mont., *Polysiphonia ferulacea* Suhr., *Polysiphonia yonakuniensis* Segi, *Polysiphonia flabellulata* Harv., and *Polysiphonia rhizoidea* sp. nov. These seven species of *Polysiphonia* were recognized primarily by their morphological features.

Some characteristics of *Polysiphonia* which have not been previously used by monographers but which appear to be important criteria for delimiting specific entities are discussed. One of these is the presence of more than one secondary pit connection between adjacent pericentral cells, a condition present in *P. rhizoidea* and *P. yonakuniensis* but not in the other species mentioned above. The other is the presence of multicellular rhizoids, a condition which was observed only in *P. rhizoidea*. Previously, authors have accepted the rhizoids of *Polysiphonia* as being unicellular.

ALTHOUGH there are a number of published articles on the marine algae of Hawaii, none of them deals specifically or intensively with the taxonomy of *Polysiphonia*. Up to the present, only six species of *Polysiphonia* have been recorded in the literature as occurring in Hawaii: *Polysiphonia aquamara* Abbott, *Polysiphonia calothrix* Harv., *Polysiphonia ferulacea* Suhr., *Polysiphonia mollis* Hook. & Harv., *Polysiphonia polyphysa* Kuetz., and *Polysiphonia tongatensis* Harv.

With respect to the published records of these six species, reference may be made to the works of Chamberlain (1860), Falkenberg (1901), Tilden (1901), Lemmermann (1905), McCaughey (1918), Yendo (1918), Weber van Bosse (1923), Neal (1930), and Abbott (1947).

The objectives of the present study were to evaluate the validity of these taxa and to determine if additional species of *Polysiphonia* are represented in Hawaii. The species included in this study were recognized primarily by morphological features.

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MATERIALS AND METHODS

The collections of *Polysiphonia* in Dr. M. S. Dory’s herbarium (DUH); *Polysiphonia* collections deposited at the Bernice P. Bishop Museum (BISH) by I. Abbott, E. Bailey, J. Rock, D. Rogers, and J. Tilden; and my own collections around Oahu (M) were the materials used in this study.

A. Collection of the Biological Materials

As much area as possible was covered at every station. The materials collected were first placed in plastic bags and later transferred to wide-mouthed bottles filled with 10 per cent formalin.

B. Investigation of the Biological Materials in the Laboratory

Little difficulty was met in the preparation of the materials for the detailed studies. There were three types of preserved materials: old mounted dry specimens, materials preserved in formalin for several years, and fresh collections in 10 per cent formalin.

A drop of water was added to each of the old mounted specimens to make them soft enough to avoid damaging any structures when preparing samples for microscopic study. It was usually necessary to boil such dry specimens for a few minutes to restore the normal cell shape. On the other hand, the old specimens preserved in formalin did not need to be boiled but had to be stained to distinguish the pericentral cells, using 1 per cent aniline blue or 1 per cent safranin O. The newly collected materials were softened in sea water-formalin solution for 24-48 hours before examination.

A dozen or more slides of each collection were prepared. A few thallus fragments were taken from each collection and placed on one or more slides with a drop of 10 per cent glycerine solution.

For counting the number of pericentral cells the materials were either crushed on the slide or cross-sections were cut. Important characteristics of the different species were illustrated with a camera lucida. Measurements were made with an ocular micrometer.

THE GENUS *Polysiphonia*

The genus *Polysiphonia*, established by Greville in 1824, belongs to the family Rhodomelaceae in the Rhodophyta. According to Falkenberg (1901), *Polysiphonia* should include all those radially symmetrical members of the Rhodomelaceae in which (1) at least the ultimate branches are evidently polysiphonous, (2) most of the branches arise exogenously by a more or less diagonal division of subapical cells before these have cut off pericentral cells, (3) all branches are essentially similar and indeterminate, and (4) only one tetrarorangium is borne normally in each segment.

IMPORTANT TAXONOMIC FEATURES

A. Trichoblasts

Rosenvinge (1903) referred to the structure that other investigators have called "leaves" as "trichoblasts." Commonly, one trichoblast occurs on each segment. Hollenberg (1942) commented on the trichoblasts as being usually arranged spirally in a counter-clockwise direction toward the tip of the branch, looking at the branch from the apex. In the present paper this would be referred to as a right-hand spiral. Hollenberg also stated that the divergence of the trichoblasts in the spiral is relatively constant and usually bears some relation to the number of pericentral cells. The trichoblasts may be simple or forked, consisting of one to several segments of cells. They are usually present at or near the apices. Generally, they are deciduous, leaving conspicuous scar cells after they fall off.

B. Branches

In the Rhodomelaceae, Falkenberg (1901) distinguished two types of branches: (1) determinate branches, which do not ordinarily give rise to further branches, and (2) indeterminate branches, those of potentially unlimited growth. The branches are either of endogenous or exogenous origin. Branches arising after the pericentral cells have been formed are designated as "endogenous," whereas those formed before the formation of the pericentral cells are referred to as "exogenous." The branches
of all the *Polysiphonia* species described in this paper are exogenous.

Hollenberg (1942) described two types of exogenous branches: (1) normally exogenous branches, arising directly from the branch primordia, and (2) cicatrogenous branches, developing from the scar cells after the trichoblast has fallen off.

**C. Antheridia**

The antheridia usually occur as primary branches of the trichoblasts or may occur on the trichoblasts, covering the lower part of the latter. At the apex of each antheridium a sterile tip of one or more cells may be found. Each antheridium is usually supported at the base by a two-celled stalk.

**D. Cystocarps**

*Polysiphonia* cystocarps are very variable in shape. They are usually urceolate, ovate, or oblong and seem to be little used for systematic or taxonomic purposes.

**E. Rhizoids**

The rhizoids occur at the base of the thallus. While they may also be found on the axis above the thallus base they are never found near the thallus apex. The rhizoids may occur singly or several may be produced from a segment of the thallus. They arise as outgrowths from the proximal end or middle of the pericentral cells. They are commonly unicellular, but sometimes multicellular. Each may or may not be cut off by a cross-wall at its proximal end from the supporting pericentral cell. The tip of the rhizoid may be simple, digitate, or discoid.

**F. Pericentral Cells and Cortical Cells**

In the tetrasiphonous species of *Polysiphonia* (Segi, 1951), the number of pericentral cells is usually constant throughout the entire thallus, while in species with more than four siphons the number of pericentral cells may vary in the different parts of the thallus.

Cortical cells may be observed in some species. They are usually formed near the base of the thallus and arise from the pericentral cells. In these corticate species the rhizoids are produced from the cortical cells. All the *Polysiphonia* species described in this paper are uncorticated.

**Observations and Results**

*Polysiphonia ferulacea* Suhringar in J. Agardh, Spec. Alg. II:980, 1863

Figure 1, **A-E**

**Type:** From the Atlantic coast of Mexico, North America, and presumed to be in the Agardhian herbarium, University of Lund.

Thalli up to 5 cm in height, usually shorter.

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**Key to the Hawaiian Species of Polysiphonia**

1. Pericentral cells 4

2. Thalli chiefly erect; segments from as long as broad to 4 times as long as broad

3. Rhizoids cut off by a cross-wall from the proximal ends of the supporting pericentral cells

4. Thalli rarely longer than 1 cm; segments about as long as broad

5. Rhizoids multicellular; thalli less than 1 cm long; forming densely matted cushions

6. Pericentral cells 6; vegetative axes tapered

7. Pericentral cells 10–12; vegetative axes approximately of equal diameter throughout
Fig. 1. *Polysiphonia ferulacea* Suhr. A, Branch showing trichoblasts. B, Rhizoids with disklike and ramified tips. C, Branch showing the spiral arrangement of tetraspores. D, Apical portion of a branch showing an antheridial cluster. E, Branch showing a young cystocarp.
Polysiphonia in Hawaii—Meñez

Pericentral cells four, ecoricate. Base composed of a few rhizoids cut off from the proximal ends of the pericentral cells by a cross-wall. Rhizoids frequently one per segment, rarely four in one segment, in some cases robust and less than 1 cm long with disklike terminal ends, in other cases slender and more than 1 cm long with terminal ends ramified into irregularly digitate tips. Rhizoids 25–80 μ in diameter and up to 680 μ long. Vegetative axes about 100 μ in diameter near the apex and up to 546 μ in the basal portion. Segments about half as long as broad. Principal axes dichotomous, angles of dichotomy 40–100 degrees, branches 5–10 segments apart. Short branchlets slightly torulose and recurved. Commonly, some of the exogenous branches arise cicatrigenously. Trichoblasts occur at the branch apices and are 3–5 times forked, up to 780 μ long and 21 μ in diameter, with a robust basal cell about 47 μ broad. Scar cells small, often indistinct, irregularly disposed, one to several segments apart and usually arranged spirally in a ¼ divergence.

Tetrasporangia tetrahedral, 20–35 μ in diameter when mature, produced in the branchlets, one in each segment, arising in a spiral running in a right-hand direction, when the branch is viewed from the point where the oldest tetrasporangium is found and following then toward the branch tip.

Antheridal clusters subcylindrical, developed as primary branches of the trichoblasts, arising from a short stalk. The apex consists of one or two sterile cells enclosed in a thick cell wall.

Cystocarps subglobose to ovate, up to 360 μ in diameter at the widest portion and 470 μ in length, with a narrow opening at the distal end; produced irregularly on the ultimate branchlets.

Materials examined: G. Andrews—78 (BISH) & 79 (BISH), from Oahu, and one other with no number, in folder "M" (BISH), collected from Waialua, Oahu, 1876; E. Bailey—8 (BISH), from Wailuku, Maui; M. Doty—8141 (BISH, DUH), on concrete wing dam east of Young Women’s Christian Association (YWCA) Beach, Waikiki, Oahu, October 7, 1950; 8755 (BISH, DUH), on Sargassum devoid of leaves and blackened, collected at Ala Moana Park, Oahu, March 19, 1951; 10999 (BISH, DUH), afloat near Abbott’s yard at Laie, Oahu, January 17, 1954; 12439 (BISH, DUH), on reef flat in front of Ala Moana Park, Oahu, April 12, 1954; 12905 (DUH), stiff bristly form afloat at Kalama Park, Maui, July 26, 1955; 12982 (BISH, DUH), tufts on pavement in less than 6 ft of water and also on a red alga apparently belonging to the family Gigartinaeaceae outside of the breakwater at Maalaea, Maui, August 27, 1955; 13005 (DUH), outside of the breakwater at Maalaea, Maui, August 27, 1955; 17373 (BISH, DUH), on Sargassum polyphyllum J. Agardh near the beach close to the natatorium at Sans Souci, Waikiki, Oahu, November 20, 1955; E. Meñez—713 (BISH, DUH, M), epiphytic on Acanthobora spicifera J. Agardh (mixed with P. mollis), collected on a reef flat at Waikiki, Oahu, February 24, 1961; 740 (BISH, DUH, M), epiphytic on Acanthobora spicifera (mixed with P. mollis), collected on a sandy reef flat with limestone rocks in the Old Sugar Mill area, Kaaawa, Oahu, July 7, 1961; J. Rock—no numbers (BISH), collected from Waikiki, Oahu, May 8, 1908, April 1908, March 1908; D. Rogers—in envelope "R" (BISH), on Padina sp., Diamond Head, Oahu, May 21, 1946; B. Stone—3137 (DUH), afloat at Waikiki, Oahu, January 10, 1959; J. Tilden—405 (BISH, DUH, M), from Waikiki, Oahu, May 28, 1900 (labelled as being "P. colensoi Hook. & Harv.").


Figure 6, D–G

Type: Type specimen collected from shores of Cayenne, France.

Thalli tufted with decumbent branches, up to 10 cm in height. Pericentral cells four, ecoricate. Base composed of rhizoids arising as protrusions from the central part of the pericentral cells, usually one per segment, occasionally two, with simple and ramified tip, 15–32 μ in diameter and up to 680 μ long. Vegetative axes 30–105 μ in diameter. Segments as long as broad. Principal branchlets dichotomous, angles of dichotomy 20–90 degrees, branches 4–20 segments apart, with fewer intervening segments in the base. Commonly, some of the exogenous branches arise cicatrigenously. Occasionally, trichoblasts may be found at the tips and on the vegetative axes, usually one in each
Fig. 2. Polysiphonia flabellulata Harv. A–C, Branches showing young trichoblasts. D, Segment of a basal thallus showing a simple rhizoid. E, Branch showing the seriate arrangement of tetraspores (small arrows indicate the point of connection of the two branch-segments flanking E). F, Branch showing young cystocarps.
segment, twice forked, 5–10 μ in diameter and up to 450 μ long. Basal cells shorter than the rest of the cells above it. Scar cells rare and irregularly disposed.

Tetrasporangia not found in the materials at hand.

Antheridia not found in the materials at hand.

Cystocarps not found in the materials at hand.

**MATERIALS EXAMINED:** E. Meñez—710 (BISH, DUH, M), collected in about 3–4.5 ft water from the bank of Waipuhi Stream above Kamehameha Highway (towards the open sea on the sea side of the bridge coming from Kaneohe), Hauula, Oahu, February 24, 1961; 711 (BISH, DUH, M), collected in about 4.5–8 ft water from the bank of Waipuhi Stream at the mountain side of the bridge at Hauula, Oahu, February 24, 1961; 728a (BISH, DUH, M), on cement wall made with basalt rock along Waipuhi Stream inland from Kamehameha Highway, near Hauula School, Hauula, Oahu, May 13, 1961; 728b (BISH, DUH, M), on cement wall along ocean side of Waipuhi Stream near Hauula School, Hauula, Oahu, May 13, 1961.

*Polysiphonia mollis* Hooker and Harvey, Ner. Austr. 2, 8:43, 1847

Figure 3, A–G

**TYPE:** A collection by R. Gunn labelled "original sp." in the Harvey Herbarium, Trinity College, Dublin. Type specimen collected from Tasmania, "parasitical on larger algae."


Thalli tufted, up to 12 cm in height. Pericentral cells four, ecoricate. Base of thalli composed of numerous slender rhizoids cut off from the proximal ends of the pericentral cells by a cross-wall, mostly one per segment, with either simple or ramified terminal ends, 20–52 μ in diameter and up to 780 μ long. Vegetative axes about 50–105 μ in diameter near the apices and up to 210 μ in the base. Segments 2–4 times as long as broad. Principal axes dichotomous, angles of dichotomies not more than 45 degrees and 3–14 segments apart, with fewer intervening segments near the apices. Trichoblasts 2 or 3 times forked, arranged in a right-hand spiral on the axis occurring one on each segment, up to 130 μ in length, attenuated towards the apex, basal cell robust and about 10 μ in diameter and much shorter than the rest of the segments above it. Scar cells one on each segment, produced near the apices, and spiralling to the right in a ⅛ divergence.

Tetrasporangia 50–115 μ in diameter, tetrahedral, globose, produced near the apices in a spiral running in a right-hand direction, when the branch is viewed from the point where the oldest tetrasporangium is found and following then toward the branch tip. Antheridial clusters borne as primary branches of the trichoblasts at the apex.

Cystocarps subglobose, stalked, on a segment of 2–4 pericentral cells, 250 μ high and 160–200 μ in diameter.

**MATERIALS EXAMINED:** I. Abbott—657 (BISH, DUH), collected from Ualapue Pond, Molokai, August 29, 1944 (labelled *P. aquamarina*); 1763 (BISH), collected from Kupeke Pond, Molokai, August 1944 (labelled *P. aquamarina*); 1767 (BISH), collected from Maupala Pond, Molokai, August 25, 1944 (labelled *P. aquamarina*); G. Andrews—49 to 52 and 79, in folder "L" (BISH), collected from Oahu; E. Bailey—in folders "K" (BISH) and "E" (BISH) without numbers, collected from Oahu, 1876; M. Doty—8817 (BISH, DUH), on rocks at 0.0 level in mud on north side of pier of Coconut Island Hotel on shore at Kaneohe Bay, Oahu, April 22, 1951; 12386 (BISH, DUH), on pond connection with muddy bottom, Coconut Island, Kaneohe Bay, Oahu, February 5, 1954; 12389 (DUH), on pond drain, Coconut Island, Kaneohe Bay, Oahu, February 5, 1954; 12684 (BISH, DUH), from a muddy area at Keehi Lagoon, Oahu, December 30, 1954; 12689 (BISH, DUH), Keehi Lagoon, airport side of the largest island (and that island formerly called Mokaua) on Diamond Head side of the runways, Oahu, December 30, 1954; 13078 (BISH, DUH),
Fig. 3. *Polysiphonia mollis* Hook. & Harv. *A*, Segment of a basal thallus showing a simple and a digitate-tipped rhizoid. *B*, A vegetative branch showing young trichoblasts. *C*, A vegetative branch. *D*, *E*, Branches showing young antheridial clusters. *F*, Branch showing the spiral arrangement of tetraspores. *G*, Branch showing a mature cystocarp.
Polysiphonia in Hawaii—MEÑEZ

collected from muddy shore of Round Pond at Ewa end of Ala Moana Park, Oahu, December 11, 1955; 17161 (BISH, DUH), on the new 1950 flow material at Hookena, Hawaii, January 29, 1955; 17213 (DUH), American Legion Post, Banyan Park, Hilo, Hawaii, February 2, 1953; E. MEÑEZ—701 (BISH, DUH, M), collected from a sandy-muddy place, on limestone rocks in about 2–4 inches of water continuously flowing at a slow rate, Maunalua Beach area, Oahu, January 29, 1961; 702 (BISH, DUH, M), collected on limestone rocks in about 5–10 inches of water, in a small pool with standing water which is muddy with a little sand, Maunalua Beach area, Oahu, January 29, 1961; 703 (BISH, DUH, M), collected on limestone rocks near the edge of the sandy-muddy shoreline with debris and a few dead animal corals, Maunalua Beach, Oahu, January 29, 1961; 704 (DUH), collected on basalt rocks just below the wall of a pond with turbid water and muddy bottom, Kuapa Pond, in the vicinity of Koko Head, Oahu, January 29, 1961; 705 (BISH, DUH, M), habitat same as 703, Maunalua Beach, Oahu, February 5, 1961; 712 (BISH, DUH, M), on cement blocks in intertidal level above high-tide line, Sans Souci Beach, Waikiki, Oahu, February 2, 1961; 713 (BISH, DUH, M), epiphytic on Acanthobora spicifera (mixed with P. farulacea), collected on a reef flat at Waikiki, Oahu, February 24, 1961; 725 (BISH, DUH, M), collected on concrete block and found growing with other algae near the bridge facing Diamond Head side of Ala Moana Park, Oahu, May 13, 1961; 730 (BISH, DUH, M), algae in thin tufts on limestone rocks covered with mud on banks of Floating Dry Dock area, West Loch of Pearl Harbor, Oahu, May 21, 1961; 731 (BISH, DUH, M), on limestone rocks covered by barnacles and mud, about 500 yards away from collecting area at 730, Pearl Harbor, Oahu, May 21, 1961; 732 (BISH, DUH, M), on mud-covered oysters, wooden poles, and galvanized iron in a tilapia and mullet fishpond at Kahua Ranch area, Ewa, Oahu, May 21, 1961; 739 (BISH, DUH, M), on top of a concrete block about 1 ft above high-tide line under the bridge at Ala Moana Park, Oahu, May 5, 1961; 740 (BISH, DUH, M), epiphytic on Acanthobora spicifera on limestone rocks, on a sandy flat near the Old Sugar Mill area, Kamehameha Highway, near Kaaawa, Oahu, July 7, 1961; 758 (BISH, DUH, M), from a muddy area at Keeki Lagoon, Oahu, February 27, 1961; J. Rock—two collections (BISH) with no numbers, one collected from Sand Island, Oahu, June 1, 1908, and another collected from Honolulu waterfront, Oahu, May 30, 1908.

Polysiphonia pulvinata (Roth) J. Agardh, Alg. Maris Medit. et Adriat. 124, 1842

Figure 4, A–D

TYPE: Type specimen presumed to be in the Agardhian herbarium, University of Lund.


Thalli tufted, with decumbent branches, up to 1 cm in height. Pericentral cells four, ecoritate. Base composed of rhizoids cut off from the proximal ends of the pericentral cells by a cross-wall. Diameter of rhizoids up to 25 μ with a length of about 625 μ. Terminal ends simple or ramified, sometimes attached to other filaments or branches, occurring singly, occasionally two or three in each segment. Vegetative axes 78–130 μ in diameter near the apices and up to 210 μ in the base. Segments approximately as long as broad. Principal axes dichotomous, angles of dichotomy not more than 45 degrees. Ultimate branchlets of tetrasperangial plants turulose, attenuated or narrowed towards the base. Cicatrogenous branches common, especially on the basal portions. Trichoblasts numerous at the apices, incurred in immature stages, 500 μ in length and 55 μ in diameter with rounded tips, forked 1–3 times, and arranged spirally in ⅓ divergence, deciduous. Basal cell shorter than the rest of the segments. Scar cells one in every segment, arising in a right-hand spiral, with ⅓ divergence.

Tetrasperangia 35–55 μ in diameter, tetrahedral, globose, produced one in each segment of the axes near the apex, arising in a spiral running in a right-hand direction, when the branch is viewed from the point where the oldest tetrasperangium is found and following then toward the branch tip.
Fig. 4. *Polysiphonia pulvinata* J. Arg. A, Basal segment of a thallus showing a rhizoid with ramified tip attached to another branch. B, Segment of a basal thallus showing a simple rhizoid. C, A branch showing young trichoblasts. D, Thallus showing the spiral arrangement of the tetraspores.
Antheridia and cystocarps were not found in the materials at hand.

**MATERIALS EXAMINED:** M. Doty—8882 (BISH, DUH), collected on exposed shoulder of lava, Halona, Oahu, May 21, 1951; 12384 (DUH), washed in at Beach Laboratory, Waikiki, Oahu, February 6, 1954; 13549 (DUH), on boulders in sand between low-tide ripples on beach flat and the exposed rock to the east, Kumim, Molokai, December 29, 1953; 17222 (BISH, DUH), collected at Punalu‘u Bay, Hawaii, January 29, 1953; E. Meñez—741 (BISH, DUH, M), collected on limestone rocks in sandy bottom, Mokuleia, Oahu, August 7, 1961.

**Polysiphonia rhizoidea** sp. nov.

Figure 5, A–H

**TYPE:** Doty 19256, on top of prehistoric lava flow dike 6–8 m above high-tide line, about 50 ft east of the 1955 lava flow at Keekee, Puna, Hawaii, December 23, 1959. This number includes antheridal and cystocarpic thalli, of which I designate the antheridal material as the type specimen.

Thalli parvi dense intricati in massos usque ad 1 cm alto, cellulae pericentrales 8–10 cellulis singulis eorticatis cum 1–3 connectivis aperturalis; basis rhizoidalis rhizoideis 15–55 μ diametro et usque ad 550 μ longis cum partitionis in latere proximale celluli pericentraei; apicibus simplicibus vel disciformibus; ramificationibus nullis vel raribus. Segmentis singulis thallorum unicum rhizoideam emitentis; segmentis alteris non rhizoidiferis. Axes vegetativi 52–115 μ diametro, ramis primariis prostratis inconspicuis, ramis secundariis dichotomis vel pseudo-dichotomis (angulis ramificationii 45°–90°); ramulis attenuatis, fere paulo curvatis vel raro recurvatis, segmentis in longitudine quam latitudine 1.5–2 X excedens; ramulis 2–18 segmentis interventanuis. Trichoblastis subapicalis 2–3 furcatis, 21 μ diametro et 625 μ longis, segmentis apicalibus fere quam segmentis basaliis longioribus, pedicellis unicellulatis 36 μ diametro. Tetrasporangii tetrahedrals, globosis, irregulariter dispositis, pseudo-spiraliter vel lineariter seriatis, usque 66 μ diametro; antheriae aggregatis, apicalis, elongatis vel cylindricis, 52 μ diametro, usque 280 μ longis, fere solitariis rare binis in pedicellum unicum. Cystocarpi globosis vel spheroidalis, breve-pedicellatis, 234 μ diametro et 286 μ altis, aperturis anterioris 57 μ latis; carposporiis clavatis, 68 μ longis et 26 μ diametro.

Thalli forming low, densely matted cushions and not more than 1 cm in height. Pericentral cells 8–10, each with 1–3 secondary pit connections, ecorticate. Base composed of multicellular rhizoids cut off by a cross-wall from the proximal ends of the pericentral cells with simple terminal ends or forming disklike structures, rarely ramified with several short cells, occurring no more than one per segment and several segments apart, 15–55 μ in diameter and up to 550 μ long. Vegetative axes 52–115 μ in diameter, branchlets attenuated, slightly curved, in rare occasions hooked, arising from an inconspicuous primary prostrate branch. Principal axes dichotomous or pseudodichotomous, angle of branching 45–90 degrees, rarely more. Segments about as long as broad, branches 2–18 segments apart. Trichoblasts developed near the apex, rare, 2 or 3 times forked, 21 μ in diameter and 625 μ long, with a short, robust one-celled stalk 36 μ in diameter. Basal trichoblast segments generally shorter than those near the apices. Scar cells rare or wanting.

Tetrasporangii 52–78 μ, tetrahedral, globose, arranged irregularly in the axes, sometimes appearing spiralled in a right-hand direction and in other cases in straight series, up to 66 μ in diameter.

Elongate or cylindrical antheridial clusters, 52 μ in diameter and up to 280 μ long, occurring near the apices of the branches. Some seem to arise as primary branches of the trichoblasts but generally are independent of the latter.

Cystocarps globose or almost spherical, shortly pedicellate, 234 μ in diameter and 286 μ high. Opening at the anterior end narrow, 57 μ. Carposporae clavate, 68 μ long and 26 μ in diameter.

**MATERIALS EXAMINED:** M. Doty—13076 (BISH, DUH, M), red-brown to maroon, velvety cushions of an extended sort around high-tide edge of a brackish fishpond at Anaehoomalu, Kona, Hawaii, November 15, 1952; 19256 (BISH, DUH), on top of prehistoric lava flow dike 6–8 m above high-tide line, about 50 ft east of the 1955 lava flow at Keekee, Puna, Hawaii,
Fig. 5. Polysiphonia rhizoidea sp. nov. A, A vegetative branch. B, Branch showing a trichoblast. C, Basal segment of a thallus showing a multicellular rhizoid with a disklike tip. D, A multicellular rhizoid with a simple tip. E, Branch showing a young and a mature antheridium. F, Branch with six mature antheridia. G, Branch showing a mature cystocarp. H, Branch with tetraspores.
December 23, 1959; 19354 (BISH, DUH), in crevices about 30 ft above high-tide line, in shaded spray-zone situations, 1/4 mile east of 1955 lava flow at Keekee, Puna, Hawaii, September 8, 1960; 19357 (BISH, DUH), extensive in spray zone on north facing consolidated cinder at Onomea Cove, Hawaii, September 13, 1960; 19359 (BISH, DUH), spray-zone pahohoe at Kings Landing, Panaewa, Hawaii, September 13, 1960; E. Meñez—733 (BISH, DUH, M), on moist clayish soil occurring in densely matted cushions in fishpond area at Kahua Ranch in Ewa, Oahu, May 21, 1961.

This species was found on solidified pahohoe lava, on moist clayish soil, and binding sand in the bottom of a shaded crevice in pahohoe. The materials from the exposed condition were collected from a hole on top of a lava-flow dike 6–8 m above high-tide line. On the other hand, the species found on moist clayish soil was collected from the bank of a fishpond, where grasses and other plants grew. These outgrowths were situated in such a way that they covered the area of collection almost completely from sunlight. The first and third habitats mentioned above are located in a spray-zone situation and are not exposed to any degree of wave action except the constant spray of water. On the other hand, the second habitat is entirely devoid of spray. The only supply of water comes from rain and the rise of probably brackish water in the pond. Under all these conditions, the thalli form densely matted cushions.

In the exposed situation, the materials were reddish-purple, whereas the materials in the shaded situation were dull in color. Those in the shaded crevices were slightly dark green in their basal portions but had purplish apices. Those on moist clayish soil were almost as brown as the substratum from which they had been collected.

This species is close to Polysiphonia howei Hollenberg from Nassau, Bahamas. Examination of Dr. Doty’s collection of Polysiphonia howei (No. 19754) from the Bahamas revealed that the general characteristics and origin of the rhizoids, the curved aspect of some branchlets, the offset position of the pericentral cells in the successive tiers, the presence of 1–3 secondary pit connections, the short basal segments of the trichoblasts, all closely resemble Polysiphonia rhizoidea sp. nov. It differs from the latter species in that 1–3 rhizoids occur in a segment, trichoblasts are 2 or 3 times forked and tapered towards the tip, vegetative axes are 55–143 μ in diameter, and pericentral cells number 8–14. Polysiphonia howei (No. 19754) was a sterile specimen.

Polysiphonia flabellulata Harvey, Proc. Am. Acad. IV:330, 1859

Figure 2, A–F

TYPE: From Japan. The type specimen is presumed to be in the Harvey Herbarium, Trinity College, Dublin.

Thalli tufted, up to 2 cm in height. Pericentral cells six, ecorticate. Base composed of simple and digitate rhizoids produced from the proximal ends of the pericentral cells. Rhizoids usually one per segment but occasionally four in a segment, whereupon each pericentral cell of the segment produces one rhizoid with a diameter of about 10 μ and a length of 835 μ. Vegetative axes 52–156 μ in diameter, with branches irregularly produced at intervals of 10–20, rarely fewer segments apart. Segments as long as broad, particularly in the ultimate branchlets. Principal axes dichotomous, angles of dichotomy 10–45 degrees. Trichoblasts produced near the apices, 2 or 3 times forked, diameter 6–12 μ, about 55 μ in length, segments as long as broad. Scar cells rare or wanting and irregularly disposed.

Tetrasporangia 45–60 μ in diameter, tetrahedral, oblong, 25 μ in diameter and arranged in a straight series.

Antheridial branches produced as primary branches of the trichoblasts.

Cystocarps subglobose, developed irregularly on the primary and secondary axes, about 160 μ in diameter at the widest portion and 210 μ in length.

MATERIAL EXAMINED: M. Doty—10820 (DUH), Kaneohe Bay, Oahu, October 10, 1953.


Figure 6, A–C

TYPE: Yonakuni Island, Loochoo Islands (T.
Polysiphonia in Hawaii—Meñez

Tanaka). Specimen presumed to be in Dr. Yukio Yamada's herbarium at Hokkaido University, Sapporo, Japan.

Thalli up to 2 cm in height, forming densely erect branches arising from a prostrate system. Pericentral cells 10–12, each with one to several secondary pit connections, ecorticate. Base composed of rhizoids cut off by a cross-wall from the proximal ends of the pericentral cells, occasionally branched. Terminal ends disklike when in contact with other filaments or branches of Polysiphonia and other algae and simple when free; diameter about 22 μ and up to 575 μ long. Vegetative axes more or less equal in diameter from the base to the segment near the apex. Branches 2–10 segments apart, rarely with as many as 20 intervening segments. Ultimate branchlets slightly recurved. Principal axes irregularly dichotomous, angle of branching 40–80 degrees. Cicatrigenous branches common, particularly on the creeping portion and occasionally on the erect axes. Trichoblasts developed on the axes and spicules, 2–5 times forked, 10–32 μ in diameter and 625 μ long. The first two segments of the base shorter than the rest, swollen in appearance in comparison to the upper segments, the cells of which have parallel walls. Scar cells small, occurring irregularly at intervals of two or three segments, with ½ to ¼ of a spiral turn in a right-hand direction between them.

Tetrasporangia, antheridia, and cystocarps were not found in the materials at hand.

MATERIALS EXAMINED: M. Doty—10816 (BISH, DUH), collected just below the upper edge of a nip, forming dense turf patches 3 × 2 × 5 inches, Kapoho Point, Kailua, Oahu, October 10, 1953; J. Tilden—508 (BISH, DUH), collected at Laie Point, Koolauloa, Oahu, June 16, 1900 (labelled P. calothrix); 602 (DUH), collected at Laie Point, Koolauloa, Oahu, June 1900 (labelled P. calothrix).

DISCUSSION

Of the six species of Polysiphonia previously recorded as occurring in the Hawaiian Islands, I examined exsiccate materials of P. aquamara, P. mollis, P. calothrix, and P. ferulacea deposited in the herbarium of the B. P. Bishop Museum. I was not able to find specimens of the other two species reported from Hawaii: P. polyphysa and P. tongatensis.

A specimen in Tilden's collection labelled "Polysiphonia colensoi Hook. & Harv.," deposited at the Bishop Museum, seems to agree well with the description of P. ferulacea and therefore is cited here as such. It was used as basis for Tilden's report of P. colensoi for Hawaii. Though unable to locate the type of Polysiphonia aquamara Abbott, and basing my observations entirely on the materials of this species sent to me by Dr. I. A. Abbott and on two other specimens deposited by her in the Bishop Museum, I conclude that these three collections of P. aquamara are not specifically distinct from the species I am calling here P. mollis. They agree well with the description of P. mollis in this paper and are therefore cited here as such.

A personal communication (Abbott, December 15, 1961) indicated her records show that she deposited the type specimen (her No. 1555) of P. aquamara in the Bishop Museum. According to Miss M. Neal, curator of the herbarium, and Mr. E. H. Bryan, curator of collections at the Museum, no record exists of this specimen having been received.

Re-examination of Tilden's collections of P. calothrix (Nos. 508, 602) revealed that they are not distinct from P. yonakuniensis as this species is described in this paper. Comparisons of the descriptions for P. calothrix and P. yonakuniensis led the author to regard Tilden's collection of P. calothrix from Hawaii as a form of P. yonakuniensis. The only satisfactory disposition, therefore, seems to be the citing of these collections (Tilden Nos. 508, 602) as P. yonakuniensis.

The seven species of Polysiphonia described in this work were recognized primarily by their morphological features using Hollenberg's (1942) criteria for distinguishing specific entities in Polysiphonia. In addition, two other characteristics of Polysiphonia, which have not been previously used by monographers but which appear to be important criteria for delimiting the Hawaiian species of Polysiphonia, have been utilized. One is the presence of more than one secondary pit connection between adjacent pericentral cells, a condition present in P. rhizoides and P. yonakuniensis but not in the other species...
included in this study. The other characteristic is the presence of multicellular rhizoids. Previously, insofar as I know, all authors have accepted the rhizoids of Polysiphonia as being unicellular. Multicellular rhizoids were observed only in P. rhizoidea.

REFERENCES


Generalized Titanomagnetite in Hawaiian Volcanic Rocks

TAKASHI KATSURA

ABSTRACT: A ferromagnetic oxide mineral with spinel structure was separated from Hawaiian volcanic rocks ranging from basalt to trachyte. The chemical compositions of all the specimens have been arranged on an oxygen reaction line, and can safely be interpreted as the result of a process of either oxidation or reduction of material with composition on or near this line. In the trachyte the mineral was found to be highly oxidized titanomagnemit. The composition of Hawaiian titanomagnetites is compared with that of titanomagnetites found in Japanese volcanic rocks belonging to the calc-alkali rock series.

It is well known that there are two kinds of ferromagnetic oxide minerals in igneous rocks, one with spinel structure and the other rhombohedral. Many investigators have studied the chemical composition, magnetism, and stability against heat of these two mineral series. In addition, phase equilibria of the system Fe-Ti-O related to the ferromagnetic minerals found in igneous rocks have been studied by Webster and Bright (1961), MacChesney and Muan (1959), and Taylor (1961) at fairly high temperatures in order to interpret the stability relationship between temperature and oxygen partial pressure at a total pressure of 1 atmosphere. The studies showed that the extremely oxidized titanomagnetite which is usually called titanomaghemite, or γ-phase, is not stable at temperatures above 1000° C, and seems to be unstable even below 1000° because the range of the solid solution field of magnetite in the system Fe-Ti-O decreases with decreasing temperature, as shown by the experimental results of Darken and Gurry (1946), Webster and Bright (1961), and Taylor (1961). In spite of this, there are a number of known occurrences of titanomaghemite in igneous rocks, sometimes with titanomagnetite and sometimes with neither titanomagnetite nor any other phase of the solid solution Fe₃O₅-FeTiO₃. In Japan, this was found to be true predominantly in alkali-rich basalts (Katsura and Kushiro, 1961).

Recent work by Macdonald and Katsura has shown that a large proportion of Hawaiian volcanic rocks are either basalt free from olivine (tholeiite basalt) or olivine-bearing tholeiite. At most 5% consist of alkali-rich types—alkali-olivine basalt, nepheline-bearing basalt, mugearite, hawaiite (as defined by Macdonald, 1960), and trachyte. In almost all cases ferric iron was more abundant in such alkali-rich types than in tholeiite, though ferric iron is generally fixed as magnetite rather than hematite. The interpretation of petrological relationships between these two types of rocks is not yet settled, but it is interesting to study the spinel-type minerals in comparison with those found in Japanese volcanic rocks, especially in Japanese alkali-olivine basalts.

By generalized titanomagnetite is meant the ferromagnetic oxide mineral with spinel structure, essentially composed of FeO, Fe₂O₃, and TiO₂, disregarding vacancies in its unit cell. If there are a large number of vacancies, as in the case of γ-hematite, we call the mineral titanomaghemite. The term titanomagnetite will be used in this paper for the mineral of stoichiometric composition, or near it.

Acknowledgments. The writer wishes to express his thanks to Dr. Gordon A. Macdonald, University of Hawaii, for encouragement when the writer was a staff member of the Hawaii Institute of Geophysics. The chemical analyses in Table 1 were made in the laboratories of the University of Hawaii under National Science
### Chemical Composition of Rocks From Which Generalized Titanomagnetites Were Separated

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### Normative Minerals

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**TABLE 1**

PACIFIC SCIENCE, Vol. XVIII, April 1964
Foundation grant G-11319 for geochemical investigations of Hawaiian lavas.

His thanks are also expressed to Dr. E. F. Osborn and Dr. A. Muan, of the Pennsylvania State University, for their kind permission to pursue the present work at Pennsylvania State University. Mr. C. O. Ingemells kindly gave permission to use the laboratory of chemical analysis at Pennsylvania State University. Dr. J. W. Greig, visiting professor at Pennsylvania State University, kindly prepared the polished sections of ferromagnetic mineral fractions separated from the rocks. Dr. I. Kushiro, of the University of Tokyo, polished the rocks to identify the presence of hematite. The writer wishes to express his deep thanks to those persons who gave him many kindnesses.

SAMPLES

About 80 samples of Hawaiian volcanic rocks were examined under the microscope to determine the grain size of the opaque mineral. In general, the grains of opaque mineral in the tholeiites were so small that it was a really difficult problem to obtain a pure separation of it from the coexisting silicate minerals. An attempt was made to separate it as purely as possible by applying the same technique as that described in a previous paper (Akimoto and Katsura, 1959). The purity of the separated ferromagnetic fraction attained was only 70% by weight in the case of sample 12 (Tables 1, 2), which may represent the tholeiite type, but the coexisting silicates consisted of felsic minerals. Therefore, when we concentrate our attention on the great difference in composition which generally exists between titanomagnetite and titanomaghemite, there may be no need to be concerned over any significant divergence from the true picture of the essential composition of the ferromagnetic minerals based on the three major components, FeO, Fe₂O₃, and TiO₂.

In contrast, it was easy to separate the opaque mineral in alkali-rich rocks when no hematite was present. The purity of the ferromagnetic fraction separated was without exception greater than 90% (the sum of FeO, Fe₂O₃, and TiO₂).

The X-ray diffraction method was used to check whether or not the separated fraction consisted of spinel. Microscopic examination of polished sections was made to identify the exsolved rhombohedral phase in titanomagnetite. In the present study only the ferromagnetic fraction that was shown by X-ray to have spinel structure was used.

Brief remarks on the volcanic rocks from which the generalized titanomagnetite was separated are given below, and their chemical compositions are given in Table 1.

No. 1. Alkali-rich type; gabbro vein cutting massive hawaiite valley-filling lava flow at Kaena Quarry, upper Waianae series, Oahu. The sum of the normative magnetite and ilmenite is about 21% (see Table 1), and the amount of ferromagnetic fraction actually separated was 18.5% by weight.

No. 2. The advanced stage of tholeiite differentiation, according to Tilley (1950); hypersthene dolerite with quartz, Palolo Quarry, Oahu. The rocks in the Palolo Quarry are somewhat complicated, and sometimes needle-like hematite is found in cavities. In the present sample a small amount of hematite was present.

No. 3. Alkali-rich type; hawaiite containing numerous flakes of dark mica, in quarry 1 mile north of Paauilo, Laupahoehoe series, Mauna Kea, Hawaii.

No. 4. Tholeiite type; reheated picrite-basalt with new hypersthene, block ejected during 1924 explosions of Kilauea, Hawaii, the same as a sample studied by Tilley (1950).

No. 5. Alkali-rich type; nepheline basalt, Kalaeo road cut, Kauai.

No. 6. Alkali-rich type; trachyte, Puu Koae dome, Honolulu series, West Maui.

No. 7. Alkali-rich type, trachyte, near the base of Ukumehame dome on west wall of Ukumehame Canyon, Honolulu series, West Maui.

No. 8. Alkali-rich type; mugearite, in highway cut at McGregor Point, Honolulu series, West Maui.

No. 9. Alkali-rich type; hawaiite containing abundant dark mica, in quarry at Keanokolu road, Laupahoehoe series, Mauna Kea, Hawaii.

No. 10. Tholeiite type; massive pahoehoe, in shallow gulch running up the face of Nanakuli Valley, Waianae Range, Oahu.

No. 11. Alkali-rich type; massive hawaiite, valley-filling flow at the same locality as No. 1.

No. 12. Tholeiite type; olivine basalt, near highway 1.4 miles south of Volcano Observa-
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<tr>
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<td>12.58</td>
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<td>22.20</td>
<td>20.59</td>
<td>25.78</td>
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</tr>
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</table>

**CALCULATED WEIGHT %**

| **FeO**  | 41.55 | 40.13 | 50.71 | 55.18 | 55.12 | 31.00 | 17.82 | 57.86 | 32.62 | 49.57 | 52.21 | 58.98 | 42.36 |
| **R₂O₃** | 26.59 | 34.82 | 25.70 | 28.06 | 19.38 | 38.15 | 58.37 | 16.63 | 37.59 | 25.60 | 18.59 | 17.96 | 31.75 |
| **TiO₂**  | 31.86 | 25.05 | 23.59 | 16.76 | 25.50 | 30.85 | 23.81 | 25.52 | 29.79 | 24.83 | 29.20 | 23.06 | 25.89 |

**MOLE RATIO**

| **Fe/(Fe+Ti)**_average | 0.748  | 0.841  | 0.812  | 0.869  | 0.786  | 0.777  | 0.850  | 0.781  | 0.850  | 0.802  | 0.754  | 0.805  | 0.803  |


| **lattice parameter (Å)** | (8.39) |
|                          |       |       |       |       |       |       |       |       |       |       |       |       |
Generalized Titanomagnetite in Hawaii—KATSURA

RESULTS AND DISCUSSION

1. Composition

Table 2 shows the chemical composition of the generalized titanomagnetite, and Figure 1 is a ternary diagram based on the components FeO, Fe₂O₃, and TiO₂. In Figure 1 a line, A–B, indicates the oxygen reaction line when material of composition A is oxidized to a final composition B. In a previous work, Katsura, Kushiro, Akimoto, Walker, and Sherman (1962) pointed out that the Hawaiian titaniferous ferruginous latosol enriched in iron and titanium has originated from titanomagnetite in volcanic rocks, and deduced the original composition of titanomagnetite from which a latosol of Naiwa type on the island of Kauai must have been formed. The chemical composition of this titanomagnetite lies just on the oxidation line A–B.

It is clear from Figure 1 that the compositions of titanomagnetite and titanomaghemite in Hawaiian volcanic rocks lie near the line A–B; and also we realize that the compositions of numbers 9, 13, and 7, which deviate somewhat from the line, represent the typical titanomaghemite studied by Basta (1959), and Katsura and Kushiro (1961).

In a series of Hawaiian volcanic rocks of alkali-rich type, the compositions of the generalized titanomagnetites are safely interpreted as resulting from either oxidation or reduction of material of a composition on or near the line A–B. In detail, for instance, number 1 is an oxidized phase of number 11, both rocks belonging to the upper Waianae series on Oahu; and number 8 is a reduced phase of number 6, both belonging to the Honolua series on West Maui.

Titanomagnetite separated from the reheated picrite basalt contained a significant amount of chromium, as shown in Table 2. In addition to this, according to Ramdohr the opaque mineral in this rock is surrounded by magnesioferrite. Thus, the titanomagnetite in the reheated basalt is much different in its constituents from that in common Hawaiian basalts.

It should be noted again, though already pointed out in this paper, that the generalized titanomagnetite is extremely oxidized to form typical titanomaghemite in the trachyte (No. 6) and hawaiite (No. 9), in which neither
titanomagnetite nor hematite were visible as independent phases under the microscope. Taking into consideration the thermodynamic equilibrium of the system, titanomaghemite in these rocks might be produced under a critical environment. If we postulate a fixed temperature and oxygen partial pressure, then the composition represented by the three components should also be fixed at the standard state. However, the study of stability relations did not reveal that titanomaghemite is experimentally stable at any temperature at a total pressure of 1 atmosphere.

2. Comparison of Composition of Generalized Titanomagnetite with Japanese Calc-Alkali Rocks

Recently, Akimoto and Katsura (1959) have studied the generalized titanomagnetite in Japanese volcanic rocks. From the data of analyzed specimens, we are able to pick out the titanomagnetics in a typical calc-alkali rock series ranging from basalt to rhyolite, and plot their compositions on the ternary diagram (Fig. 1).

As will be seen in Figure 1, the compositions of titanomagnetics in Japanese calc-alkali rocks are arranged near the Fe₂O₄-Fe₇TiO₄ join, though there is some deviation from this line. Titanium content, in general, decreases with increasing differentiation. Thus, we find 20% TiO₂ in basalt, and 5% TiO₂ in rhyolite. In contrast, the generalized titanomagnetics in Hawaiian alkali-rich rocks are arranged nearly on the oxidation line, A-B. Of course, even in the Japanese calc-alkali rocks the titanomagnetite is sometimes replaced by titanomaghemite, as described by Katsura and Kushiro (1961). Nevertheless, we were unable to find titanomaghemite as an extremely oxidized phase, as we did in Hawaiian trachyte and hawaiite.

Typical titanomaghemites were found predominantly in alkali-rich olivine basalt, such as olivine analcite basalt from Atumi, and quartz-bearing olivine-titanaugite dolerite from Kingoshi, Japan. The titanomaghemite found in Japan possesses almost the same composition as that of samples number 6 and 9 of this paper (Table 1). In consideration of this, titanomaghemite seems to be more stable in alkali-rich rocks than in rocks of the calc-alkali series, regardless of the rock province in which they occur.

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Recent Observations on Neck Extensions in Folliculinids (Protozoa)

DONALD C. MATTHEWS

Despite species variations, the process of folliculinid lorica formation is fundamentally similar (Penard, 1919; Andrews, 1923; Fauré-Fremiet, 1932; Dewey, 1939; and Das, 1947). In all a motile, nonfeeding stage becomes attached, secretes a sac and neck, and gradually metamorphoses into a sessile feeding stage characterized by peristomal lobes.

Although in certain well-established colonies restrictive attachment areas may modify sac length, breadth, and height, modifications in neck length and number of spiral whorls seem not to be thus affected (Matthews, 1963). Despite the fact that certain folliculinids with poorly developed necks (Ascobius simplex and Folliculina boltoni) seem not adversely affected, nevertheless it is commonly assumed that well-developed necks and neck extensions afford some survival value; i.e., the entrance of predators and detritus is lessened. Although this is an engaging conjecture, actually long necks and neck extensions afford little advantage. Rather, such folliculinids, responding to current disturbance, contract their peristomal lobes, whereas short-neck forms, not so affected, continue to feed. Since our knowledge of folliculinids is too meager to warrant conclusions as to why extensions are made, our attention for the present might best be focused on the stage (or stages) of the life-cycle responsible for their formation. The purpose of this paper is to place in question the limited alternatives of existing theories, and to rekindle interest in a question unsolved since 1923.

As previously stated, on completion of a lorica a nonfeeding swimmer usually metamorphoses into a feeding sessile organism characterized by peristomal lobes. It is generally assumed that, in nature, this organism responsible for the lorica remains for some time its occupant. However, once the terminal lip is completed, a disturbed organism may sever its body-attachment point and, without developing peristomal lobes or actually living in its lorica, may vacate it and subsequently begin the process anew.

Usually, however, on completion of the terminal lip the organism withdraws into its sac and, following a rest period, metamorphoses into a sessile feeding stage. Under laboratory conditions, this stage may last from one to several days. This period is followed by one of two possible courses: either metamorphosis results in a motile stage which vacates the original lorica; or, following binary fission, a distal portion metamorphoses into a motile stage whereas a proximal portion metamorphoses into a sessile stage which, for some time, occupies the original lorica.

Thus, subsequent neck extensions might be the result of (1) the stage that secreted the original lorica, (2) the stage remaining in the original lorica following binary fission, (3) the stage leaving the original lorica following binary fission, or (4) a "new" swimmer (or swimmers) entering another lorica. Although most investigators agree on the general process of lorica formation, few agree on the stage of the life cycle responsible for neck extensions. And, despite the above possibilities, the formation of neck extensions is today explained in the light of limited alternatives: either they are the result of the sessile stage which secreted the original lorica, or they are the result of a "new" swimmer which enters an empty lorica.

In a personal communication E. A. Andrews (1952) states:

No one has seen extensions actually in the process of making, but Hadzi [1951] gives some pages of argument that they are made

by swimmers locating in empty tests, while I maintain it is less improbable to imagine the adult can attempt a secondary imperfect neck or even a third while dwelling in the old test.

Following Andrew's suggestion, glass plates to which were attached Metafolliculina andrewsi, M. nordgardi, Parafolliculina violacea, and Lagotia viridis were brought into the laboratory and the following neck-extension possibilities were studied:

Fig. 1. *Metafolliculina andrewsi* as viewed from the right side showing: a, peristomial lobes; b, extended body; c, neck without extensions; d, nucleus; e, sac; and f, body attachment point.

I. Neck Extensions by the Stage that secreted the Lorica.

Although living *M. andrewsi* and *M. nordgardi* (Matthews, 1963) with and without extensions were present, these were ignored for the moment because, even if subsequent neck extensions were formed, the possibility remained that these could be the product of some stage other than that which secreted the lorica; for example, a new swimmer (or swimmers) that had entered an empty lorica. To exclude this possibility the aquarium in which these plates were held was completely covered with black paper except for one small area in which unetched glass slides were placed. By this method the entire lorica-forming process of *M. andrewsi* was observed. Thus it was made certain that the folliculinid occupying a particular lorica was indeed its original builder. Metamorphosis of these original lorica builders into swimmers was frequently observed and, as each swimmer vacated its lorica, a small, but easily distinguishable body attachment point (Fig. 5d) was left in the proximal region of the empty sac. Likewise, binary fission and the subsequent metamorphoses into sessile and motile stages was observed. In such instances the original body attachment point appeared unaltered either as to size, shape, position, or number.

In approximately 25 *M. andrewsi*, only one instance of a neck extension was observed. This particular folliculinid was brought to my attention by my inability to bring into sharp focus the region just distal to the lip. When first observed at 8:25 AM the organism, with a single point attachment, lay contracted in the proximal end of its sac. Slowly it relaxed and extended its peristomial lobes above the cloud-like, viscous mass which surrounded the lip, only to contract again into the sac. The relaxation of the body and the freeing of the peristomial lobes above the distal opening of the neck had been observed frequently in other specimens of *M. andrewsi*. In such instances, as the body relaxed the spirally twisted peristomial lobes were carried aloft where their pectinellae burst into a "running flame" of activity resembling the spiral ignition of a gas stove burner. In the present specimen such was not the case. As the body relaxed (Fig. 2g) and the peristomial lobes (a,
Neck Extensions in Folliculinids—MATTHEWS

![Diagram of Metafolliculina andrewsi](image)

**Fig. 2. Metafolliculina andrewsi** showing: *a*, slight, distal fold of right peristomal lobe; *b*, indistinct, distal region of neck extension; *c*, left peristomal lobe curved in a semicircle at right angles to main, longitudinal axis of neck; *d*, distinct, proximal region of neck extension; *e*, lip of neck; *f*, neck; and *g*, portion of body.

...were carried aloft, sometimes the right lobe (*a*) but as frequently the left (*c*) formed a semicircle at right angles to the longitudinal axis of the neck (*f*) and, in this position, was finally carried above the lip (*e*). The other lobe, which was slightly folded near its distal end (*a*), appeared as if to tap or “feel” an indiscernible neck boundary. Not once, even when both peristomal lobes were free, was any activity of the pectinellae detected. Relaxation and contraction of the body continued without interruption throughout the day. Because a slight body secretion followed each contraction, it appeared that the peristomal lobes, functioning like a plasterer’s trowel, merely carried this material aloft and spread it rather than produced it themselves. Gradually, the proximal portion of the extension (*d*) darkened somewhat and became clearly discernible, but the distal portion (*b*) became only vaguely so. At 4:00 PM the extension, still indistinct distally, measured approximately 66μ. The organism now lay in the proximal portion of the sac. After perhaps 2 hours of “inactivity,” this sessile stage metamorphosed into a motile swimmer which, following three or four unsuccessful attempts, finally swam free of the original lorica leaving, as usual, the distinct green area in the proximal region of the sac which marked the old body attachment point. Unlike other observed swimmers, this one “crawled” slowly along the surface of the submerged glass plate. Its vermiform body, only slightly attenuated posteriorly, measured 415μ long but only 33μ wide. The following morning this swimmer was found dead not far from the lorica whose neck had been extended. As far as was discernible, it had made no attempt to secrete a new lorica. The extension (Fig. 3) had darkened throughout its entire length but unfortunately was frayed distally (*a*) and devoid of lip (*a*) and spiral whorls (*b*).

Were this the only case in point, one might accept for all neck extensions Andrews’ (1923: 242) statement:

> While the original [lorica] is made by an animal without lobes which then transforms into the lobed form, it seems probable that the extensions are added by the animal when with quite different anatomy at the anterior end. . . . If true that the perfect form can secrete spiral tube and terminal lip without the usual special neck and mushroom shape it would seem to follow that it is not so much one specialized part of the body that makes the form of the dwelling as it is temporary contractions and secretions that may be active in very different parts of the body, since the area of secretion that must have been active in the secondary tube and
This stage persists under laboratory conditions from one to several days. This metamorphoses back into a swimmer but there is every reason to assume that, after a period of rest, it might undergo binary fission or indeed produce, as previously described, an imperfect neck extension. However, this is mere conjecture.

III. Neck Extension by the Stage Leaving the Lorica following Binary Fission.

Although this stage might possibly produce a neck extension, it was never observed to make one. Swimmers were often observed which seemed to experience considerable difficulty in leaving the lorica, but finally all were able to do so.

IV. Neck Extensions by a New Swimmer (or Swimmers) entering Another Lorica.

_Leptogia viridis_ (Fig. 4), with well-developed sac (g) and neck (e), was observed trapped in its lorica by a swimmer whose attachment point (b) was located either on or just below the well-developed lip (c). While at first sight this stage of neck extension might seem to fall under III (the Stage Leaving the Lorica following Binary Fission) such was not the case. As far as is known, _L. viridis_ does not make neck extensions. Although it undergoes binary fission, the distal portion metamorphoses into a swimmer which leaves the old lorica to start the process anew. Moreover, when first observed the anterior or pectinellae end of the swimmer pointed down into the neck and only later contracted and formed a living plug which completely closed the neck (e). During this time the entrapped folliculinid lay motionless at the proximal end of the sac. As in _M. andrewsi_, a viscous secretion appeared just above the lip (c). There was no apparent movement either of the swimmer or of its fused cilia. Whereas the folliculinid in the sac was a light bottle green, the swimmer attached near the lip was a deep violet. During the next 2 hours this became lighter until finally it approximated the green of the folliculinid in the sac. Slowly there emerged what at first was mistaken for a proboscis. This came not from the very top of the old lorica but rather more from the side and extended (as illustrated) to the top of the old sac. Not once, however,

Fig. 3. *Metafolliculina andrewsi* showing: a, frayed, distal end of neck extension; b, neck extension without spiral whorls; c, lip of neck; d, spiral whorl; and e, neck.

lip-making is very far removed from the area originally active in the making of the first tube [neck], ... [since] the arms are made from the region very far from the anterior end of the larval swimmer.

While my single observation proves that a neck extension, even though imperfect, can be the product of the sessile stage it does not exclude other extension possibilities.

II. Neck Extensions by the Stage Remaining in the Lorica following Binary Fission.

As previously stated, the proximal portion following binary fission metamorphoses into a sessile stage, characterized by peristomal lobes.
were observed the counter clockwise movements so characteristic of normal neck formation. This was understandable because, although it resembled a proboscis, it already possessed peristomal lobes (d).

Believing the process completed, I made a small aperture (b) in the lorica (g) in order to determine if the entrapped folliculinid would attempt to free itself. Rather more quickly than expected, it metamorphosed into a small but otherwise normal folliculinid which almost immediately gained access to the outside by means of this aperture (b). There was no “feeling around” inside the sac for the location of this opening: rather, the animal went directly to and through it.

These two folliculinids shared the same lorica from March 22 to March 24. During this time the folliculinid attached to the sac continued to use the aperture made for it. It would relax and extend its body and peristomal lobes (f) high above the dorsal surface of the old sac but made no effort to secrete a new neck. The folliculinid attached near the old lip (c) was at no time as active as the one in the old sac. Its peristomal lobes (d) were never held aloft and the beating of their pectinellae was never observed. The following morning (March 25) both folliculinids had vacated the old lorica. Whether or not they metamorphosed into swimmers was not observed. However, the swimmer that had attached itself near the old lip had secreted a strange type of neck extension (a). This consisted of a hemispherical cap whose opening was placed at right angles to the main or longitudinal axis of the original neck.

Although it is difficult to distinguish one species of swimmer from another, the fact that this swimmer was at first a deep violet and that *Parafolliculina violacea* were present on the original plate suggests that in this instance the neck extension may possibly have been the result of another species!

Because under laboratory conditions organisms frequently respond abnormally, modified experiments were performed in the organism's natural habitat. Empty loricae of *M. andrewsi* without extensions were stained with acidulated borax-carmine, washed thoroughly, and the glass plates were returned to the anchorage lagoon at Coconut Island. At the same time, other empty unstained lorica without extensions were marked and these glass plates were returned to the organisms' natural habitat. Although both stained and unstained loricae were observed over a period of 2 months, neither possessed new occupants nor extensions. And although the discouraging results of these experiments throw some doubt on the possibility that neck extensions are formed by new swimmers entering old loricae, other naturally occurring examples point very strongly to this possibility.

In *M. andrewsi* the condition illustrated in Figure 5 is frequently encountered. Two body attachment points (d, e) are clearly discernible. Although Penard (1919:317) incorrectly assumes that longitudinal fission occurs in *Folliculina boltoni* (see his Fig. 17), he correctly points out that only a single body attachment point persists, that of the original occupant. If, as suggested by Andrews, neck extensions are the result of the original occupant of the lorica, then only a single attachment point should be present. It is absurd to assign two attachment

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**Fig. 4. Lagotia viridis** as viewed from the right side showing: a, hemispherical, caplike neck extension; b, body attachment point; c, lip; d, peristomal lobes of new occupant; e, neck; f, peristomal lobes of original occupant; g, sac; and b, aperture cut in sac.
points \((d, e)\) to a folliculimid now known to undergo only binary fission. It is equally absurd to assume that the present body attachment point \((e)\) permits a better peristome exit. In light of possibility 1 (Neck Extensions by the Stage that Secreted the Lorica), two attachment points and two neck extensions might be explained as follows: the builder of the original lorica, once the neck \((c)\) was completed, contracted into its sac but, after a period of rest, instead of metamorphosing into a swimmer, relaxed and, while in the lobed stage, secreted the first imperfect neck extension \((b)\). It then withdrew and metamorphosed into a swimmer which vacated the lorica. The present body attachment point \((e)\) is that of a new swimmer which entered, became attached, and, while in the motile stage, secreted the second extension \((a)\). This may explain in part why spiral whorls are absent in the first extension \((b)\) and why they are present in the second \((a)\). This might also account for the fact that the diameter of the second extension is approximately half that of the first. While these possibilities are not conclusive, other examples suggest that neck extensions may have multiple origins.

Frequently \(M. \text{ Nordgardi}\) (Fig. 6A) is observed in which the body attachment point \((d)\) is far removed from the base of the lorica \((e)\). In such instances either the body has freed itself from its original attachment point \((e)\) and become reattached \((d)\), or another swimmer has entered the old lorica and established itself. Because many \(M. \text{ nordgardi}\) with and without extensions (Fig. 6B–C) possess loricae whose lengths exceed that illustrated in Figure 6A and yet experience no difficulty in extending their peristomial lobes, it seems rather unlikely that reattachment in the shorter form was the result of necessity. Moreover, if \(d\) (Fig. 6A) was the original body attachment point there is no way, based on our present knowledge, to explain the formation of that portion of the lorica between \(d\) and \(e\).

If one assumes that the lorica illustrated in Fig. 6A is not the product of its present occupant, how does one explain the formation of the extensions illustrated in Fig. 6C, since only one body attachment point \((e)\) is present? If one rejects Andrews’ theory that the present occupant (Fig. 6C) is responsible for the lorica \((d–e)\) and its extensions \((c–d\) and \(b–c)\) then one must extend Hadzi’s theory to include the possibility that that portion of the lorica between \(c–d\) may have been secreted by a second swimmer, and that portion between \(b–c\) by a third. As improbable as this may at first appear, there is some evidence at \(e\) (Fig. 6C) to support this view. Although it is possible that none of the original attachment-point material remains (Fig. 6A–e), occasionally (Fig. 6C–e) material accumulates whose texture and staining affinity appear identical with those of the present body attachment material.

Surely, for those examples in which swimmers have entered old lorica and built extensions, Hadzi is correct in limiting the count of the spiral whorls to those of the original lorica and excluding the number of whorls added by new swimmers. However, in cases in which the

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**Fig. 5.** *Metajolliculina andrewsi* as viewed from the right side showing: \(a\), second neck extension; \(b\), first neck extension; \(c\), neck; \(d\), original body attachment point; and \(e\), present body attachment point.
builder of the original lorica also adds extensions this method of counting may or may not result in a correct whorl number.

Although these possibilities of accounting for neck extension place in question the limited alternatives of older theories, the process must be observed in many species before these possibilities can be accepted unequivocally.

LITERATURE CITED


Tenth Pacific Science Congress Papers

The Tenth Pacific Science Congress of the Pacific Science Association was held on the campus of the University of Hawaii August 21 to September 6, 1961, under the joint auspices of the University, the Bernice P. Bishop Museum, and the National Academy of Sciences.

The University of Hawaii Press is publishing seven volumes of the distinguished papers of the Congress, each volume dealing with a different subject as it applies to the conditions that prevail in the various countries of this vast and increasingly important segment of the world scene. The second volume is:

GEOLGY AND SOLID EARTH GEOPHYSICS
OF THE PACIFIC BASIN

Report of the Standing Committee
Gordon A. Macdonald, chairman

The Greater Pacific Basin represents the major portion of the earth's surface, one which includes some of the most dramatically active areas geologically, one in which much work in geology and geophysics remains to be done. These papers go a long way toward evaluating what has been accomplished to date and establishing a basis for future studies in the area.

The monograph contains contributions covering the following countries:

Australia Malaya
Western Canada Mexico
China (Taiwan) New Zealand
El Salvador Philippines
Indonesia Thailand
Japan United States

Additional articles deal with special aspects of various areas of the Pacific. They include:

The Pacific Basin
Islands of Western North Pacific
Thermal Waters and Volcanic Emanations
British Solomon Islands

Dr. Macdonald is senior professor of geology at the University of Hawaii.

Approx. 200 pp. February 15, 1964 Paper, $5.00
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Shell Selection of Pacific Hermit Crabs

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Isopod Crustaceans from Southern California

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ANGELES ALVARIÑO
Chaetognatha in the Indian Ocean

DONALD C. MATTHEWS and SIDNEY J. TOWNSLEY
Hawaiian Platycetnea

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(Continued on inside back cover)
PACIFIC SCIENCE
A QUARTERLY DEVOTED TO THE BIOLOGICAL AND PHYSICAL SCIENCES OF THE PACIFIC REGION

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A Revision of the Genus Parapercis, Family Mugiloididae

GEORGE E. CANTWELL

This study describes the genus Parapercis Bleeker and its 26 species. The descriptions are based on anatomical studies, each structure having been analyzed statistically to determine its variation within a species and its value in identification. An effort has been made to employ those characters with the least variation within species to establish possible affinities between species, to define species groups, and to determine relationships among them. The geographic range has been determined from actual specimens and the literature.

Over 80 nominal species have been described in or placed in the genus Parapercis, but no previous attempt has been made to compare the species on a world-wide basis or to determine the value of morphological characters in the identification of them. Studies of the genus by Cuvier and Valenciennes (1829) and by Günther (1860) each included 13 nominal species. Subsequent reports have been made on a regional basis, the more important of which are listed below, along with the number of nominal species: Day (1876), India, 3; Jordan and Seale (1906), Samoa, 6; Jordan, Tanaka, and Snyder (1913), Japan, 7; McCulloch (1929), Australia, 14; Okada (1938), Japan, 12; Kamohara (1950), Japan, 11; and Beaufort and Chapman (1951), Indo-Australian Archipelago, none. The only records of Parapercis from outside the Indian and Pacific oceans are by Vaillant (1887) and Cadenat (1937), from the Cape Verde Islands off the west coast of Africa, each based on a single specimen. Arambourg (1927) identified a fossil from Oran as belonging to the genus.

Since the completion of this study, Kamohara (1960) has described a new species Parapercis okamurai from Japan. No attempt has been made to incorporate P. okamurai in this study, as no material was available for examination.

Material studied

The author is grateful to the authorities of the following institutions for the use of specimens that form the basis of this study: Academy of Natural Sciences of Philadelphia (ANSP); Australian Museum, Sydney (AM); Bernice P. Bishop Museum, Honolulu (BPBM); British Museum (Natural History), London (BMNH); California Academy of Sciences, San Francisco (CAS); Chicago Natural History Museum (CNHM); Dominion Museum, Wellington (DM); George Vanderbilt Foundation, Stanford University (GVF); Museum of Comparative Zoology, Harvard University (MCZ); Naturhistorisches Museum, Wien (NHMW); Rijksmuseum Natuurlijke Historie, Leiden (RNVH); Stanford Natural History Museum (SNHM); Tokyo University (TU); University of California, Los Angeles (UCLA); University of Michigan, Museum of Zoology, Ann Arbor (UMMZ); University of Washington, Seattle (UW); United States National Museum, Washington, D.C. (USNM); the Western Australian Museum, Perth (WAM).

The author wishes to thank Dr. L. P. Schultz, Dr. E. A. Lachner, Dr. W. R. Taylor, Mr. R. Kanazawa of the U. S. National Museum, and Dr. G. W. Wharton of the University of Maryland for their help and advice; Dr. C. M. Clifford, University of Maryland, for information on type specimens in the British Museum; Dr. K. A. Tabler, U.S. Department of Agriculture, for aid and advice on statistical analyses; and the staff of the Smithsonian Institution's Photographic Laboratory for photographs.

Definition of terms

Measurements of body parts were made with dividers and the distances recorded to the nearest half millimeter. These measurements are expressed as thousandths of the standard length. Total length: the distance from the anterior tip of the upper lip to the tip of longest caudal fin ray (except on one species, P. schauinslandi,
which has long filamentous projections from the caudal fin; in this species it was impossible to determine how much, if any, of these filamentous rays were broken; therefore the total length was taken from the anterior tip of the upper lip to the posterior end of the shortest branched caudal fin ray).

Standard length: the distance from the anterior tip of the upper lip to the posterior end of the hypural plate. When necessary the end of the hypural plate was determined by dissection or probing with a needle.

Greatest depth: the greatest vertical distance of the body at its deepest part.

Depth of caudal peduncle: least vertical distance at the caudal peduncle.

Snout length: the distance from the anterior tip of the premaxillary (upper lip) to the front edge of the orbit.

Eye diameter: the greatest horizontal distance between the margins of the bony orbit.

Postorbital length: the distance from the rear edge of the orbit to the rearmost tip of the fleshy operculum.

Interorbital width: the least distance between the bony edges of the orbits on the dorsal surface of the head.

Head length: the distance from the anterior tip of the upper lip to the posterior tip of the fleshy operculum.

Gill rakers: the anterior rightmost arch was exposed by dissection. The count includes all gill rakers and rudiments on the first arch.

Fin rays: spines are represented by Roman numerals, simple soft rays by lowercase Roman numerals, and branched soft rays by Arabic numbers. Each ray with a separate base was counted.

Abdominal vertebrae: those vertebrae from the head to, but not including, the first vertebra with transverse processes that meet midventrally.

Caudal vertebrae: those vertebrae from the most anterior one with transverse processes that meet midventrally to, but not including, the urostyle arch. Vertebral counts were made directly from radiographs and were confirmed in some instances by dissection.

Scales in a longitudinal row: the number of oblique rows of scales that cross the first lengthwise row just above the lateral line, counting from the upper angle of the gill opening along the body to the base of the caudal rays.

Scales from the soft dorsal to the lateral line: the number of scales in an oblique row running down and back from the first soft dorsal ray to the lateral line. The lateral line scale is not included in this count. Small scales near the dorsal fin are counted as whole scales.

Scales from the anal opening to the lateral line: the number of scales in an oblique row running up and back from the anterior margin of the anus to the lateral line. The lateral line scale is not included in this count.

Scales around the caudal peduncle: the number of scales in a zigzag row around the least vertical depth of the caudal peduncle.

**DIAGNOSTIC CHARACTERS**

Neither the measurements nor meristic data may be used alone to identify species. Although most of the characters vary within themselves and overlap with those of other species, in certain instances there is no variation of a character within a species nor overlapping between species.

The color pattern is of great value in identifying members of this genus when specimens are recently and/or well preserved. Very old and poorly preserved specimens, even recent poorly preserved specimens, tend to fade, and in time lose all or most of their color pattern. No sexual dimorphism in color pattern was observed.

The mean ($\bar{y}$), variance ($s^2$), and standard deviation ($s$) were obtained for all characters involving measurements or count data. In those instances where a comparison was made between species involving these data, the standard error of the difference was calculated in order to determine the statistical significance of the difference of the sample means.

**GILL RAKERS:** The total number of rakers varies between species from 9 to 25, but within each species the variation is usually 3 or 4 (Table 6). The upper arch has from 1 to 11 rakers and the lower from 7 to 15.

**FIN RAYS:** There is little variation, if any, in the fin ray counts. Without exception the pelvic fin ray count was 1, 5. The caudal fin ray formula for branched rays was 8 above and 7
below (8 plus 7), except for a few individuals in the species *P. snyderi*, in which it was 7 plus 7. The dorsal spines (Table 1) were either IV or V, with little variation within a species. The soft dorsal rays ranged from 20 to 24, and they varied little within a species (Table 1). The first ray of the anal fin was always unbranched, followed by 16 to 19 branched rays (Table 2).

PECTORAL FIN RAYS: The upper ray of the pectoral fin was always simple and unbranched, followed by 14 to 21 branched rays (Table 2). The variation within species usually did not exceed 4.

SCALE COUNTS (Tables 3, 4, 5): The number of oblique rows of scales crossing the lateral line from rear of head to base of caudal fin rays ranges from 40 to 89. The range within the genus of the number of scales from the lateral line to the anus was from 10 to 25; within each species the variation was up to 6, though usually less than 4. The number of scales from the lateral line to the first soft dorsal ray varied from 3 to 11 within the genus and up to 4 within species. The variation within a species of the number of scales around the caudal peduncle was up to 8, and the range within the genus from 15 to 44.

**VERTEBRAE:** The number of abdominal vertebrae remained constant at 10, whereas the number of caudal vertebrae ranged from 18 to 22. There was practically no variation in the number of caudal vertebrae within a species (Table 6).

**BODY MEASUREMENTS:** These data show more variation, both within and among species, than the meristic data, and therefore are not used at all.

**DENTITION:** Good diagnostic characters that do not vary within a species are the presence or absence of palatine teeth. The number of canine teeth in the outer row of the lower jaw was either 6, 8, or 10. The denticion of each species is diagrammed in Figures 2, 3, and 4.

Two other characters that show no variability

---

**Table 1**

**Number of Dorsal Fin Rays for Species of *Parapercis***

<table>
<thead>
<tr>
<th>Species</th>
<th>Spines</th>
<th>Soft Rays</th>
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<tbody>
<tr>
<td></td>
<td>IV</td>
<td>V</td>
</tr>
<tr>
<td>ramayi</td>
<td>3</td>
<td>-</td>
</tr>
<tr>
<td>aurantiaca</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>multifasciata</td>
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<td>1</td>
</tr>
<tr>
<td>binivirgata</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>sex fasciata</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>mimaseama</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>munoni</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>colias</td>
<td>-</td>
<td>16</td>
</tr>
<tr>
<td>alporti</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>gilias</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>schaunlandi</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>filamentosa</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>albotrigata</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>emeryana</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>nebulosa</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>baackei</td>
<td>-</td>
<td>25</td>
</tr>
<tr>
<td>cylindrica</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>snyderi</td>
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<td>25</td>
</tr>
<tr>
<td>pulchella</td>
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<td>-</td>
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<td>ommatura</td>
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<td>25</td>
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<tr>
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<td>-</td>
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<tr>
<td>clathrata</td>
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<td>3</td>
</tr>
<tr>
<td>hexophthalma</td>
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<td>13</td>
</tr>
<tr>
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<td>18</td>
</tr>
<tr>
<td>tetracantha</td>
<td>-</td>
<td>14</td>
</tr>
<tr>
<td>xanthozona</td>
<td>-</td>
<td>19</td>
</tr>
</tbody>
</table>
within a species are the shape of the spinous dorsal and its connection to the soft dorsal (Fig. 1). The shape of the spinous dorsal falls into two categories: (1) the middle spines are longer than the last; or (2) the spines become progressively longer posteriorly. The membranous connection between the two fins is from the tip of the last spine to the base of the first soft ray (deeply notched), or from the spine tip to the first soft ray at a level with the tip of the spine (no notch).

Along with dentition and the shape and connection of the spinous dorsal fin, other characters determined to be most useful because of their small degree of variability are the number of caudal vertebrae and the number of rays of the dorsal, anal, and pectoral fins.

**GENUS Parapercis** Bleeker

*Parapercis* Bleeker, 1863, p. 236 (type species, *Sciaena cylindrica* Block).

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>TOTAL ANAL</th>
<th>TOTAL PECTORAL</th>
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<tr>
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<td>17</td>
<td>18</td>
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<tr>
<td><em>ramsayi</em></td>
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<tr>
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<tr>
<td><em>colias</em></td>
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<td></td>
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<tr>
<td><em>allporti</em></td>
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<td></td>
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<tr>
<td><em>gilliesi</em></td>
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<td></td>
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<tr>
<td><em>schauinslandi</em></td>
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<td><em>tetragonata</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>xantbozona</em></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Neopercis** Steindachner and Döderlein, 1884, p. 212 (type species, *Parapercis ramsayi* Steindachner).


**Chilias** Ogilby, 1910, p. 40 (type species, *Percis stricticeps* De Vis).

*Neopercis* was erected using the presence of palatine teeth as the only character distinguishing it from the genus *Parapercis*. Whitley (1932) discovered *Parapercis cylindrica*, the type of *Parapercis*, also had palatine teeth. Thus *Neopercis* is a synonym of *Parapercis*.

The only character used by Jordan and Evermann to distinguish *Osurus* from *Parapercis* was the deeply forked caudal fin of *P. schauinslandi*, which I regard as an insignificant character. Ogilby did not give any valid reason for distinguishing *Chilias* from *Parapercis* and none were found.
Bloch (1801), erected the genus Percis, using as the type species Percis maculata. The genus Percis Bleeker (1844 and 1876), Dumeril (1856), and Günther (1880), is preoccupied by Scopoli, 1777, in which he used Cottus japonicus Pallas as its type species. More recent authors have placed some parapercids in the genus Percis; however, the type of Bloch’s genus Percis maculata cannot be defined as a parapercid, hence Percis and Parapercis cannot be considered synonymous.

Berg (1947) and Schultz et al. (1960) place the genus Parapercis in the family Mugiloididae. The two other genera, Mugiloides Lacepède (1802) [Pinguipes Cuvier (1829)] and Prolatilus Gill (1865) [Pseudopercis Ribeiro 1904], are restricted to South America. Characters common to the family Mugiloididae as well as the super-family Trachinoidae (of Berg) are: gill arches, 4; branchiostegals, 6; pelvics, 1, 5; nostrils, two pairs, the anterior being tubular; no scales on the dorsal or anal fins; and one opercular spine. Other characters shared by the genera of the family are: branched caudal fin rays, 8 plus 7; complete dorsal fin with IV to VII spines followed by 19 to 28 branched rays; anal fin with one simple non-cross-striped ray followed by 16 to 26 branched rays.

Mugiloides and Prolatilus differ from Parapercis as follows: the vertebrae and fin ray counts are greater in number in the South American genera than in the Indo-Pacific genus Parapercis. Vertebræ: Mugiloides and Prolatilus, 15 or 16 abdominal and 20 or 21 caudal; Parapercis, 10 abdominal and 18 to 21 caudal. Dorsal fin formula: Mugiloides, VI or VII, 26 to 28; Prolatilus, IV, 28; Parapercis, IV or V, 19 to 23. Anal fin formula: Mugiloides, I, 22 to 26; Prolatilus, I, 23; Parapercis, I, 16 to 19.

The dentition of Parapercis differs from the South American genera by having the outer row of canine teeth at the anterior end of the lower jaw well developed but separated from those teeth on the sides of the jaw by an edentulous

### TABLE 3

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>40 to</th>
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<th>50 to</th>
<th>55 to</th>
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<th>65 to</th>
<th>70 to</th>
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<th>n</th>
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**Scales Around Caudal Peduncles and Below Lateral Line in Species Parapercis**

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space. *Mugiloides* has both vomerine and palatine teeth, whereas both are absent in *Prolatilis*. Vomerine teeth are always present in *Parapercis*, whereas the palatines may be present or absent.

**GENERIC DIAGNOSIS:** Scales ctenoid, those of head and breast often cycloid; upper and lower jaws with a row of hooked conical teeth inside of which occur a band of villiform teeth. Three, four, or five canine teeth in outer row on either side of symphysis of lower jaw; vomerine teeth present; palatine teeth present or absent; upper jaw protractile; spinous dorsal rounded or progressively higher posteriorly; dorsal rays IV or V, 19 to 23, the soft portion higher than the spinous one; anal fin with I, 16 to 19 rays. Opercular spine single and sharp pointed. Caudal fin with seven branched rays in lower lobe and eight in upper lobe, except on one species, *P. snyderi*, in which a few specimens have seven; caudal truncate or slightly rounded, except in *P. schauinslandi*; pelvic fin with a short spine and five rays, the fourth longer than the others; pelvic fins inserted slightly anterior to pectorals; abdominal vertebrae 10, caudal 18, 19, or 21.

**DOUBTFUL SPECIES:** The first record of the genus *Parapercis* taken outside the Indo-Pacific Ocean was *Neopercis* [*Parapercis*] *atlantica* Vaillant (1887) from the Cape Verde Islands off the west coast of Africa. In 1937 Cadenat recorded *Neopercis ledanisi* based on a single specimen. Arambourg (1943) examined both specimens and claimed they were identical and resembled his Miocene fossil specimen *Neopercis mesogea*. An attempt was made, without success, to borrow these specimens.

Five species that Cuviers and Valenciennes recognized remain doubtful after examination of the description and/or figures: *Percis ocellata, P. punctata, P. punctulata, P. semifasciata*, and *P. nicthemera*. Other nominal species that are dubious are *Percis millepunctata* Günther (1860), *P. rose* Lienard (1893), *Neopercis macrophthalma* Pietschmann (1911), and *N. striolata* Weber (1913). The examination of *Neopercis flavofasciata* Kamohara (1936) showed it to have a subequal lower jaw and a dorsal fin formula of

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**TABLE 5**

**Scales Above Lateral Line in Parapercis**

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TABLE 6

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Revision of *Parapercis*—Cantwell

II. 22, which are not characters of the genus *Parapercis* as herein defined. Recently Kamohara (1960) made *N. flavofasciata* the type species of the new genus *Kochia*. Kamohara later (1961) discovered that the generic name *Kochia* was preoccupied and substituted for it the name *Kochichthys*.

**Artificial Key to Species of the Genus Parapercis**

1a. Palatine teeth present.

2a. Teeth in outer row of lower jaw number ten.
   3a. Soft dorsal rays 22; anal rays 18; no dark longitudinal streaks across premaxilla.....*haackei*
   3b. Soft dorsal rays 21; anal rays 17; four dark streaks running longitudinally across premaxilla.....*cylindrica*

2b. Teeth in outer row of lower jaw six or eight.

4a. Teeth in outer row of lower jaw six.
   5a. Thirteen brown bars on back; scales above lateral line 66 to 67; scales from lateral line to anus 16.....*binivirgata*
   5b. Seven or eight brown bars on back; scales above lateral line 59 to 64; scales from lateral line to anus 12 to 15.
   6a. Small light spot ringed in brown at each side of origin of spinous dorsal; brown transverse bar ringed with white across head.....*multifasciata*
   6b. No spots or bars on head or nape.....*aurantiaca*

4b. Teeth in outer row of lower jaw eight.

7a. Dorsal spines longer posteriorly.
   8a. One canine tooth on palatine; total pectoral rays 16–17; scales around caudal peduncle 30 to 34; 5 V-shaped dark markings on body between head and caudal fin.....*sexfasciata*
   8b. More than one tooth on palatine; total pectoral rays 19; scales around caudal peduncle 27; no V-shaped markings on body.....*mimaseana*

7b. Dorsal spines longest at middle.
   9a. Spinous dorsal connected by membrane to first soft ray near base.....*snydert*
   9b. Spinous dorsal connected by membrane to first soft ray along a line opposite tip of last spine.
   10a. Dorsal spines four; soft dorsal rays 24; pectoral rays 16.....*ramsayi*
   10b. Dorsal spines five; soft dorsal rays 25; pectoral rays 20.....*muronis*

1b. Palatine teeth absent.

11a. Teeth in outer row of lower jaw six.

12a. Soft dorsal rays 21; anal rays 18; upper and lower caudal rays greatly elongated.....*schaunislandi*

13b. Soft dorsal rays 22; anal rays 19; caudal rays not elongated.
   14a. Oblique rows of scales above lateral line 56 to 60; scales from lateral line to anus 11 to 14; scales from lateral line to base of first soft dorsal 4–5; scales around caudal peduncle 22 to 30.
   15a. Pectoral rays 16; scales around caudal peduncle
30; gill rakers 11; anterior soft dorsal rays greatly elongated..........................filamentosa

15b. Pectoral rays 18–19; scales around caudal peduncle 26; gill rakers 21–23; anterior soft dorsal rays not elongated..........................alboguttata

14b. Oblique rows of scales above lateral line 70 to 83; scales from lateral line to anus 20 to 24; scales from lateral line to base of first soft dorsal 9–10; scales around caudal peduncle 39 to 44.

16a. Oblique rows of scales above lateral line 70–71; scales from lateral line to soft dorsal 10; scales around caudal peduncle 39–40; pectoral rays 17; gill rakers 18–19..........................emeryana

16b. Oblique rows of scales above lateral line 80 to 83; scales from lateral line to soft dorsal 9; scales around caudal peduncle 42 to 44; pectoral rays 15–16; gill rakers 11 to 15..........................nebulosa

12b. Spinous dorsal connected to first soft ray opposite tip of last spine.

17a. Dorsal spines four; scales around caudal peduncle 25–29.

18a. Dark ocellus-like spot above operculum; one horizontal row of spots on anal fin; no rectangular white patch on caudal fin..........................clatrata

18b. No ocellus above operculum; no spots on anal fin; rectangular white patch on posterior half of caudal fin..........................cephalopunctata

17b. Dorsal spines five; scales around caudal peduncle 26–32.

19a. Large dark ocellus above lateral line at posterior part of operculum; wide dark band across cheek from below eye to interopercle; distal exposed part of each soft anal ray dark; vertical bars meet at mid-ventral line of body..........................tetracantha

19b. No ocellate spot behind or above rear of head; small dark bands across cheek; tips of soft anal rays not dark; vertical bars on body not continuous to anal fin; soft dorsal fin with 3 lengthwise rows of dark spots on membranes..........................xanthozona

11b. Teeth in outer row of lower jaw eight.

20a. Dorsal spines longer posteriorly; caudal vertebrae 18.

21a. Soft dorsal rays 20; anal rays 17; scales from lateral line to base of first soft dorsal ray 10–11; gill rakers 23–26..........................colias

21b. Soft dorsal rays 21; anal rays 19; scales from lateral line to base of first soft dorsal ray 4–7; gill rakers 15–19.

22a. Scales from lateral line to anus 16 to 17; scales around caudal peduncle 25 to 29..........................allporti

22b. Scales from lateral line to anus 18 to 19; scales around caudal peduncle 30 to 32..........................gilliesi
20b. Dorsal spines in middle portion longest; caudal vertebrae 19.

23a. Spinous dorsal connected by membrane to base of first soft ray.

24a. Soft dorsal ray 21; anal rays 18; no dark spot at base of caudal fin.................. *pulchella*

24b. Soft dorsal rays 22; anal rays 19; and ocellus at dorsal base of caudal fin.................. *ommatura*

23b. Spinous dorsal connected by membrane to first soft ray opposite tip of last spine.

25a. Two horizontal rows of brown spots across cheek; five to seven ocellus-like spots on body between pectoral and caudal fins.................. *polyophthalma*

25b. Four to eight oblique bars across cheek; three to five ocellus-like spots on body between pectoral and caudal fins........... *hexophthalma*

**DESCRIPTIONS OF SPECIES**

The descriptive data include individuals of both sexes when available. No sexual dimorphism was observed. Under "Specimens Studied" the first number refers to the total number of individuals examined. The numbers following in parentheses give the range of the total length in millimeters. In parentheses following the museum number is the number of specimens examined under that museum number.

*Parapercis ramsayi* Steindachner

Figs. 1A, 2A, 5A


*Percis novae-cambriae* Ogilby, 1885, pp. 228–229 (Port Jackson).


*Neopercis novae-cambriae* Waite, 1904, p. 50.

**SPECIMENS STUDIED:** 3 (166–192): New South Wales; Botany Bay AM IA4114 (1); Long Bay AM IA2480 (1); Newcastle USNM 179798 (1).

**DIAGNOSIS:** Eight canine teeth in outer row of lower jaw; palatine teeth present; middle dorsal spines longest; membrane from spinous dorsal connected to first soft ray opposite tip of last spine; dorsal spines y four; dorsal rays y 24.33; anal rays 19.67; caudal vertebrae 21; no serrations on opercles.

**COLOR IN ALCOHOL:** Background yellow, seven oblong dark brown spots below lateral line from back of pectoral fin to caudal peduncle; a thin dark line runs from dorsal base of pectoral fin to mid-dorsal base of caudal fin, above this line are seven wide dark brown bars reaching to dorsal fin; lower ⅔ of spinous dorsal black; anterior ⅓ of soft dorsal fin with many very fine specks, posterior ⅓ with oblique brown bars; a large dark brown spot at dorsal base of caudal fin and one at ventral base; ventral and posterior margins of caudal fin black; no markings on pectoral fin; dusky gray blotch on medial portion of pelvic fin; tip of anterior anal fin dark gray posteriorly becoming darker and including more of the fin; nape dark brown; two dark spots on opercle, one on preopercle just under the eye; upper lip gray.

**RANGE:** New South Wales and South Australia.
**Revision of Parapercis—CANTWELL**

*Parapercis aurantiaca* Steindachner and Döderlein

Figs. 1V, 4V, 9F


**SPECIMEN STUDIED:** One (162.5 mm): Joga Shima light, Japan. USNM 195872.

**DIAGNOSIS:** Six canine teeth in outer row of lower jaw; palatine teeth present; dorsal spines gradually longer posteriorly; membrane from spinous dorsal connected to first soft ray opposite tip of last spine; dorsal spines 5; dorsal rays 23; total anal rays 20; caudal vertebrae 20.

**COLOR IN ALCOHOL:** Background tan; dorsal fin with several oblique brown bars posteriorly; caudal fin with 5 or 6 wavy bars vertically; pelvics, pectorals, and anal light cream; no markings on lips.

**RANGE:** Japan.

*Parapercis multifasciata* Steindachner and Döderlein

Figs. 4V, 5B

*Parapercis multifasciatus* Steindachner and Döderlein, 1884, pp. 190–191, pl. 6, figs. 2 and 2a (type locality, Tokyo Bay). Tomiyama and Abe, 1958, p. 120, fig. 353. Kamohara, 1960, pp. 1–13.

*Percis multifasciata* Nystrom, 1887, p. 28 (Japan).


**SPECIMENS STUDIED:** 31 (45 to 162.6 mm): Pusan, Korea UMMZ 176692 (1); Japan: Ose Saki light USNM 149519 (1); Tayama Bay UMMZ 176718 (2); Owari Bay USNM 50307 (1); Yeopshima CNHM 55610 (1); Chirin Jima USNM 177908 (1); Misaki CNHM 5307 (1), 58832 (1); Hamashima USNM 59644 (1); Tokyo ANSP 26161–62 (2), SU 4984 (2), NHMW (2); Oki Shima USNM 150560 (2); Kagoshima Bay UMMZ 142750 (1); Obama Bay UMMZ

Fig. 1. Diagrams of spinous dorsal fins of species of the genus *Parapercis*: A, ramsayi; B, colias; C, clathrata and cephalopunctata; D, snyderi; E, cylindrica; F, schauinslandi; G, pulchella; H, xantozona; I, tetra-cantha; J, polyophthalmus and hexophthalmus; K, allporti; L, gilliesi; M, haacki; N, ommatura; O, filamentosa; P, alboguttata; Q, emeryana; R, nebulosa; S, munronis; T, sexfasciata; U, mimaseana; V, multifasciatus, munronis, and aurantiaca; W, binivirgata. In each instance the first soft branched ray of the soft dorsal fin is shown to the right of the last dorsal spine.
Parapercis sexfasciata (Temminck and Schlegel)  
Figs. 1T, 4T, 5D

Parapercis binivirgata (Waite)  
Figs. 1W, 4W, 5C

Neopercis binivirgata Waite, 1904, pp. 236–238, pl. 25, fig. 3 (type locality, New South Wales); 1904, p. 50.

Parapercis binivirgata McCulloch, 1922, p. 101, pl. 31, fig. 274a; 1929, pp. 331–332 (Coogee); 1934, p. 75, pl. 31, fig. 274a. Whitley, 1957, 40 pp.

SPECIMENS STUDIED: Three (142–163) New South Wales USNM 179800 (1); Sidney 179799 (1); Gunnamatta Bay AM IB3756 (1).

DIAGNOSIS: Six canine teeth in outer row of lower jaw; palatine teeth present; dorsal rays gradually longer posteriorly; membrane from spinous dorsal connected to first soft ray opposite tip of last spine; dorsal spines y 5; dorsal rays y 25; total anal rays y 20; caudal vertebrae y 21; no serrations on opercles.

COLOR IN ALCOHOL: Body light brownish yellow with 13 dark brown bars over back reaching down to the midline, the most anterior over the nape, the next two extend from the spinous dorsal, the next nine from the soft dorsal and the last over the caudal peduncle; a dark spot at the dorsal base of the caudal fin rays; seven dark oblique bars over upper 2/3 of caudal fin; a small dark brown spot at dorsal base of pectoral fin rays; middle third of median two rays of pelvic fin dark brown; anal fin with no markings.

RANGE: New South Wales.

Parapercis sexfasciata (Temminck and Schlegel)  
Figs. 1T, 4T, 5D


SPECIMENS STUDIED: 151 (78–164): Ningpo, China USNM 130538 (3); Pusan, Korea UMMZ 176691 (5); Japan USNM 57516 (3), 57732
Fig. 2. Diagrams of dental patterns of species of the genus Paraperis: A, ramsayi; B, colias; C, clathrata and cephalopunctata; D, snyderi; E, cylindrica; F, schauinslandi; G, pulchella; H, xanthozona; I, tetrancantha.
RANGE: Japan; north China; Korea.

Parapercis mimaseana (Kamohara)
Figs. 1U, 4U, 5E

Neopercis mimaseana Kamohara, 1937, pp. 189–190, fig. 3 (type locality, off Province of Tosa, 100–200 fathoms); 1938, p. 1452, fig. 3. Okada and Matsubara, 1938, p. 390, pl. 93, fig. 1 (Kochi; Kumono-nada). Kamohara, 1938, p. 63, fig. 34 (Mimase); 1950, p. 258 (Tosa and Kishu); 1952, p. 86, fig. 83. Matsubara, 1955, p. 691, pl. 74, fig. 248. Kamohara, 1955, p. 58, fig. 4; 1958, p. 67 (Mie Pref. to Kochi).

SPECIMEN STUDIED: One (126.5) Kochi Shikoku TU 7814.

DIAGNOSIS: Eight canine teeth in outer row of lower jaw; palatine teeth present; dorsal spines gradually longer posteriorly; membrane from spinous dorsal connected to first soft ray opposite tip of last spine; dorsal spines y five; dorsal rays y 23; total anal rays y 20; caudal vertebrae y 21.

COLOR IN ALCOHOL: Background light tan; upper half of body tesselated; head gray; front of upper and lower lips gray; spinous dorsal black; soft dorsal rays gray; six vertical gray bars on dorsal ½ of caudal fin; tips of anal fin rays gray, pelvic fins gray except at tips; lower ½ of pectoral fins gray; gray specks on branchiostegals.

RANGE: Japan.

Parapercis muronis (Tanaka)
Figs. 15, 45, 6A


SPECIMENS STUDIED: Three (52 to 113) Kochi TU 7815; locality unknown TU 8316; China Sea USNM 150910.

DIAGNOSIS: Eight canine teeth in outer row of lower jaw; palatine teeth present; dorsal spines gradually longer posteriorly; membrane from spinous dorsal connected to first soft ray opposite tip of last spine; dorsal spines y five; dorsal rays y 23; total anal rays y 20; caudal vertebrae y 21.

COLOR IN ALCOHOL: Background light tan; upper half of body tesselated; head gray; front of upper and lower lips gray; spinous dorsal black; soft dorsal rays gray; six vertical gray bars on dorsal ½ of caudal fin; tips of anal fin rays gray, pelvic fins gray except at tips; lower ½ of pectoral fins gray; gray specks on branchiostegals.

RANGE: Japan.
of lower jaw; palatine teeth present; middle dorsal spines longest; membrane from spinous dorsal connected to first soft ray opposite tip of last spine; dorsal spines y five; dorsal rays y 23; total anal rays y 20; caudal vertebrae y 21.

COLOR IN ALCOHOL: Background light tan; five dark brown bars on each side extend from the dorsal fin to below the midline; the lower part of each bar being darker; a light brown bar across nape; spinous dorsal light brown; soft dorsal with one or two light brown patches on the membranes between rays; tips of anal rays light gray; five vertical brown bars on caudal fin; brown patch on middle third of pelvic; no color on pectoral fins or lips.

RANGE: Japan.

**Parapercis colias** (Bloch)

Figs. 1B, 2B, 6B

**Gadus colias** Bloch, 1901, p. 54 (locality, unknown).


**Enchelyopus colias** Whitley and Phillipps, 1939, p. 235 (South Island, New Zealand).

SPECIMENS STUDIED: 17 (180.5 to 386) New Zealand: D'Urville Island BM 1890.2.26.69 (1); Wellington harbor BM 1873.12.30.34 (5); Auckland USNM 176802 (2), 176803 (1); Cook Strait DM 2093 (1); NHMW 7402 (1); Lyall Bay DM 957 (1); Makara DM 1167 (1), 1123 (1); Sinclair Head DM 2615 (2); New Zealand NHMW 59940 (1).

DIAGNOSIS: Eight canine teeth in outer row of lower jaw; palatine teeth absent; middle dorsal spines longest; membrane from spinous dorsal connected to first soft ray opposite tip of last spine; dorsal spines y 4.11; dorsal rays y 20; total anal rays y 17.12; caudal vertebrae y 18; no opercular serrations; number of scales from lateral line to soft dorsal and total number of gill rakers are greater than in any other species of *Parapercis*: proportionately larger head, snout length, and interorbital width to standard length than for any other species of *Parapercis*.

COLOR IN ALCOHOL: Upper half of body brown, lower half light tan; head brown; upper lip brown, spinous dorsal with very fine brown specks; membrane between soft dorsal rays with three or four brown spots; caudal slightly brown at base; anal with two longitudinal rows of brown spots; light brown patch at base of pectoral fin.

RANGE: New Zealand; Chatham Islands and Alderman Islands.

**Parapercis allporti** (Günther)

Figs. 1K, 3K, 6C

**Percis allporti** Günther, 1876, p. 394 (type locality, Tasmania); 1880, p. 28 (Bass Straits, 38 fathoms, Twofold Bay, 120 fathoms). Macleay, 1881, p. 564. Johnston, 1883, p. 115; 1891, p. 33.


**Parapercis allporti** Waite, 1889, p. 111. McCulloch, 1914, p. 157 (Port Stephens and Newcastle, 22–60 fathoms, Gabo Island, 200 fathoms, Bass Strait, 30 fathoms, Oyster...
Fig. 3. Diagrams of dental patterns of species of *Parapercis*: J, polyophthalma and hexophthalma K, all-porti; L, gilliesi; M, haackei; N, ommatura; O, filamentosa; P, alboguttata; Q, emeryana; R, nebulosa.

*Parapercis naevosa* Servenry, 1937, pp. 72–74 and 85, pl. 2 (type locality, Western Australia).  

**SPECIMENS STUDIED:** Nine (166 to 242) New South Wales USNM 176847 (1), 176848 (3); Tasmania; Bass Strait AM 10039 (1), USNM 179797 (3); Oyster Bay WAM P251 (1).  

**DIAGNOSIS:** Eight canine teeth in outer row of lower jaw; palatine teeth absent; dorsal spines gradually longer posteriorly; membrane from spinous dorsal connected to first soft ray opposite tip of last spine; dorsal spines y five; dorsal rays y 21; total anal rays y 18; caudal vertebrae y 18; opercles not serrated.  

**COLOR IN ALCOHOL:** Background light cream, two dark gray parallel bands extend the length of the body, the lower band from the midbase of the pectoral fin to the ventral base of the caudal fin, the upper band from above the dorsal base of the pectoral fin to the mid-dorsal base of the caudal fin; ten dark gray unevenly spaced bars extend down from the mid-dorsal line, the most anterior over the nape, the second at the origin of the spinous dorsal, the third at the beginning of the soft dorsal; the next six from the soft dorsal and the last over the caudal peduncle; the tip of the entire dorsal fin dark gray; the base of the soft dorsal dark gray where the vertical bars meet the fin; other fins with no color markings.  

**RANGE:** New Zealand.  

*Parapercis schauinslandi* (Steindacher)  

**Figs. 1F, 2F, 6E**  

*Percis schauinslandi* Steindacher, 1900, p. 175 (type locality, Hawaii); 1901, pp. 496–497, pl. 3, fig. 5.  


**SPECIMENS STUDIED:** Thirty-one (34 to 121) Hawaiian Islands CNHM 47646 (2), 4237, 4238 (2), 37088 (1); BPBM 4900 (1), 278 (1); SNHM 8543 (2), 7689 (4); USNM 47228 (2); USNM 177907 (3); USNM 151573 (1), 55301–2–3–4–5 (5), 51672 (1), 126544 (2), 78087 (2), 51054 (1), USNM 49701 holotype of *Parapercis pterostigma*. Jenkins.  

*Parapercis gilliesi* (Hutton)  

**Figs. 1L, 3L, 6D**  


**SPECIMENS STUDIED:** Seven (234 to 330) Mayor Island DM 2019 (1); Caswell Sound DM 1726 (1); Solander Island DM 2213 (3); Cape Campbell DM 2192 (1); between Plate and Whale islands DM 2535 (1).  

**DIAGNOSIS:** Eight canine teeth in outer row of lower jaw; palatine teeth absent; dorsal spines gradually longer posteriorly; membrane from spinous dorsal connected to first soft ray opposite tip of last spine; dorsal spines y five; dorsal rays y 21; total anal rays y 18; caudal vertebrae y 18; opercles not serrated.
DIAGNOSIS: Six canine teeth in outer row of lower jaw; palatine teeth absent; middle dorsal spines longest; membrane from spinous dorsal connected near base of first soft ray; dorsal spines y five; dorsal rays y 21.04; total anal rays y 18.04; caudal vertebrae y 19.04; no serrations on opercles; only species with deeply forked caudal fin in the genus *Parapercis*.

COLOR IN ALCOHOL: Background light tan; spinous dorsal membrane dusky, one lengthwise row of dark spots on soft dorsal; a faint spot at base of caudal fin; faint spots on membranes between caudal rays; dorsal and ventral extensions of caudal fin dark brown, pectoral, pelvic, and anal fins unpigmented; upper lip brown, lower lip light tan.

RANGE: Hawaiian Islands.

*Parapercis filamentosa* (Steindachner)

Figs. 10, 30, 7A

*Percis filamentosa* Steindachner 1879, pp. 386, 388 (type locality, Singapore).

*Parapercis hainanensis* Lin, 1933, pp. 95-96, fig. 2 (Southern Hainan).

*Parapercis longifilis* Herre, 1944, pp. 5–6 (Singapore).

*Parapercis filamentosa* Beaufort and Chapman, 1951, pp. 21–22 (Singapore).

SPECIMENS STUDIED: Three (85 to 117) Singapore MCZ 12887 (2); NHMW (1).

DIAGNOSIS: Six canine teeth in outer row of lower jaw; palatine teeth absent; middle spines of dorsal fin longest; membrane from spinous dorsal connected near base of first soft dorsal ray; dorsal spines y five; dorsal rays y 22; total anal rays y 19; caudal vertebrae y 19; first few soft dorsal rays greatly elongated; lowest mean ratio of head length to standard length than for any other species of *Parapercis*.

COLOR IN ALCOHOL: Background light tan; upper half of body with six faint V-shaped brown markings; cheek below eye light brown; upper lip light brown; lower lip light brown at symphysis; membrane between dorsal spine I and III brown; a lengthwise row of brown spots at base of soft dorsal; brown spot at dorsal base and a smaller one at ventral base of caudal fin; tips of caudal rays brown; tips of anal rays brown; pectorals yellow, pelvics brown at posterior half.

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RANGE: Singapore; southern Hainan.

*Parapercis alboguttata* (Günther)

Figs. 1P, 3P, 7B

*Percis alboguttata* Günther, 1872, p. 424 (type locality, Misol Island); In Brenchley, 1873, p. 422, pl. 32, fig. B. Boulenger, 1888, p. 662 (Muscat).


SPECIMENS STUDIED: Four (134 to 253) Manila Bay, Philippine Islands UW 10298 holotype of *Parapercis tesselata* Herre; China Sea 6.5 miles S.W. of Monja Islands USNM 179804 (2); Muscat, Arabia BM 1887.11.12.226 (1).

DIAGNOSIS: Six canine teeth in outer row of lower jaw; palatine teeth absent; middle spines of dorsal fin longest; membrane from spinous dorsal connected near base of first soft dorsal ray; dorsal spines y five; dorsal rays y 22; total anal rays y 19; caudal vertebrae y 19; smallest mean depth at the caudal peduncle of all species in the genus.

COLOR IN ALCOHOL: Background reddish brown; traces of about 10 blackish vertical bars below lateral line from behind pectoral fin base to caudal fin base; each scale above the lateral line margined with black; a dark diffuse spot at dorsal base of caudal fin; the middle third of the caudal fin darkened posteriorly; dorsal and anal fins with traces of dark pigment.

*Parapercis emeryana* (Richardson)

Figs. 1Q, 3Q, 7C

*Percis emeryana* Richardson, 1842, pp. 130–131 (type locality, Depuch Island); 1843, p. 4, pl. 1, fig. 1. Bleeker 1853, p. 26; 1855, p. 6.

SPECIMENS STUDIED: Eight (129.5 to 233) West Australia BM 1884.5.13 (1); Ex Mouth Gulf, West Australia AM IB3022 (1); N.W. Australia BM 1887.5.15.6 (1); Dampier Archipelago AM IB3074 (1); Shark Bay WAM P4284 (1); Mandurah WAM 71 (1); Queensland; Wide Bay WAM P249 (1); 20 miles off Bustard Head WAM P250 (1).

**DIAGNOSIS:** Six canine teeth in outer row of lower jaw; palatine teeth absent; middle dorsal spines longest; membrane from spinous dorsal connected near base of first soft dorsal ray; dorsal spines y five; dorsal rays y 22; total anal rays y 19; caudal vertebrae y 19; no serrations on opercles; three dark stripes across interorbital space.

**COLOR IN ALCOHOL:** Background brown on back, light tan ventrally, five brown bars extend from soft dorsal over the sides, the bars are narrower than the light interspaces; cheek brown; three dark stripes connecting eyes across the interorbital; two dark stripes reaching from anterior margin of each orbit to upper lip, the inner two of which are connected to each other by a transverse dark stripe; lower lip with a dark band on posterior 2/3; spinous dorsal black between spines I and V; soft dorsal with dark spots on distal part of rays and membranes; four or five wavy bars across posterior half of caudal; eight to ten oblique stripes on membranes between soft anal rays; pelvics dusky between rays.

**RANGE:** From Bustard Head, Queensland to Dampier Archipelago, Western Australia.
Fig. 5. A, Parapercis ramsayi AM IA 2480 Sidney, New South Wales, total length 236 mm; B, P. multifasciata UMMZ 176702 Japan, total length 173 mm; C, P. binivirgata AM IA 531 New South Wales, total length 142 mm; D, P. sexfasciata USNM 176715 Tateyama Bay, Japan, total length 157 mm; E, P. mimaseana TV 7814 Kochi, Japan, total length 126.5 mm.
Parapercis nebuloa (Quoy and Gaimard)  
Figs. 1R, 3R, 7D


Percis concinna De Vis, 1885, p. 546 (Moreton Bay).

Parapercis nebulosus Waite, 1899, p. 111. Waite, 1904, p. 49 (New South Wales). McCulloch, 1914, p. 156 (Queensland, off Bustard Head lighthouse, 11–21 fathoms; Fraser Island, 14–16 fathoms; Double Island Point, 29 fathoms; mouth of Wide Bay). Whitley, 1948, p. 27 (D’Entrecasteaux Point to Eighty Mile Beach). Ogilby, 1954, p. 84, fig. 99.

Percis coxi Waite, 1899, p. 111.


SPECIMENS STUDIED: 25 (71 to 275) Persian Gulf USNM 147985 (18); Durban, Natal ANSP 63834–5 (2); 53451 (1); Natal Coast ANSP 55222 (1), 54824–5 (2), 55310 (1).

DIAGNOSIS: Six canine teeth in outer row of lower jaw; palatine teeth absent; middle dorsal spines longest; membrane from spinous dorsal connected near base of first soft ray; dorsal spines y five; dorsal rays y 22; total anal rays y 19; caudal vertebræ y 19; no serrations on opercles; greatest mean number of oblique rows of scales above lateral line, scales from lateral line to the anus, and scales in a zigzag row around the caudal peduncle other than species of the genus Parapercis.

COLOR IN ALCOHOL: Background grayish brown, back darker than belly; a light brown band extends from the opercular spine to the midbase of the caudal fin; above this band are eight large black V-shaped markings; below this band are nine black bars which may or may not reach the midventral line; these nine black bars are connected dorsally by a black band that extends from the base of the pectoral fin to the midbase of the caudal fin; over the suprascapula there is a large dark blotch that may or may not be partially surrounded by a thin light ring; a faint dark band extends from the top of the snout back to each eye; a light tan bar extends vertically across the cheek; upper lip gray; lower lip tan; spinous and soft dorsal with many very fine dark brown specks; large dark spots scattered over caudal fin; a large black blotch at midbase of caudal fin which may be separated into two distinct spots; anal fin with vertical oblong spots on basal portion of membranes between rays; pectoral fin with a large dark blotch at its base; pelvic fin dusky on medial half.

RANGE: Durban, Natal; Persian Gulf; Madagascar; Reunion; West Australia; New South Wales; Queensland.

Parapercis haackei (Steindachner)  
Figs. 1M, 3M, 7E

Percis haackei Steindachner, 1884, pp. 1070–1071 (type locality, Saint Vincent Gulf).

Parapercis haackei McCulloch, 1914, pp. 155–156, pl. 34, fig. 2 (Investigator Strait, South Australia). Waite, 1923, pp. 161–162, fig. p. 162 (Investigator Strait). Waite, 1928, p. 8 (South Australia). Whitley, 1948, p. 27 (Doubtful Bay to Murchison River).

SPECIMENS STUDIED: Nine (59 to 109) Aus-
tralia; Rott Nest Island, West Australia USNM 179832 (4); Albany WAM P1224 (1); Donggarra WAM P2507 (1); Recherche Archipelago WAM P2602 (1); Gulf of St. Vincent NHMW 60747 (1); Investigator Strait NHMW (1).

DIAGNOSIS: Ten canine teeth in outer row of lower jaw; palatine teeth present; middle dorsal spines longest; membrane from spinous dorsal connected to base of first soft dorsal ray; dorsal spines y 5; dorsal rays y 22; total anal rays y 19; caudal vertebrae y 19; only species of genus with scales in interorbital space.

COLOR IN ALCOHOL: Background light gray, belly light yellow; a wide dark broken band extends from the posterior edge of the eye to the dorsal base of the caudal fin, this band covers both sides of the lateral line along the front half of the body then is above the lateral line the remaining distance; nine blackish vertical bars below lateral line from behind pectoral fin base to caudal fin base, these bars may or may not reach the midventral line; very dark spot on membranes between dorsal spines II to V; soft dorsal with two or three lengthwise rows of dark spots on membranes, lower row of spots at base of rays; of three rows present upper row of spots smallest; anal fin with two lengthwise rows of dark spots on membranes, proximal row at base of rays; dark vertical bar extends from dorsal to ventral margins at base of caudal fin rays; scattered dark spots on caudal fin; pelvics light yellow; two faint dark lines extending from tip of snout to anterior margin of eye; two dark spots on side of upper lip; dark streak on side of lower lip.

RANGE: From the Gulf of St. Vincent in South Australia to off the mouth of the Murchison River in Western Australia.

**Parapercis cylindrica** (Bloch)
Figs. 1E, 2E, 8A

**Sciaena cylindrica** Bloch, 1797, pp. 37-38, pl. 299, fig. 1 (type locality, East Indies).

**Bodianus sebae** Bloch, 1801, p. 335.

**Sciaena cylindrica** Cuvier and Valenciennes, 1829, pp. 267-268 (Molukkus). Bleeker, 1849, p. 55 (Indo-Australian Archipelago); 1851, pp. 235-236 (Banda); 1857, p. 371 (Sangi Islands); 1858, p. 199 (Goram Archipelago); 1860, p. 43 (Celebes).

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**Chilias synaphodesmus** Fowler, 1946, pp. 211 and 213, fig. p. 170 (Riu Kiu Islands).

**Cilias synaphodesmus** Matsubara, 1955, p. 692.

**SPECIMENS STUDIED:** 187 (61.5 to 125.5)
Philippine Islands: Sulu CNHM 40791-92 (2); UMMZ 100359 (3); UW 7601 (9); SNHM 34131 (9), 26498 (4); Cebu UW 7589 (8); USNM 122477 (4), 122478 (4), 122595 (1), 122480 (2), 122475 (1), 122544 (10); CNHM 47383 (3); SNHM 26499 (6); UW 7590 (45); Catalognan USNM 113227 (1); Romblon USNM 122479 (1); Pandanon USNM 122476 (1), 122545 (3); Guihulgan USNM 122481 (1); Amboina USNM 122386 (1). Fiji Islands: CNHM 47747 (1), 47748 (1), 24867 (1), 37090–92
Revision of *Parapercis*—Cantwell

Fig. 6. A, *Parapercis muronis* TU 7815 Kochi, Japan, total length 113 mm; B, *P. colias* DM 957 Lyall Bay, New Zealand, total length 191 mm; C, *P. allporti* AM 10040 Bass Strait, Tasmania, total length 234 mm; D, *P. gilliesi* DM 2535 Bay of Plenty, New Zealand, total length 234 mm; E, *P. schauinslandi* SNHM 37088 Hawaii, total length 108 mm, note deeply crescent caudal fin.
(3), 37095–4 (2); USNM 82928 (1); Marshall Islands: UW 10304 (5); USNM 140795 (1). Australia: Hayman Island, Cumberland Group USNM 177914 (3), Green Island, AM IB4073 (1); USNM 179802 (1), 179795 (1); West Cairns USNM 177915 (2); Eclipse Island, Great Barrier Reef MCZ 38508 (1), AM 2343 (1), 2344 (1); Heron Island, Capricorn Group USNM 179795 (1), 179796 (1); Rongelap Atoll USNM 140790 (1); UW 11988 (1). East Indies RVNH 5945 (27), 8537 (8); Celebes RVNH 12638 (1); locality unknown USNM 177904 (2).

**DIAGNOSIS:** Ten canine teeth in outer row of lower jaw; palatine teeth present; middle dorsal spine longest; membrane from spinous dorsal connected near base of first soft dorsal ray; dorsal spines y five; dorsal rays y 21.04; total anal rays y 18; caudal vertebrae y 19.04; only species with serrated interpercle; mean ratio of greatest depth to standard length larger than other species of the genus.

**COLOR IN ALCOHOL:** Background light tan, back dark brown with vertical lines extending ventrally to nine wide vertical bars that meet their fellow from other side at the midventral line; a brown vertical bar extends ventrally from under branchiostegals, this bar may or may not reach the midventral line; large brown blotch on spinous dorsal between spines II and V; brown spots scattered over dorsal, caudal, and anal fins; brown bar extends from lower margin of eye over cheek; a light band bordered on each side by brown extends from tip of upper lip to front of eye; lower lip with a brown spot at tip and one oblong brown spot on either side; a long brown streak on side of upper lip; top of head dark brown.

**RANGE:** Great Barrier Reef and Queensland, Australia; East Indies; Philippines; Riu Kiu; Marshall and Fiji islands.

**Parapercis snyderi** Jordan and Starks
Figs. 1D, 2D, 8B


**Neopercis snyderi** Jordan and Metz, 1914, p. 41, fig. 35.

**Cilias snyderi** Matsubara, 1955, p. 692.

**SPECIMENS STUDIED:** Eight (38 to 88.5) Korea USNM 51498 holotype of **Parapercis snyderi** Jordan and Starks, Japan, USNM 73843 (2), USNM 176719 (1), 176707 (4).

**DIAGNOSIS:** Eight canine teeth in outer row of lower jaw; palatine teeth present; middle dorsal spines longest; membrane from spinous dorsal connected near base of first soft ray; dorsal spines y five; dorsal rays y 21; total anal rays y 18.15; caudal vertebrae y 18.75; lowest mean number of scales in an oblique row above the lateral line, number of scales from the lateral line to the anus, and number of scales in a zigzag row around the caudal peduncle.

**COLOR IN ALCOHOL:** Background light tan; four dark V-shaped marks on sides above lateral line; seven faint dark bars on side below lateral line; membranes between dorsal spines dark; soft dorsal fin with three or four lengthwise rows of transparent spots each circled with a dark ring; dark patch at anterior and posterior bases of pectoral fins, pelvics with no markings; upper lip with a dark band from rictus to rictus; lower lip with three dark spots.

**RANGE:** Korea; Japan to Formosa.

**Parapercis pulchella** (Temminck and Schlegel)
Figs. 1G, 2G, 8C


**Parapercis pulchella** Bleeker, 1873, p. 127 (China); 1879, p. 18. Jordan and Snyder, 1902, p. 759 (Yokohama); 1920, pp. 463–465 and 496 (Wakanoura and Nagasaki).
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**Cilias pulchella** Matsubara, 1955, p. 692.

**SPECIMENS STUDIED:** 73 (59 to 148 mm) paratypes of Percis pulchella RVNH 416 (6), Zanbar MCZ 4494 (2); Hong Kong USNM 7649 (1); Japan USNM 57751 (5), 57517 (1), 131097 (1), CNHM 55544 (1); RVNH 5947 (6); Nagasaki UMMZ 176703 (1); USNM 50256 (5); ANSP 26192–94 (3); SNHM 7062 (2); Kagoshima USNM 59640 (1), 59641 (2); Shimizu Suruga USNM 71466 (2); Misaki UMMZ 176686 (1), 176697 (4), 176682 (1); CNHM 57490 (1); Tateyama Bay UMMZ 176716 (2), 176717 (1); Sagami Sea CNHM 55572 (4); Yokohama ANSP 615 (1); Idzui Sea CNHM 55604 (5); Suruga Bay UMMZ 176687 (6), 176710 (3); Tokyo Bay TU (2); Bali AM IB131 (1); locality unknown TU 17699 (1), 57314 (1).

**DIAGNOSIS:** Eight canine teeth in outer row of lower jaw; palatine teeth absent; middle dorsal spines longest; membrane from spinous dorsal connected near base of first soft ray; dorsal spines y five; dorsal rays y 21.1; total anal rays y 18.06; caudal vertebrae y 19; dorsal three or four branched rays of caudal fin extending beyond rest of fin; characteristic black 3-shaped mark over nape.

**COLOR IN ALCOHOL:** Background reddish brown; scales on back and side margin with black; a light band extends from the dorsal base of the pectoral fin to the midbase of the caudal fin; a characteristic 3-shaped black mark over temporal bone; behind this are two V-shaped black markings; two to four black bars extend over cheek; a black band extends over upper lip back to the eye; a black patch at base of pectoral fin; light spots margined in black on membranes between rays of caudal fin; ventral half of caudal fin has dusky appearance; lower half on spinous dorsal membrane black especially between spines III to V; soft dorsal speckled with many very fine black specks; membranes between anal fin rays with one to four light patches margined with black; near distal tip of each anal ray black, extreme tip light; a dark streak between pelvic rays III and IV, and IV and V; upper lip with black spot over premaxilla; lower lip with black spot over symphysis and one on either side; large black spots over throat region.

**RANGE:** Durban; Zanzibar; east coast of Africa; Comores; China Sea; Hong Kong; Japan.

**Parapercis ommatura** Jordan and Snyder

Figs. 1N, 3N, 8D


**Cilias ommatura** Matsubara, 1955, p. 692 (Southern Japan).

**SPECIMENS STUDIED:** 49 (67.5 to 107) Japan: RVNH 4836 (1); Nagaasaki USNM 179803 (5); co-types of **Parapercis ommatura** Jordan and Snyder, UMMZ 176705 (1), USNM 50260 (5); Tokyo USNM 50261 (2), Kobe CNHM 57174 (2), ANSP 26000–7 (8), Tsuruga MCZ 29001
FIG. 7. A, Parapercis filamentosa MCZ 12887 Singapore, total length 117 mm, showing the extremely long soft dorsal fin rays; B, P. alboguttata UW 10298 Manila Bay, Philippine Islands, total length 134 mm; C, P. emeryana AM IB 3074 Dampier Archipelago, North West Australia, total length 129.5 mm; D, P. nebulosa USNM 147985 Tarut Bay, Saudi Arabia, total length 158.5 mm; E, P. haackei USNM 179832 Rott Nest Island, West Australia, total length 98.5 mm.
(3), USNM (5), Wakanoura ANSP 26307 (1), Obama Bay UMMZ 176698 (3), Toba UMMZ 142751 (5), USNM 151813 (2); USNM 39965 (1), 59644 (1), 57527 (1); Inland Sea of Japan BM 1902.10.31.55-56 (2); Korea USNM 3776 (2); China USNM 6867 (3).

DIAGNOSIS: Eight canine teeth in outer row of lower jaw; palatine teeth absent; middle dorsal spines longest; membrane from spinous dorsal connected near base of first soft ray; dorsal spines y five; dorsal rays y 22; total anal rays y 19.04; caudal vertebrae y 19.04; lowest mean maxillary length to standard length.

COLOR IN ALCOHOL: Background light tan; three or four dark V to Y-shaped marks on sides; two narrow longitudinal dark bands across cheeks; diffuse dark spots on membranes between dorsal spines; soft dorsal fin with three rows of elongate spots on membranes; soft anal rays light yellow with a dark patch near tip; pelvics dark except at base and tips of rays; pectorals yellow; ocellus at dorsal base of caudal fin.

RANGE: North China; Korea; Japan.

*Parapercis cephalopunctata* (Seale)

Figs. 1C, 2C, 8E

*Parapercis cephalopunctata* Seale, 1901, p. 124 (type locality, Marianas).

*Parapercis montillai* Martin and Montalban, 1935, pp. 224–225, pl. 2, fig. 2 (Mindoro, Mindanao, Calapan).


SPECIMENS STUDIED: 481 (47 to 152.5) Guam BPBM 262 holotype of *Parapercis cephalopunctata*, Seale; Philippine Islands: Dasol Bay USNM 148506 (1); Dumaguete UW 7609 (1); Fiji Islands; MCZ 28303 (1); CNHM 37098–37102 (5); USNM 82786 (2); Colombo, Ceylon CNHM 47438 (1); NHMW (1); Marshall Islands: Eniwetok UW 10302 (6), 8653 (4), 12209 (1), 9136 (1), 12212 (1), 8871 (1), 12234 (1), 12210 (1); Bikini UW 10282 (2), 10291 (1), 10289 (3), 10300 (1), 10283 (2), 10292 (3), 10220 (2), 10287 (3), 10294 (2), 12211 (2), 10295 (4), 10280 (1), 10284 (4), 10303 (20), 10299 (16), 10309 (2), 10285 (3), 10569 (2), 10281 (3), 10306 (10), 10296 (7), 10420 (4), 10279 (1), 10398 (32), 10287 (2), 10564 (2), 10288 (3), 10305 (1), 10278 (1), 10290 (4), 10307 (20), 10293 (3); Kwajalein UW 10286 (3); Rongelap UW 12207 (2); Arno USNM 140784 (11), 140782 (12), 140785 (24), 140786 (31), 166740 (2), 154584 (25), 140781 (5), 140773 (14), 140777–80 (6), 140774 (6), 140800 (6), 140794 (10), 140783 (6), 140974 (1), 140776 (8), 140778 (2), 140799 (4), 140798 (4), 142280 (2); Ponaew UW 12009 (2); Ifaluk GVF (8); Raroia GVF (3); Riu Kiu Islands USNM 75502 (2); Caroline Islands: Palau GVF (5); Canton Island USNM 115413 (3), 115414 (6); Society Islands: MCZ 12889 (1), Tahiti USNM 177913 (6), 177911 (8); Samoa Islands: Rose Island USNM 115415 (2); Tau Island USNM 115418 (5); 52283 (3); CNHM 37139–37140 (2); Moorea GVF (5); Tuamotu Archipelago GVF (1); Gilbert Islands USNM 167387 (8), AM IA5346 (1), IA5347 (1), IA5348 (1); East Indies RVNH 8536 (1), 8539 (6), 5949 (3); Java RVNH 414; Mauritius NHMW (1); USNM 177905 (3).

DIAGNOSIS: Six canine teeth in outer row of lower jaw; palatine teeth absent; middle dorsal spines longest; membrane from spinous dorsal connected to first soft ray opposite tip of last spine; dorsal spines y 4.00; dorsal rays y 20.96; total anal rays y 17.98; caudal vertebrae y 19; large opaque white rectangle at distal end of caudal fin.

COLOR IN ALCOHOL: Background light yellow or reddish-brown; back with nine wide dark bars connected by an irregular band, this band extends ventrally between each of the back bars forming nine other vertical bars extending toward and may reach the midventral line; the nine ventral bars are connected by a thin dark line extending from the pectorals to the lower base of the caudal fin; over the suprascapula there is a dark patch; two dark dots over temporal bone; three dark patches on cheek, seven spots on snout, three spots on upper lip, five spots on lower lip; membrane dusky between dorsal fin spines; soft dorsal fin with three lengthwise rows of dark spots, the ventral row at base of rays; a large dark blotch at base of ventral half of caudal fin; small dark spots scattered over caudal fin; pectoral fin with a large
dark spot at ventral base; pelvics and anal yellowish white, subopercle and interopercle with a faint dark patch.

RANGE: Riu Kiu; Philippines; Marshalls; Gilberts; East Indies; Samoa Islands; Fiji Islands; Canton Islands; Caroline Islands; Guam.

*Parapercis clathrata* Ogilby
Figs. 1C, 2C, 9A

*Bodianus tetracanthus* Lacepède, 1802, pp. 285 and 302 (type locality, unknown).

*Percis tetracanthus* Kner and Steindachner, 1866, pp. 362–363, table 3, fig. 18 (Samoa Islands). Günther, 1876, p. 158, pl. 93, fig. B (Östindischen Archipels, Fidschi and Pelew Inseln, Schiffer Inseln, Gesellschafts Inseln). Garman, 1903, p. 233 (Fiji Islands).


SPECIMENS STUDIED: 84 (52.5 to 152.5) Marshall Islands, Eniwetok UW 10577 (1), 12214 (1); Bikini UW 12213 (1), 10301 (2), 10293 (3); USNM 140775 (1); Kwajalein USNM 152960 (2); Rongelap 140792–93 (3), 140791 (5); Arno USNM 166739 (2), 140787–88 (3), 140796–97 (2), 140789 (5); Ponape Islands GVf (1); Ifaluk GVf (16); Caroline Islands: Palua GVf (36); Persian Gulf USNM 196492 (2).

DIAGNOSIS: Six canine teeth in outer row of lower jaw; palatine teeth absent; middle dorsal spines longest; membrane from spinous dorsal connected to first soft ray opposite tip of last spine; dorsal spines y 4.11; dorsal rays y 20.96; total anal rays y 19; caudal vertebrae y 19; large opaque white rectangle at distal end of caudal fin; a black ocellus above operculum.

COLOR IN ALCOHOL: Background light yellow or reddish brown; back with nine wide dark bars connected by an irregular band, this band extends ventrally between each of the back bars forming nine other vertical bars extending to-ward but not reaching the midventral line; the nine ventral bars are connected by a thin dark line extending from the pectorals to the lower base of the caudal fin; these nine ventral bars may be faded so that only nine small isolated black spots remain; over the suprascapula there is an ocellus that may or may not be circled with a narrow light ring; two dark dots over temporal bone; three dark patches on cheek, seven spots on snout, three spots on upper lip, five spots on lower lip; membrane dusky between dorsal fin spines; soft dorsal fin with three lengthwise rows of dark spots, the ventral row at base of rays; a dark blotch at dorsal and ventral base of caudal fin; small dark spots scattered over caudal fin; pectoral fin with a large dark spot at ventral base; pelvics yellowish white; anal fin with one lengthwise row of dark spots; subopercle and interopercle with a faint dark pitch; cream spot at posterior tip of maxillary; light cream blotch on cheek.

RANGE: Philippines; Marshalls; Gilberts; East Indies; Samoa Islands; Fiji Islands; Canton Islands; Caroline Islands; Persian Gulf.

*Parapercis hexophthalmus* (Cuvier and Valenciennes)

Figs. 1J, 3J, 9B

*Percis cylindrica* Rüppell, 1828, pp. 19–20, pl. 5, fig. 2 (type locality, Djetta and Massaua).


*Percis caudimaculata* Rüppell, 1835, p. 98. Bleeker, 1849, p. 54 (Indo-Australian Archipelago); 1853, p. 163, Celebes; 1858, p. 459 (Cocos Islands); 1860, p. 275 (Celebes).

*Pinguipes didikuar* Thiollier, 1856, pp. 499–500.

*Parapercis hexophthalmus*, Bleeker, 1868, p.
Fig. 8. A, Parapercis cylindrica CNHM 47747 Fiji, total length 115 mm; B, P. snyderi UMMZ 176719 Japan, total length 88.5 mm; C, P. pulchella UMMZ 176682 Japan, total length 140 mm; D, P. ommatura SU 6712 Nagasaki, Japan, total length 70 mm; E, P. cephalopunctata USNM 177911 Tahiti, total length 135 mm.
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272 (Gebe); 1875, p. 78 (Madagascar and Reunion); 1878, p. 53 (New Guinea). Jordan and Seale, 1907, p. 46 (Luzon and Panay). McCulloch, 1929, pp. 331–332 (Massowah, Queensland, India, East Indies, Solomons, Shortland Islands).

Percis caudimaculatus Haly, 1875, p. 269 (North China).


Parapercis hexophthalma Fourmanoir, pp. 189 and 214 (Comores, 8–15 meters).


SPECIMENS STUDIED: Thirteen (174.5 to 226) Red Sea USNM 49310 (1); Zanzibar MCZ 4493 (1), 1070 (2), 1018 (1), 12891 (1); Society Islands MCZ 12888 (1); Fiji Islands CNHM 37095–7 (3); USNM 82926 (1), 82927 (1); Riu Kiu Islands USNM 75862 (1).

DIAGNOSIS: Eight canine teeth in outer row of lower jaw; palatine teeth absent; middle dorsal spines longest; membrane from spinous dorsal connected to first soft ray opposite tip of last spine; dorsal spines y five; dorsal rays y 21.09; total anal rays y 18.09; caudal vertebrae y 19.09; no serrations on opercles; three to seven ocelli along side of body; large oblong black spot on caudal fin; head with transverse lines across cheek.

COLOR IN ALCOHOL: Background yellowish brown with back darker brown and belly lighter yellow, back with many small dark blotches; head spotted; three to four small dark ocelli below midside from below pectoral fin base to opposite rear of anal fin base; three irregular rows of spots or oblong dashes (middle row with smaller spots or dashes) at midside from rear of pectoral fin base to base of caudal fin; a large dark spot on membrane between dorsal spines II to IV; soft dorsal fin with three or four lengthwise rows of dark spots on membranes; on middle of anal fin one row of small dark spots; a large dark oblong blotch on middle of caudal fin, remainder of fin light in color and dark spotted; usually four spots on base of pectoral fin, one or two dark spots on scaled portion of pectoral fin rays; no color markings on pelvics; four to seven transverse light or dark bars extend across cheek, preopercle, subopercle and opercle.

RANGE: Durban, Zanzibar; east coast of Africa; Madagascar; Reunion; Seychelles; Andamans; Red Sea; Cocos Islands; India; Indo-Australian Archipelago; North China; Riu Kiu; Lusiiades; Philippines; Queensland; Santa Cruz Islands; Solomons; Society Islands; New Hebrides.

Parapercis polyophthalma (Cuvier and Valenciennes)

Figs. 1J, 3J, 9C


SPECIMENS STUDIED: Nineteen (117 to 198) Red Sea CNHM 4030 (1); Zanzibar MCZ 4493 (3), 12891 (1); Rennell Islands CAS 6018 (1); Riu Kiu Islands CNHM 55531 (1); USNM 75862 (2), 75501 (4); Philippine Islands: Luzon USNM 55926 (1); Biri Channel USNM 12233–34 (2), 122484 (1), 122546 (1). Also USNM 111236, New Caledonia, dried specimen.

DIAGNOSIS: Eight canine teeth in outer row of lower jaw; palatine teeth absent; middle dorsal spines longest; membrane from spinous dorsal connected to first soft ray opposite tip of last spine; dorsal spines y five; dorsal rays y 21.05; total anal rays y 18.05; caudal vertebrae
y 19; no serrations on opercles; five to seven ocelli along side of body.

COLOR IN ALCOHOL: Background yellowish brown with back darker brown and belly lighter yellow, back with many small dark blotches; head spotted; five to seven small dark ocelli below midside from below pectoral fin base to opposite rear of anal fin base; three irregular rows of spots or oblong dashes (middle row with smaller spots or dashes) at midside from rear of pectoral fin base to base of caudal fin; a large dark spot on membrane between dorsal spines II to IV; soft dorsal fin with three or four lengthwise rows of dark spots on membranes; on middle of anal fin one row of small dark spots; a large dark oblong blotch on middle of caudal fin, remainder of fin light in color and dark spotted; usually four spots on base of pectoral fin, one or two dark spots on scaled portion of pectoral fin rays; no color markings on pelves; two horizontal rows of brown spots extend from rictus across cheek.

RANGE: Zanzibar; east coast of Africa; Red Sea; Riu Kiu Islands; Philippines; Rennell Islands.

Parapercis tetracantha (Lacepède)
Figs. 11, 21, 9D

Labrus tetracontus Lacepède, 1800, middle fig. opposite p. 493; 1802, p. 428 (type locality, unknown).


Percis tetracantha Bleeker, 1853, p. 458 (Java); 1857, p. 371 (Sangi Islands); 1859, p. 331, (Java); 1860, p. 40 (Sumatra). Kner and Steindachner, 1866, pp. 362–363, table 3, fig. 18 (S samo Islands). Alcock, 1896, p. 316 (Bay of Bengal and Andamans). Bou-lenger, 1897, p. 573 (Rotuma).


Percis tetracantha Schmeltz, 1869, p. 16 (Fjæj Insln).


SPECIMENS STUDIED: Thirteen (147.5 to 228) Philippine Islands USNM 122338 (1); Jolo uw 7607 (1); CNHM 47548 (1); UMMZ 100560 (2); East Indies RVNH 5948 (2); 8536 (1); 8539 (1); Ambon RVHN 20512 (1); locality unknown USNM 17187 (2); SU (1).

DIAGNOSIS: Six canine teeth in outer row of lower jaw; palatine teeth absent; middle dorsal spines longest; membrane from spinous dorsal connected to first soft ray opposite tip of last spines; dorsal spines y five; dorsal rays y 20.9; total anal ray y 17.9; caudal vertebrae y 19; color pattern similar to P. clathrata; large ocellus over suprascapula.

COLOR IN ALCOHOL: Background yellowish brown with back darker brown and belly lighter yellow; the upper half of the body from nape of neck to base of caudal fin with nine wide dark brown bars, the first three of which extend ventrally to the lateral line; a narrow dark brown band connects these nine bars ventrally; nine other wide dark bars extend ventrally from this longitudinal band, the last eight of which reach the midventral line; anteriorly the ventral bars are directly under the dorsal bars but become progressively more alternating toward the caudal; a narrow dark brown band extends longitudinally from the base of the pectoral fin to the ventral base of the caudal fin connecting the nine ventral bars; over the suprascapula there is a large ocellus the center of which is brown and is surrounded by a thin black ring,
Fig. 9. A. *Parapercis clathrata* UW 12214 Eniwetok, total length 133.5 mm; B. *P. hexophthalma* USNM 147454 Red Sea, total length 187 mm; C. *P. polyophthalma* CAS 6018 Rennell Islands, total length 161 mm; D. *P. tetracantha* RVNM 20512 Ambon, total length 180 mm; E. *P. xanthozona* USNM 109818 Gulf of Siam, total length 142 mm; F. *P. aurantiaca* USNM 195872 Japan, total length 162.5 mm.
this black ring may or may not be surrounded by a thin light tan ring; there is a thin dark streak across the interorbital, and another that connects the eyes just in front of the interorbital; the front half of the cheek is dark brown, the rear half light tan with many very fine dark specks; the posterior fourth of the interopercle is dark brown as well as the other opercles; each side of the upper lip has a dark brown spot at the front and a dark brown oblong spot at the side; the entire side of the lower lip is brown as well as the area immediately below the lower lip; the spinous dorsal is dusky; soft dorsal with three lengthwise rows of dark spots, the upper row near the tips of the rays, the middle row on the membranes between the rays, and the lower row partly on the membrane and rays; caudal fin with dark spots on membranes between rays; each branched anal fin ray with a dark streak near its tip; anal fin with a lengthwise row of dark spots on membrane between rays, the last few anal rays may or may not have a second spot on the membrane; pectoral fin with a dark brown spot at its base; pelvic fin light yellow.

RANGE: Bay of Bengal; Singapore; East Indies; Cocos Islands; Philippines; Society Islands; Samoa Islands; Fiji Islands; Riu Kiu; Japan.

Parapercis xanthozona (Bleeker)
Figs. 1H, 2H, 9E


Parapercis stricticeps De Vis, 1885, pp. 545-546 (type locality, Southport).

Parapercis pieurostigma Sauvage, 1891, pp. 317-318 (Batavia, Maurice, Zanzibar).

Parapercis atromaculata Fowler, 1904, pp. 548-549; pl. 24 lower fig. (Pandang, Sumatra).


Parapercis stricticeps McCulloch, 1913, p. 386; 1929, pp. 331-332.


SPECIMENS STUDIED: 19 (121 to 195) Pandang, Sumatra ANSP 27780 (1), holotype of Parapercis atromaculata Fowler; NHMW 60759 (1); Fiji Islands: CNHM 24866-7 (1); Sulu, Philippine Islands CNHM 47548 (1); Gulf of Siam USNM 109818 (2); Shortland Islands BPBM 1225 (1); Singapore RvNH 16366 (1); Amboina NHMW 60263 (1); Queensland AM II1527 (1); East Indies RvNH 5946 (8), 8538 (1).

DIAGNOSIS: Six canine teeth in outer row of lower jaw; palatine teeth absent; middle dorsal spines longest; membrane from spinous dorsal connected to first soft ray opposite tip of last spine; dorsal spines 5; dorsal rays 21; total anal rays 18; caudal vertebrae 19.

COLOR IN ALCOHOL: Background and belly light tan; upper scales on back margined with brown; below these darker scales, from the base of the pectoral fin to the base of the caudal fin occurs a light tan lengthwise band; below this band occur nine dark vertical bars; 8 to 10 dark spots on head behind the eyes; soft dorsal fin with three lengthwise rows of dark spots on membranes, lower row at base of fin; on middle of anal fin one row of spots; caudal fin with dark spots on membranes between rays; seven transverse dark bars extend across cheek and opercles on some specimens, no color markings on pelvic or pectoral fins.

RANGE: Zanzibar; Madagascar; Singapore; Gulf of Siam; Philippines; East Indies; Thursday Island; Queensland; Solomons; Japan.

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Notes on the Groupers of Tahiti, with Description of a New Serranid Fish Genus

JOHN E. RANDALL

During 1956 and part of 1957 the author carried out research on the biology of groupers (Epinephelinae; Serranidae) and snappers (Lutjanidae) in the Society Islands, with the support of a fellowship from Yale University and the Bernice P. Bishop Museum. The following 12 species of groupers were discussed in a paper by Randall and Brock (1960) which dealt primarily with food habits of Tahitian fishes:

*Epinephelus merra* Bloch  
*Epinephelus hexagonatus* (Bloch and Schneider)  
*Epinephelus fuscoguttatus* (Forskal)  
*Epinephelus elongatus* Schultz  
*Epinephelus fasciatus* (Forskal)  
*Cephalopholis argus* (Bloch and Schneider)  
*Cephalopholis urodels* (Bloch and Schneider)  
*Cephalopholis miniatus* (Forskal)  
*Cephalopholis leopardus* (Lacépède)  
*Variola louti* (Forskal)  
*Plectropomus leopardus* (Lacépède)  
*Plectropomus maculatus* (Bloch)

In addition to the above, a few specimens of four rare groupers were collected which were not positively identified in the field. Considerable museum research was needed to identify these fishes, one of which does not fit into either of two genera in which it has been previously classified. Further study has necessitated the alteration of the names of two of the more common groupers in the list of 12, *Epinephelus fuscoguttatus* and *Epinephelus elongatus*. Discussions of the four rare species and the two name changes are presented under separate headings below.

Most museum work was carried out at the U.S. National Museum (USNM), with the assistance of Leonard P. Schultz and others of the Division of Fishes. Dorothea B. Schultz made the drawing of *Epinephelus truncatus* Katayama.

**STATUS OF Cephalopholis albomarginatus**

After considerable effort a serranid fish unknown to the author, which was sighted underwater on several occasions in the Tuamotu Archipelago, was finally collected at Tetiaroa atoll in the Society Islands, near Tahiti. It was ultimately identified as *Cephalopholis albomarginatus* Fowler and Bean (1930). The specimen was deposited in the collection of the George Vanderbilt Foundation at Stanford University.

The species has been recorded on only two occasions since the original description of East Indian and Philippine specimens, once from East Africa (Smith, 1954) and once from Al-dabra in the Indian Ocean (Smith, 1955); thus a record from the Society Islands represents a noteworthy range extension.

Smith elevated the subgenus *Aethaloperca* Fowler (1904), the type species of which is *Perca roga* Forskal, to generic rank and included *albomarginata*. Although not properly belonging in *Cephalopholis*, *albomarginata* fits no better in *Aethaloperca*; therefore a new genus is proposed for this fish.

**Gracila**, n. gen.

**DIAGNOSIS.** One dorsal fin with nine spines; spines of fins slender; supramaxillary bone present; depressible teeth in jaws, those at side of lower jaw in a single row medial to a row of fixed teeth; a single pair of enlarged canine teeth at front of each jaw; head small, the length about 3.1 in standard length; depth about 2.6 in standard length; caudal fin emarginate.

**DESCRIPTION.** Dorsal rays IX, 15; anal rays III, 9 (rarely 10); dorsal and anal spines mod-

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1 Contribution from the Institute of Marine Biology, University of Puerto Rico, Mayaguez, Puerto Rico. Manuscript received August 25, 1963.
erately slender; dorsal fin unnotched, the spiny portion of fin equal in basal length to soft portion; body compressed, the width about 2 in head length and 6.5–7 in standard length; head small, about 3.1 in standard length; body depth moderate, about 2.6 in standard length; supra-maxillary (supplemental) bone present; mouth moderately large, the maxillary extending slightly posterior to eye; a pair of enlarged canine teeth anteriorly in each jaw separated by a broad gap (two adjacent canines may be present in place of a single canine), and a single row of smaller canines on sides of jaws; depressible canine teeth medial to anterior canines and in one medial row on side of lower jaw; upper jaw with a band of villiform teeth medial to fixed canines at side of jaw; a band of villiform teeth on palatines and on vomer (in V-shape on latter); tongue smooth; opercle with three flat spines, middle one closest to lower; edge of preopercle rounded with only a slight indentation above angle; upper preopercular margin finely serrate, lower margin smooth; margin of interopercle and subopercle finely serrate; head, including maxillary, scaled; scales moderately small (about 110 vertical rows between upper end of gill opening and end of hypural); scales ctenoid except on head, thorax, abdomen, and anterodorsally on body; lateral line single, continuous to base of caudal; posterior nostrils spherical; pectoral fins obliquely pointed; caudal fin emarginate; gill rakers moderately long; the one at angle slightly longer than gill filaments; 24 vertebrae.

Monotypic. Type species, Cephalopholis albolamarginatus Fowler and Bean.

DISCUSSION. Gracila shows affinities to Cephalopholis but differs principally in external morphology in its smaller head (head length of Cephalopholis 2.4–2.7 in standard length) and emarginate caudal fin (caudal always rounded in Cephalopholis). It also displays a different mode of life from Cephalopholis; it characteristically swims well above the bottom like species of Plectropomus. Cephalopholis dwells more upon the bottom and is more retiring in its habits. Gracila differs notably from Plectropomus in having 9 instead of 6–8 dorsal spines and in lacking enlarged canines of the side of the lower jaw.

Gracila is also closely related to Aethaloperca. The latter is distinctive in the steep dorsal profile of the head (the snout forms an angle of nearly 60 degrees to the horizontal; the snout angle of Gracila is about 40 degrees) and its deep body (depth about 2.2 in standard length). Also, the teeth at the side of the lower jaw of Aethaloperca (and most species of Cephalopholis) occur in more than two rows (except posteriorly on the jaw); in Gracila there are only two rows of teeth, the outer fixed and the inner depressible. Also, Gracila has much smaller anal spines.

**Gracila albolamarginata**

Figs. 1, 2


One specimen: 257 mm standard length, 318 mm total length, Tetiaroa, Society Islands, Feb. 16, 1957, J. E. Randall. Natural History Museum, Stanford University, uncatalogued.

The following counts, measurements, and observations were made from the fresh specimen: dorsal rays IX, 15; anal rays III, 9; pectoral rays 19; lateral-line scales about 115; head length 82 mm; body depth 87 mm; body width 48 mm; least depth of caudal peduncle 33 mm; diameter of eye 14.5 mm; interorbital space 18.5 mm; length of pectoral fin 52 mm; lower jaw projects 5 mm beyond upper jaw when mouth is closed; caudal concavity 13 mm; three spines on opercle, the middle located about one-third distance from lower to upper spine; preopercle entire, rounded, the upper limb finely serrate; four canine teeth in lower jaw in two close-set pairs, separated by a 5 mm gap at symphysis; teeth in upper jaw similar (only one canine on one side), separated by 11 mm; remaining teeth nearly as long, more slender, depressible, and in a double row; narrow band of villiform teeth on vomer and palatines.

Color in life reddish brown with a suffusion of orange on head, especially around mouth; numerous light grayish-blue bars on sides which nearly disappear in preservative; four diagonal
deep blue lines (dark brown in preservative) on head as in Figure 1 of an Indo-Malayan specimen, except three upper lines not continuous (uppermost line broken into two long sections and a spot; second line, from beneath eye, into a long section and two spots; and the third from maxillary groove into three spots). In preservative the edges of the fins were noted to have become white. They may have been reddish in life, as was described from African specimens by Smith (1954).

The single specimen was collected with a spear at a depth of 60 ft on the seaward side of the atoll of Tetiaroa. When seen underwater, G. albomarginata has two large white saddle-like areas on the back which are its most striking color markings. Before the speared specimen was brought to the surface, however, the white areas had disappeared and did not reappear.

The species was observed but not collected at the atolls of Takaroa, Takapoto, and Tikahau in the Tuamotu Archipelago. It was seen outside reefs and in passes, usually at depths of about 40 to at least 120 ft, but was never sighted in lagoons. Only once was it observed in water less than 50 ft deep, and when this individual was pursued it retreated into deeper water.

The largest specimen examined is the holotype (USNM 89985), 295 mm in standard length.

TAHITI RECORD OF Epinephelus truncatus

Two groupers bearing some resemblance to Epinephelus fasciatus were purchased in the market in Papeete, Tahiti, in 1957. They differ from fasciatus notably in having a shorter maxillary (maxillary of fasciatus extends to beneath posterior edge of eye), broader lips, and an opercular flap with an angularly rounded upper margin (nearly straight on fasciatus). The two fish were caught by Tahitian fishermen with hook and line at an unknown depth, but probably in excess of 100 ft, judging from the degree of distension of the stomach into the mouth from an expanded air bladder. The specimens were believed to represent an undescribed species. In the same year that they were collected a paper by Katayama appeared that described the species from islands near Japan as Epinephelus truncatus.

Epinephelus truncatus

Fig. 3

Two specimens: 222 and 238 mm standard length, Papeete market, Tahiti, May 28, 1957, J. E. Randall. USNM 75400.

Dorsal rays IX, 16 (injury to rear base of fin of one fish); anal rays III, 8; pectoral rays 19; pored scales in lateral line 68 (70); vertical scale rows from upper end of gill opening to base of caudal fin 123 (125); scale rows above lateral line 14 or 15; scales below lateral line to origin of anal fin 28 or 29; gill rakers 7 + 1 + 15 (8 + 1 + 15).

Caudal fin truncate; greatest depth of body at origin of dorsal fin, the depth contained 3 times in standard length; maxillary reaches slightly posterior to a vertical at center of eye; middle opercular spine much larger than other two, posterior in position, and slightly closer to the lower than the upper spine; opercular membrane moderately pointed, reaching posterior to a vertical at origin of pelvic fins; preopercular margin rounded, with a slight indentation above angle; 42 (48) serrations on vertical margin of preopercle, the last four enlarged; dermal flap on maxillary (continuous with upper lip) nearly reaching upper edge of maxillary; base of dorsal and anal fins moderately fleshy; origin of dorsal fin slightly posterior to a vertical at upper base of pectoral fin; anus about one-third distance from pelvic tips (when fins applied to abdomen) to origin of anal fin; first dorsal spine nearly one-third length of second, and second about three-fourths of third; third, fourth, and fifth spines the longest and nearly equal in length; remaining spines progressively shorter, the last only slightly longer than second; front of upper jaw with two large adjacent canines on each side, each of these pairs separated by a gap about equal to half eye diameter; a single row of 15 small canine teeth along side of upper jaw posterior to larger canines; lower jaw with one or a pair of large fixed canines on each side at front separated by a gap about equal to one-third eye diameter; large canines followed by a series of about 40 smaller ones extending the length of the jaw; bands of slender depressible canines medial to fixed canine teeth in both upper and lower jaws; teeth on vomer and palatines; tongue smooth.

Color when fresh dull orange, the centers of scales light greenish gray (centers now darker than edges in preservative); five faint, broad vertical bars on body which faded shortly after preservation; head mottled with light red and orange-brown; edge of orbit, except anteriodorsally, bright red (now pale in alcohol); a pale blue line adjacent to red rim of orbit and surrounding entire eye (blue line now dark in alcohol); caudal fin orange-red except olive green on upper fifth; dorsal fin olive green, the outer third of spinous portion light red basally and dark red distally (now pale with a blackish
Groupers of Tahiti—Randall

diagonal streak); a few diagonal orange lines in olive green in basal part of fin; rays orange in soft portion of dorsal; extreme base of fin with a red band; remaining fins light orange-red.

Katayama described the color of his specimens as dark red, each scale with a basal spot of greenish brown; membranes between dorsal spines tipped with black; other parts of dorsal olive; upper several rays of caudal olive, the rest of the fin red, with a dark submarginal area and a white edge; other fins red.

Because some differences seemed to exist between the Tahiti specimens and the original description given for truncatus, a request was made of Katayama for comparative material. He sent the holotype, a well-preserved specimen 319 mm in standard length. There is now little doubt that his specimen and the two from Tahiti are conspecific. Meristic data are essentially the same. The only morphological differences noted are the slightly more convex interorbital space and more rounded pectoral fins of the specimens from Tahiti. The black areas in the pale distal part of the membranes of the spinous portion of the dorsal fin of the holotype are much better developed (there are only traces of pigment distally on the spinous dorsal of the Tahitian specimens). There is no white caudal margin and dark submarginal band on the specimens from Tahiti (possibly overlooked when specimens were fresh). The border caudal markings are now very faint on the holotype. The pale edge and narrow dark submarginal line around the eye are identical on all three fish. The slight differences in morphology and color are probably due to the disparity in size of the specimens under comparison or are within the range of variability of the species. Some differences might be expected of fish collected at such distant localities as Japan and Tahiti.

ON THE VALIDITY OF Cephalopholis obtusaurus

The same fishermen who caught the two specimens of Epinephelus truncatus from relatively deep water off Tahiti brought another

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Fig. 3. Epinephelus truncatus Katayama, 238 mm standard length, Tahiti (USNM 75400). Drawing by Dorothea B. Schultz.
small grouper to market which proved difficult to identify. At first it was believed to be *Cephalopholis aurantius* (Cuvier and Valenciennes) (1828). Although this species had not been recorded previously from the Society Islands, another, *Serranus roseus* Cuvier and Valenciennes with a type locality of Tahiti, has been placed in the synonymy of *aurantius* by authors such as Boulenger (1895). Cuvier and Valenciennes described *roseus* from a painting by Parkinson in the library of Banks. A. C. Wheeler of the British Museum (Natural History) kindly sent a photograph of Parkinson’s painting. The fish is obviously *Variola lonti* (Forskal); thus it has been improperly placed in the synonymy of *aurantius*.

M. L. Bauchot of the Muséum National d’Histoire Naturelle in Paris sent the holotype of *Serranus aurantius* (Fig. 4) so that it might be compared with the specimen from Tahiti. It was soon evident that the two are not the same species.

The following observations were made of the holotype of *aurantius*, which is 165 mm in standard length and 201 mm in total length: dorsal rays IX, 15 (last ray composite, first unbranched); anal rays III, 9 (last ray composite); pectoral rays 18 (all branched except uppermost; 15 branched caudal rays; pored lateral-line scales 53 (includes 3 beyond hypural); vertical scale rows from upper end of gill opening to end of hypural about 15; gill rakers 9 + 1 + 15; depth of body 2.83 in standard length; head length 2.5 in standard length; width of body 2.3 in head length; greatest diameter of eye 6 in head length; interorbital space moderately convex, the fleshy width equal to vertical diameter of eye; maxillary reaches slightly posterior to eye; middle opercular spine slightly nearer lower than upper spine; opercular flap pointed; preopercular margin broadly rounded with a slight indentation at angle; upper limb and indentation of preopercular margin finely denticulate; small scales on head, including maxillary and mandible; scales on head and anteriorly on body cycloid; a pair of adjacent canine teeth in upper jaw (one missing on one side) separated by a space equal to .8 eye diameter; comparable canines in lower jaw separated by about .3 eye diameter; bands of villiform teeth in jaws broad anteriorly; narrow V-shaped band of villiform teeth on vomer, and narrow band on palatine in length equal to .5 eye diameter; longest gill raker at angle, about 1.5 times longer than gill filaments; pectoral fins reach a vertical at origin of anal fin; tips of pelvic fins reach slightly beyond anus; color in alcohol uniform pale yellowish; a black submarginal band at posterior

Fig. 4. Holotype of *Cephalopholis aurantius* (Cuvier and Valenciennes), 165 mm standard length, Seychelles (MNHN 765).
border of caudal fin, its width about one-third diameter of pupil; narrow blackish margin on rear half of soft portion of dorsal and all of soft portion of anal fins; a trace of dark pigment marginally on tips of pelvic fins.

Cuvier and Valenciennes described the color of the body and fins of aurantius as orange-red, without spots or bands. Bleeker (1873–1876:37, pl. 248, fig. 3) portrayed the species in color. It is rose-orange with small round blue spots on the head and the back beneath the spiny portion of dorsal fin; there is a broad yellow posterior border on the medial fins; the caudal fin has a black line within this yellow border.

The Tahiti specimen was finally identified as Cephalopholis obtusaurus Evermann and Seale (1907), after examination of the holotype in the U.S. National Museum. This species has not been recognized by authors after Evermann and Seale. Fowler and Bean (1930), Herre (1953), and Katayama (1960) have all placed it in the synonymy of aurantius; however, obtusaurus appears to be valid.

Cephalopholis obtusaurus
Figs. 5, 6.

One specimen: 185.5 mm standard length, 228 mm total length, Papeete market, Tahiti, May 28, 1957, J. E. Randall. USNM 175409.

Dorsal rays IX, 15; anal rays III, 9; pectoral rays 17; pored lateral-line scales 52 (includes 3 beyond hypural); vertical scale rows from upper end of gill opening to end of hypural 103; gill rakers 7 + 1 + 13.

Depth of body 2.77 in standard length; head length 2.50 in standard length; width of body 2.3 in head length; eye 5.1 in head length; bony interorbital nearly flat, the bony width 7.8 in head length; least depth of caudal peduncle 2.74 in head length; pectoral fins 3.83 in standard length; pelvic fins 4.52 in standard length, the tips reaching anus; third dorsal spine the longest; its length 3.36 in head length; first dorsal spine half as long as third; tenth dorsal soft ray the longest, its length 2.24 in head length; second anal spine the longest, its length 3.04 in head length; fifth anal soft ray the long-
est, its length 1.95 in head length; dorsal fin very fleshy at base; maxillary reaches posterior edge of eye; maxillary scaled, but scales mostly imbedded; opercular spines flattened, not sharp, the middle one closer to lower spine (which is somewhat anterior) than to upper; hind part of opercular membrane truncate with rounded corners; preopercular margin very finely serrate.

Color when fresh: body and fins bright orange-red, the edges of scales faintly brownish, with widely scattered small pale blue blotches; head, nape, and fins with numerous small red spots, these more evident in faint blue areas on head and caudal fin. In alcohol the specimen is pale yellowish brown with no trace of spots. Evermann and Seale described the color of the holotype as uniform yellowish, with a slight wash of dull brown, and stated that the fish was evidently uniform red in life. However, the preserved specimen shows faint, close-set pale spots (about 2 mm in diameter) on the nape.

Some differences were noted between the specimen from Tahiti and the holotype (which is nearly the same size; it measures 191 mm in standard length and approximately 238 mm in total length; the latter measurement difficult to obtain because the mouth is fully open). The holotype has a slightly smaller eye (5.64 in head length), slightly deeper caudal peduncle (3.05 in head length), maxillary not as broad (greatest width 5.5 in head length of Tahitian specimen and 6.3 in head length of holotype), longer pectoral fins, slightly longer pelvic fins (the tips reach slightly beyond anus in holotype), and longer gill rakers. In view of the many similarities, however, such as the meristic data (all counts the same except for fewer scale rows from gill opening to end of hypural—about 95 in holotype), obtuse opercular flap, position of opercular spines, fleshy dorsal fin, and color, the two specimens are regarded as belonging to the same species.

The stomach of the holotype of obtusaurus is protruding into the mouth cavity, thus suggesting that the specimen was taken from moderately deep water.

Cephalopholis obtusaurus and C. aurantius are evidently closely related species. They may be distinguished principally by the more pointed opercular flap, more convex interorbital, smaller eye, larger mouth, and higher gill raker counts of aurantius. Also, aurantius has the characteristic black submarginal line at the posterior edge of the caudal fin, which is lacking in obtusaurus.

Although other specimens of obtusaurus may be present in museums, possibly labelled as aurantius, the author knows of only the holotype from the Philippines and the one specimen from Tahiti.

ADDITIONAL SPECIMEN OF Epinephelus socialis FROM TAHI

Epinephelus socialis

Fig. 7
Serranus socialis Günther, 1873. Fische der Südsee (J. Mus. Godeffroy); vol. 1, pt. 1, p. 7, pl. 8, fig. B (type locality: Tahiti, as restricted by lectotype designation below).


Color when fresh: head and body with numerous small dark brown spots, these becoming confluent on posterior part of body to form irregular horizontal lines; caudal and soft portions of dorsal and anal fins dark brown with white spots, the anal and posterior part of caudal with a white border; spiny fins of dorsal fin light brown with irregular dark brown spots; pectorals light brown with brown spots basally, dark brown distally with a few pale spots in middle of fin; pelvic fins dark brown, the rays spotted basally, the lateral edge of the fin white near tip.

Three syntypes of Epinephelus socialis were examined in the British Museum in London. The largest of the three specimens (190 mm standard length, 236 mm total length) (BM 1873.4.3.1) from Tahiti is here designated as lectotype. Meristic data from this specimen are as follows: dorsal rays XI, 15; anal rays III, 8; pectoral rays 19; vertical scale rows from upper end of gill opening to end of hypural 103; gill rakers 9 + 1 + 16.

A year and a half of collecting fishes in Tahiti resulted in the taking of only the single specimen of this grouper. A second specimen was speared by the author in the lagoon of Takaroa in the northern Tuamotu Archipelago, at a depth of 15 ft. This was deposited in the collection of the George Vanderbilt Foundation, Stanford University.

E. socialis has been recorded from Mangareva in the southern Tuamotus (Kendall and Rcliffe, 1912). Recently it has been listed among the fishes of the Marshall Islands (Schultz et al., 1953). Poll (1942:6, fig. 1) recorded two juveniles from the lagoon of Punaauia, Tahiti.

THE IDENTITY OF Epinephelus fuscoguttatus (FORSKÅL)

Forskål (1775:42) described fuscoguttatus from the Red Sea as a variety of Perca summana. The latter is a white-spotted grouper now classified in the genus Epinephelus. The description of fuscoguttatus is brief, but the name has long been recognized as a species of Epinephelus distinct from summana. The most important characteristics given by Forskål are a black spot on the dorsal part of the caudal peduncle, circular reddish-brown spots, and 18 pectoral rays.

Morgans (1958) utilized the name fuscoguttatus for a species which Randall (1955) identified as Epinephelus horridus (Cuvier and Valenciennes). He applied the name Epinephelus dispar (Playfair) (in Playfair and Günther, 1866) to the grouper identified as fuscoguttatus by Schultz.
(1953) and Randall (1955). The confusion in deciding to which species the name fuscoguttatus should be applied is by no means confined to the authors just mentioned.

Information was requested of Jørgen Nielsen of the Universitets Zoologiske Museum in Copenhagen on the type of fuscoguttatus. He replied that the type of summana, a dried skin about 160 mm in standard length and still showing the characteristic white spots of the species, is extant, but no type material of variety fuscoguttatus is available.

The two species so long confused under the one name fuscoguttatus have numerous small reddish-brown spots and a prominent black saddle-like marking on the caudal peduncle. The one character given by Forskål which suggests one of the two species and not the other is 18 pectoral rays. The name fuscoguttatus is therefore restricted to the species with 18 or 19 pectoral rays, which is in agreement with the use of the names by Morgans, the most recent revisor (he did not, however, record pectoral ray counts).

The oldest available name for the other species appears to be Serranus microdon Bleeker (1856) (type locality, Java); thus Epinephelus microdon replaces the name Epinephelus dispar (Playfair) used by Morgans.

Data on the holotype of microdon were obtained from M. Boeseman of the Rijksmuseum van Natuurlijke Historie in Leiden, and later the specimen was examined by the author. This grouper (RMNH 5510) is now 400 mm in standard length and 490 mm in total length. Although in good condition, it was preserved with the body curved; therefore, according to Boeseman, the original length was probably a few centimeters longer. The specimen was purchased at auction in 1879, and since Bleeker (1873-1876) indicated that he had only a single 510 mm example of the species, there is little doubt that the Leiden specimen is the true holotype. Because of the curvature of the body, the photograph supplied by Boeseman (Fig. 8) shows the head foreshortened. The two broad dark bars on the body are not pigmented but shadows from large wrinkles resulting from an attempt to straighten the body before the photograph was taken. A second illustration of microdon (Fig. 9) is provided from a photograph of a smaller specimen from the Phoenix Islands.

E. fuscoguttatus and E. microdon may be distinguished as follows: fuscoguttatus, pectoral rays 18 or 19; gill rakers on lower limb of first arch 17–20 (including rudiments but not raker at angle); dorsal profile of head with an inden-

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Fig. 8. Holotype of Epinephelus microdon (Bleeker), 400 mm in standard length, Java (RMNH 5510). Photo supplied by M. Boeseman of the Rijksmuseum van Natuurlijke Historie at Leiden.
tation above hind edge of eye; maxillary extends from \( \frac{3}{4} \) to 1 eye diameter posterior to eye (seven specimens: 120–334 mm standard length, Red Sea, Zanzibar, and Gilbert Islands); microdon, pectoral rays 16 or 17 (usually 17); gill rakers on lower limb of first arch 15 or 16; dorsal profile of head smoothly convex; maxillary ends beneath hind edge of eye or extends up to half an eye diameter posterior to eye (nine specimens: 153–350 mm standard length; from Red Sea, Zanzibar, Gilbert Islands, Marshall Islands, and Phoenix Islands).

There is a slight difference in the depth of the body, microdon being the more slender form on the average (depth 2.7–3 in standard length; that of fuscoguttatus is 2.6–2.9). The dorsal soft rays of fuscoguttatus are 14 (rarely 15) and those of microdon 14 or 15 (usually 15).

Morgans (1958:656) has separated the species in a key on color. He noted that the spots of microdon (at least of adults) are more regular in outline than those of fuscoguttatus. An additional color difference is the nature of the spot beneath the spinous portion of the dorsal fin. Adults of E. microdon have a single roundish dark blotch centered at the base of the fifth dorsal spine; fuscoguttatus has two close-set blotches or a single bilobed one.

Morgans described tukula, a third species of Epinephelus from the western Indian Ocean which can be confused with fuscoguttatus and microdon. It is distinguished by the lack of small spots on the body, many rows of teeth at the front of both jaws, subequal nostrils, convex interorbital, and large size (it is believed to attain a weight of at least 240 lb). In the author's opinion tukula is the same as Playfair's Serranus dispar variety a. Since Morgans restricted dispar to variety b, his new species tukula is valid whether variety a is the same or not (unless an earlier name is found).

In view of the absence of a holotype and the instability of the classification of this complex of serranid fishes, a neotype is herein described of fuscoguttatus, based on a specimen from the Red Sea, the type locality.

**Neotype of Epinephelus fuscoguttatus (Forskal):** USNM 147594, 216 mm in standard length and 267 mm in total length, collected by Donald S. Erdman at the S.A.M. pier at Jidda, Red Sea, on July 2, 1948 (Fig. 10).

Dorsal rays XI, 14; anal rays III, 8; pectoral rays 19; gill rakers 12 + 1 + 18 (two additional small rakers between larger rakers of upper limb not counted); vertical scale rows from upper end of gill opening to end of hypural plate about 127; 25 scales in diagonal row above lateral line to origin of dorsal fin.

The following measurements are expressed as

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**Fig. 9. Epinephelus microdon (Bleeker), 153 mm standard length, Canton, Phoenix Islands (USNM 115367).**
a percentage of the standard length: greatest depth of body 38.2; width of body just behind gill opening 18.5; head length 41.4; snout length 6.1; eye diameter 6.8; postorbital length of head 27.8; horizontal distance of maxillary posterior to eye 5.4; bony interorbital space 4.9; least depth of caudal peduncle 13.0; length of caudal peduncle (to rear base of dorsal fin) 9.0; snout to origin of dorsal fin 42.4; snout to origin of anal fin 71.1; snout to origin of pelvic fin 39.8; length of dorsal fin base 57.2; length of anal fin base 17.3; length of pectoral fin 22.1; length of pelvic spine 11.1; length of pelvic fin 20.3; length of first dorsal spine 5.7; length of second dorsal spine 8.6; length of third dorsal spine 11.3; length of fourth (longest) dorsal spine 12.2; length of eleventh dorsal spine 11.4; length of first dorsal soft ray 15.0; length of longest dorsal soft ray 18.0; length of last dorsal soft ray 10.2; length of first anal spine 4.3; length of second anal spine 9.6; length of third anal spine 9.3; length of first anal soft ray 14.7; length of longest anal soft ray 18.5; length of last anal soft ray 12.2; length of caudal fin 23.6.

Profile of head consisting of two convexities which meet above center of eye; interorbital flat over most of its width (in center), rising slightly at orbits; lower jaw projecting 2.5 mm anterior to upper; middle opercular spine nearer lower than upper spine (7 mm separate tips of lower and middle spines and 12.2 mm separate tips of upper and middle spines); upper margin of opercular membrane nearly horizontal anteriorly, becoming rounded as it meets vertical hind margin (which has a protrusion slightly below level of middle opercular spine); preopercular margin very finely serrate, with no marked indentation; scales cycloid, those on head very small; maxillary finely scaled; posterior nostril subtriangular in shape, 3.8 mm in greatest measurement (height), with no rim; anterior nostril less than 1 mm in diameter, with a membranous rim which is higher posteriorly; teeth typical of genus, those on vomer small; teeth on palatine about twice as large as vomerine teeth but still not large; enlarged canines of upper jaw (a close-set pair on one side, a single tooth on the other) separated by a gap of 10 mm; single row of small, evenly spaced, fixed canine teeth along side of upper jaw; smaller depressible teeth in upper jaw in a broad patch anteriorly on each side (up to a maximum of about six irregular rows); depressible teeth of lower jaw in a band of more uniform width
(about three or four irregular rows); hind borders of all fins well-rounded; tips of pelvic fins reach within 8 mm of anus.

Color in alcohol brown with irregular dark brown blotches (those on upper third of body nearly black) and numerous small dark spots which are more evident on head and anteriorly on body. The irregular dark blotches are located as follows: an elongate one begins from lower half of hind edge of eye and angles upward to nape, meeting its fellow anterior to origin of dorsal fin; five other blotches or pairs of blotches may be seen middorsally on head anterior to one just mentioned; three irregular dark bands cross maxillary, lower jaw, and chin; all dark blotches and bands on head superimposed with the small round darker brown spots; a bilobed dark brown spot on back centered at base of fifth dorsal spine; a small dark brown spot at base of ninth and tenth dorsal spines; two irregular dark brown spots at base of soft portion of dorsal fin and a black saddle dorsally on caudal peduncle; an elongate irregular dark brown blotch below and slightly anterior to bilobed spot at base of fifth dorsal spine (lateral line runs through upper part of this blotch); a dark brown blotch in line with but posterior to the one just mentioned, also touching lateral line; five irregular brown bars on lower half of body in line with the more dorsal darker markings; dark spots along base of dorsal fin extend irregularly into fin, more obviously into spinous portion; soft portion of dorsal and other fins with interconnected round brown spots with small black centers (dark centers not very evident on pectorals); a dark brown marginal spot on each interspinous membrane of dorsal fin (except cirrus of each which is pale); other fins with very narrow pale margins.

Two syntypes of Serranus horridus Cuvier and Valenciennes from Java are also located at Leiden (RMNH 19 and 2160). Both are stuffed specimens, one 188 mm in standard length and the other 600 mm. The larger is in better condition and is here designated as the lectotype. These fish have 18 or 19 pectoral rays, a dark saddle on the caudal peduncle (not mentioned by Valenciennes in the original description), and 14 dorsal soft rays. There are two dark saddles on the back between the bases of the fourth and sixth dorsal spines, another at the end of the spinous portion of the dorsal fin, and one or two below the soft portion of the fin. S. horridus therefore seems to be a synonym of Epinephelus fuscoguttatus.

Another fish which seems to belong in the synonymy of fuscoguttatus is Serranus lutra Cuvier and Valenciennes from Mauritius. The holotype (MNHN 7278), 315 mm in standard length and 382 mm in total length, was examined by M. Blanc and R. Roux at the Muséum National d'Histoire Naturelle in Paris. They
report that it has 19 pectoral rays and 14 dorsal soft rays. A photograph was kindly supplied by Blanc, herein reproduced as Figure 11.

Blanc and Roux also examined the type of *Serranus taeniochirus* Cuvier and Valenciennes, a species which has been placed by some authors in the synonymy of *fuscoguttatus*; however this does not seem to be correct. *S. taeniochirus* has 16 dorsal soft rays and lacks a dark spot dorsally on the caudal peduncle; therefore it is probably neither *fuscoguttatus* nor *micrudon*.

At the request of the author, Eugenie Clark procured a specimen of *fuscoguttatus* from the Red Sea. The specimen (USNM 197323) measures 574 mm in standard length, 700 mm in total length, and weighs (in preservative) 9½ pounds. It was caught by trolling in 12 ft of water off Entedebin, Dahlak Archipelago, on April 5, 1962. The spots on the body were orange-brown in life, more orange ventrally, and there is a prominent black saddle on the caudal peduncle. There are 19 pectoral rays, 15 dorsal soft rays (the last two closely spaced), and 9 + 1 + 17 gill rakers. The rakers on the upper limb are sessile and difficult to count. Previous counts of the rakers on the upper limb of smaller specimens of *fuscoguttatus* were all 11–13. Possibly there is a loss of gill rakers in larger fish because of fusion.

This is the largest specimen examined by the author. Morgans (1958) reported *fuscoguttatus* from East Africa to a standard length of 760 mm, a total length of 885 mm, and a weight of 24 lb. Boulenger (1895) reported the largest as 900 mm total length. It seems obvious that it attains a greater size than does *micrudon*, the largest of which examined by Morgans is 465 mm in standard length, 565 mm in total length, and 8½ lb in weight.

A 334-mm specimen from Onotoa, Gilbert Islands, collected by the author in 1951, was colored in life as follows: light brownish yellow with numerous small orange-brown spots (more evident on head than on body) and large irregular dark brown blotches (smaller spots superimposed on the large dark blotches); one of the irregular blotches begins behind the eye and extends to the nape; those on the body occur in an irregular series of five bars, the last on the caudal peduncle beginning with the dark dorsal blotch. The large blotches are darker on the upper third of the body than on the lower two-thirds.

No individuals of *fuscoguttatus* were seen or collected in Tahiti or other islands of French Oceania. *E. micrudon*, on the other hand, is common in the Tuamotu Archipelago, although rare in the Society Islands.

**THE IDENTITY OF Epinephelus tauvina (FORSKAL)**

Figure 12 represents a photograph of the holotype of *Perea tauvina* Forskal, a dried skin, from the Red Sea. It was provided by Jørgen Nielsen of the Universitetets Zoologiske Museum in Copenhagen. He also supplied the following fin-ray counts for the specimen: dorsal rays XI, 15 or 16; anal rays III, 8; pectoral rays 18.

*Epinephelus elongatus* Schultz was described from specimens collected in the Marshall Islands, Mariana Islands, Samoa Islands, and Phoenix Islands. Two specimens in the National Museum, 110 and 218 mm in standard length, (USNM 166985–6) collected at Ghardaqa, Red Sea, by Eugenie Clark, were compared to the Pacific material of *elongatus* and proved to be the same. Specimens of *elongatus* of the same size as the holotype of *tauvina* (larger specimens have more spots than smaller ones) were compared with the photograph of the holotype, and they appear identical; thus the decision by Katayama (1960) to refer *elongatus* to the synonymy of *tauvina* seems correct.

*Epinephelus tauvina* is not common in the Society Islands. The largest of 12 specimens that were collected is 498 mm in standard length. In the smaller sizes it can be confused with two small dark-spotted groupers, *Epinephelus merra* and *E. hexagonatus*. It may be differentiated from these in having 15 instead of 16 dorsal soft rays, 27–30 gill rakers (total count) on the first arch (gill rakers of *merra* range from 20 to 23 and those of *hexagonatus* from 23 to 27), and more elongate body (depth 3.3–3.7 in standard length in contrast to 3.2–3.3 for the other two species). *E. tauvina* was observed at depths of 10–150 ft (few observations were made in deeper water) in both lagoon and outer reef environments.
Smith and Smith (1963:15, pl. 141) described *Epinephelus salonotus* from the western Indian Ocean. The type, a 10-inch specimen, was taken at Delgado, East Africa. The illustration depicts a 2-ft specimen from the Seychelles. Although the description is only 2½ lines in length and the figure small, there seems little doubt that the species is *tauvina*.

**SUMMARY**

1. *Cephalopholis albomarginatus* Fowler and Bean, known previously from the East Indies and Philippines (original description) and the western Indian Ocean, is here reported from Teriara, Society Islands. It is reclassified in the new genus *Gracila*, distinct from *Cephalopholis* principally in having a shorter head length (3.1 in standard length) and an emarginate caudal fin. The related *Aethaloperca* may be separated from *Gracila* by its steeper head profile, deeper body, more than two rows of teeth at the side of the lower jaw, and larger anal spines.

2. The range of *Epinephelus irruncatus* Katayama is extended from the Izu and Bonin islands (type locality) to Tahiti.

3. *Serranus roseus* Cuvier and Valenciennes, heretofore regarded as a synonym of *Cephalopholis aurantius* (Cuvier and Valenciennes), is synonymous with *Variola louti* (Forskal) (1775).

4. *Cephalopholis obtusaurus* Evermann and Seale, represented previously only by the type from the Philippines, is resurrected from the synonymy of *C. aurantius* and recorded from Tahiti.

5. A second specimen of the rare grouper *Epinephelus socialis* (Günther) is recorded from Tahiti. The first, the largest of three syntypes in the British Museum, is designated lectotype, thus restricting the type locality to Tahiti.

6. The name *Epinephelus fuscoguttatus* (Forskal) has been applied to either of two common groupers with reddish-brown spots and a black saddle on the caudal peduncle. It is here restricted to the species with 18 or 19 pectoral rays, 17–20 gill rakers on the lower limb of the first arch (including rudiments but not raker at angle), a more marked indentation in the profile of the head, and a larger mouth. The oldest available name for the other species, which has 16 or 17 pectoral rays and 15 or 16 gill rakers on the lower limb, is *Epinephelus microdon* (Bleeker) (1856). A neotype of *fuscoguttatus* is described.
7. *Serranus horridus* Cuvier and Valenciennes and *S. lutra* Cuvier and Valenciennes are synonyms of *fuscoguttatus*, and *S. dispar* Playfair is the same as *micronodon*. *S. taeniobrurus* Cuvier and Valenciennes, considered a synonym of *fuscoguttatus* by some authors, is neither *fuscoguttatus* nor *micronodon*.

8. *Epinephelus elongatus* Schultz and *Epinephelus salonotus* Smith and Smith appear to be synonyms of *Epinephelus tauvina* Forskål.

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Shell Selection and Invasion Rates of Some Pacific Hermit Crabs

GORDON H. ORIANS and CHARLES E. KING

ABSTRACT: Three species of littoral hermit crabs from Horseshoe Cove, Bodega Head, Sonoma County, California, and three sublittoral pagurids from Chiniimi Island, Eniwetok Atoll, Marshall Islands, have been examined with respect to their shell selection and invasion rates.

Periodic removal of crabs from marked areas resulted in immigrations of surprising magnitude. By comparison of actual collection patterns with those predictable from the alternates of density dependence and density independence, there is an indication that the observed immigration rates result from density-dependent dispersal. While our data are not conclusive, the method presented is of interest and of possible utility for examining problems of this nature.

Shell selection is discussed from the bases of both laboratory and field observations. Each of the species is shown to utilize the shells of different gastropods with different frequencies.

Finally, behavioral aspects are examined as they relate to the distribution of the California hermit crabs.

SHELLS of various species of gastropod molluscs constitute a necessary component in the environment of pagurid crabs. In addition to housing the crab the shell may act as an important determinant of behavior; for instance, several species will not feed unless in a shell (Allee and Dougish, 1945; Brightwell, 1952). Different species of pagurids regularly utilize different species of shells and it has been suggested that shell availability may be a limiting factor for some species (Provenzano, 1960).

This paper reports on observations of shell utilization by six species of Pacific hermit crabs and on some simple laboratory experiments on shell selection. In addition, a number of removal and repopulation experiments were performed. Orians worked mainly at Horseshoe Cove, Bodega Head, Sonoma County, California, during the summer of 1957, and King at Chiniimi Island of Eniwetok Atoll during the summer of 1961.

The study area at Horseshoe Cove consisted of a section of rocky, shelving shore partially

1 Dept. of Zoology, Univ. of Washington, Seattle. Manuscript received January 31, 1963. Orians' research was carried out under the auspices of the Dept. of Zoology, Univ. of California, Berkeley. King's research was supported by the U. S. Atomic Energy Commission at their Eniwetok Marine Biological Laboratory. protected from heavy ocean swell, with an abundance of small tidal pools at high and medium intertidal ranges. Twenty-seven pools in the tidal range 2.5-4.5 ft above datum (which is mean low water) and subjected to long periods of exposure at low tides, were selected because they were easily reached at most tides. They ranged in length from 0.43 to 9.5 m and in depth from 15 cm to approximately 1 m. Plant cover varied from virtually nothing to dense algal growth covering the bottoms and sides of the pools. During the period of study, temperatures never rose above 17 C in the lower and deeper pools but on warm, sunny afternoons temperatures rose to as high as 27 C in some of the higher, shallower pools. However, no correlation was found between pagurid distribution and maximum pool temperature. Three species of hermit crabs found on this study area were Pagurus berniatusculus, P. samuelis, and P. granosimanus.

The site of King's study was approximately 100 m offshore in the lagoon adjacent to Chiniimi Island of Eniwetok Atoll. At this location the depth is 7 m and the substrate is uniformly composed of coralline sand mixed with fine pieces of dead coral. A 256 m² area was divided with a thin cord into 16 squares of 16 m² each. These squares were designated by letters from
A to P as depicted in Figure 1. Three people participated in each of the four collections of these quadrats. One person started at Square A and collected in alphabetical order areas A to P while a second started at Square P and collected in reverse order P to A. The third person, after distributing labeled jars to each square, searched the area a third time. The majority of the pagurids were obtained the first time the square was examined, although two or three individuals were usually found in the second examination. Hermit crabs were rarely obtained by the third collector. Using double-block aqua-lung tanks, it was feasible to collect continuously and minimize pagurid movement into the area during the collecting process. The entire procedure required 1.5–2 hr to clear the 256 m² area of essentially all pagurids, gastropods, and empty gastropod shells. Collections were made, starting around noon, on July 10, 1961 (collection no. F-2), July 22, 1961 (F-3), July 29, 1961 (F-4), and August 7, 1961 (F-5). Three species of hermit crabs occurred consistently in most squares of each sample at Eniwetok: *Diogenes gardineri*, *Dardanus scutellatus*, and *Calcimus latens*. Their abundances (expressed as mean number/square) are presented in Table 1.

Appreciation is expressed to Anthony J. Provenzano, Jr., who identified the Eniwetok pagurids, and to David Au, David Fellows, John Shoup, and Stanley Swerdloff for their aid in making the Eniwetok collections. Ernst Reese and R. T. Paine offered many valuable comments during the preparation of the manuscript.

**INVASION RATES**

At Horseshoe Cove all of the crabs of the most abundant species were removed at weekly intervals from two pools in which *P. samuelis* was the most abundant pagurid and from one pool in which the most abundant species was *P. birsutiusculus*. The results are indicated in Figure 2D. Whereas populations of the most abundant crab were definitely reduced by the removals, the influx was of surprising magnitude, resulting in a total removal from the pools in a 3-week period of over twice the number of crabs initially present in one case. Crabs from the pool in which *P. birsutiusculus* was most abundant were removed only once due to tidal conditions, but in this pool the final population of *P. birsutiusculus* was larger than the initial one.

Since the time interval between collections was not constant, it is difficult to compare the rates of invasion after successive samples. A

**TABLE 1**

<table>
<thead>
<tr>
<th>SAMPLE</th>
<th>DATE</th>
<th>MEAN NUMBER PAGURIDS/SQUARE</th>
<th>TOTALS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td><em>Diogenes gardineri</em></td>
<td><em>Dardanus scutellatus</em></td>
</tr>
<tr>
<td>F-2</td>
<td>10 July</td>
<td>11.2</td>
<td>11.4</td>
</tr>
<tr>
<td>F-3</td>
<td>22 July</td>
<td>4.9</td>
<td>4.4</td>
</tr>
<tr>
<td>F-4</td>
<td>29 July</td>
<td>7.1</td>
<td>2.3</td>
</tr>
<tr>
<td>F-5</td>
<td>7 Aug.</td>
<td>4.9</td>
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</tr>
</tbody>
</table>
Shell Selection of Hermit Crabs—ORIANS and KING

A. Entire Area

B. Sampling Grid

C. Eniwetok

D. Horseshoe Cove

Fig. 2. Predicted and observed dispersal rates. A, Predicted rates of dispersal. Curve a—if dispersal is density independent. Curve b—if dispersal is density dependent. B, Predicted numbers of individuals entering the sampling grid. Curve a—if dispersal is density independent. Curve b—if dispersal is density dependent. C, Observed numbers of individuals entering Eniwetok sampling grid. D, Observed numbers of individuals entering pools at Horseshoe Cove.
rough, but, for the purposes of the present paper, adequate method of obtaining comparable data is to extrapolate from the original curve plotted from the data in Table 1. This has been done in Figure 2C, with the original curve being evaluated at 7-day intervals.

Andrewartha and Birch (1954) have discussed the innate tendency of animals to disperse, but apparently they attached little general significance to dispersal in response to crowding. Such a mechanism has been shown for the great tit by Kluijver (1951) and it is known that in some crab species dispersal is directly related to population density (Bovbjerg, 1960). It is obvious from Figures 2C and 2D that there are strong dispersal movements into the unoccupied area within a relatively brief period. It is not obvious, however, whether this dispersal is in response to the density of the individuals outside the sampling area. To examine this problem, two alternates may be erected:

Alternate 1: Dispersion remaining constant and independent of density. Assuming that the dispersion of pagurid populations is constant and independent of their density, all crabs would spend a great deal of their time wandering about. If the individuals found in a grid, such as that erected at Eniwetok, were removed at constant intervals, the total size of the pagurid populations would decrease at a constant rate, as is hypothetically depicted in Figure 2A (curve a). This pattern assumes both density independence and a status quo, with no death or recruitment to the population. Viewed from the number of individuals collected in the grid, however, a different pattern would result from the same assumptions. Since the total size of the pagurid populations is very large, compared to those collected in the grid, the number of individuals collected at each interval would not vary to any great extent. The result (Fig. 2B, curve a) would be a curve which was parallel to the abscissa or which decreased linearly to a very slight extent. Continued for an extremely long time, the curve would approach that obtained by viewing the entire area, since every crab would eventually wander across the grid. When crabs ceased to enter the grid, the explanation required by density-independent dispersal is that all crabs have been collected.

Alternate 2: Dispersion as a function of density. Assuming that the tendency to disperse increases with increasing population size and conversely decreases with decreasing population size, a different pattern would result. The number of pagurids in the entire area (Fig. 2A, curve b) would initially drop at a rate greater than the final rate. The curve then indicates a variable rather than a constant-rate function. At the threshold of density-dependent dispersal effects, that is, at the point above which crabs disperse and below which they do not, the number of crabs obtained in the sampling grid (Fig. 2B, curve b) would be 0. However, in contrast to density-independent dispersal, there would still be pagurids in the area (as depicted in Fig. 2A, curve b).

A final evaluation of these two alternates is not possible in the present study. For example, surf action may be responsible for most of the influx at Horseshoe Cove, and no marking and recapture experiments were made at either site. However, there are indications that Alternate 2 more adequately explains the data. If the immigration rates of the three Eniwetok crabs are examined, either lumped or separately (Fig. 2C), it is apparent that the pattern more nearly approximates that required for density-dependent dispersal than it does for density-independent dispersal (Fig. 2B). Variations in the slopes of the collecting patterns may possibly reflect differences in the initial density levels relative to the threshold of density effects.

Repopulation of two Horseshoe Cove pools (Fig. 2D) also agrees more closely with Alternate 2 than with Alternate 1.

SHELL UTILIZATION

Shells housing individual pagurids were identified whenever possible. Each pagurid species was found to utilize the shells of different gastropods with different frequencies in both the Eniwetok and Californian studies (Tables 2 and 3).

To test for homogeneity of shell utilization in various samples of the same species and to inspect the collections for interspecific differences in shell utilization, a trellis diagram was constructed (Fig. 3). For a discussion of the mechanics of this type of test, the reader is referred to Wieser (1960) and Sanders (1960).
All samples of Diogenes gardineri are uniform in their shell utilization, that is, the overlap in shells used is greater than 60% in each case. Similarly, Dardanus scutellatus is homogeneous when compared with itself. The trellis diagram indicates that sample F-4 of Calcinus latens differs from all other samples of the same species, but no significance may be attached to it, since only four individuals of this species were obtained in sample F-4.

There is very little overlap (< 30%) in the species of shells utilized by Diogenes gardineri and Dardanus scutellatus. With the exception of the F-4 sample of Calcinus latens discussed above, there is little overlap between Dardanus scutellatus and Calcinus latens, but the similarity is greater than between Diogenes gardineri and Dardanus scutellatus.

It is evident from the diagram that Diogenes gardineri and Calcinus latens are very similar in their shell requirements (> 60% overlap, with the exception of the F-4 sample of Calcinus latens), even though different samples of the shells utilized by Diogenes gardineri resemble each other, and different shell samples of Calcinus latens resemble each other more than the samples of Diogenes gardineri resemble samples of Calcinus latens.

The overlap in the Californian samples between Pagurus birstiutiscusculus and P. samuelis was 30%; between P. birstiutiscusculus and P. granosimanus, 46%; between P. samuelis and P. granosimanus, 40%.

Shell utilization is basically dependent upon the availability of shells and the morphological limitations of the individual hermit crab. Thus the shells which are available, and hence utilized, by Pagurus samuelis in northern California as determined in the present study, are markedly different from those utilized by the same species in southern California (Coffin, 1954). Similarly, it is not to be inferred that the differences in shell utilization of the three Eniwetok pagurids are due to preferences of the species. The distinct differences may be explained on the simpler basis of differences in crab size. Dardanus scutellatus, which differs most markedly from the other two species in shell utilization, is also markedly larger (with average wet weight of 0.81 g) than both Calcinus latens (0.07 g) and Diogenes gardineri (0.04 g). As might be expected, Calcinus latens and Diogenes gardineri, which are similar in shell utilization, are also similar in size.

Shells may also be selected as a function of species-specific preferences and social interactions as discussed in the next section, but data of this type are not available for the Eniwetok hermit crabs.

**EXPERIMENTS**

To test the possibility of active shell selection, crabs were taken from Horseshoe Cove and subjected to the following types of experiments in the laboratory: (1) A single crab was given a choice of several shells of different species; (2) crabs of two or more species were presented with a single unoccupied shell.

Experimental crabs were removed from their shells by the application of a lighted match to the posterior portion of the shell. When the crab relinquished its hold it was placed in a shallow petri dish with the unoccupied shells. Pagurus birstiutiscusculus consistently preferred
<table>
<thead>
<tr>
<th>GASTROPOD SHELL</th>
<th>Diogenes gardineri</th>
<th>Dardanus scutellatus</th>
<th>Calcinus latens</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F-2  F-3  F-4  F-5</td>
<td>Total</td>
<td>Total</td>
</tr>
<tr>
<td>Strombus gibberulus...</td>
<td>11  3  1  -  15  5.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Strombus mutabilis...</td>
<td>2   -   -   -  2  0.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Strombus labiata...</td>
<td>1   -   -   -  1  0.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Strombus tips...</td>
<td>54  17  3  1  151 58.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Terebra striata...</td>
<td>6   1  3  1  11  4.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Terebra crenulata...</td>
<td>-    -   -   -   -   -</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Terebra maculata...</td>
<td>-    -   -   -   -   -</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cerithium sp...</td>
<td>10  1  5  5  21  8.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mitra sp...</td>
<td>15  2  4  3  24  9.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mitra olivaceformis...</td>
<td>-    -   1  1  2  0.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mitridae...</td>
<td>-    -   6  1  3  10 3.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cymatiaidae...</td>
<td>1    -   -   -  1  0.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cymatium murexicum...</td>
<td>-    -   -   -   -   -</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nautilus onca...</td>
<td>3    2  -   2  7  2.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conus spondalis...</td>
<td>1    -   -   -  1  0.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conus consors...</td>
<td>-    -   -   -   -   -</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conus eburneus...</td>
<td>-    -   -   -   -   -</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conus pulicarius...</td>
<td>-    -   -   -   -   -</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vexillum exasperata...</td>
<td>1    2  3  5  11  4.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Merula elata...</td>
<td>1    -   -   -  1  0.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Drupa mornor...</td>
<td>-    -   -   1  1  0.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Latirus barnati...</td>
<td>-    -   -   -   -   -</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thais sp...</td>
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<tr>
<td>Trochus niloticus...</td>
<td>-    -   -   -   -   -</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhinoclavis sinus...</td>
<td>-    -   -   1  1  0.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Totals...</td>
<td>106  34  50  70  260 100</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
shells of *Thais emarginata*, leaving shells of *Tegula* and *Calliostoma* for *Thais* even when the latter were so small as to preclude the withdrawing of the carapace into the shell. Never did a crab leave a *Thais* for shells of the other two species, and in every case in which crabs were forced to use *Tegula* and *Calliostoma* they left them as soon as a *Thais* was again made available. *P. samuelis* and *P. granosimanus*, on the other hand, showed no preference between shells of *Tegula funebralis*, *T. brunnea*, and *Calliostoma costatum* as long as the shell was of proper size. A marked preference for shells of *Tegula* was noted for *P. samuelis* in southern California by Coffin (1954). However, adult *P. granosimanus* were so large that only *Tegula*

<table>
<thead>
<tr>
<th><em>Diogenes gardineri</em></th>
<th><em>Dardanus scutellatus</em></th>
<th><em>Calcinus latens</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>F-2</td>
<td>F-3</td>
<td>F-4</td>
</tr>
<tr>
<td>74.2</td>
<td>76.0</td>
<td>66.8</td>
</tr>
<tr>
<td>71.6</td>
<td>71.8</td>
<td>13.9</td>
</tr>
<tr>
<td>82.5</td>
<td>7.1</td>
<td>9.1</td>
</tr>
<tr>
<td>5.1</td>
<td>7.1</td>
<td>19.7</td>
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<tr>
<td>77.5</td>
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<td>76.5</td>
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<td>72.1</td>
<td>74.4</td>
<td>25.7</td>
</tr>
<tr>
<td>86.5</td>
<td>39.7</td>
<td>19.2</td>
</tr>
<tr>
<td>45.4</td>
<td>41.0</td>
<td>40.8</td>
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<tr>
<td>84.3</td>
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<td>71.3</td>
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<tr>
<td>20.0</td>
<td>71.6</td>
<td></td>
</tr>
<tr>
<td>11.2</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig. 3. Trellis diagram showing overlap in shell utilization in four samples of Eniwetok pagurids.
brunnea shells were of suitable size and they consequently were preferred. Both of these species chose shells of a size to permit the entire carapace to be withdrawn until the large cheliped was in a position to act as an operculum. This preference is reflected in the size of shells utilized by the crabs in nature (Fig. 4).

In eviction experiments, *P. hirsutiusculus* was dominated by the other two species, usually being evicted by crabs of the other species if they made such an attempt. In no case did a specimen of *P. hirsutiusculus* successfully evict
a crab of the other two species from a shell, even when it had a decided size advantage. Immunity from eviction was conferred only when a *P. hirsutiusculus* was in a *Thais* shell too small to interest the other crabs. No clear dominance was found between *P. samuelis* and *P. granosimanus*. Size appeared to be the critical factor in outcomes, but more experiments are needed to confirm this tentative conclusion. Interspecific dominance in hermit crabs in which species membership is more important than size has also been reported by Reese (1961).

In attempting to evict a crab from its shell, invaders of all three species follow a general behavior pattern. A crab without or with an unsuitable shell, upon making contact with a shell, immediately tests the size of the shell with its cheliped and quickly moves into a position where it is able to probe the aperture. Eviction of a crab already occupying the shell is effected by grasping either the legs or the antenna with the large cheliped and smoothly sliding the occupant from the shell. Then while holding the evicted individual at arm's length, the intruder slides out of its own shell, if it has one, and into the newly vacated shell. During the probing, shell-less crabs frequently twitch their abdomens violently.

It is interesting that a human is unable to pull either of the larger species from their shells with forceps without severely injuring the animals and yet an intruding crab is able to do so with ease (see also Allee and Douglass, 1945; Brightwell, 1952). One must therefore conclude that the evicted crab releases its hold and, though there are no data to test this, it is possible that the striking difference in behavior has important survival value. A larger crab may be able to exert enough force to sever the cheliped from the body or otherwise injure the inhabitant. If evicted, however, another shell may be found and the probability of survival increased. In contrast, if the attack is by a large predator, eviction probably means certain death, so that chances of surviving would be enhanced by remaining in the shell at all costs.

**SIGNIFICANCE OF SHELL SELECTION**

It is possible to observe a relationship between the types of shells selected and the habitat utilized by the crabs in California. *Pagurus hirsutiusculus*, which under laboratory conditions prefers smaller shells, is much more mobile than the other two species and is able to climb over the algal growth in the pools better than the other species. Both *P. samuelis* and *P. granosimanus* with their heavier shells, restrict their activities to the bottoms of the pools. This may be explained either by comparative ability to climb as related to shell weight or as the result of the aggressive dominance of *P. samuelis* and *P. granosimanus* over *P. hirsutiusculus* which was discussed earlier. Thus, though *P. hirsutiusculus* and *P. samuelis* are found together in most of the tidal pools in Horseshoe Cove, their distribution within the pools differs significantly as tested by the Fisher Exact Probability Test (Siegel, 1956). *P. hirsutiusculus* was the most common pagurid in 11 pools with good algal growth, but was the most abundant species in only 3 pools with poor algal growth. In contrast, *P. samuelis* was most common in 9 pools with few plants, but was the most abundant crab in only 2 pools with good algal growth (Table 4). Coffin (1954) also noted the importance of rocky bottoms in tidal pools containing *P. samuelis* and was able to greatly reduce crab population densities by removing rocks.

From the results of the survey of shell utilization in natural populations of hermit crabs, supported by the results of shell selection experiments, it can be concluded that not only is there active shell selection by hermit crabs which differs from species to species, but also

**TABLE 4**

<table>
<thead>
<tr>
<th>NATURE OF POOL</th>
<th>NUMBER OF POOLS IN WHICH THE MOST ABUNDANT HERMIT CRAB WAS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>Pagurus hirsutiusculus</em></td>
</tr>
<tr>
<td>Good to dense algal growth</td>
<td>11</td>
</tr>
<tr>
<td>Plants few and scattered</td>
<td>3</td>
</tr>
<tr>
<td>Sandy bottom</td>
<td>3</td>
</tr>
<tr>
<td>Rocky bottom</td>
<td>9</td>
</tr>
</tbody>
</table>
that this can be correlated with what little is known of the habits of these animals.

REFERENCES


Some Marine Isopod Crustaceans from off the Southern California Coast

GEORGE A. SCHULTZ

IN THE SUMMER OF 1962 the author identified isopods caught in the submarine canyons off the southern California coast by workers of the research vessel "Valero IV" of the Allan Hancock Foundation of the University of Southern California. The results of this work have been published (Schultz, 1964). There were additional isopods collected during the voyage which were not part of the canyon fauna and they are considered in this paper. The specimens were taken from the benthic environment by means of an Orange Peel Grab or a Campbell Grab bottom sampler. Ten species were taken, 3 of which were new to science.

After the description or mention of each species the station or collection number is given. The number in parentheses is the number of specimens of the species caught at that station. The station numbers referred to are listed in Table 1, together with publications where more precise information can be found.

The research for this project was made possible by a Teacher's Research Participation Fellowship grant by the National Science Foundation to the Biology Department of the University of Southern California. Dr. Robert J. Menzies directed the research which was done in the Allan Hancock Foundation at the University of Southern California. The author wishes to thank Dr. Menzies for his part in the work; Dr. Olga Hartman, in whose laboratory the work was done; Dr. Walter Martin, who administered the grant; and the Allan Hancock Foundation, which provided the facilities.

ASELLOTA
MUNNIDAE

Austrosignum Hodgson

Austrosignum erratum, new species

Fig. 1

DIAGNOSIS: Eyes of two or three ocelli ventrolaterally placed near antennal bases and not visible in dorsal view, but clearly visible in ventrolateral view. Front of cephalon evenly convex; first three pereonal segments with lateral margins not widely separate. Lateral margins of last four pereonal segments separated from first three and also from each other by wide gaps. Lateral margins of pereonal segments four to seven narrower than those of first three. Coxal plates conspicuously visible from dorsal view on segments five to seven, very slightly so on segments one to four. Pleotelson narrow at base; one well-defined pleonal segment present. At widest point pleotelson about two-thirds as wide as segment seven. Six setae (12 bilaterally) along apical margin of relson. Longest pereaeopod about as long as body, with knoblike merus and many spines on other segments. Dactylus on each leg elongate with several long, spined-like setae. First pereaeopod about half length of other pereaeopods; at least three large spines on carpus. First and second antennae about same length, both about half length of body. First antennal flagellum with at least four articles; second antennal flagellum with five articles; fifth article of second antennal flagellum ball-like. Maxillipedal palp of five articles, each with at least one large spine; two coupling hooks on blade. Mandible with

1 Department of Zoology, Duke University, Durham, North Carolina. Manuscript received May 29, 1965.
### TABLE 1

Additional Data for the Stations

<table>
<thead>
<tr>
<th>STATION NO. AND DATE</th>
<th>LATITUDE AND LONGITUDE (and other coordinates)</th>
<th>DEPTH m</th>
<th>TYPE OF BOTTOM</th>
<th>REMARKS AND REFERENCE TO MORE INFORMATION</th>
</tr>
</thead>
<tbody>
<tr>
<td>2842 Jan. 22, '54</td>
<td>33°-27'-57&quot; 117°-57'-56&quot; off Dana Point</td>
<td>144</td>
<td>gray-green mud</td>
<td>Orange Peel Grab took 3.15 ft(^a) (89.6 liters) Hartman, 1955</td>
</tr>
<tr>
<td>2969 Oct. 31, '54</td>
<td>33°-35'-59&quot; 119°-15'-11&quot; 13.1 miles WNW of Santa Barbara Island</td>
<td>500</td>
<td>black mud nodules and flat shaley rocks</td>
<td>Campbell Grab took 1 gal shaley rubble (unpublished)</td>
</tr>
<tr>
<td>2994 Feb. 5, '55</td>
<td>33°-55'-00&quot; 118°-30'-38&quot;</td>
<td>14.5</td>
<td>green mud</td>
<td></td>
</tr>
<tr>
<td>2998 Feb. 6, '55</td>
<td>33°-53'-22&quot; 118°-34'-40&quot; 9.9 miles SSW of Santa Monica Pier</td>
<td>approx. 80</td>
<td>black mud</td>
<td>Hartman, 1956</td>
</tr>
<tr>
<td>4767 Dec. 9, '56</td>
<td>33°-15'-45&quot; 117°-33'-15&quot;</td>
<td>102.1</td>
<td>green silt with broken shells</td>
<td>Orange Peel Grab vol. not measured Menzies &amp; Barnard (1959); Barnard et al., 1959</td>
</tr>
<tr>
<td>5102 May 24, '57</td>
<td>33°-43'-15&quot; 118°-20'-53&quot;</td>
<td>20.1</td>
<td>coarse black sand temp. 13.2° C.</td>
<td>Orange Peel Grab took 0.25 ft(^a) (7.1 liters) Barnard et al., 1959</td>
</tr>
<tr>
<td>5580 Jan. 29, '58</td>
<td>34°-22'-15&quot; 119°-39'-10&quot;</td>
<td>51.2</td>
<td>green clay temp. 14.3° C.</td>
<td>Orange Peel Grab took 2.76 ft(^a) (78.4 liters) Barnard et al., 1959</td>
</tr>
<tr>
<td>5622 Feb. 21, '58</td>
<td>33°-10'-35&quot; 117°-27'-45&quot;</td>
<td>232</td>
<td>green silty sand</td>
<td>Orange Peel Grab took 2.68 ft(^a) (76.4 liters) Barnard et al., 1959</td>
</tr>
<tr>
<td>6003 Dec. 16, '58</td>
<td>34°-24'-45&quot; 120°-08'-40&quot; 4.6 miles 137° from Gavita Pier</td>
<td>135</td>
<td>green silty sand</td>
<td>Orange Peel Grab took 1.38 ft(^a) (39.1 liters) (to be published)</td>
</tr>
<tr>
<td>6089 Jan. 4, '59</td>
<td>32°-18'-00&quot; 117°-48'-25&quot; 29.5 miles 258° T from S. Coronado Is. (south light) San Clemente Basin</td>
<td>1866</td>
<td>green silt</td>
<td>Campbell Grab took 5.53 ft(^a) (150 liters)</td>
</tr>
</tbody>
</table>

Fig. 1. *Austrosignum erratum*, new species. 1, Dorsal view of a male; 2, maxilliped; 3, mandible; 4, second maxilla; 5, first maxilla; 6, second antenna; 7, first male pleopod; 8, first antenna; 9, second male pleopod; 10, first peraeopod; 11, third peraeopod.
five teeth on incisor, leaflike lacinia mobilis, large molar process, but with no palp. First male pleopod bifurcate at tip with spines along edges. Second male pleopod with curved copulatory process (recessed under tip of pleopod itself). Uropods biramous.

MEASUREMENTS: Holotype male, 1.8 mm long.

TYPE LOCALITY: 6003; Dec. 16, 1958; 135 m; 4.6 miles 137 degrees from Gavita Pier. Taken from green silty mud by an Orange Peel Grab. Lat. 34°-24′-45″, long. 120°-08′-40″.

MATERIALS EXAMINED: One male from type locality.

DISTRIBUTION: The other species of the genus, with the exception of A. tillerae Menzies and Barnard (1959), have a circumpolar distribution in the Antarctic Sea.

AFFINITIES: A. erratum, n. sp., differs from A. tillerae by the longer lateral extensions of the pleonal segments, especially the last four. The new species is much like A. globifrons Menzies (1961), from which it differs in the type and location of the eye stalks. There are 12 rather than 10 setae along the apical edge of the pleotelson in A. erratum, n. sp.

_Munna Kroyer_

**Munna (Uromunna) magnifica**, new species

Fig. 2

This new species is placed in the subgenus _Uromunna_ Menzies (1962) because the ventral uropodal ramus is leaflike and lacks a recurved apical spine.

DIAGNOSIS: Minute unpigmented species with apparently five, but in fact seven, peraeonal segments. No spines found on frons or anterior borders of peraeonal segments. Anterior borders of cephalon convex. Coxal plates of peraeonal segments two to seven visible in dorsal view. (Segment seven underneath pleotelson.) Eyes on short stalks and with few ocelli. Peraeopods very long, about 1½ times length of body; well provided with spines; ending in clawlike dactyli. First peraeopod shorter than body, laterally compressed with many stout spines, especially on ungus. Propodus with five large spines on anterior border. Second antenna about 2½ times body length with about 45 flagellar articles. First antenna much shorter than body with about nine segments including three elongate flagellar articles of about same length plus two very short apical articles and tipped with sensory setae. Maxilliped with many large curved setae on palp. Mandible with well-developed molar process, toothed incisor and palp of three segments. Uropods biramous, ventral ramus leaflike with at least five plumose setae.

MEASUREMENTS: Holotype female (with larvae in marsupium), 2.0 mm long.

TYPE LOCALITY: 2969; Oct. 31, 1954; 500 m; 13.1 miles WNW of Santa Barbara Island; taken from black mud, nodules and flat shaley rocks by Orange Peel Grab. Lat. 33°-35′-59″, long. 119°-15′-11″.

DISTRIBUTION: Known only from two specimens from type locality.

AFFINITIES: _M. magnifica_, n. sp., is much like _M. (U.) nanna_ Nordenstam (1933) in the apparent lack of the dorsal outline of segments one and seven. The second antenna of the new species is very much like that of _M. (U.) lanuae_ Menzies (1961), except that in the new species there are three long flagellar articles, not two.

**Ilyarchnidae**

_Ilyarchna_ G. O. Sars

_Ilyarchna acarina_ Menzies and Barnard

Fig. 3

_Ilyarchna acarina_ Menzies and Barnard (1959), pp. 9, 10, fig. 2.

_Ilyarchna acarina_ Menzies and Barnard, Schultz (1964).

MATERIALS EXAMINED: 2969(1); 4767(1).

DISTRIBUTION: 13.1 miles WNW of Santa Barbara Island; 500 m.

REMARKS: Specimen 4767 is from a coastal shelf bottom station the location of which has been recorded before by Menzies and Barnard (1959:10). The single specimen taken at the station was a large male and Figure 3, 1, 2, shows the male second pleopod and the first.

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Fig. 2. _Munna (Uromunna) magnifica_, new species. 1, Dorsal view of a female; 2, maxilliped; 3, 1st maxilla; 4, 1st antenna; 5, 2nd maxilla; 6, uropod; 7, hypopharynx; 8, 1st peraeopod; 9, mandible (two views).
chelate; both peraeopods one and two with carpus attached under propodus. Peraeopods three to seven also with carpus under propodus, but not as apparently so. Seventh peraeopod with small unguis; dactylus covered with scalelike rows of setae; propodus with sensory setae near dactylus. Antennae one and two pauciarticulate each with five segments; large tufts of setae on apical segments of each antennae. Maxilliped with five (four free) segments. Third segment with ventrally projecting setae, apical segment smallest with large medially projecting setae. Uropodal endopod longer than telson. Telson and both uropodal rami with row of many setae along minutely serrated margins.

MEASUREMENTS: Holotype female, 11 mm long.

TYPE LOCALITY: 2998; Feb. 6, 1955; approx. 80 m; 9.9 miles SSW of Santa Monica Pier; taken from black mud. Lat. 33°-53'-22", long. 118°-34'-40'.

MATERIALS EXAMINED: Twelve female specimens, from several to 11 mm long.

DISTRIBUTION: Known only from type locality.

AFFINITIES: A. californiensis, n. sp., is most like A. senegalensis Barnard (1925) except that it does not have large eyes. Both species have pauciarticulate flagella with several bushlike groups of setae.

Cyathura Norman and Stebbing

Cyathura munda Menzies (1951), pp. 111-114; figs. 12, 13.
Cyathura munda Menzies, Menzies and Barnard (1959), pp. 16, 17; fig. 10.

MATERIALS EXAMINED: 5102(3).

Haliophasma Haswell

Haliophasma geminata Menzies and Barnard (1959), pp. 17-19; figs. 11, 12.
Haliophasma geminata Menzies and Barnard, Schultz (1964).

MATERIALS EXAMINED: 2842(1); 2994(1); 5580(1); 5622(1).

antenna. Menzies and Barnard did not include a picture of the male second pleopod with the description of the holotype and they pictured the first antenna incorrectly. The first antenna of the male specimen examined had 12, not 9, flagellar articles as stated in the holotype description; and the holotype description should be amended to read 12 flagellar articles in the first antenna, since other specimens were examined (male and female) and they had 12 flagellar articles.

FLABELLIFERA

ANTHURIIDAE

Apanthura Stebbing

Apanthura californiensis, new species

Fig. 4

DIAGNOSIS: Body pigmentless. Eyes present, composed of five to seven ocelli which are pinkish in alcohol preserved specimens. Peraeon smooth, without pits or keels. Rostral projection of cephalon not as far forward as anterior extent of anterolateral margins. Seventh peraeonal segment about half length of sixth segment. Pleonal segments distinct. Telson with paired statocysts, rounded with small dent in tip bearing several large, stiff setae. Peraeopod one sub-

Fig. 4. Apanthura californiensis, new species. 1, Dorsal view of a female; 2, maxilliped; 3, first maxilla; 4, mandible; 5, first peraeopod; 6, second peraeopod; 7, seventh peraeopod; 8, telson and uropod; 9, both antennae and frontal margin of cephalon.
Mesanthura K. H. Barnard

Mesanthura occidentalis Menzies and Barnard (1959), pp. 20, 21; fig. 14.

MATERIALS EXAMINED: 5102(1).

Cirolana Leach

Cirolana joanneae Schultz (1964).

MATERIALS EXAMINED: 2969(7).

GNATHIOIDEA

Gnathia Leach

Gnathia crenulatifrons Monod (1926), pp. 390-393, figs. 154, 155.
Gnathia crenulatifrons Monod, Menzies and Barnard (1959), pp. 27-29, fig. 22.
Gnathia crenulatifrons Monod, Schultz (1964).

MATERIALS EXAMINED: 5580(10).

VALVIFERA

Synidotea Harger

Synidotea calcarea Schultz (1964).

MATERIALS EXAMINED: 6069(1).

REFERENCES


Some Bathyal Pacific Amphipoda Collected by the U.S.S. Albatross

J. Laurens Barnard

Several bathyal Amphipoda from the U.S.S. "Albatross" expeditions of 1888 onward (Holmes, 1908; Shoemaker, 1925) remained to be determined in the collections of the U.S. National Museum, and the results of their study are presented here. Increasing interest is being shown in faunas on bottoms of 200–2000 m. Although these depths comprise only 8.5% of the world's sea-floor, they perhaps support the remnants of the ancient abyssal fauna occupying depths greater than 2000 m prior to the Tertiary cooling of the seas (Madsen, 1961; Barnard, 1961, 1962; and their bibliographies).

Bathyal benthic depths outside of the Norwegian polar basin have not been well explored for amphipods, so that any records are of great interest. These early Albatross collections, although small and widely scattered, contain very well-preserved and intact specimens of seven previously known and six new species.

Of especial interest is another record of Mesopleustes abyssorum Stebbing and the opportunity to discuss its relationship among three families that it intergrades. The question of speciation in the genus Eusirella is reopened. No depth is known for a new species of Melita, but its poorly pigmented eyes may indicate a deepwater origin.

Not all of the species recorded here are benthic, the members of the genera Rhachitropis, Koroga, Eusirella, Cyclocaris, and Parandania being bathypelagic or demersal.

Family Lysianassidae

Genus Aristias Boeck

Aristias adrogans, new species

Fig. 1

Diagnosis: Eyes very pale, scarcely evident, no organized ommatidea apparent, composed simply of dense tissue; antennal flagella 10-articulate; epistome and upper lip fused but bounded by a hollow incision, neither produced beyond the other; first coxa broader than long, fifth and sixth with long, broad posterior processes; palm of gnathopod 2 formed of a broad projecting thumb; all pereopods with a small conical distal process on article 6; article 4 of pereopod 3 overlapping article 5 halfway or less, article 5 half or less as long as article 4 and becoming shorter with each pereopod; second pleonal epimeron tending to project at lower corner; first urosomal segment lacking a dorsal process; uropods 1 and 2 multispinose; inner ramus of uropod 3 not quite reaching end of article 1 of outer ramus; lobes of telson relatively narrow, each armed apically with a single spine.

Holotype: USNM no. 108629, male, 15 mm.

Type Locality: Albatross Station 4781, the Near Islands, Alaska, 52° 14' 30" N, 174° 13' E, 482 fms, June 7, 1906.

Material: Two specimens from the type locality.

Relationship: Three species have been described lacking eyes according to Gurjanova's key (1962). These are A. topsenti Chevreux (1900), A. microps Sars (1895), and A. falcatus Stephensen (1923). The present species is so closely related to A. falcatus that one would consider them to be the same species, were not the trend in lysianassid systematics, especially as practiced by Gurjanova (1962), to seek extremely minute specific differences. Such has also been practiced in the genus Orchomene (= Orchomenella and Orchomenopis). Because Stephensen makes a point of using the condition of the palm of gnathopod 2 as a character of distinction between A. commensalis and A. falcatus, it may also be used in the present species, which has a distinctly produced palm and so differs from A. falcatus but is similar to A. topsenti. Aristias microps has this palm very narrowly acute. In A. falcatus the inner ramus of the third uropod exceeds article 1 of the

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1 Beaudette Foundation, Santa Ynez, California. Manuscript received March 14, 1963.
Fig. 1. Aristias adrogans, n. sp. Male, 13.0 mm, Albatross 4781: a, lateral view; b, epistome and upper lip complex; c, mandible; d, maxilla 1; e, maxilla 2; f, maxilliped; g, h, gnathopods 1, 2; i, pereopod 1; j, end of pereopod 5; k–n, uropods 1–3, 3 (enlarged); o, telson; p, posterior edge of third pleonal epimeron.
outer ramus, but in the present species it is slightly shorter. The fifth articles of pereopods 3–5 are noticeably shorter than in *A. falcatus*. *Aristias topsenti* is characterized by lateral wings on urosome segment 3. *Aristias microps* has a blunter head and poorly articulate antennal flagella and a broader telson than in the present species, and lacks the long posterior processes of coxae 5 and 6.

Because the loss of eyes may occur in different populations of the same species, I have inspected the literature on all other eyed species and find that the new species resembles *A. commensalis* Bonnier (1896), from which it differs by narrow telsonic lobes, bearing only one instead of two or three terminal spines. It differs from *A. antarcticus* Walker (1907; K. H. Barnard, 1932) by the unproduced upper lip, and from *A. colinus* K. H. Barnard (1932) by the unproduced dorum of urosomal segment 1. *Aristias pacificus* Schellenberg (1936) was described from Vancouver Island and so bears inspection as a generic relative of close geographic placement. That species has eyes, has two apical spines on each telsonic lobe, and has the inner ramus of uropod 3 exceeding the first article of the outer ramus. The second and third pleonal epimera have small posterior corner teeth, a feature showing only a tendency in the present species. The longer rami of uropod 3, longer pereopods, and more strongly spinose uropods 1 and 2 distinguish this species from *A. curtipes* Gurjanova (1962). Both *A. iaponicus* and *A. spinipes* Gurjanova (1962) have the inner ramus of uropod 3 exceeding article 1 of the outer ramus. A more careful rendering of the epistome and upper lip of species described in the last several decades would serve well in studying speciation in the group. Apparently the species are semi-parasites on ascidians and sponges, so that we may anticipate variability as seen in *Polycheira antarctica*, a dexamnid amphipod.

**GENUS Cyclocaris** Stebbing

*Cyclocaris guilelmi* Chevreux

Fig. 5K


*Cyclocaris faroensis* Norman 1900:197–198, pl. 6, figs. 5–15.

**MATERIAL:** Albatross 4793, male, 6.3 mm.

**REMARKS:** The slight differences between coxa 1 of *C. guilelmi* and of *C. tabitensis* Stebbing (1888) probably are not worthy of specific value and perhaps are only figmental. Herein the first coxa is drawn; otherwise the material corresponds with that figured by J. L. Barnard (1959), except the lower lip is like that figured by Sars (1900).

**RECORD:** East of Kamchatka, 54° 48′ N, 164° 54′ E, 2700 fms, June 16, 1906. An arctic pelagic species picked up in a deep benthic trawl.

**GENUS Koroga** Holmes

*Koroga megalops* Holmes

Fig. 2

*Koroga megalops* Holmes 1908:503–504, fig. 13; Stephens 1923:60–61, fig. 5; K. H. Barnard 1937:145–146, fig. 3; Stephens 1933:11; Thorsteinson 1941:56, pl. 2, figs. 18–20; Shoemaker 1945:186; Gurjanova 1951:192–193, fig. 62; Birstein & Vinogradov 1955:222–223; Birstein & Vinogradov 1958:224; Birstein & Vinogradov 1960:187; Gurjanova 1962:93, fig. 20.

**MATERIAL:** One specimen from Albatross Station 4785, east of Komandorskije Ostrova, 1850 fms, 53° 20′ N, 170° 33′ E, June 12, 1906; one specimen from Albatross Station 4758, off Queen Charlotte Islands, 52° 02′ N, 132° 53′ W, May 19, 1906, 300 fms.

**DISTRIBUTION:** A pelagic species, probably cosmopolitan, having been found in the north and tropical Pacific, the Arabian Sea, the high North Atlantic, and the middle Atlantic. In open-closing hauls Birstein and Vinogradov
Fig. 2. *Koroga megalops* Holmes. Female, 7.0 mm, Albatross 4758: a, lateral view; b, head and epistome-upper lip complex; c, d, antennae 1, 2; e, mandible; f, g, maxilla 1; h, maxilla 2; i, maxilliped; j, apex of inner plate of maxilliped; k, gnathopod 1; l, end of gnathopod 2; m, gnathopod 2; n, o, pereopods 1, 2; p, molar of left mandible; q–t, uropods 1, 2, 3, 3 (enlarged); u, telson.
showed its distribution to extend from a haul taken at a maximum depth of 500 m to one taken at a minimum depth of 2200 m. Other depth data are not reliable since the drags were open at all depths.

DISCUSSION OF Paracallisoma AND ALLIED GENERA

When Chevreux (1903) described Paracallisoma, only the genus Scopelocheirus Bate formed its close relative, but since that time a number of other scopelocheirid genera have been described, as reviewed by Dahl (1939). Holmes (1908) described Scopelocheirus coecus which was relegated to Paracallisoma alberti Chevreux (1903) by Schellenberg (1926a), figured his specimen sufficiently to show it corresponded with Holmes’ description more than with that of Chevreux. Indeed, no subsequent analysis of P. alberti has shown the distinctive second gnathopod as copied from the original description herein (Fig. 3n, o). Chevreux described his species as lacking a finger on gnathopod 1, but apparently subsequent reviewers have assumed Chevreux was in error. Even presuming Chevreux did not see the small finger among the distal setae as known for S. coecus, all subsequent authors have not given status to the condition of gnathopod 2 which, as drawn by Chevreux, shows a larger finger and longer palm than in S. coecus, with the finger failing to match the palm. Until Chevreux’s type material can be examined again for these features there can be no assumption that Chevreux erred in both gnathopods.

Chevreux did not distinguish Paracallisoma from Scopelocheirus, although one might believe that the obvious statement “sans trace de dactyle” would suffice; but we can see that the shorter coxae and immense disproportion of coxa 5 to coxae 6 and 7 are also of value. Scopelocheirus coecus shares these features.

Dahl (1955) described Bathycallisoma to encompass Paracallisoma sp. Schellenberg (1955), which he thought was his B. pacifica n. sp., but in a footnote he wrote that it was S. schellenbergi Birstein and Vinogradov (1958) and should be transferred to Bathycallisoma. Birstein and Vinogradov (1960) transferred it back to Scopelocheirus. But S. schellenbergi appears to be distinctly different from the only other two species in the genus Scopelocheirus and, as Dahl writes in his footnote, if S. schellenbergi belongs with Scopelocheirus then Bathycallisoma and other scopelocheirid genera should not exist.

Scopelocheirus schellenbergi differs from S. hopei and S. crenatus (see Sars, 1895: pl. 19) by the shorter coxae, especially noticeable in the poorly posteriorly excavate coxa 4, by the anterioposterior elongation of coxae 5 and 6, apparently by the lack of protrusion of the upper lip and epistome, by the very broadened plates of the maxillae and maxillipeds, and especially by the proximal inflation of the inner plate of maxilla 2, these characters all being shared by Bathycallisoma pacifica. Apparently also the lobes of the lower lip gape widely in S. schellenbergi, although Birstein and Vinogradov show only half of the lower lip and this is a criterion noted by Dahl as a generic feature of Bathycallisoma.

One character not mentioned by Dahl, but one I believe to be of significance, is the chelateness of the second gnathopod in both S. hopei and S. crenatus. This would make an excellent generic difference between Bathycallisoma and Scopelocheirus.

Until Chevreux’s Paracallisoma alberti can be rechecked I must retain P. coecus as a distinct species that indeed is questionably assigned to Paracallisoma.

Paracallisoma coecus (Holmes)

Fig. 3


MATERIAL: One juvenile 6.0 mm, Albatross Station 4760, northeastern Pacific, 53° 53’ N, 144° 53’ W, 2200 fms, May 21, 1906.

REMARKS: The mouthparts and telson correspond to those figured by J. L. Barnard (1954), but they are less setose, the outer plate of the maxilliped having only 4 lateral setae instead of 14.

FAMILY STEGOCEPHALIDAE

GENUS Parandenia Stebbing
Fig. 3. Paracallisoma coecus (Holmes). Juvenile, 6.0 mm, Albatross 4760: a, lateral view; b–d, gnathopod 1; e, f, gnathopod 2; g–j, pereopods 1, 3, 4, 5; k–m, uropods 1–3. Paracallisoma alberti Chevreux 1903, copy of original figures, n, o, gnathopods 1, 2.

Parandania boecki (Stebbing)

Andania boecki Stebbing 1888:735, pl. 36
Parandania boecki Stebbing, 1906:95–96; J. L. Barnard 1961:57–58, fig. 27 (with references).

MATERIAL: One male, 5 mm from Albatross Station 4765 southeast of Komandorskie Ostoja, 53° 12' N, 171° 37' W, 1217 fms (bottom depth), haul at 300 fms, May 29, 1906.

DISTRIBUTION: Cosmopolitan except for the
Arctic. Pelagic. Minimum recorded depth 300 m; minimum depth of closed haul 2200 m.

FAMILY PLEUSTIDAE

GENUS Mesopleustes Stebbing

This genus stands directly between the Pleustidae and the Paramphithoidae, forming almost the perfect intergrade, but in reality it is better assigned to the Calliopiidae. The two former families differ only by the lower lip and coxal structure. The lower lip of the type genus Pleustes is composed of gaping, tilted, oval outer lobes astride broad partially fused inner lobes, whereas the lower lip of the type genus Paramphithoe is composed of two upright, ungaping outer lobes with distinct mandibular processes and no inner lobes. The first four coxae of Pleustes are broadly rounded below, whereas those of Paramphithoe are sharply acute below. The lower lip of Mesopleustes is composed of distinct outer lobes, slightly tilted, slightly gaping, with poorly developed but distinct mandibular processes and indeterminate inner lobes. The coxae are attenuated but not sharply acute. The simple mandibular molar of Pleustes in contrast to the heavily ridged molar of Paramphithoe is of no consequence since other, undoubted pleustids have the paramphithiid molar. The slender gnathopods of Paramphithoe are imitated in other pleustid genera. Both families have species that are processiferous.

The fusion of Paramphithoidae and Pleustidae is not necessarily warranted by this intergrading genus, for if the importance of lower lips were discounted then the Calliopiidae should also have to be included in the complex. The Calliopiidae scarcely differ from Eusiridae (= Pontoogeneidae) and a case could then be made for their inclusion with pleustids and paramphithoids. I do not advocate such extensive recombination at this time in the Amphipoda, although the trend is obvious and, compared with other animal groups, the Amphipoda are certainly oversplit at the family level.

Mesopleustes abyssorum (Stebbing)  
Figs. 4, 5

Pleustes abyssorum Stebbing 1888:872, pl. 67.


MATERIAL: Four specimens 22 mm, 22 mm, 16 mm, and 15 mm, from Albatross Station 5082, south of Hamamatsu, Honshu, Japan, 34°05’ N, 137°59’ E, 662 fms, Oct. 20, 1906.

REMARKS: The lower lip of three of the specimens has been dissected. None shows the false inner lobes drawn by Stebbing, and I believe those may have originated from pressure on the organ while mounted under a cover slip, for by compression with a needle at the inflated median line false lobes can be inflated where shown by Stebbing. Hence the lower lip is even less like that of pleustids and more like that of paramphithoids.

Shallow pitlike thickenings of the chitin cover the body and the coxae and are drawn in enlarged figures.

DISTRIBUTION: Previously recorded from the southern Indian Ocean, near Marion Island, 3013 m; near Cape Noun, Morocco, 1180 m; NW Flores Sea, 694 m.

FAMILY EUSIRIDAE

GENUS Eusirella Chevreux

Eusirella multicalceola (Thorsteinson)  
Figs. 6, 7


Eusirella multicalceola, Birstein & Vinogradov 1955:271, fig. 30; Birstein & Vinogradov 1960:224.

MATERIAL: Figured female, 8.0 mm, and two other specimens, from Albatross Station 4758, off Queen Charlotte Islands, 52°02’N, 132°53’ W, 1600 fms, May 19, 1906.

REMARKS: This species differs from E. elegans Chevreux (1908) by the much more slender gnathopods and the truncate first coxa, and from E. longisetosa Birstein and Vinogradov (1960) by the shorter third mandibular palp article, the much more deeply cleft telson, the shorter dactyli of the gnathopods, the shorter second article of the first maxillary palp, and by
Fig. 4. *Mesopleustes abyssorum* (Stebbing). Female, 22.0 mm, Albatross 5082: a, lateral view; b, enlargement of urosome and third pleonal epimeron; c, mandible; d, lower lip; e, f, maxillae 1, 2; g, maxilliped; h, gnathopod 1; i, j, medial and lateral views of gnathopod 2; k, l, right and left pereopod 5, to show asymmetry in article 5; m–o, uropods 1–3; p, uropod 3, enlarged.
having article 5 of pereopod 1 much shorter than article 4.

The calceoli are present only on the medial faces of the articles of the antennae although in the figure of the animal drawn here they are shown rather strongly because they appear under low-powered microscopy to show through the very transparent appendages.

Birstein and Vinogradov (1960) removed Shoemaker's (1945) identification of *E. elegans* Chevreux to *E. multicalceola*, but I believe this move is premature, for Shoemaker's specimen has several good characters worthy of at least subspecific value if not more so. Especially important is coxa 1 projecting forward strongly in Shoemaker's specimen; the fifth articles of the gnathopods are of similar length in both pairs and relatively shorter than in *E. multicalceola*; the dactyli of the gnathopods extend nearly the full length of article 6, and hence the palm is longer and more distinctly defined by spines than in *E. multicalceola*; the accessory flagellum is of cylindrical, not bractiformal shape as seen on my specimen. There may be differences in the mandibular palp not mentioned by Shoemaker. Shoemaker believed that *E. multicalceola* as well as *E. valdiviae* Schellenberg (1926) were synonymous with *E. elegans* Chevreux. Since Thorsteinson had a male, and Birstein and Vinogradov and I figure females, we show that there are no sexual differences in *E. multicalceola*.

*Eusirella valdiviae* was not well figured and the gnathopods, although slender as in *E. multicalceola* and Shoemaker's specimen, may be turned and may not have been drawn flat; even so they have short dactyls as in *E. multicalceola*. The truncate first coxae also show that *E. valdiviae* is closely related and possibly the senior synonym of *E. multicalceola*.

Stephensen's (1944) figures of *E. elegans* show coxa 1 acutely pointed forward and show sexual differences only in antennae.

Because of zoogeographical considerations these species should not be fused until more material from the South Atlantic area can be examined in greater detail. *Eusirella multicalceola* is a North Pacific species, *E. valdiviae* is known from the South Atlantic, and *E. elegans* and Shoemaker's specimen are from the middle North Atlantic. Shoemaker's specimen is most closely related to *E. elegans* because of the first coxa. Hence *E. elegans* might be an endemic

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**Fig. 5. Mesoplenus abyssorum** (Stebbing). Female, 22.0 mm, Albatross 5082: a, head; b, outline of maxilla 2; c, d, dorsal and lateral views of telson; e, pleonal segments 1–3, left to right; f, enlargement of a pereonal segment above the coxa to show sculpture; g, enlargement of dorsal edge of a pleonal segment to show sculpture; h–j, distal ends of coxae 1–3. *Cyclocaris guilemi* Chevreux. Male, 6.3 mm: k, coxa and articles 2 and 3 of gnathopod 1.
Fig. 6. Eusirella multicalceola (Thorsteinson). Female, 8.0 mm, Albatross 4758: a, lateral view; b, peduncle of antenna 1; c, accessory flagellum; d, apex of antenna 1; e, antenna 2; f, calceolus; g, pereopod 1; h, end of pereopod 1; i, telson.

Atlantic species, with E. multicalceola and E. valdiviae representing a North Pacific, circumantarctic species penetrating into the South Atlantic. K. H. Barnard’s (1932) identification of E. elegans cannot be relegated either to E. elegans or E. valdiviae since the first coxa is not described and the gnathopods not figured. The very few locality collections of this species that
have been made so far do not warrant final conclusions in any of these matters yet.

**DISTRIBUTION:** North Pacific: Gulf of Alaska, 1000–1200 m tow; Kurile–Kamchatka Trench tows showing distribution between 500 and 2000 m; east of the Ramapo Deep in a 0–5500 m tow; Birstein and Vinogradov (1960) state that the distribution includes the Bering Sea but I am not aware of such a published record. *Eusirella valdiviae* is known from the South Atlantic about 30° S and K. H. Barnard’s material also came from that area.

**GENUS Rhachotropis** Smith

*Rhachotropis natator* (Holmes)

*Gracilipes natator* Holmes 1908:527–529, figs. 32–34; Thorsteinson 1941:85, pl. 6, figs. 67–70.


**MATERIAL:** One specimen from Albatross Station 4760, northeastern Pacific, 53° 53' N, 144° 53' W, 2200 fms, May 21, 1906.

**DISTRIBUTION:** Northern Pacific: Gulf of Alaska, Hokkaido, southern California, and east of the Ramapo Deep, shallowest depth 930 m, greatest haul 5500 m but no closing hauls yet available defining greatest depth.

**FAMILY GAMMARIDAE**

**GENUS Melita** Leach

*Melita kodiakensis*, new species

Fig. 8

**DIAGNOSIS:** Antenna 1 scarcely longer than
FIG. 8. *Melita kodiakensis*, n. sp. Holotype, male, 12.0 mm: *a*, lateral view; *b*, head; *c*, peduncle of antenna 1; *d*, mandible; *e*, lower lip; *f, g*, ends of gnathopods 1, 2; *h*, pereopod 1; *i–k*, uropods 1–3; *l*, telson.
the second; head with accessory lobe at anterolateral corner behind which is the sharp tooth generally present in Melitas; eyes present, with well-developed ommatidea but bleached to ochre in alcohol; article 1 of mandibular palp not produced; inner lobes of lower lip well developed; coxa 1 not produced forward; articles 5 and 6 of gnathopod 1 equal in length, finger normal; palm of male gnathopod 2 oblique, with three processes, finger overriding palmar edge and slightly longer than palm, article 4 with distal tooth; pereopods 3–5 rather short and stout, posterodistal corners of article 2 not strongly produced; pleonal epimera rounded or quadrate at posterior lower corners; pleonal segments 1–5 increasingly strongly dentate dorsally, on segment 1 there are two obsolete teeth, on segment 2 there are three obtuse teeth, on segment 3 there are five teeth, on segment 4 there are three teeth, the middle-most of which is more erect than the two laterals, on segment 5 there are three teeth, the middle of which is shortest but possibly because of damage; hence the pleonal tooth formula is (2)–3–5–3–3–0.

**HOLOTYPE:** USNM no. 108631, male, 12 mm.

**TYPE LOCALITY:** Chogafka Cove, Kodiak Island, Alaska, July 10, 1880, W. H. Dall, no. 3371 (1948).

**RELATIONSHIP:** This species is related to *M. valida* Shoemaker (1955) but differs by the quadrate third pleonal epimera, the smaller forward extension of the first coxa, and the larger teeth of the urosome. It differs from *M. dentata* (Kroyer) (see Sars, 1895: pl. 181) by the quadrate third pleonal epimera, the unproduced first mandibular palp article, and the accessory lobe at the lower anterior corner of the head. From *M. gladiosa* Bate (Chevreux and Fage, 1925:233) it differs by the unproduced first to third pleonal epimera and the male second gnathopodal palmar armature. From *M. pallida* Sars (1886: pl. 15) the new species differs by the unproduced second and third pleonal epimera and the shape of the head.

**FAMILY PHOTIDAE**

**GENUS *Photis* Kroyer**

*Photis chiconola*, new species

**Fig. 9**

**DIAGNOSIS OF MALE:** Coxae 1 and 2 similar to coxae 3 and 4, longer than broad; third coxa not wider than second; gnathopod 1 with palm slightly excavate, distinctly defined by a shallow bump armed with a spine; palm of gnathopod 2 oblique, with a deep, narrow conical invagination, the defining tooth slender but not reaching a transverse line from the dactylar hinge, the palmar process near finger hinge not protruding strongly, article 7 slender, tapering evenly, with several inner serrations and articulated spines, the largest occurring distally and forming a slight notch, tip of article 7 strongly overlapping defining tooth; article 2 of gnathopod 2 poorly produced anterodistally, its lateral face with a single, obscure striating ridge.

**FEMALE:** Palm of gnathopod 2 slightly excavate, its article 7 overlapping palm, anterodistal end of article 2 with a small, narrow process.

**HOLOTYPE:** USNM no. 108632, male, 5 mm.

**TYPE LOCALITY:** Albatross Station 4530, Monterey Bay, California, Pt. Pinos Lighthouse, S 78° E, 6.8 miles, 847–755 fms, beam trawl on soft gray mud, May 27, 1904.

**MATERIAL:** Station 4530 (25 specimens).

**RELATIONSHIP:** This species is most closely related to *Photis conchicola* Alderman (see J. L. Barnard, 1962a) and the differences herein noted may be those of only racial value. *Photis chiconola* differs from *P. conchicola* especially by the slender dactyl of the female gnathopod 2, which strongly overlaps the palm, in contrast to the short, stout dactyl fitting the palm in *P. conchicola*. Articles 3–6 of pereopods 3–5 are more slender in *P. chiconola*, the dactyl of male gnathopod 1 is longer, and the male coxa 2 is longer than broad but this probably is a feature of its juvenility. The distal lobe of article 2 on the female second gnathopod is small and slender in contrast to that of female *P. conchicola*.

The new species is related to *P. reinhardti* Kroyer (see Sars, 1895:pl. 202), differing from it by the narrower palmar excavation of male gnathopod 2, which may be a feature of juvenility, but the dactyl strongly overlaps the palm, indicating sufficient difference.
Fig. 9. *Photis chiconola*, n. sp. Female, 4.5 mm, Albatross 4530: a, b, head; c, d, gnathopod 1; e, f, gnathopod 2; g, pereopod 1; h, end of pereopod 3; i, pereopod 5; j, coxa 5; k, coxa 6; l–n, uropods 1, 2, 3 (enlarged); o, telson; p, pleonal segments 1–3, left to right. Holotype, male, 5.0 mm: q–s, gnathopods 1, 2, 2 (enlarged); t, pereopod 2; u–w, pereopods 3–5; x, coxa 3.

**GENUS Podoceropsis** Boeck

**Podoceropsis nitida** (Stimpson)

Selected references:


**MATERIAL:** One female from Chiniak Bay, Kodiak Island, Alaska, July 12, 1880, W. H. Dall coll. no. 3413 (1527).
**Distribution**: Boreal species: North Atlantic at Norway, Kattegat, Holland, France as far south as Boulange, British Isles, New England as far south as Connecticut; Arctic at Bering, Chukchi, and East Siberian seas; North Pacific at Kodiak Island, Alaska. Depth range 40–150 m.

**Family Ischyroceridae**

**Genus Ischyrocerus** Kroyer

*Ischyrocerus bortator*, new species

Fig. 10

**Diagnosis**: Eyes obsolete, forming a barely perceptible white mass composed of finely particulate tissue; antenna 1 shorter than antenna 2; flagellum of antenna 2 not longer than article 5 of peduncle; coxa 5 half as long as coxa 4; pereopods 4 and 5 with lower posterior corners of second articles subconically produced, pereopod 3 less produced; uropod 3 very slender, elongated, rami about 37% as long as peduncle, apex of outer ramus ornamented (see figures), inner ramus with a single apical spine; telson linguiform, apically rounded, armed with two lateral spines; gnathopod 2 with long palm, scarcely distinct from but longer than hind margin of article 6, near finger hinge bearing a poorly bifurcate process.

**Holotype**: USNM no. 108634, female, 13.8 mm. ovigerous.

**Type Locality**: Albatross Station 2789, off Isla de Chiloe, Chile, 42° 36' 00" S, 75° 28' 00" W, 1342 fms, Feb. 12, 1888.

**Material**: Albatross 2788 (specimen 9.0 mm); Albatross 2789 (holotype, and a 9.5-mm specimen).

**Relationship**: In the obsolescent eyes and the short rami of uropod 3 this species resembles *I. tenuicornis* (Sars 1885) and *I. brevicornis* (Sars 1885), but differs by the produced posteriorventral corners of the second articles of pereopods 4 and 5 and the distal palmar process of gnathopod 2. It has different proportions of the antennae than *I. tenuicornis*, and different proportions of the peduncle and rami of uropod 3 than does *I. brevicornis*.

The new species differs from *I. commensalis* Chevreux (1900) by the shorter fifth coxa, the obsolescent eyes, and shorter rami of uropod 3, but in other respects the two species are similar.

This species is related to *I. chamissoni* Gurjanova (1951), but differs by the produced lower corners of the second articles on pereopods 3–5. The shorter rami of uropod 3 distinguish the species from *I. krascheninnikovi* Gurjanova (1951), according to her key and description. The new species lacks the distal peduncular seta on uropod 3 shown for *I. rhodomelae* by Gurjanova (1951).

The epistome is similar to that drawn herein for *I. malacus*, n. sp.

**Diagnosis**: Eyes obsolete, pigmentless in alcohol but bearing tiny distinct ommatidia moderately scattered; antennae about equal in length, flagellum of antenna 2 not longer than article 5 of peduncle; coxa 5 three-fourths as long as coxa 4; pereopod 5 with lower posterior corner of article 2 subacutely produced, the corners of pereopods 3 and 4 bluntly produced; uropod 3 slender, elongated, rami half as long as peduncle, apex of outer ramus ornamented (see figures), inner ramus with a single apical spine; telson linguiform, apically rounded, armed with two spines; gnathopod 2 with long palm, scarcely distinct from but longer than hind margin of article 6, near finger hinge bearing a poorly bifurcate process.

**Holotype**: USNM no. 108636, female, 9.0 mm. Unique.

**Type Locality**: Albatross Station 4538, Monterey Bay, California, 6.5 miles S, 85° E of Pt. Pinos Lighthouse, 871 fms, May 31, 1904.

**Relationship**: This species resembles *I. bortator*, n. sp., in its general appearance but from the diagnoses one may see innumerable small differences. The eyes of *I. malacus* are slightly better composed, coxa 5 is longer, the rami of uropod 3 are longer, and the antennae are equal in length.

The produced lower corner of article 2 on pereopod 5 removes this species from these relatives: *I. megacheir* (Boeck), *I. hansenii
**Fig. 10.** *Ischyrocerus bortator*, n. sp. Holotype, female, 13.8 mm, Albatross 2789: *a*, lateral view; *b*, accessory flagellum; *c, d*, gnathopod 1, medial and lateral; *e, f*, gnathopod 2, medial and lateral; *g*, pereopod 1; *h–j*, uropods 1–3; *k*, two views of uropod 3, enlarged; *l*, apex of inner ramus of uropod 3; *m*, apex of outer ramus of uropod 3; *n*, telson.

**Fig. 11.** *Ischyrocerus malacus*, n. sp. Holotype, female, 9.0 mm, Albatross 4538: *a*, lateral view; *b*, upper lip and epistome complex; *c*, gnathopod 1; *d, e*, gnathopod 2, medial and lateral views; *f–h*, uropods 1–3; *i*, two enlarged views of uropod 3; *j*, apex of inner ramus of uropod 3; *k*, apex of outer ramus of uropod 3; *l*, telson.
Stephensen, *I. tenuicornis* (Sars), *I. brevicornis* (Sars), and *I. brasilovi* (Gurjanova).

From *I. chlamissoi* Gurjanova it differs by the equal antennae and the longer rami of uropod 3; from *I. kracheninnikovi* by the equal antennae and the weak eyes. From *I. commensalis* Chevreux the new species differs mainly by coxa 5 being slightly shorter than coxa 4 and by the weak eyes.

**FAMILY COROPHIIDAE**

**GENUS Ericthonius** Milne Edwards

*Ericthonius hunteri* (Bate)

Selected references: Sars 1895:605, pl. 216, fig. 2; Holmes 1908:543; Chevreux & Page 1925: 354–356, fig. 363; Stephensen 1940:65; Stephensen 1942:403; Stephensen 1944:128; Enequist 1950:344–345, fig. 62; Gurjanova 1951:951, fig. 662; Shoemaker 1955:68.

**MATERIAL:** Pacific Grove, California, 300 + fathoms, USNM no. 105349, no. 42, 2 (1 male).

**DISTRIBUTION:** Subarctic at Murman Coast, White Sea, Okhotsk Sea, Barents Sea, north of Russia; northeastern Atlantic south to Gulf of Gascogne but also penetrating into the Black Sea, as yet unreocnzed in the Mediterranean; Alaska at Pt. Barrow and recorded here as far south in the eastern Pacific as Monterey Bay, descending apparently to greater depth with temperature. Previously recorded from 0–235 m, here to 550 m.

**FAMILY PODOCERIDAE**

**GENUS Dulichia** Kröyer

*Dulichia remis*, new species

Fig. 12

**DIAGNOSIS OF MALE:** Pereonal and pleonal segments lacking dorsal projections; head lacking eyes and lateral bulges, lateral lobes and rostrum small; coxa 1 small, not spiniform, other coxae not acuminate, rounded below; palmar defining tooth of gnathopod 2 oblique, quite proximal, inner edge of article 7 bearing a long proximal tooth, article 2 broadly lobed on its distal half; pereopods 3–5 subprehensile, article 6 inflated and strongly spinose, the serrate finger turned back on palm; telson with a dorsal accessory lobe. Mouthparts like those figured by Sars (1895, pl. 228) for *D. spinossissima* except for the longer fourth maxillipedal palp article.

**HOLOTYPE:** USNM no. 108637, male, 13.0 mm.

**TYPE LOCALITY:** Albatross Sta. 4781, the Near Islands, Alaska, 52° 14’ 30” N, 174° 13’ E, 482 fms, June 7, 1906.

**FEMALE:** If indeed these three specimens represent the female of this species there is a remarkable sexual differentiation. They differ from the male by the deeper head having lateral eye bulges filled with dispersed white cells; shorter outer rami of uropods 1 and 2; less inflated, yet distinctively prehensile sixth articles of the pereopods; relatively longer fifth articles of pereopods 3 and 4 (possibly on missing pereopod 5 of male also); and the distinct ventral bumps on coxae 3 and 4.

Three criteria indicating that the two sexes belong to the same species are: (1) the prehensile pereopods 3 and 4 (?), (2) the rather long fourth maxillipedal palp article, and (3) the peculiar dorsal accessory lobe of the telson.

**RELATIONSHIP OF MALE:** In its second gnathopod it is closely related to *D. tuberculata* (see *D. curticauda*, Sars, 1895: pl. 230, fig. 2) but lacks eyes, has a larger dactylar process on gnathopod 2, and has distinctly prehensile pereopods 3–5. In addition to the above notes it differs from *D. porrecta* (see Sars, 1895: pl. 229) by the nonacuminate second coxa. The new species differs from *D. knipowitschi* Gurjanova (see 1951) by the same criteria mentioned above for *D. tuberculata*.

Species noted for poorly developed eyes and for having second gnathopods reasonably similar to the new species are *D. normani* Sars (1895: suppl. pl. 8), of which only the female has been described; *D. hirticornis* Sars (1885) and Stephensen (1944), and *D. abyssi*. The first two of these species have poorly prehensile pereopods. *D. abyssi* Stephensen (1944) lacks pereopods, and perhaps represents earlier growth stages of the present new species, since gnathopod 2 is shown in two stages which conceivably could lead to the present stage; terminal developments in the specimens at hand are the long dactylar tooth and the strongly broadened distal end of article 2 on gnathopod 2.
Fig. 12. Dulichia remis, n. sp. Holotype, male, 13.0 mm, Albatross 4781: a, lateral view, antennae and pereopod 5 broken; b, telson; c, end of maxillipetal palp; d, e, coxae 3, 4; f, end of gnathopod 1; g–i, details of gnathopod 2; j, k, end of pereopod 1; l, end of pereopod 3. Female, 16.0 mm, Albatross 4781: m, head and antennae; n, head, arrow indicating dorsum; o, p, gnathopods 1, 2; q–s, pereopods 3–5; t, end of pereopod 4; u, urosome.
REFERENCES


Bathyal Amphipoda—BARNARD


—— 1895. Amphipoda. An account of the Crustacea of Norway with short descriptions and figures of all the species. 1:viii and 711 pp., 240 pls., 8 suppl. pls.


The Chaetognatha of the Monsoon Expedition in the Indian Ocean

ANGELES ALVARIÑO

This report deals with the chaetognaths collected by the "R/V Argo" during the Monsoon Expedition in the Indian Ocean in 1960 and 1961. The Monsoon collections extended from about 8° S to 42° S (Fig. 1); that is, the region roughly limited by the Equatorial Countercurrent and the Subantarctic West Wind Drift (the Indian Central waters extending to the Subtropical Convergence); and also the Indonesian seas and the South Australian waters. This report includes only data from the Indian Ocean. Data from collections made by the same Expedition in the Pacific have been added to the study of the chaetognaths of the Pacific. However, data derived from the Pacific are used here also in discussing the distribution of the species. The Monsoon Expedition covered in part the regions surveyed for chaetognaths by the Gazette, Gauss, Sealark, Siberia, and Snellius expeditions, with the following exceptions: the Bay of Bengal, west coast of Ceylon, and waters of Somalia and eastern Africa.

The samples were taken with a 1-m open net, towed obliquely from a depth of 200 or 360 m to the surface; and several mid-water trawls are also included (see Table 1).

It is well known that the hydrographic changes taking place in the Indian Ocean are influenced by the monsoon regime. The sampling extended from November 1960 to January 1961. This is the season of the northeast monsoon (Mattheus, 1926).

Two well-defined zoogeographical boundaries were indicated in the Indian Ocean by the study of the Chaetognatha population: (1) the equatorial boundary extending south of the equator (from about 5° S in the West to 15° S in the East), and (2) the Subtropical Convergence region (at about 40° S). These well-defined boundaries frame latitudinally three main regions: Equatorial, Central, and Subantarctic.

Typical equatorial species of the Pacific that occur also in the Indian Ocean appear to be restricted to the Equatorial waters. Warm-water species that are cosmopolitan in distribution, extend along the Equatorial and Central Indian waters, while cold-water species do not extend to the Central waters. The Subtropical Convergence appears to be the fluctuating northern boundary for the latter.

The data obtained aid in filling the gap that existed in the zoogeography of the chaetognaths by adding information from the Indian Ocean. These observations make it easy to compare the relationships found in the distributional pattern shown by each of the species in the Indian Ocean and their respective allies in the Atlantic and Pacific oceans.

The Indian Ocean collection contains 23 oceanic species of chaetognaths, already known from the Atlantic and the Pacific oceans.

The following species were observed in the samples from the Monsoon Expedition in the Indian Ocean:

1 Contribution from the Scripps Institution of Oceanography, University of California, San Diego. Manuscript received May 13, 1963.
Fig. 1. Stations plan for the zooplankton collections of the Monsoon Expedition in the Indian Ocean.

O — 1-m net
Δ — mid-water trawl

Stations corresponding to previous work in this region are:

F — Siboga Expedition (Fowler, 1906)
R — Gazelle Expedition, Fauna Southwestern Australia, Deutsche Südpolar Expedition
(Ritter-Zahony, 1909, 1910, 1911)
B — Sealark Expedition (Burfield and Harvey, 1926)
S — Snellius Expedition (Schilp, 1941)
T — (Tokioka, 1956b)
D — (David, 1958, 1959)

*S. planctonis* Steinhaus
*S. pulchra* Doncaster
*S. regularis* Aida
*S. robusta* Doncaster
*S. tasmanica* Thomson
*S. zetesios* Fowler

Seventeen of the 23 species recorded are epiplanktonic. Ten of these are cosmopolitan and seven are Indo-Pacific. Fifteen of the 17 epiplanktonic species in the Indian Ocean connect with their respective regions of distribution in the Pacific Ocean along the Indonesian seas. The mesoplanktonic species *S. decipiens* and *S. zetesios* apparently connect with the Pacific population along the same route, while *S. planctonis* extends into the Pacific following the South Australian waters. These mesoplanktonic species are also cosmopolitan. However, *E. bathypelagica*, obtained previously only in the Pacific at great depths, was recorded here once at the northern part of the region covered by the "R/V Argo" in the Indian Ocean (mid-water trawl no. 3, at 11° 56' 42" S—115° 22'
### List of Stations of the Monsoon Expedition in the Indian Ocean

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<td></td>
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### Mid-Water Trawls

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</table>
12° E, from 2179 m depth). No typical Indian Ocean species was found. The sampling only covered the oceanic regions, and it is assumed that some neritic species of chaetognaths may be restricted to the Indian waters.

Important previous works on the Chaetognatha in the Indian Ocean and adjacent waters include:

<table>
<thead>
<tr>
<th>Authority</th>
<th>Number of valid species observed</th>
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<td>Béraneck (1895), Bay of Amboine</td>
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<td>Burfield and Harvey (1926), Indian Ocean</td>
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<td>Doncaster (1903), Maldive-Laccadive Archipelago</td>
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<td>Fowler (1906), Indian Ocean</td>
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<td>George (1952), Indian coastal waters</td>
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<td>Lele and Gae (1936), Bombay harbor</td>
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<td>Oye (1918), Java Sea</td>
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<td>Rao (1958), Lawson’s Bay, Waltair, Bay of Bengal</td>
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<td>Rao and Ganapati (1958), off east coast of India and Ceylon</td>
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<td>Ritter-Zahony (1909), southern Indian Ocean</td>
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<td>(1910), southwest Australia</td>
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<td>(1911), Deutsche Südpolar Expedition</td>
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<td>Schilp (1941), Indian Ocean</td>
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<td>(1956), Central Indian Ocean</td>
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<td>(1956), Arafura Sea</td>
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</table>

The chaetognaths observed in the Indian Ocean can be grouped as follows:


b) Cold-water representants: *S. gazellae, S. tasmanica, E. hamata.*


d) Mesoplanktonic: *S. decipiens, S. planctonis, S. zetesios.*


It is important to notice that *Sagitta macrocephala* Fowler was not recorded here. The absence of this species from the samples may be due to its scarcity and to the small number of deep samplings. It was previously recorded in the Indian Ocean by Fowler (1906), Burfield and Harvey (1926), and Schilp (1941).

*Sagitta gazellae,* an oceanic species with a circumpolar distribution in the Antarctic and Subantarctic waters, enters the Atlantic, Indian, and Pacific oceans up to the Subtropical Convergence, often extending further north in deep levels in the Atlantic and Pacific (Alvariño, 1964b). In the Monsoon collections (Fig. 2), *S. gazellae* occurred as far north as 36° S—98° E and 37° S—71° E; whereas David (1958) reported it extending along the 90° E meridian from 65° S to approximately 41° 30′ S (Fig. 2), and David (1959) from 66° 35′ S to 42° 35′ S (south of the Indian Ocean). The specimens of *S. gazellae* recorded in the Monsoon region might very well represent penetrations of the Subantarctic waters below the Subtropical. The penetration apparently does not extend farther north, because none were recorded at the midwater trawl station 9 situated north of the septentrional boundary of this species in the Indian Ocean, although the sampling went to 1878–2000 m deep. The northernmost records of *S. gazellae* in the Indian Ocean (David, 1955) were at 40° 30’ S—90° E, and in the Pacific at 39° 20’ S—180° E and 38° 30’ S—126° W.

At station 22 (37° 49.6’ S—85° 21.7’ E) only young specimens 28–30 mm long at early maturity stage 1 were found; while at station 25 (57° 43’ S—169° 12’ E) some were 50–60 mm long and still at maturity stage 1. In the Pacific, at station 29 (40° 37’ S—164° 08’ W) the specimens were 20–30 mm in length, and at station 32 (28° 35.3’ S—158° 57.5’ W) they were 20–30 mm long and at maturity stage 1.

David (1955) points out that *S. gazellae* was occasionally taken north of the Subtropical Convergence at 41° 49.7’ S—18° 49.9’ E, and that the hydrographical data showed a northward extension of the Subantarctic waters. The observations in the Pacific (Alvariño, 1964b) showed the progression of the Subantarctic waters at deep levels far north of the Subtropical Con-
vergence. In the Pacific (Alvarino, loc. cit.), at about 35° S—21° S, there is an overlapping of the populations of *S. gazellae* and *S. pacifica* at about 200–400 m depth. In the Indian Ocean, the northern boundary of *S. gazellae* and the southern boundary of *S. pacifica* did not overlap, and do not even appear well juxtaposed. However, this pattern cannot be admitted as definitive; it may be due to scarcity of sampling in these localities. More data from this region will eventually show if this distributional pattern persists, or if both species occur in a pattern similar to that shown in the Pacific.

*S. lyra* recorded by Tokioka (1940) is most probably *S. gazellae* because of the geographic localities of the records (33° and 35° S and 151° E); and the *S. lyra* recorded by David (1939) and by Johnson and Taylor (1921) may also be *S. gazellae*.

*S. pacifica* populations of the Pacific and Indian oceans connect along the Indonesian seas (author’s records; Tokioka, 1955, 1956b; and possibly also the report of Béranecq, 1895). It appears to extend with the South Equatorial Current to the Indonesian seas and then into the Indian Ocean (Fig. 2). It cannot be ascertained if some representatives of this species enter the Agulhas Current, since they have not yet been observed in the Atlantic.

Previous records of *S. serratodentata* in the Indian Ocean by Burfield and Harvey (1926), Doncaster (1903), Fowler (1906), John (1937), Ritter-Zahony (1910, 1911), and Schilp (1941), could be considered to be *S. pacifica*. Baldasseroni (1915) was the first to distinguish Atlantic specimens of *serratodentata* from those of the Pacific; he gave a short diagnosis and published drawings of the seminal vesicles of the species. Tokioka (1940) published a complete diagnosis and named the species. Cleve’s (1901) records of *S. serratodentata* Krohn should correspond to *S. pacifica*. The John (1937),
Chaetognatha of the Monsoon Expedition—Alvarino

Rao (1958a, b) Rao and Ganapati (1958), and Ritter-Zahony (1910, 1911) records of S. serratodentata correspond to S. pacifica. Other records of S. pacifica in the Indian Ocean are given by Tokioka (1940, 1955, 1956a, b).

S. tasmanica populates the Atlantic and the southernmost part of both the Indian and Pacific oceans up to the Subtropical Convergence. The northern boundary follows a pattern similar to that of S. gazellae, although it does not progress northward in deep layers as S. gazellae does. More data are needed to establish the extension of the distribution.

This species extends along southern Australia into the Pacific (Alvarino, 1964b); and it appears from the S. tasmanica records in the Pacific and Indian oceans that the Subtropical Convergence acts as a barrier which interrupts the distribution of the species northward from that boundary. With these findings in mind, and the fact that this species is recorded widely in the Atlantic, more data are needed before definitive conclusions may be drawn (Fig. 3).

Unfortunately, some of the expeditions in the Indian Ocean did not cover the distributional region of S. tasmanica, and most of the data from the Atlantic are difficult to interpret, because this species has been recorded together with S. serratodentata under Krohn's synonymy.

David's (1958, 1959) records of S. serratodentata Krohn refer probably to both S. tasmanica and S. pacifica and to S. tasmanica respectively.

S. lyra, a typical Atlantic chaetognath, appeared in small numbers and only in the West-Central Indian waters (Fig. 3). Other records are given by Baldasseroni (1915), Burfield and Harvey (1926), Fowler (1906) as S. furcata, Oye (1918), Ritter-Zahony (1911), Schilp (1941), and Tokioka (1956a).

S. enflata extends along the Indian Equatorial waters. It is heavily distributed in the eastern

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Fig. 3. Distribution of S. lyra and S. tasmanica in the Indian Ocean, including positive records from previous expeditions.
part of these waters and in the Sunda Sea. I suspect that it will also extend along the Indian Central waters, but lack of sampling in the East-Central Indian Ocean does not permit a complete picture of the distribution of this species (Fig. 4). Other records in the Indian Ocean: Baldasseroni (1915), Béraneck (1895), Burfield and Harvey (1926), Chacko (1950), Cleve (1901), Doncaster (1903), Fowler (1906), George (1952), John (1933, 1937), Lele and Gae (1936) as S. gardineri, Menon (1945), Oye (1918), Pillai (1944), Rao (1958a, b), Rao and Ganapati (1958), Ritter-Zahony (1909, 1910, 1911), Schilp (1941), and Tokioka (1940, 1955, 1956a).

S. robusta was observed in the Indonesian seas and at the northeastern stations in the Equatorial Indian Ocean. It apparently remains (Fig. 5) restricted to the Equatorial waters, whereas S. ferox (also an Equatorial species) spreads further south into the Tropical region. A similar pattern was observed in the Pacific (Alvariño, 1962b). It is obvious that the populations of both the Pacific and the Indian oceans connect along the Indonesian seas. Other records in the Indian Ocean: Baldasseroni (1915, S. robusta), Doncaster (1903), and Fowler (1906), recorded both species. Burfield and Harvey

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Fig. 4. Distribution of S. enflata and S. hexaptera in the Indian Ocean, including positive records from previous expeditions.
Chaetognatha of the Monsoon Expedition—Alvarino

FIG. 5. Distribution of S. robusta and S. ferox in the Indian Ocean, including positive records from previous expeditions.

(1926), George (1949, 1952), Oye (1918), Ritter-Zahony (1909, 1910, 1911), and Schilp (1941) recorded both under the S. robusta synonymy. Rao (1958a, b) and Rao and Ganapati (1958) records of S. robusta probably correspond to S. ferox and those of S. hispida to S. robusta. Tokioka (1940) recorded both species in 1955, and in 1956b only S. robusta, in 1956a, both species, although S. ferox is recorded under the S. ai Tokioka synonymy. Other records: Chacko (1950), John (1933, 1937), and Varadarajan and Chacko (1945).

S. bipunctata was abundant in the stations north of 30° S. According to the data obtained, it appears that the populations of S. bipunctata of the Indian and Pacific oceans connect along the Indonesian seas, as no S. bipunctata was observed south of parallel 30° S; while the 35° S parallel appears to be the southern boundary for this species in the Pacific (Alvarino, 1964a, and other unpublished data; Bieri, 1959). It inhabits the Tropical Equatorial and Central Pacific waters. Other records in the Indian Ocean: Baldasseroni (1915), Béraneck (1895), Cleve (1901), Oye (1918), Rao (1958a), Rao and Ganapati (1958), Ritter-Zahony (1910, 1911), Schilp (1941), Thomson (1948), and Tokioka (1940, 1955, 1956b). The Burfield and Harvey (1926) and George (1952) drawings of S. hispida are more likely to be of S. bipunctata.

S. bedoti appeared abundantly in the Indonesian seas to the southwest of Java, a position between Cocos Keeling Isl. and the Christmas Islands. Other records in the Indian Ocean: Baldasseroni (1915), Béraneck (1895), Burfield and Harvey (1926), Doncaster (1903, as S. polydon), Fowler (1906), George (1952), Lele and Gae (1936), Pillai (1944), Rao (1958a), Rao and Ganapati (1958), Ritter-Zahony (1910) Schilp (1941), Subramanian (1940), and Tokioka (1955, 1956a, b).

S. neglecta was recorded only at station 11 (11° 15′ S—103° 32′ E). Other records in the Indian Ocean: Baldasseroni (1915), Burfield
and Harvey (1926), Chacko (1950), Doncaster (1903, as *S. septata*), Fowler (1906), George (1949, 1952), John (1933, 1937), Oye (1918), Rao (1958a, b), Rao and Ganapati (1958), Schilp (1941), Tokioka (1955, 1956b), Varadarajan and Chacko (1943).

*S. pulchra* was observed in the Indonesian seas and in the Equatorial Indian waters as far as the Mauritius Islands. Other records in the Indian Ocean: Baldasseroni (1915), Burfield and Harvey (1926), Doncaster (1903), Fowler (1906), George (1949, 1952), Oye (1918), Rao (1958a, b), Rao and Ganapati (1958), Ritter-Zahony (1910, 1911), Schilp (1941), and Tokioka (1955, 1956a, b).

*S. minima*, cosmopolitan in the warm and temperate waters, should be expected in the Central Indian Ocean waters. However, it was only observed in very small numbers at stations 11, 13, 15 (11° 15' S—103° 32' E, 17° 01' S—93° 28.6' E, 12° 57.9' S—75° 13.6' E) respectively. The samples examined showed an abundance of *S. bipunctata* and a scarcity of *S. minima*, whereas the opposite was found by Tokioka (1956a). The samples examined by Tokioka (loc. cit.) were taken on December 11, 1954—January 16, 1955, and the Monsoon samples from October 22, 1960—January 9, 1961, which is practically during the same monsoon regimen. Therefore, no speculation could be made based on the monsoon influence in the distribution of these species. In the samples from the Naga Expedition in the South China Sea and the Gulf of Siam (Alvariño, unpublished data), *S. bipunctata* appeared also more abundant than *S. minima*, unlike the quantitative pattern shown by both species in the North Pacific. Other records of *S. minima* in this ocean: Ritter-Zahony (1910, 1911), Schilp (1941), Thomson (1948), and Tokioka (1955, 1956a).

*S. regularis* extended in the Equatorial waters as far as the Mauritius Islands. Although no specimens of *S. regularis* were observed at the stations in the Indonesian seas, it is reasonable to assume that the species extends along those paths to the Pacific. Large numbers of *S. regularis* were observed in the samples of the Naga Expedition, from the Gulf of Thailand and the South China Sea (Alvariño, unpublished data). The lack of positive records in regions where the presence of this species is to be expected, is likely due to the small size of the *S. regularis* which could easily escape owing to the size of the mesh used in the nets. The species has been recorded by previous workers in the Indonesian region. Other records in the Indian Ocean: Burfield and Harvey (1926), Doncaster (1903), Fowler (1906), George (1952), Menon (1945), Oye (1918), Rao (1958a, b), Rao and Ganapati (1958), Ritter-Zahony (1910, 1911), Schilp (1941), and Tokioka (1955, 1956a, b).

*S. decipiens* extended along the strata below 250 m from the northern part of the region covered in the Indian Ocean to 37° S. In the Pacific it extended along those strata from 40° S (Alvariño, 1964b; Bieri, 1959). Other records in the Indian Ocean: Burfield and Harvey (1926), David (1958), Fowler (1906) as *S. sbagae*, Rao and Ganapati (1958), Ritter-Zahony (1911), and Schilp (1941).

*S. planctonis* was observed along the northern part of the Subantarctic West Wind Drift extending into the Subtropical Convergence in the Indian Ocean. It was found below the 200-m level up to 36° S, and in deeper waters up to 22° S (mid-water trawl from 2000 m deep, one specimen). The connection of the populations of *S. planctonis* of the Indian and Pacific oceans evidently occurs along the south Australian seas. Its distribution in the Pacific was also found limited by the Subtropical Convergence towards the north (Alvariño, 1964b). *S. zetesios*, a species closely related to *S. planctonis*, extends along the mesoplanktonic domain of the Tropical, Equatorial, and Central Indian waters. The two-dimensional pattern of distribution for *S. zetesios* overlaps that of *S. planctonis* at mid-water trawl station 8 (22° 04' S—63° 02' E), where one specimen of *S. planctonis* and two of *S. zetesios* were observed in a haul taken from 2000 m. At mid-water trawl 9 (33° 19' S—72° 34' E) taken from 1878 m, 38 specimen of *S. zetesios* were recorded with only three specimens of *S. planctonis*. The *S. planctonis* domain, then, extended south of that boundary.

The Burfield and Harvey (1926), George (1952), and John (1937) records of *S. planctonis* are most likely to be *S. zetesios* in view of the location of the observations and the drawings and descriptions of the species included in the
respective publications. David's (1959) records of *S. zetesios* should have included *S. planctonis*. Fowler (1906) recorded *S. zetesios* and, in species "incertae," *S. planctonis*. Schilp's (1941) records of *S. planctonis* may apply to *S. zetesios*. Ritter-Zahony (1911) observed *S. planctonis* at about 44°S in the Southwest Indian Ocean and in the Subantarctic-Antarctic waters of the Southwest Indian Ocean. Tokioka's (1940) records of *S. planctonis* from Australian waters are accurate, but those of *S. planctonis* from Japanese waters may apply to *S. zetesios*. The discrepancy Tokioka refers to in relation to the percentage of the length of the tail segment to the total length between those populations indicates that he was dealing with two different species: *S. zetesios* in the Japanese waters and *S. planctonis* in the New South Wales region. This is also understood when observing the drawings that appear on page 374 (loc. cit.): Fig. 8A is *S. planctonis* (the anterior end of the anterior fins reaches the level of the middle of the ventral ganglion); and Fig. 8D is *S. zetesios* (the anterior end of the anterior fins reaches the level of the posterior end of the ventral ganglion). (See original descriptions of Steinhaus, 1896, and Fowler, 1905.)

*Krobnitta subtilis* populates the Equatorial and Central Indian Ocean, and does not reach the boundaries of the Subtropical Convergence. The Indo-Pacific populations connect through the Indonesian seas. Other records in the Indian Ocean: Burfield and Harvey (1926), Fowler (1906, 1950), George (1952), Rao (1958a, b), Ritter-Zahony (1910, 1911), Schilp (1941), and Tokioka (1940, 1955, 1956a, b).

*K. pacifica* was observed only at station 8 (north of Flores Island). This species is not so widely distributed as is its congeneric *K. subtilis*, and is for the most part restricted to the Equatorial waters. This is the only equatorial-tropical species of chaetognath common to these regions in the Atlantic, Indian, and Pacific oceans. The presence of this species in the Equatorial-Tropical Atlantic suggested one of two hypotheses: either it is conveyed by the Agulhas Current into the Benguela Current and assimilated by the Equatorial Current, or the populations of *K. pacifica* at both sides of Central America, although long isolated, still somehow remain unchanged morphologically, but the process of divergence is noticed. There are no conveniently available samples and data from the Atlantic to explain this problem. However, Heydorn (1959) did not observe it in the Benguela region.

Other records in the Indian Ocean: Burfield and Harvey (1926) under the *K. subtilis* synonymy; Chacko (1950), Doncaster (1903), Fowler (1906), George (1952), Oye (1918) as *K. kerierti*; Pillai (1945), Rao (1958a, b), Rao and Ganapati (1958), Ritter-Zahony (1910), Schilp (1941), Tokioka (1955, 1956a, b), and Varadarajan and Chacko (1943).

*Pterosagitta draco* inhabits the Equatorial and Central Indian waters, and its extension southward is apparently limited by the Subtropical Convergence. Other records in the Indian Ocean: Baldasseroni (1915), Béranec (1895), Burfield and Harvey (1926), Doncaster (1903), Fowler (1906), George (1952), Rao (1958a, b), Rao and Ganapati (1958), Ritter-Zahony (1910, 1911), Schilp (1941), and Tokioka (1940, 1955, 1956a, b).

*Eukrohnia hamata* was recorded at the stations along the southernmost part of the region sampled, in hauls taken from 283 and 268 m deep, and the records taken in the central gyral were from 1878 m deep. There are two possible alternatives: (1) *E. hamata* does not progress northward from the boundary of the Subtropical Convergence in the Indian Ocean, or (2) if it does progress northward it is not very abundant and hence is missed by the sampling, or it may appear in layers deeper than those mostly sampled. Other records in the Indian Ocean: Burfield and Harvey (1926), Fowler (1906), Ritter-Zahony (1911), and Schilp (1941).

*E. fowleri* was recorded at the mid-water trawls 2, 3, 4, and 10, taken from 2121, 2179, 1721, and 2060 m deep, respectively. In all probability, *E. fowleri* populates the deep layers (below 1600 m) of the Indian Ocean, as it does in the Pacific and Atlantic. The species *E. fowleri* was only recorded at the boundary of the Indian Ocean and the Indonesian seas. A peculiarity of this species is that it emerges to higher levels in the Equatorial regions than in others in the Pacific (author's unpublished data), and that the populations extend along deeper levels in other parts of the oceans. Other records
in this region: Ritter-Zahony (1911), and Schilp (1941).

E. bathypelagica was represented by only one specimen at mid-water trawl 3 (11° 56' S—115° 22' E) taken from 2179 m. This single record could be considered as a stray of the population extending along deeper levels. This is the first record of the species occurring other than in the Pacific Ocean (Alvarino, 1962a). This species could not be the spent stage of E. hamata, in view of the morphological characteristics and the size reached at maturity (E. bathypelagica 23 mm, and E. hamata 43 mm).

Sagitta hexaperta is the most common species in the region of the Indian Ocean covered by the Monsoon Expedition, followed by P. draco, S. pacifica, S. ferox, S. bipunctata, and K. subtiliss. The species appearing in the highest number relative to the frequency were, in regressive order: S. gazellae, S. bedoti, S. enflata, S. pacifica, and S. tasmanica.

ACKNOWLEDGMENTS

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Additional Records of Hawaiian Platycetenea (Ctenophora)

DONALD C. MATTHEWS AND SIDNEY J. TOWNSLEY

IN A PREVIOUS PAPER (Matthews, 1954:282) representative samples of all orders of Ctenophora were reported for Hawaii. Of these, the platycetids were represented by only two immature specimens of Coeloplana dubosequii collected on the reef of the Hawaii Marine Laboratory on December 31, 1952. This small, pale, yellowish-green platycetid has not been collected since, although the alga (Hypnea nidifica) on which it was found has been periodically examined. Also, continuous examination of spines of the slate-pencil urchin, Heterocentrotus mamillatus (viz. Utinomi, 1961:116, pl. 58, no. 9), has failed to reveal platycetids, although Dawydoff (1938:161) reported having collected Coeloplana weilli on this urchin in the region of Ream (Gulf of Siam, Cambodia). It is rather ironical that, quite by chance, platycetids were taken in 1961 on the spines of the black urchin, Echinosbrix diadema, collected from the sandy bottom in about 10 m of water at the seaward edge of Waikiki reef. Again, in January, April, and May 1962, and in April 1963, platycetids were taken on E. diadema at about the same depth, near Buoy No. 8, Kaneohe Bay, Oahu.

Coeloplana willeyi Abbott, 1902

Fortunately, as many as 50 platycetids may crowd the spines of E. diadema in Hawaii. Thus, sufficient numbers are available from which a composite picture of this beautiful but extremely variable species can be made. Although their color is described as "scarlet or carmine red, fading toward the edges to a yellowish pink" (Abbott, 1902:108), this characteristic in Hawaiian specimens warrants further explanation. Distribution on spines seems color-correlated. Alternate purple and white rings characteristic of large spines of young E. diadema (vide Utinomi, 1961:113, pl. 57, no. 6) ultimately darken and fuse into black. Small C. willeyi, whose tentacular axes do not exceed ring widths, occur more frequently on dark rings; whereas large C. willeyi, whose tentacular axes exceed ring widths, occur more frequently spirally arranged on dark rings. However, both small and large platycetids seem distributed indiscriminately over black spines of older urchins. Both small and large specimens appear lighter when removed to a light background.

Background, however, is only one factor which affects color; another is their ever-changing shape. As described by Abbott (1907:46), certain relaxed regions may flow in one direction like a thin film which, because of widely separated pigment granules, appears extremely light in contrast to certain contracted regions which appear dark. These "flows" may be limited to one side of the main (tentacular) axis, resulting in a highly asymmetrical, partially light and partially dark body, or they may proceed simultaneously in all radii, resulting in a thin, almost circular, pinkish-yellow film. Although Abbott (1907:47) states: "about the periphery there is a series of white or yellowish-white spots or flecks of color . . . ," and Komai (1922:93) extends these to include the bases of the dorsal papillae, in the Hawaiian representatives of this species these spots or flecks are only weakly developed. Dependent, then, upon the above considerations C. willeyi in Hawaii may be described as deep purple, red, pink, or yellowish-white, and any one animal may reveal simultaneously all of these various colors. There is, however, an overall tendency for the region along the tentacular axis to be darkest. The ventral surface is uniformly grayish-white.

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As mentioned by Abbott (1907:47) "... measurements of *Coeloplana* are not of much value in an animal of such great mobility. When fully contracted the shape of the body ... is nearly circular. *C. willeyi*, in such conditions usually measures 1–2 cm. across. ..." Komai (1922:93) gives the range of the Misake representatives of this species as "... 20–60 mm. (in extended state)." The range of the Hawaiian representatives is from 2 mm (contracted) to 32 mm (relaxed).

Besides the well-developed tentacular apparatus, which may extend colorless, cydippid-like tentacles to many times the body diameter, numerous dorsal tentacles (papillae) are present. Komai (1922:9) gives the number of these dorsal papillae as commonly 20–30. Yet, these minute, club-shaped outgrowths of the gastrovascular canals are not well developed in Hawaiian representatives of this species for, as stated by Abbott (1907:48), "The body tissue of *C. willeyi* is so loose and the animal itself so 'amoeboid' in its movements that it is impossible to tell, in the living specimen, just what arrangement these dorsal tentacles have. ... They tend to disappear when the animal relaxes, and reappear, especially when contraction is along the tentacular axis. In such instances, two poorly defined sagittal "rows" appear, but it is difficult to determine which papillae are derived from paratentacular canals and which are derived from parastomacal canals. While dorsal papillae may be arranged on one side of the tentacular axis in a 2–4–4–2 series, the other side may be arranged in a 2–3–4–1 series. In other specimens only the 2–3 series is present on one side, while on the opposite side, a 2–3–5–1 series is present. Of the many specimens observed, not one exhibited a symmetrical arrangement of dorsal papillae. Their total number ranged from 18–24. Variations in size, number, and arrangement of dorsal papillae are not restricted to *C. willeyi*. Dawydoff (1938:160) says of *C. perrieri*:

Close examination shows that the apparatus in question is based, in our species, on the most diffuse scheme in the *Coeloplanidae*, that is to say, that the aboral papillae are arranged in four irregular rows (each one containing 4 or 5 papillae) so that the paratentacular papillae cannot be distinguished externally from the parastomal papillae. Moreover, in each row, the papillae have lost their usual alignment and generally show an embarrassing disorder to the observer. [Authors' translation.]

The aboral sense organ is clearly discernible as a small, unpigmented area in the center of the tentacular axis. Although Abbott (1907:47) states that the comparatively small otolith of living *C. willeyi* is frequently difficult to find, in Hawaiian representatives the pit in which it lies is closed by fleshy lips only when this region of the organism contracts. When this region relaxes, the otolithic mass is clearly seen and displays the usual, constant vibrating motion. The internal (concave) and external (convex) surfaces of the two slightly elevated semicircular polar plates are devoid of digitiform papillae, thus conforming to Komai's (1922:14) statement that in *C. willeyi* lobation of polar plates does not occur. Rudimentary ciliary bands are present, but beating cilia are seen only on polar plates and oral surface.

As previously reported for *C. dubosequii* (Matthews, 1954:284), prominent excretory pores are located just outside the border of each polar plate. These pores appear and disappear as the gastrovascular system relaxes and contracts. In *C. willeyi* the region beneath an excretory pore forms a large temporary reservoir which, as it fills, protrudes as a light thin-walled hemisphere equal in size to the dorsal sense organ. The excretory "pore" is thus carried aloft and, as it opens, expulsion of materials quickly obliterates the reservoir. These "reservoirs" fill and empty neither simultaneously nor alternately; but, rather, one may function many times before the other becomes operative.

Both living and stained (with acidulated borax-carmine and indulin) specimens show no trace of gonadal development, despite the fact that their size suggests sexual maturity. This, however, strengthens Komai's (1922:32) contention that "... besides some negligible exceptions, the breeding season of *Coeloplana* may be said to extend from early summer to early fall, the gonads developing in the main during summer months and the spawning taking place generally in late summer or in early autumn."

The fact that three urchins are now known to serve as hosts for platyctenids (*C. echinica...
Tanaka on *Toxopneustes pileolus*; and *C. willeyi* Abbott on *Heteroctentrotus mamillatus* and *Echinothrix diadema* suggests an extensive fauna on these widely distributed echinoderms.

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NEWS NOTE

Tenth Pacific Science Congress Papers

The Tenth Pacific Science Congress of the Pacific Science Association was held on the campus of the University of Hawaii August 21 to September 6, 1961, under the joint auspices of the University, the Bernice P. Bishop Museum, and the National Academy of Sciences.

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Dr. Szent-Ivany is senior entomologist in the Department of Agriculture, Stock and Fisheries of the Territory of Papua and New Guinea.

94 pp. May 5, 1964 Paper, $2.50

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B. J. MARPLES
Pacific Island Spiders

M. J. COOPER
Ciguatera Poisoning in the Gilbert Islands

MAXWELL S. DOTY and ISABELLA A. ABBOTT
Liagoropsis

D. L. PAWSON
Holothuroidea Collected off Southern Chile

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Thoracic Cirripedia from a Southeast Pacific Guyot

VICTOR A. ZULLO1 AND WILLIAM A. NEWMAN2

A DREDGE HAUL taken at a depth of 228 m from a flat-topped seamount (guyot) by the "R/V Horizon" in January 1958, during the Scripps Institution of Oceanography IGY cruise to the southeast Pacific, has yielded specimens of four genera of barnacles representing three extant suborders of the order Thoracica. The Lepadomorpha are represented by a new species of Megalasma s. str. Hoek (1883) and by a new species of Heteralepas s. str. Pilsbry (1907). The Verrucomorpha are represented by a new species of Verruca Schumacher (1817), and the Balanomorpha by a new species of the subgenus Solidobalanus Hoek (1913) of the genus Balanus Da Costa (1778).

Neither Megalasma nor Solidobalanus has been previously reported from the eastern Pacific. The former is but the second member of the family Poeclismatidae known from this zoogeographic province. Heteralepas has been recorded twice from the eastern Pacific: Heteralepas quadrata (Aurivillius, 1894) from Lower California, and H. cygnus Pilsbry, 1907, presumably from Monterey, California. No other reports on members of the entire family Heteralepidae in the eastern Pacific have been made since, although one of us (W.A.N.) has recently examined specimens referable to H. quadrata, occurring on Panulirus penicillatus (Oliver) from the Galapagos Islands.

Verruca had previously been known from the west coast of South America by the extant littoral species V. laevigata Sowerby (Darwin, 1854:520), and from the Pliocene in the vicinity of Nome, Alaska, by the presumed littoral species V. alaskana Pilsbry (MacNeil et al., 1943:95). In addition to the published fossil record of Verruca in the eastern Pacific, several isolated compartmental plates of a new species of this genus from the Oligocene Gries Ranch beds of Washington are contained in the Museum of Paleontology of the University of California, Berkeley (hereafter referred to by the abbreviation UCMP).

The unnamed guyot from which the present sample was taken is located on the southwest end of Nasca Ridge (Fig. 1) at 85° 25' W, 25° 44' S, about 1280 km (800 miles) off the coast of Chile and 480 km (300 miles) approximately N 80° W of San Felix Island (Fisher, 1958, fig. 8, station HD-73). A triglid fish has been described from the same sample (Hubbs, 1959:313-315), and a manuscript on a new species of the stiroid echinoid Salenia Gray is in press (Zullo, Kaar, Durham, and Allison).

We wish to extend our thanks to Mr. Robert H. Parker of the Scripps Institution of Oceanography for making available the material described in this paper. The descriptions and figures of the new species of Megalasma and Heteralepas were prepared by W. A. Newman. The new species of Verruca and Balanus were described by V. A. Zullo and illustrated by Ruth L. von Arx.

SUBORDER LEPADOMORPHA Pilsbry

FAMILY POECILASMATIDAE Annandale

Synonymy: Nilsson-Cantell, 1921; Trilasmatidae Nilsson-Cantell, 1934a.

GENUS Megalasma Hoek

Megalasma (Megalasma) elegans Newman, sp. nov.

Figs. 2A-I

DIAGNOSIS: Capitulum of five completely calcified, fully approximate valves; carina with internal transverse plate forming a single internal
tooth on either side; occludent margin of tergum nearly one-third length of occludent margin of scutum; portion of scutum below umbo rotated approximately 90°, forming continuation of occludent margin below scutal umbo; outer surface of basal portion of carina marked by approximately six rows of low, weak ridges; strong beaded ridge seen in M. (M.) striatum Hoek, running in arc from below the scutal umbones across the basal portion of the scuta and carina to the carinal umbo, lacking.

Prosoma strongly developed; insertion of cirrus I widely separated from that of cirrus II, on posteroverentral margin of prosoma; single pair of dorsal thoracic filamentary appendages situated approximately halfway between the insertions of cirri I and II; cirri long, ctenopod; five pairs of setae on intermediate articles of posterior cirri, major pairs pinnate; outer surface of pedicles of all cirri marked by finely spaced lines or broad scales; major spines of caudal appendage plumose.

DESCRIPTION: Terga (Figs. 2A, B, C-1) triangular, occludent margins approximately one-third, and scutal margins nearly two-thirds length of scuta; outer surface nearly flat, lightly marked by transverse growth lines and minute longitudinal ridges; terga form a flat continua-
tion of the carinal margin and are marked by chevron-shaped growth lines; primordial valves apical; interior moderately concave, smooth; scuto-occludent angle with fossa to receive projection formed by tergo-occludent angle of scutum.

Scutum (Figs. 2A, B, C–2) broadly triangular, divided into two portions by a ridge running from the umbones to the tergolateral angles; exterior marked by distinct growth lines running transversely above, and nearly longitudinally below the dividing ridge; minute ridges running perpendicularly or nearly perpendicularly to them; surface above dividing ridge broadly convex; below ridge, reflexed laterally to form, with its neighbor and the expanded basal portion of the carina, a receptacle for the peduncle; interior smooth, broadly concave; elevated occludent margin terminating in a smooth articular surface at the umbo; portion basal to umbo forming ventrolateral elements of peduncular receptacle; carinal margin supporting shallow fossa in lower third, receiving lateral tooth of carina; umbo situated approximately one-fifth the length of the occludent margin of the scutum from the base; faint scar of the strong scutal adductor muscle located just inside the ridge of the occludent margin opposite the tergolateral angle.

Carina (Figs. 2A, B, C–3, D) indistinctly divided into two regions due to expansion and flection of basal portions in forming the carinolateral elements of the peduncular receptacle; external surface of basolateral portions supporting about six rows of short, small, weak ridges; entire valve crossed by longitudinal growth lines running nearly parallel to the scutal margin; carinal margin with chevron-shaped growth lines running into a shallow V-shaped trough or depression; this depression not continued forward onto the carinal ridge formed by the carinal margins of the terga; primordial valve occasionally supported on a projecting umbonal portion (cf Figs. 2B, D); this arrangement apparently not correlated with size in the dozen specimens examined, as suggested by Barnard (1924); inner cup-shaped plate, along with expanded lateral portions, forming carinal contribution to the peduncular receptacle, produced laterally as a pair of teeth; distal angles flared laterally, forming articular surfaces on which the terga and scuta bear; capitulum of holotype UCMP 37860, the largest specimen, measured 9.5 mm high, 3.8 mm deep, and 3.6 mm wide; peduncle had average diameter of 1.2 mm and extended 0.82 mm below basal margin of carina; orange ovigerous lamellae visible through semi-translucent shell; smallest specimen in series 3 mm high.

Labrum (Fig. 2E) produced anteriorly in a V-shaped trough, divided into right and left portions by a medial ridge in the chitin; supporting 22–24 small, stout, sharp teeth; mandibular palps spatulate, attached to labrum; superior margin slightly concave, supporting numerous spines along superior and inner margins (left palp in Fig. 2E aberrant); mandible (Fig. 2F) remarkably long, with four teeth, not including inferior angle; inferior angle bifid; surface clothed with short spines, a few of which extend over cutting edge; superior and inferior margins and notch between first and second teeth supporting long spines; inner maxilla (Fig. 2G) with three major spines above and many below notch; notch, and superior and inferior margins, supporting several spines; surface clothed sparsely with degenerate spines occurring in groups of one to four; outer maxilla (not figured) nearly one-third again as long as high; superior margin slightly concave; superior and inner margins supporting long, relatively heavy setae or spines.

Cirrus I widely separated from II; attached to posteroventral margin of prosoma; rami subequal; outer ramus approximately twice as wide as inner ramus, setae arranged nearly symmetrically on both lesser and greater curvatures; terminal article supporting about six strong spines; inner ramus densely setose on lesser curvature, a few spines at each articulation on greater curvature, articles slightly longer than wide; setal arrangement essentially ctenopod and normal in appearance; remaining cirri clearly ctenopod; each cirrus in turn longer than the preceding; rami subequal; proximal articles (except the first) nearly as long as wide; intermediate articles nearly 4 times as long as wide, each with five pairs of setae, the two or three stronger pairs pinnate; first proximal article long, apparently composed of several fused segments; pedicles of all cirri supporting a single row of minute spines along posterior margins.
and fine closely spaced scales on raised postero-lateral surfaces; despite the long, delicate and ctenopod nature of the cirri, apparently adapted to capture small particles or prey, the rami are made up of relatively few articles; counts for a single ovigerous specimen (holotype UCMP 37860) given below:

<table>
<thead>
<tr>
<th>Cirrus</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
<th>VI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Outer ramus:</td>
<td>10</td>
<td>13</td>
<td>16</td>
<td>16</td>
<td>17</td>
<td>14</td>
</tr>
<tr>
<td>Inner ramus:</td>
<td>10</td>
<td>12</td>
<td>15</td>
<td>18</td>
<td>16</td>
<td>14</td>
</tr>
</tbody>
</table>

Caudal appendage (Fig. 21) short, supporting approximately four plumose spines and occasionally one or two small spinules. Penis (not figured) relatively small, slender and in-
conspicuous; surface clothed sparsely throughout with long, soft setae and an occasional short spine; distal end supporting numerous long, soft setae which obscure details of apex; surface irregular and lumpy, no annulations observable.


**DISCUSSION:** The status and definition of the genus *Megalasma*, especially of the less clearly defined subgenus *Megalasma* (*Glyptelasma*), has been discussed and emended by a number of authors, particularly Calman (1918, 1919). Kriger (1940:29, table 1) indicates that at least five species of the subgenus *Megalasma* (*Megalasma*) have been described. These can be divided into two series: "Striatum," the type series of the genus and subgenus, and "Minus," the second form of the subgenus to be described. The latter series may contain as many as three species. However, the views of Barnard (1924), Nilsson-Cantell (1938), and Utinomi (1958), when taken together, suggest that there is only one species contained in the "Minus" complex. The inclusion of *M. striatum* in a portion of the *M. minus* synonymy by Weltner (1922) is apparently by *lapsus calami*. The present report is not directly concerned with the "Minus" synonymy, having no additional data, and simply follows the synonymy proposed by these workers:

1. *Megalasma* (*Megalasma*) *striatum* Hoek, 1883
2. *Megalasma* (*Megalasma*) *minus* Annandale, 1906b
   *Megalasma striatum minus* Annandale, 1906b
   *Megalasma lineatum* Hoek, 1907
   ?*Megalasma bellum* (Pilsbry, 1907c)
   ?*Megalasma carinodontatum* Weltner, 1894

The two series are closely related, differing in proportions and details of the articulations of the valves. Following the views of Pilsbry (1907c) and Broch (1922), the degree and specialization in armament seen in *Megalasma* *s. str.* has progressed, from *Poecilasma* through *Glyptelasma*. The most highly developed form is *Megalasma striatum*, in which the terga are enlarged (a condition that reduces the relative height of the carina to half the height of the entire capitulum) and the lateral margins of the distal portions of the carina are strongly developed articular surfaces. It is to the *striatum* section of the subgenus that the new species described here belongs.

*Megalasma* (*Megalasma*) *striatum* is very similar to the form described here. The lateral view of *M. (M.) striatum* depicted by Hoen (1883, pl. 2, fig. 5) and Broch (1922, text fig. 29) shows a ridge of coarse beads or elevations running in an arc across the basal portion of the scutum from the umbo to the lateral margin. The arc then continues to the basal portion of the carina and terminates at its umbo. The dorsal aspect given by Hoen (loc. cit., pl. 2, fig. 6) does not show the course of this beaded ridge on the carina as one would expect, but only a peculiar elevation formed along the lateral margin of the scutum. At first inspection it would appear that Gruvel (1905, text fig. 126) had merely traced Hoen's drawings; however, the dorsal aspect of the basal portion of the carina is considerably different than that illustrated by Hoen. It shows clearly the course of the beaded ridge extending outwardly from the carinal umbo. The form described here clearly lacks this ridge as viewed from both lateral and dorsal aspects. The basal portion of the scutum (Fig. 2A) is essentially smooth, unmarked by beads or ridges. The basal portion of the carina (Figs. 2A, B) also lacks the ridge seen in *M. (M.) striatum* figured by Hoen, Gruvel, and Broch, but below this area there are approximately 6 rows, each of 2-10 short ridges, running to the basal margin.

Of the trophi only minor differences were found. The lower angle of the mandible, including the fourth tooth (Fig. 2F), is much more strongly produced than that figured by Hoen (loc. cit., pl. 1, fig. 8) and by Utinomi (loc. cit., text fig. 4b) for *Megalasma* (*Megalasma*) *striatum*. The notch of the first maxilla (Fig. 2G) is less pronounced and the setae clothing its surface are short and weak, appearing vestigial. The second maxilla is longer than high, probably corresponding to the proportionately greater length of the mandible.

The ctenopod chaetotaxis (Fig. 2H) appears the same as that of *Megalasma* (*Megalasma*) *striatum*. However, in the new species the major
sae are pinnate. In a figure titled "Caudal Appendage" drawn by Utinomi (loc. cit., text fig. 4E), a portion of the first article of the peduncle of the sixth cirrus is illustrated. Utinomi figures two rows of conspicuous small, stout barbs (it is possible that the two-row effect is produced by an approaching molt), and a major simple spine of the caudal appendage. The present species has but a single inconspicuous row of smaller, less numerous barbs and these occur on the pedicels of all cirri. The major spines of the caudal appendage are densely and conspicuously plumose, an unusual feature, one apparently lacking in M. striatum. Finally, the outer surface of the pedicels of all cirri are transversely marked by fine, closely spaced lines.

_Megalasma_ (Megalasma) _striatum_ is reported from the spines of sea urchins from deep waters of the Indo-Pacific and Japan, while the species described here is so far known only from gorgonacean skeletons in the eastern Pacific, nearly 9000 miles from the known range of _M._ (M.) _striatum._

FAMILY HETERALEPADIDAE

_Nilsson-Cantell_, 1921.

GENUS Heteralepas _Pilsbry_

_Heteralepas mystacophora_ _Newman, sp. nov._

_Figs. 3A–H_

**DIAGNOSIS:** Capitulum ovoid, slightly compressed, lacking valves; cuticle smooth, with or without indistinct carinal ridge; orifice one-fourth length of capitulum; lips protuberant, margins crenulate; position of scuta marked by slightly elevated oval thickenings below and to either side of the orifice; peduncle approximately one-half length of and distinct from capitulum; cuticle smooth, marked by fine lines; peduncle expanded into attachment disc; labrum slightly bullate, bearing a remarkable growth of fine, soft setae; crest toothed; lateral portions squamous; mandible with four teeth, including inferior angle; superior margins of second and third teeth supporting several widely spaced spines; first maxilla with three major spines above and approximately seven major spines below notch; lower margin of cutting edge equal to half the length of the entire cutting edge; second maxilla broadly rounded, spines lacking along median portion of inner margin; inner rami of cirri V and VI atrophied; penis with long setae and short, sharp spines scattered over surface, inconspicuously annulated, without minute, specialized, ricer-like structures.

**DESCRIPTION:** Capitulum (Figs. 3A, B) ovoid in lateral aspect, carinal margin broadly convex; convex curvature of occludent margin interrupted by protuberant lips of orifice; carinal ridge, when present, indistinct (the animals were received dry and one cannot tell how much the effect of drying is responsible for the condition of the indistinct carinal ridge); no other prominent distinguishing warts, bumps or protuberances were observed other than an inconspicuous but definite thickening, a little less than one-half the distance up the carinal margin of the capitulum. This thickening is rather peculiar. In two specimens (including the holotype) a small tear or perforation, communicating with the mantle cavity, was evident at the upper end, and in one specimen the cirri protruded through to the outside. U-shaped orifice relatively small, approximately one-fourth the height of the capitulum; slightly crenulate lips continuous above but not below; mantle wall thin, cuticle smooth, except where marked by fine lines and minute folds about the orifice and at the capitulo-peduncular junction. Dried specimens were an opaque, reddish-brown color. Peduncle essentially one-half length of capitulum, about as long as wide, marked by several folds and by fine lines in the otherwise smooth cuticle; basal portion of peduncle expanded into attachment disc; holotype UCMP 37863 (Figs. 3A, B) measured:

<table>
<thead>
<tr>
<th>Capitulum</th>
<th>Peduncle</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length:</td>
<td>1.6 mm</td>
</tr>
<tr>
<td>Width:</td>
<td>1.4 mm</td>
</tr>
<tr>
<td>Depth:</td>
<td>1.6 mm</td>
</tr>
</tbody>
</table>

Labrum (Fig. 3C) slightly bullate, anterior portion covered with numerous long, fine, soft setae; crest supporting 12–14 equally spaced, small, sharp teeth; sides of labrum, posterior to insertion of palps, finely squamous. Palp (Fig. 3C) nearly triangular, superior margin supporting several long spines, outer surface sparsely scaled. Mandible (Fig. 3D) with five teeth
Fig. 3. Heteralepas mystacophora Newman, sp. nov. Figs. A, B, Holotype UCMP 37863. Fig. C, Labrum and palps. Fig. D, Mandible. Fig. E, First maxilla. Fig. F, Second maxilla. Fig. G, Intermediate articles of outer ramus of cirrus V. Fig. H, Distal quarter of penis. (Figs. A, B same scale, D–H same scale.)
including inferior angle; upper surface of second and third teeth supporting a few widely spaced spinules; fourth tooth with a few small accessory spines near base; superior margin of mandible with row of numerous paired setae; inferior margin supporting approximately eight spines; a group of several spines near superior angle, and a lower group of numerous short spines in groups or singly similar in arrangement to that seen in *Heteralepas gigas* (Anandale, 1905, pl. 8, fig. 3b). First maxilla (Fig. 3E) with three major spines above and approximately seven major spines below prominent notch; a few long spines in a group along superior margin, and two long spines near the base of first major spine; cutting edge composed of notch and superior spines equal in length to cutting edge below notch; surface clothed with numerous slender spinules arranged in groups and rows; notch supporting a few strong spines; inferior margin with approximately eight long spines. Second maxilla (Fig. 3F) broadly rounded; superior margin with minute and widely spaced serrations and a few spines; inner margin supporting long plumose spines in two groups, one at the superior and the other at the inferior angle; space between these two groups without spines (a condition occasionally seen in *Heteralepas japonica* according to Nilsson-Canrell, 1927). At least two very long pinnate spines on swelling at proximal portion of inferior margin.

Insertion of cirrus II widely separated from cirrus II, attached to posterior margin of prosoma; cirrus I approximately one-half length of cirrus II, supporting a single posteriorly directed ensiform filamentary appendage at its base; cirri II–VI essentially equal in length; inner ramus of cirri V and VI atrophied; pedicles of all cirri faintly squamous; long setae of all cirri finely pinnate, but becoming progressively less so posteriorly; inner ramus of cirrus I somewhat shorter than the outer, and more heavily clothed with setae; rami equal in width, arrangement of setae lasiopod (as many as 12 long, strong setae in staggered transverse whorl), with at least one major spine at each articulation along the greater curvature on intermediate articles; outer ramus of cirrus II slightly longer than the inner, setae arranged normally (cf Fig. 3G); setal arrangement of inner ramus intermediate between normal form and that of outer ramus of cirrus I; inner rami of cirri V and VI atrophied, approximately one-fifth length of outer rami; proximal articles of all cirri tending to fuse; unfused proximal articles two-thirds wider than long, intermediate articles as wide as long, distal articles essentially one-half as wide as long; counts for cirri of the holotype UCMP 37863 and a paratype (in parentheses) are given below. Unfortunately, the tips of many rami had been nipped off and no count could be made.

Caudal appendages of five articles nearly as long as the first article of the pedicle of cirrus VI, last two articles supporting a few long spinules, apex with a tuft of several short and two long spinules. Penis (Fig. 3H) weakly annulated, relatively short, slender, tapering gradually throughout its length; clothed with numerous long, soft setae and occasional short spines; apex truncate, supporting a tuft of short stiff bristles.


**DISCUSSION:** Although the species described here cannot be assigned to any of the known forms of *Heteralepas s. str.*, it is similar to several, some of which are of uncertain status. These are:

1. *Heteralepas japonica* (Aurivillius, 1894)
2. *H. indica* (Gruvel, 1902)
3. *H. gigas* (Anandale, 1905)
4. *H. cygnus* Pilsbry, 1907
5. *H. lankesteri* (Gruvel, 1901)
6. *H. quadrata* (Aurivillius, 1894)

Except for *H. quadrata*, these forms generally occur on the spines of sea urchins. They are characterized externally by an ovoid, slightly compressed, relatively smooth capitulum, and protuberant or slightly protuberant lips. Except

<table>
<thead>
<tr>
<th>Cirrus:</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
<th>VI</th>
<th>CA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Right outer ramus:</td>
<td>16 (19)</td>
<td>- (37)</td>
<td>- (42)</td>
<td>- (41)</td>
<td>- (40)</td>
<td>35 (45)</td>
<td>- (5)</td>
</tr>
<tr>
<td>Right inner ramus:</td>
<td>10 (13)</td>
<td>29 (27)</td>
<td>- (43)</td>
<td>- (39)</td>
<td>6 (11)</td>
<td>8 (8)</td>
<td></td>
</tr>
<tr>
<td>Left outer ramus:</td>
<td>16 (19)</td>
<td>21 (39)</td>
<td>- (41)</td>
<td>- (40)</td>
<td>- (45)</td>
<td>- (11)</td>
<td>5 (11)</td>
</tr>
<tr>
<td>Left inner ramus:</td>
<td>11 (13)</td>
<td>25 (31)</td>
<td>- (42)</td>
<td>- (41)</td>
<td>10 (10)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
for *H. lankesteri* from the West Indies, they are reported from the Pacific and Indian oceans.

Nilsson-Cantell (1927) discusses variability in certain external and internal characteristics ordinarily utilized in distinguishing members of the genus. In an extensive study of *H. japonica*, he concluded that *H. indica* is but a form of this species and that the status of *H. nicobarcia* Annandale, *H. gigas*, and *H. cygnus* is subject to re-examination in the light of his findings. Broch (1931), Nilsson-Cantell (1938), and Utinomi (1958) list *H. indica* as a synonym of *H. japonica*, but the status of the other species has not been altered. Whatever the status of these species, the form described here differs from them in a number of ways, in that *H. japonica* and its allies have a rather large orifice, occupying essentially one-half the occludent margin of the capitulum, and the mandible, at least of *H. japonica*, has pectinations on the underside of the first, second, and third teeth. The orifice of *H. lankesteri* is a little less than one-half the height of the capitulum, but the mandible is essentially that of *H. japonica*. Remaining then is *H. quadrata*. It generally occurs on *Panthirius* in the Pacific. Despite its similar appearance, it can be separated from the species described here by the presence of minute rivet-like structures (figured by Utinomi, 1949) on the penis.

The nearly naked Lepadomorpha present a difficult problem for the systematist since, being unarmed, they lack a number of distinctive features customarily utilized in separating genera and species. Turning to a comparative study of the appendages, Pilsbry (1907) was able to separate *Heteralepas s. l.* from *Alepas*, and to split the genus into two distinct subgenera: *Heteralepas s. str.* and *Paralepas*. However, he retained the heterogeneous assemblage Alepadiniae. Nilsson-Cantell (1921) furthered our understanding of this group by placing *Heteralepas s. l.* in a separate subfamily, the Heteralepidae. Further work sustained Pilsbry's subgeneric distinctions, and, as a consequence of his suggestion, the subgenera were finally recognized as separate genera (Newman, 1960).

At higher taxonomic levels the group would appear to be in fairly good order. However, as has been discussed above, this is not true as far as many of the species are concerned. In fact, it seems fair to say that we simply do not know what morphological and zoogeographic data are really applicable in making judgments at the specific level, there being so little information to go on. Aside from the work of Nilsson-Cantell (1927), no critical studies have been made. Thus it is difficult to establish a new form with any degree of certainty, for extensive collections would be required and they are simply not available. Therefore much of the time spent in study of this form was devoted to comparing characters with the known range of variability. Even so, with the extreme latitude allowed by synonymy, the present form could not be assigned to any known species.

The new species has been named *H. mystacophora* ("mustache bearer") for the numerous soft setae clothing the bullate portion of the labrum or upper lip. This condition is indeed unusual, and it is difficult to conceive what function it may serve. Yet the palps are provided with long setae or spines, perhaps stronger and certainly fewer than is usual in cirripedes, and they are in a position to be drawn through the labral setae. Perhaps in this way material entangled there could be brought to the mouth field.

**Suborder Verrucomorpha** Pilsbry

**Family Verrucidae** Darwin

**Genus Verruca** Schumacher, 1817

**Subgenus Verruca s. str.**


*Verruca (Verruca) scrippse* Zullo, sp. nov.

Figs. 4A–K

Dimensions of holotype UCMP 34713: height of shell, 2.5 mm; carinorostral diameter of base, 6 mm; lateral diameter of base, 4 mm; carinorostral diameter of orifice, 2.5 mm.

Shell (Figs. 4A, B) depressed, boxlike, colored white in dried specimen with adherent particles of yellow-brown epidermis; fixed plates steep, approaching perpendicular; movable valves flat, parallel to base; base of fixed plates thin, not
inflected, regularly and coarsely denticulate; basal denticulae impressed into shell of gastropod to which attached, leaving circular scar upon removal.

Movable scutum (Figs. 4E, F) with two articular ridges separated by narrow, shallow furrow; first ridge forming large tooth on otherwise unadorned tergal margin; second or crescentic ridge extending to basitergal angle; remainder of exterior of valve without ridges, ornamented only by deep, regularly spaced grooves separating growth increments; interior of movable scutum with large, distinct, kidney-shaped adductor pit in apical part of valve; upper and
tergal margins of adductor pit bounded by high ridge separating pit from deep, narrow articular furrow at apex.

Moveable tergum (Figs. 4C, D) squared, but with carinal margin longer than occludent margin; three prominent articolar ridges present; occludent margin bearing small, thin ridge not extending to apex; remainder of exterior without ridges, ornamented only by deep, narrow, closely spaced grooves separating growth increments; interior of movable tergum flat, smooth.

Carina (Fig. 4A) with four ridges terminating in articular teeth at rostral border; low, indistinct ridge borders tergal margin above uppermost articulating ridge; basal margin indistinctly lobed; lobes corresponding to basal denticulae.

Rostrum (Fig. 4A) with five ridges terminating in articular teeth at carinal border; apex at margin of plate; margin of uppermost ridge forming scutal margin; lowermost two ridges eroded and indistinct; basal margin deeply and irregularly lobed, corresponding to basal denticulae.

Articulation between fixed scutum and fixed tergum linear (Fig. 4B) obscured from exterior; fixed scutum (Figs. 4A, B) articulating with rostrum by means of three ridges interposed with four ridges on rostrum; main part of plates ornamented by low, indistinct, longitudinal ribs terminating in basal lobes; depressed triangular area bordering movable scutum ornamented by deep, sinuous, irregularly spaced, vertical grooves; interior of fixed scutum with indistinct adductor pit bordered below by thin, low, erect, concave adductor myophore or ridge.

Fixed tergum (Fig. 4B) with two ridges articulating with three ridges on carina; main part of plate ornamented by eroded, low, broad, longitudinal ribs terminating in regularly spaced lobes on basal margin; depressed triangular area bordering movable tergum ornamented as in fixed scutum; interior of tergum smooth.

Labrum (Fig. 4G) concave, bearing several minute, conical teeth on crest.

Palpus (Fig. 4H) elongate-triangular with apex at inner margin; row of short spines along superior margin, and tuft of longer, curved spines at apex on inner margin.

Mandible (Fig. 4I) with three teeth; uppermost tooth largest; cutting edge below third tooth, and inferior angle pectinate; single, large toothlike spine amid smaller spines above inferior angle.

Inner maxilla (Fig. 4J) without notch below upper two large spines; area between upper two large spines and large spines on lower half concave, bearing several short spines; lower part of cutting edge protrudent, bearing four larger spines followed by several small, slender spines at inferior angle.

Outer maxilla (Fig. 4K) notched in center of inner margin; inner margin on either side of notch bearing row of short spines; superior margin bearing numerous long, curved spines.

Cirrus I densely setose; posterior ramus about twice as long as anterior ramus; segments of anterior and posterior rami becoming long and slender terminally.

Cirrus II densely setose; posterior ramus about one-third again as long as anterior ramus; segments of anterior ramus somewhat protrudent; segments of posterior ramus becoming long and slender terminally.

Cirrus III more similar to cirri IV—VI than to cirri I and II; rami slender, subequal, with posterior ramus slightly longer and stouter; three to four pairs of spines per segment.

The number of segments on the cirri of holotype UCMP 34713 are as follows:

<table>
<thead>
<tr>
<th>Cirrus</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
<th>VI</th>
</tr>
</thead>
<tbody>
<tr>
<td>anterior</td>
<td>11</td>
<td>8–9</td>
<td>17</td>
<td>18</td>
<td>22</td>
<td>27</td>
</tr>
<tr>
<td>posterior</td>
<td>15</td>
<td>13–16</td>
<td>21–22</td>
<td>24</td>
<td>24</td>
<td>26</td>
</tr>
</tbody>
</table>

Caudal appendage long, about 2½ times length of pedicel of cirrus VI, with 18 segments.

Penis not known.

**TYPE DESIGNATION:** A single specimen on shell of *Sipho* sp. with *Balanus nascanus* Zullo sp. nov., designated as holotype UCMP 34713.

**DISCUSSION:** *Verruca scrippsa* is assigned to the typical subgenus of *Verruca* on the basis of the indistinct, linear nature of the suture between fixed scutum and tergum, and the horizontal plane of the movable scutum and tergum. Pilsbry (1916) recognized four groups of species within the subgenus *Verruca* based on characteristics of the cirri, the caudal appendage, and the base of the shell wall. *Verruca scrippsa* cannot definitely be assigned to any one of these groups.

In the slender nature of the cirri, the moderately long caudal appendage, and the low ad-
ductor ridge, *V. scrippsae* resembles members of the *V. alba* group, but differs in the absence of ribs which terminate on the scutotergal margins of the scutum and carina. *Verruca scrippsae* also bears resemblance to members of the *V. calotheca* group, especially in the presence of large unribbed areas on the exterior of the movable scutum and tergum, and in the absence of short, curved ribs on the scutotergal margins of the rostrum and carina (i.e., *V. entobapta* Pilsbry and *V. macani* Stubbings). *Verruca scrippsae* is most easily distinguished from the *V. nixa* group by the vertical rather than inflected basal margin of the shell wall, and by the marginal rather than submarginal apex of the rostrum. The sharp basal edge of the shell wall, and the presence of well-defined articulating ribs between rostrum and fixed scutum and carina and fixed tergum in *V. scrippsae* suggest affinities with the shallow-water *V. stromia* group. In these two features *V. scrippsae* differs from members of the “deep-water” groups.

**Suborder Balanomorpha** Pilsbry

**Family Balanidae** Gray, emended

**Subfamily Balaninae** Gray, emended

**Genus Balanus** Da Costa, 1778

**Subgenus Solidobalanus** Hoek, 1913

*Solidobalanus* Hoek, 1913, *Siboga-Expedition*, mon. 31b, p. 159.


**Balanus (Solidobalanus) nascanus** Zullo, sp. nov.

Figs. 5A–K

Dimensions of holotype UCMP 37855: height of shell, 2.5 mm; carinorostral diameter of base, 3 mm; greatest lateral diameter of shell, 2 mm; carinorostral diameter of orifice, 2 mm.

Shell high conic or cylindric; holotype UCMP 37855 (Fig. 5A) and paratype UCMP 37858 small, elongate along carinorostral axis, with deeply concave basis resulting from attachment on gorgonians; specimen on shell of *Sipho* sp. (UCMP paratype 37856) larger, up to 6 mm in height and basal diameter, with flat basis and nearly circular basal outline; dried specimens colored white or mottled orange; parieties smooth or longitudinally plicate; exterior of parieties and radii covered by adherent, buff-colored epidermis; orifice large, moderately toothed, diamond-shaped; radii thick, wide, with irregularly crenulated sutural edges; surface of radii glossy with distinct, regularly spaced, transverse striae; summits of radii oblique, about 30° from plane of orifice; alae thick with indistinctly crenulated sutural edges; summits of alae oblique, convex, projecting above radii; parieties solid, ribbed interiorly near the basis, the ribs fadding about half-way to the sheath; base of parieties with sharp ribs for attachment to basis; sheath from one-fourth to one-half length of compartmental plate, without space beneath lower edge; basis solid, thickened on periphery; periphery furnished with denticulae for articulation with compartmental plates; inner surface of basis with distinct radial ribs.

Scutum (Figs. 5B, C) white, externally ornamented by shallow, regularly spaced grooves separating flat growth increments; alternate increments forming sharp, sinuous teeth on occludent margin; growth increments ornamented by indistinct, closely spaced, radial striae; occludent margin straight; tergal margin concave, reflexed almost 90°; basal margin sinuous, shorter than tergal margin; surface of scutum concave exteriorly; articular furrow broad, shallow, and finely denticulate; articular ridge long, four-fifths length of tergal margin, erect, and high, especially in lower half; no adductor ridge; pit for adductor muscle small, oval, shallow, situated near occludent margin; pit for lateral depressor muscle small, deep; lower fourth of occludent margin inflected, forming small pit in basioccludent angle.

Tergum (Figs. 5D, E) narrow, almost twice as long as broad; color white; apex not produced; exterior ornamented by closely spaced growth lines which are finely striate on either side of spur fasciole; spur fasciole delimited by impressed grooves on either side; spur narrow, about as long as wide, terminating in rounded point; spur close to but distinct from basicalcular angle, and curving with only a slight break into the basal margin on the carinal side; scutal margin straight, reflected 90°, denticulate in some specimens; carinal margin convex, delimited by
upturned growth lines; basal margin concave; articular furrow broad, shallow; articular ridge high, sharp, not overhanging furrow; crests for lateral depressor muscles well developed, short, usually three in adults.

Labrum (Fig. 5F) notched, with three sharp, prominent teeth on either side paratype UCMP 37857, and three on the left and two on the right side in holotype UCMP 37855; margin of labrum sinuous, a small, prominent convexity bordering on either side of notch, followed by a broad, shallow concavity in which teeth are primarily situated; concavity followed distally by broad, low convexity terminating at edge of labrum.

Palpi (Fig. 5G) with numerous, short, pectinate spines irregularly arranged along superior margins; three or four long, curved, pectinate spines situated on inner margin.

Mandibles (Figs. 5H, I) with five teeth including inferior angle, excepting one mandible of holotype UCMP 37855 with only four teeth, the second and third appearing fused; first tooth largest; second and third teeth approximately equal in size; third tooth bifid, terminating in point; fourth tooth smaller than preceding teeth, bifid, with one or two small, sharp accessory denticles above and below; inferior angle trispidose; uppermost spine of inferior angle broadest, lowermost spine longest; row of 10 or 11 long, slender spines on inferior margin; spines nearest inferior angle usually pectinate curved towards inferior angle; anterior and posterior surfaces of mandible densely spinose.

Inner maxillae (Fig. 5J) notched below uppermost two large spines; one or two small, slender spines in notch; four spines below notch followed by two large spines; large spines followed by two or three small spines on inferior angle; inferior margin bearing several small, slender spines.

Outer maxillae (Fig. 5K) oval, bearing a few long, slender, distantly spaced spines arranged in three parallel rows.

Rami of cirri I and II densely setose, unequal, with outer rami longer; segments slightly protrudent.

Rami of cirrus III similar in structure to those of cirri I and II, excepting in fewer number of spines on segments.

Cirri IV–VI longer than preceding cirri, with four to five pairs of spines per segment; short hairs present at base of spines.

The number of segments on cirri I–III of the right side of paratype UCMP 37857 is as follows:

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
</tr>
</thead>
<tbody>
<tr>
<td>outer ramus:</td>
<td>6</td>
<td>8</td>
<td>9</td>
</tr>
<tr>
<td>inner ramus:</td>
<td>5</td>
<td>7</td>
<td>9</td>
</tr>
</tbody>
</table>

Penis long, with small tufts of spines scattered sparingly over surface; tufts common on annulations near extremity of penis; extremity blunt, covered with thick tuft of long spines; no basidorsal point seen.

**TYPE DESIGNATION:** Four specimens on gorgonians, holotype UCMP 37855, paratypes UCMP 37857; one on shell of *Siphon* sp. with *Verruca scrippssae* Zullo, sp. nov., paratype UCMP 37856.

**DISCUSSION:** Thirteen species of the subgenus *Solidobalanus* have previously been described from the Western Pacific, eastern Atlantic, and Indian oceans. They are:

*Balanus (Solidobalanus) astacophilus* Barnard (1925:128); Mozambique coast.

*Balanus (Solidobalanus) auricoma* Hoek (1913:199, pl. 18, figs. 20–22; pl. 19, figs. 1–7); Moluccan Straits (Hoek, 1913; Broch, 1931); southeast Australian coast (Broch, 1922); Persian Gulf (Nilsson-Cantell, 1938).

*Balanus (Solidobalanus) ciliatus* Hoek (1913: 199, figs. 8–16); Flores Sea (Hoek, 1913); Sulu Archipelago (Broch, 1931); Siam Bay (Nilsson-Cantell, 1934a); Strait of Malacca, Indian Ocean (Nilsson-Cantell, 1934b); Andaman Sea, east coast of India, Ceylon, Gulf of Manaar, Arabian Sea, Persian Gulf (Nilsson-Cantell, 1938); Gulf of Aden, Red Sea (Stubbings, 1936).

**Synonym:** *Balanus maldivensis* Borradale,
of Annandale (1906a, p. 148) from the Gulf of Manaa (Nilsson-Cantell, 1938:50).

_Balanus (Solidobalanus) compressus_ Hoek (1913:202, pl. 19, fig. 17; pl. 20, figs. 1–7);
Banda Sea, Timor Sea.

_Balanus (Solidobalanus) echinoplacis_ Stubbings (1956:45, figs. 20a–k); Zanzibar area.

_Balanus (Solidobalanus) hawaiensis_ Pillsby (1916:222, pl. 48, figs. 1–1g; text figs.
70a–c); Hawaiian Islands.

_Balanus (Solidobalanus) malddivensis_ Borradale (1903:442, fig. 118); Maldives Islands.

_Balanus (Solidobalanus) occidentalis_ Stubbings (1961:34, text figs. 8–11); tropical
West Africa.

_Balanus (Solidobalanus) pseudauricoma_ Broch (1951:72, figs. 25a–i); Molucca Sea, Japan.

_Balanus (Solidobalanus) socialis_ Hoek (1883:
150, pl. 13, figs. 23–28); Arafura Sea
(Hoek, 1883); Moluccas, Flores Sea (Hoek,
1913); Java Sea (Nilsson-Cantell, 1934a);
British North Borneo (Nilsson-Cantell,
1937); Gulf of Manaa, Ceylon (Nilsson-
Cantell, 1938); Japan (Utinomi, 1949).

_Synonyms: Balanus aeneas_ Lanchester
(1902:370) and _B. aeneas_ Lanchester of
Annandale (1906a:148) from the Malay
Peninsula and the Gulf of Manaa,
respectively (Pilsbry, 1916; Nilsson-Cantell,
1938).

_Balanus (Solidobalanus) solidus_ Broch (1931:
76, figs. 26a–i); Japan.

_Balanus (Solidobalanus) tantillus_ Pillsby
(1916:224, pl. 48, figs. 2–2e; text figs.
72a–c); Sulu Archipelago.

_Balanus (Solidobalanus) thompsoni_ Stubbings
(1936:43, figs. 19a–h); Gulf of Aden.

_Balanus nascanus_ resembles _B. hawaiensis_
Pilsbry from the Hawaiian Islands. However,
there are certain characters which distinguish
the new species. The articular ridge of the scutum of _B. nascanus_ is erect, whereas Pillsby
(1916:222) describes that of _B. hawaiensis_ as
"somewhat reflexed." Pillsby did not describe
the pit for the lateral depressor muscle, but that
of the figured scutum (Pilsbry, 1916, pl. 48, fig.
1f) is only vaguely indicated, whereas the lat-
eral depressor pit of _B. nascanus_ is deep and
prominent. The exterior of the scutum of the
new species is ornamented by fine, closely spaced,
radial striae which are not present in _B. hawai-
ensis_. The tergum of _B. nascanus_ is narrower
than that of _B. hawaiensis_. In addition Pillsbry
(1916:222) describes the tergal spur of _B. ha-
awaiensis_ as "very short, tapering to a rounded
end." Measurements of his figures indicate
that the length of the spur is approximately equal to
one-half the width of the spur at the basal
margin. The spur of _B. nascanus_ is longer (its
length being nearly equal to the spur width),
more pointed distally, and placed closer to the
basiscutal angle. The margin of the labrum of
_B. nascanus_ differs in being sinuous rather than
straight, and the mandible differs in having a
pointed, bifid third tooth on the cutting edge
and accessory teeth above and below the fourth
tooth as in _B. tantillus_ (Pilsbry, 1916, text fig.
72c).

_Balanus nascanus_ can be distinguished from
_B. ciliatus_, _B. compressus_, and _B. socialis_ by
the absence of teeth or hooks on cirri III and IV.
_Balanus astacophilus_ can be separated by the
shorter, broader tergal spur, and by the greater
number of teeth both on the mandibles and on
the labrum. In _B. auricoma_ the tergal spur is
more distantly removed from the tergal margin
and the mandible does not possess the distinct-
ive trispinose inferior angle of _B. nascanus_ and
_B. hawaiensis_. _Balanus echinoplacis_, _B. pseu-
dauricoma_, _B. solidus_, and _B. thompsoni_ also
lack the trispinose inferior angle on the man-
dible, and can further be distinguished by their
possession of a short, broad, obliquely truncate
tergal spur. In addition; _B. echinoplacis_ is de-
scribed as having a porous basis, whereas that
of _B. nascanus_ is solid.

_Balanus malddivensis_ and _B. tantillus_ are sim-
ilar to _B. nascanus_ in the form of the opercular
valves. _Balanus malddivensis_, however, can be
distinguished by the horizontal summits of the
radii and the form of the mandible, and _B. tan-
tillus_ differs in having the tergal spur confluent
with the basiscutal angle. The recently described
West African species _B. occidentalis_ resembles
_B. nascanus_ in the characters of the trophi, but
differs in the possession of teeth on the anterior
border of the posterior ramus of cirrus III, in
the lack of radial striae on the exterior of the
scutum, and in the broader tergal spur placed
farther from the basiscutal angle.
Species of the subgenus Solidobalanus, being for the most part restricted to subtidal depths, are known by relatively few individuals, and as a result little information is available concerning the range of variation of the characters which are presently considered significant at the specific level. Future collections, especially from the Pacific, may indicate that the characters used in separating such geographically widespread, morphologically similar species as Balanus auricoma, B. bawaiensis, and B. nascanus are variable, and that these three species, and perhaps others, may be merged into a single species. At the present time, however, it would appear more prudent to differentiate the eastern Pacific solidobalanid by establishing a new species.

SUMMARY

Representatives of four new species of thoracic cirripedes were obtained in a dredge haul at 228 m depth on a guyot on the southwest end of Nasca Ridge about 1280 km off the coast of Chile.

1) Megalasma elegans Newman, sp. nov., is related to M. sriiatum Hoek, but differs in the absence of the beaded ridge extending from below the scutal umbones across the scuta and carina to the carinal umbones; in the form of the trophi; and in the presence of pinnate setae on the cirri and plumose spines on the caudal appendage.

2) Heteralepas mystacophora Newman, sp. nov., is remarkable for the presence of numerous soft setae clothing the bullate portion of the labrum.

3) Verruca scrippseae Zullo, sp. nov., resembles members of the shallow-water V. stroemia group in the sharpness of the basal edge of the shell wall and the presence of well-developed articulating ridges between rostrum and fixed scutum and carina and fixed tergum, but differs in the more slender cirri, longer caudal appendage, and low adductor ridge.

4) Balanus (Solidobalanus) nascanus Zullo, sp. nov., is related to B. bawaiensis Pilsbry, but can be distinguished by the narrower tergum with a longer tergal spur, and by the presence of radial striae on the scutal exterior.

Megalasma, Solidobalanus, and the "deep-water" verrucids have not been reported previously from the eastern Pacific.

REFERENCES


——— 1931. Papers from Dr. Th. Mortensen’s Pacific Expedition 1914–16, LVI. Indoma-


A Hypomaxillary Bone in *Harengula* (Pisces: Clupeidae)

**Frederick H. Berry**

*Harengula* Valenciennes 1847, *Lile* Jordan and Evermann 1896, *Sardinella* Valenciennes 1847, and one whose designation currently is uncertain, but here is referred to as *Clupalosa* Bleeker 1851. (The distinguishing characteristics are listed below.)

The position of the hypomaxillary in *Harengula* is shown in Figure 1A. Its posterior end overlaps the maxillary laterally. The hypomaxillary, premaxillary, and maxillary all bear a single row of small pointed teeth. The connective tissue in the space between the hypomaxillary may also bear teeth. The hypomaxillary was ossified in the smallest specimen examined (16 mm S.L.). The presence of the hypomaxillary and the characteristic elongation of the posterior supramaxillary (Fig. 2A) in *Harengula* have been verified in the following species:

- *H. clupeola* (Cuvier 1829), St. Lucia, British West Indies, SU35458, and syntype of *H. latulus* Valenciennes, SU32769
- *H. humeralis* (Cuvier 1829), Jamaica, SU5041
- *H. pensacolae* Goode and Bean 1880, Sanibel Island, Florida, SU36092, and Santos, Brazil, SU36065 (as *S. majorina* Storey 1938)
- *H. peruana* Fowler and Bean 1924, many specimens from Peru to Costa Rica in several institutions
- *H. thrissina* Jordan and Gilbert 1882, many specimens from Pacific Mexico in several institutions

<table>
<thead>
<tr>
<th>HYPOMAXILLARY</th>
<th>SHAPE OF POSTERIOR SUPRAMAXILLARY</th>
<th>BILOBED FOLD ON CLEITHRUM</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Harengula</em>...</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td><em>Lile</em>...</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td><em>Sardinella</em>..</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td><em>Clupalosa</em>...</td>
<td>absent</td>
<td>present</td>
</tr>
</tbody>
</table>

1 U.S. Bureau of Commercial Fisheries, Biological Laboratory, Brunswick, Georgia. Manuscript received August 1, 1963.
The presence of the hypomaxillary in the syn-type of Harengula latulus, the type species of the genus, is considered to restrict the genus Harengula to comparable species possessing this structure. The synonymy of H. latulus, the probability of the erroneous original locality designation, and the type species designation were detailed by Storey (1938:36-39), who gave evidence that Harengula does not occur in the eastern Atlantic. Based on present information, the genus Harengula apparently occurs only in the western Atlantic and the eastern Pacific.

Lile lacks the hypomaxillary bones, and the intervening space along the gape between the premaxillary and the maxillary is occupied by unossified connective tissue (Fig. 1B). The elongated supramaxillary is shown in Figure 2B. These two characters have been verified in

L. stolifera (Jordan and Gilbert 1881) on specimens from many eastern Pacific localities in the collections of several institutions. Lile apparently only occurs in American waters.

Sardinella is similar to Lile in lacking hypomaxillaries (Fig. 1C). The expanded distal end of the posterior supramaxillary is rounded, with the dorsal constriction about vertical to the ventral constriction (Fig. 2C). This has been verified in the following species:

S. aurita Valenciennes 1847, Florinopolis, Brazil, SU53863 and SU51662
S. brachysoma Bleeker 1852, Tai Ping, China, SU25701
S. cameronensis Regan 1917, West Africa, RGMAC 94987
S. clupeoides (Bleeker 1849), Singapore, China, SU33838
S. dayi Regan 1917, Ceylon, SU22866
S. eba (Valenciennes 1847), eastern Atlantic, RGMAC 94994
S. fimbriata (Valenciennes 1847), Manila, Philippines, SU20350
S. jussieu (Lacépède 1803), Manila, Philippines, SU60478
S. leiogaster Valenciennes 1847, Sulu Prov., Philippines, SU28571
S. longiceps Valenciennes 1847, Madras, India, SU35273
S. melanura (Cuvier 1829), Malekula Island, New Hebrides, SU25031
S. perforata (Cantor 1850), Formosa, SU7420
S. rouxi (Poll 1953), West Africa, RGMAC 94999
S. sindensis (Day 1878), Manila, Philippines, SU38369
S. sirm (Walbaum 1792), Apia, Samoa, SU 8984
S. zunasi (Bleeker 1854), Onomichi, Japan, SU20140

Sardinella occurs in the Atlantic and Indian oceans and in the western Pacific, but not in the eastern Pacific.

Because the genus Harengula is restricted to species possessing hypomaxillaries, certain Indo-Pacific species, which have usually been placed in Harengula, but which lack this pair of bones, are tentatively assigned to the genus Chiplalosa. They have the posterior pair of supramaxillaries
elongated, with the ventral constriction anterior to the dorsal constriction. Species of this genus that I have examined are:

*C. dispilonotus* (Bleeker 1852), Philippines, su35345

*C. punctata* (Riippell 1835), Philippines, su20885; Pelew Islands, su37332; Ceylon, su22892; South Andaman Islands, su37100; Philippines, su28556

*C. schrammi* (Bleeker 1849), Philippines, su33538

*C. tawilis* Herre 1927, Philippines, su28559

Bleeker erected the genus *Clupalosa* for his monotypic new species *C. bulan* from the Java Sea in 1849. *Clupalosa* has subsequently been placed in synonymy of both *Harengula* and *Sardinella*. I have not seen this species, and the type specimens, if extant, should be examined to confirm its relationships. I presume that it is distinct from the hypomaxillary-bearing *Harengula*, because no species of *Harengula* (as restricted) have been observed from the Indo-Pacific. I presume that it is distinct from the genus *Sardinella*, because it was not included in a recent and comprehensive review of the Indo-Pacific species of *Sardinella* by Chan (ms). However, Regan (1917), who said he examined Bleeker’s types of *bulan*, placed that species in synonymy of *Sardinella perforata* (Cantor 1850). Subsequent authors have listed *bulan* as a distinct species, notably Fowler (1941). If *Clupalosa* proves to be unavailable for this genus, the following generic names might apply: *Paralosa* Bleeker 1868 (type species *Harengula valenciennesi* Bleeker 1868), Wilкesina Fowler and Bean 1923 (type species *Harengula fijiensis* Fowler and Bean 1923), *Herklotsichthys* Whitley 1951 for *Herklotsiella* Fowler 1933 (type species *Harengula dispilonotus* Bleeker 1852), or *Escualosa* Whitley 1940 (type species *Clupea macrolepis* Steindachner 1879). The status and identity of *Macrura* van Hasselt 1823 is uncertain; it has been proposed for species of this group, but also has been suggested as a synonym of *Hilsa* Regan 1916.

Of the four genera discussed above, I have not examined the following nominal species and am not certain of their generic or specific status:

*Harengula callolepis* Goode 1880

*Sardinella albella* (Valenciennes 1847)

*Sardinella allecia* (Rafinesque 1810)

*Sardinella aurovittata* (Swainson 1839)

*Sardinella caeruleovittata* (Richardson 1846)

*Sardinella dactylolepis* (Whitley 1940)

*Sardinella desmaresi* (Risso 1826)

*Sardinella maderensis* (Lowe 1836)

*Sardinella nymphaea* (Richardson 1848)

*Sardinella posterus* (Whitley 1931)

*Lile piqutinga* (Schreiner and Miranda Ribeiro 1903)

*Lile platana* Regan 1917

*Harengula abbreviata* Valenciennes 1847

*Harengula blackburni* (Whitley 1948)

*Clupalosa bulan* Bleeker 1849

*Harengula dollfusi* Chabanaud 1933

*Harengula bualiensis* Chu and Tsai 1958

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**Fig. 2.** Posterior supramaxillaries of *Harengula* (*A*), *Lile* (*B*), and *Sardinella* (*C*), showing their characteristic shapes and the relative positions of the dorsal and ventral constrictions.
Harengula konigsbergeri (Weber and de Beaufort 1912)
Clupalosa lippa (Whitley 1931)
Harengula maccullochi Whitley 1931
Harengula macrolepis (Steindachner 1879)
Harengula ovalis (Bennett 1830)
Harengula vittata (Valenciennes 1847)

The last 11 species are Indo-Pacific and may all belong to Clupalosa.

I have tabulated 110 nominal species that appear to belong to these four genera, of which only about 43–51 species may be valid. There are many conflicting opinions and uncertainties concerning the synonymies of these nominal species. In listing the species above I have used and attempted to reconcile the works of Chan (1941), Fowler (1941), Herre (1953), Regan (1917), Rivas (1950), and Whitley (1940, 1941, 1948).

The separation of Harengula and Sardinella was discussed by Chan (1941), who was the first to emphasize the differences in the larger and more posterior of the two supramaxillaries in these two genera. Chan also detailed differences in scale sculpture between these genera and commented upon the two enlarged terminal anal fin rays in Sardinella. Whitehead (1962) suggested that Harengula might have a greater number of parietal striae than Sardinella; but this difference, if valid, is complex, because the number of parietal striae in Harengula thrisina progressively increases from about 5 at 50 mm S.L. to about 13 at 130 mm. Chan and previous authors were unaware of the hypomaxillary bones in American species assigned to Harengula, however, and considered Harengula in its broad sense to include the Indo-Pacific species which lack hypomaxillaries.

The phylogenetic significance of the hypomaxillary and its importance in the classification of the Clupeidae are subject to various interpretations. A thorough knowledge of the morphology of the genera and species of Clupeidae and of the origin and development of this bone will furnish a more definitive answer to these issues.

The hypomaxillary is a specialized structure that must have developed independently in two phylectic lines of the Clupeidae—in the typical herring genus, Harengula, and in Pellona and Pliosteostoma of the group of clupeids with a high number of anal rays and greatly compressed bodies, sometimes referred to as “bloodless clupeids.” It probably arose as a permanent splitting off of a portion of the maxillary or premaxillary; it is less probable that its origin was the spontaneous development of a new site of ossification.

In Aphredoderus (Percopsiformes) and in certain species of Amblyopsidae (Amblyopsiformes) each premaxillary is divided distally into from 2 to about 7 distinct but closely associated parts of progressively decreasing size (Rosen, 1962). These smaller terminal portions of the premaxillaries were termed segments, and Rosen (1962:23) suggested that these segments produced a flexibility to the upper jaw in full extension of the mouth. This might indicate that these segments were developed in response to a need for additional flexibility, or that, after they had developed, additional flexibility was possible. The clupeid hypomaxillary undoubtedly developed independently from the premaxillary segments of Aphredoderus and the amblyopsids, and, if any such functionalism were once a factor in the origin of the hypomaxillary in these clupeids, it has subsequently been lost or occluded.

My studies have led me to believe that, within the two clupeid groups concerned, the hypomaxillary must be significant in indicating a distinct phylogenetic (and taxonomic) difference between the species which have it and those which lack it. Myers (1950) found the hypomaxillary present on one side and absent on the other in a large specimen of Pellona and questioned its significance; but in the hundreds of specimens of all species of Pellona, Pliosteostoma, and Harengula that I have examined, both sides of the upper jaw have hypomaxillaries of similar size.

To stabilize the nomenclature until extant uncertainties are clarified, and because published generic names are available, I have proposed above that the presence of the hypomaxillary be regarded as a criterion of generic distinction, and restriction of the genus Harengula.

ACKNOWLEDGMENTS

I am grateful to Franklin G. Alverson, Iza-

REFERENCES


A Study of the Hatching Process in Aquatic Invertebrates

IX. Hatching within the Brood Sac of the Ooviviparous Isopod, *Cirolana* sp. (Isopoda, Cirolanidae)

X. Hatching in the Fresh-water Shrimp, *Potimirim glabra* (Kingsley) (Macrura, Atyidae)

Charles C. Davis

Through the kind cooperation of the Instituto Tropical de Investigaciones Científicas of the Universidad de El Salvador, and through a travel grant provided by the Graduate Research Fund of Western Reserve University, it was possible to continue, in the summer of 1962, a study of the hatching processes of aquatic invertebrates in the tropical environment of El Salvador, Central America. I wish to express my gratitude to the sponsoring agencies for their aid in making the study possible.

Previous publications in the present series are listed in Davis (1964). As has been shown in these publications, hatching may be achieved by the swelling of the embryo (growth or water uptake), by mechanical means, by osmosis through a nonliving egg membrane, by enzymatic action or by some combination of these methods.

**IX. HATCHING WITHIN THE BROOD SAC OF THE OVOVIVIPAROUS ISOPOD, *Cirolana* sp. (ISOPODA, CIROLANIDAE)**

Numerous specimens of *Cirolana* sp. were collected on July 23, 1962, from empty shipworm galleries in pieces of old wood wedged in the rocks between the tide marks near the village of Mizata, in the eastern portion of El Salvador (Departamento de La Libertad). Specimens were identified as possibly a new species of *Cirolana* by Dr. H.-E. Gruner, Zoologisches Museum, Berlin, and as being close to *C. diminuta* Menzies (but possibly as a new species) by Dr. Robert J. Menzies, Duke University Marine Laboratory, Beaufort, N.C. 2

Living specimens were returned to the laboratory for study. Many of them contained eggs or young in their brood pouches at all stages of development. The earlier stages of embryonic development were enclosed in definite egg membranes, but later stages were free in the pouches.

In *Cirolana* sp. the brood pouch is so firmly enclosed that the eggs and young could be removed only by disruption of the body of the mother. Recently laid eggs removed in this fashion (Fig. 1) were ovoid, about 730μ long and 600μ wide. The egg membrane was not turgid, and fit rather loosely, leaving a considerable space between it and the embryo. Later, when the young isopod took on more definitive form (Fig. 2), the entire mass increased greatly in size so that, although the width decreased somewhat to 540μ, the length became 1,350μ. At this time the egg membrane had come to fit the embryo much more tightly but, as shown in the figure, small fluid-filled spaces still occurred in front and just behind the head, as well as lateral and posterior to the abdominal segments. The beating heart could be seen clearly in the region between the thorax and the abdomen. Just before hatching from the egg membrane, all fluid-filled spaces disappeared, and the embryo increased to an average of 1,590μ X 580μ (10 measurements), an increase of 2.2 times in length.

Hatching itself was passive as far as movements of the appendages of the embryo were concerned. Swelling became much more rapid, so that the length increased within 15 min...

1 Department of Biology, Western Reserve University, Cleveland, Ohio. Manuscript received August 13, 1963.

2 I wish to express my thanks to both of these men for their help.
from an average of 1,590 to 1,770\(\mu\). No signs of drinking were observed at this time, and therefore the obvious uptake of water must have been across the surface of the embryo after the water had permeated through the egg membrane. Thereupon the embryo squirmed and twisted, and the membrane broke at the anterior end, liberating some of the anterior appendages. It took approximately 1 min for the membrane to slip off, thus completing the hatching. At an average of 7 min after the break in the membrane occurred, the young isopods had increased to a length of 1,890\(\mu\).

It was observed that embryos within their membranes, whether some time before hatching, or nearly ready to hatch, were able to live for over 24 hr in the external sea water, but they became weaker and weaker, and shortly thereafter death ensued. In those ready to hatch, hatching was unsuccessful if they had been out of the brood pouch more than about an hour before initiation of eclosion. It is not thought that the sea water used was toxic, for the parents were living in it. Either lack of nutrients pro-

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**Fig. 1.** *Cirolana* sp. Early egg removed from the brood pouch. There is a large fluid-filled space between the developing embryo and the loosely fitting egg membrane.

**Fig. 2.** *Cirolana* sp. An embryo shortly before hatching. There has been a great increase in size, compared to the early stage shown in Figure 1. The membrane is thin and tightly stretched. A fluid-filled space remains, however, between it and the embryo.
vided to the embryos within the brood pouch by the mother or lack of ventilation of the embryos may have contributed to their weakening. Secretion of nutrients by the mother has long been suspected for isopods, but no definite evidence proves its occurrence, at least prior to hatching. Wesenberg-Lund (1939) has questioned the production of such nutrient substances in fresh-water isopods. Based on length measurements of marsupial young, and on ex-marsupial cultures of embryos, Lemercier (1957) denied the existence of such secretions by the aquatic *Jaera marina*. Saudray and Lamercier (1960), on the other hand, showed that although there was a decrease of vitelline reserves (and of dry weight) before hatching in eggs of the terrestrial *Ligia oceanica*, there was a considerable increase of weight, in great part from minerals, after hatching, and that this increase probably was of maternal origin.

The newly hatched young were by no means able to care for themselves. Locomotion was impossible; although in the experimental containers they appeared to attempt to right themselves after hatching from their (invariable) position on their backs, they never succeeded in doing so. Specimens that were pushed by the investigator into a position with the ventral side down always rolled over on their backs immediately when the supports were removed. Likewise, embryos within the egg membranes were almost invariably lying dorsal side down, though a few were not.

After hatching the young remained in the brood pouch for a considerable period of time (the length of their stay could not be ascertained). During their sojourn in the brood pouch they developed a great deal more pigmentation than the small amount present at the time of hatching, and they increased considerably in size. Some attained a length of a little more than 2 mm, or one-third the length of the parent. Liberation of the young from the brood pouch was not observed.

**Discussion**

There was considerable increase in size of the embryo before hatching, and even more subsequently. It was not possible to distinguish between true growth (i.e., increase of biomass) and false growth by intake of water. True growth could occur only if the mother provided some nutrition to the developing young.

The extremely rapid growth occurring at the time of hatching could not have been a true growth, for new protoplasm cannot be formed so rapidly. It is believed that the size increase came about by the absorption of water from the environment, and that it probably was associated with the liberation of osmovalent substances in the protoplasm or the hemocoel at this time.

Experimental tests of the permeability of the egg membrane could not be undertaken, but the steady growth of the embryo and of the postembryonic animal, and the rapid growth at the time of hatching, indicate that the membrane was permeable both to water and to any nutrient substances the mother may have secreted into the brood pouch. Originally loosely surrounding the egg, the egg membrane later became taut and invested the embryo closely. This does not suggest that the membrane itself was osmotically active, as occurs in hatching copepods and in some insects (Davis, 1959, 1961).

Hence the hatching process appears to proceed somewhat as suggested by Przylecki (1921) for *Daphnia*, where the embryo swells (in *Daphnia* only by the uptake of water) until finally the egg membrane is sloughed off.

Hatching has previously been described briefly for isopods by Ellis (1961), who said that in *Asellus intermedius* there is an outer egg membrane, an inner egg membrane, and a larval membrane. The outer membrane splits and is shed at an early stage of development. The other two membranes are shed later. Nothing is said of an increase of embryo size, however. Earlier investigators (Verhoeff, 1920; Forsman, 1944; Naylor, 1955) mentioned an increase of size. Both Forsman and Naylor studied aquatic isopods (respectively, *Jaera albifrons* and *Idotea emarginata*). Forsman said that the first stage of life in the brood pouch terminated when the egg shell suddenly burst and slipped off. The enclosed embryo immediately increased in size but was still enclosed in an "embryonic membrane." Only after some time the latter suddenly ruptured. It is not clear from Forsman's description that the size increase caused either of the eclosions, but he specifically stated that final
emergence from the second membrane was by the struggles of the animal. Naylor (op. cit.) observed that the originally spherical egg became ovoid after a period of development, and that this was followed by the rupture of the egg membrane. There was a growth from 0.7-mm diameter in the spherical egg to an embryo 1.2 mm long. This embryo was still enclosed in an "embryonic membrane." After appendages appeared in the developing embryo, this membrane also ruptured.

In the present study only a single egg membrane was observed, but the inability of the embryos to continue living normally outside of the brood pouch, combined with the rapidity of movement of the parent animals and the opacity of their bodies, may have led to a second membrane being overlooked. In the earliest stages observed there was no sign of more than one membrane; the fact that this one membrane lay rather loosely around the embryo does not suggest that an outer membrane had been sloughed off earlier.

**Summary**

Eggs at various stages of development, and hatched young, were taken from the brood pouches of *Cirolana* sp. There was approximately a doubling of the size of the eggs from time of oviposition to hatching, and the young increased in size even more after hatching. It remains unclear whether the mother secretes a nutritive substance into the brood pouch. Hatching itself was accompanied by, and partly caused by, a sudden and rapid increase of volume of the embryo, evidently through a rapid uptake of water across the body surface. The stretched egg membrane, however, was burst by squirming action of the embryo.

**X. HATCHING IN THE FRESH-WATER SHRIMP, Potimirim glabra (Kingsley) (MACRURA, ATYIDAE)**

Several small shrimps were obtained from their shelter beneath rocks in a small stream (Río Chiquileco), near Mizata, Departamento de La Libertad, El Salvador on July 23, 1962. They were found not more than 20–30 m from the ocean beach, but the water in which they lived was fully fresh (though probably subject to salt-water contamination during storms). One of the shrimps was ovigerous and was returned to the laboratory for closer study. The shrimp was identified as *Potimirim glabra*, and the determination has been confirmed by Prof. Dr. L. B. Holthuis of the Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands. Evidently the species has been reported only twice before, by Kingsley (1878) from the west coast of Nicaragua, and by Holthuis (1954a, b) from the Rio Jiboa in El Salvador, about 60 km east of the present find.

When the specimen was captured the eggs were at a very early stage of development, but the shrimp and its eggs lived well in fresh water in the laboratory. Five days later the eggs were far advanced, for the eyes were conspicuous, the hearts were beating (the rate of the heart beat varied in the different specimens), and there were vigorous intestinal movements. Occasionally there was a sudden twitch of the body. The average size of seven eggs was 500μ × 300μ (they varied little in their dimensions).

Within the egg (Fig. 3) the lengthy young were coiled into an oval. The first two abdominal segments lay more or less along the same axis as the cephalothorax, but the rest of the abdomen folded under so that most of the segments lay ventral to the cephalothorax and its appendages. The furca was folded over the head, terminating

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**Fig. 3. Potimirim glabra.** The young within the egg shortly before hatching. The telson passes anteriorly in front of the head, to terminate dorsally over the yolk mass.
dorsally. The furcal setae passed back to the region between or just posterior to the eyes (hence over the region of the anterior part of the yolk mass).

Because of the proximity of the habitat to the sea, it was uncertain whether hatching occurred in fresh water or in sea water. Some of the eggs were placed in sea water, but after a couple of hours they showed distinct signs of degeneration. Controls in fresh water remained normal.

Hatching commenced on the sixth day after capture of the animal. The size of the eggs had increased slightly to an average of 520μ × 310μ. At this time some more eggs were placed in sea water; they did not hatch successfully, whereas nearly all of the controls in fresh water did so.

Hatching was observed many times. Two membranes surrounded the egg (a third membrane, as described by Burkenroad, 1947, was not observed). Before hatching, the embryo lay snug within the two membranes, but it was able to move around in such a fashion that it was clear the embryo itself was not exerting pressure on the outer membrane.

The first event of hatching was the sudden bursting of the outer membrane, always at the cephalic end of the embryo. Immediately afterwards the inner contents, surrounded by a second membrane, almost explosively increased in size, showing that they were under considerable internal pressure. At this time the dimensions of the embryo and its membrane were about 600μ × 320μ. Soon there was a rather rapid enlargement to 650μ × 330μ. As this swelling occurred, the outer membrane slipped to the posterior end of the egg and was sloughed off.

At first after the bursting of the outer membrane the inner membrane lay tightly appressed against the body of the embryo, but later a fairly large space developed between the living animal and the nonliving membrane. At the same time the folds of the animal loosened up somewhat within the membrane, so that spaces appeared ventrally between the thorax and the abdomen.

Then the young animal commenced to struggle, primarily by movements of the abdomen. Eventually the inner membrane broke over the end of the telson, hence over the head (no egg burster was evident on the telson), and the animal straightened out. In this manner the membrane was torn still more. Then a single vigorous flip was sufficient to liberate the zoea from the remains of the egg membrane.

Five specimens were timed in their emergence. They took from 2 min 15 sec to 17 min 5 sec (average of 6 min 35 sec) from the first bursting of the outer membrane to the last flip from the inner membrane.

Discussion

Hatching in decapod crustaceans has seldom been described heretofore. Among publications touching on the process, Davis (1959) sketchily observed hatching in the Ohio fresh-water shrimp, *Palaemonetes kadiakensis*, and stated that osmotic forces were involved. R. L. Robertson, writing in Truitt (1941:10), gave a figure showing hatching of an egg of the crab, *Callinectes sapidus*. The prezoea is shown escaping backwards, with the rear of the head coming out first; only an outer membrane is shown. Churchill (1917–1918) stated concerning the same species: "...the shell of the egg split into two parts, the young crab emerged and, after freeing itself from a thin membrane which covered it, swam away." Gray (1942) briefly described hatching of the fiddler crab, *Uca minax*. She intimated it was caused entirely through the vigorous mechanical action of the crab; only one egg membrane was mentioned. Andrews (1904, 1907) studied hatching in the crayfishes *Astacus leniusculus* and *Cambarus affinis*, but merely stated that: "In hatching, the egg capsule burst open over the back of the embryo, and... then the embryo slowly glided out backward." According to his observations the embryo at hatching was very inactive and helpless, unable to use its limbs. More recently, Burkenroad (1947) described hatching in the marine shrimp *Palaemonetes vulgaris* and in its close relative from fresh water, *P. exilipes*. In the marine species, the outer two membranes were burst by swelling of the young within, and the embryo, enclosed in the third membrane, emerged passively. It then tore its way from the third membrane by active extension of the pleon. In the fresh-water form, on the other hand, the outer membranes were split through the pressure...
caused by an osmotic swelling of the inner membrane. The swelling continued until the outer membranes were sloughed off and until the inner membrane burst and liberated the young. Herrick (1911) has described some aspects of hatching in the American lobster, *Homarus americanus*. He observed that an outer membrane burst first, and that an inner membrane, which was attached to the outer one, remained surrounding the hatching larva. When the inner membrane was shed the larva emerged, but must then molt before it was free-swimming.

The bursting of the outer egg membrane in *Potimirim glabra* could not have been associated with the presence of any hatching spines or egg bursters. The only structures so placed on the embryo that they might have acted in this manner were the anteriorly directed lateral spines on the carapace, but if these had caused the bursting of the outer membrane they would also have done so to the inner membrane, which remained intact. It was clear that the bursting was caused by considerable pressure from within, and it is postulated that this occurred by the osmotic uptake of water through the inner membrane, although perhaps the embryo itself took up water also, as indicated by the fact that there was no space between the embryo and the inner membrane at the time that the outer membrane broke. That such a space appeared later, however, suggests that osmotic water was being taken in through the membrane. Estimates of possible further increase in size of the embryo itself at this time, however, were not possible because of the manner in which it loosened up its compact folds within the inner membrane. This made accurate comparative measurements impracticable.

The fact that the outer membrane invariably burst over the cephalic region suggests a weakened line of dehiscence there, although before bursting no such line was visible with the high power of a compound microscope.

Hence, in *Potimirim glabra* the hatching process is a combination of osmotic bursting of an outer membrane and active mechanical exit by the animal through the inner membrane. Evidently no enzymatic action is involved, unless there is an enzymatically caused change in the permeability of the inner membrane at hatching time.

**Summary**

*Potimirim glabra* hatched through the osmotic swelling of an inner egg membrane; the pressure caused the rupture of the outer membrane, which then was sloughed off by continued swelling of the inner one. Final hatching from the inner membrane was accomplished by the struggles of the young shrimp, which broke the membrane over the head by action of its telson, then tore the membrane further by straightening out its highly coiled body.

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Native Hawaiian Cotton (*Gossypium tomentosum* Nutt.)

S. G. Stephens

Although the wild cotton, *Gossypium tomentosum* Nutt., is one of the more common of the few endemic species which still survive on the coastal plains of the Hawaiian Islands, it remains relatively unknown to the geneticist. Elsewhere it has been grown with indifferent success in experimental culture. Under such diverse conditions as those found in the West Indies, southern Mexico, the U. S. cotton belt, and in greenhouse culture, it flowers sparingly and even less frequently sets seeds. As a consequence, experimental studies have been very restricted, and cytogenetic analysis has been confined almost entirely to the few crosses which have been made with annual forms of the related New World species, *G. barbadense* L. and *G. hirsutum* L. To the technical difficulties may be added the lack of representative collections of the species in culture. The few accessions studied have usually been obtained from the more readily available Oahu populations, and less frequently from Molokai. These have been supplied to cotton geneticists through the courtesy of resident Hawaiian botanists, J. F. Rock, O. Degener, A. Mangelsdorf, and others, and patiently resupplied as fast as the stocks in culture expired.

As seen in culture, the different accessions show little morphological variation (finely tomentose vegetative parts, sulphur-yellow and spotless flowers, long anther filaments partly fused in pairs, nectarless leaves, and undifferentiated seed fibers). More recently, visitors to the islands, unacquainted with the taxonomy of the species, have sent seed samples to the mainland, and the plants grown from some of these appear to differ rather widely from earlier “authentic” accessions.

It has long been recognized that an understanding of the degree of relationship existing between *G. tomentosum* and the other 52-

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1 Contribution from Genetics Department, University of Hawaii. Manuscript received May 23, 1963.
2 On leave of absence from Genetics Department, North Carolina State College, Raleigh, N. C.

chromosome species of *Gossypium* is fundamental for a satisfactory interpretation of the evolution of the genus as a whole. It is somewhat disturbing for the cytogeneticists not to know if the limited samples of the species studied in culture are at all representative of its natural range of variation, nor to be confident that some of the “off-types” which have been collected recently may safely be attributed to the effects of hybridization with those 19th–20th century introductions of *barbadense* and *hirsutum* which still persist in the islands (Stephens, 1963).

In the spring semester, 1963, a temporary appointment to the staff of the Genetics Department, University of Hawaii, gave me the opportunity to make a field study of the native species. I should like here to record my thanks to the University of Hawaii for inviting me to their campus and to my home institution, North Carolina State College, for granting me the necessary leave of absence. Thanks are also due to the National Science Foundation for defraying a major part of the travel expenses (NSF Grant G-14203).

GEOGRAPHICAL RANGE

*G. tomentosum* has never been found beyond the limits of the Hawaiian Islands. Statements to the contrary have arisen through nomenclatural confusion (Watt, 1907:69–71). Hillebrand’s statement (1888:51) that it occurred on all the Hawaiian Islands probably referred only to some or all of the eight major islands of the group—Niilhau, Kauai, Oahu, Molokai, Lanai, Kahoolawe, Maui, and Hawaii. The smaller leeward islands from Nihoa and Necker and beyond to Midway and Kure were studied by the Tanager Expedition, and the list of vascular plant collect-

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8 The matter has recently been re-investigated by Dr. R. Wilbur (Pacif. Sci. 18 (1):101–103, 1964), who concludes that "G. sandviicensis Parl." is the correct name for the Hawaiian native cotton, not "G. tomentosum Nutt." as used throughout this article.
tions (Christopherson and Caum, 1931:20–39) includes only one malvaceous species, *Sida fallax*. Nor was *tomentosum* found on the small island of Molokini, which lies in the channel between Kaho'olawe and Maui, by Forbes (1913a:10).

Collections from five of the eight major islands are preserved in the herbarium of the Bernice P. Bishop Museum. A total of 40 accesses includes no specimens from the other three islands, Ni'ihau, Kauai, and Hawaii. Ni'ihau is a privately owned cattle ranch, and few botanists have had the opportunity to visit it. Mrs. Sinclair (1885:23) included a painting of *tomentosum* in her "Indigenous Flowers of the Hawaiian Islands" which, according to St. John (1954:144–145), was probably made from living material near her home in Keiki, Ni'ihau. The only published record of *tomentosum* on Ni'ihau is that of Forbes (1913b:23).

I have been able to find only one definite record of the occurrence of this species on Kauai. This is a very old record (Wawra, 1873) which was kindly drawn to my attention by Dr. O. Degener. In recent years it has apparently not been seen, though St. John (loc. cit.) listed it among plants common to Ni'ihau and Kauai. Ripperton and Hosaka (1942) did not record it from Kauai, and Mr. Stephen Au and Mr. A. W. Duvel, who are familiar with the botany of the island, inform me that they have never seen it there. Dr. C. M. Rick recently searched for it among the dry western foothills in the Mana–Kekaha region without success. This suggests that *tomentosum* is very rare, or possibly extinct, on Kauai.

Concerning Hawaii, there is a rather puzzling conflict of evidence. MacCaughey (1917:414–418) described *tomentosum* as one of the species adapted to the colonization of lava flows, with an altitudinal range of 0–2000 ft. Although he did not state explicitly that the species occurred on Hawaii, his paper was concerned entirely with the (geologically) recent flows which are confined to Hawaii and East Maui. I have been able to find no independent record of the occurrence of *tomentosum* in either of these areas. Further, an altitude of 2000 ft is a considerably higher elevation than any recorded for the Bishop Museum collections, or found during the present study. As will be evident later, *tomentosum* is usually found as a component of *Prosopis* scrub, the altitudinal ranges of which have been mapped for the Hawaiian Islands by Ripperton and Hosaka (1942:maps 1–3). According to their maps there is one—and only one—region where this type of vegetation ("Zone A" in their terminology) extends to an elevation of 2000 ft. This is the Kau Desert region in southeast Hawaii, and if MacCaughey's statements concerning *tomentosum* applied to Hawaii, this would seem to be the only region which could have provided the necessary range in altitude. On the other hand, botanists who are very familiar with the Hawaiian flora (Miss Marie C. Neal, Mr. L. W. Bryan, and Mrs. C. K. Wentworth) have informed me that they have never seen the species on Hawaii, except in culture. It was not listed by Ripperton and Hosaka (1942) as a component of their "Zone A" vegetation on Hawaii, nor by Fagerlund and Mitchell (1944) in their check list of plants in the Hawaii National Park.

The map in Figure 1 shows the probable geographic range of *tomentosum* as it exists today. Sites collected during the present study are indicated by solid circles. These do not differ materially from earlier collections recorded in the herbarium of the Bishop Museum. Sites recorded by earlier collectors, but not checked during the present study, are represented by solid circles enclosed in rings. The open circle shows the locations of hybrid populations on Oahu which will be considered later. Shaded portions of the map show the approximate areas in which the average annual rainfall is 20 inches or less (Leopold, 1951:2).

In the case of the Oahu populations the apparent negative relation between rainfall and collection sites is quite significant, since the time available allowed for a careful search to be made on an island-wide basis, and no populations were found outside these dry areas. Elsewhere, owing to time limitations, only the drier areas were carefully studied. However, none of the collections in the Bishop Museum for which locations are recorded, appears to have been collected outside the low rainfall areas, and it seems likely that in the neighbor islands, as in Oahu, rainfall is a primary factor limiting the range of the species.

The negative relationship between rainfall and habitat is also indicated by the altitudinal
Fig. 1. Geographic range of Gossypium tomentosum Nutt. in the Hawaiian Islands (1963). Solid circles indicate collection sites; those enclosed in rings represent sites of former collections unchecked during the present study. The open circle indicates site of hybrid populations. Shaded areas correspond to regions with an average annual rainfall of 20 inches or less.

range of the species. On Oahu rainfall rises rapidly with elevation, and tomentosum was not found above an altitude of 100 ft. On Lanai, a low island in the rain-shadows of Molokai and Maui, scattered populations were found extending from sea level to almost 1000 ft. The collections from Molokai and Maui were obtained between 100 and 250 ft. These differences in altitudinal ranges agree quite well with the vegetation maps published by Ripperton and Hosaka (loc. cit.).

**ISLAND HABITATS**

1. *Oahu*

As shown in Figure 1, tomentosum is found most extensively on the western coastal plain in the rain-shadow of the Waianae Range. Here it extends in scattered populations from the southern extremity of the range, north of Barber's Point, to the outskirts of Nanakuli. North of this village is another population around Maile Point and extending for about 2 miles inland along the Hakimo Valley. Elsewhere along the coast only scattered plants were found around Kaena Point (from north of Makua extending around the point to the north coast). South of Nanakuli, tomentosum is found almost exclusively as an understory, along with Sida spp. and occasional Opuntia, in Prosopis (ke-awe) scrub. It appears to grow best under partial shade, i.e., wherever the stands of Prosopis are relatively thin. A similar habitat occurs around Maile Point, but there a semiprocumbent form (ecotype or plastic variant?) has extended away from the scrub to the edge of the exposed beach. Inland it extends along the Hakimo Valley as a component of mixed Prosopis and Leucaena scrub. On the whole the populations are found most commonly on the coastal flats, extending a little way up the slopes of the Waianae Range, but not ascending to a height of more than 100 ft. On the ocean side they rarely extend to the strand; the Maile Point population is exceptional in this respect.
A relic population occurs at the southern limit of the Koolau Range, west of Makapuu Point. Earlier records suggest that this population may once have extended farther west, at least to Koko Head and possibly as far as Diamond Head. All the area west of Koko Head is being absorbed rapidly in housing developments. The relic population is found along the roadside and extending inland to the west of the Mauka Kai golf course. Here the former cover of Prosopis has been cleared in recent years and the present habitat is obviously not a natural one. A small population is also found as a component of Prosopis scrub inside Diamond Head Crater.

Two other interesting features of the habitat are worth noting at this time, since they apply to the other islands also. Without exception the wild cotton was not found growing in friable soil, but always rooted deeply among outcrops of volcanic boulders, presumably the results of ancient lava flows. It was always found in association with Sida, but was far more restricted than the latter in range and habitat. Three different habitats on Oahu are illustrated in Figure 2.

2. Molokai

According to Degener (1937: fam. 221), tomentosum is commonly found in the dry southwest end of the island, but is rare elsewhere except in the Kawela area, east of Kaunakakai. Unusually heavy rains prevented a visit to the main region, which is only accessible by traces crossing the pineapple plantations west of Mauana. The most recent collection from this area appears to be Degener no. 9589 (Bishop Museum) which was collected at Kamakaipo in 1928.

Two populations, both of limited size, were found along the coastal region between Kaunakakai and Kawela. One of these occurred on a moderate slope about 50 ft above the highway, 2 miles east of Kaunakakai under a thin stand of Prosopis. It was absent among the taller stands bordering the highway and did not extend to an elevation of more than 100 ft inland. The other population consisted of thinly scattered plants rooted among large volcanic boulders lining the sides of Onini Gulch in the Kamilolola–Alii Pond district. The population extended from approximately 150–250 ft elevation. At lower levels, plants were not found among the dense stands of Prosopis, nor at higher levels where Prosopis was replaced by Leucaena. No other populations were found in a search extending as far east as Kamalo.

3. Lanai

The range of tomentosum appears to be greater on Lanai than on any of the other islands. At sea level on the south coast around Manele Bay and near the east coast in the Keomuku district there are areas where it forms an almost solid understory in tall Prosopis scrub. At higher elevations the populations thin out, and in the neighborhood of 1000 ft scattered plants occur in quite exposed positions, rooted on old lava flows among low and sparse vegetation. In such open habitats tomentosum occurs as a sprawling or semiprocumbent shrub and the characteristic tomentose surface of stems and leaves becomes intensified. Time did not permit collection on the north coast of the island, which is not readily accessible. A collection from this area (Awalua) was made in 1961 by Kondo (nos. 1b and 1c in the Bishop Museum). It seems likely that it is a common plant all around the periphery of the island in those areas which have not been brought into pineapple cultivation.

4. Maui

No collections have been recorded from the eastern, and geologically much younger, region of this saddle-shaped island. The herbarium in the Bishop Museum has two collections, both made by Degener (nos. 3650, 17624), in or near Pohakea Gulch, which is situated above
the eastern coastal plain on West Maui. In 1962 another population, 10 miles west of this area, near Ukumhame Shaft, was collected by Mr. Craig Whitesell. According to his notes, the population was scattered over 2-3 acres at about 250 ft elevation. This population was not located during the present study, but plants were found in the Pohakea Gulch region at an elevation of about 100 ft. These occurred under a thin cover of Prosopis immediately above a cane field and extending up into the gulch.

Most of the dry area in the "saddle" of the island which is shown in Figure 1 is in cane cultivation. Judging by the habitat of tomentosum on the other islands, the only likely area for its occurrence on East Maui would be the dry southernmost region lying between Makena and Kamanamana Point. Its vegetation is composed principally of tall Prosopis scrub with frequent Opanitia, which is traversed in places by bare, or almost bare, lava flows. This area was visited but no tomentosum was found.

5. Kaboolawe

This island is uninhabited and has been used for some years by the U.S. Navy as a target for bombing practice. Its low-altitude location in the rain-shadow of Maui and a past history of heavy overgrazing combine to make it the most barren of all the major islands in the group. From the air it appears as a low plateau, practically devoid of vegetation, with dry scrub lining the steep gullies which surround its coast.

Fifty years ago Forbes (1913:a:7), on the last recorded botanical exploration of the island, found a population of tomentosum near the southwest end.

6. Hawaii

Three areas which would seem to offer appropriate habitats for the establishment of the species were searched without success:

(a) The dry coastal flats north of Kona Airport, Kailua

(b) The area bordering the coastal road between Kealakekua Bay and the City of Refuge in the South Kona District

(c) A small area between Honuapo and Punaluu Beach in the southern Kau District

Time did not permit a visit to the Kau Desert and Hilina Pali areas which, as noted earlier, may have provided the necessary combination of altitudinal range and vegetational type for Mac-Caughey's observations.

CLIMATE AND "SOIL"

The climatic conditions to which tomentosum is adapted would appear to differ rather sharply from those under which the wild forms of birsutum flourish in the Caribbean. Honolulu weather records from 1948-1960 indicate that the average temperature on coastal Oahu varies (in round figures) between 70 and 80 F, with a mean of about 75 F, and a diurnal range of 9 F. The winter (short-day) months tend to be cool and wet, though the monthly distribution of rainfall is very erratic. In contrast, the Caribbean climate has a higher mean temperature, and short day length usually coincides with a pronounced dry season and cooler night temperatures. The Caribbean cottons grow vegetatively during the long wet days, and flower and set seed during the dry season. Flower initiation seems to be determined in part by day length and in part by night temperature (Mauney and Phillips, 1963), so that there is a seasonal flowering cycle. This regular cycle is missing in tomentosum. Mrs. Sinclair (1885:23) noted that it flowered the year round; and the herbarium specimens in the Bishop Museum were collected in every month of the year except December. During the present study it was found that in any population—at least from February through May—most of the plants are vegetative and the remainder may have young flower buds, open flowers, or ripe bolls. Seeds can therefore be collected over a long period, but only from relatively few plants at any given time. Although tomentosum can be considered a dry-land plant, it appears to be less xerophytic than Caribbean birsutum. Wild forms of the latter species will often thrive around salt ponds, and immediately exposed to strong winds and salt spray. Forms which grow in dry scrubland away from the coast tend to be components of more open vegetation, or else to grow tall. Typically they are not found as an understory among taller plants. In contrast, the most vig-
ors stands of tomentosum were found under light shade.

The virtual restriction of tomentosum to old volcanic outcrops, as opposed to friable soil, suggests that it possibly may have rather specialized physical and nutritional requirements. MacCaughey (loc. cit.) included it in a list of species which he considered to be particularly adapted to the colonization of lava flows and which were characterized by certain xerophytic features. Some of these features are clearly applicable to tomentosum (viz., woody perennial growth form, with slow growth and deep root penetration; foliage often pubescent; and a tendency to assume a decumbent habit on bare substrates). He also pointed out the extremely xerophytic conditions which are generated on recent lava flows through a combination of high evaporation, free drainage, and rapid heating of black or almost black surfaces. However, these conditions apply particularly to recent lava flows, and in the present study no tomentosum was found in those areas (Hawaii and East Maui) to which recent flows are restricted.

It seems likely that some of the difficulties of growing the species in culture may be associated with (a) failure to provide sufficiently rapid drainage, (b) too high a mean temperature, and (c) too acid soil conditions. With regard to the third factor, MacCaughey (1917: 408) noted that soils derived from Hawaiian lava flows have a far higher proportion of basic constituents than comparable mainland soils (64% as compared with 19%, according to his figures). The following analysis of igneous rocks in Hawaii was obtained from “Handbook of Hawaiian Soils” (1932):

<table>
<thead>
<tr>
<th>Average of 56 Analyses of Lavas from Island of Hawaii</th>
</tr>
</thead>
<tbody>
<tr>
<td>SiO₂</td>
</tr>
<tr>
<td>Al₂O₃</td>
</tr>
<tr>
<td>Fe₂O₃</td>
</tr>
<tr>
<td>FeO</td>
</tr>
<tr>
<td>MgO</td>
</tr>
<tr>
<td>CaO</td>
</tr>
</tbody>
</table>

MORPHOLOGICAL VARIATION

Those morphological characteristics of tomentosum which distinguish it taxonomically from the other New World species of Gossypium (long anther filaments, partly fused in pairs; absence of leaf nectary; intense yellow flower color; undifferentiated and strongly adherent seed fibers) were found to be quite uniform. On the other hand, characters which previous experience had shown to be rather variable (leaf shape; bracteole form and section; degree of pubescence; plant habit) were found to be extremely variable. There was little if any tendency for these variations to follow a geographical pattern; i.e., it was not possible to distinguish morphologically between different island races. In this respect, G. tomentosum contrasts strongly with the native species of the Galapagos Islands (G. darwinii), in which each island has tended to develop its own well-marked morphological race. It is somewhat surprising that two archipelagos, of comparable size and origin, and offering similar arid habitats to related colonizing species, should have produced such different evolutionary results.

The nature of variation in leaf shape and bracteole form is illustrated in Table 1 and Figure 3, respectively. The data show the considerable range of variation within any one population, and the extensive overlap that exists when different populations are compared. Varia-

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**Fig. 3.** Outline drawings, approximate half natural size, of tomentosum bracteoles. All bracteoles were obtained from open flowers. Top row, Oahu; 2nd row, Lanai; 3rd row, Molokai; 4th row, Maui.
TABLE 1

VARIATION IN LEAF SHAPE IN 11 POPULATIONS OF Gossypium tomentosum
COLLECTED FROM FOUR DIFFERENT ISLANDS*

(Measurements based on ten mature leaves per population)

<table>
<thead>
<tr>
<th>Island</th>
<th>Leaf Description</th>
<th>L</th>
<th>S</th>
<th>Mean</th>
<th>Index</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>OAHU</td>
<td>1. Barber's Point—Kahe Point</td>
<td>84.1</td>
<td>32.2</td>
<td>38.3</td>
<td>31-49</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2. Kahe Point—Nanakuli</td>
<td>78.8</td>
<td>30.8</td>
<td>39.1</td>
<td>28-49</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3. Maile Point (procumbent form)</td>
<td>80.0</td>
<td>29.0</td>
<td>36.3</td>
<td>30-45</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4. Maile Point (shade form)</td>
<td>100.0</td>
<td>39.4</td>
<td>39.4</td>
<td>31-46</td>
<td></td>
</tr>
<tr>
<td></td>
<td>5. Makapuu Point</td>
<td>79.6</td>
<td>32.4</td>
<td>40.7</td>
<td>36-47</td>
<td></td>
</tr>
<tr>
<td>MOLOKAI</td>
<td>6. Kaunakakai</td>
<td>74.7</td>
<td>28.8</td>
<td>38.6</td>
<td>27-50</td>
<td></td>
</tr>
<tr>
<td></td>
<td>7. Onini Gulch (100 ft elev.)</td>
<td>64.4</td>
<td>24.7</td>
<td>38.4</td>
<td>35-45</td>
<td></td>
</tr>
<tr>
<td></td>
<td>8. Onini Gulch (200 ft elev.)</td>
<td>81.0</td>
<td>34.6</td>
<td>42.7</td>
<td>36-49</td>
<td></td>
</tr>
<tr>
<td>LANAI</td>
<td>9. Keomuku</td>
<td>71.1</td>
<td>32.4</td>
<td>45.6</td>
<td>38-53</td>
<td></td>
</tr>
<tr>
<td></td>
<td>10. Manele</td>
<td>71.7</td>
<td>31.2</td>
<td>43.5</td>
<td>36-55</td>
<td></td>
</tr>
<tr>
<td>MAUI</td>
<td>11. Pohakea Gulch</td>
<td>71.1</td>
<td>33.0</td>
<td>46.4</td>
<td>42-51</td>
<td></td>
</tr>
</tbody>
</table>

The degree of hairiness can also be modified to a lesser extent by transferring the plants from a shaded greenhouse to full sunlight. Comparative studies under controlled environmental conditions would therefore be necessary to determine whether the variation observed in natural stands of tomentosum is phenotypic only or the result of ecotypic differentiation.

POLLINATION AND INTROGRESSION

1. The Primary Breeding System

It has been pointed out by Baker (1955:347–349) and Stebbins (1957:343–344) that an autogamous breeding system would be initially advantageous to a colonizing plant species, since it would render the latter independent of pollen vectors. On the contrary, it would be most unlikely for appropriate pollen vectors to be introduced into a new habitat along with the cross-pollinated species dependent upon them. This argument is particularly pertinent if applied to the colonization of isolated volcanic islands like the Hawaiian group.

All species of Gossypium are self-compatible with radially symmetrical flowers, large numbers of anthers, and a true floral nectary located in a deep circular groove lined with glandular hairs at the inner base of the calyx. The nectary can be seen only under low-power magnification of a vertical section of the receptacle. It is accessible both to long-tongued insects and to insects small enough to crawl between the bases of the petals. Usually there are also extrafloral nectaries located (1) at the bases of the bracteoles and (2)
on the outer surface of the calyx alternating with the bracteoles, and there is a leaf nectary on the midrib of the under surface of each leaf. It is thus possible for insects to obtain nectar without entering the flowers at all. These characteristics do not suggest floral adaptation to any specific insect vector (Grant, 1950:392).

In *tomentosum* extrafloral nectaries and leaf nectaries are lacking entirely, but a true floral nectary can be seen in vertical section. There is reason to suppose that the latter is nonfunctional or only weakly functional. When the corolla is removed from a fresh flower of *barbadense* or *birsutum*, a pool of nectar can be seen within the calyx cup, but the secretion is weak or absent in *tomentosum*. This observation, based on the relatively few flowers available at the time of study, was confirmed later by Mr. Frank Johnson. He informs me that only a fraction of the flowers he examined appeared to contain nectar. It seems likely, therefore, that insects would visit *tomentosum* flowers primarily to feed on pollen or to gather pollen. Further, because a limited number of plants are in flower at any one time in *tomentosum* populations, they would not be likely to furnish a main source of supply to pollen-gathering insects. Under these circumstances a mainly autogamous breeding system is to be expected, with visits by pollen-gathering insects restricted to temporary periods of over-all pollen shortage.

In Central America and the Caribbean, the relatively small and scattered populations of wild and dooryard forms of *G. birsutum* do not impress the observer as being heavily stocked with pollinating insects. Those commonly found in the flowers are small ants and beetles which probably function more effectively as agents of self- rather than cross-pollination. The situation in *tomentosum* populations appears to be similar, though the number of observations which could be made was too small to be very reliable. Unusually heavy and persistent rains occurred throughout March and well into April in this normally dry habitat; thereafter there was a temporary cessation of flowering until toward the end of May. In the latter part of April the combined results of three separate searches through the Oahu populations yielded less than 50 flowers. It was noted that although honeybees and small moths (occasionally) and carpenter bees and scavenger flies (rarely) were visiting *Sida* flowers in the immediate neighborhood, none of these potential pollinating agents visited *tomentosum* flowers. Most of the latter were entirely devoid of insects, though occasional flowers containing a few small ants or fruit-bud beetles (*Conotetus mexicanus*) were seen.

These observations, though limited, do not suggest that insects play an important role in the breeding system of *tomentosum*. On the other hand, a strictly autogamous system is difficult to reconcile with the fact that *tomentosum* flowers, like those of other wild forms of the New World species, have long styles with the receptive stigmatic surfaces borne high above the staminal column (cultivated forms usually have short styles with the stigmatic surfaces in contact with, or immediately above, the staminal column). An interesting feature of the *tomentosum* style is the fact that it is often recurved, assuming a crozier-like structure with the stigmatic surface nearly approximated to the staminal column.

2. The Effects of Insect Introduction

In oceanic islands like the Hawaiian group with a numerically poor indigenous insect fauna (Zimmerman, 1948:94–95), the introduction of beekeeping as a local industry could have potentially disturbing effects on the taxonomy of the local flora. A likely example is provided by the dooryard cottons (*G. barbadense*), which still may be found in gardens and along roadsides on the islands. As early as 1812, cotton was introduced into Oahu (Jones, 1937:17) and, later, in the early 20th century, serious attempts were made to establish it as a crop (Krauss, 1909:1–16). Commercial varieties of Sea Island (*barbadense*) and Upland (*birsutum*) were both introduced without lasting success. Around 1857 the first shipment of honeybees arrived from California (Eckert, 1951:1). According to Van Dine and Thompson (1908:8), *Prosopis* soon became the primary source of nectar, and on the western side of the island apiaries were moved to the coastal areas under the shelter of the *Prosopis* forests, where many of them are found today. During the past 10 years this source of nectar has been seriously diminished by the activities of an immigrant moth, *Ithome concolorella*, which destroys the
florets of *Prosopis* and certain other leguminous shrubs (Namba, 1956:100). As a consequence the relatively flower-constant honeybee has been forced to forage among a variety of nectar (and pollen) sources.

The village of Nanakuli is located on a crescent-shaped coastal plain of western Oahu, bounded by the Waianae Range which juts into the sea to the north at Maile Point and to the south at Kahe Point. The lower slopes of the range are dominated by a zone of *Prosopis* scrub, and where this zone approaches the coast, populations of *tomentosum* are very common in the understory. Occasional *barbadense* plants occur along the coastal highway which runs through Nanakuli, and also in gardens in the village itself. In two small areas, (a) south of Piliokahe Beach and (b) in a waste lot adjoining the Texaco Service Station in the village, outlying plants of *tomentosum* and *barbadense* are growing within 50 yards of each other. Less than a quarter mile inland, two colonies of honeybees are established in hives under the *Prosopis* trees. And in the areas where *tomentosum* and *barbadense* are in close proximity, two obviously hybrid populations are found whose taxonomic properties are illustrated by the data presented in Table 2 and Figure 4.

Table 2 gives the results of scoring the populations for four qualitative or semiqualitative characters which distinguish the two species. The scoring was necessarily limited to those plants which were flowering at the time the study was made. The 11 plants scored include 9 different combinations of characters, none of which was identical with either parental combination. The populations were therefore segregating for characters which distinguish the two species.

The plants were also scored for certain metrical characters which previous experience has shown to be useful in discriminating between species of New World cottons. These are presented as a scatter diagram in Figure 4, according to the methods developed by Anderson (1949: 81–101). The characters measured are listed below; methods of measurement will be found in the Appendix to this paper:

- Br. T.—Number of bract teeth
- Br. D.—Bract dissection index
- Br. S.—Bract size
- L. I.—Leaf index
- P. L.—Petal length
- S. I.—Staminal index

In Figure 4 staminal index is plotted on the horizontal axis, petal length on the vertical axis. The other characters are symbolized according

### TABLE 2

**HYBRID COTTON POPULATIONS AT NANAKULI, OAHU; SEGREGATION IN QUALITATIVE CHARACTERS**

Symbols used: *H* (tomentum); *Ne* (leaf nectary); *Y* (bright yellow petal); *R* (petal spot). Presence of each character is indicated by (+), absence by (o) and intermediate condition by (−).

<table>
<thead>
<tr>
<th>Hybrid No.</th>
<th><em>H</em></th>
<th><em>Ne</em></th>
<th><em>Y</em></th>
<th><em>R</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>+</td>
<td>o</td>
<td>+</td>
<td>o</td>
</tr>
<tr>
<td>2</td>
<td>−</td>
<td>o</td>
<td>+</td>
<td>−</td>
</tr>
<tr>
<td>3</td>
<td>+</td>
<td>−</td>
<td>o</td>
<td>o</td>
</tr>
<tr>
<td>4</td>
<td>o</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>5</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
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<td>6</td>
<td>−</td>
<td>o</td>
<td>+</td>
<td>−</td>
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</tr>
<tr>
<td>9</td>
<td>−</td>
<td>o</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>10</td>
<td>o</td>
<td>+</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>11</td>
<td>o</td>
<td>+</td>
<td>−</td>
<td>o</td>
</tr>
</tbody>
</table>

Parent type; in *Prosopis* scrub south of Nanakuli

Waste ground near service station, Nanakuli

Roadside behind Piliokahe Beach, Nanakuli

Parent type; Dooryards, Nanakuli
to the key accompanying the figure. Solid circles refer to the parental species (barbadense to the left, and tomentosum to the right of the chart). Open circles represent the plants under study, the “Texaco” plants being distinguished from the “Piliokahe” plants by dots placed within the circles.

It is evident that although most of the plants resemble barbadense with respect to the characters measured, they all deviate in one or more characters in the direction of tomentosum. This would be expected if they were hybrids segregating from backcrosses of tomentosum to barbadense. A few of the plants had open bolls, and the seeds they contained bore fibers of two distinct kinds—medium to long lint fibers, more or less adherent to the seed-coat; and coarse, strongly adherent fuzz fibers. Both lint and fuzz fibers were light brown in color. These fiber characteristics are typical of barbadense × tomentosum hybrids studied previously in culture.

Several visits were made to the hybrid populations from the beginning of March through May, but at no time was insect activity among them very great. The pollen-feeding beetle (Conotelus) was quite common inside the open flowers, but it is not likely that it would be effective as a cross-pollinating agent. A few small ants were also found in the flowers from time to time, but the only “prospects” likely to be concerned in natural crossing were the rare visits by honeybees, and one solitary visit by a syrphid fly, which were observed. Similarly, it was noted that Conotelus was common inside the flowers of dooryard barbadense in the same area, and rather infrequently honeybees were seen to enter the flowers also. A few carpenter bees and hornets were observed around the plants, but their attention appeared to be confined to the extrafloral nectaries, and they were not seen to enter the flowers. During the same period honeybees in particular, syrphids, and occasionally carpenter bees and small moths were seen to be actively visiting the flowers of Sida and a variety of garden ornamentals in the neighborhood.

Thus it appears that rather infrequent visits by honeybees were most likely responsible for the origin of the hybrid populations, and for the subsequent backcrossing and intercrossing which have probably taken place. However, the relatively few observations which could be made on tomentosum provided no direct evidence that honeybees, or any other pollen-gathering insects, visit flowers of this species.

LOCAL NAMES AND USE

There are two Hawaiian names for Gossypium tomentosum: ma‘o (“yellow-green”) and hulu hulu (“hairy hairy”). Two independent sources suggest that the plant was used by the ancient Hawaiians as a source of green dye for their kapa cloth. Malo (1903:43, 74), writing about 1836, stated definitely that ma‘o was Gossypium tomentosum, and that its flower was used as a dye to color “tapa and the loin cloths of the women etc.” Bennett (1840:217), who was a surgeon on a whaling ship, stated that “a delicate green-yellow dye” obtained “from an infusion of the flowers of the cotton plant” was used for dyeing kapa in Oahu. Later in the same narrative (1840:235) he said: “Several exotic kinds of the cotton-shrub (pulu or soft of the natives) grow wild in the plains, and include that rare species, the yellow or nankeen cotton (Gossypium religiosum) called by the natives marou.”

Brigham (1911:50, 144) referred to Bennett’s statement, and assumed that the latter had con-
fused cotton with *Abutilon incanum*, which also had the Hawaiian name *ma'o* and which also was used as a dye. That Brigham was in error is suggested from the following considerations:

1. Bennett's use of the (then) accepted Latin nomenclature in identifying the numerous plants he described in his narrative, indicates that he was a competent botanist.

2. Bennett stated explicitly that the flowers were used as a source of the dye: according to Brigham it was the leaves of *Abutilon* which were used.

3. The name *ma'o* is applied both to *G. tomentosum* and to *A. incanum*. The name is incomprehensible as a description of either plant, but quite understandable if it refers to a common dyeing property.

4. The word "nankeen" was used nonspecifically in the 18th and 19th centuries to describe a brown-fibered cotton. It was applied both to Asiatic and to New World cottons and could reasonably have been applied by Bennett to the brown-fibered *tomentosum*. Bennett's identification of this species as "*G. religiosum*" is consistent with other nomenclature of the same period. (An obvious specimen of *G. tomentosum*, no. 12935 in the National Herbarium, Washington, D.C., which was collected in 1845 by the U.S. Exploring Expedition under the command of Charles Wilkes, is labelled "*Gossypium religiosum*.")

5. It has been known for some time that the flowers of the cotton plant contain pigments, once thought to be of potential importance to the dyeing industry (Perkin, 1899:825). Dr. C. R. Parks (1963) has recently made a chromatographic survey of these pigments and has shown that the depth of the yellow color in the petal is primarily determined by the relative amount of the flavon pigment, gossypetin, which it contains in various glycosidal forms. Further he has shown that the petals of *tomentosum* have larger amounts of this pigment than those of other species. (This explains the bright sulphur-yellow shade of *tomentosum* flowers, as compared with the lemon-yellow of *barbadense* and the cream shades of many *birsutum* forms). Solutions of gossypetin glycosides are bright yellow in color, but separate out in greenish crystals when concentrated. Slightly alkaline solutions produce a green dye. According to Bennett (loc. cit.), the "astringent water of the taro patch" was used to mordant the dye—possibly a matter of pH adjustment.

The other Hawaiian name, *bula bula* ("hairy hairy"), does not seem to be a particularly apt description of the finely tomentose surface of the plant. One wonders whether the name may not, in fact, be a corrupted version of *boola*, which, according to Brigham (1911:171) is "the principal Hawaiian word meaning to color ... to dive into the water, to plunge into a liquid, hence to dye. . . ."

**SUMMARY**

1. The wild cotton of the Hawaiian Islands, *G. tomentosum* Nutt., has never been found beyond the limits of the eight major islands of the group. Today it is only known on six of the islands: Niihau, Oahu, Molokai, Maui, Lanai, and Kahoolawe. There is apparently no definite record of its occurrence, or former occurrence, on Hawaii, despite general statements to that effect in the literature.

2. Within its current geographical range, the species is found only in dry areas with an average annual rainfall of 20 inches or less. Its altitudinal range on any particular island therefore depends on local topography and position relative to rain-shadows.

3. The most common habitat is as an understory in thin *Prosopis* scrub, growing among partially weathered volcanic boulders. Less frequently it is found in more exposed positions, i.e., near beaches or (at relatively high altitudes) among thin low scrub.

4. The species has not evolved morphologically distinct island races. Those morphological characters which differentiate it taxonomically from other species of *Gossypium* are remarkably uniform. Other characters may vary apparently
Native Hawaiian Cotton—STEPHENS

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at random (leaf shape and bract form), or may be associated with the particular environment in which the plant is growing (pubescence and plant habit).

5. In one area in Oahu two populations were found of undoubtedly hybrid origin (G. barbadense × G. tomentosum). The underlying reasons for this situation are discussed.

6. Evidence is presented for the belief that the flowers of G. tomentosum were used by the ancient Hawaiian people as a source of green dye.

ACKNOWLEDGMENTS

In the course of this study I have drawn freely on the time, combined experience, and special knowledge of the following people: Dr. O. Degener, Waialua, Oahu; Miss Marie C. Neal and Mr. Alvin K. Chock, Bernice P. Bishop Museum; Dr. C. Lamoureux, Botany Department, University of Hawaii; Dr. Dale Habeck, Entomology Department, University of Hawaii; Mr. Stephen Au and Mr. A. W. Duvel, Department of Agriculture, Kauai; Mr. Henry Wiebke, Hooluhua, Molokai; Mrs. Juliette Wentworth, Hawaii National Park, Hawaii; Mr. L. W. Bryan, Kailua, Hawaii; Mr. Craig Whitesell, U.S. Forest Service, Hilo, Hawaii.

I am greatly indebted also to Mr. G. Yamane and Mr. W. Bonsey for transport and help with the location of collecting sites on Lanai and Maui, respectively, and to Dr. C. M. Rick for the photographs reproduced in Figure 2. Finally I wish to thank my host, Dr. J. B. Smith, for the excellent facilities provided in the Genetics Department, University of Hawaii, for his continued interest in the study, and for "stage managing" my travel in the neighbor islands.

REFERENCES


**APPENDIX**

Methods of measuring characters shown in Figure 4:

**Br. T.**—The average number of teeth per bracteole, based on counts of 10 bracteoles.

**Br. D.**—Bract dissection index: S expressed as a percentage of L, where S is the distance from bracteole base to base of the sinuses on either side of the median tooth, and L is the distance from bracteole base to apex of median tooth. Measurements averaged from three bracteoles each removed from a flower in bloom.

**Br. S.**—Bract size: The geometric mean of bracteole length and bracteole breadth. Averaged from three bracteoles, each removed from a flower in bloom.

**L. I.**—Leaf index: S expressed as a percentage of L, where S is the distance from leaf pulvinus to base of median lobe, and L is the distance from leaf pulvinus to apex of median lobe. Measurements averaged from three climax leaves.

**P. L.**—Petal length, measured from claw of petal to maximum distance on outer edge. Averaged from three fresh petals from different flowers.

**S. I.**—Staminal index: Maximum diameter of staminal column expressed as a percentage of the length of the column. Measurements averaged from three flowers.
Spiders from Some Pacific Islands, Part V

B. J. Marples

A COLLECTION OF SPIDERS from various Pacific islands was entrusted to me for examination by the Director of the Bernice P. Bishop Museum in Honolulu, to whom I am indebted. There were 146 tubes, mostly containing a number of specimens, and they had been collected by different people at different times from islands between New Caledonia in the west and Tahiti in the east. Five new species are described and also four allotypes, and a number of additions to faunal lists have been made. The islands, or island groups, will be mentioned in alphabetical order, and the descriptions given at the end. Unless otherwise stated the specimens are in the Bernice P. Bishop Museum.

AITUTAKI

Aitutaki is an island, partly volcanic and partly of coral, lying 140 miles north of Raratonga. It has 6 square miles. Twenty-four species have been recorded and the present collection adds three more. Smeringopus pallidus (Blackwall) (formerly S. elongatus Vinson) has a very widespread distribution and has been recorded in Samoa and in Raratonga and the Northern Cook Islands. Chiracanthium longimanum L. Koch has previously been recorded only as far east as Tonga and Samoa. The third new record is a salticid here described as Placilla kraussi n. sp.

LINE ISLANDS

These are very isolated atolls situated more or less on the equator, east of the Gilbert Islands and north of the Tokelau Islands. The fauna of such islands is of course poor in the extreme, and consists for the most part of species accidentally introduced by man. This was well shown by Sakagami (1961) for Marcus Island,

which lies in a very isolated position to the northeast of the Mariana Islands. In 1902 only one spider species was present, while in 1961 there were four: a pholcid, an epeirid, a salticid, and Heteropoda venatoria. In the present collection 15 species were present from six islands, and six of these have been left unidentifed. It was felt that they may have been introduced from anywhere and are not part of the normal Pacific fauna. To describe them as new would only tend to cause confusion. Table 1 shows the distribution of the species between the islands.

NEW CALEDONIA

About 150 species have been recorded from New Caledonia, many of them not extending into the more easterly islands but no doubt having a wider distribution towards the northwest. In the present collection 14 species have been identified, all but two of which have been recorded previously. The two new records are Prychia gracilis L. Koch, previously known from New Hebrides and Fiji, and Poicilopachys bispinosa (Keyserling) (formerly Cyrtarachne), known from New Hebrides and Samoa.

SAMOA

The spider fauna of Upolu is probably as well known as that of any of the Pacific islands. The larger island of Savaii to the west, and the smaller Tutuila to the east, are less well known. However, as their distances from Upolu are only 8 and 47 miles respectively, their faunae are probably very similar. All are large, mountainous, volcanic islands.

In 1955 I published a list of the spiders of Upolu, including 123 species. Since then six have been added: Drassodes ciusi Berland, Clabiona upoluensis n. sp., Eurypattus lautos Keyserling, Trite longipalpis Marples, Leucauge granulata Walckenaer, and Eppeira pogisa Marples. Tetrablemma samoensis n. sp., recorded in 1955

\footnote{Department of Zoology, University of Otago, Dunedin, New Zealand. Manuscript received September 6, 1963.}
from an incomplete specimen, is here described fully. Thirty-five species are recorded from Savaii and 34 from Tutuila, these being listed below, and the total for the Samoan Group is now 136.

**SOCIETY ISLANDS**

Forty species have been recorded from the Society Islands. The present collection includes 12 species, mostly from Tahiti, and two of them are new records for the group. These are both clubionids, *Australaena histricina* Berland, previously recorded from Rapa, and *Chiracanthium gilvum* L. Koch, previously recorded from New Caledonia and Samoa.

**SWAINS ISLAND**

This is a small island situated between Samoa and the Tokelau Islands to the north. No spiders seem to have been recorded from it before, but the collection includes four species. Two of them are very widespread species, *Thorellia ensifera* Thorell and *Epeira theisi* Walckenaer. *Ceruleocera ransfordi* Marples, recorded from Upolu, Samoa, is surprising, as its habitat there is under stones in rather moist situations. The fourth species is an agelenid, described below as a new genus and species.

**TONGA**

New records are *Uloborus gibbosus* L. Koch from Nukualofa, previously recorded from New Hebrides, Fiji, Samoa, and Tokelau, and *Theridion albidum* Berland from Vavau, previously recorded from Samoa. It had seemed curious that no uloborids were known from Tonga; this is the first record of the genus. The total number of species for Tonga is now 51.

**TETRABLEMMIDAE**

*Tetramelema samoensis* n. sp.


**Male:** Length 1.16 mm. Bright chestnut brown, legs a little paler.

**Carapace:** Length 0.52 mm, breadth 0.23 mm. Outline from above pear-shaped, widest opposite leg II, rounded in front and behind. Profile rises steeply to the apex opposite leg I, where the eyes are situated.

**Eyes:** Four, white, central area of the group black. Ratios of the diameters of the eyes and of their distances apart: AE, 65; PE, 56; A–A, 0; A–P, 0; P–P, 40. Width of the eye-group 0.09 mm; clypeus 0.25 mm.

**Chelicerae:** Stout, with a large, anteriorly directed, upward-curving horn arising near the base. Ventral end of the retromargin of the groove with a large sharp angle.

**Maxillae:** Sharply inclined inwards, the scopulae meeting in front of the lip.
<table>
<thead>
<tr>
<th>TABLE 2</th>
<th>LIST OF THE SPIDERS KNOWN FROM THE SAMOAN ISLANDS OF SAVAII AND TUTUILA</th>
</tr>
</thead>
</table>

<table>
<thead>
<tr>
<th>Spider Name</th>
<th>Savaii</th>
<th>Tutuila</th>
</tr>
</thead>
</table>
| Filistata bakeri Berland........ | ✔️ | |}
| Uloborus bistratias L. Koch. ... | ✔️ | ✔️ |
| Uloborus geniculatus Olivier ... | ✔️ | ✔️ |
| Uloborus gibbosus L. Koch ... | ✔️ | ✔️ |
| Dictyna bifasciata L. Koch .... | ✔️ | ✔️ |
| Loxoselet refractens L. Dufour ... | ✔️ | ✔️ |
| Scytodes striatipes (L. Koch) ... | ✔️ | ✔️ |
| Artina mauriaca Walckenaer .... | ✔️ | |}
| Philocus ancoralis L. Koch. ... | ✔️ | ✔️ |
| Physocyclus globosus Taczanowski | ✔️ | |}
| Smeringopus pallidus (Blackwall) | ✔️ | |}
| Chiracanthium furax L. Koch ... | ✔️ | ✔️ |
| Clubiona alveolata L. Koch .... | ✔️ | ✔️ |
| Clubiona samoensis Berland ... | ✔️ | ✔️ |
| Clubiona zimmermani n. sp ... | ✔️ | ✔️ |
| Heteropoda venatoria Linn ... | ✔️ | |}
| Diasea pristexa L. Koch ... | ✔️ | ✔️ |
| Athamas whitmevi Cambridge ... | ✔️ | ✔️ |
| Arcylus terygodori L. Koch ... | ✔️ | ✔️ |
| Bavia aericeps E. Simon ... | ✔️ | ✔️ |
| Bianor maculatus Keyserling ... | ✔️ | ✔️ |
| Cytaea piscula L. Koch ... | ✔️ | ✔️ |
| Flacilla minuta Berland ... | ✔️ | ✔️ |
| Menemems bivittatus Dufour ... | ✔️ | ✔️ |
| Mollicia microphthalmal L. Koch ... | ✔️ | ✔️ |
| Mollicia pusilla Strand ... | ✔️ | ✔️ |
| Plexippus paycelli Audouin ... | ✔️ | ✔️ |
| Savaiia punctata Marples ... | ✔️ | ✔️ |
| Thoreilla ensifer Thorell ... | ✔️ | ✔️ |
| Hahnia berlandi Marples ... | ✔️ | ✔️ |
| Argyodes cometes L. Koch ... | ✔️ | ✔️ |
| Argyodes gracilis L. Koch ... | ✔️ | ✔️ |
| Cylognatha affinis Berland ... | ✔️ | ✔️ |
| Mysmena rotunda (Marples) ... | ✔️ | ✔️ |
| Phoroneidia personata (L. Koch) ... | ✔️ | ✔️ |
| Theridion adamsoni Berland ... | ✔️ | ✔️ |
| Theridion abosiriatum L. Koch ... | ✔️ | ✔️ |
| Theridion aleipata Marples ... | ✔️ | ✔️ |
| Theridion busonoi Berland ... | ✔️ | ✔️ |
| Theridion hopkinsi Berland ... | ✔️ | ✔️ |
| Linyphia suavis Marples ... | ✔️ | ✔️ |
| Leucauge ilatele Marples ... | ✔️ | ✔️ |
| Leucauge taberculata Keyserling ... | ✔️ | ✔️ |
| Leucauge prodiga L. Koch ... | ✔️ | ✔️ |
| Tetragnatha macilentu L. Koch ... | ✔️ | ✔️ |
| Tetragnatha panopoe L. Koch ... | ✔️ | ✔️ |
| Anepion ramboides (L. Koch) ... | ✔️ | ✔️ |
| Cyclota littoralis L. Koch ... | ✔️ | ✔️ |
| Cyrtophora moluccensis Doleschal ... | ✔️ | ✔️ |
| Epeira maculaticeps L. Koch ... | ✔️ | ✔️ |
| Epeira pagisa Marples ... | ✔️ | ✔️ |
| Epeira thesi Walckenaer ... | ✔️ | ✔️ |
| Poiciopachys bispinosa (Keyserling) ... | ✔️ | ✔️ |
| Theridiosoma lopelli Marples ... | ✔️ | ✔️ |
Lip: Free, much wider than long.
Sternum: Length 0.31 mm, breadth 0.34 mm, convex. Prolonged upwards between the bases of the legs. Hind legs widely separated.
Palp: Long, tibia stout, tarsus large, smooth and pear-shaped with an upcurved spine at the tip. As in Figure 1.

<table>
<thead>
<tr>
<th>Legs</th>
<th>I</th>
<th>IV</th>
<th>II</th>
<th>III</th>
<th>Palp</th>
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<tbody>
<tr>
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<td>2.0</td>
<td>1.9</td>
<td>1.8</td>
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</table>

Three claws. Tarsi with serrated bristles. Metatarsi with one and tibiae with three dorsal trichobothria. No spines.

Abdomen: Length 0.75 mm, breadth 0.63 mm. Large dorsal and ventral sclerites. Spinnerets surrounded by a conical sclerite. Each side of the abdomen with three long narrow sclerites, and three similar ones between the dorsal sclerite and that surrounding the spinnerets. Two broader ones in the corresponding space below.

FEMALE: Length 1.18 mm. Color as in male.
Carapace: Length 0.56 mm, breadth 0.42 mm. While in the male the carapace in side view is conical, with the eye-group at the apex, in the female the eye-group is more anteriorly placed, so that the carapace has a horizontal dorsal ridge.

Eyes: Ratios of the diameters of the eyes and of their distances apart: AE, 56; PE, 64; A–A, 17; A–P, 0; P–P, 41. Width of eye-group 0.11 mm. Clypeus 0.16 mm.

Chelicerae: Without the anterior horns.
Maxillae and lip: As in male.
Sternum: Length 0.31 mm, breadth 0.34 mm. Palp: Short and slender. No claw.

<table>
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<tr>
<th>Legs</th>
<th>IV</th>
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<th>II</th>
<th>III</th>
<th>Palp</th>
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<td>2.0</td>
<td>1.8</td>
<td>1.7</td>
<td>0.5</td>
</tr>
</tbody>
</table>

A single male, collected by E. C. Zimmerman viii–20–40 on Swains Island, appears to belong to the Agelenidae. This family is most unusual in the Pacific, and the only species attributed to

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A-P, 0; P-P, 41. Width of eye-group 0.11
mm. Clypeus 0.16 mm.

Chelicerae: Without the anterior horns.
Maxillae and lip: As in male.
Sternum: Length 0.31 mm, breadth 0.34 mm.
Palp: Short and slender. No claw.

<table>
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<th>Legs</th>
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<td>2.0</td>
<td>1.8</td>
<td>1.7</td>
<td>0.5</td>
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</table>

Abdomen: Length 0.82 mm, breadth 0.61 mm. As in the male. Strong transverse fold near the posterior margin of the large ventral sclerite.

The family Tetrablemmidae was erected by Cambridge (1873) for a single male *T. medioculatum* from Ceylon. The present male differs from this in the carapace, there being no prominence bearing small points anterior to the eyes, nor any row of prominent points round the margin. The shape of the horns on the chelicerae and of the palpal organ also appear somewhat different. Another species, *T. okei*, was described by Butler (1922) from a female from Victoria, Australia. The shape of the carapace is slightly different but, otherwise, except for the presence of trichobothria in the present specimen, they are very similar. Because of these differences and the great geographical separation, a new species is established.

AGELENIDAE

A single male, collected by E. C. Zimmerman viii–20–40 on Swains Island, appears to belong to the Agelenidae. This family is most unusual in the Pacific, and the only species attributed to

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it, *Paro simoni* Berland from Rapa, may actually be a linyphiid. The present specimen may have been accidentally introduced to Swains Island from some other part of the world, as suggested above for the specimens from the Line Islands. As the island is not so isolated, and the other three species are found also in Samoa, the present specimen is described as *Swainsia armata* gen. et sp. nov.

*Swainsia armata* gen. et sp. nov.

**MALE:** Swains Island. Length 3.72 mm. General color pale brown, the chelicerae and cephalic part of the carapace being darker, the abdomen lighter. Black around the eyes and between AME and LE.

**Carapace:** Length 1.87 mm, breadth 1.38 mm. Cephalic part parallel-sided, posterior part broad and rounded in outline, widest opposite legs II. Thoracic groove longitudinal.

**Eyes:** Eight. From above, both rows recurved. Ratios of the diameters of the eyes and of their distances apart: AM, 112; AL, 147; PM, 113; PL, 131; AM–AM, 113; AM–AL, 84; AM–PM, 97; PM–PM, 188; PM–PL, 135; L–L, 62; clypeus 148. Breadth of eye-group 0.60 mm.

**Chelicerae:** With boss. Strong and geniculate at the base with a posterior swelling also. Groove oblique and somewhat concave, especially the promargin. Ventral end of the promargin with two large conjoined teeth and one small one. Retromargin with a row of eight teeth decreasing in size from the base of the fang.

**Maxillae:** Rather long, slightly converging, pointed in front.

**Lip:** Free, as wide as long and rounded anteriorly. About half the length of the maxillae.

**Sternum:** Length 0.89 mm, breadth 0.94 mm. Convex, almost circular but truncated anteriorly.

**Palp:** Tibia with a large rounded distally directed lobe on the retrolateral side and a very large pointed process on the prolateral side, curving dorsally. Cymbium with a rounded swollen body and slender distal extremity. As in Figure 2.

<table>
<thead>
<tr>
<th>Legs</th>
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<th>II</th>
<th>III</th>
<th>Palp</th>
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<td>3.41</td>
<td>3.38</td>
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<table>
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<tr>
<th>Femur</th>
<th>Tibia</th>
<th>Metatarsus</th>
<th>Tarsus</th>
<th>Total</th>
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<tbody>
<tr>
<td>Palp</td>
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<td>1.07</td>
<td>....</td>
<td>0.82</td>
</tr>
<tr>
<td>I</td>
<td>1.75</td>
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<tr>
<td>II</td>
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<td>1.57</td>
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<tr>
<td>III</td>
<td>1.59</td>
<td>1.73</td>
<td>1.36</td>
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<tr>
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<td>2.29</td>
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<table>
<thead>
<tr>
<th>Tibial Index I</th>
<th>Tibial Index IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>14.5</td>
<td>10.8</td>
</tr>
</tbody>
</table>

Legs slender and with slender spines. Three claws, the dorsal similar with 12 long pectinations, the ventral with three small ones. Tarsi

Fig. 2. *Swainsia armata*. Ventral, dorsal, and retrolateral views of the male palp.
and metatarsi with a single dorsal row of trichobothria increasing in length distally.

Abdomen: Length 1.78 mm, breadth 1.19 mm. Colulus a broad lobe. Anterior spinnerets narrow and cylindrical, posterior spinnerets conspicuously long and slender, twice the length of the anterior ones.

CLUBIONIDAE

Clubiona upoluensis n. sp.


Carapace: Length 3.33 mm, breadth 2.40 mm. Smooth oval.

Eyes: Eight, posterior row straight, anterior row slightly recurved. Ratios of the diameters of the eyes and of their distances apart: AM, 161; AL, 221; PM, 173; PL, 200; AM–AM, 222; AM–AL, 178; AM–PM, 218; PM–PM, 435; PM–PL, 342; L–L, 160; clypeus, 95. Breadth of eye-group, 1.15 mm.

Chelicerae: Promargin of the groove with three teeth, the smallest nearest the fang, the largest in the middle, the third prolonged proximally as a ridge. Retromargin with two small teeth, one opposite the small promarginal one, the other nearer to the fang.

Maxillae: Long, constricted in the middle, wide and rounded distally.

Lip: Little more than half the length of the maxillae.

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Fig. 3. Clubiona upoluensis. Ventral and retrolateral views of the male palp.
lateral teeth opposite to them, the one nearest the fang being the largest. A sharp retrolateral tooth close to the base of the fang.

**Maxillae:** Rounded and expanded distally, the median corner truncated.

**Lip:** Slightly more than half the length of the maxillae. Concave distally.

**Sternum:** Length 1.37 mm, breadth 0.94 mm. Convex.

**Palp:** Spines: femur, one dorsal and four distal; patella, three dorsal; tibia, two pairs prolateral-dorsal. Tibia with a long slender retrolateral apophysis, about half the length of the tarsus, with a short one ventral to its base. Details as in Figure 4.

<table>
<thead>
<tr>
<th>Legs:</th>
<th>IV</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>Palp</th>
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<tbody>
<tr>
<td></td>
<td>3.0</td>
<td>2.4</td>
<td>...</td>
<td>1.8</td>
<td>0.8</td>
</tr>
</tbody>
</table>

| Patella and Tibia Metatarsus Tarsus Total |
|-----|-----|-----|-----|------|
| Palp | 0.74 | 0.66 | ... | 0.68 | 2.08 |
| I    | 1.81 | 2.68 | 1.19 | 0.65 | 6.33 |
| II   | 1.90 | 2.66 | ... | ... | ... |
| III  | 1.42 | 1.71 | 1.11 | 0.42 | 4.66 |
| IV   | 2.28 | 2.61 | 2.21 | 0.65 | 7.75 |

Tibial Index I 10.3 Tibial Index IV 8.5

Scopulae on tarsi, metatarsi and very slightly on tibiae I and II. Legs I and II have two pairs of spines on the tibiae, and three dorsal and one prolateral-distal spine on the femora.

**Abdomen:** Length 2.94 mm, breadth 1.37 mm. Stout bristles anterodorsally and a few above the spinnerets.

Differs from *C. alveolata* in the large tibial apophysis on the palp and the absence of hairs on the chelicerae. The ridge on the chelicerae is much smaller and more oblique than that of *C. samoensis*, whose chelicerae are also hairy.

**SALTICIDAE**

**Flacilla kraussi** n. sp.

**Male:** Aitutaki. Collected by N. L. H. Krauss in 1960. Length 4.79 mm. Carapace brown, darker round the edge and especially in the ocular area where the eyes are surrounded by black. Chelicerae, maxillae, lip, and legs I, dark brown. Palps, remaining legs, sternum, and abdomen pale brown. The dorsal surface of the abdomen with a darker ill-defined pattern consisting of a dark mark over the heart, anterior dorsolateral parches and posteriorly three transverse bands somewhat interrupted and irregular near the middle line.

**Carapace:** Length 1.95 mm, breadth 1.37 mm. Flat and rectangular in appearance. Anteriorly directed hairs around the eyes and flattened pale ones within the ocular quadrangle.

**Eyes:** Anterior row recurved. Ratios of the diameters of the eyes and of their distances apart: AM, 157; AL, 62; PM, 40; PL, 74; AM–AM, 18; AM–AL, 39; AL–PM, 126; PM–PL, 102; PL–PL, 445. AM in contact with the margin of the carapace. Ratios of the dimensions of the ocular quadrangle, including the eyes: AL–AL, 517; AL–PL, 388; PL–PL, 545.

**Chelicerae:** Small, with oblique groove. On the ventral promargin are two teeth, the one nearer to the fang being the larger. One retro-marginal tooth opposite to this and of equal size.

**Maxillae:** Long.

**Lip:** More than half the length of the maxillae, narrow, rounded anteriorly.

**Sternum:** Length 0.95 mm, breadth 0.55 mm. Convex, narrow anteriorly between the large coxae I and with a slender posterior point between coxae IV.

**Palp:** Well-developed tibial apophysis. As in Figure 5.
Leg I very large and stout, tarsi and metatarsi being much narrower. All joints except the tarsi with a small number of long outstanding hairs. Metatarsus I with a short stout prolateral-ventral spine at the distal end, and a small retrolateral-ventral one also. There is also a small prolateral-ventral spine about the middle of metatarsus I. Tibia I with a short stout prolateral-ventral spine a short distance from the distal end. There is a smaller ventral spine close to it and a minute one about one-third of the length of the tibia from the proximal end. No other spines on leg I, and those on the other legs slender, not very numerous and of the usual type. No scopulæ.

**Abdomen:** Length 2.69 mm, breadth 1.42 mm. Truncated in front, narrow behind. This specimen is doubtfully placed in the genus *Flacilla.*

**Mollicia pusilla* Strand**

A specimen collected at Amouli, Tutuila, Samoa, by E. C. Zimmerman viii–2–40 is attributed to this species described from Tahiti.

**MALE:** Length 3.85 mm. Chestnut, paler in the ocular area with an oval pale mark behind. Black around the eyes. Remainder pale brown, the abdomen with two poorly defined dorso-lateral darker bands.

**Carapace:** Length 1.94 mm, breadth 1.46 mm. Slightly convex in the ocular area, sloping steeply down behind. General impression high and short.

**Eyes:** Ratios of the diameters of the eyes and of their distances apart: AM, 228; AL, 143; PM, 27; PL, 113; AM–AM, 18; AM–AL, 25; AL–PM, 165; PM–PL, 103; PL–PL, 535; clypeus, 45. Ratios of the dimensions of the ocular quadrangle, including the eyes: AL–AL, 734; AL–PL, 482; PL–PL, 685. From above anterior row of eyes recurved. Breadth of eye-group 1.45 mm.

**Chelicerae:** Short and slightly swollen, fang short. Two teeth on the promargin of the groove and one larger one on the retromargin.

**Maxillae:** Broad and semicircular distally. **Lip:** Lozenge-shaped, about half the length of the maxillae.

**Sternum:** Length 0.87 mm, breadth 0.69 mm. Convex.

**Palp:** As in Figure 6.
All parts of the legs, except the tarsi, with spines including dorsal ones on tibia IV. Tarsi without scopulæ.

Abdomen: Length 1.87 mm, breadth 1.17 mm.

**Rarahu nitida** Berland

This genus and species were described by Berland (1929) from a single male from Malololelei, Upolu, Samoa. In the Otago Museum collection are four females and one male collected from moss in the rain forest at Afiamalu, very close to Malololelei. The male is smaller than Berland’s specimen and differs in color and in slight details, but it seems to belong to the same species. Its measurements and brief description are given here for comparison with those of the female.

**Male:** Length 1.90 mm. General color pale brown, the margin of the carapace dark, the ocular area almost black, the abdomen with a broad anterior transverse band followed by four narrow ones. This differs from Berland’s specimen, which was dark brown with lighter parts on the legs.

**Carapace:** Length 1.02 mm, breadth 0.63 mm.

**Eyes:** Ratios of the diameters of the eyes and of their distances apart: AM, 118; AL, 61; PM, 27; PL, 71; AL–PM, 100; PM–PL, 92; PM–PL, 273. Anterior eyes in contact, row strongly recurved. This is essentially as described by Berland.

**Palp:** As in Figure 7 and as figured by Berland.

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Tibial Index I 4.9  Tibial Index IV 5.8

Details of legs as described by Berland.

**Abdomen:** Length 0.85 mm, breadth 0.55 mm. The chitinous plates above and below, mentioned by Berland, are scarcely perceptible.

**Female Allotype:** Length 2.34 mm. Color as in male.

**Carapace:** Length 1.25 mm, breadth 0.76 mm. As in male.

**Eyes:** Ratios of the diameters of the eyes and of their distances apart: AM, 134; AL, 95; PM, 33; PL, 80; AL–PM, 132; PM–PL, 105; PL–PL, 330. Anterior eyes in contact.

**Chelicerae, maxillae, and lip:** As in male.

**Sternum:** Length 0.52 mm, breadth 0.39 mm.

### Legs:

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**Fig. 7. Rarahu nitida. Ventral and retrolateral views of the male palp.**
**Abdomen:** Length 1.18 mm, breadth 0.87 mm. Spinnerets terminal. No noticeable chitinous plates. Epigynum as in Figure 8.

**Trite longipalpis** Marples

**FEMALE ALLOTYPE:** Afiamalu, Upolu, Samoa. 2,200’, collected by E. C. Zimmerman vi–14–40. Length 7.72 mm. Color similar to male.

**Carapace:** Length 3.77 mm, breadth 2.85 mm.

**Eyes:** Ratios of the diameters of the eyes and of their distances apart: AM, 221; AL, 125; PM, 23; PL, 118; AM–AM, 27; AM–AL, 45; AL–PM, 150; PM–PM, 654; PM–PL, 144; PL–PL, 635. Breadth of eye-group 2.22 mm.

**Chelicerae:** Simpler and straighter than those of the male. Promargin of the groove with two teeth as in the male. Retromargin with five teeth, the largest nearest to the fang and not separated from it by a concavity. Fang without the flange present in the male.

**Maxillae and lip:** As in male, but the pit in the maxilla shallower.

**Sternum:** Length 1.59 mm, breadth 0.89 mm.

**Palp:** Long. Patella, tibia, and tarsus flattened dorsally, where they are somewhat darker in color and fringed with light hairs.

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**Abdomen:** Length 4.41 mm, breadth 2.18 mm. Epigynum as in Figure 9.

**MALE:** In the males from Samoa the carapace, mouthparts, palps, and leg I are much paler chestnut-colored than in the type from Tonga. They correspond, however, in structure. A correction to the measurements of the type are the tibial indices, which should be 8.8 and 7.2.

**Salticid**

A single mature male from Jarvis Island does not seem to belong to any species known from the Pacific area. It almost certainly must have been accidentally introduced by man and a few details and figures of the palps are given in the hope that it may be recognized.

**MALE:** Length 4.9 mm. General color dark chestnut with very little abdominal pattern. Carapace broad and high. Chelicerae with two proteral teeth, the nearer the fang being the larger, and one retrolateral tooth deeply divided

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into two equal cusps. Palps long and slender with a small tibial apophysis and short embolus, as in Figure 10. Very long thin white hairs along the prolateral side of the tibia and to a lesser extent on the patella.

**THERIDIIDAE**

*Theridion adamsoni* Berland

**MALE ALLOTYPE:** Taparatapo, Upolu, Samoa. Collected by E. C. Zimmerman, 19/7/40. Female described from Tahiti. Length 2.71 mm. Carapace, sternum, legs, and mouthparts light brown. Legs with faint annulations, strongest on IV, scarcely perceptible on I. Abdomen pale greyish brown, the upper surface with stout bristles each arising from a conspicuous dark base. Posterior half of dorsal surface with pairs of irregular dark marks extending back as far as the spinnerets. Single pair of dark marks near the anterior end.

**Carapace:** Length 1.31 mm, breadth 1.09 mm. Groove longitudinal. Upper surface sloping up steeply to the ocular area.

**Eyes:** Eight. AM dark. From in front the anterior row straight, from above the posterior row straight. Ratios of the diameters of the eyes and of their distances apart: AM, 200; AL, 131; PM, 142; PL, 129; AM–AM, 128; AM–AL, 87; AM–PM, 145; PM–PM, 151; PM–PL, 130; L–L, 18; clypeus, 264. Breadth of eye-group 0.62 mm.

**Chelicerae:** Long and tapering, groove unarmed and very oblique.

![Figure 10. Unidentified salticid. Ventral and retrolateral views of the male palp.](image)

**EPEIRIDAE**

*Epeira pogisa* Marples

A single female collected by E. C. Zimmerman, Afona Trail, Tutuila, Samoa, at 200' on 1/8/40, is doubtfully assigned to this species. The epigynum and cheliceral teeth are similar. The present specimen has a length of 9.5 mm compared with 5.28 mm for the type, and the abdomen, instead of being dark, is pale with a dark trident marking anteriorly, the central branch over the heart, the lateral ones continued...
irregularly back to meet behind. A band of oblique dark marks on each side.

**SUMMARY**

Additions are made to the lists of spiders known from various Pacific islands, and five new species and one new genus are erected: *Tetrablemma samoensis*, Tetrablemmidae from Samoa; *Clubiona upoluensis* and *C. zimmermani*, Clubionidae, from Samoa; *Flacilla kraussi*, Salticidae, from Aitutaki; *Swainsia armata* gen. et sp. nov., Agelenidae, from Swains Island.

**REFERENCES**


Ciguatera and Other Marine Poisoning in the Gilbert Islands¹

M. J. Cooper²

Among the animals that live in the sea are many that may be poisonous to eat; these animals include fish, sharks, crabs, molluscs, and turtles. Of all marine animals the most important are fish, which are for so many people an essential source of food. There are a number of different ways in which teleost fish may be poisonous. Some fish are naturally poisonous; others for instance are always toxic. Some species of fish can be poisonous at certain seasons; in Fiji there is a species of sardine which may be deadly poisonous in the later months of the year. A third type of poisoning is found where some fish are poisonous to eat when they are caught on certain reefs or parts of a reef, and yet when caught on other reefs of the same species, are perfectly safe to eat. This type of poisoning, known as ciguatera, is common throughout the tropical Pacific, usually on oceanic islands and isolated reefs.

Ciguatera is not, as many people think, a recent development. Captain Cook, in the journal of his second voyage to the Pacific in 1772–1775, relates how all of his officers who ate "two red-dish fish, about the size of bream and not unlike them" were poisoned and the pigs, that were given the offal, died. These fish were taken in the New Hebrides, and Cook refers to an earlier record of poisonous fish in those waters when he remarks that these redfish must be the same kind as those mentioned by Quiros, and called by him "pargos." Pedro de Quiros was in the New Hebrides in 1606. However, prior to World War II there were few reports of ciguatera poisoning in the Pacific; cases of poisoning did occur, but unless a stranger to the Pacific was involved little notice was taken. During and after World War II attention was drawn to the problem, as there were many more people in the Pacific who were poisoned by supposedly good food fish, often in areas where toxic fish had been previously unknown.

Although the symptoms of ciguatera poisoning, the species of fish likely to cause it, and many of the areas harboring toxic species have been recorded, several aspects of the problem still remain to be solved. In spite of recent research into ciguatera poisoning an antidote to the poison, a field test for distinguishing a toxic fish from a nontoxic one, the true nature of the toxin, and the cause of the development of ciguatera among fishes have not yet been discovered.

This paper is a review of the history and location of ciguatera poisoning in the Gilbert Archipelago and of the various Gilbertese beliefs about marine poisoning, together with identifications of the species considered toxic by the Gilbertese, and some of the author's opinions on the development, cause, and spread of toxicity.

The Gilbert Islands are a group of 16 atolls lying north and south of the equator; latitude 5° N passes through the most northerly island and latitude 3° S passes a few miles south of the most southerly island. The group lies between longitude 172° and 173° E of Greenwich. From north to south the 16 atolls are Makin, Butaritari, Marakei, Abaiang, Tarawa, Maiana, Abemama, Kuria, Arunuka, Nonouti, Tabiteuea, Beru, Nikunau, Onotoa, Tamana, and Arorae. Atolls are of two distinct kinds, lagoon islands and reef islands. A simple lagoon island consists of a lagoon, a body of fairly shallow water set off from the ocean, according to tradition, by a ring of small islets; in fact, the islets are usually in a chain lying on the weather side of the lagoon, with submerged barrier reefs on the lee side. A simple reef island is a small island with a fringing reef round it and no enclosed body of water. Many islands appear to be a mixture of both types. The total land area was estimated

¹ Contribution No. 214, Hawaii Marine Laboratory, University of Hawaii. Manuscript received September 24, 1963.
² Research Associate, Hawaii Marine Laboratory, University of Hawaii. (Home address: 28 Statham Street, Laucala Bay, Suva, Fiji.) Study in part supported by National Institutes of Health Contract SA-43-ph-3741.
by Dr. Rene Catala at 114 square miles. The population in 1947, the time of the last census, was 27,000; in 1958 the Gilbertese population was estimated to be 32,652 (Doran, 1960).

The information presented here was collected during the period 1953–1962 while the author was resident in the Gilbert and Ellice Islands Colony with her husband, who was an administrative officer with the Gilbert and Ellice Islands Colony Government. Residence was maintained for varying periods of time on Tarawa, Christmas Island (in the Line Islands), and Ocean Island; personal visits were made to all the Line and Phoenix islands, including Washington Island, and to almost all of those in the Gilbert group. During this time the author learned the Gilbertese language, which permitted her to gather information directly from the islanders.

In the course of a study of the scientific equivalents of the Gilbertese names for fish it was found that while some names would encompass all members of a whole family of fish, other names were restricted to a single species, and some names defined the development stages of a generic group. Through the initial study of Gilbertese names for fish, the author became interested in Gilbertese traditions and customs associated with fish, and finally in an investigation of fish toxicity in the archipelago.

The intimate association of the Gilbertese with the sea, almost their only source of dietary protein and fat, makes them reliable givers of factual information about fish poisoning. This dependence upon the sea means that every adult member of a community must have a basic knowledge about the reefs and the fish species around his island, particularly in the area of his village. Although in recent years the traditional dependence on fish as a major source of food has been lessened to some extent by introduction of imported foodstuffs, the detailed knowledge of environment has been preserved and is still known by the elders of the Gilbertese community who are the traditional custodians of natural lore. These "old men"—the term in Gilbertese is traditionally one of respect—have proved to be the most fruitful source of information when dealing with the history of fish toxicity. Younger men, active fishermen, have provided information on the species caught and the areas fished.

Due to the restricted nature of the Gilbertese diet, there are very marked preferences for certain species of fish. Fish considered to be very fatty or greasy are greatly sought after, because the Gilbertese at times develop a craving for animal fats. These sought-after species include Latianus bohar, Lethrinus variegatus, Acanthurus xanthopterus, Epinephelus fascoguttatus, Cephalopholis miniatus, Myripristis spp., Chanos chanos, and Muraenidae spp. The larger these fish, the more tasty they are considered to be. Some of these species have been found to be toxic, even dangerously so, in certain areas in the Gilberts. But even if a species is known to be toxic, there comes a time when the Gilbertese find it impossible to resist the temptation of a good fatty meal. This craving for animal fats is not restricted to the Gilbertese. Harry (1955) relates that the islanders of Raroia Aroll, in the Tuamotus, were unable to resist eating certain species of fat fish even when they knew that these species were toxic, and that as a result there were frequent cases of poisoning. Population pressure, together with particular food preferences, forces the Gilbertese to continue sampling a known toxic area. On account of this, a fairly accurate picture of the evolution of toxicity in an area may be obtained.

Considerable information was collected from Gilbertese visiting Tarawa, from assistant medical officers (graduates of the Fiji School of Medicine), and from officers and crews of the various ships operating in the colony. This information was later checked by the author, who was able to visit all the "toxic islands" with the exception of Tabiteuea and Arunuka, and by her husband, whose duties took him to all the Gilbert Islands. A special visit was made by the author to Marakei to obtain a more detailed picture of a toxic area than was possible when surveying the group as a whole.

ACKNOWLEDGMENTS

It is impossible to list by name all the very many people who have helped me and given me the information contained in this paper, but I should like to express my thanks to all of them. In particular I should like to thank the staff of the Colony Medical Department; Captain E. V. Ward, acting marine superintendent, for infor-
mation on currents, anchorages, and wrecks; officers and crews of all the ships in the colony, especially the Co-operative Society vessels; members of all the missions working in the Gilberts; Mr. G. Palmer of the British Museum (Natural History), London, and Dr. D. W. Strasburg of the U. S. Bureau of Commercial Fisheries, Hawaii, for identifications of unrecorded species; and Dr. A. H. Banner and Dr. P. Helfrich of the Marine Laboratory of the University of Hawaii for advice in preparing this paper.

The population statistics were taken from the "Report on Tarawa Atoll," by E. Doran (1960); the land areas are taken from "Report on the Gilbert Islands: Some Aspects of Human Ecology," by Rene L. A. Catala (1957). The rainfall figures were kindly given me by the New Zealand Meteorological Service, Laucala Bay, Suva. The maps, except that of Onotoa, are adapted from admiralty charts. The Fiji Government Printer gave great assistance in preparing the maps of Nikunau and Tabiteuea. The map of Onotoa was adapted from P. E. Cloud's map, based on aerial surveys (Atoll Research Bulletin 12, 1952).

Above all, the greatest acknowledgment and thanks are due to the many Gilbertese old men and women, fishermen, and the "general public," who patiently discussed for endless hours just "fish."

SYMPTOMS OF CIGUATERA POISONING IN THE GILBERTS

Ciguatera poisoning is regarded as an occupational hazard by the Gilbertese, especially by those who have lived all their lives in a toxic area. As a result, they consider ciguatera poisoning to be a "Gilbertese sickness," and they prefer to treat such sicknesses with their own remedies, as opposed to what they consider to be imported "European illnesses," for which European medicines are logically more suitable. Gilbertese do not normally go to a medical officer when poisoned by a fish, except on rare occasions when the victim is obviously on the point of death. Colony medical officers, therefore, do not see or record many cases of fish poisoning. Although mild cases of poisoning are very frequent on some islands, medical department records are relatively few.

The following sequence of symptoms of ciguatera poisoning has been collected from talks with several assistant medical officers and colony dressers (male nurses trained at the Colony Central Hospital, Tarawa). At first, several hours after eating a toxic fish, there is nausea, followed by vomiting and severe stomach pains, which may be accompanied by diarrhea and fever. There is tingling of the arms and legs followed by numbness and a heaviness of the limbs, which may lead to complete loss of coordination or even to paralysis. The sense of balance is lost. In severe cases there may be great thirst. Intense itchiness is followed by peeling of the skin. Finally, in fatal cases the victim lapses into coma and dies.

The following case histories were taken from the assistant medical officer stationed on Betio, Tarawa. He, his wife, mother-in-law, and two teenage boys were poisoned in March, 1962. He caught a small Lutianus bohar on the Betio lagoon reef. The fish was cooked and eaten on his return home, but no symptoms of poisoning appeared until 12 hr later. The five people involved ate varying amounts of the fish and had different symptoms.

The assistant medical officer and his wife are only a little of the fish. His symptoms, which appeared about 10 PM, were nausea but no vomiting; his legs tingled and then felt numb; next morning the cement floor felt like ice to his bare feet and he was "very shivery" in the wind, but far too hot out of it. He managed to work for half the day, but then he felt too ill so went to bed. Next day he was better, the symptoms had all gone, but on the third day the tingling sensation in his legs returned and persisted for several days. His wife suffered nausea, vomiting all night, and a severe stomach-ache. She stayed in bed the next morning and complained of numbness in her arms and legs all day. She recovered by the second day, except for a shivery feeling and an intensified tingling in her legs every time she put her hands in water. These feelings persisted for about a week.

The old woman, the mother-in-law, ate more fish than the preceding two. She suffered from nausea, vomiting, and a severe stomach-ache all night. Next day and the day after, the vomiting and stomach-ache continued; she complained that she could not walk, her legs felt heavy, and
she remained lying on her mat. By the fourth
day she could walk again, but she vomited and
complained that her legs felt tingly for a week,
by which time she was well enough to travel to
another part of the island where she considered
she could get more expert treatment. It is pos-
sible that her vomiting was aggravated by her
own home-made medicines.

One of the boys ate but little of the fish; he
suffered from nausea during the night, and the
next morning his legs tingled but he was able
to go to work. The other boy finished the fish,
and in doing so ate far more than the others.
He was taken ill about 2 hr before the rest of
the family, at about eight o’clock, with nausea,
vomiting, severe stomach-ache, and a fever of
102 F. The assistant medical officer did not re-
alize that it was ciguatera poisoning until the
others became ill as well, so at first he treated
the boy with penicillin for appendicitis. The
boy vomited all night, as well as having acute
diarrhea and pain. The next day he was still ill,
with fever, nausea, vomiting, and diarrhea; he
lost his sense of balance, his legs were power-
less, and he remained on his bed. By the third
day he had completely recovered; he returned
to work and suffered no lingering symptoms or
after-effects.

The three adults were in agreement on cer-
tain symptoms; they all say that one of the first
signs, which at the time they did not realize was
the start of an attack of poisoning, was a funny
feeling in their noses, as if the air passages were
enlarged and they could breathe more freely.
They also agreed that the numbness in their legs
persisted for several days, and that water on
their skins caused shivery feelings, as well as
making their legs tingle again.

Another man who was poisoned by a Luti-
amus bohar, also in March, 1962, from the Betio,
Tarawa, toxic reef, said that he had nausea and
vomiting, but he complained that the most per-
sistent symptom was a feeling of numbness and
swelling of his lips and tongue. This sensation,
together with pins and needles in his legs, per-
sisted for about 10 days.

It has not yet been proved whether the severe
poisoning caused by large Muraenidae is true
ciguatera or is caused by a different, although
perhaps allied, toxin (Banner et al., 1960; Hel-
frich, 1961; Bouver et al., 1962). The Gilbertese
consider it to be ciguatera poisoning but very
much more severe than that from other fishes.
They say that moray eels grow large, have voro-
cious appetites, and are able to eat so many
smaller toxic fish that they become deadly from
the stored toxin. It has been proved that cigua-
tera toxin is passed along the food chain, at
least for toxic Latiumus bohar, which when fed
to a previously nontoxic Acanthurus xanthop-
terus Cuvier and Valenciennes, made the flesh
of the latter toxic (Helfrich and Banner, 1963).
In the Gilberts large moray eels may be deadly
poisonous but only when caught in an area in
which other species of fish are toxic. Outside
these areas large moray eels are a popular food
fish (see section on Nonouti). In 1961 two men
died after eating part of a large moray eel
cought on the Betio, Tarawa, toxic reef. The eel
was cooked in the usual manner, without gut-
ting or cleaning, and the family went to the
cinema without eating any of it. While they
were away two men, an old man and a young
one, ate part of this eel. When the family re-
turned from the cinema they found both men
very ill, with violent vomiting and severe stom-
ach-ache. They were both taken to the Betio
hospital, in charge of the assistant medical offi-
cer, where the old man lapsed into a coma and
died at 2 AM the same night. The younger man
lived for a week, but the only symptoms remem-
bered by the assistant medical officer were that
he suffered intense itchiness, that his skin peed
away, and that finally he went into a coma and
died.

The following history was supplied by an as-
istant administrative officer who was poisoned
by an eel on Canton Island, in the Phoenix
Islands, in 1947. The eel, a big, black moray,
was caught in the lagoon and cooked and eaten
by six men. True to normal practice, it was not
gutted before being cooked. Of the six men who
ate the eel, only this one man was poisoned; the
others were completely unaffected. He was a
newcomer to Canton Island and was given the
choicest part of the eel, the fatty part from the
belly, whereas the others ate only the meat.
About half an hour after eating the eel, he be-
gan to feel very ill. At first he felt very cold in
the wind, so he moved out of it, and then felt
far too hot. Then he felt as if he were standing
on the bows of a ship in a rolling sea; this was
followed by a severe pain high in his stomach, accompanied by violent vomiting and diarrhea. He lost his sense of balance, his legs became powerless, and he just lay on his bed, suffering from acute pain in his stomach for a week. After this time the pain in his stomach eased, and he felt that perhaps he was not going to die. During the second week, although he suffered from intense itchiness, he began to feel much better and slowly regained his sense of balance. When he left his bed, he said, he almost had to relearn to walk. By the third week he was very much better, the itchiness finally having subsided with the flaking away of the skin from all over his body. This was the first time that this man had been poisoned, and he thought that it was because he was a newcomer to the island and had not had time to build up an immunity to the poison. The other five men, who ate the eel with him, had been living on Canton Island for some months, and considered that they had become partly immune to toxic fish during the time they had lived there. At that time, 1947, mild cases of ciguatera poisoning on Canton Island were not infrequent.

SOME GILBERTSE OPINIONS ABOUT CIGUATERA POISONING

Gilbertese opinions as to the cause of toxicity in fishes vary from island to island, and even between individuals. On Abemama, Nonouti, Tabiteuea, Onotoa, Beru, and Nukunau the islanders say that the fish have been toxic since a vessel was wrecked on the reef which is toxic at the present time, and blame the wrecks for the toxicity. On Tarawa the war with its resulting bombs, increase in shipping and in rubbish of various sorts dumped in the sea, is blamed for the violent increase in toxicity which began in about 1944. On Butaritari the increase in shipping and above all the rubbish dumped by the ships during the war is thought to have caused the poisoning there. All these islanders agree with Randall (1958), who found that on many islands wrecks were cited as the location of a toxic reef, and that rubbish dumped in the sea was often blamed for toxicity. Randall's hypothesis (1958) that toxicity may be caused by an alga that is the first alga to grow on a new substrate appears at first sight to be borne out by these Gilbertese statements. Wrecks, rubbish, and bomb craters all form new surfaces in the sea.

On Marakei, where toxicity suddenly appeared in 1946, the people blame a certain kind...
of alga. They say that their fish became toxic when this alga, which they had not seen before, began to grow on the now toxic reef. This alga, a blue-green *Schizothrix calciola* (Agardh) Gomont, grows on top of fine algae already growing on the reef (see section on Marakei). If this alga should be associated with toxic conditions, then this upholds Randall’s hypothesis (1958) that a fine, blue-green alga might be one of the basic causes of toxicity in fishes.

Many Gilbertese believe that certain people are immune to fish poison, and many even eat a toxic fish without harm. It is commonly said that there have been occasions when a family group has partaken of a large fish, and some of them have been severely poisoned, others not at all. However, neither the amount of fish nor the parts eaten are taken into consideration. A little-known belief which still lingers, especially among the older people, is that of family totem fishes. It is almost impossible to find out very much about this belief, as the Gilbertese are very loathe to talk about it. When discussing toxic fish with Gilbertese it should be realized that some older people still consider that certain families may be magically affected by certain species of fish.

Some Gilbertese think that the toxin is concentrated in the liver and guts of a fish, and that the viscera may be toxic when the flesh is not. This idea has been confirmed by Halstead and Bunker (1954). Other Gilbertese think that the toxin is concentrated in the blood, and that if the throat, guts, and large blood vessels are ripped from a still living *Lutjanus bohar* then that fish will be safe to eat. Banner *et al.* (1963) report that large specimens of *Lutjanus bohar* killed, filled, and frozen within half an hour of catching proved just as toxic as specimens kept for several hours after death. In spite of these ideas the Gilbertese do not usually bother to clean or gut carnivorous or small fish before cooking them. It is considered a waste of time to gut such fish as *Lutjanus bohar* or species of Muraenidae, as the Gilbertese say the guts are too small to bother about. It is customary, how-

ever, to clean and gut certain herbivorous fish such as *Mugil* spp. or *Kyphosus* sp.

Randall (1958) mentions that if a person who is recovering from an attack of ciguatera poisoning eats a reef fish he may experience a return of certain symptoms. He suggests that therefore the fish must contain toxin at a level sufficient to raise the toxin in the eater to the threshold level, but not sufficient to affect people who have not been recently poisoned. The Gilbertese people agree with this contention, but maintain that *all* fish will accentuate the neurologic symptoms in someone who is recovering from ciguatera poisoning, including species that have never been known to cause ciguatera, for instance flying fish.

The Gilbertese have the usual superstitions, proved false by Banner *et al.* (1963), that flies will never settle on a toxic fish, that a silver coin will turn black if it is cooked with a toxic fish, and, one superstition that appears to be peculiar to the Gilbertese, that grated coconut will turn bright green if baked inside a toxic fish. A more promising method of testing for a toxic fish occasionally practiced is to give one of the household cats a sizable piece of the suspect fish; if the cat is not ill in a few hours then the fish is not toxic. Another, probably more frequent "test," is for one of the family to act as guinea pig and eat some of the fish, although this is not considered foolproof because people react differently to the toxin. It is customary in toxic areas for old people to eat part of a large fish first. Later, if no symptoms of poisoning develop, the rest of the family will finish the fish. Experienced residents of toxic areas never allow their children to eat doubtful or uncommon fish until several hours, preferably a night, after it has been tried by the older members of the family.

This custom makes most puzzling the statement of Cavallo and Boudet (1961) and of Boudet *et al.* (1962) that ciguatera poisoning was a primary cause of infant mortality on Sydney Island (which the author visited in 1953). Sydney Island, in the Phoenix group, had no indigenous population prior to 1939, when it was settled by Gilbertese from the southern Gilberts, but had at times been worked for guano and copra. It is a most unfertile, drought-stricken atoll, the enclosed lagoon being too salty to sup-

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8 This alga, originally identified as *Plectonema terrebrans* (Borini and Flahaut) by Dr. Franci Drouet, has been assigned to the above species by Drouet. See Drouet, 1963, Ecophenes of *Schizothrix calciola*, Proc. Acad. Nat. Sci. Phila. 115(9):261–281.
port marine life. The whole population suffered severe protein deficiency, certainly due in large measure to the toxicity of the reef fish, which deprived the settlers of their natural source of animal protein. This general deficiency undoubtedly contributed to the infant mortality referred to above. The population of Sydney Island was evacuated to the Solomon Islands in 1958, the island having been found unsuitable for permanent settlement.

EVOLUTION OF TOXICITY IN THE GILBERTS

In the Gilbert Islands the evolution of toxicity of an island seems to follow a pattern. When toxicity first appears in an area only a few fish caught on a small patch of reef are found to be toxic. Within a few months many more fish become toxic, the toxicity is more severe, and the area where toxic fish are caught extends over some of the neighboring reefs. Within a short while (on Marakei about 2 years), nearly all species of reef-dwelling food fish and the roving carnivores that normally prey on them have become very poisonous. After some years have passed (on Marakei about 10), the toxicity begins to decrease. Small specimens of certain species become safe to eat; this improvement appears to start at the periphery of the toxic area and gradually works its way toward the center. The small fish of a species become safe to eat before the large ones of the same species, and the “safe” size becomes progressively larger; certain species become safe to eat before others. Eventually a stage is reached when all fish are being eaten, although sporadic cases of poisoning may still occur; at this stage the Gilbertese do not admit to having a toxic area on their island. It is not known whether a reef, once “poisoned,” ever becomes completely free of all toxic fish, but from accounts collected in the Gilberts it seems highly unlikely. The reefs appear to go into a “quiescent stage” when only an occasional large specimen of *Lutianus bohar*, *Promicrops lanceolatus* (specimens of 200–300 lb are sometimes landed, but they are very uncommon), or of Muraenidae may cause poisoning. The toxicity may flare up again, when the cycle will be repeated, and it appears that, until a valid field test for toxicity has been discovered, any fish caught in a known toxic area should be regarded with suspicion.

Unfortunately, due to the rapidity with which toxicity increases, it has not been possible to determine either the order in which species become toxic, or the first species to become toxic. However, at the height of toxicity most members of the following families or genera of fish are toxic: Acanthuridae, Balistidae, *Caranx* spp., Cirrhitidae, Holocentridae, Lethrinidae, Lutinidae, Mugilidae, Muraenidae, Scaridae, Serranidae, and Sphyraenidae; certain Mullidae may be toxic, and Labridae are also probably toxic, especially the larger ones, but information on this family is lacking, as the Gilbertese do not like their taste and prefer not to eat them.

As the toxicity declines, amongst the first fish that become safe to eat are the Holocentridae, Mugilidae, Cirrhitidae, Mullidae; the smaller species of grouper, *Epinephelus merra*, and allied species and *Cephalopholis* *urodelus*; small specimens of *Lutianus kasmira* and *L. vaigiensis*. On the other hand, some species remain toxic far longer than others, and among the ones that may remain toxic for many years are the following: *Acanthus xanthonotus*, *Ctenochaetus* spp., *Lutianus bohar*, *L. semincinctus*, *L. monostigma*, *Lethrinus variegatus*, *Epinephelus fuscoguttatus*, *Cephalopholis argus*, *C. mineatus*, *Variola louti*, *Plectropomus truncatus*, *Promicrops lanceolatus*, large *Caranx* spp., *Scarus* spp., large *Sphyraena* spp., large Muraenidae. *Monotaxis grandoculis* and *Gnathodonurus aureolinesatus* may also remain toxic, but these fish are not at all common. More and more species become safe to eat, but *C. mineatus* and *P. truncatus* are particularly slow, and *E. fuscoguttatus* even slower to improve. Finally the reefs enter the quiescent stage with only a few species, *Lutianus bohar*, *Promicrops lanceolatus*, and large Muraenidae, remaining potentially toxic. Large *Sphyraena* spp. have been found to remain very toxic in the vicinity of a toxic area, which in the Gilbert Islands may be almost anywhere in the colony.

WINDS AND CURRENTS

Throughout the Gilbert Islands the prevailing winds are the trade winds, blowing from the northeast, east, or southeast, with an occa-
sional stronger wind blowing from the north, usually after a period of calm. The prevailing ocean current is from the southeast; this current splits on coming to an atoll, sending a very strong current sweeping northward up the eastern side, with a much slacker current being deflected round the southern tip and up the western side. The effect of these winds and currents on the atolls is very marked. On the eastern weather sides there is constant heavy surf, while on the western lee sides calmer seas prevail. The "land" of the atolls is often more developed on the weather side than on the lee. This is especially noticeable on the larger lagoon islands, which have islets all along the weather sides, while the lee remains a mass of barrier reefs and shoal patches (as in Butaritari, Abaian, Tarawa, Maiana, and in particular Arunuka, Nonouti, and Tabiteuea). The main anchorages on all the atolls are on the western lee sides, and, in the case of lagoon islands, so are the main ship or boat channels into the lagoon.

Between the months of October and March, there may be gales from the west bringing heavy rain, but several years may pass without any westerly weather developing. In years of heavy or continual westerly winds, an ocean current may develop from the southwest; the Gilbertese believe that a change in current actually precedes a severe westerly gale. During this westerly weather, big seas develop on the usually calm western sides, heavy surf breaks on the barrier reefs and may even sweep right across the lagoons. These westerly gales do not normally last for more than a few days, but they may blow up without warning and may be the cause of an occasional shipwreck, even in these days of motor vessels (as at Nikunau, in 1955).

DETAILS OF TOXIC AREAS BY ISLANDS

Makin

Makin (in U. S. Sailing Directions, Little Makin or Makin Meang) is the most northerly of the Gilbert Islands. It is small, about 2.8 square miles in land area, with a population in 1958 of 1,130. Annual average rainfall is 107 inches, which makes it one of the wettest islands in the Gilberts. Toxic fish are unknown to the Makin people. Although Makin is classed as a reef island, it is unusual in having a shallow lagoon on the eastern side of the island. On the western or lee side there is a narrow fringing reef, which at low tide is covered by about 4 ft of water; this reef drops away suddenly and steeply to deep water. Vessels may anchor only during exceptionally calm weather, and even then they must moor onto the edge of the reef.

In 1956 this narrow lee reef was a mass of luxuriant corals, with deep sandy-bottomed surge channels lined with many species of corals and a large and varied population of fish. In November, 1961, this magnificent reef was found to be completely changed; the corals were broken and the surge channels full of the debris, and there were not nearly so many fish. Enquiries showed that this very extensive damage had been caused by an exceptionally severe gale accompanied by heavy seas just before Christmas, 1960. However, no toxic fish have yet appeared.

Butaritari

Butaritari (in U. S. Sailing Directions, Makin Atoll) is a large lagoon island in the northern Gilberts with a land area of some 4.5 square miles and a population in 1958 of 2,118. It is the wettest island in the group, with an annual average rainfall of 125 inches. Poisonous fish were first reported from Butaritari after World War II. Small ships may enter Butaritari lagoon, which is large, through a passage in the southwest by Kotabu Islet, but large ships must remain outside the lagoon. During the war many ships were anchored in the passage and there are wrecks both here and inside the lagoon. About 25 years ago the "St. George" was wrecked in the lagoon opposite Ukianang village; and nearby the "Alexis" was bombed and sunk by the Japanese a couple of years later. No toxicity followed the earlier wreck, nor appeared for some years after the latter. The remains of a crashed Catalina flying boat are still to be seen near Butaritari village.

The toxic area, which is in the southeastern part of the island (Fig. 1), extends from a point somewhere between Butaritari village and Ukianang village inside the lagoon southward through the South Channel by Kotabu, thence to the northwest along the fringing and barrier reefs both inside and outside the lagoon, as far as Tukurere Islet. This toxic area is composed of
Ciguatera in the Gilbert Islands—COOPER

**Fig. 1. Map of Butaritari Atoll.**

Sandy-bottomed lagoon opposite Ukianang village, deep water in the passage and anchorage outside, and living coral on the reefs.

Toxic fish were first reported from Butaritari about 1947–1948, and one of the earliest recorded cases of poisoning was the crew of the London Missionary Society’s vessel, “John Williams VI.” They caught a number of *Acanthurus xanthopterus* in the lagoon anchorage near Ukianang and, having had no previous experience of poisonous fish in Butaritari, they ate them. So many of the crew were poisoned that the vessel was unable to sail on time.

It is not known when the toxicity began to clear, but by 1956 there was already a great improvement in the condition of the reefs around Kotabu and Tukurere, where many species of fish were safe to eat. The toxicity took much longer to clear in the lagoon by Ukianang, the South Passage, and anchorage. The “John Williams VI” was again involved in a case of poisoning in 1956, but this time it was the European passengers and the captain of the ship who were very severely poisoned by an unidentified fish. The health of one of the passengers was so seriously affected that he was forced to resign from his work.

By 1959 all species of fish, with the exception of large *Lutjanus bohar* and the Muraenidae, were again being eaten in all toxic areas. By 1961 the Butaritari people claimed that they were free of poisonous fish, except for an occa-
sional specimen of Latianus bohar or an exceptionally large Promicrops lanceolatus or muraenid. However, early in 1962 the crew of the Sacred Hearts Mission ship, "St. Teretia," were poisoned by a barracuda (Sphyraena sp.) said to be about 3.5 ft long, which they had caught just outside the South Passage.

Marakei

Marakei is a small lagoon island in the northern Gilberts, lying some 60 miles to the northeast of Tarawa. The lagoon on Marakei is shallow, although full of fish, and is connected with the sea by only two passages, one on the southwest and one on the east. Both passages are very shallow and almost dry at low spring tides. There are seven villages; the largest is Rawanawi, in the northwest, which is also the Government Station where the medical dispensary and wireless station are situated. The Sacred Hearts Mission maintain a school at Rawanawi with two resident sisters and a resident parish priest, who were most helpful in this survey. There are two anchorages. The main one, for ships up to 150 tons and usable only during east to southerly winds, is off Rawanawi, where there is a boat passage through the fringing reef. This anchorage, although poor, is better than the more southerly one by the western lagoon entrance.

A more detailed survey of the toxic fish problem was made on Marakei than on the other islands. Marakei was chosen for a variety of reasons, the most important being that the start of the toxicity in 1946 was recent enough to be clearly remembered by the Marakei people and it was said that they knew which alga was responsible. The population on Marakei, about 1,790 in 1958, is rather large for the size of the island, which is a mere 3.94 square miles in land area, and it is one of the most densely populated islands in the group. Although Marakei is not one of the "drought" islands, the rainfall, averaging 79 inches a year, is not high, and the people are accustomed to finding a large proportion of their food from marine sources. Thus, when the reef fronting the main village, Rawanawi, the most heavily populated area of a heavily populated island, suddenly began producing toxic fish, the Marakei people were very hard hit by the loss of a good proportion of their food supply. They were forced by the need for protein food to keep sampling this reef, in an effort to find out just what they could eat without fear of poisoning and what was too toxic. In this way a good local knowledge of the behavior of the toxicity on this reef was gradually amassed by the older people of Marakei.

The toxic reef on Marakei is the fringing reef on the west or lee side of the island (Fig. 2), extending from the vicinity of the village of Rawanawi southward to the village of Buota.

The reef flat is narrow, with a few very shallow tide pools and small boulders. It is covered with fine algae and has a greenish aspect. Just below low water mark (see Fig. 3) where the reef never dries out, there is a belt of red-colored algae. Beyond this the reef drops a little and is covered with a dense growth of millipore coral. Between the stands of coral there are deep sandy-bottomed channels, whose sides are lined with a great variety of marine life. There are a few red algae between the branches of the millipore coral, and some brilliant green species on the floor and sides of the channels; in places there...
are dead coral pinnacles which reach almost to the surface, and the tops of these are covered with red algae. On the whole there was little algal growth below low water mark compared with the quantity on the reef flat. Beyond the belt of millipore coral, the reef face drops away fairly steeply to deep water. Many fish of different species were swimming above the coral, in the channels, and over the edge in the deeper water.

With the exception of tetraodonts and diodonts, toxic fish were unknown on Marakei prior to 1946. In that year a few fish caught on the reef near Rawanawi were found to be poisonous. By 1947 the affected area had spread southward along the reef as far as Buota, and many more fish were found to be toxic. By 1948 "all" fish were said to be toxic in some degree, when caught anywhere along this reef. Although the Gilbertese say "all" fish were poisonous, there were a few species, chiefly pelagic and oceanic, that were not affected, but it was not safe to eat most reef-dwelling or reef-hunting species. Many people were poisoned but few died, the only remembered deaths being the very old people and those already debilitated by disease. The Marakei people were forced to discontinue regular fishing on this reef, although they continued to collect octopus and other molluscs, none of which became toxic.

When toxic fish first appeared the Marakei people, having had no previous experience of toxicity, did not know what was making them ill. As more fish became toxic and the intoxications increased in severity, they realized that the fish had become poisonous; they were exceedingly angry and surprised, and immediately sought advice for a reason. At first many people blamed the medical dresser, saying that he had fouled the reef with old medicines and dressings. Even to this day the Marakei people are loath to go to any medical officer when poisoned by a fish.

Another idea, a usual one throughout the Gilberts in an unknown, unpleasant situation, was that someone was making black magic and had poisoned the reef. The blame for this was put on a Maiana man who had been imprisoned on Marakei by the Marakei Island magistrate. Some people blamed a party from Butaritari, who arrived on the Sacred Hearts Mission ship, "St. Teretia"; they brought with them some alumi-
num from the wrecked catalina in Butaritari lagoon. Aluminum is a highly prized metal in the Gilberts, used for making combs; when the visitors landed on Marakei they were swamped in the boat passage and the aluminum was swept onto the reef. Although an attempt was made to recover it, some metal remained on the reef, and this metal was thought to have affected the fish.

Other people blamed "the Americans," in particular "an American ship which came to Marakei, grounded on the reef at Rawanawi, and when the tide came in again, left." Enquiries at Tarawa showed that a United States L.S.T. had made several trips to Marakei from Tarawa sometime in 1945 or early 1946, to load thatch and wood for the new houses that were then being built on Tarawa. At that time toxic fish were a serious problem on Betio, Tarawa, and this L.S.T. was based on Betio.

The "old men," on this occasion a specially called-together group of experienced fishermen as well as the usual village elders, aver that when the poisoning started they noticed a change in the appearance of the reef flat fronting Rawanawi. They say it appeared to have tan-tan, a Gilbertese word used to describe lichens and also certain fungus diseases of the skin. This tan-tan was caused by a brown-colored alga of a kind which they had never seen before. The alga began as a small circular patch growing on top of existing algae, sand, or stones, and as the patches grew larger small pieces broke away from the center. As in tan-tan, or fungal skin infections, this alga first appeared as a few small patches but spread rapidly, and then gradually died away until only a few patches were left, as at the present time. The "old men" say that this alga first appeared at Rawanawi, and spread along the reef to Buota; they insist that they have never seen it on any other reef on Marakei. This alga was clearly seen on the reef flat at low tide; it is orange-brown in color and grows in circular patches which may be picked up together with the underlying algae. At high tide vast numbers of acanthurids graze along this reef, and appear to nibble at this alga in turn with the other fine varieties on the reef flat.

This alga has been identified by Dr. Drouet of the Philadelphia Academy of Science as the blue-green alga Schizothrix calciosa (Agardh) Gomont.

Unfortunately the "old men" could not remember which species of fish was first noticed to be toxic, but they agree that a specimen of Cephalopholis argus was responsible for one of the earliest cases of severe poisoning.

The "old men" said that they continued to eat Albula vulpes (Linnaeus), Chanos chanos, and one unidentified species of Mullidae, together with flying fish—luckily very plentiful off Marakei—tunas and other deep-sea fishes, and of course fish from the other reefs and the lagoon. Strangely enough, one of the most popular and safe species, provided it was cleaned correctly, was puffer fish.

By 1962, although there had been a great improvement in the condition of the reef, many fish were still toxic. The fish population had increased enormously during the many years' rest, and the Marakei people (whose population had also increased) were not able to resist the easy fishing and disregarded the risk of being poisoned. Cases of poisoning were frequent and became an accepted part of Rawanawi village life.

**Abaiang**

Abaiang (in U.S. Sailing Directions, Apaiaing Island) is a lagoon island just north of Tarawa, with a land area of 11 square miles, a population in 1958 of 3,234, and an annual average rainfall of 83 inches. There is a large lagoon, deep in parts, with an abundance of fish. Small vessels may enter the lagoon but larger ones must remain outside. There was no increase in shipping during the war.

Poisonous fish have never been reported from Abaiang; its people claim that this is entirely due to the efficacy of their magic.

**Tarawa**

Tarawa, the headquarters of the Colony Government, is a large lagoon island with a land area of 7.5 square miles. The population in 1958 was 6,982 Gilbertese and 141 expatriates; this includes some 1,500 on Betio, a small islet in the southwest. There is an annual average rainfall of 70 inches. Poisonous fish have been known on Tarawa for as long as anyone can remember. The lagoon is large, with extensive barrier reefs on the western side, in the midst of which is the main deep-water entrance to the
The anchorage, which is in the southwestern part of the lagoon, is an excellent deep-water anchorage and small ships may anchor very close to Betio. Tarawa, and in particular Betio, may be remembered as the site of the World War II Battle of Tarawa in 1943.

The toxic area on Tarawa (see Fig. 4) is situated in the southwestern part of the atoll. It is centered round the reef which runs north from the west end of Betio, and includes the deep water on the ocean side of the reef and the deep-water entrance which marks its northern extremity. Part of the reefs bordering the other side of the entrance, the ship passage inside the lagoon from the entrance to the anchorage and the parts of the lagoon bordering this passage, and the lagoon beach west of Betio are also toxic.

This toxic area includes deep water, a sub-
merged barrier reef, living coral, sandy areas, and a fringing reef flat that dries out at low-water springs. During normal weather conditions seas are slight on these reefs, but at times of westerly gales heavy surf develops. A very strong current sweeps out over the toxic area from the lagoon during the ebbing tide.

It is not known when poisonous fish first appeared on Tarawa. According to Gilbertese tradition, Betio was notorious for being the place where strangers dare not eat fish for fear of being poisoned. Among the old people the idea is held that toxic fish always have been, and always will be, found on this reef—it is part of the natural order of things. However the war, with the resultant increase in shipping, bombs, wrecks, rubbish, and surplus war material dumped on the reef, is blamed for the violent increase in toxicity in the late forties and early fifties.

There still remains about Betio much of the wreckage of the invasion of 1943, but these wrecks are not well correlated with the toxic areas. Thus landing craft left stranded, now rusted out and disintegrating, are present not only on the toxic reef flat but also on the edges of the inshore reefs all along the lagoon side of the island. Other war wreckage may be found in the deeper parts of the toxic section of the lagoon, but is also found in the nontoxic areas.

![Map of Abemama](image-url)
Finally, although there is a large quantity of ammunition and other materials to be found on the toxic reef flat, there is a considerably greater amount on other reefs which are not toxic. At various times from 1944 to 1963, coral heads have been blasted from the main lagoon entrance and passage to Betio, and from the seaplane alighting area near Bairiki; the former area is toxic, the latter is not.

There are several well-remembered cases of poisoning from before the war, mostly attributed to *te maneku*, large spotted grouper (probably *Epinephelus fuscoguttatus*) and red snapper (probably *Lutianus bohar*). However, the first recorded case was that of an elderly Australian shipmaster in 1944 (Halstead and Lively, 1954) who ate a red snapper. This is commonly thought to have been the start of the toxicity on Tarawa, whereas it was merely the first time it had been brought to the notice of the outside world. It was, however, the start of the resurgence of poisoning.

From 1944 onwards the toxicity increased rapidly, until nearly all the food fish caught in the toxic area were poisonous. The Betio people ceased to fish that area. In about 1956 a slow amelioration began, and by 1960 the reef was considered safe enough for fishing to be generally resumed. In 1961, although sporadic cases of poisoning still occurred, the reef was considered to be clear of toxic fish, and all species were being eaten. A few recorded cases of poisoning since 1958 are as follows:

1958 A Betio woman died after eating an 18-inch *Epinephelus fuscoguttatus*. I personally investigated this case, as the woman was the wife of a fisherman employed by me. This fisherman had brought this grouper to my house, where he was told it was a toxic fish and was sacked on the spot. He then took the fish home to his wife, who ate it and died.

1959 Several people ate a large *Lutianus bohar* and two of them were mildly poisoned.

1961 Two men died after eating a large moray eel. (See above, under Symptoms.)

1961 Two men were mildly poisoned by a *Lutianus bohar*.

1962 A man was mildly poisoned by a *Lutianus bohar*.

1962 The assistant medical officer stationed on Betio and his family were poisoned by a *Lutianus bohar*. (See above, under Symptoms.)

1962 Two children were mildly poisoned by an *Epinephelus fuscoguttatus*.

**Maiana**

Maiana is a lagoon island just south of Tarawa. There is a land area of about 10.2 square miles, a population in 1958 of 1,359, and an annual average rainfall of 62 inches. Maiana lagoon is fairly large but very shallow, navigable by the smaller colony vessels at high spring tides only. Toxic fish have not been reported from Maiana.

**Abemama**

Abemama (in U. S. Sailing Directions, Ape-mama) is a lagoon island in the central Gilberts. It is a fertile island, 6.5 square miles in land area, and has an annual average rainfall of 57 inches. The population in 1958 was 1,341, but settlers from the overpopulated southern islands have increased it. There is a large lagoon with two deep water entrances through the reefs on the western side. Toxic fish have been found in both these passages for many years. (See Fig. 5).

The northernmost toxic area is around the Western Passage; it comprises the passage itself, the reefs both inside and outside the lagoon around the point of "land" (in fact, a reef flat known as Te Tutongo) on the north side of the passage, and the reefs around the islet of Abatiku on the south side of the passage. A vessel owned by Burns Philip and Co. was wrecked on Te Tutongo about 1917, and the poisoning is said to date from this time. Parts of the engines of this vessel are still visible on Te Tutongo at low tide, and the Abemaman people think that some fish will remain toxic until all the ship’s remnants have disintegrated. The condition of the reefs around the islet of Abatiku began to improve about 1947; and in December, 1961, both there and in the passage, an occasional *Lutianus bohar* or *Epinephelus fuscoguttatus* were the only fish found to be poisonous. On the reefs around Te Tutongo some acanthurids were still poisonous, as well as the above species.

The southernmost toxic area comprises the South Passage and the reefs around the islet of
Ireef reported to extend 2 miles further west.

KURIA and ARANUKA

Kuria

Kuria is a reef island, 5 square miles in land area, in the central Gilberts, with a population of 541 in 1958; the annual average rainfall is 55 inches. There are two islets, joined and surrounded by extensive reefs. Toxic fish have not been reported from Kuria.

Arunuka

Arunuka is a lagoon island in the central Gilberts, with an annual average rainfall of 53 inches. The lagoon is full of coral heads and is not navigable except by launches. Ships must anchor by the entrance to the lagoon on the west side of the island. (See Fig. 6.)

The population of Arunuka, a mere 571 in 1958, is very small for the size of the island, which is nearly 6 square miles in land area. Many of these people are settlers from the overpopulated southern islands. These settlers do not
know the reefs around the island, nor the traditions associated with fish on Arunuka. This and the fact that the small population finds plenty of fish in the lagoon for all their needs, mean that there is a lack of local knowledge concerning the outside reefs. In fact, the present Arunukans maintain that there are no poisonous fish on the island. However, many people, all members of ships’ crews, have been poisoned at Arunuka; the fish have been caught either in or somewhere near the anchorage, or on the reefs on the north side of the anchorage by an uninhabited islet. It has not been possible to find out the exact positions of the reefs that are considered to be toxic, and those marked on the map of Arunuka are tentative only. It is definite, however, that toxic fish have not been found inside the lagoon.

It is not known when fish became toxic on Arunuka, but between 1929 and 1937 many species are reputed to have been dangerous to eat. Just before World War II two members of the crew of the Burns Philip vessel Moamoa ate a large Epinephelus fuscoguttatus which had (probably Epinephelus fuscoguttatus), and were severely poisoned. Another time, according to one old Arunukan, a whole village went out communal fishing and caught “over one hundred big grouper,” of which only one fish was poisonous, and the unlucky family who consumed it were very ill.

Despite the Arunukans’ ideas to the contrary, all the ships’ crews still consider that large Lutianus bohar, Epinephelus fuscoguttatus, and Muraenidae are toxic when caught in or near the anchorage. In January, 1962, the crew of the Co-operative vessel “Aratoba” were poisoned by a large Epinephelus fuscoguttatus which had been caught by the reefs on the north side of the anchorage.

Nonouti

Nonouti is a lagoon island in the southern Gilberts, with a land area of nearly 10 square miles and a population in 1958 of 2,143. There is an annual average rainfall of about 50 inches. Poisonous fish have been known on Nonouti for many years. Ships may enter Nonouti lagoon, which is large, north of Autaken reef (see Fig. 7), but the passage is not easy and many ships’ masters prefer to remain at anchor just south of Autaken reef and work the island by boat. The toxic area is around this southern anchorage and includes the neighboring reefs. There are no toxic fish inside the lagoon.

The “old men” of Nonouti told us that they could not remember a time when fish were not toxic on this reef—which memory probably dates back 50 years to 1910—but that they remember hearing that a vessel was wrecked there in 1890, and that this was the start of the poisoning in the area. The Gilbertese name for this area, Te Tamni (not on the Admiralty charts), was derived from the name of the wrecked ship. The Nonouti people are not quite certain which species are still toxic there because, from long-standing custom, they do not fish on those reefs. However, crews of all ships do fish in the anchorage, and they say that in 1948 and 1949 very many fish were toxic on these reefs and that by 1958 only a few species remained poisonous. In 1962 Lutianus bohar, all large Muraenidae, and any particularly large groupers (Serranidae) were the only fish they considered still remained toxic.

Eels are very plentiful on Nonouti, and a specialty of the island is dried eel. Eel traps are set in the deep water of the lagoon and boat passages. The large eels which are so caught are cut into pieces and dried in the sun. The resulting rather smelly, very greasy pieces of fish are sold for a remarkably high price to the Chinese on Nauru. The “old men” say that, as long as the eels are taken only from the lagoon and boat passages, they are not toxic, and that by customary law no Nonouti fisherman would dare to trap eels outside the lagoon.

Tabiteuea

Tabiteuea (in U. S. Sailing Directions, Tapi-teua), the largest of the Gilbert Islands, with a land area of 19 square miles, is a lagoon island in the south. The population in 1958 was 3,266, and the annual average rainfall is 47 inches. There is an extensive area of reefs and shoal patches lying to the west of the southern portion of Tabiteuea. These reefs are not shown on the Admiralty chart, as the survey of Tabiteuea is not yet completed. Somewhere among these reefs is a shoal patch known on Tabiteuea as Takoronga Inanon, which at times is large enough to be covered with a growth of Scævolæ frutescens, and at other times is a mere sandbank
awash at high tide. The reefs all around this islet harbor toxic fish, and the area is extensive enough to include the entrance channels into south Tabiteuea (see Fig. 8).

A vessel of some sort is said to have been wrecked on Takorongo about 1919, and the poisoning dates from that time. Although many fish remained very toxic for many years, occasional fishermen continued to visit the area because there were so very many fish there that the temptation was great enough to risk poisoning. Men who had dived there said that the ribs and keel of a vessel are to be seen near Takorongo, and that other remains are scattered over the area.

In 1958 many species still remained toxic off Tabiteuea, although the Tabiteueans considered that there were fewer than there had been. By 1962 still fewer species were considered toxic, but it was not possible to obtain details of which

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**Fig. 7. Map of Nonouti.**
species remained poisonous. In December, 1961, both the mate of the colony vessel "Moanaroi" and a passenger, Mr. H. R. Cooper (husband of the author), were mildly poisoned by an unidentified fish caught in the entrance passage to south Tabiteuea.

**Beru**

Beru is a lagoon island in the southern Gilberts, with a land area of 8.15 square miles. The population in 1958 was 1,968 and the annual average rainfall is 49 inches. Until recently, the headquarters of the Gilberts Mission of the London Missionary Society was located there. Toxic fish have been known on Beru for as long as anyone can remember. Ships cannot enter the lagoon, which is very shallow with extensive sandbanks at low tide and is considered to be silting up. (See Fig. 9.)

There are three anchorages on Beru, one in the south, off the village of Taboiaki, which was in use many years ago. In about 1936 a boat passage was blasted at Espiegle Anchorage in central Beru by the London Missionary Society and this became the main anchorage. The boat passage has gradually silted up, and the southern and northern anchorages have been used more than Espiegle Anchorage in recent years. It is around the southwestern anchorage that toxic fish are found, opposite the village of Taboiaki. This area is a leeward fringing reef and does not include any part of the lagoon.

The Beru people say that long ago a New Zealand ship was wrecked on this reef, and that the poisoning dates from that time. They say that at times many species may be toxic, at other times only a few, but that this variation appears to follow no rules. Beru is a dry, poor island and population pressure forces the people to continue to fish this reef in spite of the risk of severe poisoning.

The poisoning caused by toxic fish on Beru appears to be more severe than on other islands. The staff of the London Missionary Society report that cases of poisoning among their students—many of whom were from other islands—were often severe enough to cause paralysis. In the late thirties several people became ill after eating a *Lutianus bohar* and were taken to the London Missionary Society's headquarters, where two men died. (This is a well-remembered incident, as the victims were all Roman Catholics.) Other deaths are remembered and red snapper (probably *Lutianus bohar*), *te ingo*, is blamed for most of them.

In January, 1962, the Beru people said that there were far fewer fish toxic than in 1958,
and that they were eating everything except large Muraenidae and the uncommon, enormous Promicrops lanceolatus. However, they said that they were taking a risk, and that any specimen of Lutianus bohar, Epinephelus fuscoguttatus, or Cephalopholis mineatus could be poisonous.

Nikunau

Nikunau is a reef island in the southern Gilberts with a population in 1958 of 2,011 and a land area of about 7 square miles. Although the average annual rainfall on Nikunau is the same as Onotoa's, 44 inches, and differs only by a few inches from several other islands, it appears to be a much drier island and is subject to severe droughts. Poisonous fish have been known on Nikunau for a very long time.

The toxic area is on the western or lee side of the island (see Fig. 10), and stretches along the fringing reef from the village of Tabutoa in the north to the village of Manriki in the south. Between these two villages is the village of Rungata, the Government Station and main anchorage. There is a boat passage through the fringing reef in front of the village. The reef flat is alga-covered and there are luxuriant corals in the deeper water.

A vessel is said to have been wrecked on the reef by Rungata village at some time in the past, and the poisoning dates from that wreck. The Nikunau people say that the poisoning began at Rungata, but spread north and south along the reef. After a while it began to recede and the reefs near Manriki and Tabutoa have always produced fewer toxic fish than those in the center by Rungata. At one time very many species were toxic, but by January, 1962, all species, except large Muraenidae, were being eaten; the occasional large specimen of Lutianus bohar may still cause mild poisoning.

In 1955 the Sacred Hearts Mission ship, "St. Teretia II," driven on to the reef by a very local westerly current and wind, was wrecked opposite Rungata village. However, this accident appears to have made no difference to the toxicity of the reef.

Onotoa

Onotoa is a lagoon island in the southern Gilberts with a land area of 5.21 square miles and a population in 1958 of 1,542 people. It is another dry island subject to drought and having an average annual rainfall of 44 inches. Poisonous fish have been known on Onotoa for many years. The toxic reef is in northwest Onotoa, is known as Aontebeba (see Fig. 11), and is considerably smaller than other toxic areas in the Gilbert Islands. There are three anchorages outside the lagoon on Onotoa, and the toxic reef lies just to the north of the northernmost anchorage. A ship is said to have been wrecked on Aontebeba during a southwesterly gale, and the poisoning dates from that time. It has not been possible to discover when this wreck took place; it was, however, a very long time ago.

Onotoans say that at one time very many species of fish were toxic on Aontebeba, but that their numbers have declined and the reef has been considered to be clear of toxic fish for some years. However, Onotoans still will not eat large Muraenidae caught there and admit, though somewhat reluctantly, that the occasional large Lutianus bohar is still found to be mildly poisonous.

Tamana

Tamana is a very tiny reef island in the southern Gilberts; the land area is a mere 2 square
miles, the population in 1958 was 1,142, and the average annual rainfall is 48 inches. There is a poor anchorage on the western side of the island, opposite the only village. Toxic fish have never been reported from Tamana.

**Arorae**

Arorae is a small reef island and the most southerly of the Gilbert Islands. There was a population in 1958 of 1,551 and a land area of 5 square miles. There are three anchorages, all described as poor. Toxic fish have never been reported from Arorae, and both the Tamana and Arorae people are most indignant at the idea that either island could ever produce a toxic fish.

The fringing reefs on Arorae are wide, especially in the north and south. A ship is reputed to have been wrecked on the southernmost tip of Arorae, but there is no sign of any remains.

**Ocean Island**

Ocean Island, lying 160 miles west-southwest of Tarawa, is not in the Gilbert Archipelago although it is a part of the Gilbert and Ellice Islands Colony. Ocean Island is a higher island than the low atolls of the Gilberts, and has an annual average rainfall of 68 inches. It rises to 265 ft, and beyond the fringing reefs drops abruptly to great depths. The fringing reef is rather different from those of the atolls, being composed in places of much rougher rocks; there are steep cliffs of very sharp weathered rock and few sandy beaches. There are, as on the atolls, deep surge channels in the edges of the reefs. There are deep pools on the reef flat, joined by tunnels in the reef, and living corals grow luxuriantly in these more protected waters. There is a very large fish population, composed not only of reef dwellers, but also of oceanic and deepwater species.

Ocean Island has large deposits of phosphates which have been worked since the early 1900s. Phosphate-loading vessels tie to moorings laid in very deep water. There is an old boat harbor with a wide deep passage through the reef on the western side which was blasted out of the reef in 1904. Since then a large new harbor has been built on the southeastern side, entailing extensive blasting of the reef. There is much cement and iron work on the reef, both in use and in the process of disintegrating from the old and new cantilever piers.

All rubbish is thrown over a chute on these cliffs, to fall on the reef beneath; from there it is slowly washed away by high tides. Sewage is pumped out over the reef. The "Ocean Trader" was wrecked sometime ago on the southeast side, and was followed in 1952 by the "Kelvinbank," which went on the reef on top of the remains of the previous vessel. The wrecks are still there, slowly disintegrating. During normal trade winds, blowing from the northeast through southeast, there is heavy surf on the eastern side of the island, but westerly weather is apt to cause heavy seas to beat all round the coast.

In spite of all this reef damage extending back over 60 years, no poisonous fish have ever been reported from Ocean Island.

**Discussion**

Of the 16 islands in the Gilbert Island archipelago, 10 have toxic reefs where certain species of fish have been poisonous for varying lengths of time. These "toxic" islands are Tarawa, Abemama, Arunuka, Tabiteuea, Beru, Nonouti, and Onotoa, lagoon islands, and Nikunau, a reef island, on all of which some fish have been toxic for many years; on Butaritari and Marakei, toxic
fish have appeared only comparatively recently. The remaining six islands, Abaiang and Maiana, lagoon islands, Makin, Kuria, Tamana, and Aroae, reef islands, have no history of toxic fish.

The toxic area on all these islands is in the same relative position on the atoll; that is, each toxic area is on the sheltered lee side, either in the northwest, west, or southwest. This finding does not agree with Brown (1945), who reports that in the Bahamas the windward, exposed areas are more likely to be toxic than the leeward, sheltered ones. On a few islands part of the lagoon is toxic, but in no case is the toxicity confined to the lagoon; no non-navigable lagoon has any toxic reefs. Randall (1958) suggests that a body of water set off from the ocean by reefs may be more likely to contain toxic fish than more open water. In the Gilberts, although all the toxic reefs are in reasonably sheltered areas, there is a steady but not powerful ocean current, as well as currents caused by ebbing and flowing tides constantly washing over them.

The islands of the Gilberts vary from wet toxic Butaritari (125 inches) and dry toxic Nikunau (44 inches), to wet nontoxic Makin (107 inches) to dry nontoxic Tamana (48 inches). There is no island in the Gilberts with a fresh water stream, nor is the rainfall ever heavy enough to cause run-off.

Wrecks are often cited as the location and cause of a toxic area (Randall, 1958). In the Gilberts, on no less than seven toxic reefs out of eleven, wrecks are given as the reason for the start of the toxicity. Of these seven wrecks only one may still be seen (on northern Abemama); the rest are merely remembered. Within the last thirty years there have been five authenticated wrecks, two at Ocean Island, two at Butaritari, and one at Nikunau, none of which appear to have had any effect on the areas concerned. The Nikunau reef was already toxic when the wreck occurred, but the toxicity was not increased. The two wrecks at Butaritari occurred within a couple of years of each other, during the Pacific war, but the toxicity was not reported from Butaritari until some years later. It should be noted that all the wrecks referred to are in or very near anchorages or passages to navigable lagoons.

Again, heavy reef damage has been suggested as a possible factor in the chain of events leading to toxicity (Randall, 1958). Yet damage to the Makin lee fringing reef (by storm), to Beru lagoon reef (by blasting), and to Ocean Island reefs (by continual blasting and workings) produced no change in toxicity. Of particular interest is Beru, where the fringing reef downstream from the blasted area was already toxic. However, on Tarawa there was a resurgence of the toxicity following the Battle of Tarawa with its reef damage, wrecks, and heavy casualties on the reefs, all of which must have produced at least a temporary change in the ecology of the reef areas around Betio.

Vessels not only anchor in the usual cargo-working anchorages, as at Tarawa, Butaritari, Arunuka, Onoota, and south Nonouti, where all these anchorages are in toxic areas, but, as may not be generally realized, vessels planning to enter a lagoon often must first anchor outside, in the entrance, or even in the passage itself, to await the optimum angle of the sun's rays before navigating the unmarked channels through the reef patches. In these days of radar and depth indicators this approach is not so vital as it was a few years ago. It has been found that these anchorages at lagoon entrances and in reef passages are frequently toxic, as at Tarawa, Abemama, Butaritari, and Tabiteuea. Nonouti is an island with a very difficult entrance into the lagoon, and many ships' masters prefer to work the island from the southern anchorage (which is toxic), or to wait there before attempting to navigate the entrance which is to the north of Autaken reef. Nikunau and south Beru have rather poorer anchorages than the islands so far mentioned, but nevertheless vessels do anchor off these places to load cargo and, once again, these anchorages are toxic.

Fanning Island, often quoted in papers on ciguatera (Randall, 1958; Banner et al., 1960), is another example of an atoll where the anchorage is toxic. In fact P. F. D. Palmer is quoted by Randall (1958) as saying that the areas where fish were toxic were only where the ships anchored. Randall continues to say that in the Line Islands where toxic fish appeared large ships had previously been anchored. The toxic area on Palmyra is also near the channel entrance (Banner et al., 1960). The toxic area on Christmas Island in 1955–56 was in and around the anchorage by the main lagoon entrance; since that time it has extended southward a con-
Considerable distance (Helfrich, unpublished data).

It is of interest that, with the exception of Abaiang, islands which are free of toxicity have the worst anchorages and are islands where vessels must often drift while working cargo (for instance Makin, Kuria, Tamana, and Arorae). Marakei, another island with a very poor anchorage, is toxic, but it has been suggested that the cause of toxicity was an L.S.T. which was able to "land" on the reef. Abaiang, an island with excellent anchorages for small ships inside the lagoon, is near enough to Tarawa for vessels to time their arrival so that they may enter the lagoon at daylight without anchoring in the entrance. Larger vessels, infrequent at Abaiang, must drift off the island. Maiana, another non-toxic island very close to Tarawa, has a very shallow lagoon, navigable only by the smaller colony vessels (length about 50 ft) at high spring tides. All cargo and copra is worked on Maiana by these vessels or by larger vessels on the drift.

Washington Island, in the Line Islands, so often cited as one which is inexplicably free of toxic fish (Randall, 1958; Banner et al., 1960; Boucher et al., 1962), under normal conditions has no anchorage. Continual, heavy surf beats all around the atoll. Cargo, copra, and passengers must be moved in surf boats, while the vessel being loaded drifts some way off the island.

From evidence in the Gilbert and Ellice Islands Colony, it would appear that shipping may in some way be associated with the spread of toxicity. Allen (1953) discusses the large part played by ships in the world-wide distribution of a variety of marine invertebrates. He suggests that, as well as invertebrates, certain algae, in particular Enteromorpha intestinalis (Linné) and Ulva lactuca (Linné), may owe their almost universal distribution to ships. There is a minimum number of new organisms, he says, that must be introduced to start a new population, and concludes that in Australia harbors are the logical place for this to happen. In the Gilbert Islands there are no harbors, but merely anchorages; and it may be noted that all the most frequently used anchorages (lying outside lagoons) in the Gilbert Islands are toxic. Perhaps this means that there is a particular organism found in and around these anchorages which is not found elsewhere in the Gilbert Islands. If wrecks are indeed "the cause" of toxicity, perhaps the wrecked vessels were carrying this organism, which then spread along the reef.

OTHER TYPES OF POISONING

Sharks' Liver Poisoning

The liver from large sharks is thought to be potentially poisonous throughout the Gilberts, whether the shark is caught in a lagoon or in the ocean. The Gilbertese have a great liking for shark flesh, considering it more digestible than the flesh of other fish. In particular they like the liver; sometimes this is made into a kind of sausage, using the shark intestines as the casing. Not all large sharks have toxic livers; certain species are more likely to be toxic than others. According to the Gilbertese the most dangerous species are the tiger shark, Galeocero cuvieri (Lesueur), and the "white-tipped lagoon shark" (possibly Triakodon obesus [Ruppell]), but they say that any exceptionally large shark may have a toxic liver.

The different assistant medical officers consulted say that there appears to be no difference in the symptoms caused by sharks' liver poisoning and those caused by toxic teleost fishes; their list of symptoms for sharks' liver poisoning is the same as that described under ciguatera poisoning. However, the poisoning caused by toxic sharks' liver is extremely rapid and severe; the victims often become comatose after suffering from severe vomiting, stomach cramps, and diarrhea. There are no Gilbertese remedies for sharks' liver poisoning other than those given for ciguatera.

It has been considered that sharks' liver poisoning may be due to an excess of Vitamin A (Lonis, 1950). However, in 1949 samples of sharks' livers from the Gilberts were analyzed for Vitamin A content with a view to starting an industry. The report stated that there was insufficient Vitamin A to make commercial extraction worthwhile. The Vitamin A content of livers from several species of sharks from various areas in the tropical Pacific was also investigated by the U.S. Fish and Wildlife Service in 1949; none were found to contain enough to be used as a commercial source (unpublished report).

The traditions associated with sharks' liver poisoning vary slightly from island to island, but
inhabitants of all islands, with the exception of Abaiang, agree that the liver of large sharks can be very poisonous. The Abaiang people maintain that their magic prevents sharks from having toxic livers in the same way as it prevents their fish from producing ciguatera; they are not really believed by other islanders, who ridicule them, but not within their hearing. The Marakei people say that sharks caught at night are much more likely to have poisonous livers than those taken during the day. Arunukans, Abemaman, and Butaritarians say that a toxic liver is always longer than a nontoxic one and has one lobe doubled back underneath itself. Others say that a toxic liver is darker than a nontoxic one or has dark spots on it. There are the same superstitions as there are for toxic fish; i.e., flies will not settle on a toxic liver, a silver coin is blackened, or grated coconut turns green when cooked with a toxic liver.

Several people died on Beru in 1957 after eating some tiger shark liver; again in 1960 and 1961 people died on Tabiteuea, poisoned by liver from the same species.

Shark flesh has never been reported to be toxic in the Gilbert Islands.

**Poisoning by Tetradont and other Plectognath Fishes**

Puffer fishes, species of the family Tetraodontidae, are rather uncommon in the Gilberts, although on certain islands in other parts of the colony, particularly Fanning Island, they are very plentiful. Puffer fish poisoning is well known to the Gilbertese who, on the whole, do not especially like to eat these fish. Nevertheless, there are many people who do eat them; and they say that, provided the fish is skinned and gutted and the ovaries are removed immediately while the fish is still alive, the flesh will not be poisonous. Sometimes, despite these precautions, a puffer may still be deadly. On Maiana a large blue puffer fish, probably *Lagocephalus lagocephalus* (Linnaeus), which was taken at sea on a bait for flying fish, severely poisoned all who ate it, killing two, in spite of being "correctly" cleaned when it was caught.

Porcupine fish, Diodontidae, are considered far too toxic to risk eating. The toxin is thought by the Gilbertese to be concentrated in the ovaries, and they say that "even if only one egg is broken" the fish will be deadly. Sharp back puffers, *Canthigaster* spp., are also known to be deadly poisonous, but these little fish are too small to be used as food; *Canthigaster solandri* (Richardson) is the only species of any interest to the Gilbertese, as this species is used for fighting in the same way as are the Siamese fighting fish.

Trigger fish, Balistidae, are eaten whenever caught, but the majority are not particularly liked. Large specimens of *Pseudobalistes flavimarginatus* (Ruppell) or *Rhinecanthus aculeatus* (Linnaeus) are considered to be more tasty than other kinds of Balistidae. These fish do not appear to be toxic all the time, and the Gilbertese say that they have always eaten them with impunity. Trigger fish may be very poisonous, however, in a ciguatera-producing area, but only when the outbreak of poisoning is at its height.

File fish, Monocanthidae, are not at all liked as food fish, but are occasionally eaten and do not appear to cause poisoning. The flesh of *Aleutea scripta* (Osbeck) is described as being rather bitter, but this fish was eaten in times of famine and does not have the reputation of being poisonous.

**Hallucinatory Mullet Poisoning**

The heads of certain species of mullets, Mugilidae, and of certain species of surmullets, Mullidae, have the reputation of causing a mild form of poisoning, described by some Gilbertese as a "madness," by others as a "forgetfulness," or "sleepiness." It was very difficult to get Gilbertese to admit to any knowledge of this form of poisoning. Fuller inquiries showed that the heads of certain of these fish were eaten with the full expectation and possible enjoyment of the hallucinations or dreams which followed.

Helfrich and Banner (1960) reported that in Hawaii this form of poisoning is restricted to certain localities and times of the year. Sufficient information was not obtained from the Gilbertese to be able to decide if this was true in the Gilberts or not.

It may be of interest to note that the Gilbertese consider two more species of fish capable of causing a "madness" or "forgetfulness" form of poisoning, *Epinephelus coralicola* (Cuvier
and Valenciennes) and Abudesuda septemfasciatus (Kendall and Goldsborough). These fish are customarily eaten only by the old people—
who are forgetful anyway. It was not possible to find out if these fish were at times genuinely "toxic," or merely considered so on account of their habits.

Scombroid Poisoning

There is no evidence of any scombroid poisoning in the Gilbert or Ellice islands. This type of poisoning appears to be caused by a bacterium (Kawabata et al., 1956), which may be found in the flesh of certain scombroid fishes. This microbe reacts on certain chemicals in the flesh of the fish when too long a time is allowed to elapse between catching and cooking the fish. The reaction is quickened by tropical temperatures. In the Gilberts scombroid fishes of various species are frequently caught early in the morning and left in the sun, and later the flesh is salted for consumption the next day. No poisoning has been reported, and it is thought that the scombroid fishes inhabiting this part of the Pacific are not infected with the specific bacterium (Banner, personal communication).

"Castor Oil" Fish Poisoning

On a few islands where the sea is very deep, close to the shore is found the castor oil fish, Ruvettus sp. Although this is a favorite food, it has the reputation of causing poisoning from the purgative properties of the oil in its flesh (Fish and Cobb, 1954). The choicest part of the fish is considered to be the roe, which is boiled whole, but the flesh is eaten as well. If the fish is cooked soon after catching, no "poisoning" results. However, the Gilbertese, and in particular the Ellice people, are well aware of its purga-
tive properties; indeed, if there is a prolonged shortage of them, perhaps due to rough seas, the amount of epson salts sold by the stores in- creases to quite staggering proportions.

Clupeoid Poisoning

During the time that the author was in the Gilberts, clupeoid poisoning was unreported. However, in November 1962 two children are reported to have died and other people have been taken ill after eating "sardines" (te tara-but) caught off Betio, Tarawa. No details are known, except that there were two separate catches involved.

Some years ago at Bairiki, Tarawa, a woman died after eating what was described as "sardines" (possibly Harengula sp.). This woman was the only person taken ill among a number of people who ate the catch. At the time she was blamed for her own death, as she threaded her fish on an old piece of corroded brass wire before cooking them, instead of using a piece of coconut midrib: it was considered that she had died from copper poisoning.

Turtle Poisoning

The hawksbill turtle, Eretmochelys imbricata (Linnaeus), is considered to be deadly poisonous throughout the Gilbert and Ellice islands. It is not generally eaten, but occasionally one will be eaten in error, either in mistake for the green turtle or by someone who does not know the hawksbill's reputation.

The poisoning caused by the hawksbill is very severe, and the Gilbertese describe it as being similar to ciguatera but very much worse. It is so rare for anyone to eat this turtle, and so to be poisoned, that none of the assistant medical officers who were consulted had ever seen a case. The details of the following cases were supplied by eye witnesses on whom the severity of the poisoning had made an everlasting impression.

On Arorae, about 15 years ago, a group of people ate a hawksbill turtle. All of them became very ill and five of them died. Their symptoms were described as follows: vomiting; very severe stomach ache, and diarrhea; their skin was "very hot to touch; they were very thirsty, but something was wrong with their mouths and they were unable to drink; they were unable to move their arms and legs; finally, their skin peeled off as if they had been cooked." One man was so severely poisoned that he is said to have died less than a day after he ate the turtle, but even in that short time he peeled. The others died at various intervals, the longest surviving about a week.

The symptoms in a more recent incident on Tabiteuea involving an unknown number of people were described as follows: vomiting; severe stomach ache, and diarrhea; gradual paralysis; flaking skin, leaving great sores, especially
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<th>MARAKEI Lagoon</th>
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<td>49</td>
<td>44</td>
<td>44</td>
</tr>
<tr>
<td>YEAR TOXICITY COMMENCED</td>
<td>About 1948</td>
<td>1946</td>
<td>Unknown; resurgence 1944–1945</td>
<td>Unknown (1917?)</td>
<td>Unknown (more than 50 years)</td>
<td>Unknown; but resurgence 1929–37</td>
<td>Unknown (1890?)</td>
<td>Unknown (1919?)</td>
<td>Unknown (more than 40 years ago)</td>
<td>Unknown (more than 40 years ago)</td>
<td>Unknown (more than 40 years ago)</td>
</tr>
<tr>
<td>Holocentrus spp. (Gunther)</td>
<td>Ku</td>
<td>+</td>
<td></td>
<td>+</td>
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<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Myripristis spp. (Cuvier)</td>
<td>Mon</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Epinephelus merra (Bloch), and allied species</td>
<td>Kuau</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>E. corallocola (Cuv. &amp; Val.)</td>
<td>Kuaurang</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>L+</td>
<td>L+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>E. fasciculatus (Forskål)</td>
<td>Maneku</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>L+</td>
<td>L+</td>
<td>+</td>
<td>+</td>
<td>+</td>
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<tr>
<td>Cephalopholis argus (Bloch &amp; Schneider)</td>
<td>Nimanang</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>?</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
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<tr>
<td>C. minuta (Forskål)</td>
<td>Nrekereke</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Plectropomus truncatus (Fowler)</td>
<td>Rekimoa</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>?</td>
<td>?</td>
<td>+</td>
<td>+</td>
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</tr>
<tr>
<td>Variola louti (Forskål)</td>
<td>Bukitakeiau</td>
<td>?</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Promicrops lanceolatus (Bloch)</td>
<td>Bakati</td>
<td>L+</td>
<td>L+</td>
<td>+</td>
<td>L+</td>
<td>L+</td>
<td>+</td>
<td>L+</td>
<td>+</td>
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<td>+</td>
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<tr>
<td>C. lugubris (Poey)</td>
<td>Aongo</td>
<td>L+</td>
<td>+</td>
<td>L+</td>
<td>L+</td>
<td>+</td>
<td>L+</td>
<td>?</td>
<td>L+</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>A. triostegus (Linnaeus)</td>
<td>Koinawa</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>TARI ISLAND TYPE</td>
<td>PHOLLY</td>
<td>PHOTIS</td>
<td>PHOTIS</td>
<td>PHOTIS</td>
<td>PHOTIS</td>
<td>PHOTIS</td>
<td>PHOTIS</td>
<td>PHOTIS</td>
<td>PHOTIS</td>
<td>PHOTIS</td>
<td>PHOTIS</td>
</tr>
<tr>
<td>YEAR TOXICITY COMMENCED</td>
<td>Unknown (1917?)</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>ISLAND TYPE</td>
<td>BUTARITARI Lagoon</td>
<td>MARAKEI Lagoon</td>
<td>TARAWA Lagoon</td>
<td>ABEMAMA N. Lagoon</td>
<td>ABEMAMA S. Lagoon</td>
<td>ARUNUKA Lagoon</td>
<td>NONOUTI Lagoon</td>
<td>TABITUEA Lagoon</td>
<td>BERU Lagoon</td>
<td>NIKUNAU Reef</td>
<td>ONOTOA Lagoon</td>
</tr>
<tr>
<td>-------------</td>
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</tr>
<tr>
<td>ANNUAL AVERAGE RAINFALL (IN INCHES)</td>
<td>125</td>
<td>79</td>
<td>70</td>
<td>57</td>
<td>57</td>
<td>53</td>
<td>50</td>
<td>47</td>
<td>49</td>
<td>44</td>
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</tr>
<tr>
<td>YEAR TOXICITY COMMENCED</td>
<td>About 1948</td>
<td>1946</td>
<td>Unknown; resurgence 1944-</td>
<td>Unknown (1917?)</td>
<td>Unknown (more than 50 years)</td>
<td>Unknown; but resurgence 1929-37</td>
<td>Unknown (1890?)</td>
<td>Unknown (1919?)</td>
<td>Unknown (more than 40 years ago)</td>
<td>Unknown (more than 40 years ago)</td>
<td>Unknown (more than 40 years ago)</td>
</tr>
<tr>
<td>A. lineatus (Linnaeus)</td>
<td>Karawa</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
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<td></td>
</tr>
<tr>
<td>A. xanthopterus (Val.)</td>
<td>Mako</td>
<td>? + + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ctenochaetus spp. (striatus and strigosus)</td>
<td>Ribabui</td>
<td>? + + +</td>
<td>? ? ?</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aprion virens (Val.)</td>
<td>Awai</td>
<td>? + + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lettia vaigieniiis ... (Quoy &amp; Gaimard)</td>
<td>Bawe</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L. monostigma (Cuvier)</td>
<td>Baweina</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L. bobar (Forskål)</td>
<td>Ingo</td>
<td>L+ L+</td>
<td>+ + +</td>
<td>L+</td>
<td>L+</td>
<td>+ + +</td>
<td>L+</td>
<td>L+</td>
<td>L+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L. gibbus (Forskål)</td>
<td>Ikanibong</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L. semicinctus (Quoy &amp; Gaimard)</td>
<td>Tanaesa</td>
<td>? + + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Letbrinus spp. (undetermined species)</td>
<td>Rou</td>
<td>? + + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
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</tr>
<tr>
<td>Scarus spp.</td>
<td>Inai</td>
<td>? ? ?</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sphyraena sp. (undetermined species)</td>
<td>Nunua</td>
<td>+ L+</td>
<td>+ + +</td>
<td>L+</td>
<td>L+</td>
<td>+ L+</td>
<td>L+</td>
<td>L+</td>
<td>L+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mugil spp. and other mullets</td>
<td>Aua</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td>+ + +</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mutaenidae</td>
<td>Rabono</td>
<td>+ L+</td>
<td>+ + +</td>
<td>L+</td>
<td>L+</td>
<td>L+</td>
<td>L+</td>
<td>L+</td>
<td>L+</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

+ Denotes a species which may be toxic.
L+ Denotes a species in which large specimens only are potentially toxic.
? Denotes a species about which there is insufficient information on its toxicity.

The author would like to point out that the above list refers to the more common toxic species in the Gilberts. To discuss the degree of toxicity of all possible species is beyond the scope of this paper.
on the mouth, lips, and in the armpits; intense thirst, but due to the condition of the mouth, inability to drink; finally, the victims died, described as being unable to breathe.

The green turtle, *Chelonia mydas* (Linnaeus), is eaten throughout the Gilbert Islands and has not been implicated in any poisoning.

It should be noted that the hawksbill turtle is primarily a carnivore (Loveridge, 1946), preferring crabs and molluscs, although in captivity they will eat fish as well as seaweeds. On the other hand, the green turtle is primarily a herbivore, grazing many hours a day on beds of *Thalassia* (Loveridge, 1946, citing Deraniyagala, 1939). In captivity the green turtle may prefer animal food (Loveridge, 1946). In the Gilberts young green turtles are sometimes kept until they are large enough to eat, being fed almost exclusively on fish.

The hawksbill and green turtles were and still are Gilbertese family totems. Members of the families concerned will often maintain that all turtles are poisonous.

**Invertebrate Poisoning**

Several species of crabs are considered by the Gilbertese to be deadly poisonous, but very few species of crabs are commonly eaten. *Te kukua, Zozymus aenens* (Linnaeus), is reported by Banner and Randall (1952) to be deadly poisonous on Onotoa; although Tarawa people would agree that it is toxic, this species is eaten on Arorae, Beru, and Nonouti. Another species, *Carplus convexus* (Forskål) generally considered to be poisonous, is similar to a commonly eaten species, *te ntababa*, the red-eyed crab, and in the dark may easily be confused with it, especially by an inexperienced fisherman. Another with the reputation of being deadly poisonous is an uncommon small black and green or yellow crab. Because of its size it would never be taken for food; but it is said to have been used by the practitioners of black magic to poison their victims. However, the Gilbertese are reluctant to discuss such practices and the crabs involved.

In September 1961 a Bairiki, Tarawa, woman died after eating crabs. The crabs had been collected by torch fishermen on the Bairiki reef. When they returned they flung the whole catch on the ashes of a fire, an unusual procedure, boiling being the usual Gilbertese method of cooking crabs. It is said that the woman, being greedy, did not wait until the crabs were fully cooked, but grabbed them half-cooked from the fire and ate them. She was taken ill, removed to the Colony Central Hospital, and died. The assistant medical officer who dealt with the case described her death as being due to acute allergy poisoning. As it was dark when the crabs were cooked and eaten, identifying the species responsible was not possible.

Molluscs are not considered to be toxic by the Gilbertese on any island. Banner and Randall (1952) stated that the Onotoans reported that large tritons, *Charonia tritonis* (Linnaeus), were toxic; however, they could find no specific case of intoxication from this snail (Banner, personal communication). The large conch, *Strombus sp.*, has been reported as toxic from certain areas in the Bahamas (Randall, 1958), but apparently this mollusc is not found in the Gilberts. The blood-mouth conch, *Strombus sp.*, is one of the most common shellfish in the Gilberts. Vast numbers are collected and eaten, either raw or cooked, but so far none have caused any poisoning. Both small and large spider conches, *Lambis spp.*, found on the algae-covered reef flats as well as in deeper water, are commonly eaten by the Gilbertese, but have never been reported toxic. The commercial trochus, *Trochus niloticus* (Linnaeus), is not found in the Gilberts, but smaller *Trochus spp.* are not uncommon; although these are eaten when collected during general gleaning on the reef, they are considered somewhat small for food. Turban shells, *Turbo spp.*, are eaten and are commonly used for bait. These snails are picked up on the reef, broken open, a piece is bitten off and put on the hook, and the rest is eaten raw at the time. Cowries of various kinds are found throughout the Gilberts, but are never eaten by the Gilbertese. Many varieties of pelycopods are eaten without any causing illness.

The Gilbertese, surprisingly enough, do not make as much use of the various seafoods on their reefs as do many islanders in the Pacific. Sea urchins, again reported by Randall (1958) as causing a ciguatera-like poisoning, are not eaten by the Gilbertese.

During the Japanese occupation some varieties of seaweeds were eaten by the Gilbertese, but as soon as food supplies returned to normal
Islands That Are Free from Toxicity

<table>
<thead>
<tr>
<th>ISLAND</th>
<th>MAKIN</th>
<th>ABAIANG</th>
<th>MAIANA</th>
<th>KURIA</th>
<th>TAMANA</th>
<th>ARORAE</th>
<th>OCEAN ISLAND</th>
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</thead>
<tbody>
<tr>
<td>TYPE</td>
<td>Reef</td>
<td>Lagoon</td>
<td>Lagoon</td>
<td>Reef</td>
<td>Reef</td>
<td>Reef</td>
<td>High, reef</td>
</tr>
<tr>
<td>RAINFALL</td>
<td>107&quot;</td>
<td>83&quot;</td>
<td>62&quot;</td>
<td>55&quot;</td>
<td>48&quot;</td>
<td>56&quot;</td>
<td>63&quot;</td>
</tr>
<tr>
<td>ANCHORAGE</td>
<td>Very Poor</td>
<td>Poor</td>
<td>Nil</td>
<td>Poor</td>
<td>Very Poor or Nil</td>
<td>Poor</td>
<td>Moorings only</td>
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</table>

This ceased. No information is available, therefore, as to the toxicity of any alga in the Gilbert Islands.

**SUMMARY**

The Gilbert Islands were surveyed for fish poisoning, using local Gilbertese as informants. The following observations were made:

1. Ten out of 16 Gilbert Islands have fish that cause ciguatera.
2. The toxic areas are all found on the western lee sides, and are usually confined to open sea reefs and anchorages in this area, seldom penetrating into lagoons.
3. There is a definite evolution of toxic conditions over the years, with a few species being initially toxic, almost all reef fish being toxic at maximum, and, in the final stages, only large eels, certain snappers, and groupers remaining toxic. This cycle appears to take at least 8 years.
4. Of the other fish in the archipelago, the liver of some sharks, the heads of some mullets and surfmulls, the “castor oil fish,” and some sardines all have reputations for varying degrees of toxicity. In addition, the hawksbill turtle is also reported to be toxic. At least the shark’s liver and the hawksbill turtle produce symptoms somewhat similar to those of ciguatera.
5. Of the invertebrates, only two species of crab and one species of gastropod have been said to be toxic; no other crustaceans or molluscs were considered as being toxic.

**REFERENCES**


PACIFIC SCIENCE, Vol. XVIII, October 1964


Studies in the Helminthocladiaceae, III

Liagoropsis

MAXWELL S. DOTY and ISABELLA A. ABBOTT

In the first paper in this series of studies of the Helminthocladiaceae (Doty and Abbott, 1961), we have shown that, in two species of Helminthocladius from Hawaii, the female reproductive structures are generally similar to those described by other workers for other species in the genus, and that vegetative structures such as internal cortical rhizoids may be used to distinguish at least the Hawaiian species. In the second paper of this series (Abbott and Doty, 1960) a new genus, Trichogloeopsis, was described as containing three species, one new and two transfers from the genus Liagora. They share a major character in common, that of sterile rhizoidal extensions of the gonimoblast, but again the three species may be distinguished from each other by their vegetative structures.

Liagoropsis was first described by Yamada (1944) from material collected in Taiwan (Formosa). The type and only known species was L. maxima. The type specimens of all the species concerned here have been studied by us and we have included illustrations of them (Figs. 1–4) when they have not been illustrated before. We have studied two thalli from Yamada's collections of the type species: the type (Yamada, 1944: fig. 5), a male thallus; and a cotype, a female specimen. It is upon the characteristics of the female thallus that the main description of the generic taxon rested. In examining specimens (Table 1) of eight of the nine collections which we believe constitute Liagoropsis, we are of the opinion that the structural vegetative differences seen, whether external or internal, are without taxonomic significance at either the generic or specific level. Thus, we believe that the genus can be amply delineated on the basis of characters possessed by the female reproductive apparatus alone, and that Liagoropsis as known at present should be considered monotypic.

1 This work was made possible through financial assistance from the National Science Foundation on Contract G3833, from the Philippine National Research Council by funds for expenses provided under Republic Act 1606, and from the Graduate Committee of the University of Hawaii.

For the loans of critical materials used in this study we wish to thank Dr. Yamada, Hokkaido University; P. Bourrelly, Museum National d'Histoire Naturelle, Paris; T. Norlindh, Lund University; The Botanical Museum of the University of Copenhagen; T. V. Desikachary, R. Subramanyan, and V. Krishnamurthy, Madras University; Laura Huerta, Escuela Nacional de Ciencias Biologicas, Mexico City; and L. Williams, Duke University. We are also indebted to Gregorio Velasquez, University of the Philippines, who accompanied the senior author and made possible some of the field trips in the Philippines.

2 Department of Botany, University of Hawaii, Honolulu, Hawaii.

3 Hopkins Marine Station of Stanford University, Pacific Grove, California.

4 Desikachary published (1957: fig. 1) a photograph of his material. Yamada (1944: fig. 5) has an excellent drawing of the type of Liagoropsis maxima, which specimen we have studied. Boergesen published (1909: plates I and II, respectively) photographs of one of his sheets of Nemalion schrammi and of the type of Nemalion longicolle.

5 By using "cotype" here the authors mean not to derogate the more precise terms isotype and paratype. The thalli under consideration are parts of the same collection but were separate thalli and of different sex. To use isotype would be akin to using this term for both the male and female branches collected at one time from, respectively, separate staminate and pistillate flower-bearing trees. To use paratype would imply that in the original place of publication this was a specimen other than the holotype cited with the original description. This specimen was not cited by Yamada although the dioecious nature of the species as represented by the specimens examined was mentioned and aspects of both the male and female thalli were described.
In external appearances (Figs. 1–4) Liagoropsis resembles some species of Liagora (Abbott, 1945), especially L. farinosa, but it is more robust and taller, and the branches are more irregular than those of any species of Liagora known to us. In its slightly calcareous nature it lies between the noncalcareous genera, such as Nemalion (which may have carbonate deposits in the base of the thallus), and generally strongly calcified genera, such as Trichogloea and Liagora. The fresh thalli resemble Trichogloeopsis sequenii and T. lubrica or the Trichogloeopsis species in texture, being soft and mucilaginous to gelatinous, though limy or slightly calcified. The dried thalli do not reveal this very soft nature but in herbarium specimens that have been dried without decalcification the liminess shows, usually in a reticulate pattern.

Yamada distinguished the genus from Liagora on the basis of the slight amount of calcification possessed by Liagoropsis, the paucity of involucral filaments, and the equality of the sometimes terminal carpogonial branches to vegetative branches. From his illustrations of the reproductive features it is clear at once that his genus is indeed different from Liagora. The extent of these differences was not known, however, in reference to the other criteria used for distinguishing genera among the simpler Nemalionales, and our present study was made largely to gather further information in this regard.

Table 1 reveals the geographic distribution of this genus. In consideration of these locations it appears that one can expect to find this genus most often in the same areas where one finds the greatest degree of coral development, that is, in the warmer parts of the western Pacific and the western Atlantic. Yet it is not reported by Taylor (1942), Bernatowicz (1952 a,b),

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**Fig. 1, 2.** Photographs of female carpogonial thalli believed to be representative and accepted as representative of Liagoropsis Schrammi; these are, respectively, the type and an isotype of Helminthocladia schrammi. Fig. 1, The type specimen in the Thuret herbarium. Fig. 2, The isotype bearing the number 21962 in the Agardh herbarium.
Liagoropsis—Doty and Abbott

Fig. 3, M. Doty no. 16954 from the Philippines. Fig. 4, A cotype of Liagoropsis maxima from Y. Yamada's herbarium.

Collins and Hervey (1917), or Howe (1918, 1920) in their several floristic treatises of the western warmer Atlantic. Strangely enough it is not yet known, seemingly, from south of the equator except for the Williams collection. This is certainly due in part to a lack of habitats in the western Atlantic and Indian oceans south of the equator, but perhaps even more likely due to our lack of floristic information on these areas. However, it appears neither elsewhere in the studies of Boergesen nor in those of Weber Van Bosse, whose works on Indian Ocean and Indonesian algae were both intensive and extensive. The relative abundance of records from the Indian Ocean north of the equator is less easy to explain, unless it is the result of a greater collecting intensity in these waters.

DESCRIPTION AND DISCUSSION OF THE SPECIES

It is our intention to continue use of the oldest legitimate specific epithet published which applies to the one species we feel should be recognized; and this is accepted here as "schrammi," validly published in the combination Helminthocladia schrammi, with the very poor description, "Pourpré jaunatre a l'etat frais," by Maze and Schramm (1870-77:177-178). As Boergesen (1909:4) points out, J. Agardh (1890:41), in treating this alga as a Helminthocladia, suggested it might better be treated as a member of the Chordariaceae (Phaeophyta). There seems to be no question, applying contemporary criteria, but that this is a member of the rhodophyta order Nemalionales, the classification, nomenclature, and nature of which are discussed below.

Liagoropsis schrammi (Maze et Schramm) comb. nov.

Type: Maze and Schramm (loc. cit.) say their only collection was found cast onto the beach at "Capesterre." It is accepted that the type of *Helminthocladia schrammi* was washed onto the beach at Capesterre, Guadeloupe (16° N, 62° 40' W), in November, 1870, collected, and later numbered "1572." The collection was said by Maze and Schramm to be of only one specimen. Possibly, this specimen was divided (Boergesen, 1909) into at least three parts, one deposited in the Thuret herbarium, a second in the general cryptogamic herbarium of the Museum d'Histoire Naturelle (Paris), and a third in the Agardh herbarium. We accept the specimen (Fig. 1) in the Thuret-Bornet herbarium at the Paris Museum as the holotype. An isotype (Fig. 2) has been located, as number 31962, in the Agardh herbarium, but no third part has been located.

*Nemalion schrammi* (Maze et Schramm) Boergesen. 1909. Some new or little-known West Indian Florideae. I. Botanisk Tidsk. 30:4, pl. 1, text fig. 3 (obligate synonym, tynonym).

*Nemalion longicolle* Boergesen. 1909. Some new or little-known West Indian Florideae, K. Botanisk Tidsk. 30:8, pl. 2, text fig. 4 (faculative synonym).

*Liagoropsis maxima* Yamada. 1944: 19 ff., figs. 5, 6 (faculative synonym and generic holotype*). Cotype illustrated here as Figure 4.

Thalli up to 1 m tall, primarily pinnate (Fig. 3) to irregularly branched, becoming pseudodichotomously branched distally (Fig. 4); lightly calcified, soft and gelatinous; of multiaxial construction; central axes cylindrical, becoming compressed often up to 1 cm, or even 3.3 cm

### Table 1

<table>
<thead>
<tr>
<th>Author, Citation, Collection Numbers, and Geographic Origins of the Collections*</th>
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<tr>
<td><strong>Positions of Known Collections</strong></td>
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<td>Latitude</td>
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<tr>
<td>1. <em>Nemalion schrammi</em> (Williams and Blomquist, 1947)</td>
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<td>2. <em>Helminthocladia schrammi</em> (Maze and Schramm, 1870–77)</td>
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<td>3. <em>Nemalion schrammi</em> (Boergesen, 1909 [#1614])</td>
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<td>4. <em>Nemalion longicolle</em> (Boergesen, 1909 [#1614])</td>
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<tr>
<td>5. <em>Liagoropsis schrammi</em> ([M. Dory coll. #16954])</td>
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<td>6. <em>Liagoropsis maxima</em> (Yamada, 1944)</td>
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<td>7. <em>Liagoropsis maxima</em>† (Desikachary, 1957)</td>
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<td>8. <em>Liagoropsis schrammi</em> (Subramanyan [M. Dory coll. #19686])</td>
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<tr>
<td>9. <em>Liagoropsis schrammi</em> (Desikachary [M. Dory coll. #19687])</td>
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</table>

* The material reported (Huerta, 1960) as *Nemalion schrammi* seems to be, according to a communication from the author of that article and the material of the collection seen by the present authors, *Helminthocladia calvadotii* (Lamx.) Setchell.
† Specimens not seen.
broad. Assimilatory filaments thin, the cells cylindrical to obovate, frequently tipped with a hair, and then resembling those of Liagora rather than Nemalion. Terminal cells of vegetative filaments not specially differen tiated. Male gametes becoming spherical, produced (Fig. 5) in grapelike superficial clusters. Male and female structures produced on the same or on different thalli. Carpogonial branch apparently a modified vegetative branch, or an outgrowth from the basal first or second cell of a vegetative system, or one member of a pair of branches arising (Figs. 6, 7) from the basal or second dichotomy in a vegetative branch, or in still other (but much more rare) cases a lateral branch of a vegetative system. In the order of these positions as given, the cell number in the carpogonial branch seems to decrease variably from eight to five cells. Carpogonial branches shorter than the vegetative branches near them and usually straight as in Nemalion rather than curved as usual in Liagora. Carpogonial branches usually with two (one to three) cells at the base (Fig. 6) similar to the other vegetative cells near them. Hypogynous cells three to five, forming a stalk below the carpogonium.

After fertilization the trichogyne separates from the zygote and withers away except at the base. The zygote itself does not always conspicuously divide transversely but produces prominent filaments (Figs. 8–10) rarely protruding horizontally from the carpogonial axes, usually protruding toward the thallus surface and often even nearly parallel to the trichogyne. Our observations are in general agreement with those of Desikachary (1957) who illustrates this process well. In some cases it seemed that the more basal carpogonial protoplasm had become highly vacuolated, pushing the goni moblast-forming cytoplasm out into the developing goni moblast filament initials without a previous division of the zygote. In other cases the zygote cytoplasm seemed to have become divided after much of the cytoplasm had collected in the apex of the carpogonium under the separated trichogyne but before goni moblast filaments appeared. Clearly in the latter case a sterile stalk cell is produced between the hypogynous cells and the goni moblast initial. Soon (developmentally) several more goni moblast filaments are produced parallel to those first formed.

The upper part of the carpogonial cytoplasm was the only part seen giving rise to goni moblast filaments, whether or not the cell had divided into two cytoplasts following fertilization. Very rarely, however, in older stages it appeared that some goni moblast filaments had their origin below the line above which one would say the dense cytoplasm would have aggregated and separated by cell division after fertilization typically, but, in the poorly fixed material at hand, observations of a cytological nature could only lead to tentative conclusions.

The goni moblast filaments at maturity are pseudo-dichotomously divided, perhaps up to as many as four times. The individual segments are rather straight and uniformly diverging throughout, yet always directed toward the surface of the thallus (Figs. 11–14) so that the mature goni moblast forms an inwardly pointing cone of rather closely placed, rather straight and free filaments. The terminal carposporangia bear but one spore each. In age the carpospores may be gone from the terminal cells of the firstformed erect filaments. The empty carposporangia then form an apically colorless central mass surrounded by younger, secondary goni moblast.

Desikachary (1957: figs. 1, 2, 4, 5) shows sterile or vegetative filaments arising from the base of some carpogonial branches. Neither he (1962) nor we consider these to be sterile filaments produced as special branches in association with the reproduction process, but rather as less well-developed vegetative branches. In the various materials examined we have found no sterile filaments developed around the goni moblast from either the carpogonial branch or from the surrounding vegetative cells as is the case in Trichogloea or Liagora. However, from the base of the carpogonial branch there develop rhizoids which run in straight courses away from the supporting cells. From some mature goni moblasts such rhizoids were seen protruding from the basal few cells in the carpogonial branch itself. We saw no such rhizoids arising from the carposporophyte.

The thalli collected by the senior author (Fig. 3) were attached to stones and sunken logs in 2–3 m of water off the mouth of a small stream near the village of Libog, Albay Province, Philippines (13° 14' N; 123° 46' 8" E), V–19–1958. Hundreds of thalli could have been col-
lected over a 0.25 hectare area. About 1 liter of specimens was preserved with strong formalin on the spot. It may be added, in passing, that Boergesen’s (1909) materials came from a similar habitat.

The Philippine material on which the descriptive paragraphs above were written consists of herbarium sheets of the collection bearing the senior author’s number 16954. The specimen deposited in the Bishop Museum herbarium in Honolulu, Hawaii, is presented here as Figure 3. Portions of the same collection, but not parts of the same thallus, are being distributed to the herbaria of the University of the Philippines, Hopkins Marine Station, Hokkaido University, Kagoshima University, Museum of Natural History (Paris), Copenhagen University, Lund University, University of California (Berkeley), Adelaide University, and Madras University.

OTHER SPECIMENS EXAMINED (Table 1): the type of Helminthocladius schrammi (Paris); specimens of Boergesen (Botanical Museum, Copenhagen) under the name of Nemalion schrammi; the type of Nemalion longicolle (Botanical Museum, Copenhagen); the type and cotype of Liagoropsis maxima (Y. Yamada’s herbarium, Sapporo, Hokkaido); the specimen of Williams (Duke University, Durham, N. C.) from Brazil as Nemalion schrammi; specimens of Desikachary (University of Madras) from Tuticorin and of Krishnamurthy and Subraman-yan (University of Madras) from the Andaman Islands. There seem to be no specifically significant or consistent reproductive or vegetative differences between these materials.

Boergesen (1915) distinguished the more slender species, Nemalion longicolle, on the basis of the solitary central or terminal position of the carpogonial branch from the broader species, Nemalion schrammi, where he found the carpogonial branches to be both terminal and otherwise. Our study leads us to believe that the vegetative morphological differences and the carpogonial branch differences between these two species may be due to age.

The Philippine collection may be divided into thalli of two sorts on the same basis used by Boergesen (1915) for distinguishing Nemalion schrammi and Nemalion longicolle. The coarser of the two (as in N. schrammi) was whiter (more calcified) when alive; now dry, it is more yellow or brown in color, the axes are usually about 1.5 cm, but up to 3.3 cm, broad on the herbarium sheets. The surface is more strongly reticulate (i.e., the reticula are morphologically distinguishable). The more delicate form of the two was pinker (less calcified) when alive; now dry, it is still the pinker in color, the axes are only rarely over 1.0 cm broad; and the surface is more aereolate than reticulate (i.e., the reticulum is distinguished predominately by color).

Boergesen (1915) does not mention calcification and, indeed, basing his studies on exsiccati of previously wet-preserved materials, classified his two species as members of Nemalion, a genus generally considered to be noncalcareous. Neither Maze and Schramm nor Agardh mention liminess. After decalcification our own quite limy specimens strongly resembled the specimens of Boergesen’s taxotype. Boergesen’s specimens produced some gas when we put strong hydrochloric acid on them.

The term “taxotype” is employed by the present authors to designate a specimen used by an individual as either typical of a taxon or as the element in the taxon to which other elements are compared. It is, thus, a standard for taxonomic purposes, rather than a nomenclatural standard for application of priority by means of the type method.

Figs. 5–14. Reproductive structures of Liagoropsis schrammi, drawn with the aid of a camera lucida from the various collections studied. The sizes are indicated by the index lines provided for the different figures. In general no attempt was made to indicate pit connections or the thickness of the gel or wall material surrounding the cytoplasts. Fig. 5, Spermatangial clusters, with a dotted line to indicate the outer limit of the gelatinous walls around the individual spermatangia. In spreading the spermatangia sufficiently to show some of their relationship to the stalks bearing them, several were broken away from the cluster and lost. (Type specimen of Liagoropsis maxima Yamada.) Figs. 6, 7, Monocarpogonial cortical branch systems bearing carpogonial branches, as well as spermatangial clusters. A rhizoid (rh) is shown at the base of the cortical system near the medullary (med) strands. Respectively, M. Doty nos. 19687 and 16954. Figs. 8–14, Gonimoblast development as generally found in all collections. Respectively, M. Doty no. 16954; cotype of Liagoropsis maxima: M. Doty no. 16954; M. Doty no. 16954; type of Nemalion schrammi; cotype of Liagoropsis maxima, and type of Nemalion longicolle [Boergesen no. 1614b].
Morphology of the male structures (Fig. 5) has proven of little value to us in the taxonomy of this genus, nor has the fact that some collections are monoecious and some dioecious been of value. Our Philippine material (no. 16954) is monoecious, as Desikachary (1957) reports to be the case in his material, whereas Yamada reports (1944:21) dioecious material. We have substantiated this latter point by our study of Yamada's specimens. Boergesen apparently did not see convincing evidence of spermatium production in either of the specific taxa he recognized, but expected his material of at least one of them to be dioecious.

SYSTEMATIC DISCUSSION

Though often in Liagoropsis they are solitary (Figs. 7, 8), usually one finds many carpogonial branches in clusters (Figs. 15–18). Figure 156C in Newton's book (1931) illustrates a similar situation for Nemalion, and see Boergesen (1915: fig. 68) for the same situation in Liagora elongata Zanardini, a species that perhaps should be transferred to Liagoropsis, along with some Nemalion spp. When the carpogonial branch clusters are large, containing five or more branches, their derivation seems clearly that of replacing vegetative (assimilatory) filaments. At one time we considered such "polycarpogonial" systems to be hair clusters with an occasional hair-bearing branch developing as a carpogonial branch. This was because at first we found many with short trichogynes and we interpreted them as hairs, for the hypogynous cells were not strongly differentiated. We now consider such to be merely young, for in almost each collection such branches in some clusters have been found bearing gonimoblast filaments. The similarities in hair and carpogonial development have been noted (e.g., Rosenvinge, 1911) by a good many authors. At least in ontogeny, in Liagoropsis, the determination process must remain labile for a long time and the hypogynous cells are never strongly specialized.

![Figures 15-18. Polycarpogonial branch systems bearing, in one case, a gonimoblast. Respectively, type of Nemalion longicolle [Boergesen no. 1614b]; type of Nemalion schrammi from Paris specimen; M. Doty no. 16954; Boergesen no. 1614.]
Perhaps the nature of the carpogonial branch itself is of systematic value. The straight carpogonial branch of *Liagoropsis* with a relatively large and somewhat variable number of not highly differentiated cells can be considered simpler than the curved carpogonial branches consisting of fewer, more highly differentiated and numerically and morphologically more uniform cells, for example, of *Helminthbora*. In this respect *Liagoropsis*, *Nemalion*, *Trichogloea*, and *Trichogloeopsis* are similar.

Kylin (1956:108) distinguished *Liagoropsis* from *Nemalion* on the basis of the carpogonial branches, which in *Liagoropsis* were said to be accessory lateral branches on the cortical filaments, whereas in *Nemalion* the carpogonial branches were said to correspond to young branches of the cortical filaments. While this distinction may be useful for separating *Liagora*, *Helminthbora*, and *Helminthocladiella* from *Nemalion* or *Trichogloea*, it is not a valid one for distinguishing *Liagoropsis*, for this genus shows both derivations of the carpogonial branches but, particularly frequently, the more terminal, less specialized *Nemalion* type.

When the carpogonial clusters containing two or three carpogonial branches in a vegetative branch system are considered, the attachment and derivation of the different branches appear to be so different that some may be interpreted as replacing vegetative branches terminally (Figs. 12, 13), and others, either in the same (Fig. 15) or separate (Figs. 10, 11) fertile clusters, appear to have arisen laterally on, respectively, a carpogonial or a vegetative filament. In these small clusters the carpogonial branches also may seem to be attached to each other (Fig. 10), or in larger clusters they may appear to be (Figs. 15-18) parts of a cyphomorphy system. Thus the position or attachment of the carpogonial branches is not a very useful systematic criterion in this genus.

The first and subsequent divisions of the fertilized carpogonium do not show regularity and thus the sequences described by Pappenfuss (1946) for various of the Helminthocladiaceae are not applicable to *Liagoropsis*. Some oblique and some transverse divisions have been seen in the zygote contents as well as many cases where gonimoblast initials seem to have been produced without any division at all. No consistency was found. This is quite different from the situation in *Trichogloeopsis* or *Helminthbora*. This could be considered as primitive variability, whatever the unknown nuclear cytology.

The gonimoblast is small when compared to the size of the carpogonial branch. Its size is comparable to the cystocarp of *Nemalion* (Kylin, 1916), but in most other genera in the Helminthocladiaceae sensu Kylin the mature cystocarp is large and conspicuous and almost always associated with a large number of sterile filaments. The gonimoblast of *Liagoropsis* consists of but a few fertile filaments developing terminal carpospores on the more centrally formed filaments first. Subsequently carpospores are produced, also terminally, on the surrounding and later formed gonimoblast filaments. This sequence is not that of either *Liagora* or *Nemalion*. It would appear that the gonimoblast grows by producing young branches radially, which in age produce terminal carposporangia successively more distant from those first produced. This cymose development is not precisely the indeterminate growth of the gonimoblast initials described for the classical *Nemalion elminiboides* (Vell.) Batters (1902); nor is it that of *Trichogloeopsis*, where the primary gonimoblast filaments terminate in rhizoids. Neither does it, in its development, lead to the mixture of young, mature, and empty carposporangia characteristic of most *Liagora* species. In other words, it seems to be intermediate of, or perhaps more primitive than, these other two types.

In *Trichogloeopsis* (Abbott and Doyt, 1960) and in *Nemalion*, as classically illustrated by Kylin (1956: figs. 57, 58A), the zygote divides transversely, and the primary gonimoblast filaments protrude radially and develop most at 90° or more from the trichogyne. With further growth the gonimoblast filaments curve toward the base of the carpogonial branch, and they may become parallel and close to it. The carpospores are produced terminally on secondary gonimoblast filaments which radiate or curve toward the outside of the thallus and which are branches of the primary gonimoblast filaments. Though differing in detail, the gonimoblast in

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*However, further on in his key and descriptions Kylin says "terminal or subterminal," but still places the genus near *Liagora* rather than near *Nemalion.*
Nemalion elminthoides collected at Pacific Grove, California, is similar to the above two genera in that a rather dense knotlike gonimoblast is produced wherein any filamentous nature is obscured.

In Liagoropsis (16954 and cotype of L. maxima Yamada) the gonimoblast filaments are loosely composed from the first and are clearly filamentous. This is another unique feature of Liagoropsis and was previously reported by Desikachary (1957) and is verified here by us. The gonimoblast filaments of Liagoropsis first appear (Figs. 8–11) straight and closely erect (i.e., they tend to parallel the trichogyne). These primary gonimoblast filaments differentiate (Figs. 12–14) carpospores at their tips later. The secondary gonimoblast filaments appear later as branches that are likewise erect and directed toward the exterior of the thallus. These secondary gonimoblast filaments arise from the nondifferentiated more basal cells of primary gonimoblast filaments and appear, when mature, as though they were sterile filaments surrounding and appressed to, or at least close to, the more matured primary filaments.

In the lack of sterile filaments, in the lack of a closely packed knot of gonimoblast initials, and in the direct growth of the gonimoblast initials toward the thallus surface, Liagoropsis is perhaps simpler than Liagora or Helminthocladia. In these two genera a knot of gonimoblast initials may form before the later formed filaments protrude toward the surface, and also sterile filaments may be present. At least sterile filaments of some kind are also present in Trichogloeia and Trichogloeopsis. In this respect Liagoropsis is most like Nemalion elminthoides, which usually lacks the sterile filaments but has, apparently, the knot of cells developing from the zygote.

In surveying the genera of Helminthocladiaceae, we have come to the conclusion that those with a low definite number of cells forming curved lateral carposgonal branches, with no vegetative cells between the hypogynous cells and the supporting cell, are more advanced than those which have larger and more variable numbers of cells forming straight carposgonal branches which often have one or more vegetative cells between the hypogynous cells and the supporting cell. In the first category with lateral carposgonal branches which largely arise along the basal two-thirds of the supporting cell, are Helminthocladia, Helminthora, Liagora (in sensu nostro), Dernonema, and Camagloia. In the second group, with terminal or lateral carposgonal branches, are Liagoropsis, Nemalion, Trichogloeia, and Trichogloeopsis.

Desikachary (1962) interpreted the carposgonal branches of Liagoropsis as consisting entirely of hypogynous cells and the carpogonium. As noted above, it appeared to us that in some cases (e.g., Figs. 6, 11) there were cells of normal vegetative appearance at the base of the branch bearing the carpogonium, and in other cases (e.g., Figs. 7, 13, 18) none. We interpret this situation as evidence of primitive variability. Following our interpretation of the vegetative nature of some of these cells, we would say there were not even any “less well developed vegetative branches” arising from the carposgonal branches such as Desikachary (1957) shows in some of his illustrations.

The diffuse gonimoblasts of the two genera Dernonema and Camagloia set them apart from all other members of this family.

Svedelius (1939), as a result of his study of Dernonema, thought Schmitz and Hauptfleisch's (1896) Dernonemeae, established for Dernonema, could well be treated as a separate family. Gardner (1917), as a result of his study of Cumagloia, thought they represented merely extremes in a family, the members of which had gonimoblasts of varying degrees of compactness. Desikachary (1962), in making a close study of the point, found Dernonema to be without the fusions, the earlier reported presence of which has led others to feel the genus might not belong to the Helminthocladiaceae at all. Desikachary, however, feels as we do, that there is not enough known about the related genera to justify establishment of a family for these two, and possibly other, genera at this time. Insofar as we know, no one has erected a familial taxon for this group. Should this be done it would appear, from the results of Desikachary's study, that this family should contain both Dernonema and Camagloia.

In Trichogloeopsis mucosissima (Abbott and Doty, 1960) the carposgonal branches may occur in groups, somewhat similar to the clusters of carposgonal branches in Liagoropsis (Figs.
Liagoropsis—DOY and ABBOTT

15–18); and it appears in both species that in this polycarposgonial condition the remaining nearby carposgonial branches are suppressed in their development after one of the group has begun to develop a gonimoblast. However, Trichogloeopsis differs from all Helminthocladiaceae in that it possesses sterile gonimoblastic rhizoids as daughter cells or continuations of the fertile system. In Liagoropsis there are no sterile cells associated with the gonimoblast, an unusual condition in this family.

The unique way in which the gonimoblast is formed from irregular division of the zygote (i.e., fertilized carposgonium) and the sequence of carpospore production would also lead us to believe that Liagoropsis is more primitive than any other member of this family—certainly more primitive than Nemalion, which has been used classically as a "primitive" red alga.

These latter two genera are rather distinctive in that the vegetative systems originating from the supporting cell tend to continue to grow beyond the carposgonial branches they produce, so that some of the carposgonia appear to be lateral in age but not by an epinastic development of the apex of the supporting cell. This lack of epinastic development of the supporting cell we consider to be one of the most primitive of the attributes of Liagoropsis.

Certainly, of the genera included in the Helminthocladiaceae by Kylin (1956), Liagoropsis is the least specialized and seems to stand with the simplest of the groups of genera we recognize. Table 2 presents our views of the general relationships of these major groups of genera and Liagoropsis. We (Abbott and Doty, 1960) have made a suggestion as to the family names, but have continued the use of Helminthocladiaceae above and in the title under which the present work was undertaken. We expect, however, to continue the use of the name Nemalionaceae for a family of algal genera of which Nemalion Duby (1830) is the type. We do not care to indicate a closer affinity for the Dermenemeae at this time though, in relation to the lateral position of their carposgonial branches and the degree of specialization of their carposgonial branches, they would seem perhaps to be more closely related to the Helminthocladiaceae than to the Nemalionaceae. Similarly, and in agreement with Desikachary (1962), we do not feel it possible to postulate a generic phylogeny or family tree for the genera until more species have been studied in detail.

SUMMARY

One species, Liagoropsis schrammi (Maze and Schramm) Doty and Abbott, is recognized as occurring in both the western Atlantic and western Pacific, whereas three species have been recognized previously. The genus Liagoropsis is proposed for recognition as the simplest genus among the genera of a group we propose to treat as the Nemalionaceae, a subfamily suggested to include (in addition to the type, Nemalion) the genera Liagoropsis, Trichogloea, and Trichogloeopsis. However, we recognize Liagoropsis to be quite distinct in several respects from these other three genera.

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The Holothuroidea Collected by the Royal Society Expedition to Southern Chile, 1958–1959

D. L. Pawson

ABSTRACT: The holothurians collected by the Royal Society Expedition to southern Chile, totalling 180 specimens, are described. Ten genera (of which one is new) and ten species are represented. Neopsolidium n.g., type species Psolidium convergens (Herouard), is erected to accommodate those species in the genus Psolidium (sensu lato) in which the dorsal plates are reduced to a diameter of about 0.4 mm.

The holothurian fauna of southern Chile is generalised, containing few restricted species, and sharing many elements with distant subantarctic islands and with Antarctica.

DURING late 1958 and early 1959 an expedition sponsored by the Royal Society carried out marine and terrestrial observations and collections in southern Chile. Stations were established in three separate areas, namely:

1. Isla Chiloe (approx. 42° S)
2. Puerto Eden to Punta Arenas (approx. 49° S to 52° S)
3. Isla Navarino and southern regions (approx. 55° S).

These three areas, considered together, were expected to provide a good picture of the changes in flora and fauna along the Patagonian coastline. The present paper contains an account of the holothurians collected by the marine biologist to the expedition, Prof. G. A. Knox, of Canterbury University, Christchurch.

A total of 180 specimens of holothurians were collected, and these comprise 10 genera and 10 species. The collection represents a good cross-section of the known fauna, although a number of species, hitherto regarded as common, were not found.

The shallow-water holothurian fauna of southern Chile is not large in terms of species, although a wide variety of genera are represented. This is particularly true for the order Dendrochirotida. Previous authors such as Ludwig (1898a, 1898b), Perrier (1905), Ekman (1925), and Deichmann (1947) have provided a clear picture of the composition of the fauna. It is unlikely that many new shallow-water species will be taken from this region.

I am grateful for the opportunity to study this most interesting collection, and I would like to thank Prof. G. A. Knox and the Royal Society for making this material available to me.

LIST OF SPECIES COLLECTED

Order Dendrochirotida
Family Phyllophoridae
Subfamily Thyoniidae Heding and Panning, 1954
Attanidium chilensis (Semper)

Family Cucumariidae
Subfamily Cucumariinae
Cladodactyla crocea (Lesson)
Stereodermia laevigata (Verrill)
Pseudocnus dubiosus (Semper)
Subfamily Colochirinacea Panning, 1949
Trachythyone lechleri (Lampert)

Family Psolidae
Neopsolidium convergens (Herouard)
Psolus patagonicus (Ekman)

Order Apodida
Family Chiridotidae
Chiridota pisanii (Ludwig)
Trochoboda purpurea (Lesson)
Taeniogyrus contortus (Ludwig)

Order Molpadida—none

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²Department of Zoology, Victoria University of Wellington, Wellington, New Zealand. Manuscript received September 27, 1963.
Order Aspidochirotida—none
Order Elasipodida—none

MATERIAL EXAMINED

180 specimens were collected from 12 of the 78 stations worked. Collecting was done by hand in the intertidal zone, by diving, dredging, or seine netting.

Area 1, Isla Chiloe, Stations 1–18
Sta. 4. Punta Gaviota, 42° 03’ 50” S, 74° 02’ 50” W; intertidal boulder beach, volcanic rocks; hand collecting; Oct. 4, 11, and 16, 1958.

Astbyonidium chilensis (Semper), 4 specimens

Area 2, Puerto Eden to Punta Arenas, Stations 19–49
Sta. 19. Puerto Eden, Isla Wellington, the point to the north of the FACH base, 49° 08’ 20” S, 74° 26’ 55” W; intertidal granitic gneiss rocks, sheltered; hand collecting, also collection from Macrocystis fronds and holdfasts and sublittoral collection by diving; Nov. 29 and 30, 1958.

Pseudocnus dubiosus (Semper), 1 specimen
Sta. 27. Isla Carlos, 49° 09’ 35” S, 74° 25’ 24” W; collection from Macrocystis fronds and holdfasts; Dec. 5, 1958.

Pseudocnus dubiosus (Semper), 57 specimens
Sta. 37. Caletta Lackawana, 49° 10’ 32” S, 74° 25’ 52” W; depth 18 m, sand, rock, shell; dredge; Dec. 9, 1958.

Stereoedera laevigata (Verrill), 1 specimen
Sta. 39. Puerto Eden, west side of Canal Sur, 49° 09’ 52” S, 74° 26’ 08” W; intertidal boulder beach of granitic gneiss; hand collecting and collection from Macrocystis fronds and holdfasts; Dec. 9 and 11, 1958.

Pseudocnus dubiosus (Semper), 15 specimens
Psolus patagonicus Ekman, 30 specimens
Sta. 40. Isla Dulce and Isla Levinson, Puerto Eden, 49° 09’ 02” S, 74° 25’ 10” W; intertidal and sublittoral granitic gneiss rocks; hand collecting; Dec. 12 and 13, 1958.

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Psolus dubiosus (Semper), 2 specimens
Psolus patagonicus Ekman, 1 specimen
Area 3, Isla Navarino and Southern Regions, Stations 50–78

Neopsolidium convergens (Herouard), fragment
Sta. 52. Puerto Robalo, Isla Navarino, 54° 55’ 50” S, 67° 41’ 40” W; intertidal argillite rock; hand collecting and collecting from Macrocystis fronds and holdfasts; Jan. 10, 16, 23, and 30, 1959.

Psolus dubiosus (Semper), 10 specimens
Neopsolidium convergens (Herouard), 2 specimens
Sta. 54. Puerto Grandi, Isla Bertrand, 55° 12’ S, 67° 55’ 30” W; boulder beach; intertidal hand collecting; Jan. 12, 1959.

Psolus dubiosus (Semper), 4 specimens
Trachythyone lechleri (Lampert), 9 specimens
Sta. 73. Seno Grandi, small island opposite Puerto Grandi, 55° 15’ S, 67° 56’ W; collection from Macrocystis fronds and holdfasts; Jan. 5, 1959.

Cladodactyla crocea (Lesson), 24 specimens
Neopsolidium convergens (Herouard), 1 specimen (juvenile)
Chiridota pisamii (Ludwig), 4 specimens
Trochodota purpurea (Lesson), 8 specimens
Taeniogyrus contortus (Ludwig), 1 specimen

Trochodota purpurea (Lesson), 2 specimens
Sta. 77. Puerto Grandi, Isla Bertrand, to the west of the wharf; 55° 12’ S, 67° 55’ 30” W; intertidal granitic rocks and boulder beach, semi-sheltered, hand collecting; Feb. 7, 1959; collection by diving among Macrocystis; Feb. 8, 1959.
*Pseudocanus dubiosus* (Semper), 1 specimen
*Neopsolidium convergens* (Herouard), 2 specimens
*Trochodota purpurea* (Lesson), 1 specimen

**SYSTEMATIC ACCOUNT**

**Order DENDROCHIROTIDA**

**Family PHYLLOPHORIDAE**

**Subfamily THYONIDINAE** Heding and Panning, 1954

**Genus Athyonidium** Deichmann, 1941

*Eucyclus* Lampert, 1885, p. 920; Theel, 1886a, p. 268; Ludwig, 1887, p. 1239; Heding and Panning, 1954, p. 36: name preoccupied.

**TYPE SPECIES:** *Athyonidium chilensis* (Semper).

**REMARKS:** This genus is monotypic. Deichmann (1941) pointed out that the generic name *Eucyclus* was preoccupied, having been claimed some years earlier for the Mollusca. Heding and Panning (1954) unfortunately persisted with the old generic name.

*Athyoniium chilensis* (Semper)

*Thyone* (*Stolus*) *chilensis* Semper, 1868, p. 241, pl. 40, figs. 3–6; Lampert, 1885, p. 156.

*Eucyclus duplicatus* Lampert, 1885, p. 250; Theel, 1886a, p. 268.

*Thyone chilensis* Theel, 1886a, p. 139.


*Athyonidium chilensis* Deichmann, 1941, p. 127.

*Eucyclus chilensis* Heding and Panning, 1954, p. 36, fig. 2.

**DIAGNOSIS:** Large forms (25 cm) with thick, soft skin and numerous stout feet. Tentacles, five large external pairs and five small inner pairs. Calcareous ring with five stout, almost rectangular radials and five insignificant interradials, often completely concealed in surrounding tissue. One large dorsal stone canal, often branched, and one or two tufts of smaller stone canals with minute heads. Numerous tufts of branched Polian vesicles. Inner anatomy otherwise typical of the family.

Deposits large, well-developed end plates, a few perforated spinous rods; tentacles with few rosettes in younger individuals. Colour greyish mottled to almost black, ventrum paler, tentacles dark. Shallow-water forms. (After Deichmann, 1941.)

**MATERIAL EXAMINED:** Sta. 4, four specimens from *Macrocytis* zone.

**REMARKS:** The four specimens in the present collection range in length between 140 mm and 185 mm. The body is covered in tube feet, which are more numerous ventrally. Colour in alcohol is dark brown to blackish dorsally, fading to light brownish-grey on the ventral surface. There are 20 black tentacles arranged in two rings. The outer ring has 10 regularly spaced, profusely branched larger tentacles, averaging about 25 mm in length. The inner ring lies close around the mouth, and comprises five radially placed pairs of short, sparsely branched tentacles of 8 mm average length. The oral field is about 20 mm in diameter. Immediately outside the ring of large tentacles, in the middorsal interradius, lies a small approximately circular mound of tissue about 1 mm high and 2 mm broad, which supports the genial aperture.

The mouth is large, and examination of the intestinal contents in a dissected specimen showed that hard pieces of *Macrocytis* stipe up to 42 mm long and 6 mm wide, or 25 mm × 10 mm can be ingested. The intestine also contains fragments of green algae, both filamentous and thalloid, brown algae (*predominantly Macrocytis*), appendages of small crustaceans, and hydroids. This species seems to be primarily a vegetarian browser.

The calcareous ring is large, and has been illustrated by Heding and Panning (1954).

The gut is thin-walled, and takes a large S-shaped loop. The cloaca is broad, thick-walled, attached to the body wall by very numerous muscle strands. Respiratory trees take the form of two broad flat tubes with scattered, profusely branched tufts of respiratory tubules. The trees arise from the anterior end of the cloaca in the lateral dorsal interradius, and extend anteriorly for about half the length of the body cavity.

A tuft of numerous Polian vesicles arises from the ventral side of the water-vascular ring. The stone canal stems from the dorsal side of the ring, and gives off smaller canals which lie to each side of the strong dorsal mesentery, and terminate in nodular madreporites.
The gonad almost fills the rest of the body cavity, and consists of two bunches of sparsely branched genital caeca, lying one to each side of the dorsal mesentery. The caeca are orange in colour, with white thickenings scattered along their length.

Radial muscles are represented as broad flat straps. The retractor muscles are each split into two or three narrow bands, joined by a thin web of tissue for most of their length. In the specimen dissected a commensal pinnotherid crab was found in the last branch of the intestine, half way along the body cavity. The crab appeared to have caused little damage to adjacent tissues, apart from a slight rupturing of the wall of the intestine. This rupture might conceivably have been caused during preservation or transport of the specimens.

I found no calcareous deposits in the body wall or in the tube feet, although end plates are known to occur in the tube feet of this species.

Due to the work of Deichmann (1941) and Heding and Panning (1954), the systematic position of this species is now quite clear.

**DISTRIBUTION:** Deichmann (1941) notes that *Athyonidium chilensis* is probably "the most common phyllophorid known from Chile." The species is also found along the coast of Peru. The present locality record does not affect the known distribution pattern, and it is apparent that this species is reasonably common in the *Macrocystis* zone, immediately below low-tide mark.

**Family CUCUMARIIDAE**

**Subfamily CUCUMARIINAE**

Genus *Cladodactyla* Brandt, 1835 emend.

Panning, 1940

**DIAGNOSIS:** Tentacles 10. Calcareous ring small, without bifurcating processes. Skin deposits merely plates. The plates are thin, smooth, developed from forked rods. (After Panning, 1949.)

**TYPE SPECIES:** *Cladodactyla crocea* (Lesson).

**REMARKS:** The genus *Cladodactyla* contains three species at the present time. *C. senegalensis* Panning and *C. monodi* Cherbonnier are known from Dakar and the Cameroons coast, respectively.

**Cladodactyla crocea** (Lesson)

*Cladodactyla crocea* Lesson, 1830, p. 153, pl. 52, figs. 1, 1r; Theel, 1886a, pp. 58, 110, pl. 12, figs. 1, 2; Ludvig, 1898a, p. 15, pl. 1, figs. 6–13 (list of references); Bell, 1908, p. 2; Ekman, 1925, p. 75, figs. 15, 16; Deichmann, 1947, p. 331.

*Cladodactyla crocea* Panning, 1940, p. 172; Panning, 1949, p. 413; Panning, 1957, p. 27, figs. 12, 13.

**DIAGNOSIS:** Thin-skinned, small (up to 100 mm), dendrochirotides with equal-sized tentacles. Tube feet restricted to the ambulacra, larger ventrally, smaller and more numerous dorsally (when present); usually arranged into double rows. Calcareous ring simple, with no posterior processes. Deposits perforated rods or platelets, reduced or lacking in older specimens. Tube feet with end plates. Brood-protecting.

**MATERIAL EXAMINED:** Sta. 73, 24 specimens.

**REMARKS:** *Cladodactyla crocea* is one of the best-known of the holothurians from southern waters, and I have little to add to the thorough accounts given by the workers listed in the synonymy above. The specimens in the present collection range in total length from 10 mm to 27 mm. Colour in alcohol is light brown to dark greyish-brown. In some specimens, tube feet are entirely lacking from the dorsal radii. Theel (1886) noted that in the 20–40 mm specimens, dorsal tube feet were wanting, but this is not the case in all of the specimens in the present collection. I found no juveniles on the dorsal surface of any specimens, although Theel's (1886) material, which was collected at about the same time of the year, included some specimens carrying broods of juveniles. Examination of the gonad in the larger specimens in my collection indicated that sexual maturity had not as yet been reached.

Calcareous deposits proved to be very rare, the tentacles sometimes containing isolated perforated rods in the smallest specimens (Fig. 1, 1). In larger specimens the tentacle rods were mainly absent. With the exception of the end plates in the tube feet (Fig. 1, 2), body wall deposits tend to be very scarce or lacking altogether. In a single 14 mm specimen I found but three deposits in the skin of the dorsal side (Fig. 1, 3). These took the form of perforated platelets.
The features of the internal anatomy have already been described.

**DISTRIBUTION:** Cladodactyla crocea is most commonly found at the southern tip of South America, about the Straits of Magellan, and along the eastern coast of southern South America, as far north as the mouth of the Rio de la Plata. The species is also known from Kerguelen, South Georgia, and Antarctica (Coulman Is., Hut Point, and Franklin Is.) (Bell, 1908). C. crocea has been taken between low-tide mark and 4,300 m, but is most common to depths of about 30 m, often associated with seaweed.

Genus Stereoderma Ayres, 1851 emend. Panning, 1949

**Pentactella** Verrill, 1876.

**DIAGNOSIS:** Tentacles 10. Calcareous ring simple, without forked processes. Body wall deposits are knobbed plates, all of the same shape, and arranged in one layer; no tables, no rosettes, no cups. (After Panning, 1949.)

**TYPE SPECIES:** Stereoderma unisemita (Simpson).

**REMARKS:** The genus Stereoderma contains about 12 species at the present time. Four of the species have a circumpolar distribution when considered together. S. leoninoides (Mortensen), Auckland and Campbell islands. S. godefroyi (Semper), west coast of South America 20°-40° S (Deichmann, 1947).

S. laevigata (Verrill), southern end of South America, Falkland Is., Kerguelen Is., Marion Is., the Crozets, Antarctica.

S. perrieri (Ekman), southern Chile, Falkland Is., South Georgia.

These four species seem to be closely related to each other, and their distribution parallels the case of certain species of Trachysbyone (Pawson, 1962).

Stereoderma laevigata (Verrill)

Pentactella laevigata Verrill, 1876, p. 68; Studer, 1876; Studer, 1879; Smith, 1879, p. 271.

Cucumaria laevigata Theel, 1886a, p. 57, pl. III, fig. 5, pl. IV, fig. 13; Lampert, 1886, p. 828; Ludwig, 1898a, p. 32, pl. II, fig. 25;

Herouard, 1901, p. 44; Perrier, 1905, p. 22; Herouard, 1906, p. 12, pl. 2, figs. 5, 6; Bell, 1908, p. 2; Helfer, 1917, p. 164; Ekman, 1925, p. 56, text fig. 11; Deichmann, 1947.

Cucumaria serrata Theel, 1886a, p. 73.

**Stereoderma laevigata** Panning, 1949, p. 422.

**DIAGNOSIS:** Tentacles of equal size, feet restricted to the ambulacra, calcareous ring simple. Spicules as oblong plates with one end denticulate, sometimes knobbed with a reticulated network; they are numerous in smaller specimens, more scattered in larger ones. Tube feet have end plates and three-armed rods. Tentacles with perforated rods; introvert with four-holed buttons sometimes with an external reticulum. Total length up to 120 mm. (After Deichmann, 1947.)

**MATERIAL EXAMINED:** Sta. 37, one specimen.

**REMARKS:** The single specimen is small (total length 8 mm), and is strongly contracted, with many deep transverse wrinkles. Colour in alcohol is light brown. The calcareous deposits are typical of this species and need no further discussion here. Stereoderma laevigata is a species which is readily recognised because of its distinctive calcareous deposits.

**DISTRIBUTION:** Deichmann (1947) notes that S. laevigata is known from the southern tip of South America, the Chile coast, Falkland Is., Kerguelen Is., the Crozets, Marion Is. Bell (1908) reported specimens from the vicinity of McMurdo Bay, Antarctica, to depths of about 41 fathoms.

Genus Pseudocnus Panning, 1949

**DIAGNOSIS:** Tentacles 10. Calcareous ring simple, without posterior processes. In the body wall are knobbed plates of two types in two layers. (After Panning, 1949.)

**TYPE SPECIES:** Pseudocnus kollikeri (Semper).

**Pseudocnus dubiosus** (Semper)

For synonymy see Panning (1950).

**DIAGNOSIS:** Medium-sized, length up to 100 mm. Tube feet in five bands, numerous in the dorsal ambulacra. Tentacles bushy, of unequal size. Calcareous ring simple. Deposits numerous oblong knobbed plates (of average length 0.12 mm) with one end denticulate, and four-hole
knobbed buttons (0.9 mm average length). Tube feet with rudimentary end plates or none at all, and numerous perforated supporting rods, mostly three-armed. Introvert and tentacles have perforated plates and rods. (After Deichmann, 1941.)

**MATERIAL EXAMINED:** Sta. 19, 1 specimen; Sta. 27, 57 specimens; Sta. 39, 15 specimens; Sta. 40, 2 specimens; Sta. 52, 10 specimens; Sta. 54, 4 specimens; Sta. 77, 1 specimen.

**REMARKS:** The 90 specimens range in length from 10 mm to 50 mm. The colour varies between white and pink. This species is one of the best-known from Chile and has been described by many workers. Panning (1950, 1952) has suggested that there are three "forms" of this species. They are *P. dubiosus-leonina*, from the southern end of South America (all of the present specimens are of this type); *P. dubiosus-dubiosa* ranges the Atlantic and eastern Pacific shores, as far south as Chile; *P. dubiosus-jageri* is known from South Africa.

The deposits of the body wall in the present material (Fig. 1, 5, 7) are those of the *leonina* form. Small specimens may show stages in the development of knobbed buttons (Fig. 1, 8). The tube foot deposits (Fig. 1, 4) are perforated plates, often three-armed, about 0.22 mm in average length. The tentacles contain perforated rods and small plates up to 0.32 mm long (Fig. 1, 6).

A thorough investigation of all of the species in the genus *Pseudocnus* is urgently needed, particularly those species which have the body wall deposits as plates with one end denticulate, and buttons. For a successful attempt at a revision, a representative range of specimens of each species would be required, and unfortunately these are not available to the writer at the present time.

**DISTRIBUTION:** The *leonina*-form of this species is known from southern Peru in the west of South America to the Rio de la Plata in the east, and the Falkland Is., from the intertidal zone to approximately 100 m.

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**Subfamily COLOCHIRINAE**

**Genus Trachythone Studer, 1876**

For synonymy, see Panning (1949).

**DIAGNOSIS:** Calcareous ring simple, without forked processes. In the skin are cups and smooth plates, the plates imbricating in some species. (After Panning, 1949.)

**TYPE SPECIES:** *Trachythone muricata* (Studer).

**REMARKS:** This genus comprises about 20 species, of which 11 are distributed in the southern Pacific Ocean from Australia to South America and also Kerguelen Is. The remaining species are found in the Indo-West-Pacific and Mediterranean regions.

*Trachythone lechleri* (Lampert)

*Thyone lechleri* Lampert, 1885, p. 253, fig. 64; Theel, 1886a, p. 267; Ludwig 1898a, p. 44, pls. 2, 3, figs. 26–33; Perrier, 1905, p. 35; Ekman, 1925, p. 101, fig. 22; Deichmann, 1947, p. 335.

*Thyone hassleri* Theel, 1886b, pp. 11–12.

*Trachythone lechleri* Panning, 1949, p. 426, figs. 12–14.

**DIAGNOSIS:** Medium-sized (up to 15 cm total length); colour in alcohol, brown. Tube feet numerous, scattered. Deposits thick oval plates, sparsely perforated, length 0.07–0.2 mm, overlain by rudimentary “cups” of varying shapes. End plates in tube feet surrounded by perforated supporting plates of 0.2 mm average length.

**MATERIAL EXAMINED:** Sta. 54, nine specimens.

**REMARKS:** These are typical specimens of this unusual species. The total length ranges from 47 mm (a strongly contracted specimen) to 130 mm. The colour in alcohol is mottled light brown to dark orange-brown. The tube feet are lighter in colour than the rest of the body. In most cases the tentacles are completely retracted. The calcareous ring is simple, with no posterior processes, and is solid, with the five radials and five interradials firmly fused together. The
Fig. 2. 1–5, *Trachythyone lechleri* (Lampert). 1, Radial and interradial pieces of calcareous ring. 2, Plates from the body wall. 3, Tube foot deposits. 4, Plates from the posterior extremity of the body. 5, Rudimentary cups.

6–10, *Neopsolidium convergens* (Herouard). 6, Cups from the dorsal skin. 7, Tentacle deposits. 8, Plates from the dorsal body wall. 9, Buttons from the ventral body wall. 10, Plates from the ventral body wall.
radials each have an anterior notch for insertion of retractor muscles (Fig. 2, 1). There is a single tubular Polian vesicle about 40 mm in length, which arises from the water-vascular ring in the left dorsal interradius; the madreporite is a very small nodule about 1.5 mm in diameter, lying near the posterior edge of the calcareous ring in the middorsal interradius. The gonad comprises two bunches of elongate unbranched orange-coloured caeca, which attach to the long genital duct near the middle of the body in the middorsal interradius.

The skin is packed with great numbers of calcareous deposits, which chiefly take the form of thick, oval plates, with few perforations or none, and a length varying between 0.07 mm and 0.2 mm (Fig. 1, 2). Overlying the plates are a small number of rudimentary “cups” which vary considerably in shape (Fig. 2, 5), and occasionally carry short, blunt knobs, and may have up to three perforations. At the extreme posterior end of the body the plates are larger, and more complex, with a great number of perforations, and a tendency to become knobbed or two-layered (Fig. 2, 4). These plates are up to 0.3 mm long. The tube feet contain stout end plates which are surrounded by perforated supporting deposits (Fig. 2, 3), having an average length of about 0.2 mm.

Lampert (1895) apparently stated that this species has a calcareous ring with posterior prolongations, as Theel (1886a), after examining the “Challenger” specimens of Thyone leclleri, stated that “each piece of (the calcareous ring) ...has a bifurcate projection posteriorly.” Then Theel (1886b) described a new species, Thyone basleri, which resembled Lampert’s Thyone leclleri in most respects, but lacks posterior processes on the calcareous ring. Ludwig (1898a) illustrated the calcareous ring of what he believed to be Thyone leclleri, and it is similar in every way to the ring illustrated in this paper (Fig. 2, 1), and lacks forked posterior processes. Panning (1949) also states that the calcareous ring in species leclleri lacks posterior processes. Either Theel (1886b) was quite correct in erecting the species basleri for those specimens with no posterior processes on the calcareous ring (in which case some specimens previous workers have assigned to species leclleri are in fact basleri), or Lampert’s type specimen of leclleri may have been unusual in possessing posterior processes. The calcareous deposits of species leclleri and basleri are apparently identical and are so unique in character that it seems logical to leave the two species as synonyms. The problem cannot finally be resolved until Lampert’s type material can be re-examined.

**DISTRIBUTION:** Trachythyme leclleri is known from the vicinity of Magellan Straits and Tierra del Fuego in depths up to 30 m. A single holothurian from Heard Is., resting in the collection of the Dominion Museum, Wellington, was identified by the author as Trachythyme leclleri, and thus the range of this species is now considerably extended.

**Family PSOLIDAE**

**Genus Neopsolidium n. gen.**

**DIAGNOSIS:** Small forms, with sole not sharply distinguished from the rest of the body. Dorsal deposits small (up to 0.4 mm) smooth perforated plates, and cups. Ventral deposits plates similar to dorsal plates and perforated buttons; no cups ventrally.

**TYPE SPECIES:** Psolidium convergens (Herouard).

**REMARKS:** Deichmann (1941, 1947) stated that the species Psolidium convergens deserves a separate genus because of the nature of its dorsal deposits, which differ from those in most other Psolidium species. This opinion was based chiefly on the thorough description and figures given by Perrier (1905) of this species. Clark (1946) agreed with Deichmann, but neither of these workers elected to propose a new generic name. Examination of specimens of Psolidium convergens in the Royal Society collection has convinced me that this species should be assigned to a separate genus. Although Neopsolidium is monotypic at present, it may accommodate some other Psolidium species, and future work will show whether or not this is possible.

The family Psolidae contains but a small number of genera, and the genus Psolus itself is in urgent need of revision. Such a revision is beyond the scope of this work.

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This text is an excerpt from a scientific paper discussing the morphology and taxonomy of the genus Neopsolidium, specifically focusing on the species Trachythyme leclleri and its distinguishing features. The description includes detailed observations on the structure of the calcareous deposits, the presence of cups and knobs, and the differences between the dorsal and ventral deposits. The text also touches on the classification of the species and the potential for further research in the family Psolidae.
KEY TO THE GENERA IN THE FAMILY PSOLIDAE

1(10). Tentacles 10.
2(7). Dorsal surface with tube feet.
3(4). Dorsal deposits include hourglass-shaped bodies, but lack cups or baskets.............. Thyoneposolus Clark
4(3). Hourglass-shaped bodies lacking, cups or baskets present.
5(6). Sole sharply set off; dorsal deposits conspicuous scales, and small cups. Dorsal tube feet may pass through some of the scales. Sole deposits plates or buttons, usually with an external layer of small deep cups.............. Psolidium Ludwig
6(5). Sole not sharply set off; dorsal deposits small (up to 0.4 mm), smooth perforated plates, and cups. Ventral deposits plates (similar to dorsal plates), and buttons (no cups).............. Pseudopsolus Ludwig
7(2). Dorsal surface without tube feet.
8(9). Dorsal surface with imbricating scales. Mouth and anus dorsal.............. Psolus Oken
9(8). Dorsal surface smooth, deposits sparingly scattered oval perforated plates, sometimes with warty surfaces, of average diameter 0.1 mm. Mouth terminal, anus subdorsal.............. Pseudopsolus Ludwig
10(1). Tentacles 15.............. Stolius Selenka

Neopsolidium convergens (Herouard)


DIAGNOSIS: As for the genus.

MATERIAL EXAMINED: Sta. 50, fragment of anterior end; Sta. 52, 2 specimens; Sta. 73, 1 specimen; Sta. 77, 2 specimens.

REMARKS: The material examined agrees well in most respects with the excellent descriptions and figures given by Perrier (1905) and Herouard (1906). The total length ranges between 18 mm and 22 mm while the juvenile specimen is 4 mm in length. Colour in alcohol is dirty white to light brown. The tentacles are orange to light brown, darker in colour than the rest of the body. Tube feet are restricted to the radii ventrally, where they are arranged in a double row in each radius. Near the extreme anterior and posterior ends of the body, the feet decrease in numbers and adopt a biserial arrangement. Dorsally the feet are scattered over both radii and interradii. The mouth and anus are slightly upturned. There are about 10 anal teeth or papillae.

Deposits in the dorsal skin are thick perforated plates 0.2–0.4 mm in length (Fig. 2, 8). The plates are closely aggregated together and overlain by cups, which are 0.14 mm in diameter (Fig. 2, 6). The cups are lacking in the juvenile specimen. Ventrally the plates are slightly more irregular in outline and are not so closely crowded together (Fig. 2, 10). Intermingled with the ventral plates, and more numerous than they are irregular perforated buttons (Fig. 2, 9). The tentacles contain perforated plates and button-like deposits in great numbers (Fig. 2, 7). Some of these deposits are curved and carry small knobs.

This species differs from the others known in the region (Psolidium dorisipes and P. disciformis) in possessing the characteristic small dorsal plates, which have warranted erection of a new genus to accommodate it.

DISTRIBUTION: Neopsolidium convergens has been taken from the waters about Cape Horn, Magellan Straits, Falkland Is., and South Georgia, in depths ranging to about 15 m, and seems to favour life in the Macroystis zone, where Herouard (1901) first discovered the species.

Genus Psolus Oken, 1815

DIAGNOSIS: Tentacles 10. Dorsal surface lacking tube feet, covered by imbricating scales. Sole sharply defined, deposits smooth or knobbed plates or buttons.

TYPE SPECIES: Psolus phantapus (Strussenfeldt).

REMARKS: This genus now contains over 30 species, which are spread widely over the Arctic and Antarctic regions and in the tropics. Psolus species are most common in shallow water, but some types are known from considerable depths.
Holothuroidea from Southern Chile—Pawson

Psolus patagonicus Ekman

Psolus patagonicus Ekman, 1925, p. 140, text figs. 35, 36; Deichmann, 1941, p. 148, pl. 30, fig. 8; Deichmann, 1947, p. 339, figs. 1, 2.

DIAGNOSIS: A small psolid, up to 20 mm in total length, with oral and anal valves, and radial teeth between them. Few scales between mouth and anus. Sole distinct with one or two marginal rows of tube feet. Mid-ventral radius naked. Sole deposits mostly four-holed knobbed buttons (average length 0.1 mm), together with a few small plates. Tentacles invested in smooth or knobbed perforated plates (0.07–0.17 mm in length).

MATERIAL EXAMINED: Sta. 39, 30, specimens; Sta. 40, 1 specimen.

DESCRIPTION: The specimens are small (total length ranges from 2.5 mm to 11 mm), dorso-ventrally flattened, oval in outline, broadest near the anterior end. The dorsal surface carries mouth and anus, and is invested in overlapping plates. The ventral sole is soft. Colour in life "salmon-pink"; in alcohol, light yellowish-brown dorsally, orange-brown ventrally. The tentacles are orange-yellow, with some small brown spots.

The dorsal plates are about 0.8 mm broad and tend to overlap towards the midline, while the dorsal surface is bordered by one to three rows of smaller marginal plates (Fig. 3, 1). The plates are thick, reticulated, and beset with minute knobs. The plates also carry a small number of tiny pearl-like grains, which are less common in smaller specimens. There are about five plates between mouth and anus.

The dendritic tentacles are extended in most specimens, and the ventral pair are somewhat smaller than the rest, unbranched or weakly branched. There are five conspicuous triangular interradial oral valves (Fig. 3, 1), between and below which lie five radial valves, which are in the form of elongate isosceles triangles. In a small number of specimens, one to four smaller plates lie near the base of the oral valves, but these are not always present. The anal aperture is also covered by five radial valves and five anal valves (Fig. 3, 1).

The soft sole is semitransparent and is bordered by a ring of tube feet in a single or sometimes double row. The mid-ventral radius is naked (Fig. 3, 2).

The calcareous ring comprises five radials and five interradials fused together. Each radial piece has an anterior process with a deep, narrow notch. Interradials each have an anterior process with no notch. There are no posterior processes (Fig. 3, 6). The ring is turned so as to lie parallel with the dorsal surface of the body to correspond with the dorsal position of the mouth. Therefore the mid-ventral radial piece is the most anterior portion of the ring.

The thin-walled intestine is coiled into three loops, and the mesentery of the posterior loop of the intestine lies as usual in the right ventral interradius. Overall, the intestine is a dark orange-brown in colour. A single bulbous Polian vesicle arises from the water vascular ring in the left ventral radius. The short stone canal and nodular madreporite lie in the middorsal interradius.

The gonads in the larger specimens are well developed as two bunches of light brown tubular unbranched caeca, which extend for the length of the body cavity. The genital duct proceeds along the dorsal side of the calcareous ring (or more correctly, the "posterior" side), and opens to the exterior immediately behind the tentacles, but apparently within the oral valves.

Apart from the dorsal surface, calcareous deposits are present in the sole, the tentacles, and the tube feet.

1. Sole deposits: The thin sole contains four-holed button (Fig. 3, 3), and some slightly larger knobbed or smooth plates (Fig. 3, 3). These deposits are sparingly scattered in the sole.

2. Tube foot deposits: Each tube foot has an end plate (Fig. 3, 7) of average diameter 0.23 mm, which is surrounded by some curved perforated rods and plates, which may carry knob-like projections (Fig. 3, 5). The length of these deposits varies between 0.06 mm and 0.2 mm.

3. Tentacle deposits: The tentacles are invested in a network of perforated rods and plates, some of which carry knobs (Fig. 3, 4).

REMARKS: After having examined these specimens, I thought that I had found a new species, as they differ in some respects from Ekman's (1925) type specimen. Both Ekman (1925) and Deichmann (1941) state that Psolus patagonicus can have small intercalary plates between the larger dorsal plates. The photograph of Ekman's
(1925) specimen clearly shows these plates. None of the specimens I examined possess these intercalary plates. Ekman's specimen was 20 mm long, while the largest in the present collection is 11 mm in total length. This size discrepancy could explain the absence of intercalary plates in my material, as they may develop later in the life of the animal.

The present specimens closely resemble the type of P. patagonicus when their calcareous deposits are considered, and thus there is little doubt that they are in fact examples of Ekman's species.

**Distribution:** The type specimen (Ekman, 1925) was collected from the Patagonian bank, 46° S, at a depth of 110 m. Deichmann (1941, 1947) states that the species has been taken from the type locality and various other localities in the Straits of Magellan. Present records indicate that *Psolus patagonicus* may be quite common in some localities, its small size perhaps enabling it to escape notice by the collector.

**ORDER APODIDA**

Family CHIRIDOTIDAE

Genus *Chiridota* Eschscholtz, 1829

*Dactylota* Brandt, 1835; *Liosoma* Brandt, 1835; *Trochinites* Ayres, 1852; *Lioderma* Bronn, 1860.

**Diagnosis:** Tentacles 12, digits 3–10 on each side, the terminal pair being the longest. Polian vesicles numerous (3–20). Deposits six-spoked wheels collected into small papillae containing varying numbers of wheels of diverse sizes. No sigmoid rods, but small curved rods with enlarged ends may be present. Minute milliary granules often occur in the longitudinal muscles.

**Type Species:** *Chiridota discolor* Eschscholtz.

**Remarks:** This is a well-defined genus of world-wide distribution, containing about 25 species, none of which have a very extensive geographic range. Most species occur in shallow waters, although some have been taken at depths in excess of 3,500 m.

*Chiridota pisanii* Ludwig

*Chiridota pisanii* Ludwig, 1886, p. 29, pl. 2, fig. 14; Ludwig, 1898a, p. 71 (complete list of references); Ludwig, 1898b, p. 445; Clark, 1907, p. 118; Ekman, 1925, p. 145, text fig. 62; Heding, 1928, p. 297, text fig. 62; Heding, 1931, p. 676; Deichmann, 1947, p. 347.

*Chiridota purpurea* Theel, 1886a, pp. 15, 35, pl. 2, fig. 1; Lampert, 1889, p. 851.

**Diagnosis:** Tentacles 12, usually with five pairs of digits each. Calcareous deposits wheels, which are arranged in papillae up to 1.5 mm in diameter. Papillae confined to the interradii, and are more numerous dorsally, where they are arranged in a single row in each interradius. No other deposits in the skin. Radial muscles contain milliary granules. Tentacle rods brackish-shaped, with branched ends, average length 0.05 mm.

**Material Examined:** Sta. 73, four specimens.

**Remarks:** The total length of the four specimens ranges between 11 mm and 60 mm. Colour in alcohol dirty white to light brown. There are 12 tentacles, each with five pairs of digits. The wheel papillae vary considerably in diameter, up to a maximum of 1 mm.

Dissection of the largest specimens revealed the presence of seven Polian vesicles, the largest being 7 mm in length. Rows of closely aggregated ciliated funnels lie in the middorsal and left lateral interradii, the rows commencing about 6 mm from the anterior end of the body cavity, and extending to the extreme posterior end. The genital tubules are long, sparsely branched, and packed with eggs averaging 0.3 mm in diameter. Deichmann (1947) has commented on the relationships of this species, and notes that deeper water forms are known which may perhaps be assigned to *Chiridota purpurea* Theel.

**Distribution:** *Chiridota pisanii* is known from both coasts of southern South America, and the Falkland Is., from the intertidal zone to about 100 m.

Genus *Trochodota* Ludwig, 1892

**Diagnosis:** Tentacles 10, digits 2–6 on each side. One Polian vesicle and one stone canal. Calcareous ring comprises 10 pieces, the radial unperforated. Calcareous deposits sigmoid hooks, scattered or arranged into groups, and wheels.
Fig. 3. 1-7, *Psolus patagonicus* Ekman. 1, Dorsal view of 9 mm specimen. 2, Ventral view of same specimen, showing disposition of tube feet. 3, Plates and buttons. 4, Tentacle deposits. 5, Tube foot deposits. 6, Portion of calcareous ring. 7, End plate of tube foot.

8, *Trochodota purpurea* (Lesson), tentacle deposits.
scattered and never grouped into papillae. (After Clark, 1907.)

**TYPE SPECIES:** *Trochodota purpurea* (Lesson).

**REMARKS:** This is a well-defined, cosmopolitan genus, containing about a dozen species, some of which are inadequately described. There are three species in Australia, two in New Zealand, and one in southern South America. *T. dunedinensis* from New Zealand resembles *T. purpurea* from South America in many respects, and the two species may be related.

*Trochodota purpurea* (Lesson)

*Holothuria (Fistularia) purpurea* Lesson, 1830, p. 155, pl. 53, fig. 1.

*Chiridotana purpurea* Jager, 1833, p. 16; Dujardin and Hupé, 1862, p. 616.

*Chiridotana purpurea* Brandt, 1835, p. 259.

*Sigmodota purpurea* Studer, 1876, p. 454 (partim).

*Chiridota australiana* Theel, 1886a, p. 16.

*Chiridotana studeri* Lampert, 1889, p. 839, pl. XXIV, fig. 12.

*Trochodota studeri* Ludwig, 1892, p. 359.

*Sigmodota studeri* Oestergren, 1898.

*Trochodota purpurea* Ludwig, 1898a, p. 83, pl. III, figs. 43–45; Perrier, 1905, p. 76; Clark, 1907, p. 123; Clark, 1921, p. 166; Ekman, 1925, p. 149; Deichmann, 1947, p. 351.

**DIAGNOSIS:** Tentacles 10, each with 2–6 pairs of digits. Wheels (0.13–0.18 mm diameter) scattered in the skin, together with sigmoid hooks (0.12–0.13 mm long). Tentacle deposits, when present, average 0.078 mm in length, and are bracket-shaped, with dichotomously branching ends. Colour in life commonly purple.

**MATERIAL EXAMINED:** Sta. 73, 8 specimens; Sta. 74, 2 specimens; Sta. 77, 1 specimen.

**REMARKS:** The smallest specimen in the collection is 4 mm in total length, and the largest is 100 mm. Colour in alcohol ranges from off white to light brown or violet. The number of tentacle digits varies. Clark (1921) in his key to the species of *Trochodota* stated that species *purpurea* has tentacles with six digits each. In the present collection, one specimen has 12 digits per tentacle, and another has eight. Clearly the number of tentacle digits is not a reliable diagnostic character in this species. The calcareous deposits in the skin have been well described.

The tentacles in some of the specimens contain a number of bracket-shaped rods with dichotomously branching ends (Fig. 3, 8). Perrier (1905) stated that the tentacles in his material were "totally devoid of calcareous deposits," while Deichmann (1947), in diagnosing this species, wrote "... no spicules in the tentacles." Ludwig (1898a) illustrated a single tentacle rod, and it closely resembles those illustrated here. There is no doubt, then, that tentacle deposits may be present, perhaps in young stages, and become rare or disappear as a specimen grows, as can happen with the wheels and hooks in the body wall.

**DISTRIBUTION:** *Trochodota purpurea* is recorded from the southern tip of South America and the Falkland Is., to depths of about 50 m. Habitat includes sand, shelly bottom, and holdfasts and fronds of seaweed, especially *Macrocystis*.

Genus *Taeniogyrus* Semper, 1868

*Sigmodota* Studer, 1876.

**DIAGNOSIS:** Tentacles peltato-digitate, 10 or 12. Digits five to seven pairs per tentacle, the terminal pair being the longest. Calcereous deposits are wheels gathered into papillae, and sigmoid hooks (about 0.2 mm long), scattered in the skin. No miliary granules in radial longitudinal muscles.

**TYPE SPECIES:** *Taeniogyrus australianus* Stimpson.

**REMARKS:** This is a small genus containing about six species. Three species are known from Australia, one from Japan, one from Hawaii, and one from the southeast Pacific Ocean.

*Taeniogyrus* lies intermediate between *Chiridota* (wheels and occasionally curved rods, no sigmoid hooks) and *Trochodota* (wheels, and sigmoid hooks, the wheels not grouped into papillae).

*Taeniogyrus contortus* (Ludwig)

*Chiridotana contorta* Ludwig, 1874, p. 80, pl. VI, fig. 6; Lampert, 1885, p. 234; Theel, 1886a, pp. 16, 33, pl. 2, fig. 2; Theel, 1886b, p. 20; Lampert, 1889, pp. 851, 853.

*Sigmodota purpurea* Studer, 1876, p. 454; Studer, 1879, p. 123.
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*Chirodota purpurea* Bell, 1881, p. 101; Lampert, 1885, p. 236; Lampert, 1886, p. 18, figs. 17–20; Ludwig, 1886, p. 29.

*Chirodota studerii* Theel, 1886a, p. 33.

*Chiridota contorta* Ludwig, 1892, p. 359; Ludwig, 1897, p. 217; Ludwig, 1898a, p. 73, pl. III, figs. 37–42.

*Sigmodota contorta* Ostergren, 1898; Sluiter, 1901, p. 154.

*Taeniogyrus contortus* Clark, 1907, p. 122, pl. VII, figs. 8–13; Clark, 1921, p. 165; Ekman, 1925, p. 147; Heding, 1928, p. 311, text fig. 66, 1–9; Deichmann, 1947, p. 348.

**DIAGNOSIS:** Tentacles 12, with five to seven pairs of digits. Wheels (diameter 0.042–0.13 mm) gathered into well-defined papillae; sigmoid hooks large (0.14–0.2 mm long) scattered in the skin. Tentacle rods 0.17 mm in length.

**MATERIAL EXAMINED:** Sta. 73, one specimen.

**REMARKS:** The single specimen is 50 mm in total length and has only 11 tentacles. Colour in alcohol is a dull, dark brown. The systematic position of *Taeniogyrus contortus* is now quite clear as a result of the work of Clark (1907, 1921) and Heding (1928).

**DISTRIBUTION:** The species is known from the southern tip of South America, Falkland Is., South Georgia, Burwood Bank, and Kerguelen Is., to depths of about 200 m. Sluiter (1901) recorded *Sigmodota contorta* from the Java Sea at a depth of 82 m. Clark (1921) doubted the accuracy of the identification, and it might well be that Sluiter's material represents yet another species. Fisher (1907) found a close relative to *T. contortus* in Hawaii.

**DISCUSSION**

1. The Holothurian Fauna of Southern Chile

Collections made at 18 stations in the Isla Chiloe area revealed only one species, namely *Abyonidium chilensis*, while at least seven shallow-water species are known from this region. *Abyonidium chilensis* is one of the most conspicuous holothurians in Peru and Chile, and Isla Chiloe represents the extreme southern limit of the range of the species.

From Puerto Eden to Punta Arenas, 31 stations were worked, and holothurians were taken from five stations. They were *Pseudocnus dubiosus*, *Stereoderma laevigata*, and *Psolus patagonicus*.

By far the most common species here was *Pseudocnus dubiosus*, which was collected in numbers at four of the five stations. This species, together with *Cladodactyla crocea* and *Stereoderma laevigata*, seems to favour the Macrocystis zone as a habitat.

Seven species were found at Isla Navarino and the southern regions, at six of the 29 stations worked. They were *Pseudocnus dubiosus*, *Cladodactyla crocea*, *Trachytyone lechleri*, *Neopsolidium convergens*, *Chiridota pisani*, *Trochoda purpurea*, and *Taeniogyrus contortus*.

Of these seven species, three are apodous forms. In an account of the marine work carried out by the Royal Society Expedition, Prof. Knox (personal communication) noted that "one of the salient features of the southern region is the reduction which has occurred in the number of species present," and he cited the case of species of Brachyura (Crustacea), of which there were 15 at Chepu (Isla Chiloe), and only two in the southern regions. This state of affairs clearly does not apply to the holothurians, as at least 14 species are known from the southern region, while approximately seven have been recorded from the Isla Chiloe area.

Between Isla Chiloe and Isla Navarino the character of the holothurian fauna changes, and the number of species gradually increases. There are no drastic changes which might indicate a provincial pattern, although the number of species shows a definite increase at about 52° S, immediately north of the western entrance to the Straits of Magellan.

Apodous species (e.g., *Trochoda purpurea*, *Chiridota pisani*, and *Taeniogyrus contortus*) are more numerous in the southern regions than elsewhere on the Chile coast, but there is no apparent reason why this should be the case.

The fauna of Chile contains a remarkably high percentage of cucumariids (ca. 40%), compared with that of New Zealand (33%) and Australia (22%). This is a striking feature of the fauna, as also is the virtual absence of phyllophorids below about 42° S, whereas New Zealand has 15%, and Australia 14%.

2. Relationships of the Fauna

A. With Australia, New Zealand, and the
Antipodean Province Islands: The holothurian fauna of southern Chile bears no close relationship to that of New Zealand and Australia. A single species, Paracandina chilenis, is common to New Zealand and southern Chile, and this species is a circum-Pacific eurybath form. Ocnus calcareus is known from New Zealand and Juan Fernandez, but has not as yet been recorded from the Chilean coast. The Antipodean Province Islands (Auckland Is., Campbell Is. in particular) of New Zealand support a holothurian fauna of New Zealand character, and thus the fauna differs fundamentally from that of other southern islands such as Kerguelen, Macquarie, South Georgia. However, one Antipodean Province species, Stereoderm a leoninoides (Mortensen) is a close relative of Stereoderm a laevigata from southern Chile, and it is quite possible that these two species may have been derived from some common source.

B. With that of Antarctica: Some species, including Cladodactyla crocea, Stereoderm a laevigata, Trachbythone parva, and Psolus antarcticus, are shared with the fauna of Antarctica. Fell (1961), in discussing the Ophiuroidea of Antarctica, stated that the Magellanic ophiuroid fauna is predominantly of southern American type, mingled with a few Antarctic species which are eurythermal. The four species mentioned above are probably eurythermal and can readily survive the difference in temperature between Antarctica and southern Chile.

C. With that of the Subantarctic Islands: The Falkland Islands (Islas Malvinas) have a holothurian fauna which is scarcely distinguishable from that of southern Chile. This is understandable when one considers that the islands are but 300 miles east of Tierra del Fuego, in a good position to accept species carried from southern South America by the westwind drift.

Among the Kerguelen Island holothurians are Cladodactyla crocea, Stereoderm a laevigata, Trachbythone parva, and Taeniogyrus contortus. Thus the fauna here also bears a remarkable likeness to that of southern Chile.

South Georgia, regarded as a separate biotic province by Knox (1960), shares Cladodactyla crocea, Trachbythone parva, Stereoderm a laevigata, Neoplosolidium convergens, Taeniogyrus contortus, and (with doubt) Anapta fallax with southern Chile.

Stereoderm a laevigata is also known in the fauna of Marion Island and the Crozets.

When considered overall, these islands have faunas which are similar to that of southern Chile, and the similarity is at the specific level. The dispersal of species to these widely separated areas is probably effected epiplanktonically (perhaps on rafts of seaweed), with the aid of the westwind drift. This is quite conceivable for such species as Stereoderm a laevigata and Cladodactyla crocea, which commonly live on the fronds and holdfasts of Macrocystis, a brown seaweed which is found on all of the islands mentioned above. The westwind drift dispersal mechanism for echinoderms has already been discussed by Mortensen (1925), Fell (1953, 1962), and Ekman (1953), and others.

The holothurian fauna of southern Chile is a generalised fauna, containing few restricted species, and notable because of the number of species which are shared with distant islands, and the Antarctic continent.

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Tenth Pacific Science Congress Papers

The Tenth Pacific Science Congress of the Pacific Science Association was held on the campus of the University of Hawaii August 21 to September 6, 1961, under the joint auspices of the University, the Bernice P. Bishop Museum, and the National Academy of Sciences.

The University of Hawaii Press is publishing seven volumes of the distinguished papers of the Congress, each volume dealing with a different subject as it applies to the conditions that prevail in the various countries of this vast and increasingly important segment of the world scene. They include:

ANCIENT PACIFIC FLORAS

The Pollen Story

Lucy M. Cranwell, editor

The papers collected in this volume record the existence, identity, and geographical location of fossil pollens, correlating them with climatic changes and glacial and geological periods. Fourteen articles contributed by eleven authors deal specifically with Australia, Borneo, Chile, Japan, New Zealand, and islands of the Pacific, and range from Eurasia and Antarctica to the sediment of the ocean floor.

In the course of outlining this method of attacking the eternally intriguing mystery of the earth's age, the authors have enumerated species and the places where they are to be found—findings which should be of interest to the petroleum industry as well as to the paleobotanist. The collection exemplifies the coordination of scientific studies for which the Pacific Science Association is noted.

Dr. Cranwell is associated with the Geochronological Laboratories at the University of Arizona, Tucson, Arizona.

114 pp., illus. Winter, 1964 Paper, $3.50

PUBLIC HEALTH AND MEDICAL SCIENCES

IN THE PACIFIC

A Forty-year Review

J. Ralph Audy, editor

The period covered by these reports—approximately 1920 to 1960—was one of turmoil, war, and political, social and cultural upheaval. The reports reflect strenuous efforts to salvage what was good in health practices and procedure in the past and to make all further progress possible in the face of adverse circumstances.

The countries reporting are: Australia, Canada, Chile, China (Taiwan), Indonesia, Japan, Malaya, the Philippines, Thailand, and the United States.

The report on the United States includes California and Hawaii.

This collection of reports will be of particular interest to those engaged in the various aspects of medical and public health work and to students of these areas. The material has been designed to appeal to the general scientist as well.

Dr. Audy is director of the George Williams Hooper Foundation, San Francisco Medical Center, University of California, Berkeley, California.

Approx. 300 pp. Winter, 1964 Paper, $7.50
SOIL CONSERVATION IN THE PACIFIC

A Symposium and Panel Discussion

J. C. Christ, convener and chairman

Conservation of our resources is of supreme importance, due to the fact that a food deficit exists in most of the countries of the Pacific. This monograph outlines workable plans for preserving resources that exist and developing new ones. The symposiums include the following subjects:

- The Use of Soil Surveys in Conservation Planning
- Watershed Management
- Economics of Conservation Programs
- Soil and Water Conservation in Relation to Wildlife Habitat
- Forestry Potential in Hawaii
- Plant Selection for Conservation Purposes

Mr. Christ was formerly state conservationist, U. S. Department of Agriculture, Soil Conservation Service, Honolulu, Hawaii.

viii, 58 pp. Ready Paper, $1.50

GEOL OGY AND SOLID EARTH GEOPHYSICS OF THE PACIFIC BASIN

Report of the Standing Committee

Gordon A. Macdonald, chairman

The Greater Pacific Basin represents the major portion of the earth’s surface, one which includes some of the most dramatically active areas geologically, one in which much work in geology and geophysics remains to be done. These papers go a long way toward evaluating what has been accomplished to date and establishing a basis for future studies in the area.

The monograph contains contributions covering the following countries:

- Australia
- Western Canada
- China (Taiwan)
- El Salvador
- Malaya
- Mexico
- Indonesia
- Japan
- New Zealand
- Philippines
- Thailand
- United States

Additional articles deal with special aspects of various areas of the Pacific. They include:

- The Pacific Basin
- Islands of Western North Pacific
- Thermal Waters and Volcanic Emanations
- British Solomon Islands

Dr. Macdonald is senior professor of geology at the University of Hawaii.

xii, 180 pp., 15 figs., tables Ready Paper, $5.00
Pacific Entomology

Report of the Standing Committee Chairman

J. J. H. Szent-Ivany

This volume is a survey of the extraordinary progress made in the study of insects of the Pacific area between 1958 and 1961, based on reports by Standing Committee members and published articles.

The possibilities of the spread of harmful or potentially harmful insects have been greatly increased by recent rapid expansion of swift communication facilities. As a result of introduced pests and methods used to control them, the balance of nature has in some areas been seriously disturbed.

The author not only treats thirty-seven countries and island groups in considerable detail, but gives a comprehensive picture of the entomological status in the area as a whole as he takes the reader on an orderly tour clockwise around the Pacific rim from Alaska to Japan.

Dr. Szent-Ivany is senior entomologist in the Department of Agriculture, Stock and Fisheries of the Territory of Papua and New Guinea.

x, 93 pp. Ready Paper, $2.50

Physical Aspects of Light in the Sea

A Symposium

John E. Tyler, editor

A dozen authorities from France, Japan, Sweden, and the United States describe and demonstrate, through detailed text and copious illustrations, techniques useful in the physical aspects of marine or fresh-water research.

Described and illustrated with photographs, diagrams, charts, and detailed construction plans are an underwater observation vessel and its photographic equipment; apparatus for measuring water samples and determining turbidity; instruments for photography in the sea and for measuring the angular distribution of submarine daylight.

In addition to the practical aspects of submarine light, theoretical calculations for light fields and for the scattering function of small particles are provided.

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