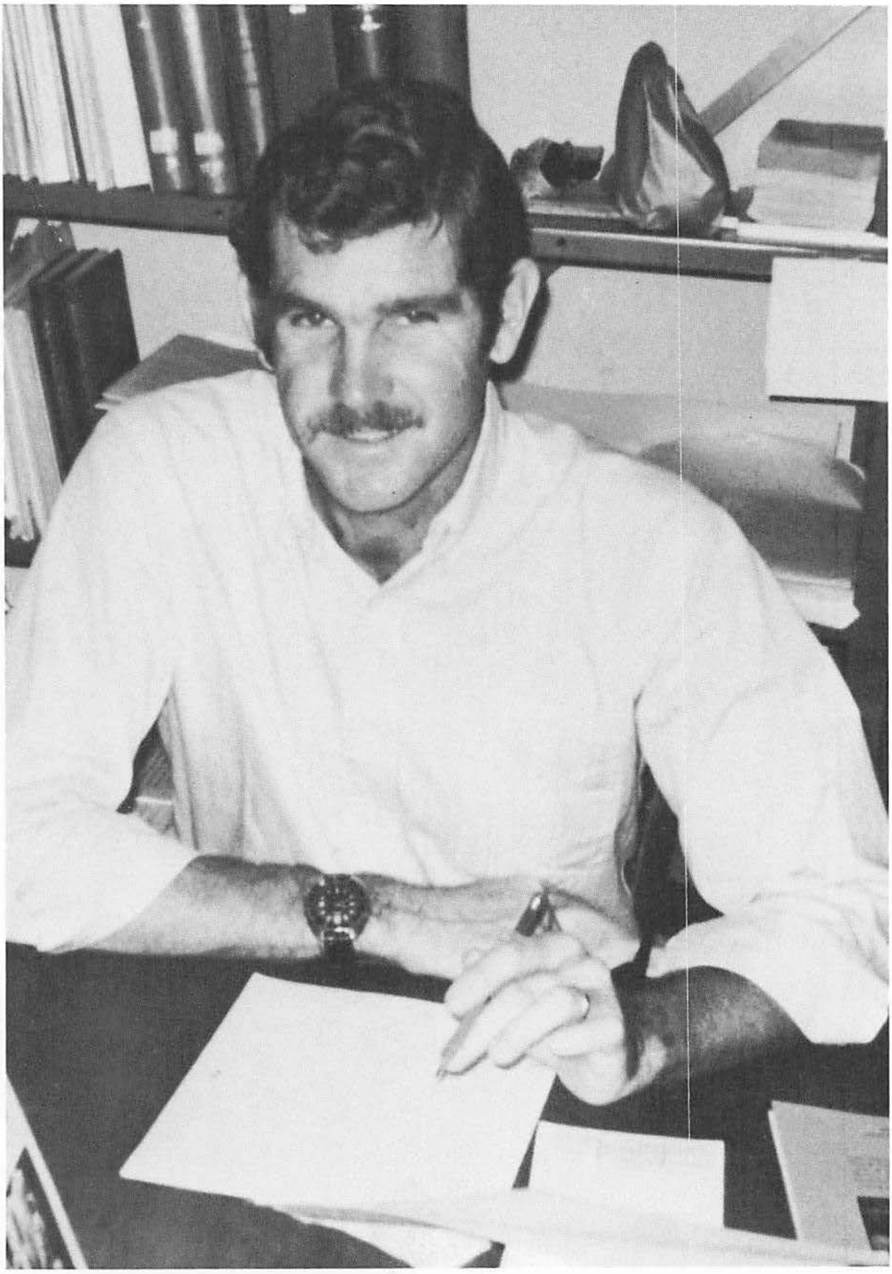
REEF AND SHORE FAUNA OF HAWAII

Sections 2 and 3



DENNIS M. DEVANEY
1938–1983

REEF AND SHORE FAUNA OF HAWAII

Section 2: Platyhelminthes through Phoronida
and
Section 3: Sipuncula through Annelida

Edited by
DENNIS M. DEVANEY
and
LUCIUS G. ELDREDGE

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DENNIS M. DEVANEY
1938–1983

THIS VOLUME, THE SECOND AND THIRD SECTIONS of the revised *Reef and Shore Fauna of Hawaii,* is dedicated to Dennis M. Devaney, the senior editor of the first 4 sections (section 4 having been published previous to this volume). As second editor of the series, I should like to have this volume added to the remembrance of Dennis, whose untimely disappearance while pursuing his research ended a most productive career in marine biology.

Born in Los Angeles on August 9, 1938, Dennis attended Occidental College, where he earned his A.B. degree in 1960. He continued his education with an M.A. degree at the University of California, Los Angeles, in 1962. That same year Dennis and his wife, Gail, moved to Hawaii, where Dennis attended the University of Hawaii and studied systematics and post-larval skeletal changes in ophiocomid brittlestars. His Ph.D. was awarded in June 1968. The following year he participated in post-doctoral research at the Smithsonian Institution in Washington, D.C.

Ophiuroids (brittlestars) were Dennis's prime interest. He worked painstakingly over their minute and often-times microscopic anatomy. His studies included systematics, and he described several new forms, including the genus *Clarkcoma*. Additionally, he conducted biological and ecological investigations on ophiuroids and other echinoderms.

Dennis joined Bishop Museum in 1967 as an assistant invertebrate zoologist, sharing his time between the Division of Invertebrate Zoology and the Pacific Scientific Information Center. After earning his doctorate, he became full-time invertebrate zoologist. Here he reorganized and extensively augmented and rearranged the collection. In 1979, he assumed the duties of Chairman of the Department of Zoology.

In 1977, the University of Hawaii invited Dennis to become an Affiliate Graduate Faculty member of the Department of Zoology.

During his research he travelled extensively in the Pacific. Even as an undergraduate student he spent time at Enewetak Atoll in the Marshall Islands as a research assistant. Poison fish and ecological surveys later took him to the Line Islands and Johnston Atoll. Much of his doctoral dissertation research was conducted at Enewetak. During the summer and fall of 1967, Dennis participated in a National Geographic Society expedition in southeastern Polynesia. Two years later, he visited Bermuda and Belize reefs, investigating the larval development of ophiuroids. The same year, 1969, he participated in the crown-of-thorns (*Acanthaster planci*) starfish survey at Guam and Yap.

Subsequently, Dennis joined a Bishop Museum-sponsored and National Geographic Society-supported expedition, again to southeastern Polynesia, in 1970–1971 aboard the schooner *Westward*. Collections made at Rapa and the Austral Islands were among the first subtidal marine animals collected there and resulted in numerous new records.

Dennis visited American Samoa several times to carry out environmental surveys. In April–May 1974 and March–April 1977, he conducted surveys for the U.S. Army Corps of Engineers. During October 1979, he researched the coral reefs of Tutuila and Manua Islands. Numerous visits were also made to Enewetak, where he was responsible for curating the invertebrate collection under contract with the Mid-Pacific Research Laboratory. In the fall of 1976, he participated in a National Science Foundation-sponsored Coral Reef Taxonomy Workshop, also at Enewetak. In early 1975, Dennis visited Truk briefly to investigate the impact of the runway extension.

Dennis was honored with a National Science Foundation United States-Australian Program grant award to conduct research on the systematics of Indian Ocean ophiuroids based on collections from the International Indian Ocean Expedition and from the Western Australian Museum. The entire family enjoyed Perth between November 1977 and August 1978. For the next 2 months, Dennis reviewed ophiuroids at the Zoological Survey of India at Calcutta and at other institutions on a Smithsonian travel grant.

In Hawaii, he studied reefs on the islands of Hawaii, Maui, and Oahu. Most recently he participated in research with the submersible *Makali'i* under the auspices of the Hawaii Undersea Research Laboratory and the U.S. Army Corps of Engineers, investigating dredge spoil sites and natural-products chemistry of gold corals at depths to 360 meters.

Dennis's interests were broad. His first publication pertained to a worm associated with echinoderms. He coauthored a new species of stenopididean shrimp and investigated the shell-forming sea anemone *Stylobates*. In the first section of *Reef and Shore Fauna of Hawaii,* he wrote the octocoral and ctenophore parts and coauthored the scyphozoan and other hydrozoan parts, as well as the nemertine part in this volume. Without his dedicated efforts, this multi-volume series would not have materialized.

Additionally, Dennis was very committed to museum studies. He was one of several authors who described problems and suggested recommendations for invertebrate collection resources. He was a member of the National Science Foundation Advisory Committee on the U.S. Systematics Resources in Invertebrate Zoology between 1974 and 1978. He presented a paper on "Functions and Services of Systematics Collections in the Pacific" at the Association of Systematics Collections Forum held at Bishop Museum in May 1982.

Dennis disappeared while scuba diving to collect shrimp off the northwest coast of the island of Hawaii, near Mahukona, on August 13, 1983. His memory will be continued by the animals named in his honor, as well as by his publications. The starfish genus *Devania* Marsh, 1974, is known only from Raivavae Island, Austral Group, French Polynesia. The soft coral *Cladiella devaneyi* Verseveldt, 1977, was collected by Dennis at Rurutu Island in the same island group. The brachyuran crab *Dynomene devaneyi* Takeda, 1977, was dredged off the southeast coast of Oahu. The banded shrimp *Stenopus devaneyi*

Goy and Randall, 1984, was first observed by Dennis; the shrimp was living in association with a moray eel from the Marquesas. Undoubtedly, additional remembrances will honor the memory of Dennis M. Devaney in the future.

LUCIUS G. ELDREDGE

University of Guam
Mangilao, Guam
Summer 1986

Note on the Series

REEF AND SHORE FAUNA OF HAWAII

INTEREST IN THIS SERIES, begun with Charles Howard Edmondson's single-volume publication in 1933, has remained strong for over half a century. A revised edition was published in 1946, and in 1965 a decision was made to generate an expanded series based on the original work.

The series was originally planned for 6 volumes:

Section 1:	Protozoa, Porifera, Cnidaria, and Ctenophora
Section 2:	Platyhelminthes, Nemertina, Aschelminthes, Ecto-Endoprocta, Brachiopoda, and Phoronida
Section 3:	Sipuncula, Echiura, and Annelida
Section 4:	Mollusca
Section 5:	Arthropoda
Seciton 6:	Echinodermata, Chaetognatha, Hemichordata, and Chordata (excluding vertebrates)

Section 1: Protozoa through Ctenophora was published in 1977. This was followed in 1979 by *Section 4: Mollusca* (*Hawaiian Marine Shells*), with Dr. E. Alison Kay as sole author. Other than *Mollusca,* all volumes are expected to be multi-author works. In the present volume we have combined sections 2 and 3 to produce a work broadly inclusive of all the marine "worm" phyla.

This combined volume could not have been realized without the efforts of the contributing authors and their own personal assistants. Additionally, the revision has benefited from the invaluable aid of Drs. A. H. Banner, M. G. Hadfield, E. A. Kay, and S. J. Townsley, all of the University of Hawaii.

Further acknowledgments are extended to the present Director of Bishop Museum, Dr. W. Donald Duckworth, and to staff and former staff of Bishop Museum Press—Henry Bennett, Keith Leber, Dr. JoAnn Tenorio, and Andrew Elston. The continued support and assistance of Drs. Richard Titgen and Allen Allison have been much appreciated.

L.G.E.

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INTRODUCTION

E. ALISON KAY

THE MARINE BIOTA of the Hawaiian Islands consists of the descendants of organisms that have been able to disperse successfully over thousands of miles of ocean. The biota has been recognized since the mid-nineteenth century as related to that of the Indo-West Pacific—that region of the tropical and subtropical ocean extending from the east coast of Africa in the Indian Ocean to Hawaii, the Line Islands, the Marquesas, and Easter Island in the Pacific. The Hawaiian marine biota, however, constitutes a distinct component within the Indo-West Pacific and is noted especially for its relatively high degree of endemism (Ekman 1953; Briggs 1974; Kay 1980). The Hawaiian marine biota is also distinguished by attenuation, that is, by having fewer species than are found among other island groups in the western Pacific; by disharmony, in that many species common elsewhere in the region are absent; and by the dominance of some species particularly associated with high islands.

Endemism is a characteristic feature of the Hawaiian marine biota and is almost entirely restricted to the species and subspecies levels; there are no endemic families, and only 3 genera each of mollusks, echinoderms, and fish are thought to be endemic (Ely 1942; Gosline and Brock 1960; Kay 1984). Various levels of endemism exist at the species level: 18% of the algae (Doty, pers. comm.); 25% of the polychaetes (Bailey-Brock, this volume); 20% of the mollusks (Kay 1967, 1979); 20% of the shallow-water asteroids and ophiuroids (Ely 1942); 40% of the crustacean family Alpheidae (Banner and Banner, in prep.); and 19% of the fish (Randall, pers. comm.).

Patterns of endemism are not clear-cut. High-shoreline and brackish-water mollusks appear to exhibit consistently higher proportions of endemism than do subtidal forms. Among the fish, not only are endemics abundant, but "they are represented with surprising regularity among the various reef fish families. There is not a single family represented in Hawaii by ten or more species in which there are not endemics" (Gosline and Brock 1960). Differences in size and habitat among the mollusks (Kay 1967, 1979) and fin-ray counts among the fish (Strasburg 1955; Gosline and Brock 1960), compared with those of the same species elsewhere in their range, suggest incipient speciation or isolation of gene pools. In *Cypraea caputserpentis* (Gastropoda: Cypraeidae) the interstices of the apertural teeth are brown in Hawaii and white elsewhere in its range. In the *manini*

(*Acanthurus sandvicensis*) the mark at the base of the pectoral fin is longer than it is elswhere (Gosline and Brock 1960). Among the fish, "when there is a difference in fin-ray counts, the Hawaiian form usually has more fin rays than its representative further south" (Strasburg 1955; Gosline and Brock 1960).

Comparison of the numbers of shallow-water species of corals, mollusks, echinoderms, and fish recorded from Hawaii with those found in other island groups within the western Pacific reveals attenuation. Seventeen genera and subgenera of corals are recorded from Hawaii, 59 in the Marshall Islands and 59 in the Line Islands (Maragos 1986); about 1,000 species of marine mollusks are found in Hawaii, 2,500 in the Ryukyu Islands (Kay 1967); 90 species of echinoderms are known in Hawaii, 345 in the Philippines (Clark and Rowe 1971); and 700 species of reef and shore fish are recorded from Hawaii (Randall 1981), about 1,000 in the Marshall Islands (Randall and Randall 1987).

Several groups of well-known Indo-West Pacific organisms have either never reached the Hawaiian Islands, or were here during the Pleistocene and have since become extinct. Among the mollusks that apparently never reached Hawaii are *Tridacna* (Bivalvia: Tridacnidae), cuttlefish (Cephalopoda: Sepeidae), and the Haliotidae and Vasidae (Gastropoda). The spider shell *Lambis* (Gastropoda: Strombidae) and the oyster *Pycnodonta* (Bivalvia) are examples of mollusks present during the Pleistocene but now extinct in the Hawaiian Islands. In the Crustacea there are no fiddler crabs (*Uca*). Among the fish there are no native snappers of the genus *Lutjanus* or shallow-water groupers of the genera *Epinephalus* or *Cephalophis,* genera important in the Indo-West Pacific ichthyofauna elsewhere (Randall and Kanayama 1973).

The dominance of some marine organisms along Hawaiian shorelines and their absence among the atolls of the central Pacific are also noteworthy. The algae *Ulva* and *Sargassum,* for example, are curiously restricted to high islands (Doty 1973; Tsuda 1968). The gastropod mollusks *Cellana* (Patellidae), *Hipponix* (Hipponicidae), *Littorina pintado* (Littorinidae), and *Nerita picea* (Neritidae) have a similar distribution (Kay 1979; Vermeij et al., 1983).

Within an area comprising a chain of islands that extends 2,451 km from north to south, which encompasses various topographical features and depths and where average water temperatures differ by as much as 4 °C, anomalies in distribution are perhaps not unexpected. Only 9 of the 15 genera of Hawaiian reef corals occur in the Northwestern Hawaiian Islands, where water temperatures are consistently lower than among the main islands (Ladd et al. 1967; Dana 1971). Fossils of Midway dating back to the Miocene, however, suggest a more diverse coral fauna there than now occurs (Ladd et al. 1967; Wells 1982). Several species of endemic mollusks, among them the limpets *Cellana exarata* and *C. sandwicensis* and the muricid *Neothais harpa,* are common on basalt shorelines of the windward islands but apparently absent on the calcareous shorelines of the northwestern islands (Kay 1979). Conversely, other molluscan species such as *Drupa grossularia* and *Nerita plicata* are common on the atoll shorelines of the northwestern islands but absent in the windward islands. Among the fish, melanistic forms are well known off the Kona coast of Hawaii Island but unknown from other areas in the Hawaiian chain (Gosline and Brock 1960).

HAWAIIAN MARINE ECOSYSTEMS

Benthic marine habitats are traditionally divided into 3 major zones: the littoral, the sublittoral, and the deep sea. The littoral zone has been further subdivided into a littoral fringe, where marine and terrestrial organisms intermingle but where marine organisms predominate; and a eulittoral zone, occupied by marine organisms adapted to, or requiring, alternating conditions of submersion and emersion (Lewis 1964). In the Hawaiian Islands, where tidal range is limited to less than 1 m and where wave action may not only effectively submerge shoreline benches and tide pools but also scour sublittoral substrates to depths of more than 15 m, Gosline and Brock (1960) recognize a suprasurge, a surge, and a subsurge zone in describing the vertical zonation of fish. A modification of Lewis's (1964) scheme and that of Gosline and Brock (1960) is used here.

SHORELINE ECOSYSTEMS

The littoral fringe. The littoral fringe is that area of shoreline fringed by the seaward edge of the maritime vegetation, comprising in Hawaii largely *naupaka* (*Scaevola*), *hau* (*Hibiscus*), sea heliotrope (*Messerschmidia*), and *Panicum*. The zone is above the reach of waves and tides but is markedly affected by salt spray. Two regions are distinguishable: an upper region, somewhat localized in occurrence, with broken limestone and/or basalt boulders, and a lower region of more or less continuous rocky substrate of cemented limestone (Emery and Cox 1956) or basalt. In the upper region, where boulders are covered by a canopy of maritime vegetation and the undersurfaces are subject to conditions of high humidity, at least 6 species of mollusks (among them the pulmonates *Melampus, Laemodonta,* and *Pedipes*) and the isopod *Ligia* are commonly found. Seaward of the boulder region the shoreline is dominated by 2 species of littorine, *Littorina pintado,* which is widespread in the Indo-West Pacific, and *Nodilittorina hawaiiensis,* which is endemic to Hawaii. Both have a pelagic veliger larval stage during their life histories and hence both are tied to the sea by their mode of reproduction. The littorines are replaced seaward but still above the reach of waves and tides by the black nerite, or *pipipi, Nerita picea.* The grapsid crabs *Pachygrapsus plicatus* and *Grapsus tenuicrustatus* range through both regions, from the maritime vegetation to the reach of waves and tides.

Basalt shorelines. Where basalt outcrops extend seaward from the shore, extensive areas of water-leveled benches, vertical cliff faces, and boulder beaches are prominent features of the coastline on all windward islands. The shoreward portions of benches and beaches are part of the littoral fringe, but the seaward sections are alternately exposed and immersed by tides twice daily and scoured by waves seasonally. On basalt benches the highest level of wave action may be marked by a line of the crisp red alga, *Ahnfeltia.* Below the *Ahnfeltia* line a variety of frondose algae such as *Ulva, Rhizoclonium,* and *Jania* cover the substrate. This section of the shore is, in turn, succeeded seaward by a broad band of pink "paint," the growth form of the calcareous alga *Porolithon.* The interface between the shore and the sea is marked by either the red alga *Pterocladia* or by a mix of the brown seaweeds *Sargassum* and *Ectocarpus*. The dominant mollusks seaward of *Ahnfeltia* are the black foot *opihi, Cellana exarata,* the pulmonate limpet *Siphonaria,* the opisthobranch *Smaragdinella calyculata,* and the predator gastropods *Morula granulata* and *Neothais harpa*. The *Porolithon*-encrusted area of these shorelines is dominated by the yellow foot *opihi, Cellana sandwicensis,* and the shingle urchin, *Colobocentrotus atratus*. The frontal slope is riddled with borings of the sea urchin *Echinometra mathaei,* and a variety of mollusks is found in pockets and crevices of the cliff face: the cowry *Cypraea caputserpentis,* the vermetid *Petaloconchus keenae,* and the bivalve *Isognomon incisum*. Several carnivorous fish are also associated with this ecosystem, among them the damselfish *Abudefduf imparipennis,* the wrasse *Thalassoma umbrostigum,* and the goby *Bathygobius cotticeps*.

The pattern described above represents the broadest expression of littoral zonation found in Hawaii, and it is variously modified on vertical cliff faces and in sheltered coves and bays. On cliff faces, the *Ahnfeltia* zone and the succeeding frondose algal zone are absent, and the littorines and nerites of the littoral fringe merge directly into the *Porolithon*-encrusted zone. In sheltered coves and bays, especially where there are intrusions of fresh water, the native Hawaiian oyster *Ostrea sandvicensis* encrusts vertical substrates between the littoral fringe and the subtidal region, and the bivalve *Isognomon californicum* forms dense mats on the horizontal substrate.

Calcareous shorelines. Calcareous or carbonate shorelines are dominant features of the coastlines of all major windward islands except Hawaii; on Oahu 87 km (32%) of the coastline is composed of this type of shoreline (Wentworth 1939).

Topographically, solution benches resemble atoll reef flats, consisting of sea-level platforms extending from 1 to 30 m seaward from the shore. The benches are separated from shore by a raised, sharply pitted limestone zone and a nip, an indentation at the base of the vertical section. Seaward of the nip the flat-topped surface is densely matted with an algal turf. At the sloping outer edge calcareous algae and, to a lesser extent, corals contribute to the structure of the bench. Because the bench height is above sea level, the surface may be exposed at low spring tides for periods of as long as 4 hours.

The biota of calcareous shorelines is distinguished from that of basalt shorelines by its cover of thick algal turf. The turf is interspersed with grazing herbivorous mollusks such as the cowry *Cypraea caputserpentis* and the opisthobranch *Haminoea crocata,* with mats of the suspension-feeding mollusks *Brachidontes crebristriatus* and *Dendropoma gregaria,* and with active carnivorous snails such as *Morula,* miters, and cones. *Morula granulata* feeds on *Brachidontes* and *Dendropoma;* the miters feed on sipunculans that infiltrate the substrate (Kohn 1970); and most of the cones ingest polychaetes (Kohn 1959). Both the flora and the fauna are conspicuously zoned. The pools of the pitted zone, which are in effect in the littoral fringe, are inhabited by the small littorine *Peasiella tantilla* and the blenny *Istiblennius zebra;* on the bench itself the cones, especially, form a series from *Conus abbreviatus* at the shoreward edge to *C. chaldaeus* at the seaward edge (Kohn 1959).

Marine tide pools. Tide pools occur on sea-level basalt outcrops, some formed by depressions in the water-leveled benches, others formed by massive boulders fronting the sea; tide pools also occur on the benches of calcareous shorelines. Physical conditions in marine pools vary with exposure, those pools farthest from the sea undergoing striking variations in temperature and salinity, those at the seaward edge exhibiting essentially subtidal marine conditions. The most exposed pools are characterized by sand substrates bound with blue-green algae. In them are found 2 or 3 species of small mollusks, occasional grapsid crabs, and 2 fishes, the blenny *Istiblennius zebra* and the goby *Bathygobius fuscus*. Seaward pools are progressively more densely turfed with algae such as *Padina, Jania,* and *Boodlea,* and a variety of worms, mollusks, crustaceans, and echinoderms are found in them. The spaghetti worm, *Loimia medusa* (Polychaeta: Terebellidae), and the bandana shrimp, *Stenopus hispidus* (Crustacea: Stenopodidae), are especially conspicuous. Seaward pools also serve as incubators for juvenile fishes such as *manini, Acanthurus sandvicensis,* and *aholehole, Kuhlia sandvicensis.*

Anchialine pools. Anchialine pools, shoreline pools without surface connection to the sea but having waters of measurable salinity (0.5 to 30 ‰) and showing tidal fluctuations, are found only on the southwest coast of east Maui and the west coast of Hawaii, from Kau to Kohala (Maciolek and Brock 1974). These ponds are recent geological features, subject to obliteration by lava flows and to senescence. As organic and mineral deposits accumulate, the ponds fill in and disappear.

The aquatic vegetation of anchialine pools is dominated by benthic algae such as *Rhizoclonium* or nonencrusting mats of the cyanophytes (blue-green algae) *Scytonema* and *Lyngbya,* as well as the vascular aquatic plant *Ruppia maritima.* Four decapod crustaceans, 2 mollusks, and 2 native fishes are characteristic of the fauna. As on rocky coasts, there is a high degree of endemism: the mollusks *Theodoxus neglectus* and *T. cariosus,* the small red shrimps *Metabetaeus lohena, Procaris hawaiana,* and *Halocaridina rubra,* and the fishes are all endemic to the Hawaiian Islands.

Sandy beaches. The sand shorelines of the windward Hawaiian Islands are, in general, low, sloping beaches backed by a wall or raised coral platform. Except on Hawaii, sand is largely calcareous, composed of foraminiferan tests, mollusks, echinoderms, and coralline algae (Moberly et al. 1965). On Hawaii there are many black-sand and olivine beaches. The most extensive beach development occurs on Kauai; shorter stretches of beach are characteristic of the other islands.

Hawaiian beaches may be subdivided into 3 zones: an upper beach including the vegetation line; a mid-beach between the high-tide line and the vegetation line, its extent dependent on slope and tide; and the lower beach, which is continually awash with waves. The biota of sandy beaches is related to both sand-grain size and beach slope. The upper beach is characterized by amphipods, isopods, and males of the ghost crab, *Ocypode laevis,* which burrow in the area (Fellows 1966). Females of *O. laevis* and males of another species, *O. ceratophthalmus,* burrow in the mid-beach area. The mole crab, *Hippa pacifica,* scavenges for food, and 4 species of the gastropod genus *Terebra* prey on spionid polychaetes in the low beach (Miller 1970). The color of *Hippa, Ocypode,* and *Terebra* is associated with the color of the beach sand: lighter crabs and shells are found on the yellow-sand beaches of Oahu, darker forms on the darker beach sands of Maui and Hawaii (Fellows 1966; Miller 1970; Wenner 1972).

Fringing reefs. Hawaiian reefs are neither so spectacularly developed nor so diverse as are the reefs of other Pacific islands, a circumstance associated with the location of the Hawaiian Islands at the northern edge of the coral reef zone of tropical and subtropical seas and, therefore, near the low-temperature extreme to which corals are sensitive.

More than half the shoreline of Oahu and comparable portions of Kauai, Molokai, Lanai, and Maui are fringed by reef, but only a small section of the northwest coast of Hawaii, at Kawaihae, is fringed by reef. The reefs are wide, shallow platforms extending as much as 300 m seaward from the shore. The reef platforms are typically subtidal, 1 to 3 m below mean sea level, although occasional sections may be exposed at low spring tides. The reef flat consists predominantly of sand, coral rubble, and coralline algae. Crustose coralline algae exceed other organisms as the dominant reef builders in Hawaii, with cnidarian corals relatively unimportant in the overall fringing reef habitat (Littler 1973). Vigorous coral growth does occur, however, off the frontal edge of the reef flats.

Reef flat assemblages are perhaps the most diverse of those occurring along Hawaiian shorelines, reflecting a variety of habitats: solid substrates of calcareous algae and cnidarian corals; stands of frondose algae such as *Sargassum;* rubble; and sand patches. Because of the variety of habitats, the distribution of reef organisms is patchy. Where there are sand patches, infaunal organisms such as the mollusks *Conus pulicarius* and *Terebra* spp. occur, and the polychaetes *Mesochaetopterus sagittarius* and *Phyllochaetopterus verrilli* form sand-grain tubes that project above the sand. Where there is rubble or living coral, other mollusks, fish, and echinoderms are common and the large fan worm *Sabellastarte sanctijosephi* occurs in pockets and crevices. On the Waikiki reef it has been shown that cardinal fish, especially, are associated with different substrates, *Apogon snyderi* feeding over light, sandy substrates, *A. menesmus* over living coral (Chave 1971).

Estuaries. Estuaries are defined both as river valleys that receive freshwater discharge and as the tidal portions of streams. As many as 35 estuarine ecosystems have been identified in the Hawaiian Islands (Cox and Gordon 1970). Three major estuaries are Nawiliwili Bay, Kauai, and Pearl Harbor and Kaneohe Bay, Oahu.

Estuarine ecosystems support an endemic fauna of about 40 species. Most estuarine species in Hawaii are euryhaline and most are derived from marine rather than freshwater ancestors (Timbol 1972). Typical estuarine endemic fishes include the *oopu* (*Chonophorous genivittatus*), *oopu nakea* (*Chonophorous stamineus*), *aholehole* (*Kuhlia sandvicensis*), and the mollusks *hapawai* (*Theodoxus vespertinus*) and *hihiwai* (*Neritina granosa*). Estuaries are also the primary habitats of a few species utilized for food, such as the Samoan crab, and they are nursery areas for the inshore marine fishes *amaama, awa, kaku,* and *aholehole*. Many estuaries in Hawaii are now affected by the invasion of exotic species; for example, the Tahitian prawn *Macrobrachium lar,* crayfish, *Tilapia,* and water hyacinth, *Eichornea crassipes,* are replacing native forms.

Mangroves. Mangroves were introduced on Molokai in 1902 and on Oahu in 1922. On both these islands several developed stands now exhibit many of the properties attributed to mangrove swamps in other tropical areas, but the Hawaiian stands lack the extensive flora and fauna of typical large mangrove stands because of their relatively recent development (Walsh 1963).

SUBTIDAL ECOSYSTEMS

In addition to coral communities associated with fringing reefs, corals extend subtidally to depths of at least 50 m in Hawaiian waters, and spectacular coral development occurs on submarine surfaces of recent lava flows off the coasts of the islands of Maui and Hawaii, and in the waters between Maui and Molokai, for example, off Molokini islet and on Penguin Bank. Subtidal coral communities along the Kona coast of Hawaii Island appear to be better developed than those off the leeward coasts of other windward islands, perhaps because of the large size of the island and the height of the 3 major volcanic peaks, Hualalai, Mauna Kea, and Mauna Loa, which provide protection from trade-wind generated seas. Subtidal coral communities are, however, characteristic of all the windward islands, and 3 distinctive assemblages are recognized.

A *Pocillopora meandrina* assemblage is associated with coastlines where there is considerable wave action and a basalt boulder or rubble substrate, from depths of 1 m to more than 30 m. *Pocillopora meandrina* is the first coral to appear on new lava flows (Grigg and Maragos 1974), and this coral forms a dominant element in the shoreline zone off the Kona coast of Hawaii (Dollar 1973) and in most shoreline areas off Kauai and the windward coast of Oahu. The *P. meandrina* assemblage is often interspersed with other species of corals such as *Porites lobata* and *Montipora verrucosa,* by soft zoanthid coelenterates such as *Palythoa* and *Zoanthus,* and the sea urchins *Echinometra, Echinothrix,* and *Tripneustes.* Fifty-four species of fishes have been reported in the habitat off the Kona coast of Hawaii Island (Hobson 1974).

Coral communities dominated by *Porites lobata* also occur in shallow water. On the Kona coast of Hawaii island this assemblage is found seaward of *Pocillopora meandrina* assemblages; elsewhere it is found in protected bays (Dollar 1973). *Porites lobata* is apparently successful in populating almost any consolidated area from shallow depths down to 30 m, but modifies its growth form in response to the physical conditions of the environment (Maragos 1972). Where there is surge, the coral is usually flat and encrusting; in deeper waters the coral occurs as large, lobate or platelike colonies. Other corals found in the assemblage include *Pocillopora meandrina, Fungia scutaria,* and *Porites compressa.* The dominant reef fish in the assemblage are chaetodons, and algae such as *Halimeda* and *Turbinaria* may also be prominent members.

Porites compressa-dominated assemblages are found at depths ranging from less than 1 m to more than 50 m. Colonies of *P. compressa* are distinct from those of *Pocillopora meandrina* and *Porites lobata* in that the coral is of a branching type, forming fragile thickets that may extend for hundreds of square meters. On the Kona coast of Hawaii Island, *P. compressa* assemblages form a zone seaward of *P. lobata*; elsewhere the corals are prominent in protected bays such as Kaneohe Bay, Oahu, and on Penguin Bank, between Molokai and Maui. Other organisms associated with this assemblage include a variety of reef fish, including chaetodons, and sea urchins such as *Echinometra, Echinothrix,* and *Tripneustes.*

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SECTION

2

Chapter I

Phylum PLATYHELMINTHES

JEAN POULTER

THE PLATYHELMINTHES are acoelomate worms characterized by bilateral symmetry, an anterior-posterior axis, and, often, a differentiated head or cerebral region. Although the Platyhelminthes, or flatworms, represent a reasonably cohesive unit, they include a broad spectrum of organizational levels ranging from simple to complex. Some groups demonstrate well-developed organ systems, such as a digestive system (generally without an anus), a reproductive system (most species are hermaphroditic, with reproductive structures often occupying extensive internal areas), a central nervous system, and often an excretory system. A wide array of adhesive structures and/or adhesive glandular regions are a dominant feature among the phylum members. Flatworms lack a circulatory system and, generally, hard supporting structures (accounting for their soft bodies). They are free-living, commensal, or parasitic, and the three classes embraced by the phylum are to some extent distinguished by these ecological preferences. The class Turbellaria primarily comprises free-living forms, with few commensals or parasites. For reviews of commensalism and parasitism among turbellarians see Jennings (1971, 1974) and, for more recent investigations, see Jennings (1981), Christensen (1981), and Shinn (1981). The free-living species are restricted to aquatic or moist environments. In contrast to most turbellarians, members of the classes Trematoda and Cestoda are parasitic.

Definitive systematics of flatworms are based primarily on, and include, internal features revealed by whole-mount preparations, reconstructions of systems from sectioned (microtomized) material, or both. Many of these details, including information on parasitic forms, are beyond the scope of this presentation, and interested readers are directed to the references cited.

Class TREMATODA

The trematodes (flukes) have a nonciliated epidermis, a digestive system, and an unsegmented body. In Hawaiian marine waters adult trematodes are found

LEGEND FOR FIGURES (PLATYHELMINTHES)

A	acetabulum	MG	male gonopore
B	bothrium	MI	main intestine
BC	*bursa copulatrix*	MT	marginal tentacles
CE	cerebral eyes	NT	nuchal tentacles
CG	cement glands	O	ovary
CP	cirrus pouch	OP	opistaptor
CR	copulatory region	P	papilla
CS	cirrus sac	PB	proboscis
CT	small teeth in cirrus sac	PH	pharynx
E	eye(s)	PR	prohaptor
ED	ejaculatory duct	PV	prostatic vesicle
FE	frontal eyes	S	sucker
FG	female gonopore	ST	statocyst
G	gut	SV	seminal vesicle
LT	large teeth in cirrus sac	T	testis
LV	Lang's vesicle	TE	tentacular eyes
M	mouth	U	uterus
ME	marginal eyes	VT	vitellarium

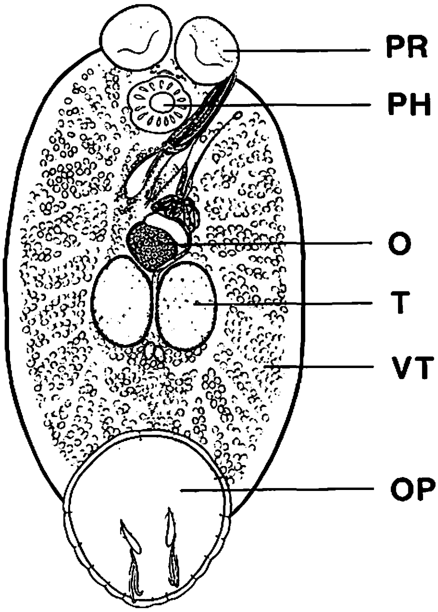

Figure 2.I.1.—*Benedenia hawaiiensis*, a monogenetic fish fluke: cleared specimen revealing internal anatomy. (After Yamaguti 1968a.) For abbreviations, see Legend above.

as ectoparasites attached to the gills and body surfaces of fishes or as endoparasites in the digestive tract of fishes. Ectoparasitic forms, the monogenetic trematodes, are best known from Hawaiian marine fishes through studies by Yamaguti (1965a, 1966, 1968a). The last work monographs the Hawaiian forms and includes 147 monogenes from 122 host fish species.

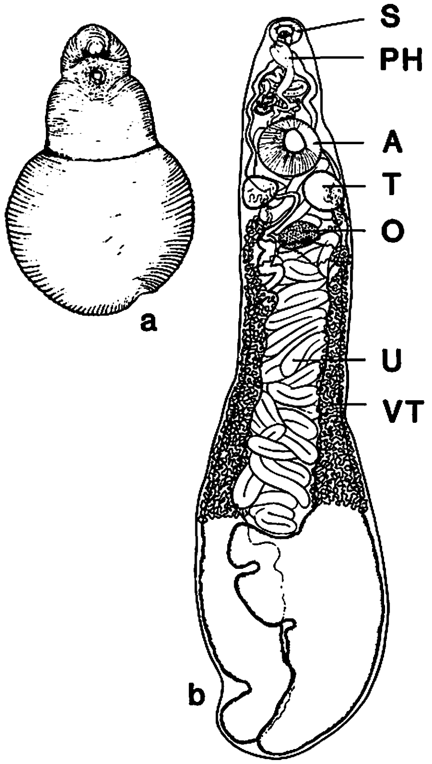

Figure 2.I.2.—*Hirudinella beebei*, a digenetic fish fluke: a, view of contracted worm; b, ventral view of expanded, cleared specimen revealing internal anatomy. (After Yamaguti 1970.) For abbreviations, see Legend preceding Figure 2.I.1.

Benedenia hawaiiensis (Fig. 2.I.1) is a monogene reported from the gills and body surface of at least 24 species of shallow-water Hawaiian fishes (Yamaguti 1968a).

Endoparasitic Hawaiian marine fish flukes, the digenetic trematodes, are also known mainly through work by Yamaguti (1965b, 1970). In his 1970 publication, 314 identified digenes were recorded from 144 species of fishes. *Hirudinella beebei* (Fig. 2.I.2) exemplifies a digenetic trematode which is found in the stomach of the fish *Acanthocybium solandri,* known in Hawaii as *ono. Hirudinella beebei* has a thick, pyriform body with a tough epithelium. There are 2 suckers on the ventral surface.

Identification of both mono- and digenetic trematodes requires examination of internal anatomy, which necessitates staining of whole-mounted specimens. The complete life cycles of the Hawaiian marine parasitic trematodes are unknown, and larval stages of digenetic species develop within other organisms that are the prey of fishes which may become hosts of adult flukes. The final larval stage (metacercaria) of an apparently undescribed digenetic trematode in the genus *Plagioporus* has been found encysted in polyps of the Hawaiian corals *Porites* spp. (Cheng and Wong 1974). Adults of 7 species of *Plagioporus* have been found in the intestines of Hawaiian fishes (Yamaguti 1970).

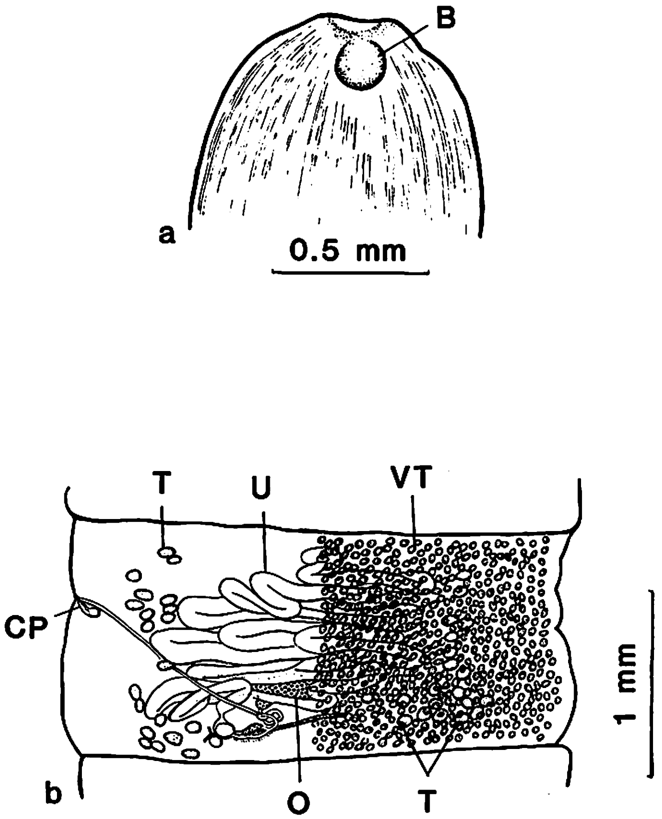

Figure 2.I.3.—*Metabothriocephalus menpachi*, a tapeworm from a fish (*Myripristis argyromus*): a, ventral view of scolex; b, dorsal view of mature proglottid. (After Yamaguti 1968b).

Class CESTODA

Seven cestodes (tapeworms) have been described by Yamaguti (1968b) from Hawaiian marine fishes. Adult tapeworms are usually elongate flatworms having a nonciliated epidermis. The head (scolex) is provided with hooks or suckers or both, followed by a series of segmentlike sections (or serially linked individuals) called proglottids (Fig. 2.I.3). Each mature proglottid lacks a digestive system but has a well-developed reproductive system. Adult cestodes have been found in Hawaiian fishes, including *mahimahi* (*Coryphaena hippurus*) and *menpachi* (*Myripristis argyromus*). The complete life histories of Hawaiian marine cestodes are unknown. At least 2 hosts are necessary for maturation, with the larval stage carried by another organism and the adult stage by the fish.

Larval tapeworms of the genus *Tylocephalum* (order Lecanicephaloidea) have been reported by Sparks (1963) from the digestive diverticula of the introduced eastern oyster *Crassostrea virginica* from Pearl Harbor, Oahu. Cheng (1967) considered this oyster an accidental rather than a natural intermediate host. Adult members of this order of cestodes are parasites of sharks. A mature tapeworm was found in the visceral region of a cephalopod, *Octopus cyanea*, captured off Kahe, Oahu, in December 1979 (Devaney 1981).

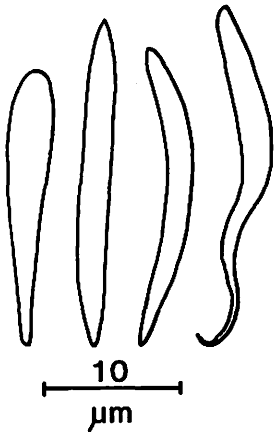

Figure 2.I.4.—Rhabdites from papillae of *Thysanozoon tentaculatum.*

Class TURBELLARIA

Turbellarian flatworms include marine, freshwater, and terrestrial species. They generally have specialized structures in their ciliated epithelium known as rhabdoids. The more commonly occurring rhabdoids are referred to as rhabdites, which are rodlike structures in the epidermis with their long axes directed outward (Fig. 2.I.4). The major external features of Hawaiian marine turbellarians are given here, but these generally cannot be regarded as diagnostic without consideration of internal anatomy. Several terrestrial triclads are known from Hawaii, but marine triclads are unreported.

Turbellarian classification is not firmly settled and new concepts or information may modify the arrangement of existing orders (cf. Hyman 1951, 1959a; Ax 1963; Karling 1974).

Karling et al. (1972) described or identified 12 marine microturbellarians from Hawaii. Microturbellarians are usually regarded as inclusive of all turbellarians except the Tricladida and Polycladida, which generally represent larger forms. Members of the orders Acoela, Prolecithophora, Proseriata, and Rhabdocoela are represented. The reported species are based on collections made on the sandy bottom and coral reefs around Coconut Island (Moku-o-Loe) and near Sand Island (Ahu-o-Laka) in Kaneohe Bay, Oahu. This is undoubtedly but a fraction of the microturbellarian fauna present in Hawaiian marine environments. Collection methods and study techniques were described by Karling et al. (1972, p. 251) as follows.

Substrate samples—pebbles, gravel, pieces of coral with sand, and algae—are collected in buckets, the contents sieved in seawater, and the smallest material retained for examination. Sand collected from different depths with a spade or small net is placed in glass jars. Specimens are isolated from this sandy material using methods described by Sterrer (1968, p. 4) for interstitial organisms. Animals are studied alive by squeezing them lightly under a cover slip on a glass slide. Specimens are fixed in Bouin's or mercuric chloride solution for sectioning. Whole-mounts are prepared in a clearing agent, CMCP-9AB (Turtox).

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HAWAIIAN TURBELLARIA

- 54 Order ACOELA
    - **Otocelididae**
        - *Notocelis gullmarensis maculata* Karling et al., 1972
    - **Convolutidae**
        - ?*Convoluta* sp.
- 59 Order PROLECITHOPHORA (Holocoela)
    - Suborder COMBINATA
        - **Cylindrostomidae**
            - *Cylindrostoma ?monotrochum* (Graff, 1882)
    - Suborder SEPARATA
        - **Plagiostomidae**
            - *Plagiostomum acoluthum* Marcus, 1948
- 60 Order PROSERIATA
    - **Monocelididae**
        - *Archiloa subtilis* Karling et al., 1972
        - *Archimonocelis helfrichi* Karling et al., 1972
        - *Duplominona kaneohei* Karling et al., 1972
        - *Minona bistylifera* Karling et al., 1972
- 58 Order RHABDOCOELA (Neorhabdocoela)
    - Suborder TYPHLOPLANOIDA
        - **Trigonostomidae**
            - *Cilionema hawaiiensis* Karling et al., 1972
            - *Microvahine corallicola* Karling et al., 1972
    - Suborder KALYPTORHYNCHIA
        - Group EUKALYPTORHYNCHIA
            - **Polycystidae**
                - *Austrorhynchus hawaiiensis* Karling, 1977
                - *Gyratrix hermaphroditus* Ehrenberg, 1831
            - **Koinocystididae**
                - *Utelga variodentata* Karling et al., 1972
        - Group SCHIZORHYNCHIA
            - **Schizorhynchidae**
                - *Carcharodorhynchus* sp.
- 62 Order POLYCLADIDA
    - Suborder ACOTYLEA
        - Superfamily ILYPLANOIDEA
            - **Euplanidae**
                - *Aprostatum longipenis* (Kato, 1943)
                - *Euplanoida tropicalis* (Hyman, 1954)
                - *Taenioplana teredini* Hyman, 1944
        - Superfamily STYLOCHOIDEA
            - **Callioplanidae**
                - *Discostylochus parcus* Bock, 1925
            - **Stylochidae**
                - *Stylochus (Imogine)* sp.
                - *Stylochus (Stylochus)* sp.

Planoceridae
Aquaplana pacifica (Hyman, 1954)
Paraplanocera marginata Meyer, 1921
Paraplanocera oligoglena (Schmarda, 1859)
Planocera hawaiiensis Heath, 1907
Superfamily LEPTOPLANOIDEA
Stylochoplanidae
Ceratoplana hawaiiensis Bock, 1925
Emprosthopharynx rasae Prudhoe, 1968
Stylochoplana inquilina Hyman, 1950
Suborder COTYLEA
Superfamily PSEUDOCEROTOIDEA
Pericelidae
Pericelis hymanae Poulter, 1974
Pseudocerotidae
Pseudocerotidae spp.
Pseudobiceros ?affinis (Kelaart-Collingwood, 1876)
Pseudobiceros gratus (Kato, 1937)
Pseudobiceros sp.
Pseudoceros ?kentii Graff in Saville-kent, 1893
Pseudoceros sp.
Thysanozoon tentaculatum (Pease, 1860)
Thysanozoon cf. *brocchii* (Risso, 1818)
Superfamily EURYLEPTOIDEA
Prosthiostomidae
Enchiridium japonicum Kato, 1943
Prosthiostomum (Lurymare) katoi Poulter, 1975
Prosthiostomum (Prosthiostomum) montiporae Poulter, 1975
Prosthiostomum (Prosthiostomum) ?trilineatum Yeri and Kaburaki, 1920
?Peasia irrorata Pease, 1860
Uncertain Status
Peasia inconspicua Pease, 1860

Order ACOELA

Acoel turbellarians are generally plump marine forms up to a few millimeters long; they usually have a statocyst and frontal glands. Eyes are absent or paired. A mouth is present, sometimes with a pharynx simplex, but an intestinal cavity and protonephridia are lacking. Dörjes (1968) reorganized the systematics of the acoels and included a key to genera. One representative of each family, Otocelididae and Convolutidae, is known from Hawaii.

? *Convoluta* sp.

This acoel has a rectangular form, reaches 6 mm in length, and is slightly narrower than long. It is greenish brown overlaid dorsally by orange pigment granules that are often concentrated posteriorly. The posterior margin of the body

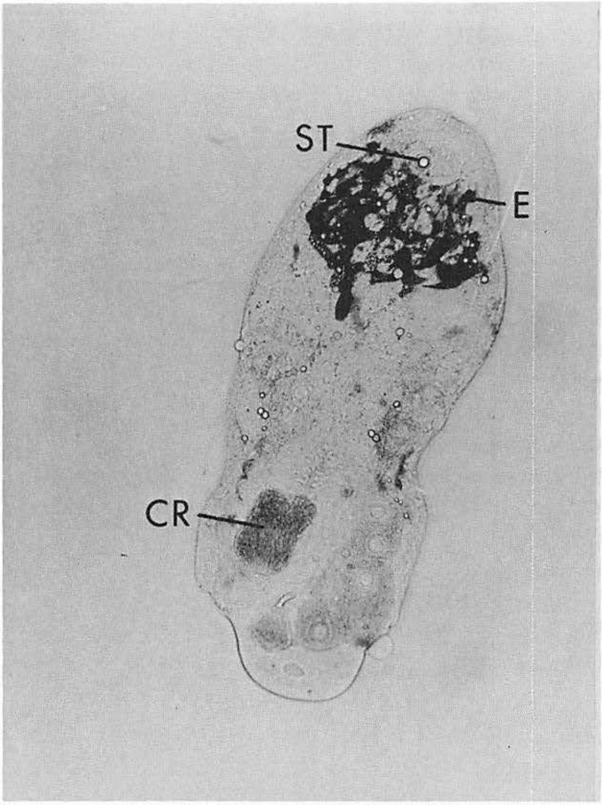

Figure 2.I.5.—*Notocelis gullmarensis maculata*: living specimen, slightly compressed. (Courtesy T. G. Karling.) For abbreviations, see Legend preceding Figure 2.I.1.

is trilobed with the lateral lobes extending farthest posteriorly (Plate. 2.I.1a). Details of anatomy and reproduction of this species are contained in an unpublished senior honors thesis by Jerome Kim completed at the University of Hawaii in 1980. Provisional assignment to the genus *Convoluta* is based on reproductive anatomy and pigment analysis. Plant pigments extracted from the Hawaiian specimens are characteristic of those of the single-cell phytoflagellate genus *Platymonas* (R. Trench, pers. comm.). This is a typical algal symbiont of the French species *Convoluta roscoffensis,* but not of *Amphiscolops langerhansi,* which the Hawaiian worms decidedly resemble superficially.

While sexual reproduction is limited to a short midwinter period, this undetermined species reproduces asexually through most of the year by transverse fission, a process which bisects the posterior third of the body. The posterior portion further differentiates into 2 small worms from the right and left halves, maintaining the antero-posterior axis of the parent. The worms resulting from the posterior portion develop into individuals that externally appear identical to the anterior parent portion except they lack a statocyst, which only sexually reproduced worms possess [see Hyman (1951) for additional information on the anatomical implications of specimens lacking a statocyst]. This flatworm has been seen frequently in the University of Hawaii's marine laboratory aquaria at Kewalo Basin and Coconut Island and has been found in Kaneohe Bay, Oahu (M. Hadfield, pers. comm.).

This species does not appear to have been previously recorded from Hawaii. The author is uncertain, from the information given about this acoel, of its taxonomic position. Examination of specimens by an acoel specialist is necessary for a specific determination.

Notocelis gullmarensis maculata Karling et al., 1972

The body is 0.6 mm long, anteriorly rounded, posteriorly tapering (Fig. 2.I.5), and is transparent except for brown pigment around the statocyst and 2 yellowish eyespots located anterolaterally to the statocyst. The mouth occurs at about 30% of the body length[1] and leads to a simple pharynx. A common gonopore is located at about 75% of the body length. Specimens of this subspecies have been reported in sand and on algae on coral reefs in Kaneohe Bay, Oahu.

Order PROLECITHOPHORA (Holocoela)

These are small marine or freshwater turbellarians of fusiform or cylindrical shape. The pharynx is either a plicate or variabilis type and the intestine is saclike.

Suborder COMBINATA

In members of this suborder, there is a common mouth and genital aperture and a plicate pharynx is present. One species in the family Cylindrostomidae has been reported from Hawaii.

Cylindrostoma ?monotrochum (Graff, 1882)

This worm is 1 mm long, anteriorly rounded, with a necklike constriction designating a ciliary furrow; the body is bluntly pointed posteriorly (Figs. 2.I.6–7). Specimens are opaque, with dark brown spots resulting from ingested material. Two pairs of anteriorly located eyes and frontal glands are present. A common mouth and genital pore is located at about 75% of the body length. The tubular pharynx is conical and posteriorly directed. Karling et al. (1972) identified Hawaiian specimens as somewhat distinct forms of *C. monotrochum*. The worms were washed from coral blocks, sand, and stones taken from the tidal zone at Coconut Island, Oahu. *Cylindrostoma monotrochum* has been reported from the European Atlantic coast, Mediterranean Sea, Sea of Marmara, Black Sea, and from the coasts of California and possibly Brazil.

Suborder SEPARATA

Members of this suborder have the mouth and genital openings separated and a pharynx generally of the variabilis type (a form of bulbous pharynx). One species in the family Plagiostomidae is known from Hawaii.

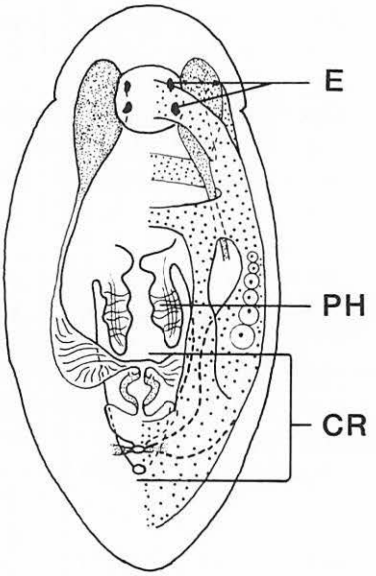

Figure 2.I.6.—*Cylindrostoma ?monotrochum*: general anatomy from dorsal aspect; right side showing female reproductive system, left side showing male reproductive system. (After Karling et al. 1972.) For abbreviations, see Legend preceding Figure 2.I.1.

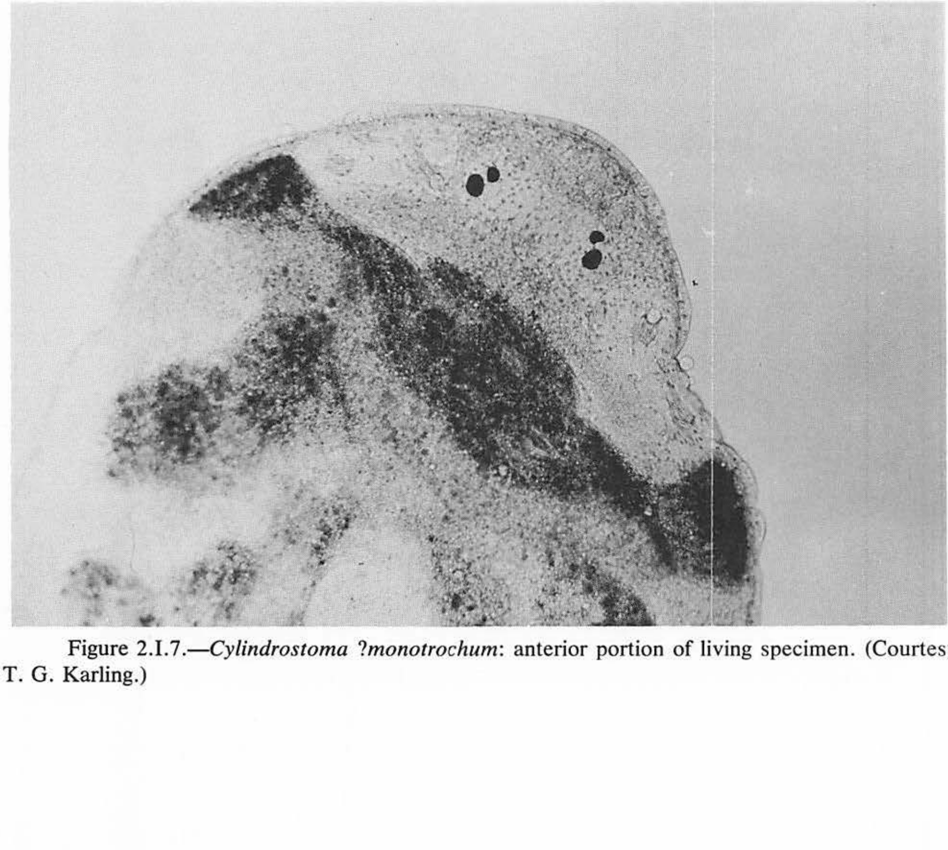

Figure 2.I.7.—*Cylindrostoma ?monotrochum*: anterior portion of living specimen. (Courtesy T. G. Karling.)

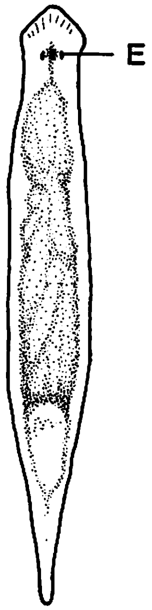

Figure 2.I.8.—*Plagiostomum acoluthum*: dorsal aspect. (After Karling et al. 1972.) For abbreviations, see Legend preceding Figure 2.I.1.

Plagiostomum acoluthum Marcus, 1948

The body is cylindrical, 2 mm long, and has a triangular "head" (with frontal glands) distinguished from the rest of the body by a constriction (Fig. 2.I.8). The color is yellowish white with 2 brownish eyespots and a spot of similar pigment lying between the eyes. The mouth and pharynx are located anteriorly at about 20% of the body length. The copulatory region lies at about 75% of the body length. Karling et al. (1972) identified this species taken in the intertidal zone from fine sand and coral at Coconut Island, Oahu. Extra-Hawaiian records include the Brazilian coast.

Order PROSERIATA

These are generally slender turbellarians with a plicate pharynx and serially arranged testes and yolk follicles. The intestine may be slightly or deeply diverticulate. Most species are marine. A single family, Monocelididae, is recorded from Hawaii. Members of this family have a statocyst, a posterior adhesive region, and a tubular plicate pharynx. The anterior region is equipped with sensory "hairs" but lacks sensory pits. Karling et al. (1966) revised the Monocelididae and included a key to genera. Four Hawaiian species are known.

Archiloa subtilis Karling et al., 1972

The body is filiform, 1.5 mm long, colorless, lacks eyes, and has a caudal adhesive region. Specimens have only been reported from below the low-tide level in coarse and fine sand at Sand Island and Coconut Island in Kaneohe Bay, Oahu.

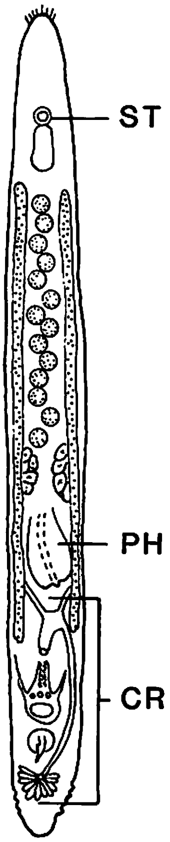

Figure 2.I.9.—*Duplominona kaneohei*: dorsal aspect, slightly compressed. (After Karling et al. 1972.) For abbreviations, see Legend preceding Figure 2.I.1.

Archimonocelis helfrichi Karling et al., 1972

The body is filiform, about 3 mm long, colorless, and lacks eyes. Definitive diagnostic characters are internal. Specimens were washed out of sand, stones, and corals from Coconut Island, Kaneohe Bay, Oahu. This is an endemic species.

Duplominona kaneohei Karling et al., 1972

The body is filiform, 1 to 2 mm long, colorless, and lacks eyes. The pharynx lies at about 60% of the body length and the copulatory region is midway between the pharynx and the posterior end (Fig. 2.I.9). Specimens adhere to the substrate by means of an adhesive girdle in the region of the statocyst, located at about 12% of the body length, as well as by the triangular posterior end. This endemic species was discovered among sand and stones in the intertidal zone and also on coral reefs near Coconut Island in Kaneohe Bay, Oahu.

Minona bistylifera Karling et al., 1972

Externally, living specimens strikingly resemble *Duplominona kaneohei,* and differences are restricted to internal morphology. This endemic species has been reported among coarse sand below the low-tide level in Kaneohe Bay, Oahu.

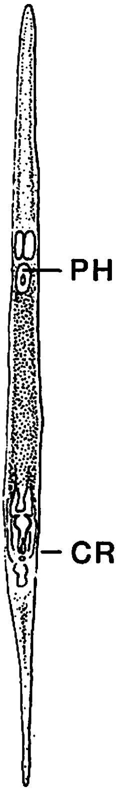

Figure 2.I.10.—*Cilionema hawaiiensis*: based on free-swimming specimen. (After Karling et al. 1972.) For abbreviations, see Legend preceding Figure 2.I.1.

Order RHABDOCOELA (Neorhabdocoela)

These turbellarians are small, usually less than 3 mm long, but are occasionally longer. The body is usually elongate, and normally there is a pair of eyes. A bulbous pharynx leads into a saclike main intestine.

Suborder TYPHLOPLANOIDA

Members of this suborder usually lack an anteriorly terminal proboscis, typically have a rosulate pharynx, and often have rhammites forming rod tracks. The 2 Hawaiian species of the family Trigonostomidae are endemic.

Cilionema hawaiiensis Karling et al., 1972

The body is filiform and cylindrical, about 3 mm long, and pointed at both ends (Fig. 2.I.10). This species is colorless, has well-developed rod tracks anteriorly, an adhesive girdle located at about 50% of the body length, and a caudal adhesive girdle. The mouth lies at about 40% of the body length and leads into a small rosulate pharynx. The copulatory region lies posteriorly, with a common gonopore situated at about 70% of the body length. Specimens have been reported in shelly sand below the low-tide level at Sand Island in Kaneohe Bay, Oahu.

Microvahine corallicola Karling et al., 1972

The body is cylindrical, 1 mm long (Fig. 2.I.11), with a necklike constriction at the level of the paired eyes forming a head with a proboscis. This yellowish-brown worm is pointed at each end when swimming, but when attached to the substrate it is broadened caudally in the region of an adhesive disc. The rosulate pharynx lies at 50% of the body length. The copulatory region is situated posteriorly, with a common gonopore lying at about 90% of the body length. This worm can adhere strongly to the substrate or glide rapidly. Worms of this species were washed from sand and algae occurring in the intertidal zone on coral blocks near Coconut Island, Oahu. Specimens were found on most coral examined.

Suborder KALYPTORHYNCHIA

Members of this suborder have an anterior terminal protrusile proboscis independent of the mouth. The pharynx is of the rosulate type. Rod tracks are lacking. Representatives are generally marine and 2 groups can be recognized.

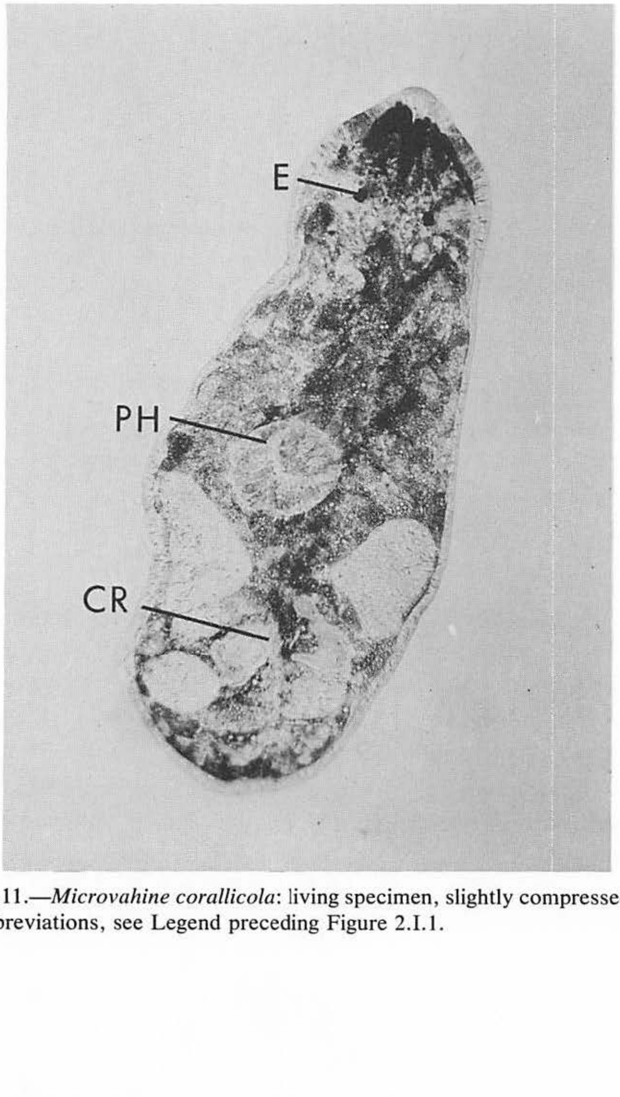

Figure 2.I.11.—*Microvahine corallicola*: living specimen, slightly compressed. (Courtesy T. G. Karling.) For abbreviations, see Legend preceding Figure 2.I.1.

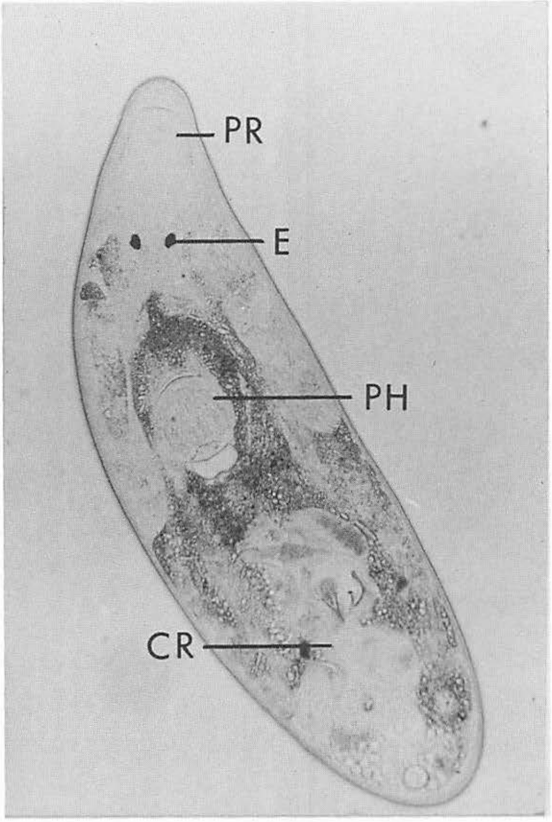

Figure 2.I.12.—*Austrorhynchus hawaiiensis*: living specimen, slightly compressed. (Courtesy T. G. Karling.) For abbreviations, see Legend preceding Figure 2.I.1.

Group EUKALYPTORHYNCHIA

Three species known from Hawaii belong to this group, which is characterized by having an undivided proboscis. The first 2 species belong to the family Polycystidae, the third to the family Koinocystididae.

Austrorhynchus hawaiiensis Karling, 1977
[syn. *Austrorhynchus pectatus* Karling, 1952: Karling et al., 1972]

The body is cylindrical, anteriorly tapering to a rounded apex with an anterior proboscis, and is rounded posteriorly (Fig. 2.I.12). There is a pair of eyes. The mouth and pharynx lie at about 40% of the body length. Karling et al. (1972) reported this species as abundant in sand in the intertidal region and on corals at Coconut Island, Oahu; it is an endemic species.

Gyratrix hermaphroditus Ehrenberg, 1831

The body is cylindrical, tapers to a blunt point at each end, has a terminal anterior proboscis, and has a pair of eyes (Fig. 2.I.13). The mouth and rosulate pharynx lie at about 50% of the body length. The copulatory region is in the posterior quarter

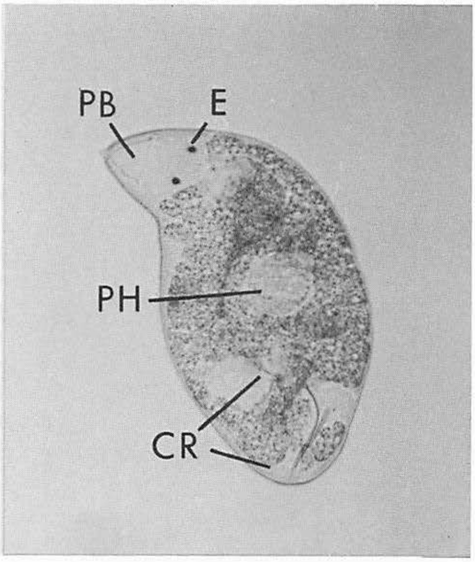

Figure 2.I.13.—*Gyratrix hermaphroditus*: living Hawaiian specimen. (Courtesy T. G. Karling.) For abbreviations, see Legend preceding Figure 2.I.1.

of the body. Specimens were collected from coral formations and sand intertidally at Coconut Island, Oahu (Karling et al. 1972). This species is cosmopolitan.

Utelga variodentata Karling et al., 1972

The body is 3 mm long, cylindrical, tapering anteriorly, rounded posteriorly, and has a large proboscis (Figs. 2.I.14,15). It is colorless except for a pair of small eyes. These worms adhere to the substrate by adhesive cells in the eye region and by the caudal end. The mouth and rosulate pharynx lie at about 35% of the body length. The copulatory region is in the posterior quarter of the body with the

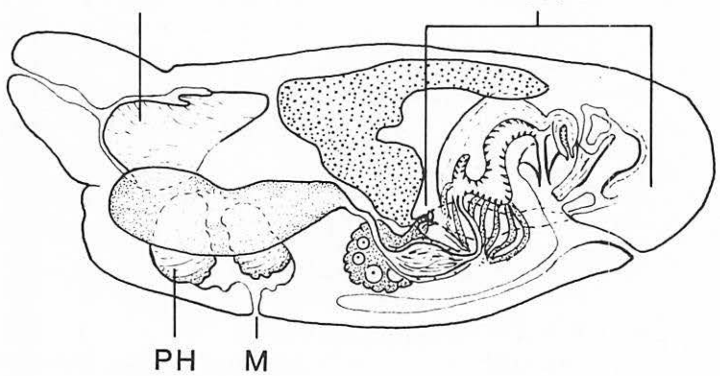

Figure 2.I.14.—*Utelga variodentata*: sagittal reconstruction. (After Karling et al. 1972.) For abbreviations, see Legend preceding Figure 2.I.1.

Figure 2.I.15.—*Utelga variodentata*: posterior portion of living specimen, slightly compressed, showing features of copulatory apparatus. (Courtesy T. G. Karling.) For abbreviations, see Legend preceding Figure 2.I.1.

common gonopore at about 90% of the body length. Specimens of this endemic species have been reported from sand at the low-tide level at Coconut Island, Oahu.

Group SCHIZORHYNCHIA

Members of this group have a bifurcate proboscis. One undetermined species in the family Schizorhynchidae is known from Hawaii.

Carcharodorhynchus sp.

Karling et al. (1972) mentioned finding a bright red member of this genus at Sand Island, Kaneohe Bay, Oahu. No further details were given.

Order POLYCLADIDA

The polyclads are the largest and most conspicuous Hawaiian marine turbellarians. Their dorsoventrally compressed bodies, occasionally exceeding 10 cm in length, include numerous gut branches arising from a median main intestine which extend toward the body perimeter, many eyes, numerous scattered ovaries and testes, and a well-developed central nervous system.

Polyclads, with a single known exception, are marine or estuarine forms. They are well represented in Hawaiian shallow waters. Most polyclads are bottom dwellers (benthic), inhabiting dark places; they are usually found on a firm substrate, such as rock or coral. Some species are decidedly nocturnal.

Many polyclads are predators on various invertebrates (e.g., corals, mollusks, small crustaceans, and worms, including other polyclads). While it has been suggested that polyclads have few predators, the author has observed that they are consumed by some sea anemones and, in 1 case, by a reef fish (Poulter 1975). Riser (1974) reported the polychaete worm *Nereis arenaceodentata* from Florida as a predator of *Taenioplana teredini*, a polyclad originally described from Hawaii.

Whereas there have been several publications on Hawaiian polyclads, the reported species constitute only a fraction of the total number present. For the most part, interest in these worms has been ancillary to other zoological investigations. The known Hawaiian polyclads demonstrate an endemicity of less than 60%, a figure that will probably decrease with further reports from the Indo-West Pacific region where, with the exception of southern Japan, the polyclad fauna is poorly known. As expected, many polyclads recorded from Hawaii are members of genera restricted to or largely represented in tropical seas.

The earliest reports on polyclads from Hawaii and nearby islands are deficient in detail and difficult or impossible to verify. Pease (1860) reported 5 species, of which only 2 (*Paraplanocera oligoglena* and *Thysanozoon tentaculatum*) can be identified; 2 others (*Peasia inconspicua* and *Peasia irrorata*) have not been subsequently identified; the remaining species, *Peasia maculata*, is probably not a polyclad. Plehn (1899) reported a *Thysanozoon* from Laysan, considering it conspecific with *Thysanozoon brocchii* (Risso, 1818). Heath (1907) described *Planocera hawaiiensis* but neglected to section a specimen; consequently, the internal anatomy is incompletely known. Subsequent reports on Hawaiian polyclads have generally been more comprehensive and usually include relevant internal morphology, thus permitting reliable identifications.

With regard to the ensuing systematic treatment, several publications are pertinent (Hyman 1953 and Marcus and Marcus 1966). Recently, Faubel (1983, 1984) has undertaken the monumental task of completely and extensively revising the Polycladida and includes anatomical definitions (cf. Hyman 1953), definitions of taxa and keys down through the generic level. The system proposed by Faubel emphasizes internal morphology with particular attention to the prostatic vesicle(s). Faubel's system will be applied here with only minor variations.

Whole-mount figures of 2 of the more common Hawaiian polyclads are presented to illustrate salient features of the 2 suborders: the Acotylea, represented by *Paraplanocera oligoglena* (Fig. 2.I.16), and the Cotylea, represented by *Thysanozoon tentaculatum* (Fig. 2.I.17). In comparing these 2 representatives, tentacular position (e.g., marginal or nuchal), presence or absence of a ventral sucker, and location of the pharynx and copulatory region are useful characteristics for assigning specimens to a suborder. More detailed microscopic examination of whole-mount and sectioned specimens is often necessary for more specific determination. Sometimes conspicuous color patterns can be used to identify live specimens. Information on specific habitats or symbiotic associations known for some species also can assist in identification.

POLYCLAD STUDY TECHNIQUES

Observations on living polyclads should include size, color pattern, eye arrangement, tentacular placement and development, type and shape of pharynx,

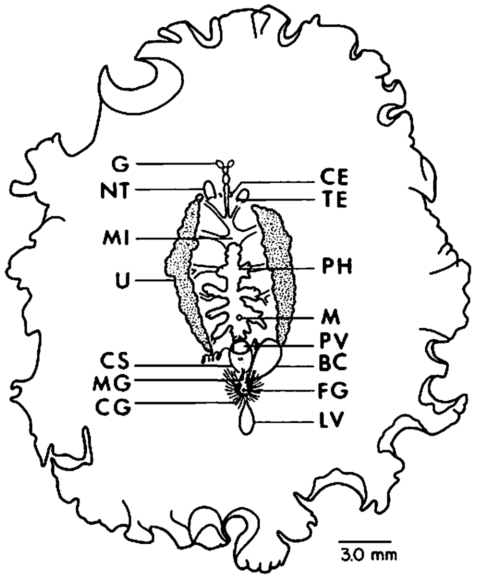

Figure 2.I.16.—Representative Acotylea, *Paraplanocera oligoglena*: note presence of nuchal tentacle (NT), lack of ventral sucker, and posterior location of copulatory apparatus. For abbreviations, see Legend preceding Figure 2.I.1.

position of the mouth, location of the male and female gonopores, presence or absence of a ventral sucker (adhesive disc), and other anatomical features.

Definitive taxonomic identifications require the examination of internal structures; thus, it is essential to prepare specimens for microscopic inspection by adequate fixation and preservation. A saturated solution of mercuric chloride ($HgCl_2$)

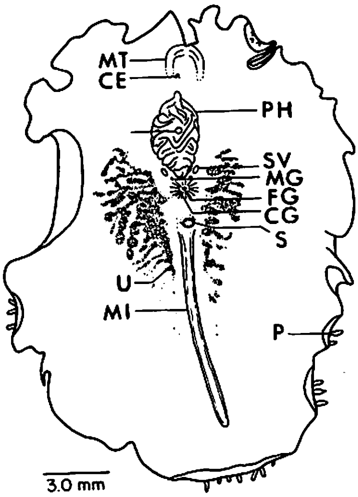

Figure 2.I.17.—Representative Cotylea, *Thysanozoon tentaculatum*: note marginal tentacle (MT), ventral sucker (S), and more anterior location of copulatory apparatus. For abbreviations, see Legend preceding Figure 2.I.1.

in seawater (about 9% $HgCl_2$ solution) is a recommended fixative for polyclads. The fixation procedure should be conducted in a chemical fume hood or with a mercury vapor mask, owing to the toxicity of mercuric compounds. Place the worm in a 6-cm or smaller petri dish with as little seawater as is practical. Heat the seawater-$HgCl_2$ solution in a fume hood until it begins to steam (about 80 °C). Pour a generous amount of the solution into the petri dish near but not on the worm. Allow the worm to remain in the fixative for an hour. Many polyclads become distorted with this treatment. However, do not attempt to flatten or restrain the worm at this point. Decant the fixative and wash the specimen quickly but thoroughly with water. Start the alcoholic dehydration procedure. Two changes of 1 hour each in 35% alcohol followed by 2 similar changes in 55% and then 70% alcohol are essential to preserve the worm. The specimen can now be removed from the petri dish and stored indefinitely in 70 or 80% alcohol.

After preservation for several days (usually no less than a week) in 70% alcohol, the worm can be flattened for examination as a cleared specimen or for sectioning. Flattening is often a tedious procedure. Again place the worm in a petri dish with a moderate amount of 70% alcohol. With camel-hair brushes gently unroll or uncurl the worm, placing small pieces of glass slides on flattened areas as progress is made until a glass slide or other appropriately sized piece of glass is lying on top of the entire worm and holding it in the desired position by gravity. The alcohol in the petri dish is changed successively through 80, 85, 90, and 95% using generous amounts, and then is changed to absolute alcohol (at least 2 changes). A Pasteur pipette is recommended for making these and subsequent changes. After the last alcohol is decanted, a clearing agent is used; oil of wintergreen (methyl salicylate) is recommended. After about 2 hours in methyl salicylate, the restraining glass slide is removed. The cleared worm may be examined for whole-mount features.

Once the extent of the copulatory region is determined, it can be excised while the specimen is cleared, but, owing to possible fracturing, it is suggested that the specimen be returned to 80% alcohol through the graded alcohols. The desired portion may then be excised, dehydrated, cleared, and embedded in paraffin. After sectioning (usually 10 μm) and partial rehydration of the serial sections on glass slides (in 70% alcohol), transfer slides to a port-wine-colored solution of Lugol's iodine in 70% alcohol for 5 minutes to remove any mercuric precipitates remaining in the tissue and follow by a running tap water wash. Then treat with an aqueous 5% solution of sodium thiosulfate ($Na_2S_2O_3.5H_2O$) for 2 minutes to bleach the iodine stain. Following a half-hour running tap water wash, the sections are ready for staining with any of the various stains compatible with a mercuric fixation (e.g., hematoxylin and various counterstains, periodic acid-Schiff or Feulgen reaction and counterstain).

KEY TO HAWAIIAN POLYCLAD SUBORDERS AND ACOTYLEAN SUPERFAMILIES[2]

1 No sucker posterior to female gonopore; tentacles, when present, of the nuchal type; marginal eyes, when present, forming a band,

never limited to a pair of clusters on the anterior margin; copulatory region usually in posterior half of body (Fig. 2.I.16) .... Suborder ACOTYLEA ... 2

A sucker posterior to female gonopore; tentacles, when present, of the marginal type; eyes in and around tentacles (when tentacles are present), and sometimes present as a pair of clusters on the anterior margin; copulatory region usually in anterior half of body; female system with a characteristic cement gland pouch (Fig. 2.I.17) .... Suborder COTYLEA

2(1) Prostatic vesicle present 3
Prostatic vesicle absent (Fig. 2.I.18b) .... Superfamily ILYPLANOIDEA (syn. Emprosthommatidea)

3(2) Prostatic vesicle free (Fig. 2.I.20b) .... Superfamily STYLOCHOIDEA (syn. Craspedommatidea)
Prostatic vesicle interpolated (Fig. 2.I.26b) .... Superfamily LEPTOPLANOIDEA (syn. Schematommatidea)

Suborder ACOTYLEA
Superfamily ILYPLANOIDEA
(syn. Emprosthommatidea)

The 3 known species representing the Ilyplanoidea in Hawaii are members of the family Euplanidae, which is characterized by: a central or slightly anteriorly disposed pharynx; male copulatory apparatus posteriorly directed and without prostatic glands entering its distal tract; gonopores separate; tentacles absent or rudimentary.

Family **Euplanidae**

Aprostatum longipenis (Kato, 1943b)

This polyclad is elongate oval, rounded anteriorly, bluntly pointed posteriorly, with little crenulation of the margin (Fig. 2.I.18a). Living specimens may be 62 mm long and 25 mm wide. The ground color is translucent white and is usually altered in specimens collected in the field, which are often almost uniformly colored opaque bright orange, pink, or light green owing to ingested matter. Brown pigment spots scattered at random and forming aggregates are also found on the dorsum. Over the pharynx, this brown pigment forms an irregular line with random lateral branches. Cerebral eyes form a paired aggregation. While notable nuchal tentacles are lacking, conspicuous paired tentacular eye groups are found posteriorly and lateral to the cerebral eyes. The ruffled pharynx occupies about 35% of the body length and is disposed toward the anterior. The copulatory region (male complex shown: Fig. 2.I.18b) lies close to the posterior end of the pharynx. This species has been collected in areas of moderate wave action from the undersides of rocks at Ala Moana Beach Park, Swanzy Beach Park, and Kualoa, Oahu. Outside of Hawaii, *Aprostatum longipenis* has been reported from Palau.

The color pattern of *A. longipenis* is similar to that of *Ilyella gigas* (Schmarda, 1859) (Ilyplanidae). The latter species occurs throughout much of the

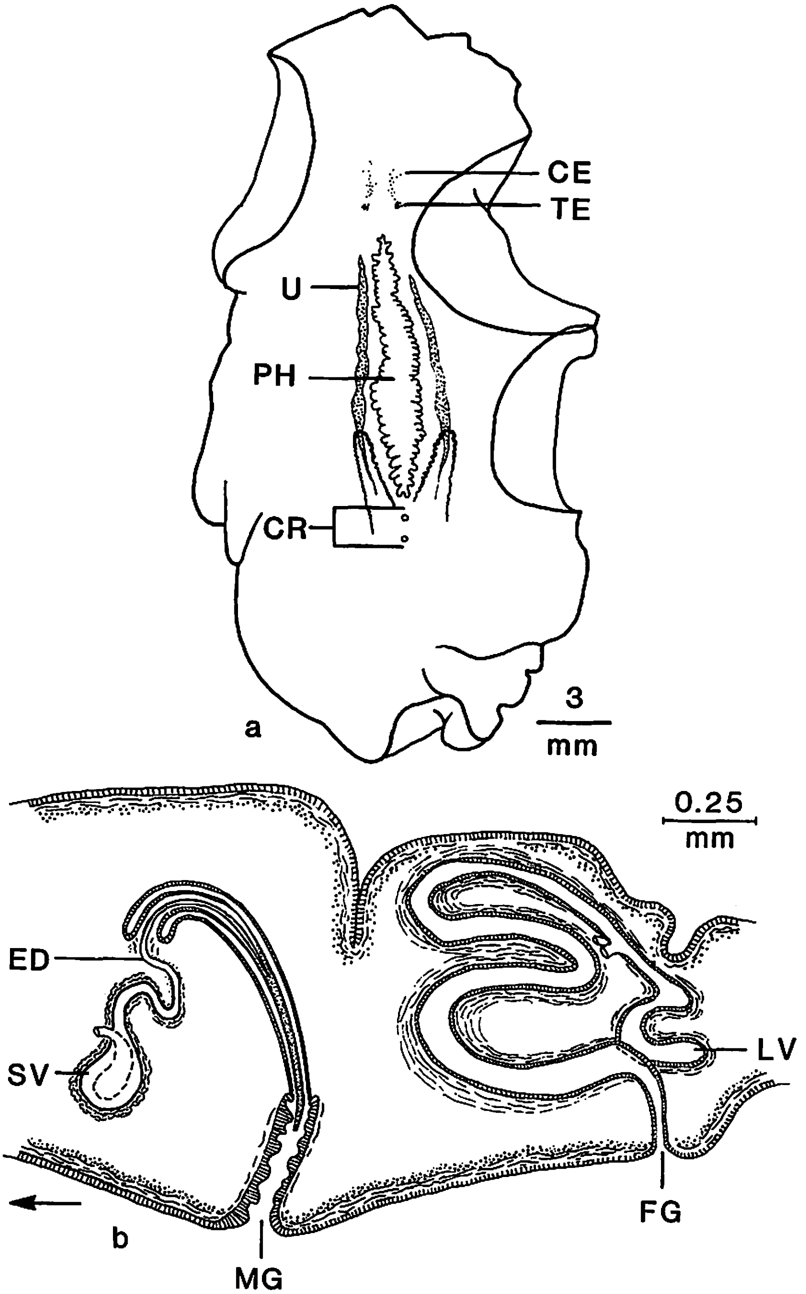

Figure 2.I.18.—*Aprostatum longipenis*: a, general anatomy; b, sagittal reconstruction of the copulatory apparatus. For abbreviations, see Legend preceding Figure 2.I.1.

Indo-West Pacific. The specimen shown in Plate 2.I.1b, because of its large size (over 100 mm long and 46 mm wide) and different habitat (under coral block on a coral reef), could represent the similarly colored species *I. gigas* and will require more detailed examination for a specific determination.

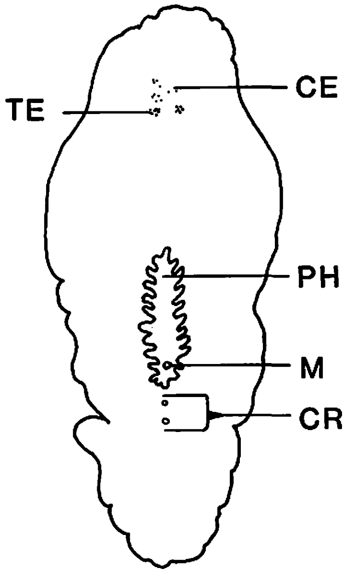

Figure 2.I.19.—*Euplanoida tropicalis*: general anatomy. (After Hyman 1954.) For abbreviations, see Legend preceding Figure 2.I.1.

Euplanoida tropicalis (Hyman, 1954)
[syn. *Euplana tropicalis* Hyman]

The only preserved specimen is elongate oval and measures 38 mm long and 17 mm wide (Fig. 2.I.19). The color of the living animal was not described, but Hyman suggested that it was probably tan with dark-brown spots. Cerebral eyes are present but difficult to discern. A pair of tentacular eye clusters is conspicuous, but nuchal tentacles are lacking. The ruffled pharynx, occupying about 25% of the body length, is disposed posteriorly. The copulatory region is near the posterior end of the pharynx. This polyclad was reported from Kapoho, Hawaii, the only known record of this species.

Taenioplana teredini Hyman, 1944

These worms are long and narrow, with a maximum length of 90 mm and a breadth of 4 mm. The ground color of living worms is opaque cream to pink; on each side of the middorsal line is a band composed of brown-black maculae, and these bands tend to converge over the pharynx; near the margin is another region of dark pigmentation; the ventral side is cream colored (Plate 2.I.1c). Marginal eyes are restricted to the anterior region. Cerebral eyes form paired clusters, and a few frontal eyes are present. The ruffled pharynx lies anteriorly and occupies about 15% of the body length. The copulatory region lies some distance behind the posterior end of the pharynx but a little anterior to the body middle.

Specimens of *T. teredini* have been found in burrows of the mollusk *Teredo*[3] (shipworm) in Honolulu Harbor, Waikiki, and Kaneohe Bay, Oahu. Although originally described from Hawaii, *T. teredini* was reported by Riser (1974) from

Florida, Israel, Panama, and possibly New Guinea, also in association with shipworms.

Other Euplanidae

Other Euplanidae have been observed in Hawaiian shallow waters but will require more detailed study to be identified or described.

Superfamily STYLOCHOIDEA
(syn. Craspedommatidea)

KEY TO THE KNOWN HAWAIIAN STYLOCHOIDEA FAMILIES

1 Prostatic vesicle lining undulated 2
Prostatic vesicle lining smooth .... **Callioplanidae**
2(1) Cirri present in terminal portion of male tract .... **Planoceridae**
Cirri absent.. **Stylochidae**

Family **Callioplanidae**

Discostylochus parcus Bock, 1925

The worm is ovate, broadly rounded anteriorly, and measures 14 mm long and 10 mm wide (Fig. 2.I.20a). The color of the living specimen is unknown. Marginal eyes are restricted to the anterior margin. Cerebral eyes are arranged in a single dispersed group and are difficult to distinguish from frontal eyes. Tentacular eye clusters are present under inconspicuous nuchal tentacles. The ruffled pharynx, occupying about 36% of the body length, is disposed posteriorly. The copulatory region is behind the posterior end of the pharynx, well anterior to the posterior margin; the male system is shown in Fig. 2.I.20b. The only reported specimen was taken from under the sea urchin *Colobocentrotus atratus* at Hilo, Hawaii. Another polyclad species, *Ceratoplana hawaiiensis,* has also been found under *C. atratus.*

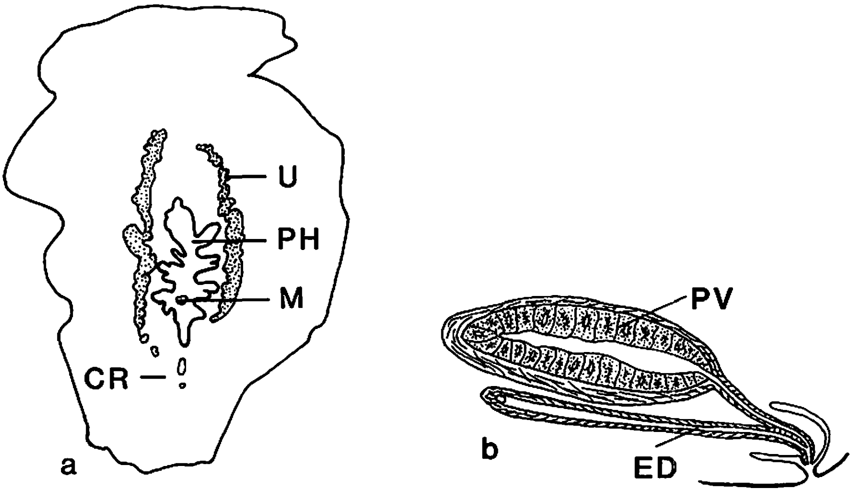

Figure 2.I.20.—*Discostylochus parcus*: a, ventral aspect; b, sagittal reconstruction of male copulatory apparatus showing free prostatic vesicle. For Abbreviations, see Legend preceding Figure 2.I.1. (After Bock 1925.)

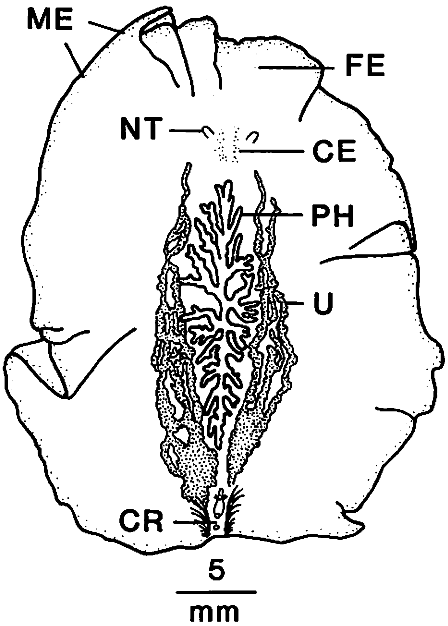

Figure 2.I.21.—*Stylochus* (*Imogine*) sp.: ventral aspect of cleared specimen. For abbreviations, see Legend preceding Figure 2.I.1.

Family **Stylochidae**

Stylochus (Imogine) sp.

Alive and extended, this worm may exceed a length of 60 mm and a breadth of 30 mm. At rest it is ovate to round (Fig. 2.I.21) and the body is of firm consistency. The dorsal surface (Plate 2.I.1d) is brown, punctuated by regions of greater and lesser pigmentation, usually more intense over the pharynx. Conspicuous nuchal tentacles are gold, and this color is also evident along the edge of the anterior margin of the body. The ventral side is off-white. A band of marginal eyes encircles the entire body margin. Cerebral eyes form an incompletely separated aggregate and also indistinctly blend with the frontal eyes. Tentacular eyes are densely grouped within each nuchal tentacle. The pharynx, occupying about 55% of the body length, is central and deeply ruffled. The copulatory region usually lies midway between the posterior end of the pharynx and the posterior margin. While the golden coloration of this *Stylochus* sp. might serve to differentiate it from the following *Stylochus* sp. in the field, the definitive differences lie in its internal morphology where the male system demonstrates a seminal vesicle characteristic of the subgenus *Imogine*.

This species of *Stylochus* is very common, especially during the summer, under rocks harboring the common rock oyster, *Ostrea sandvichensis*, upon which it is a likely predator; the author observed this species clinging to oysters, the upper valves of which could often easily be removed. Presumably, in some manner (enzymatic digestion, oxygen deprivation, fatigue, or a combination of these) the polyclad is able to invade the shell and prey upon the oyster. This behavior is probably what Kato (1944, p. 264) referred to as the "hanging method" of predation, based on observations of another *Stylochus* species. This

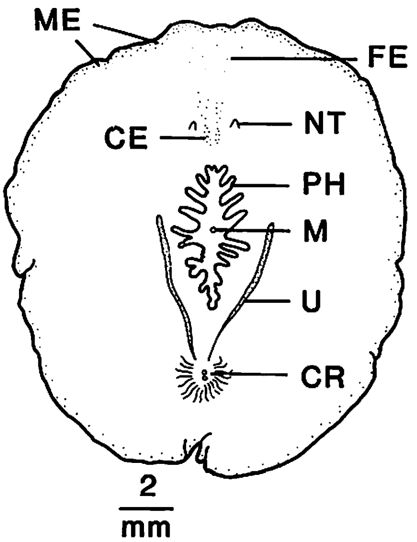

Figure 2.I.22.—*Stylochus* (*Stylochus*) sp.: ventral aspect of cleared specimen. For abbreviations, see Legend preceding Figure 2.I.1.

clinging behavior was not observed on empty oyster shells. These worms occur on Oahu along Ala Moana Beach Park, Fort Kamehameha reef, and in Kaneohe Bay.

Stylochus (Stylochus) sp.

At rest, this unidentified species of *Stylochus* is round to ovate (Fig. 2.I.22), but when crawling and extended it is elongate, measuring 30 mm long and 9 mm wide. The body is of firm consistency. It is gray on the dorsal side, with pigmentation reduced over the pharyngeal region and along the margin; the ventral surface is off-white. Marginal eyes completely encircle the body margin. Cerebral eyes form a pair of aggregations indistinctly separated at some points and also indistinguishable from the few frontal eyes. Paired nuchal tentacles contain numerous tentacular eyes. The ruffled pharynx occupies about 30% of the body length and is slightly displaced anteriorly. The copulatory region lies midway between the posterior end of the pharynx and posterior margin. The male system has a seminal vesicle characteristic of the subgenus *Stylochus*. This species of *Stylochus* has been found at Ala Moana Beach Park, Oahu, in shallow water.

Family **Planoceridae**

Aquaplana pacifica (Hyman, 1954)
[syn. *Planocera pacifica* Hyman, 1954]

The body is oval and the margin is ruffled (Fig. 2.I.23a). It is 40 mm long and 25 mm wide; there is no information on the color in life. The cerebral eyes form a distinctly paired aggregation, and tentacular eyes form rings at the bases of the pair of nuchal tentacles. The ruffled pharynx, occupying about 30% of the body length, is disposed anteriorly. The copulatory region lies near the posterior end of

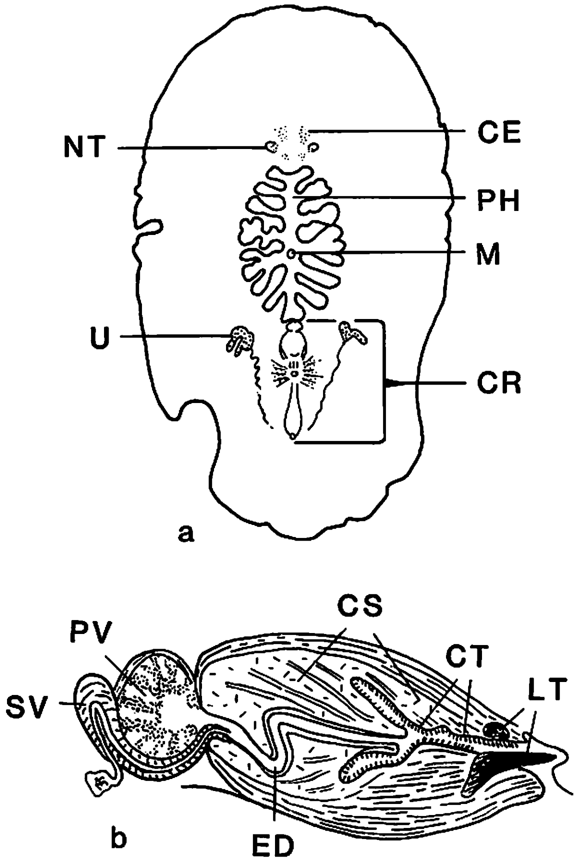

Figure 2.I.23.—*Aquaplana pacifica*: a, general anatomy; b, sagittal reconstruction of male copulatory region showing free prostatic vesicle. (After Hyman 1954.) For abbreviations, see Legend preceding Figure 2.I.1.

the pharynx; the male system is shown in Fig. 2.I.23b. A single specimen is recorded from Hawaii, but the collection site is unknown.

Paraplanocera marginata Meyer, 1921

This polyclad is rounded (Fig. 2.I.24), with a moderately ruffled margin. Specimens reach a length of 40 mm and a breadth of 30 mm. The dorsum is predominantly light to rust brown, with a lighter midregion (Plate 2.I.1e). White maculae are found randomly dispersed, and white pigment forms a symmetrical, finely radiating nebulous pattern from the central region toward the periphery. The extreme margin is white, and interior to this are dashes of deep purple parallel with the margin. To the inside of this is a buff region broken by perpendicular, club-shaped pigmented areas that are white toward the center, blending to yellow toward the periphery, and interrupting the deep purple dashes. These clavate pigments are regularly spaced but are not present between all deep purple dashes. Cerebral eyes form a distinctly paired group. The conspicuous paired nuchal tentacles lie lateral to the cerebral eyes, and the base of each tentacle is ringed by numerous tentacular eyes. Small eyes are also found in the apex of each tentacle.

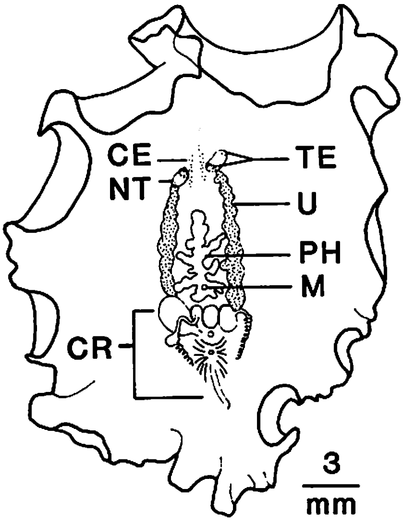

Figure 2.I.24.—*Paraplanocera marginata*: general anatomy of cleared specimen. For abbreviations, see Legend preceding Figure 2.I.1.

The deeply branched, ruffled pharynx occupies about 20% of the body length and is centrally located. The copulatory region lies close to the posterior end of the pharynx. Representatives of this species have been collected from the undersides of rocks at Ala Moana Beach Park and Black Point, Oahu. Outside of Hawaii, *P. marginata* is reported only from the Red Sea.

Paraplanocera oligoglena (Schmarda, 1859)
[syn. *Peasia reticulata* Pease, 1860]

The animal is ovate to circular, has a highly ruffled margin (Fig. 2.I.16), and reaches a length of 70 mm and a breadth of 62 mm. Smaller worms are translucent buff, but with increasing size the specimens generally become more densely pigmented (Plates 2.I.1f,2a). The color pattern of larger specimens is complexly mottled or reticulated dark brown. Dense pigmentation usually accumulates near the gut branches on an opaque tan background. White maculae are also present and are more prevalent peripherally. Abundant cerebral eyes form a paired aggregation. Tentacular eyes form rings at the bases of the pair of conspicuous nuchal tentacles. The ruffled pharynx, occupying 20 to 30% of the body length, is centrally located. The copulatory region lies behind the posterior end of the pharynx.

This is possibly the most common and conspicuous polyclad in the Hawaiian littoral zone. It was initially reported from Hawaii by Pease (1860) and more recently by Hyman (1954, 1960). This polyclad is usually found under rocks below the intertidal zone on reefs and lava benches in areas of moderate to heavy wave action. On Oahu specimens have been found at Ala Moana Beach Park, Black Point, Swanzy Beach Park, and Hauula Beach Park. On Kauai they have been collected at Haena and at Poipu Beach Park, and on the island of Hawaii at Hilo and Honaunau (City of Refuge). *Paraplanocera oligoglena* occurs throughout the Indo-West Pacific and its range may extend to Baja California.

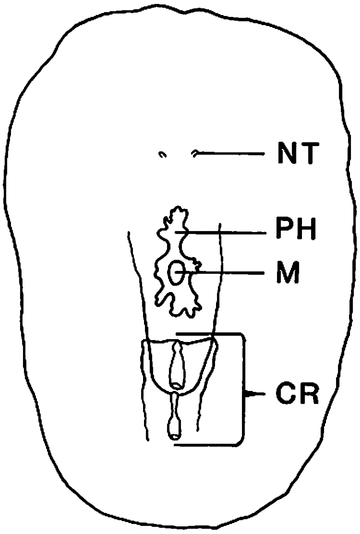

Figure 2.I.25.—*Planocera hawaiiensis*: general anatomy. (After Heath 1907.) For abbreviations, see Legend preceding Figure 2.I.1.

Other *Paraplanocera* Species

At least 1 other *Paraplanocera* species is present in the Hawaiian littoral zone but is as yet undetermined.

Planocera hawaiiensis Heath, 1907

This species is circular to ovate (Fig. 2.I.25). The length of the largest specimen is 39 mm, the breadth 33 or 35 mm. The coloration in life is not recorded, but the dorsum of preserved specimens is stippled with minute black pigments forming streaks and blotches. Cerebral eyes form a paired aggregation. A pair of nuchal tentacles is present, with a ring of tentacular eyes at their bases. The ruffled pharynx, occupying about 25% of the body length, is centrally located. The copulatory region lies behind the posterior end of the pharynx. This species is known only from specimens dredged at a depth of 51 to 79 m (28 to 43 fm) in the Auau Channel between Maui and Lanai. A specimen was not sectioned and internal morphology is incompletely known.

Superfamily LEPTOPLANOIDEA
[syn. Schematommatidea]

The 3 known members of the superfamily Leptoplanoidea from Hawaii are assigned to the family Stylochoplanidae and are characterized by various body outlines; an anteriorly disposed ruffled pharynx; and posteriorly directed male complex posterior to the pharynx, prostatic vesicle with smooth lining, and prostatic glands mostly extravesicular.

Family **Stylochoplanidae**

Ceratoplana hawaiiensis Bock, 1925

This species is elongate oval, and the largest preserved specimen is 14 mm long and 6 mm wide. Alive, it is a translucent light yellowish tan color dorsally

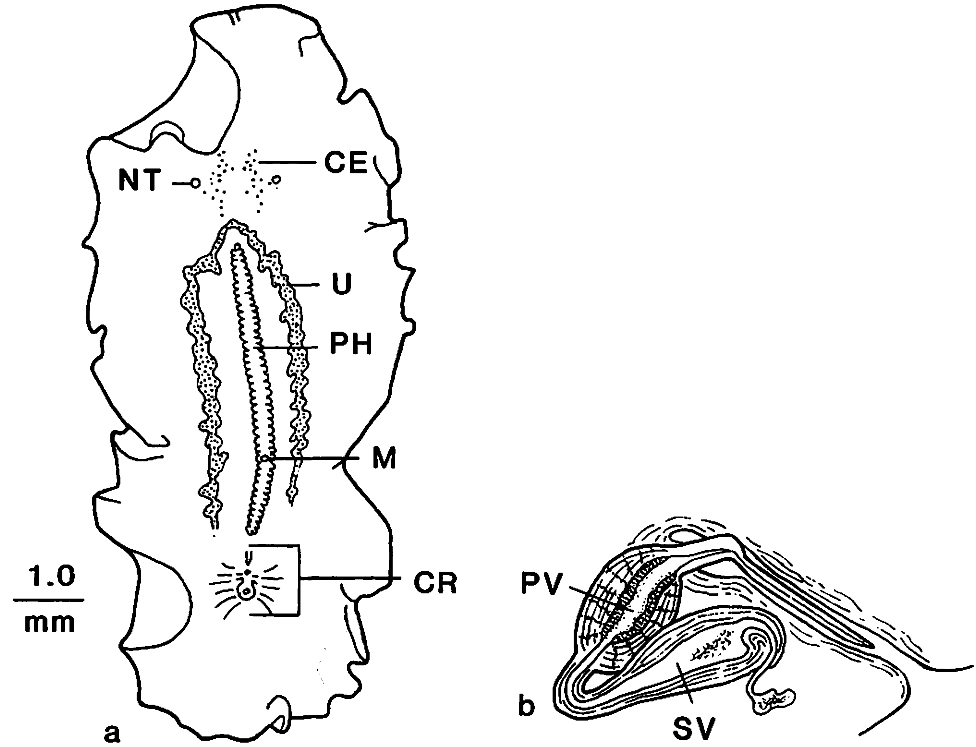

Figure 2.I.26.—*Ceratoplana hawaiiensis*: a, cleared specimen; b, sagittal reconstruction of male copulatory apparatus showing an interpolated prostatic vesicle. For abbreviations, see Legend preceding Figure 2.I.1.

(Plate 2.I.2b). Cerebral eyes form a paired aggregation, whereas larger tentacular eyes are found within conspicuous tapering nuchal tentacles. A ruffled pharynx occupies about 42% of the body length and is centrally located (Fig. 2.I.26a). The copulatory region lies a short distance behind the posterior end of the pharynx; the male system is shown in Fig. 2.I.26b.

Specimens were first reported from Hilo, Hawaii, where they were taken under the sea urchin *Colobocentrotus atratus*. Living specimens have been observed and collected at Ala Moana Beach Park (Magic Island), Oahu, under this sea urchin. Smaller but similar specimens were collected under the same species of sea urchin at Krakatau Island in the Sunda Strait (Indonesia). Bock (1925) noted differences in the shape and position of the pharynx and mouth as well as in the male and female genital structures and suggested that the Hawaiian form be considered a subspecies. Based on the new material examined and the above anatomical differences, especially in the female reproductive system, the Hawaiian and Indonesian forms can be considered separate species. The very prominent nuchal tentacles distinguish this species from another polyclad, *Discostylochus parcus*, also collected under *Colobocentrotus atratus* in Hawaii.

Emprosthopharynx rasae Prudhoe, 1968

The maximum recorded length is 20 mm and breadth is 6.5 mm for preserved specimens. The worm is elongate oval (Fig. 2.I.27). Alive, it is a light reddish

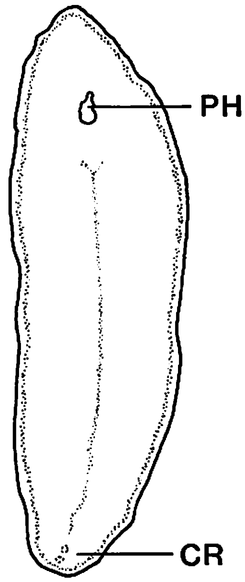

Figure 2.I.27.—*Emprosthopharynx rasae*: ventral aspect. (After Prudhoe 1968.) For abbreviations, see Legend preceding Figure 2.I.1.

brown to tan with paler margins. Anterior marginal eyes are present and cerebral eyes are few and in a paired aggregation. A few tentacular eyes are present but nuchal tentacles are absent. Frontal eyes are apparently absent. The pharynx is small, occupying 3% of the body length, and is anteriorly located. The copulatory region lies far behind the pharynx near the posterior margin.

This polyclad has been found curled about the abdomen of the hermit crab *Calcinus latens* within the shell of *Trochus intextus*. Prudhoe (1968) reported that the polyclad occurred on 3 to 7% of *C. latens* in Kaneohe Bay, Oahu, whereas 2 other species of hermit crabs occupying shells of *T. intextus* (as *T. sandwichiensis*) did not harbor this polyclad. *Emprosthopharynx rasae* is endemic to Hawaii.

Stylochoplana inquilina Hyman, 1950

This polyclad is elongate and bluntly pointed at each end (Fig. 2.I.28). A preserved specimen is 25 mm long and 7 mm wide. The dorsal ground color is white, and some distance from the median line 2 broad bands of tawny brown extend the entire length of the body. The margin is white. The color pattern is said to correspond well with that of both the gastropod shell and the sea anemone with which it is associated. Eyes are restricted to a pair of indistinctly separated cerebral and tentacular clusters, but nuchal tentacles are lacking. A ruffled pharynx, occupying about 40% of the body length, is distinctly disposed posteriorly. The copulatory region is adjacent to the posterior end of the pharynx.

Specimens of this polyclad were first collected off Oahu at a depth of 29 m (16 fm). This species, known only from the Hawaiian Islands, is associated with hermit crabs in the genus *Dardanus* occupying the molluscan shells of *Tonna* adorned with the sea anemone *Calliactis polypus*. The worm uses the umbilicus of the shell as a haven and also crawls about on the anemones. Hyman (1950) suggested that the

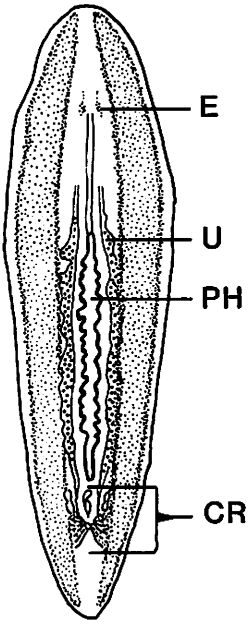

Figure 2.I.28.—*Stylochoplana inquilina*: dorsal aspect. (After Hyman 1950.) For abbreviations, see Legend preceding Figure 2.I.1.

polyclad obtains some of its food from the crab, the anemone, or both. Poulter (1975, p. 334) found spirocysts (a type of nematocyst) in the gut of 1 of Hyman's original sectioned specimens of *S. inquilina*, suggesting either their ingestion along with food stolen from, or possible predation on, the anemone.

A superficial resemblance is shared by *E. rasae* and *S. inquilina* and, further, both are associated with a hermit crab species. However, the reported eye arrangements along with the large differences in pharyngeal location and length in each respective species are distinguishing features. These features along with attention to the different hermit crab species associated with each polyclad species should serve as distinguishing field characters.

Suborder COTYLEA

KEY TO THE KNOWN HAWAIIAN COTYLEAN SUPERFAMILIES

Pharynx ruffled and hanging in the pharyngeal cavity .... PSEUDOCEROTOIDEA
Pharynx cylindrical and directed anteriorly .... EURYLEPTOIDEA

KEY TO THE KNOWN HAWAIIAN PSEUDOCEROTID FAMILIES

Prostatic region interpolated .... **Pericelidae**
Prostatic vesicle(s) free .... **Pseudocerotidae**

Family **Pericelidae**

Pericelis hymanae Poulter, 1974

Crawling and extended, living specimens may attain a length of 48 mm and a breadth of 16 mm. The body at rest is ovate to circular with a moderately ruffled margin (Plate 2.I.2c). The ground color is off-white. Dorsally there is a narrow median brown stripe that does not quite reach the anterior margin; the stripe is discontinuous through the cerebral region and terminates posteriorly at various levels over the pharynx. A pair of inconspicuous, V-shaped marginal tentacles bearing eyes is present. Eyes also encircle the body margin. A paired cerebral eye aggregation lies over the brain, and frontal eyes are also present. The ruffled pharynx occupies about 40% of the body length (Fig. 2.I.29) and is slightly disposed towards the anterior. The copulatory region lies behind the posterior end of the pharynx, and a rudimentary sucker is present posterior to the copulatory region. This polyclad has been reported from Swanzy Beach Park, Hauula Beach Park, and Black Point, Oahu. These worms are usually found under rocks that harbor the bivalve mollusk *Isognomon perna* and often use the underside of the lower valve of *Isognomon* as a refuge.

Family **Pseudocerotidae**

Many members of this family are found in the Hawaiian littoral zone. The revision of the Cotylea by Faubel (1984) requires that at least the recognition of the single or dual nature of the male system be known prior to provisional generic assignment; additionally, information on the internal morphology of the copulatory complex with emphasis on the male apparatus must be available for a firm assignment to genera.

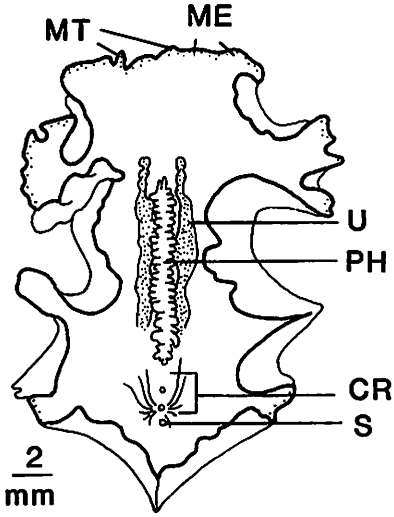

Figure 2.I.29.—*Pericelis hymanae*: general anatomy. For abbreviations, see Legend preceding Figure 2.I.1.

Pseudobiceros ?affinis (Kelaart-Collingwood, 1876)
[syn. *Pseudoceros affinis* Hyman, 1960]

The body is ovate and the margins are ruffled. This worm attains a length of 30 mm and a breadth of 20 mm. The dorsum is deep violet with an orange margin edged with black. Marginal tentacles are present. The cerebral eye arrangement and pharyngeal configuration have not been reported. The male reproductive system is paired and the female gonopore, followed by the sucker, lies a little posterior to the male copulatory systems.

The identification of this polyclad by Hyman (1960) was based on a single specimen collected from the underside of a rock in the intertidal zone at Makapuu Point, Oahu. This identification from the Hawaiian Islands, based mainly on color pattern, is dubious. In contrast to the color pattern of the Hawaiian specimen, neither the original description nor the illustration of *P. affinis* in Stummer-Traunfels (1933) definitely indicates that the edge of the margin is black (Fig. 2.I.30). The polyclads with which Hyman (1960) considered this species conspecific are reported from Ceylon and the Philippines (or Palau).

Faubel (1984) has placed *P. affinis* in his list of species of uncertain status. However, Hyman's (1960) identification does recognize the dual nature of the male apparatus of the local species. To avoid further systematic confusion, this local form can only be considered a provisional *Pseudobiceros* sp. until further information is available.

Pseudobiceros gratus (Kato, 1937)
[syn. *Pseudoceros gratus* Kato, 1937. *Pseudobiceros strigosus* Marcus, 1950: see Faubel, 1984]

The species is elongate oval and has a ruffled margin. Crawling and extended, individuals may exceed a length of 55 mm and a breadth of 15 mm. The ground color is white. The dorsum is distinctively marked (Plate 2.I.2d) with a

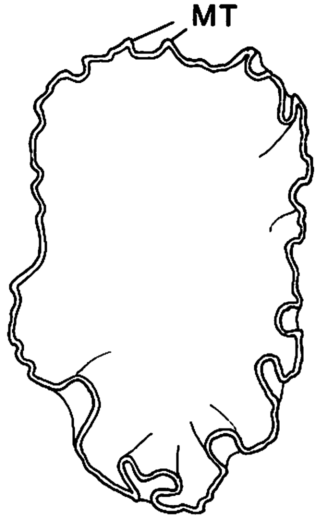

Figure 2.I.30.—*Pseudobiceros affinis*: redrawn from painting of living specimen (position of MT conjectural). (After Stummer-Traunfels 1933.)

broad median dark band, which begins behind the cerebral eyes and ends before the posterior margin. On each side of the midline is another dark band originating at each tentacular base. These lateral bands unite posteriorly behind the end of the median band. The margin is narrowly edged with black. Cerebral eyes are arranged in a V-shaped aggregation, and eyes are present on the tentacular folds. A compact ruffled pharynx, occupying about 15% of the body length, lies anteriorly. The male reproductive system is bilaterally paired and ends near the posterior termination of the pharynx. The female reproductive system lies posterior to the male systems and a sucker is present behind the female gonopore. This species has been found at Ala Moana Beach Park, Black Point, near the mouth of Kuapa Pond, and at Swanzy Beach Park, Oahu. Outside of Hawaii, *Pseudoceros gratus* is known from Japan and Palau. Hyman (1959b, p. 566) suggested, and the author agrees, that it is probably conspecific with *P. striata,* a species Schmarda (1859) recorded from Ceylon.

Hyman's (1959b, p. 566) "opinion" concerning the validity of the specific name *P. gratus* is concurred with. Faubel's (1984) list of synonmyms decidedly recognizes this priority and Faubel's declaration of *P. strigosus* as the specific name for this species does not seem appropriate. Thus the name *P. gratus* is maintained and *P. strigosus* is a recognized synonym.

Pseudobiceros sp.

This elongate or ovate worm with ruffled margin (Fig. 2.I.31) reaches a length of 70 mm or more and a breadth of 35 mm when crawling and extended. The dorsum (Plate 2.I.2e) is iridescent black, usually with tiny scattered white spots. The ventral side is white. A pair of deeply infolded tentacles is present, and cerebral eyes form a single heart-shaped cluster in an area of diminished pigment. Within the tentacles, eyes are present but difficult to discern. The pharynx is

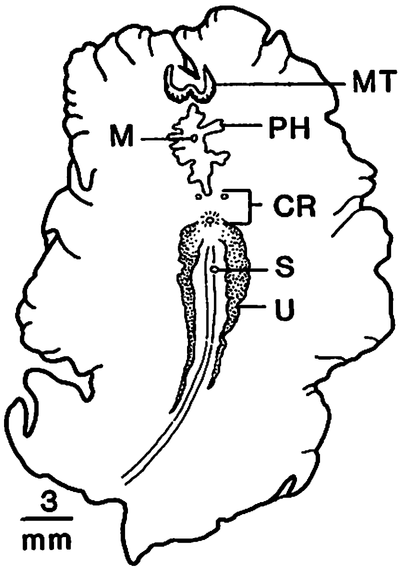

Figure 2.I.31.—*Pseudobiceros* sp: general anatomy. For abbreviations, see Legend preceding Figure 2.I.1.

compact and occupies about 20% of the body length. The male reproductive system is armed and bilaterally paired and lies near the posterior end of the pharynx. The female gonopore and the sucker lie posterior to the male reproductive system. This *Pseudobiceros* has been found commonly at Ala Moana Beach Park, as well as at many other locations around Oahu.

Pseudoceros sp.

This is an elongate species with a moderately ruffled margin (Fig. 2.I.32). The maximum length noted is 60 mm (breadth 17 mm) when crawling and extended. Generally the dorsum is black, with the medial region and margins yellow (Plate 2.I.2f). In gravid specimens the medial region may be mottled, with a bright fuchsia color imparted by ova in the female tract. The paired marginal tentacles are simple upfoldings of the margin, and the cerebral eyes form a single V-shaped cluster. Eyes are also present in and between the tentacles. The pharynx, occupying about 15% of the body length, is deeply branched. The male reproductive system is unpaired and armed and lies just behind the posterior end of the pharynx. The female gonopore lies just posterior to the male system, and behind it is the sucker. This is a relatively common *Pseudoceros* and is found along Ala Moana Beach Park, Oahu.

Other Pseudocerotidae

A number of other Pseudocerotidae have been observed in Hawaiian shallow waters. One (Plate 2.I.3a) is similar to that recorded as *Pseudoceros kentii*, which is shown in a color illustration by Saville-Kent (1893). However, the Hawaiian specimen examined had pale green dots. The male system is single, indicative of a *Pseudoceros* sp.

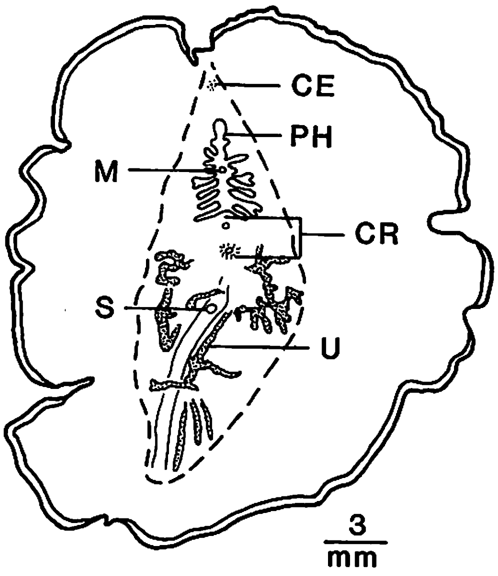

Figure 2.I.32.—*Pseudoceros* sp.: general anatomy. For abbreviations, see Legend preceding Figure 2.I.1.

A specimen figured by Edmondson (1946, p. 51) is also a likely member of the Pseudocerotidae. He described it as having a black upper surface with pale yellow or white oval spots and a violet ventral surface. A length of 2 inches (51 mm) was given. This is likely the same species as shown in Plate 2.I.3b. However, the specimens examined and those photographed have a dark purple dorsum.

Another likely Pseudocerotidae (Plate 2.I.3c) is similar or identical to that shown by Stummer-Traunfels (1933, Pl. 1, fig. 1) which is an undescribed species from Ambon, Indonesia (morphology of the male system unknown).

Additional probable representatives of the family Pseudocerotidae are shown in Plates 2.I.3d–f and 2.I.4a–e.

Thysanozoon tentaculatum (Pease, 1860)
[syn. *Peasia tentaculata* Pease, 1860. *Thysanozoon hawaiiensis* Hyman, 1960]

The species is elongate oval (Fig. 2.I.17) when crawling and extended, and has a maximum recorded length of 32 mm and breadth of 17 mm. The ground color is cream but may be altered by ingested material. The dorsum, including papillae, is dusted with dark pigment (Plate 2.I.4f). Small red pigment granules, restricted to the margin edge, form a narrow red to pink band that is usually more vivid anteriorly and discontinuous over the paired marginal tentacles. The tentacular bases are black and the tips white. The ventral side is off-white (Plate 2.I.5a). Cerebral eyes form a single, heart-shaped aggregate, and additional eyes are present within and between the tentacles. A compact, ruffled, anteriorly located pharynx occupies about 20% of the body length. The male reproductive system is bilaterally paired, armed, and lies in the region of the posterior portion of the pharynx. The female system lies behind the posterior end of the pharynx. A sucker is present posterior to the female gonopore. This endemic polyclad has been found under rocks in the littoral zone, usually in areas of mild to moderate wave action. It has been observed at Ala Moana Beach Park, Waikiki, Black Point, Makapuu Point, and Kualoa, Oahu, as well as at Poipu Beach Park, Kauai.

Other *Thysanozoon* Species

A *Thysanozoon* (Plate 2.I.5b) anatomically similar to *Thysanozoon brocchii* described by Risso (1818) and, perhaps, corresponding to this species as identified by Plehn (1899) from Laysan Island has been observed in the Hawaiian littoral zone (male system paired and armed). Several other undetermined species with a papillose dorsum are found in Hawaii and one is represented in Plate 2.I.4e.

Superfamily EURYLEPTOIDEA

All the known Hawaiian members of the superfamily Euryleptoidea are members of the family Prosthiostomidae. This group is characterized by its anteriorly rounded, elongate form; lack of tentacles; and paired cerebral eye group and marginal eyes either forming a band along the anterior or completely encircling the margin. The pharynx is cylindrical and directed forward; uterine vesicles usually lacking.

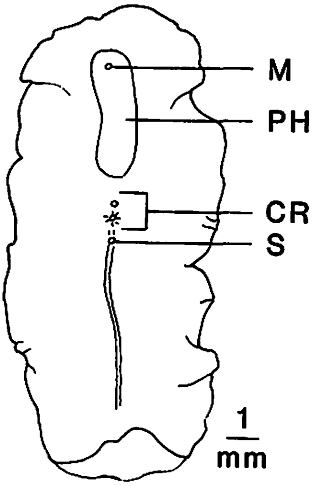

Figure 2.I.33.—*Enchiridium japonicum*: general anatomy. For abbreviations, see Legend preceding Figure 2.I.1.

Family **Prosthiostomidae**

Enchiridium japonicum Kato, 1943a

This worm is elongate, anteriorly truncate (sometimes with an indentation on the anterior midline), and posteriorly cuspate (Fig. 2.I.33). The maximum length may be 30 mm or more, and the breadth is 6 mm. The ground color is off-white. On the dorsum are scattered cocoa-brown maculae, which form a median band that does not reach either the anterior or posterior margins and is disrupted through the cerebral region (Plate 2.I.5c). Golden yellow pigment spherules also punctuate the dorsum, appearing more prevalent peripherally. Tentacles are absent. Marginal eyes form a band along most of the body. Cerebral eyes form paired clusters and include a ventral eye in each group. The pharynx is tubular and occupies about 37% of the body length. The copulatory region, followed by the sucker, lies just behind the posterior end of the pharynx.

Specimens collected at Black Point, Oahu, were reported by Poulter (1975). These worms were found in a shallow area of relatively heavy wave action at the reef front under basalt rocks. These rocks harbored the bivalve mollusk *Isognomon perna* [as *I.* (*Melina*) *costellatum*] and patches of the alga *Sargassum* were among the rocks. Another polyclad, *Pericelis hymanae,* was found in the same area. *Enchiridium japonicum* is also reported from Taiwan.

Prosthiostomum (*Lurymare*) *katoi* Poulter, 1975[4]

The worm at rest is elongate oval, rounded anteriorly, and bluntly pointed posteriorly (Fig. 2.I.34). The maximum length is 28 mm and the breadth is 6 mm. The ground color is off-white, and the dorsum is dusted with minute brown pigments, which are more prevalent medially (Plate 2.I.5d). Larger gold to orange pigment spherules are also present and are more prevalent medially. Tentacles are lacking. Marginal eyes form a continuous band along the anterior margin.

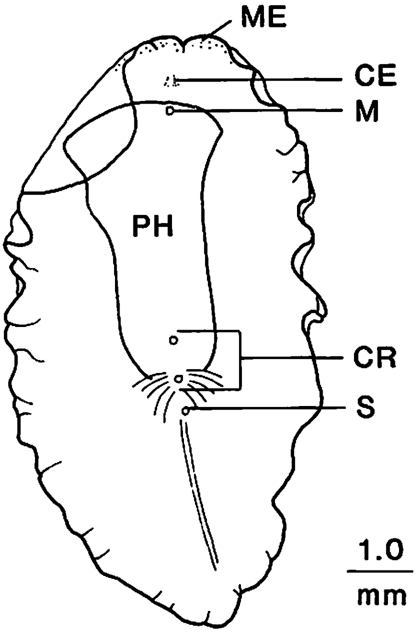

Figure 2.1.34.—*Prosthiostomum* (*L.*) *katoi*: general anatomy. For abbreviations, see Legend preceding Figure 2.1.1.

Cerebral eyes form a paired aggregate, and each aggregate usually includes a ventral eye. A tubular pharynx is present, occupying about 50% of the body length. The copulatory region lies near the posterior end of the pharynx, and the sucker is near the posterior end of the copulatory complex. This species has been collected in areas of relatively mild wave action from the undersides of rocks usually harboring the common oyster *Ostrea sandvichensis*. Specimens of *P. katoi* have been reported only from Ala Moana Beach Park and Kualoa, Oahu.

Prosthiostomum (*Prosthiostomum*) *montiporae* Poulter, 1975[5]

The worm is elongate, rounded anteriorly, and cuspate posteriorly (Fig. 2.1.35). Living specimens may attain a length of 12 mm, whereas the length of preserved specimens examined is 10 mm and the breadth is 3 mm. The dorsum is off-white (Plate 2.1.5e). The gut is delineated by a dendritic, rust-brown pigmentation resulting from ingested symbiotic algae (zooxanthellae) from the coral upon which it feeds. Tentacles are lacking, and a crescentic band of marginal eyes is found along the anterior margin of the body. Cerebral eyes form a paired aggregate over the brain region and each aggregate includes a ventral eye. The tubular pharynx, occupying about 10% of the body length, is located anteriorly and is modified by a unique longitudinal cleft. The copulatory region, followed by the sucker, lies near the posterior end of the pharynx. This endemic species, reported from Kaneohe Bay, Oahu, is a predator or ectoparasite on scleractinians (stony corals) of the genus *Montipora*, especially *M. verrucosa*, as reported by Jokiel and Townsley (1974).

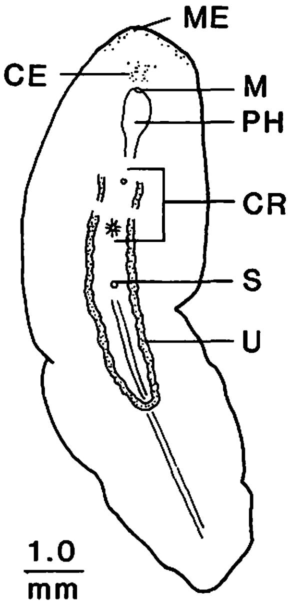

Figure 2.I.35.—*Prosthiostomum* (*P.*) *montiporae*: general anatomy. For abbreviations, see Legend preceding Figure 2.I.1.

Other Prosthiostomidae

The specimens represented in Plate 2.I.5f are possible members of the Prosthiostomidae. The color pattern of the specimen shown in Plate 2.I.6a is similar to the distinctive color pattern of *Prosthiostomum trilineatum* Yeri and Kaburaki, 1920, reported from Japan and more recently from Palau by Kato (1943b).

Peasia irrorata Pease, 1860

This worm is elliptical and is rounded at both ends; the length is 19 mm. The dorsum is pale yellowish fawn, irregularly dotted with brown and white and densely punctuated with minute fawn spots. Tentacles are lacking. Pease recorded an oblong "cluster of dots" that may be cerebral eyes. He also reported a tube under the epithelium, which suggests a tubular pharynx, occupying about 40% of the body length and lying in the anterior half of the body. Pease noted 2 ventral openings anterior to the middle of the body and just posterior to the tubelike structure. The anterior opening with white radiations might indicate the cement glands of the terminal portion of the female reproductive system. The more posterior opening may be a sucker. The male reproductive system, which would lie anterior to the female system, may have been overlooked or was perhaps in an immature state.

Pease also mentioned that these worms are very active, "creeping by very slight but rapid undulations of the body" and floating with its dorsum downward on the surface of the water. While the latter is a common behavior among some polyclads, it has not generally been noted among the Prosthiostomidae. No collection site is given for this Hawaiian species.

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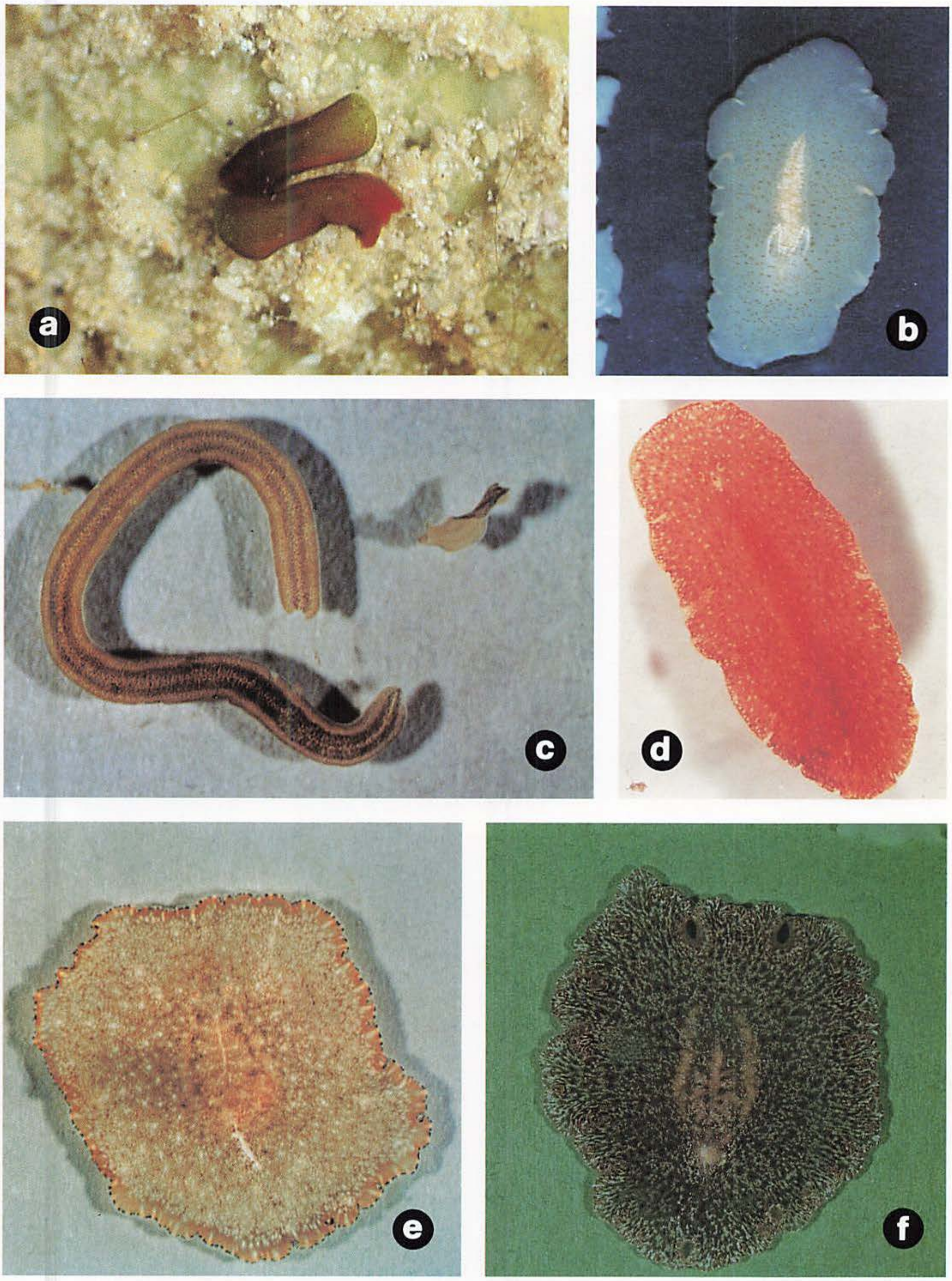

Plate 2.1.1

a. *Convoluta* sp., living specimens. (Courtesy M. Hadfield.)
b. *Aprostatum longipenis* or possibly the similarly colored ilyplanoid polyclad *Ilyella gigas*.
c. *Taenioplana teredini:* note smaller specimen in lower left.
d. *Stylochus (Imogine)* sp.
e. *Paraplanocera marginata*.
f. *Paraplanocera oligoglena:* larger specimen with more intense pigmentation.

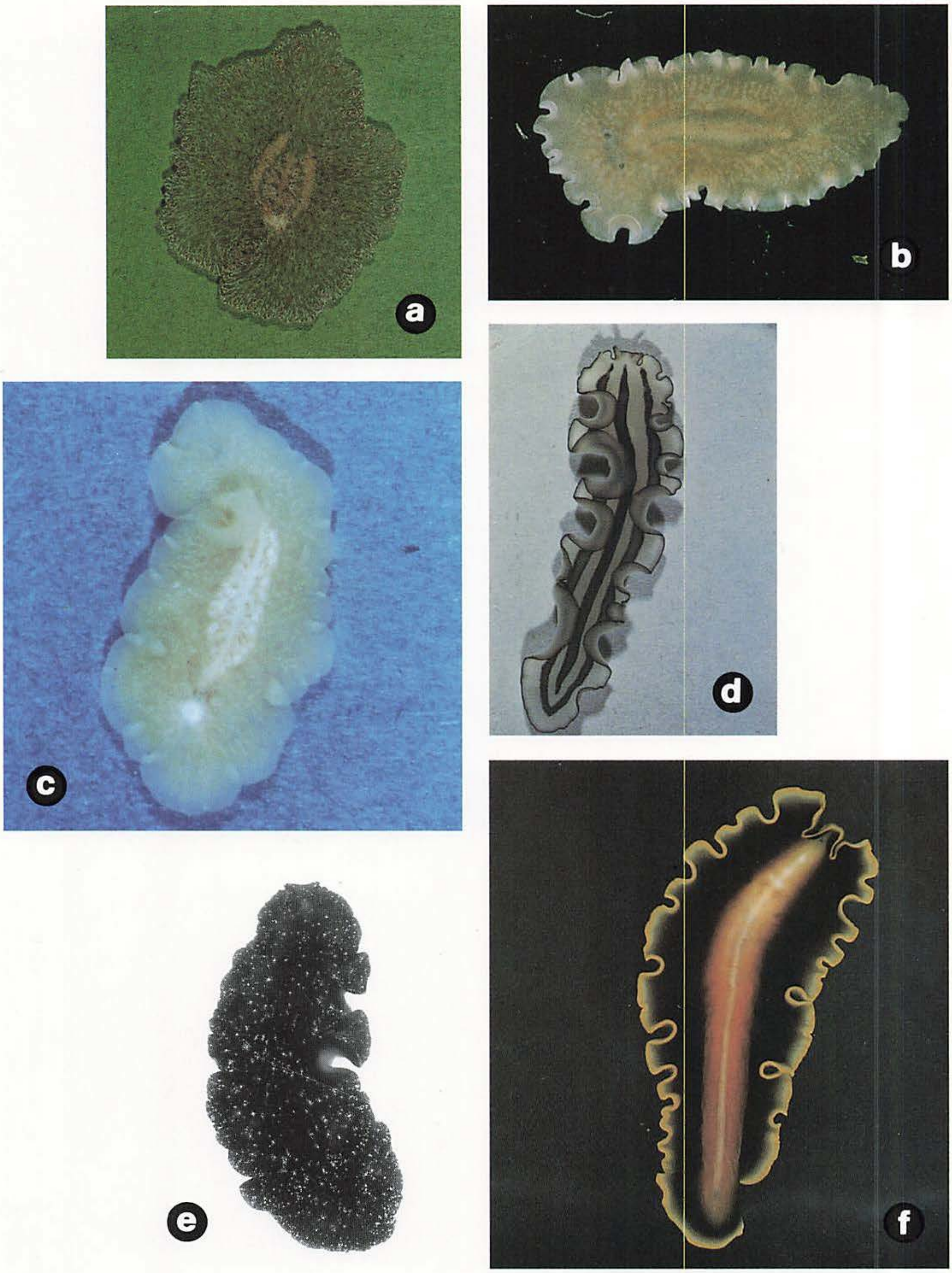

Plate 2.I.2

a. *Paraplanocera oligoglena:* smaller specimen showing internal anatomy.

b. *Ceratoplana hawaiiensis:* Magic Island, Ala Moana Beach Park, Oahu, found beneath *Colobocentrotus.* (Courtesy D. M. Devaney.)

c. *Pericelis hymanae.*

d. *Pseudobiceros gratus.*

e. *Pseudobiceros* sp.

f. *Pseudoceros* sp.

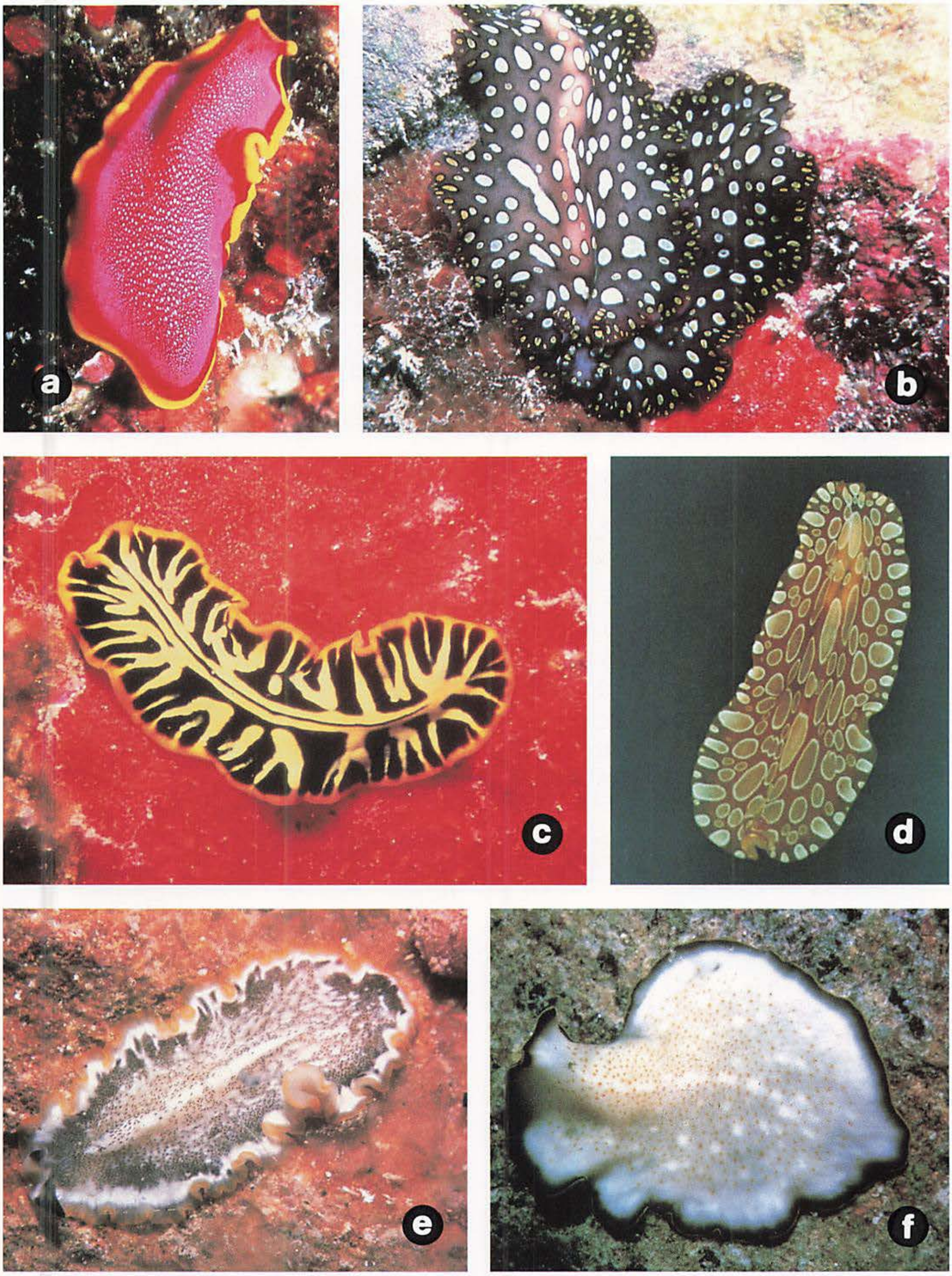

Plate 2.I.3

a. *Pseudoceros? kentii.*

b. *?Pseudocerotid:* Barbers Pt., Oahu, 5–25 m, under rocks and on ledges; length 35–40 mm.

c. *?Pseudocerotid* sp.: Pupukea, Oahu, 10–20 m, in ledges and caves; length ca. 25 mm.

d. *?Pseudocerotid.*

e. *?Pseudocerotid* sp.: Kewalo, Oahu, intertidal under rocks; length 20–40 mm. (Courtesy S. Johnson.)

f. *?Pseudocerotid* sp.: note cerebral eye group. Pupukea, Oahu, 10 m, under rocks; length ca. 12 mm.

(All photos courtesy S. Johnson.)

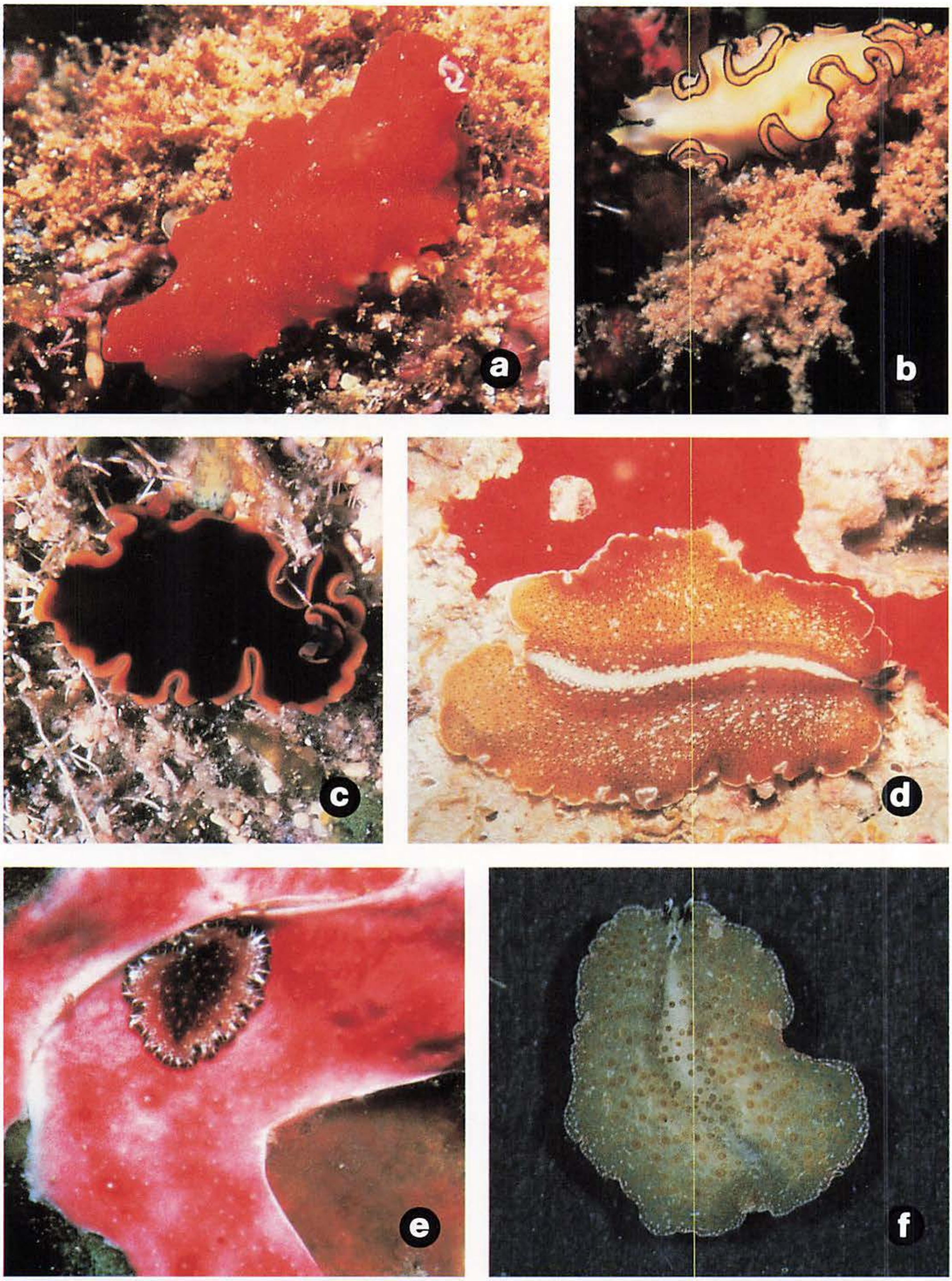

Plate 2.I.4

a. *?Pseudocerotid* sp.: note white over tentacles and lighter color of pharyngeal region. Pupukea, Oahu, 10 m, under rocks; length ca. 15 mm. (Courtesy S. Johnson.)

b. *?Pseudocerotid* sp.: note cerebral eye group. Pupukea, Oahu, 10 m, under rocks; length ca. 10mm. (Courtesy S. Johnson.)

c. *?Pseudocerotid* sp.: Makua, Oahu, 0–15m; length 8–20 mm. (Courtesy S. Johnson.)

d. *?Pseudocerotid:* note cerebral eye group. Ewa, Oahu, 8–15 m, under rocks and in caves; length 35–40 mm. (Courtesy S. Johnson.)

e. *?Pseudocerotid* sp.: Maile, Oahu, 15 m. under rocks and in caves; length 8–25 mm. (Courtesy S. Johnson.)

f. *Thysanozoon tentaculatum:* dorsal aspect.

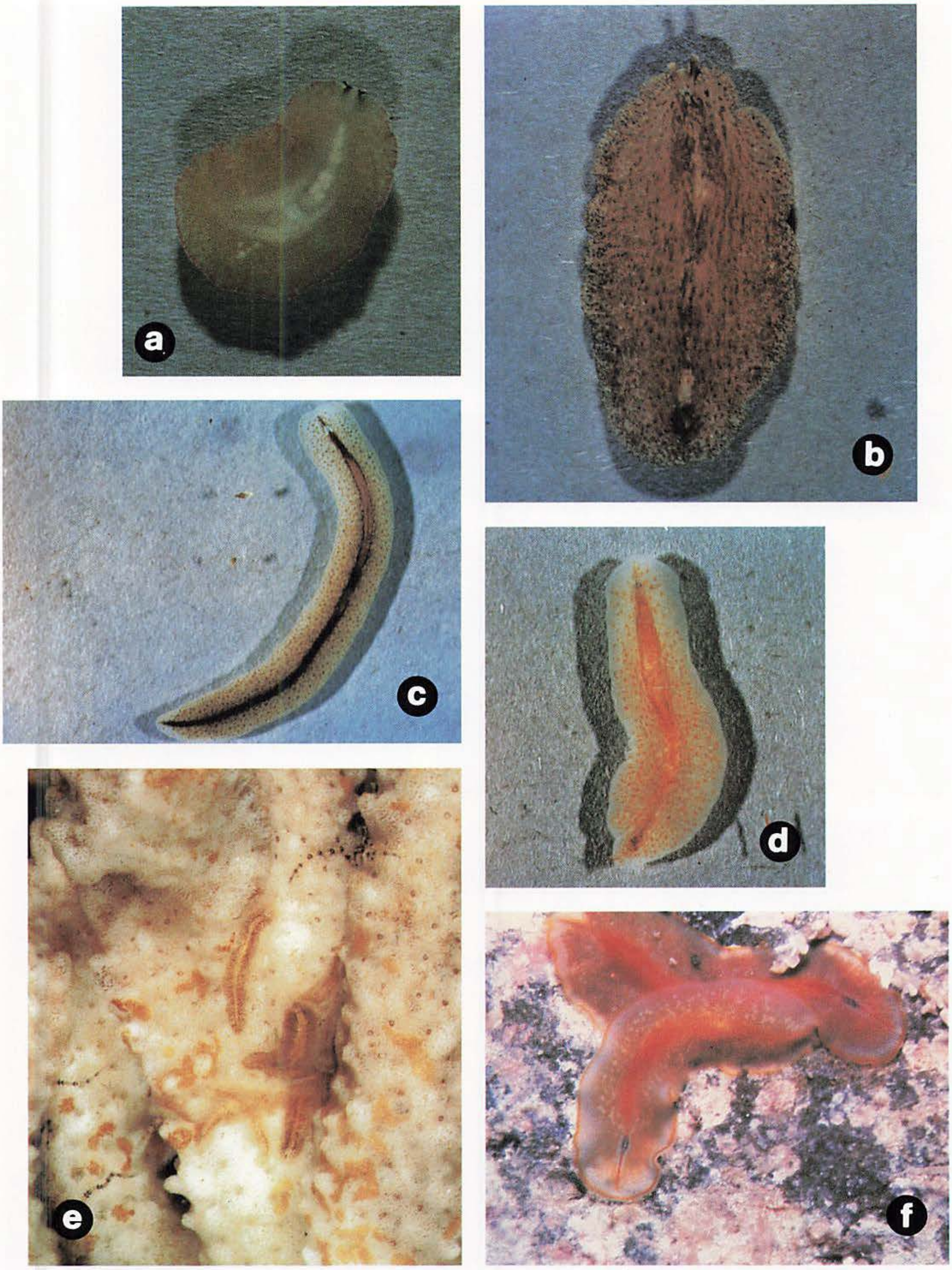

Plate 2.I.5

a. *Thysanozoon tentaculatum:* ventral aspect.
b. *Thysanozoon* cf. *T. brocchii.*
c. *Enchiridium japonicum.*
d. *Prosthiostomum (L.) katoi.*
e. *Prosthiostomum (P.) montiporae.* (Courtesy P. Jokiel.)
f. *?Prosthiostomidae:* Makua, Oahu, 5 m. (Courtesy S. Johnson.)

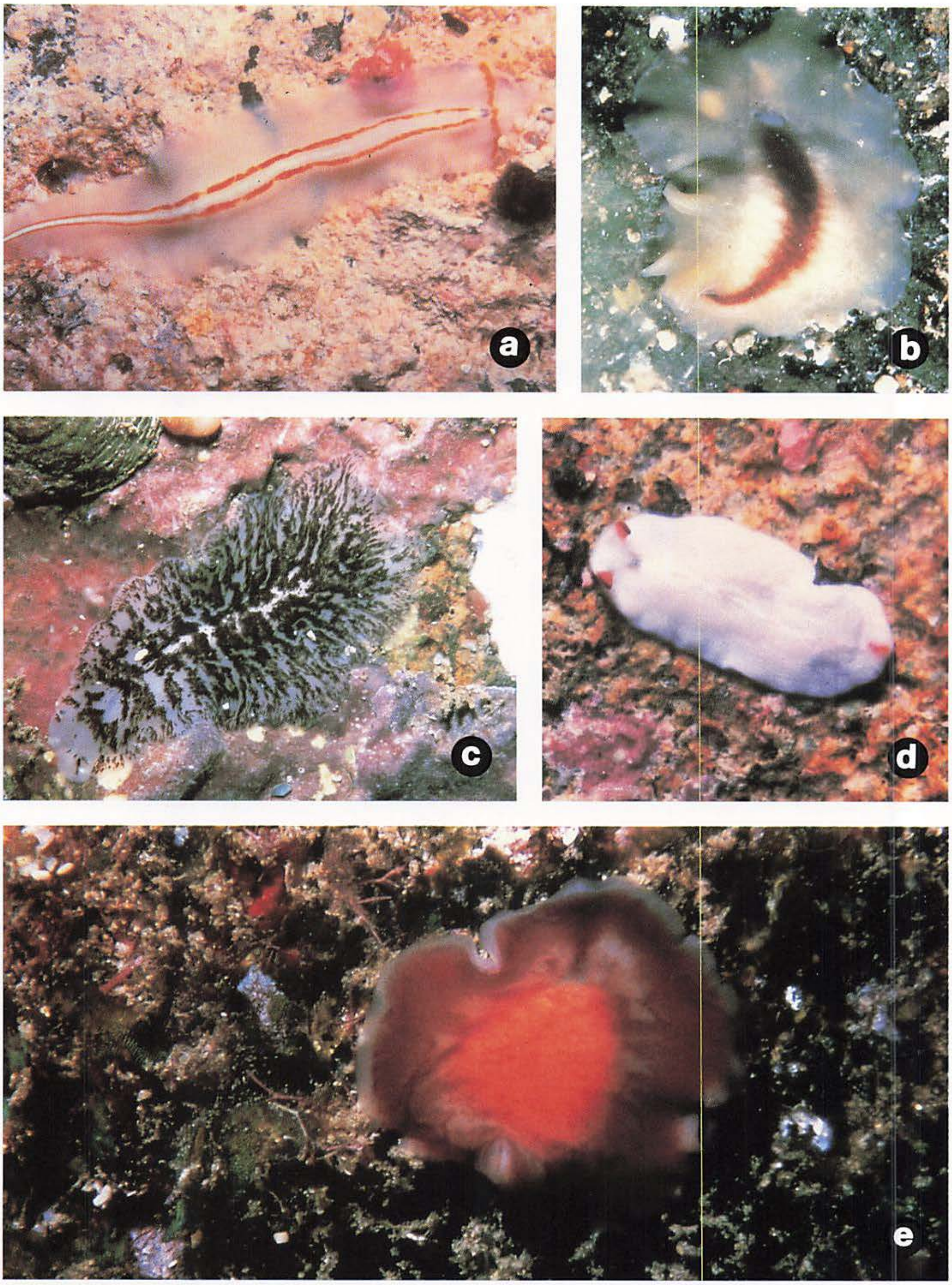

Plate 2.I.6

a. *Prosthiostomum ?trilineatum:* Makua, Oahu, 5m, under rocks; length ca. 30 mm.

b. Undet. Acotlylea: note nuchal tentacles. Kewalo, Oahu, intertidal under rocks; length 25–30 mm.

c. Undet. Acotylea: Kewalo, Oahu, intertidal under rocks; length 25–30 mm.

d. Cotylean sp.: Kewalo, Oahu, 1 m, under rocks; length 25–30 mm.

e. Acotylea sp.: Makua, Oahu, 5 m, on ledge; length 15 mm.

(All photos courtesy S. Johnson.)

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Plates for section 2: Chapter IV appear on following page.

Plate 2.II.1

Baseodiscus edmondsoni: dorsolateral view; Kewalo, Oahu at 1 m. (Courtesy S. Johnson.)

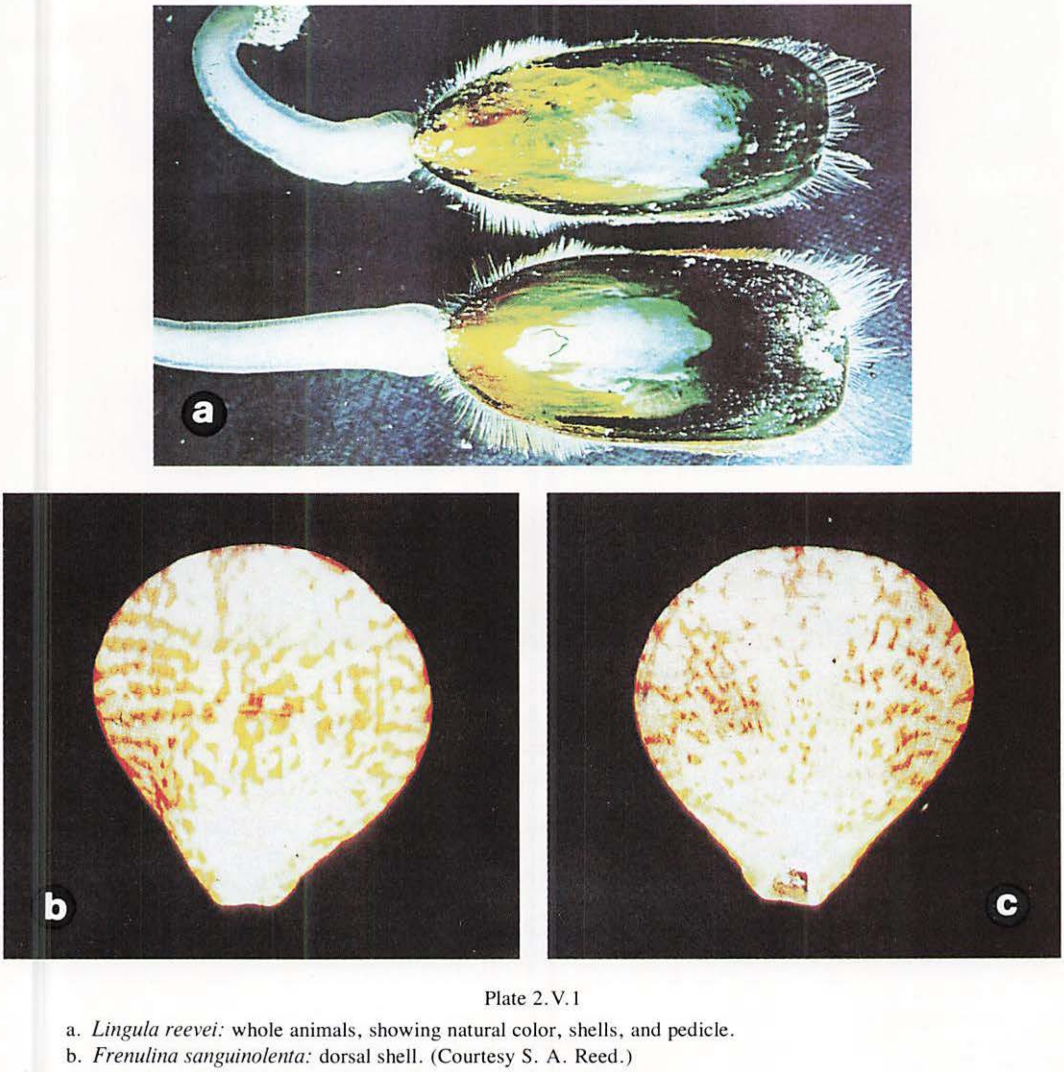

Plate 2.V.1

a. *Lingula reevei:* whole animals, showing natural color, shells, and pedicle.
b. *Frenulina sanguinolenta:* dorsal shell. (Courtesy S. A. Reed.)
c. *Frenulina sanguinolenta:* ventral shell. (Courtesy S. A. Reed.)

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Plates for section 2: Chapter V appear on preceeding page.

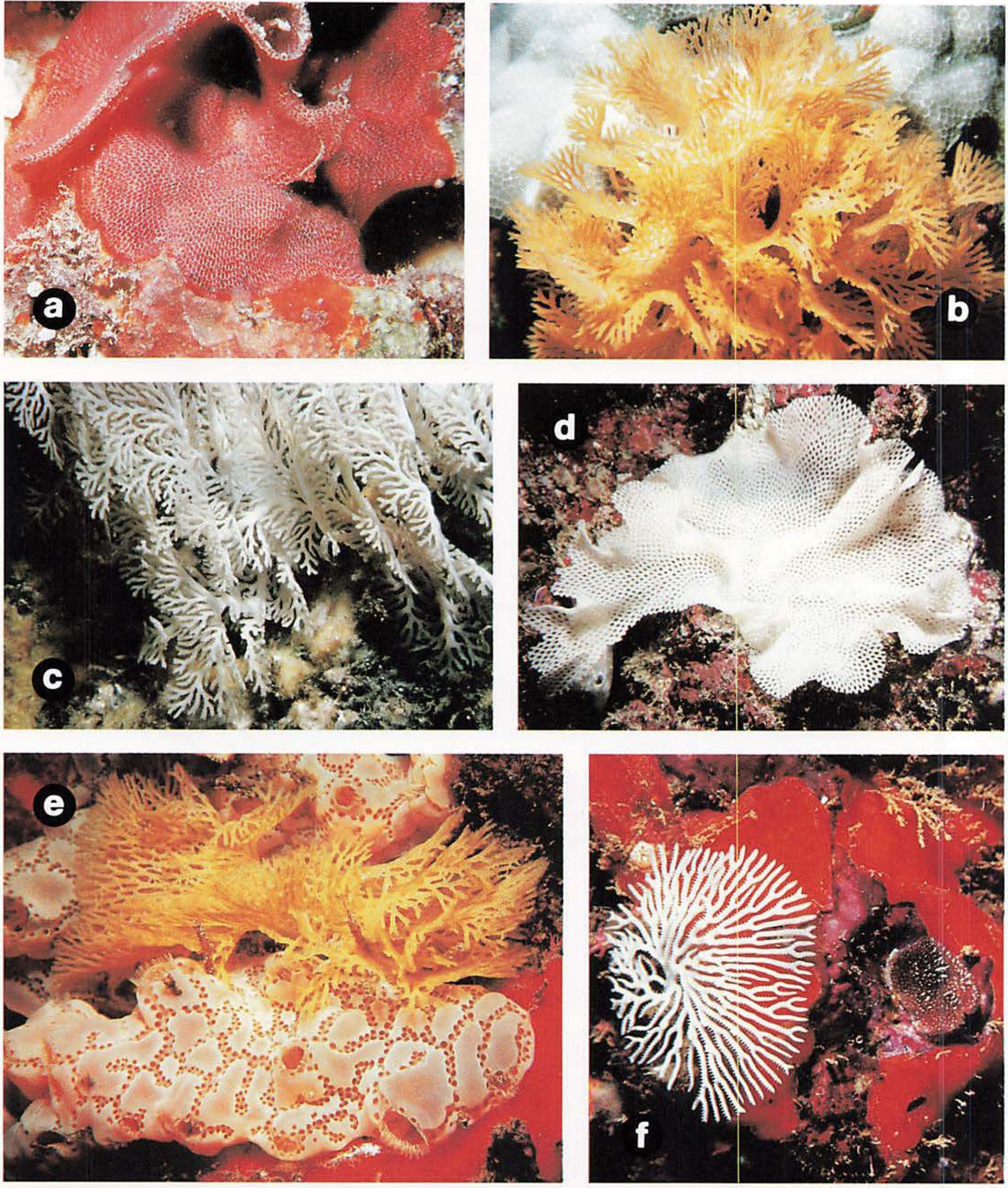

Plate 2.IV.1

a. *Steginoporella magnilabris.* Colony with incrusting base, rising in foliaceous bilaminar growth (top center). Photographed within lava tube at 10 m. Keahole Point, Kona, Hawaii.

b. *Reteporellina denticulata.* On coral colony surrounded by tunicate and red sponge. Photographed under ledges at 10–15 m. Kailua Bay, Kailua, Kona, Hawaii.

c. *Reteporella graeffei.* Photographed from underneath large coral head. Kailua Bay, Kailua, Kona, Hawaii.

d. *Triphyllozoon* sp. Photographed within lava tube. Keahole Point, Kona, Hawaii.

e. *Reteporellina denticulata.* Colony surrounded by colonial tunicate and red sponge. Kailua Bay, Kailua, Kona, Hawaii.

f. *Crisina radians.* White "tuning fork" colony above red sponge; cupped shape, purplish colony of *Holoporella* in right center. Taken within lava tube on wall at 10–12 m. Kaupulehu, Kona, Hawaii.

Until additional specimens come to hand, it can only be speculated, as suggested by Lang (1884), that *Peasia irrorata* may belong to the family Prosthiostomidae. The available information on this species permits rather wide interpretation and does not allow a clear assignment even to family.

Uncertain Status: *Peasia inconspicua* Pease, 1860

The incomplete description of this species precludes conjecture as to its systematic placement. Specimens are "elliptically oval" and equally rounded at both ends. The length is about 15 mm. The color is "pale" and the body translucent. Tentacles are lacking. An anterior cluster of minute black dots (cerebral eyes?) was noted. Specimens were found under stones at the low-tide level but the Hawaiian locality was not given.

Other Hawaiian Polyclads

In addition to the identified polyclads reported above, many remain to be identified or described from Hawaiian waters. A number of these colorful animals have drawn the attention of underwater photographers. Some representatives are shown in Plates. 2.I.6b–e to alert readers to the necessity of collecting these and other species for examination and identification by specialists.

ACKNOWLEDGMENTS

Professor Dr. Tor G. Karling of the Swedish Naturhistoriska Riksmuseet has been most gracious of his time and energy with respect to the microturbellarians. He read the manuscript, offered advice, suggestions, and corrections and generously provided the original photographs of Hawaiian microturbellarians. Prof. Karling's interest and support has been greatly appreciated, and he has contributed a far greater depth to the microturbellarian portion than the author could possibly have provided. However, errors are those of the author.

The description and photograph of the acoel ?*Convoluta* sp. was generously prepared by Dr. Michael J. Hadfield, University of Hawaii. Specimens of this species have not been examined by the author. Scott Johnson has made his extraordinary collection of color photographs of polyclads available for publication here, and the author thanks him for sharing them. The photograph of *Prosthiostomum* (*Prosthiostomum*) *montiporae* was made available by Paul Jokiel and the author wishes to thank him.

The material on the trematodes and cestodes is the result of the energy and interest of the late Dr. Dennis M. Devaney, whose constructive contributions to this chapter are enormous.

NOTES

1. Percent values given are based on overall length as measured from the anterior to posterior ends.
2. Adapted from Faubel (1983, 1984) here and throughout the following text.
3. Kay (1979, p. 578) records this as *T. clappi*.
4. Faubel (1984) lists this as *Lurymare katoi*.
5. Faubel (1984) lists this as *Prosthiostomum montiporae*.

GLOSSARY (PLATYHELMINTHES)

acetabulum (see **adhesive region: true sucker**).

acoelmate: Condition where the space between body organs and body wall is filled with mesenchyme and muscle fibers.

adhesive region: A common feature of Platyhelminthes, referring to any of several kinds of adherent structures, e.g.:

- —**bothrium:** Weakly muscularized, shallow sucking depressions characteristic of some cestode orders.
- —**glandular epithelial region:** Found among many microturbellarians.
- —**glandular muscular sites:** Found among many of the platyhelminths; includes the "sucker" (ventral adhesive disc) generally characteristic of the polyclad suborder Cotylea.
- —**true sucker:** Rarely found among turbellarians but common among digenetic trematodes; known as the acetabulum.
- —**opisthaptor:** Large posterior attachment organ in monogenetic trematodes.
- —**prohaptor:** Anterior adhesive organ characteristic of some monogenetic trematodes.

antrum: Cavern or cavity; usually a dilation of a canal.

bothrium (see **adhesive region**).

cirrus sac (pouch): Enlargement of a passage containing cirri; usually referable to an eversible portion of the male reproductive system found in some platyhelminths.

copulatory region: General site of the terminal portions (reproductive complex or apparatus) of the male or female, or both reproductive systems, usually lying near the gonopore(s).

digenetic: Pertaining to the order Digenea of the class Trematoda, consisting of mostly endoparasitic organisms with 2 to 4 hosts (the adult stage residing in the primary host, developmental stages or larvae residing in intermediate hosts).

eyes: Within the Turbellaria these usually refer to light-sensitive structures (ocelli) of varying complexity. Eyes tend to be numerous within the order Polycladida and are defined by their location:

- —**cerebral eyes:** Over or near the brain.
- —**frontal eyes:** Between the brain region and the anterior body margin.
- —**marginal eyes:** Along the body margin.
- —**tentacular eyes:** Within or in the immediate vicinity of the tentacles, or where the tentacles would be located if present.
- —**ventral eyes:** Eyes near the ventral body wall and associated with the cerebral eyes.

frontal glands: An aggregation of gland cells near the brain.

gonopore: Aperture of the reproductive system through which reproductive cells or reproductive organs communicate with the exterior. There are 3 types characteristic of turbellarians:

- —**common gonopore:** Aperture serving both male and female reproductive systems.
- —**female gonopore:** Aperture to the exterior through which ova pass and that in many turbellarians also receives the terminal portion of the male system at copulation.
- —**male gonopore:** Aperture through which the terminal male reproductive system communicates with the exterior.

hermaphrodite: An organism equipped with both male and female reproductive organs.

interstitial: Living in spaces between closely set objects; here referring to animals living between sand grains or other particulate matter.

monogenetic: Pertaining to the order Monogenea of the class Trematoda; these organisms are mostly ectoparasitic and are usually limited to a single host.

opisthaptor (see **adhesive region**).

papillae: Projections of varying shapes (e.g., clavate, mucronate); particularly characteristic of the cotylean polyclad genera *Thysanozoon* or *Acanthozoon*, in which the dorsum is adorned with numerous papillae and where in some species a branch of the gut may enter the papillae.

pharynx: Muscular tube for grasping and conveying food to the body mass or to the main intestine; among the Turbellaria the pharynx is of various types:

- —**bulbous pharynx:** A pharynx where the proximal portion of the pharyngeal tube is muscularly thickened and well delineated from adjacent mesenchyme. Three general forms of the bulbous pharynx are encountered in turbellarians:
  - —**doliiform pharynx:** Barrel-shaped pharynx oriented to the antero-posterior axis.

—**rosulate pharynx:** Spherical pharynx oriented parallel to the dorsoventral axis.

—**variable pharynx** or ***pharynx variabilis:*** Pharynx of less rigid shape and delineation, having alternations in various muscle layers.

—**plicate pharynx:** A muscular fold freely projecting into the pharyngeal cavity. Two general variations are found:

—**ruffled pharynx:** Pharynx suspended from the dorsal pharyngeal cavity.

—**tubular pharynx:** A pharynx lying parallel to the anteroposterior axis and attached at one end of the pharyngeal cavity.

—**simple pharynx** or ***pharynx simplex:*** Generally, a tube of invaginated epithelium.

proboscis: Protrusile structure, especially characteristic of the rhabdocoels of the suborder Kalyptorhynchia. This structure aids in the capture of prey and conveys it to the mouth.

prohaptor (see **adhesive region**).

rhabdoid: Rodlike structure found in the epithelium of turbellarians; among the several types of rhabdoids are the following:

—**rhabdite:** The most common rhabdoid type, generally shorter than the height of the epithelium.

—**rhammite:** Long and often sinuous rhabdoid, longer than the epithelial height. Anterior rhammite glands form rod tracks found in some rhabdocoels, which result from rhammites moving anteriorly along the necks of rhammite-forming glands.

rod tracks (see **rhabdoid: rhammite**).

sensory pit: Generally an anteriorly located indentation.

statocyst: Organ of balance.

sucker (see **adhesive region**).

tentacles: Usually referring to, but not limited to, a pair of protuberances often found in polyclads and distinguished as follows:

—**marginal tentacles:** A pair formed by folds and/or extensions of the anterior margin (characteristic of the suborder Cotylea).

—**nuchal tentacles:** A pair situated on the dorsum, usually near the brain (characteristic of the suborder Acotylea).

vitellaria: Yolk-producing glands that in most of the platyhelminths are anatomically separated from the ovaries; exceptions include members of the turbellarian orders Acoela and Polycladida and a few other turbellarians.

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Chapter II

Phylum NEMERTEA (RHYNCHOCOELA)

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NEMERTEANS (ribbon or proboscis worms) are unsegmented, soft-bodied worms capable of a high degree of elongation and contraction. The presence of an eversible tubular proboscis enclosed in a hollow proboscis sheath (the rhynchocoel), which lies above the digestive tract, characterizes and distinguishes this group of worms (Fig. 2.II.1). The specialized proboscis is regarded by Hyman (1951) as further development of the proboscis noted in 1 group of turbellarian flatworms (phylum Platyhelminthes). Other similarities to flatworms include an acoelomate body construction, often with a mass of tissue (parenchyma) filling the space between the body wall and intestine; a ciliated epidermis; and protonephridial excretory organs (when present). The general organization of the nervous system is also similar to that of flatworms. However, in contrast to Platyhelminthes, nemerteans possess a simple, closed circulatory system containing a colorless blood, which sometimes carries variously pigmented corpuscles. Moreover, the nemertean digestive tract is tubular, with separate oral and anal openings.

Most nemerteans are less than 20 cm in length when extended, and many are only a few millimetres long; however, some are known to reach a length of several meters or more. Body-wall musculature, composed of circular and longitudinal smooth layers, facilitates the remarkable elongation and contraction noted in many members of this phylum. Gland cells in the skin of nemerteans produce a sticky mucus, providing a surface on which beating cilia and waves of muscular contraction produce a gliding movement by bottom-dwelling forms.

Externally, the anterior head region in some species is provided with lobes, but in others the head is simply straight and tapering. Light-sensitive, pigmented eyespots (ocelli) as well as ciliated cephalic grooves and pits or other sense organs occur on the head of many species.

The proboscis opens to the outside, either through a separate proboscis pore

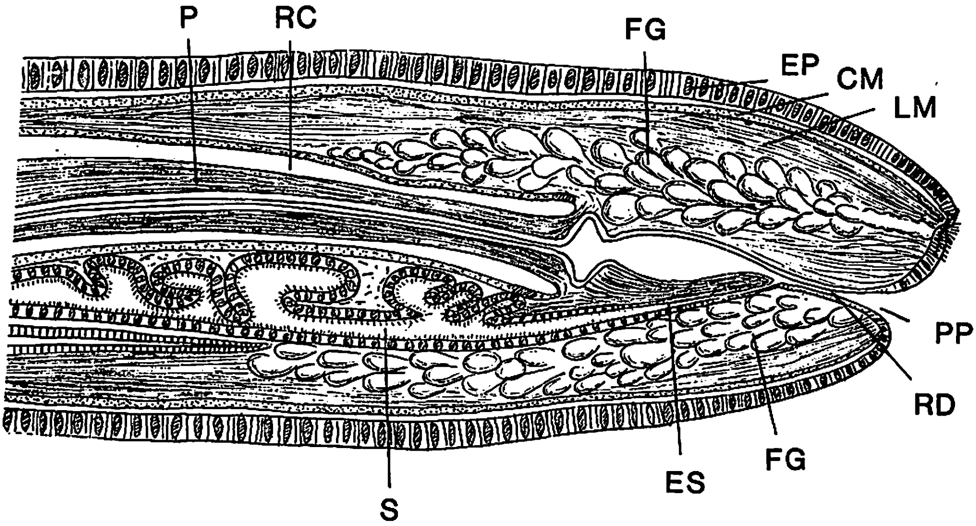

Figure 2.II.1.—Hoplonemertean (*Nemertopsis*): anterior sagittal section. (CM, circular muscle; EP, epidermal glands; ES, esophagus; FG, fontal glands; LM, longitudinal muscle; P, proboscis; PP, proboscis pore; RC, rhynchocoel; RD, rhynchodaeum; S, stomach.) (After Hyman 1951.)

anterior to the mouth or through a pore shared by the proboscis and the digestive system. Eversion of the proboscis—in which it is turned inside-out like a finger of a glove—results from muscular contraction that exerts pressure on fluid within the rhynchocoel. Withdrawal of the proboscis in most nemerteans is accomplished by a retractor muscle at the base of the rhynchocoel. In species lacking this muscle, proboscis retraction is presumably achieved hydraulically. By widely accepted convention, the position and names of proboscis muscle layers are designated when the proboscis is retracted. In this state, the proboscis epithelium is nearest the center of the proboscis. The muscle layer adjacent to the epithelium is termed "outer" (since it will be to the outside when the proboscis is everted), while those muscle layers farther from the epithelium are termed "inner." When extended, the proboscis is used to obtain food, act in defense, or enable rapid escape. Most nemerteans feed mainly on other invertebrates or are scavengers. In the group known as hoplonemerteans, the proboscis is armed with 1 or more small, pointed stylets, which aid in the capture of prey. Wrapping the prey in coils of the proboscis is another method of capture.

Although some nemerteans lack conspicuous colors, others are distinctively pigmented with lines or rings of contrasting color over the body. Color patterns present in adult specimens may be absent in juveniles.

In most nemerteans the sexes are separate and fertilization takes place after the eggs are released to the outside. Fertilized eggs are often deposited in strings or clusters enclosed in a gelatinous matrix. The embryos either develop directly or metamorphically; in the latter case, larvae are produced. Several larval forms are recognized. Among these are the transparent, free-swimming, ciliated pilidium larva and the Desor larva that remains within the egg membrane. These larvae undergo metamorphosis and become typical nemertean worms.

Most nemerteans are benthic and are found crawling on rocky or soft substrate, burrowing in sediments, or intertwined among algae or sessile animals such as mussels, tunicates, and bryozoans. A few species are planktonic and some are parasitic on or within other invertebrates. Only 7 free-living benthic and 1 symbiotic nemertean species have been reported from Hawaiian waters. Five of the benthic species have been reported only from the Hawaiian area. Little is known about nemerteans in the tropical Pacific, and the exceptionally high level of apparent endemicity and low number of Hawaiian species may well be a reflection of inadequate collecting. More study in Hawaii and other Pacific island areas is needed to establish the distribution and composition of the Hawaiian nemertean fauna.

NEMERTEAN STUDY TECHNIQUES

Study techniques for nemerteans given below are based on Kirsteuer (1967, 1978), except as indicated. A proven method for collecting nemerteans from tropical coral habitats relies on the tendency of these worms to come to the surface when water becomes depleted of oxygen and carbon dioxide builds up. After collecting a sample (e.g., pieces of coral, other hard substrate, or marine plants), a 30- to 40-liter glass or clear plastic container, which is higher than wide, is filled about three-quarters with loosely placed material. Seawater is then added some 5 cm above the sample. The container should be entirely shaded or, at most, with only a small portion in brighter light. Depending upon the ambient temperature, nemerteans and other worms will move up on the walls of the container within 4 to 8 hours. Close inspection of all small worms on the container walls and water surface may be necessary to recognize the nemerteans. A pipette can be used to transfer specimens to a small dish where they are best examined under a dissecting microscope.

Notes and simple drawings of living animals aid in identification. In addition to measurements of length and width (in the noncontracted condition), the shape of the head, presence of cephalic slits and grooves, presence, number, and arrangement of ocelli, as well as colors and color pattern, are important external features. Outlines of internal organs can be seen through the body surface of some light-colored and semitransparent species. Methods of microscopic examination of living nemerteans are reviewed by Kirsteuer (1967).

Prior to preservation, nemerteans should be anesthetized or relaxed to avoid undue contraction and fragmentation of the body or eversion of the proboscis. Urethane or chloral hydrate can be used as anesthetics in the following way: to a dish of seawater containing the nemertean, a few crystals of the anesthetic are gradually added at 10-minute intervals; generally within 1/2 to 2 hours the worm will be motionless and expanded. However, partial body contraction and eversion of the proboscis during this procedure indicates that too much anesthetic has been added. In this case the specimen should be returned to clear seawater and the operation started again. A 7.5 to 8% magnesium chloride solution made up in distilled water is also recommended and has no adverse effects on the worms. In this solution, anesthetization is usually complete in 10 to 30 minutes and only infrequently leads to proboscis eversion (R. Gibson, pers. comm.).

After complete relaxation and expansion, nemerteans should be transferred to a fixing agent. Bouin's fluid is a good fixative, rendering the tissues suitable for histological examination. Fixation for 3 to 5 hours for small specimens, and 12 to 24 hours for larger ones, is usually sufficient, after which the animals are transferred from Bouin's to 70% ethyl alcohol. Periodic changes of the alcohol for a few days removes any remaining fixative, which is indicated by a yellow color.

For identification at the specific and higher levels of classification, an examination of the internal anatomy is necessary. This can be accomplished by studying 7–μm-thick cross sections of the animal with a compound microscope. For details of histological preparation methods, see Guyer (1953). A working knowledge of the group and familiarity with the literature are required. Two books in English that review many aspects of nemertean biology and contain extensive bibliographic citations are Hyman (1951) and Gibson (1972). A recent systematic resumé of the group, including definitions often to the genetic level, has been presented by Gibson (1982). Hawaiian nemerteans have been described by Coe (1906, 1934, 1947) and Humes (1942).

Class ANOPLA

Nemerteans in this class have the mouth located below or behind the brain, the central nervous system within the body wall epidermis, dermis, or musculature (Fig. 2.II.2), and the proboscis lacking armature (stylets). The 5 Hawaiian species belonging to this class are members of the order Heteronemertea, which has a body-wall musculature in 3 layers (a middle layer of circular muscle between inner and outer layers of longitudinal muscle) (Fig. 2.II.2).

Two genera, *Baseodiscus* and *Lineus,* are recorded from Hawaiian waters and, with the exception of 1 species that is also known from Wake Island, each of the species has been reported only from the Hawaiian Islands.

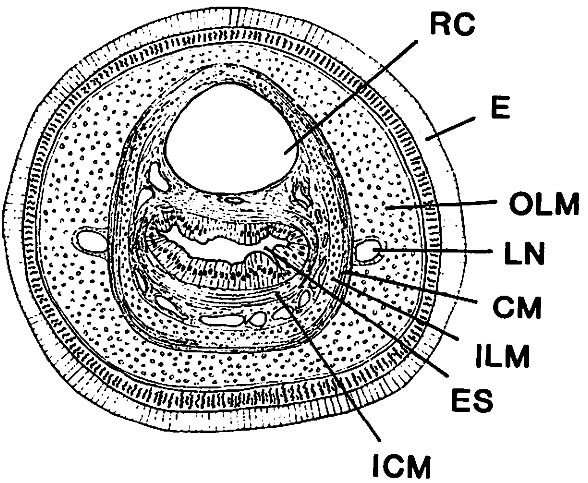

Figure 2.II.2.—*Baseodiscus cingulatus:* cross section through posterior end of foregut. [E, epidermis; ICM, inner circular (splanchnic) muscle; ILM, inner longitudinal muscle; LN, lateral nerve; OLM, outer longitudinal muscle; see Fig. 2.II.1 for other abbreviations.] (From Coe 1906.)

KEY TO HAWAIIAN HETERONEMERTEA

1 Cephalic grooves absent; proboscis and proboscis sheath short, seldom more than one-third body length; proboscis musculature in 2 layers of which the outer is longitudinal .... *Baseodiscus* ... 2
   Horizontal cephalic grooves present on sides of head; proboscis longer than body but coiled in shorter proboscis sheath; proboscis musculature in 2 or 3 layers, of which outer is circular............ *Lineus* ... 4
2(1) Body with reddish brown rings separated by lighter areas (Fig. 2.II.3) .... *B. cingulatus*
   Body lacking reddish brown rings but with reddish brown middorsal stripe 3
3(2) Transverse band of reddish brown present on head between laterally placed ocelli and separated from usually broad middorsal stripe (Plate 2.II.1) .... *B. edmondsoni*
   Transverse band absent and ocelli absent or inconspicuous; continuous middorsal stripe along entire body (Fig. 2.II.5) .... *B. univittatus*
4(1) Tip of head pale gray (as well as margins of cephalic grooves), overall body color otherwise brown .... *L. hiatti*
   Tip of head white beyond which anterior part of body dark, with posterior half of body lighter (Fig. 2.II.6)................ *L. albifrons*

Baseodiscus cingulatus (Coe, 1906)
[syn. *Taeniosoma cingulatum* Coe]

Living, extended specimens are known to reach a meter or more in length and to be as wide as 4 mm, making this the largest recorded nemertean in Hawaiian waters. There are numerous reddish brown rings (often incomplete ventrally) contrasting with a pale yellowish or flesh color on the rest of the body. In living specimens a longitudinal brown line can be present on the dorsal side. Each lateral margin of the head bears 35 to 50 cup-shaped black ocelli (Fig. 2.II.3). The body is firm, not easily fragmented, and has a distinct annular groove in front of the mouth separating the head from the rest of the body.

Although originally recorded from dredge hauls between Maui and Lanai at depths approaching 80 m (44 fm), *B. cingulatus* has been found on shallow reef areas from Necker Island to Halape, Hawaii (Coe 1934, 1947). Nematode parasites (Fig. 2.II.4) were observed in 2 of the specimens taken in deeper water (Coe 1906).

Baseodiscus edmondsoni Coe, 1934

This is a slender species with a maximum recorded diameter of 3.5 mm and length of 50 cm. A dark reddish brown median stripe, becoming more or less divided into alternating light and dark bands, runs the length of the body dorsally and contrasts with a pale yellowish or flesh-colored background. In some specimens the median longitudinal stripe can be narrow with 20 to 30 transverse bands of darker color extending laterally on each side. Toward the front of the body, the dorsal stripe is separated by a light area from a broad, transverse

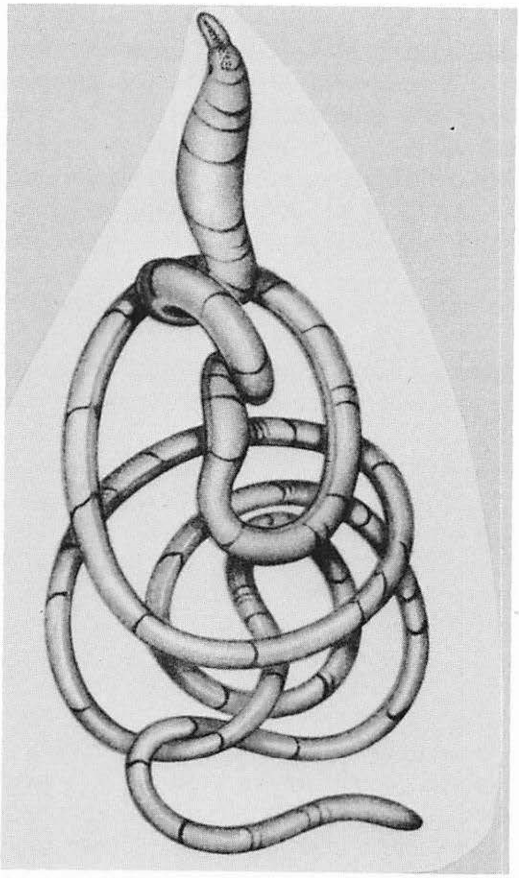

Figure 2.II.3.—*Baseodiscus cingulatus:* entire specimen. (From Coe 1906.)

reddish brown band over the head (Plate 2.II.1); on either side of the head there are 20 or more small black ocelli and 15 or more similar ocelli behind the pigmented band on the head. Two types of internal parasites were recorded from *B. edmondsoni:* slender "nematode-like" worms encysted in connective tissue between the lateral cord and midgut wall, and elongated gregarine protozoans in the intestinal tract (Coe 1934). Specimens of *B. edmondsoni* have been recorded from several locations around Oahu, the shore at Lihue, Kauai, and from Wake Island in the central Pacific. Gibson (1979) included *B. edmondsoni* as a questionable junior synonym of *B. hemprichii* (Ehrenberg, 1831), a widespread Indo-West Pacific species.

Baseodiscus univittatus (Coe, 1906)
[syn. *Taeniosoma univittatum* Coe]

The body of this nemertean may exceed 10 cm in length and have a diameter between 1.5 and 2.0 mm. A single, dark reddish brown stripe of variable width extends the length of the entire body dorsally (Fig. 2.II.5) and contrasts with a creamy white or flesh-colored background color; ocelli are absent or inconspicuous. *Baseodiscus univittatus* was first collected in deep water off Molokai and

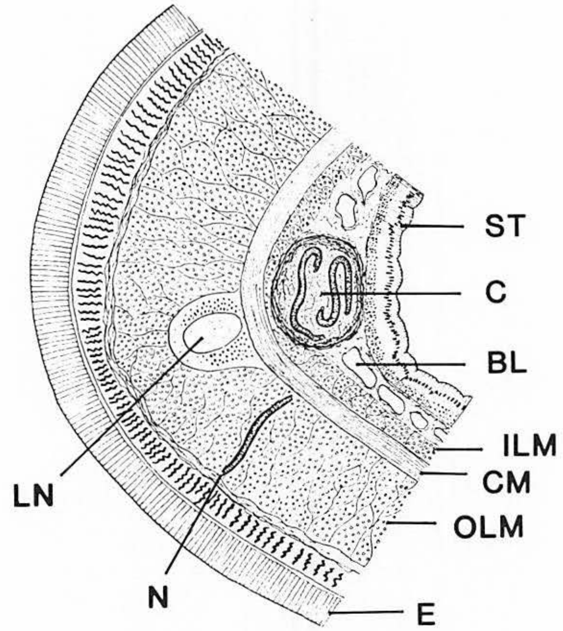

Figure 2.II.4.—*Baseodiscus cingulatus:* cross section through anterior end, stomach region. (BL, blood lacuna; C, cyst containing 2 nematode parasites; N, nematode parasite; ST, stomach lining; see Figs. 2.II.1, 2 for other abbreviations.) (From Coe 1906.)

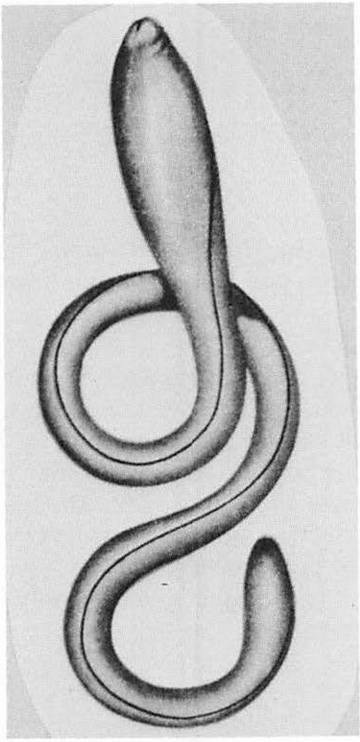

Figure 2.II.5.—*Baseodiscus univittatus:* form with narrow dorsal stripe. (From Coe 1906.)

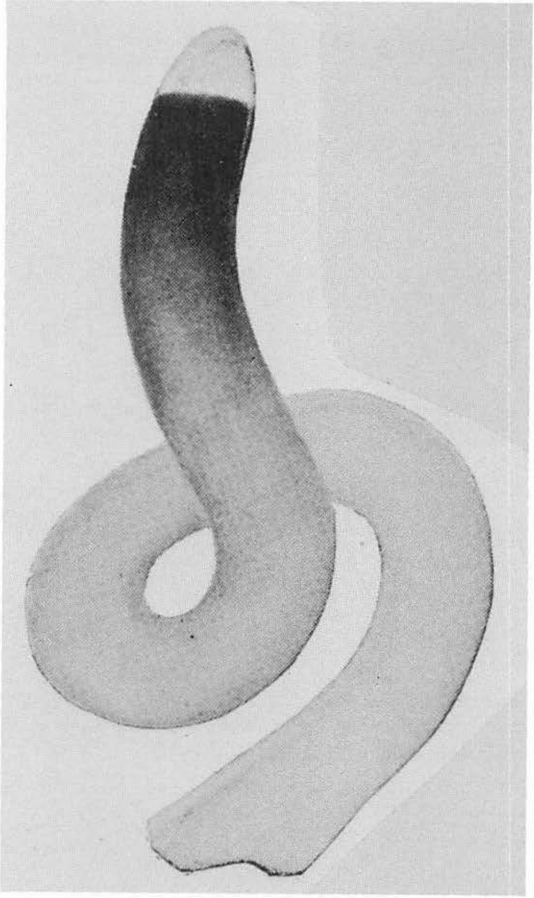

Figure 2.II.6.—*Lineus albifrons:* dorsal view of anterior end of body showing pigmentation. (From Coe 1934.)

Maui at 232 to 325 m (127 to 178 fm); additional specimens are known from shallow reef areas at Kaaawa and Waikiki, Oahu (Coe 1934).

Lineus albifrons Coe, 1934

The size of this species, extended and alive, is unknown. The only recorded specimen was 14 mm long and 1.5 mm wide when preserved. This species can be recognized by the white or colorless anterior tip of the head followed by a darker pigmented region covering about one-third of the body; the body gradually lightens toward the posterior end (Fig. 2.II.6). The living color is unknown. The cephalic grooves are described as moderate in length but not deep, with the mouth located directly behind the posterior end of these grooves. Ocelli are inconspicuous or absent. *Lineus albifrons* was collected only at Kahala, Oahu, and no additional records are known.

Lineus hiatti Coe, 1947

Preserved specimens are 10 to 15 cm long and 4 mm wide. Alive, this worm is brown, and it darkens upon preservation. The body is reportedly fragile; the worm easily fragments when collected. The head is slender, much narrower than the adjacent portion of the body, and the tip is pointed. The cephalic grooves are long and deep. Ocelli are inconspicuous or absent. Both edges of the cephalic grooves and the extreme tip of the head are pale gray.

Four specimens, the only records of this species, were collected beneath stones and matted algae at Halape, Hawaii.

Class ENOPLA

In this group of nemerteans the mouth is located in front of the brain, frequently there is only a common mouth and proboscis opening to the exterior, and the central nervous system is internal to the body-wall musculature (composed of an outer circular and inner longitudinal muscle layer) (Fig. 2.II.1). In the order Hoplonemertea, to which the recorded Hawaiian species belong, needlelike stylets are located at the tip of the everted proboscis. Members of the enoplan order Bdellonemertea have an unarmed proboscis, a ventral sucker, and live within the mantle cavity of bivalve mollusks.

Shallow-water hoplonemerteans recorded in Hawaii belong to the suborder Monostilifera, which is characterized by having a central proboscis stylet embedded in a conical, granular mass called the basis. There are also usually 2 or more lateral accessory pouches containing several reserve stylets in various stages of development. One Hawaiian member of the suborder Polystilifera has been recorded (Coe 1906) as an undetermined species of *Drepanophorus* known only from a proboscis recovered in a dredge haul at a depth of 462 to 516 m (250 to 282 fm) off northwest Oahu. The proboscis armature of polystiliferans is distinctive, consisting of a pad or shield that bears numerous small stylets.

KEY TO HAWAIIAN MONOSTILIFERA

1 Symbiotic on egg masses of portunid crabs .. *Carcinonemertes mitsukurii*
  Free-living 2
2(1) Proboscis sheath less than half of body length; red when alive
  .... *Nemertopsis exilis*
  Proboscis sheath extending to, or nearly to, posterior end of body;
    uniformly flesh-colored when alive .... *Tetrastemma* sp.

Carcinonemertes mitsukurii Takakura, 1910

The body[1] is cylindrical, very narrow, and with both ends bluntly pointed. Extended, males are as long as 10 mm; females, 30 mm. The width of both is as much as 0.5 mm. Two black eyespots (ocelli) lie slightly back of the anterior end, and the overall color is light brown, light yellow, or milky white. The brain is visible through the body as a fleshy mass. Internally, the proboscis stylet is 8 μm or less in length, with the basis elongate-oval, 20 to 27 μm long, and 5 to 7 μm broad. In members of this genus the accessory stylets and stylet sacs have been secondarily lost. In the male a specialized duct (Takakura's duct) is considered to be a pinched-off portion of the rhynchocoel and lies behind the proboscis. This

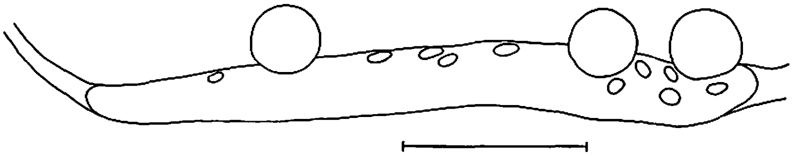

Figure 2.II.7.—*Carcinonemertes mitsukurii:* mucus sheath from egg mass of crab, showing 3 crab eggs. (From Humes 1942.) Scale line = 1 mm.

duct serves to transport sperm cells, which empty into the intestine where they exit through the anal opening.

Carcinonemertes mitsukurii secretes a semitransparent mucus sheath (Fig. 2.II.7), which is attached to setae (bristles) on the abdominal appendages (pleopods or swimmerets) of egg-bearing host crabs. Adult specimens have been recovered from the egg masses of crabs upon which they probably feed. Individuals of other species in the genus *Carcinonemertes* move to the gills of crabs when there are no eggs. *C. mitsukurii* was originally described from specimens collected on the grapsid crab *Eriocheir japonicus* in Yokahama Bay, Japan. Additional specimens have been recorded from 3 species of portunid crabs in the Philippines, Hong Kong, and Singapore, as well as in the Gilbert, Society, and Hawaiian Islands (Humes 1942). The host in Hawaii is reported as the portunid *Charybdis erythrodactyla.*

Nemertopsis exilis Coe, 1947

This slender worm, 0.5 to 1.5 mm in diameter, reaches a length of at least 60 mm when fully extended. The body is firm and not easily broken. One of the original specimens was red when alive. The rhynchocoel is about one-third the body length. The proboscis is more than half the body width in places and the stylet and stylet basis are slender. Two stylet sacs bear accessory stylets. The only recorded specimens were collected at Halape, Hawaii, under rocks in shallow water.

Tetrastemma sp.

An undetermined species of *Tetrastemma* was recorded by Coe (1934). The body of this nemertean was uniformly flesh-colored. No morphological details were given. This species was collected on a reef at Lihue, Kauai, by A. E. Verrill, who also made the generic determination (Coe 1947).

ACKNOWLEDGMENTS

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NOTE

1. Much of the description of external features is based on Humes' (1942) translation of the original description by Takakura for specimens collected in Japan.

GLOSSARY (NEMERTEA)

blood lacunae: One of 2 types of blood channels that are spaces in the closed circulatory system, lined with a thin membrane. The true blood vessels with distinct walls represent the other type.

epidermal glands: Mostly unicellular glands that produce mucus that aids in movement, as well as in maintaining a moist body surface and protecting the animal from predators.

frontal glands: Mucus-secreting structures in the anterior end of nemerteans, often opening by a separate pore above the proboscis pore; also called cephalic glands.

rhynchodaeum: A cavity between the proboscis and proboscis pore. In most Enopla the rhynchodaeum leads to a common anterior external opening for proboscis and digestive system.

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Chapter III

THE ASCHELMINTH COMPLEX

W. DUANE HOPE

THE PHYLA ROTIFERA, Gastrotricha, Kinorhyncha, Nematoda, and Nematomorpha were at one time grouped together as classes of the phylum Aschelminthes, but currently each is regarded as a separate phylum. Members of these phyla are typically small (except the relatively long nematomorphans and some parasitic nematodes), usually ranging from microscopic to a centimeter or more in length; the body is often elongate, transparent, covered with a thin cuticle, and without true segmentation. Surface ciliation is limited to specialized areas or it may be absent, but modified cilia are associated with sensory spines and setae. The body cavity is a pseudocoelom, and the digestive tract is usually complete with mouth, gut, and anus. Members of most species are dioecious.

Phyla ROTIFERA, GASTROTRICHA, NEMATOMORPHA

Very little research has been done on the Aschelminthes from the Hawaiian Islands. Three species of marine rotifers (phylum Rotifera) have been reported (Weber 1906), which were collected ". . . dans des fosses et mares, entre Honolulu et Waikiki (Ile Oahu) . . . " on October 13, 1902. They are as follows[1]:

Dipleuchlanis propatula (Gosse, 1886)
  [syn. *Euchlanis plicata* Levander, 1894]
Lecane (Lecane) luna (O. F. Müller, 1776)
  [syn. *Cathypna luna* (Müller), lapsus (Ehrenberg) in Weber (1906)]
Lecane (Monostyla) lunaris (Ehrenberg, 1832)
  [syn. *Monostyla lunaris* Ehrenberg, 1832]

Unidentified members of the phylum Rotifera, as well as unidentified members of the Gastrotricha, were found in a study of sand samples taken at Kaneohe Bay, Oahu (Emig 1981). Members of the phylum Nematomorpha have only been informally reported as inhabitants of freshwater in the islands.

Members of the phylum Kinorhyncha are entirely unknown from Hawaiian waters, although undoubtedly they are present.

Phylum NEMATODA

This is by far the largest and most diverse phylum of the aschelminth complex, with over 5,000 nominal species known from the marine environment alone. Many more species are known from soil and freshwater environments, and a very large number of species are parasitic in invertebrates and vertebrates. Yet judging from the large number of new species being described, only a relatively small percentage of the existing species is known. Marine free-living nematodes (Fig. 2.III.1) are present in sediments from the tidal areas of estuaries, marshes, and mudflats and from the spray zone of open beaches to deep abyssal plains. They are often the most abundant metazoans in numbers of species and individuals in these intertidal and subtidal environments (Hope and Murphy 1972). Individuals of most marine species are quite small. Those reported from Hawaii by Allgén (1951), for example, range from 0.760 to 9.0 mm with a mean length of 2.4 mm.

STUDY TECHNIQUES FOR MARINE SPECIES

Marine nematodes may be extracted from sandy sediments by placing a sample of sediment in a volume of seawater that is about 20 times larger than that of the sediment itself and stirring the mixture to suspend the sediment particles and meiofauna. After allowing about 30 seconds for the sand particles to settle, the seawater and meiofauna are decanted through a sieve having openings about 50 μm in width. The sieve is then inverted and flushed with seawater to rinse the meiofauna into a beaker or other suitable container. If the sampling is quantitative, it may be necessary to repeat the above procedure 2 or more times to extract essentially all of the organisms.

The sieving technique described above is not satisfactory for the extraction of nematodes from sediment consisting of fine organic detritus, because the suspended detritus does not settle faster than nematodes and other meiofauna. Laborious hand sorting of meiofauna after sieving such samples is usually necessary, although it may be made easier by first staining the sample with Rose Bengal. More effective methods of removing nematodes from detritus-laden samples are density gradient centrifugation and density gradient flotation using Ludox TM (de Jonge and Bouwman 1977; Price et al. 1977) or Ludox AM (Nichols 1979) as the gradient materials.[2] De Jonge and Bouwman (1977) found that extraction with Ludox is more complete if the sample is shaken beforehand and immediately fixed with formalin. This breaks the attachment nematodes often make by way of their caudal glands to sediment particles, thus reducing the chances that such particles will carry nematodes out of suspension. Ludox AM is preferred because it does not gel immediately when mixed with seawater, as does Ludox TM (Nichols 1979). Hulings and Gray (1971) and Nicholas (1975) may be consulted for other specialized extraction techniques.

It is preferable to extract nematodes from sediment prior to fixation, especially if they are in fine sediment. Convulsive contractions of the esophagus as the nematodes die may cause detritus to be drawn into the stoma, thus making it difficult later to resolve teeth and other details within the stoma.

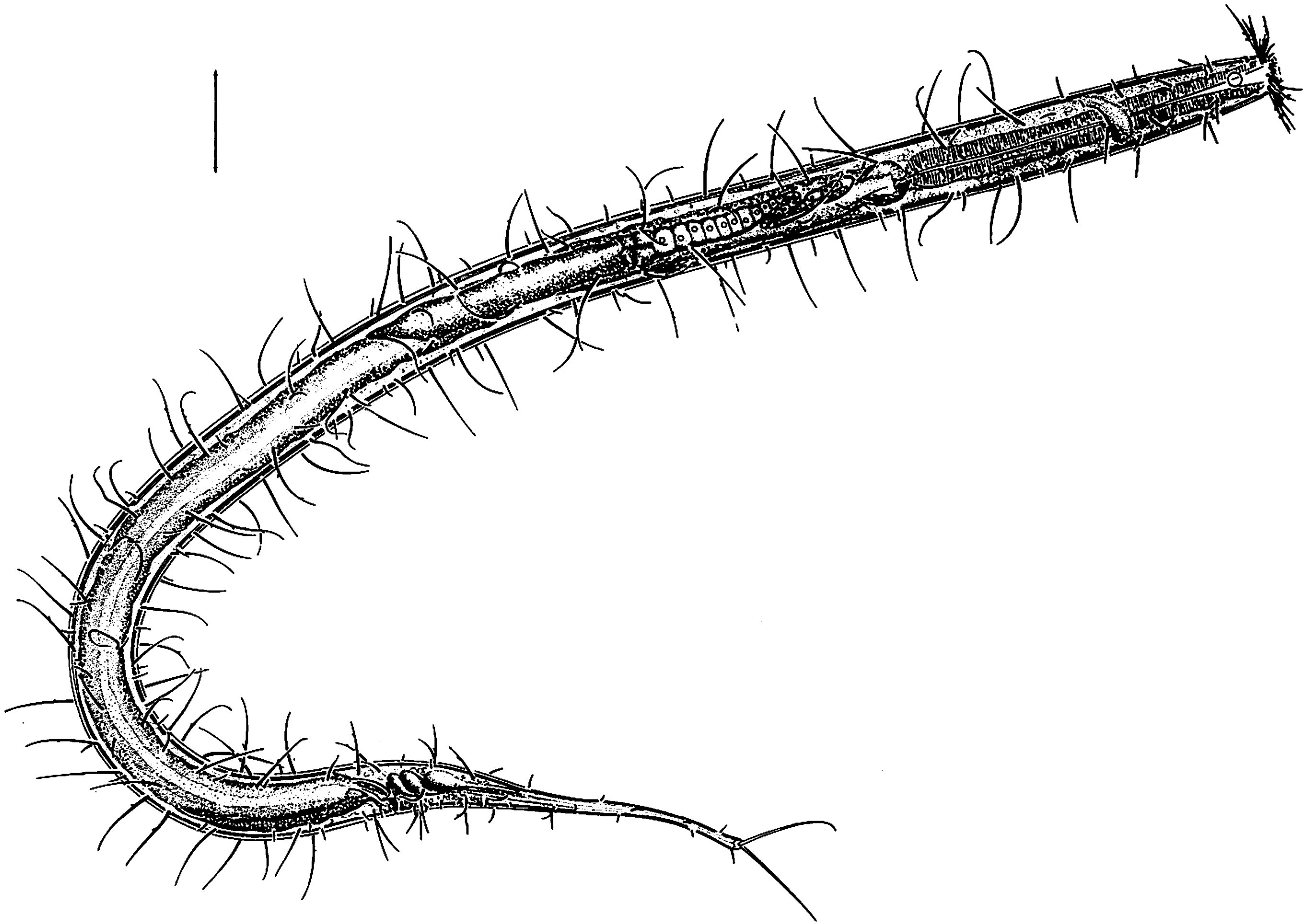

Figure 2.III.1.—*Steineria* sp.: adult male from fine sand collected during low tide at about 3 m depth behind a breakwater at the Makapuu Pier, Oahu, Hawaii. Scale line = 50 μm.

Nematodes are fixed and preserved in 3 to 5% buffered formalin in seawater. Alcohol should not be used as a fixative, and it should be avoided as a preservative because of the shrinkage and distortion that results.

Because of their small size, marine nematodes cannot be identified without the high magnifications obtainable with a compound microscope. For that reason, it is necessary to mount specimens whole on microscope slides before they are studied; usually they are permanently mounted in anhydrous glycerine.

Nematodes are processed into anhydrous glycerine by transferring fixed specimens into a small dish, preferably with a concave bottom, containing several milliliters of 2% glycerine in distilled water. The dish is partially covered so that evaporation of the water is prolonged over a period of about 1 week, at which time the nematodes are left in a thin layer of glycerine. Sufficient stock (hydrous) glycerine is added to ensure complete immersion of the specimens, and the specimens are then dehydrated by placing the dish and its contents in a desiccator for a week or longer. Desiccated specimens may be mounted on glass slides or between coverslips mounted in Cobb aluminum frames using anhydrous glycerine as the mountant. Compression of the specimen must be avoided by using coverslip supports because measurements of body width at 1 or more points along the length of a specimen are often essential for identification. The coverslip is sealed by pipetting Permount[3] under the edge of coverslip. To ensure enough space under the edge of the coverslip for Permount, care must be taken not to use too much glycerine. Also, care should be taken to not trap air bubbles between the glycerine mountant and Permount.

Nematode taxonomy is based on such anatomical characters as striations, punctations, and other features of the cuticle; shape and size of the amphid; structure of the esophagus; number and arrangement of setiform and/or papilliform sensory receptors (especially on the head); and various structures of the reproductive system, such as the number and position of the gonads and morphology of the male copulatory apparatus.

Allgén (1951) reported 53 species of free-living nematodes collected off the coast of Honolulu at 20 to 80 m and from washings of *Sargassum* and *Lithothamnion* collected at about 20 m near Hilo. Twenty-two of these species were reported as new. Unfortunately, Allgén's identifications are not reliable and many of his new species descriptions are inadequate. A list of the species described by Allgén with current valid names is included in the list of Hawaiian free-living marine nematodes. Also included is a species described by Murphy (1964) based upon specimens extracted from inter-tidal sand collected at Kawaihae, Hawaii.

In a study on community structure in sediments associated with chaetopterid polychaete mounds, unidentified free-living nematodes were found to be very abundant (Bailey-Brock 1979). Furthermore, an analysis of the fauna associated with the brachiopod *Lingula reevei* in Kaneohe Bay revealed numerous unspecified free-living nematodes (Emig 1981).

Adult nematodes may be parasitic in the digestive tracts of marine fishes, invertebrates, and mammals (Yamaguti 1962), and larval stages infect numerous fish and invertebrates. A study of the nematode parasites of the fishes of the Hawaiian Islands has been initiated by Drs. T. L. Deardorff, M. M. Kliks, and R. S. Desowitz of the University of Hawaii, Department of Tropical Medicine. To date, 1 new species of nematode has been described (Deardorff and Overstreet

1982), and adult members of the genus *Spirocamallanus* have been reported from reef fishes (Rychinski and Deardorff 1983). Detailed host-parasite lists and analysis of larval nematode infestations from fishes caught in the vicinity of the Hawaiian Islands have been reported by Deardorff et al. (1982). Some of these larvae may be of public health significance. Coe (1906) reported the presence of nematode parasites in 2 specimens of the nemertean *Baseodiscus cingulatus* taken at depths between 38 to 79 m (21 to 43 fms) between Maui and Lanai.

HAWAIIAN FREE-LIVING MARINE NEMATODES[4]

√√ Class ADENOPHOREA
Order ENOPLIDA
Suborder ENOPLINA

57 spp.

Superfamily ENOPLOIDEA
Leptosomatidae
Leptosomatinae
Leptosomatum bacillatum (Eberth, 1863) Bastian, 1865
See Allgén 1951:269
Enoplidae
Enoplinae
Enoplus meridionalis Steiner, 1921
See Allgén 1951:273
Enoplolaiminae
Mesacanthion hawaiiense (Allgén, 1951) Wieser, 1953
[syn: *Enoplolaimus hawaiiensis* Allgén, 1951:274]
= species indeterminata[5] op Wieser 1953
Mesacanthion pacificum (Allgén, 1947) Wieser, 1953
[syn: *Enoplolaimus pacificus* Allgén, 1947]
= species indeterminata op Wieser 1953
See Allgén 1951:275
Oxyonchus stateni (Allgén, 1930) DeConinck and Stekhoven, 1933
[syn: *Enoplolaimus stateni* Allgén, 1930]
= species inquirenda[6] or synonym of *Oxyonchus australis* (De Man, 1904) Filipjev, 1927, op Wieser 1953
See Allgén 1951:277
Phanodermatidae
Phanodermatinae
Phanoderma (Phanoderma) hawaiiense Allgén, 1951:270
Phanoderma (Phanoderma) tenuicaudum Allgén, 1951:271
Phanoderma (Phanoderma) tuberculatum (Eberth, 1863) Bastian, 1865
= doubtful identification op Wieser 1953
See Allgén 1951:269
Anticomidae
Anticominae
Anticoma acuminata (Eberth, 1863) Bastian, 1865
[syn: *Anticoma limalis* Bastian, 1865, op Cobb 1891]
See Allgén 1951:267
Anticomopsis typica Micoletzky, 1930

[syn: *Paranticoma tenuicollis* Allgén, 1951, op Gerlach 1962]
See Allgén 1951:268
Superfamily OXYSTOMINOIDEA
Oxystominidae
Halalaiminae
Halalaimus (Halalaimus) gracilis De Man, 1888
See Allgén 1951:272

Suborder ONCHOLAIMINA

Superfamily ONCHOLAIMOIDEA
Enchelidiidae
Enchelidiinae
Polygastrophora hexabulba (Filipjev, 1918) Filipjev in Kreis, 1926
[syn: *Bolbella pacifica* Ditlevsen, 1930, op Wieser 1953]
See Allgén 1951:283
Polygastrophora tenuicollis (Allgén, 1951) Wieser, 1953
[syn: *Bolbella tenuicollis* Allgén, 1951:284]
= species inquirenda op Wieser and Hopper 1967
Enchelidium brevicaudatum Allgén, 1947
See Allgén 1951:281
Enchelidium microlaimum Allgén, 1951:282
= species inquirenda to *Calyptronema* op Wieser 1953
Enchelidium pacificum Allgén, 1951:281
= species inquirenda op Wieser 1953
Eurystomininae
Eurystomina ornata (Eberth, 1863) Marion, 1870
[syn: *Eurystomatina ornatum* (Eberth, 1863)]
Eurystomatina is an invalid emendation by Stekhoven 1935
See Allgén 1951:285
Oncholaimidae
Oncholaimellinae
Viscosia glabra (Bastian, 1865) De Man, 1890
= questionable identification op Wieser 1954
See Allgén 1951:278
Oncholaiminae
Oncholaimus rapax Kreis, 1932
[syn: *Viscosia pacifica* Allgén, 1951:278, op Wieser 1953]
Pontonematinae
Pontonema californicum Allgén, 1947
See Allgén 1951:277

Order CHROMADORIDA
Suborder CHROMADORINA

Superfamily CHROMADOROIDEA
Comesomatidae
Dorylaimopsinae
Dorylaimopsis hawaiiensis Allgén, 1951:310
Chromadoridae
Chromadorinae

Chromadorella filiformis (Bastian, 1865) Filipjev, 1918
See Allgén 1951:309
Chromadorina pacifica (Allgén, 1947) Wieser, 1954
[syn: *Chromadora pacifica* Allgén, 1947]
See Allgén 1951:309

Euchromadorinae

Euchromadora vulgaris (Bastian, 1865) De Man, 1886
See Allgén 1951:307
Graphonema amokurae (Ditlevsen, 1921) Inglis, 1969
[syn: *Euchromadora amokurae* Ditlevsen, 1921]
See Allgén 1951:308
Steineridora loricata (Steiner, 1916) Inglis, 1969
[syn: *Euchromadora loricata* Steiner, 1916]
See Allgén 1951:307

Hypodontolaiminae

Spilophorella campbelli Allgén, 1928
See Allgén 1951:307

Spilipherinae

Spiliphera gracilicauda De Man, 1893, var. *breviseta* Allgén, 1951
[syn: *Spilophera gracilicauda dolichura* De Man, 1893, var. *breviseta* sensu Allgén 1951:304 op Allgén 1959]
= variety inquirenda op Wieser 1954
Spiliphera longiseta Allgén, 1951
[syn: *Spilophora longiseta* Allgén, 1951:305]
= species indeterminata op Wieser 1954
Spiliphera tenuicauda Allgén, 1951
[syn: *Spilophora tenuicauda* Allgén, 1951:305]
= species indeterminata op Wieser 1954

Cyatholaimidae

Cyatholaiminae

Cyatholaimus gracilis (Eberth, 1863) Bastian, 1865
= doubtful identification op Wieser 1954
See Allgén 1951:291

Paracanthonchinae

Acanthonchus (Acanthonchus) californicus (Allgén, 1947) Wieser, 1955
[syn: *Seuratiella californica* Allgén, 1947]
= species inquirenda op Wieser 1955
See Allgén 1951:293
Paracanthonchus brachyuris Allgén, 1951:290
= species indeterminata op Wieser 1954
Paracanthonchus caecus (Bastian, 1865) Micoletzky, 1924
See Allgén 1951:286
Paracanthonchus hawaiiensis Allgén, 1951:288
Paracanthonchus mortenseni Allgén, 1947
See Allgén 1951:287
Paracanthonchus pacificus Allgén, 1951:289
= species indeterminata op Wieser 1954
Paracyatholaimus tenuispiculum (Allgén, 1951) Wieser, 1954
[syn: *Paracanthonchus tenuispiculum* Allgén, 1951:287]

Selachinematidae
Selachinematinae
Demonema rapax Cobb, 1894
[syn: *Dignathonema mirabile* Allgén, 1951:294, op Gerlach 1964]
Choniolaiminae
Halichoanolaimus robustus (Bastian, 1865) De Man, 1886
[syn: *Halichoanolaimus hinemoae* Ditlevsen, 1930, op Gerlach 1964]
See Allgén 1951:293
Superfamily DESMODOROIDEA
Desmodoridae
Desmodorinae
Acanthopharynx brachycapitata (Allgén, 1947) Gerlach, 1963a
[syn: *Desmodora brachycapitata* Allgén, 1947]
See Allgén 1951:298
Acanthopharynx merostomacha (Steiner, 1921) Stekhoven, 1943
[syn: *Desmodora merostomacha* Steiner, 1921]
See Allgén 1951:300
Desmodora (Subgenus ?) *crassa* Allgén, 1951:299
= species indeterminata op Gerlach 1963a
Desmodora (Desmodora) californica Allgén, 1947
See Allgén 1951:300
Desmodora (Desmodora) scaldensis De Man, 1889
[syn: *Desmodora paramicrochaeta* Allgén, 1947, op Wieser 1955]
See Allgén 1951:296
Desmodora (Pseudochromadora) microchaeta Allgén, 1929
See Allgén 1951:296
Desmodora (Zalonema) propinqua Allgén, 1951:297
Spiriniinae
Spirinia (Spirinia) septentrionalis (Cobb, 1914) Wieser, 1954
[syn: *Spirina pacifica* Allgén, 1951:302, op Wieser 1954]
Aponchiidae
Aponchiinae
Aponchium conicaudatum Allgén, 1951:291
= species indeterminata op Gerlach 1963b
Superfamily MONOPOSTHIOIDEA
Monoposthiidae
Monoposthiinae
Monoposthia pacifica Allgén, 1951:301
= species indeterminata op Wieser 1954

Order MONHYSTERIDA
Suborder MONHYSTERINA

Superfamily MONHYSTEROIDEA
Xyalidae
Xyalinae
Daptonema tenuispiculum (Ditlevsen, 1918) Lorenzen, 1977

[syn: *Cylindrotheristus tenuispiculum* (Ditlevsen, 1918) Wieser, 1956. *Theristus tenuispiculum* (Ditlevsen, 1918) DeConinck and Stekhoven, 1933]
See Allgén 1951:313
Steineria sp.[7]

Superfamily AXONOLAIMOIDEA
Diplopeltidae
Diplopeltinae
Diplopeltis cirrhatus (Eberth, 1863) Cobb, 1891
[syn: *Diplopeltis longisetosus* Allgén, 1928, op Gerlach 1962]
See Allgén 1951:312
Onchium hawaiiense (Allgén, 1951) Gerlach, 1962
[syn: *Araeolaimus hawaiiensis* Allgén, 1951:311]
= species inquirenda op Gerlach 1962
Southerniella youngi Murphy, 1964

23 Class SECERNENTEA
Order RHABDITIDA
Suborder CEPHALOBINA

Superfamily RHABDITOIDEA
Cephalobidae
Cephalobinae
Cephalobus marinus Allgén, 1951:313

NOTES

1. The names used by Weber (1906) are junior subjective synonyms, and only those names appear in the synonymy for each species.

2. Ludox Colloidal Silica may be purchased from E. I. Du Pont De Nemours and Company (Inc.), Wilmington, Delaware 19898, USA.

3. Permount is a trademark for a synthetic resin marketed by Fisher Scientific. Before using, 2 volumes of Permount should be diluted with 1 volume of xylene.

4. The names in this list are current valid names. The synonymies are not complete. They include only those names used by Allgén (1951) that are now regarded as junior subjective synonyms.

5. Species indeterminata is used in the same sense as Blackwelder (1967:267), i.e., the species in question is not identifiable from the original description.

6. Species inquirenda is also used in the same sense as Blackwelder, i.e., the classification of the species in question is doubtful.

7. This is an undescribed species (Fig. 2.III.1) identified by the author. Insufficient material prevents a proper description.

GLOSSARY (ASCHELMINTH COMPLEX)

amphid: Sense organ on each side of the head region of nematodes, the external portion of which is in the shape of a pocket, circular depression, spiral, or other shape derived from one of the above.

dioecious: Sexes separate, having male and female individuals.

meiofauna: Interstitial benthic organisms, mostly metazoans, that can pass through a 1.0 mm but not through a 0.05 mm screen.

pseudocoelom: A persistent blastocoel forming a "cavity" between the body wall and the internal organs.

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Chapter IV

Phyla ENTOPROCTA and BRYOZOA (ECTOPROCTA)

JOHN D. SOULE, DOROTHY F. SOULE,
and HENRY W. CHANEY

BRYOZOANS are minute, attached (sessile) animals that for the most part are marine and colonial, distributed worldwide from tropical to polar seas. They occur from intertidal to abyssal depths but are most abundant in the sublittoral and neritic zones to about 200 m. In Hawaiian waters bryozoans are often not found intertidally unless they are sheltered by natural rocky overhangs or rubble, or by docks and boat hulls. Some tropical reefs contain an intertidal fauna, whereas others are barren at intertidal depths. This contrasts with the richer fauna found in the extensive intertidal zone in temperate areas where tidal heights range from 1 to 2 m to more than 5 m (Ryland 1970). The more intense light and heat of the tropical and subtropical intertidal zone militates against bryozoan colonization in the shallowest water, although some species do occur there.

Although bryozoans are quite small, with individuals generally less than 1 mm in length, a colony may cover substrates for several centimeters. Multiple colonies may completely cover submerged non-living surfaces, as well as some species of living mollusks, crustaceans, and echinoderms; in the temperate zone, kelp fronds may be coated for several meters. Most bryozoans tend to be inconspicuous and often are not recognized because they occur in mixed associations with algae, hydroids, sponges, and tunicates, especially on older portions of coral reefs. While bryozoans have sometimes been called moss animals because some species blend with the smallest tuftlike algae, a few erect species in the family Sertellidae (= Reteporidae) are quite attractive and have been called lace corals by divers (Plate 2.IV.1b–e). One unique genus of Ectoprocta, *Monobryozoon*, is not colonial, occurring as separate individuals found in the soft sediments of some European seas. Members of the entoproct family Loxosomatidae are also solitary.

Historical Background. Historically the phylogeny, anatomy, and function of bryozoans has been subject to a wide variety of interpretations and classifications—first as plants and subsequently as animal-plants, the Zoophyta of the eighteenth and nineteenth century scientists. Hyman (1959), in reviewing the historical background of the group, noted that the first recognizable illustration published may have been that of Rondelet in 1558, which he regarded as that of a sea plant.

It is not surprising that the animal nature of bryozoans was not recognized because optics and facilities to observe living colonies were lacking and because the polyps were already dead in the plantlike, frondose colonies commonly washed ashore in Europe after storms. What is surprising is that the well-known biologists of the latter eighteenth century such as Linnaeus, Pallas, and Cuvier disregarded the studies of earlier workers, who had finally asserted the animal nature of both the bryozoans and the corals (known together as the corallines). Instead they lent the weight of their prestige in perpetuating the classifications Zoophyta (animal-plants) and Lithophyta (stony-plants). Linnaeus classified all other invertebrates except insects as Vermes.

Imperato, a Naples apothecary, had suggested in his *Historia Naturale* in 1599 that corals were at least partly animal in nature. The bryozoans that encrusted the corals he considered to be "pores" in the coral. In 1729, de Peyssonnel, a Marseilles physician, went to sea with red coral fishermen and observed the "insects" (the extended tentacles), which he believed were the animals that formed the colonies. His views were derided by other naturalists, including the then eminent Count Marsigli, who had apparently been the first to observe tentacles unfolding and believed they were flowers blooming. In 1742 de Jussieu, who created the word polyp, finally announced that he agreed with de Peyssonnel, having observed many of the zoophytes along the Normandy coast, and concluded that they were animals rather than plants. Abraham Trembley, who became famous for his research on the animal nature of the freshwater hydra, also discovered the first freshwater bryozoan in 1744.

John Ellis, a London merchant, in 1755 published one of the great zoological books of the eighteenth century, the *Natural History of the Corallines*, based on his microscopic studies of seaweeds and bryozoans, which he called corallines. Even though Linnaeus (Carl von Linné) in 1758 used Ellis's meticulous illustrations as the basis of his zoophyte species, he still insisted that the corallines were intermediate between plants and animals (Ryland 1970).

Bryozoans were classified with polypoid organisms such as the coelenterate corals and hydroids until it was confirmed by de Blainville in 1820 that bryozoans have a much more complex level of organization, including a one-way digestive tract with a separate mouth and anus, whereas coelenterates bear only a single opening to a gastrovascular cavity. By 1827, Grant noted that bryozoans also differed from coelenterates by having ciliated tentacles (Hyman 1959; D. F. and J. D. Soule 1979a; Boardman et al. 1983). In addition to being classified with coelenterates during the early nineteenth century, bryozoans were also grouped systematically with morphologically more advanced taxa. Because of a perceived similarity with compound ascidians, Milne-Edwards combined the Bryozoa with tunicates under the Molluscoidea in 1843. Lang in 1888 placed bryozoans in phylum Vermes as class Prosopygii, which included brachiopods, phoronids, sipunculids, and priapulids.

The name Bryozoa was given by the German scientist Ehrenberg in 1831 to the group of organismsh that then encompassed forms now known as the Entoprocta and Ectoprocta, whereas the British scientist Thompson in 1830 created the term Polyzoa to characterize approximately the same group of colonial organisms. This led to an extensive and acrimonious battle in the literature that lasted for over 100 years (J. D. Soule 1958; J. D. and D. F. Soule 1968), over priority of the names and definition of the phylum. However, the term "Polyzoa" has disappeared from the recent literature.

Recognizing that there were 2 major groupings within the Bryozoa, Nitsche (1869) and others designated those with the anal opening located inside the tentacle circle as the Entoprocta, while those with the anal opening outside the tentacle circle were designated as the Ectoprocta. These 2 categories were elevated to phylum level by Hyman (1959), precipitating another round of debate in the literature (D. F. and J. D. Soule 1979a).

The Entoproct-Ectoproct Relationship. The matter of the relationship between the 2 groups is by no means resolved and further research is needed to provide definitive answers. There are other differences between the 2 groups in addition to the location of the anus. For example, the entoproct ovum undergoes modified spiral cleavage, while ectoproct cleavage is biradial. Also, while the Entoprocta were said by Hyman (1959) to be pseudocoelomates and the Ectoprocta to be coelomates, Nielsen (1977a,b) and others do not interpret the Ectoprocta as having a coelom. Metamorphosis in the entoprocts is protostomial, while metamorphosis in the ectoproct larvae has been said by some to be deuterostomial and by others to be protostomial. Mesoderm may be of ectodermal origin; however, it is not possible to make the usual associations about the derivation of the mesoderm in ectoprocts since metamorphosis is so radical that the larval gut is completely destroyed (Nielsen 1977a,b; Zimmer and Woollacott 1977a,b). There are also differences in the derivation of the tentacles and their cilia between the 2 groups (Emschermann 1982).

Both groups have a U-shaped digestive tract, but this feature is common to many sessile animals. The Entoprocta have a pair of flame bulb nephridia reminiscent of the Rotifera, whereas the Ectoprocta have no excretory system. Neither has a circulatory system. Both have a nervous system that includes a cerebral ganglion and nerve net but the 2 differ in structure and location. (See Barnes 1980 for general descriptions of Entoprocta and Ectoprocta and Woollacott and Zimmer 1977 for detailed discussions of the biology of ectoprocts.)

The result of the various interpretations of the differences between the 2 groups is that some researchers use the terms Entoprocta and Ectoprocta with phylum status; "bryozoan" is then used as a descriptive word without phylum status to include both groups. However, if one wishes to research the literature, confusion can arise because certain authors retain both the Entoprocta and Ectoprocta in the phylum Bryozoa (e.g., Nielsen 1971, 1977a,b, 1985). Others regard the Entoprocta as a separate phylum, in which case the phylum Bryozoa then includes only ectoprocts (e.g., Boardman et al. 1983). Since the same research scientists often work on both groups, the term "bryozoans" has considerable utility, but in the present volume the authors restrict their usage to the Ectoprocta. The differences alluded to must be kept in mind when using the systematic literature, recognizing that future research may resolve these questions.

Phylum ENTOPROCTA

MORPHOLOGY

The Entoprocta are solitary or colonial, usually stalked, uncalcified animals that superficially resemble hydroid polyps but are much more complex in structure. The generalized body plan consists of a pedicel (stalk), which may be reduced or absent in some genera, topped by a calyx (head), which may or may not be partially separated from the stalk by a septum (Fig. 2.IV.1a,b). The face of the calyx bears the genital and excretory pores and a crown of tentacles that surrounds the mouth as well as the anal prominence (cone); hence the name Entoprocta, or "inside anus." Individuals may be connected by stolons or not, a

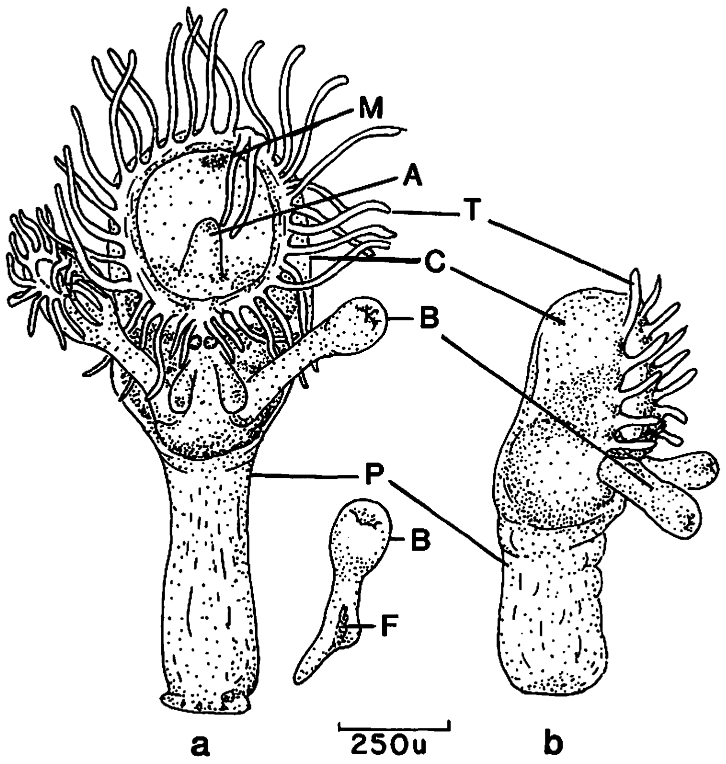


Figure 2.IV.1.—Two species of *Loxosomella*: a, frontal (ventral) view with attached buds, detached bud to the right; b, lateral view. (M, mouth; A, anus; T, tentacle; C, calyx; B, bud; P, pedicel; F, foot gland.) (After D. F. and J. D. Soule 1965.)

characteristic used in defining the families. In entoprocts the tentacles, when contracted, roll in upon themselves but cannot be withdrawn inside the calyx, although they are protected by an external body wall fold. In contrast, the ectoprocts are able to retract the entire tentacle crown (lophophore), base-first, and tentacle sheath into the body cavity and cannot roll up the tentacles. The stalked entoprocts are able to bend, tipping the calyx about, giving the appearance of nodding heads. In some genera the base of the stalk has a muscular thickening that acts like a socket, allowing a more rigid stalk and calyx to bend.

The entoproct calyx contains the internal organs: the digestive tract, which consists of a mouth, esophagus, stomach, intestine, and rectum, plus the gonads, the nephridia (excretory organs), a nerve ganglion, and retractor muscles. Because body and tentacles are filled with parenchymal connective tissue and lack a peritoneal lining, entoprocts are said to be pseudocoelomate. Both sexual and asexual reproduction occur. Some species brood their embryos on the face of the calyx inside the tentacle circle. Asexual buds may be produced on the calyx, stalk, or stolon and will drop off or remain attached to the stalk, providing features used to characterize the families and genera of the phylum.

ECOLOGY

Entoprocts are so small and inconspicuous that they are easily overlooked during collecting, often forming a whitish fuzz of individuals or colonies on the surfaces where they attach. Most species are quite selective in choice of substrate. Some species are epizoic only on worms or worm tubes, some prefer other invertebrates such as hydroids, sponges, ascidians, ectoprocts, or crustaceans, and others attach only to algae. A few species settle on inanimate objects. Nielsen (1964) listed the 36 loxosomatid species then known, only 2 of which were found on non-living substrata. The majority of the entoprocts are marine or brackish water inhabitants. Only 1 genus occurs in freshwater.

SYSTEMATICS

The usual system of entoproct classification gives no categories higher than the family level and employs 2 families, the Loxosomatidae and the Pedicellinidae, which together contain some 60 species. Emschermann (1972) created 2 orders, Solitaria and Coloniales, with the Loxosomatidae as the only family in the order Solitaria. He designated 2 suborders in the order Coloniales, the Astolonata, which contains the new family Loxokalpodidae, and the Stolonata. In the latter he placed the family Pedicellinidae and established the family Barentsiidae for members of the long-known genus *Barentsia* and some related genera such as the freshwater *Urnatella.*

There are 2 different larval types, which are consistent with the separation of the Solitaria (Loxosomatidae) from the Coloniales, except that the colonial but astolonate *Loxokalypus* has the solitary larval type. There are some other anomalies in this system, because the genus *Loxosomatoides* is included in the Coloniales with the Pedicellinidae but shares characteristics with the Loxosomatidae as well. Emschermann (1972, in German) presented a diagram of the musculature that clearly differentiated the genera and indicated possible phylogenetic relationships. The diagram with translated caption (Fig. 2.IV.2) and

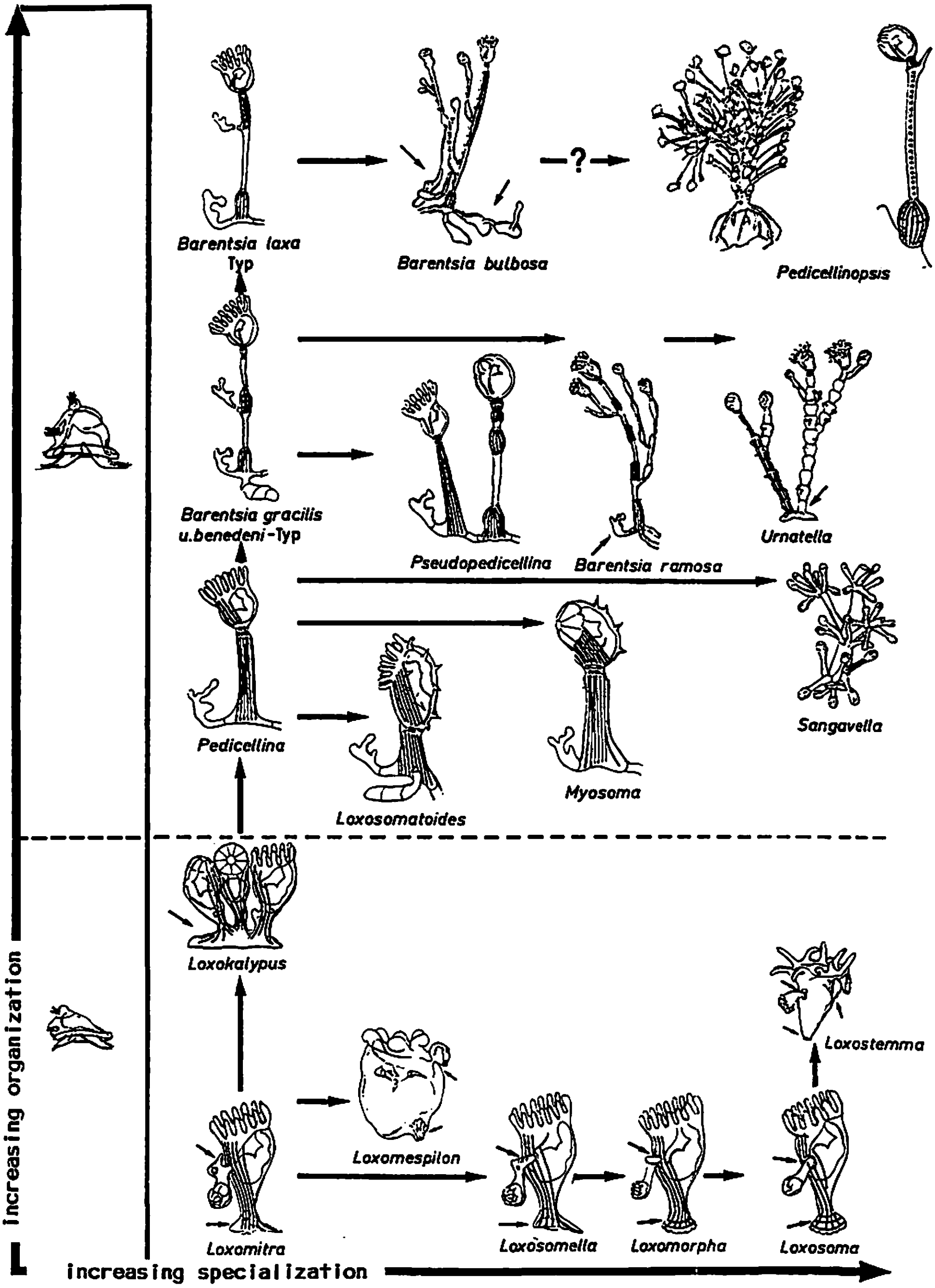


Figure 2.IV.2.—Diagram of entoproct morphological characteristics and probable phylogenetic relationships, according to increasing levels of organization and specialization. Larval types are on left. Longitudinal body muscles (dark lines) and their derivatives are indicated for each genus (trunk muscles are not visible under the light microscope in *Loxomespilon*; literature does not contain comparable data for *Loxostemma*). (Courtesy P. Emschermann.)

the classification presented below are based on an unpublished manuscript kindly provided to us by Dr. Emschermann.

Entoprocts have not been studied systematically in Hawaii, although many Loxosomatidae and Pedicellinidae occur in Hawaiian waters and await taxonomic treatment. Edmondson (1933, 1946) figured a loxosomatid collected on the green alga *Ulva* at the water's edge, and Hadfield (unpubl.) has found them on sponges at 20 m. We collected an undescribed *Loxosomella* on settling racks at Pokai Bay (unpubl.). Many of the loxosomatids are commensal on other invertebrates, including bryozoans, polychaetes, sipunculids, sponges, echinoderms, tunicates, coelenterates, pterobranchs, and mollusks (Nielsen 1964); D. F. and J. D. Soule (1965) reported them on the gills of mantis shrimp.

To identify the entoprocts, particular care is necessary in collecting and preservation. Some specimens should be anesthetized ($MgCl_2$, Stovaine) and some unanesthetized before fixation in seawater and 4% formalin. The narcotizing agent relaxes the tentacles and pedicel, and the addition of borax carmine stain reveals the presence or absence of the foot gland. The muscles, which are crucial to some identifications, stand out more clearly in contracted, unanesthetized specimens. Emschermann (pers. comm.) stated that the muscles are best studied under polarization microscope or, if that is not available, with the help of polarization foils slid into the ocular and condenser. Brightening of the black and white polarization view and transportation into the blue and yellow shades can be achieved by using a thin quartz plate. The Nomarski interference contrast method is also recommended for examining the muscles. This can be replaced by slanted lighting by means of sideway rotation of the condenser (easily done with revolving condensers in Zeiss or Wild systems, according to Emschermann).

A simplified summary of the Entoprocta families and genera that might be found in Hawaiian waters is presented below. There are many difficulties in identification of species, in part because some descriptions in the literature are inadequate, and in part because there appears to be a wide range of variability. Other reasons include the lack of clearcut features that separate the species unambiguously, possible cross breeding between genera, or lack of information on the phenotypic effects of environmental differences on the species. For further information on species known elsewhere see, for example, Prenant and Bobin 1956; Osburn 1953; D. F. and J. D. Soule 1965; Nielsen 1964, 1971; and Emschermann 1972.

Order SOLITARIA

Small solitary forms with continuous longitudinal muscles in calyx and stalk; asexual budding of new individuals on the calyx; buds detach from the parent.

Family **Loxosomatidae**

Solitary individuals, many commensal on other invertebrates; calyx not separated from the pedicel by a septum; calyx cannot be shed; asexual buds drop off parent. Some species capable of limited mobility after initial attachment.

Genus *Loxomespilon*: Pedicel reduced in buds, absent in adults; calyx attached directly to polychaete host.

Genus *Loxostemma*: Like *Loxomespilon* except that tentacles bear large suckers.

Genus *Loxosoma*: No foot gland; bud attached to parent by central part of pedal suction disc with unicellular gland; adult can move attachment site.

Genus *Loxomorpha*: Formerly part of *Loxosoma*; bud attached to mother by posterior edge of pedal disc.

Genus *Loxocalyx*: Foot gland well developed in bud and adult; adult of some species capable of moving site of attachment; most species with winglike expansions (alae) on calyx, stalk, or foot; considered by some to be included in *Loxosomella*.

Genus *Loxosomella*: Pedicel base contains a foot gland (visible in stained whole mounts) that is large in bud but degenerates in adult; bud attached to mother by tip of foot; adult permanently attached to host at original site of settlement; no alae on calyx, pedicel, or foot.

Genus *Loxometra*: Formerly part of *Loxosomella*; bud attached to mother by back of pedicel or calyx.

Order COLONIALES

Suborder ASTOLONATA

Small colonies of individual animals on a common base, without stolon formation; continuous longitudinal muscles in calyx and pedicel.

Family **Loxokalypodidae**

Like Loxosomatidae, without separation between calyx and pedicel; bud originates and remains attached at base of parent to form colony without stolons.

Genus *Loxokalypus*: With characters of the family.

Suborder STOLONATA

Colony formed with stolonal budding; can develop into very large plane or treelike colonies; separate calyx and pedicel muscles; stolons separated into zooid-bearing and non-bearing segments.

Family **Pedicellinidae**

Calyx separated from pedicel by a partial septum, pedicel and calyx pseudocoelom remain confluent; calyx can be shed and regenerated; pedicel unjointed, entirely muscular; buds attached to colony by stolons.

Genus *Pedicellina*: Pedicel thin, with longitudinal muscles but not diagonal muscles, flexible, without muscular enlargement at base.

Genus *Myosoma*: Pedicel thick, with longitudinal and diagonal muscles, sometimes with cuticular spines; stolons recumbent (adnate).

Genus *Pseudopedicellina*: Colony with 2 types of zooids; one with flexible pedicellinid-like muscular stalks and the other with barentsiid-like rigid stalks with muscle sockets.

Genus *Pedicellinopsis*: Colony treelike, with upright stems in 20 cm, dichotomous branching, basal rhizoids; growing tip of each branch bears numerous zooid buds arranged spirally around branches.

Genus *Sangavella*: Colony irregularly branching; zooids arranged in circlets at internodes and points of branching.

Genus *Coriella*: Colonies partly upright to 10 cm, stolons thick, rigid, sticking together in upright rhizocaulomes.

Family **Barentsiidae**

Genus *Barentsia*: Calyx separated from pedicel by partial septum, pseudocoelom confluent; pedicel more chitinized, inflexible, erect, separated into muscular and non-muscular segments, with barrel-shaped muscular socket enlargement at base of pedicel; with pores and muscular thickenings along pedicel in some species.

Phylum BRYOZOA (ECTOPROCTA)

ZOOGEOGRAPHY

The zoogeographic patterns of major invertebrate phyla in the tropical Pacific islands have been described as representing the distribution of descendants of organisms that have been dispersed successfully over thousands of miles of ocean (Kay 1977). Known as the Indo-Pacific or Indo-West Pacific since the nineteenth century, this biogeographic province has been identified as extending from the east coast of Africa across the Indian Ocean, through the tropical and subtropical western and mid-Pacific islands to the so-called East Pacific barrier (Ekman 1953). This barrier theoretically separates the Hawaiian Islands, the Line Islands (Kiribati), the Marquesas Islands, and Easter Island (Rapa Nui) from the American continents.

Whether the fauna of the Indo-Pacific peripheral island areas such as Hawaii is attenuated by distance from a distributional center or is a relict of a previously worldwide distribution during periods of tropical environment, endemism is clearly characteristic at the species or subspecies level in many groups. Examples include Hawaiian mollusks (Hertlein and Emerson 1953, 1957; Kay 1982), crustaceans (Garth 1965), echinoderms (Ely 1942), polychaete worms (Hartman 1966), and fish (Gosline and Brock 1960). Kay (1977) presented endemism estimates for various phyla that range from 18 to 40% of the biota in the Hawaiian Islands. The extent of endemism in Pacific island bryozoans is unknown, however, because there has been insufficient bryozoan collecting in the geographic reaches of the tropical Pacific islands, especially in habitats of the shallow subtidal zone reached by divers. There is no fully curated collection in the Pacific Basin available for reference, and no extensive keys or illustrated guides have been published that would assist in making essential taxonomic comparisons.

The bryozoan fauna of the Pacific islands is still poorly described, although bryozoans form significant components of tropical coral reef habitats. They serve as food for a wide variety of invertebrates and fishes and as blastic stabilizers of reef structure while clastic processes erode older, senescent coral colonies (J. D. and D. F. Soule 1974).

When Soule and Soule began their initial bryozoan investigations in the

Hawaiian Islands in 1966, fewer than 60 species had been reported from the Hawaiian Archipelago; these were from the dredging expeditions of the *Challenger* (Busk 1881, 1884) and the *Albatross* (Canu and Bassler 1927) and the shoreline collections of Edmondson (1944, 1946). From the western Pacific islands, the *Siboga* Expedition Reports (Harmer 1915, 1926, 1934, 1957) and Canu and Bassler's "Bryozoa of the Philippine Region" (1929) provide the only major taxonomic monographs.

The works of Hincks (1880–1889), P. H. MacGillivray (1869–1895), Waters (1887–1889), and Hastings (1932) provide much of the available information on the Bryozoa of temperate and tropical eastern Australian waters. Bryozoan information from the African margin of the Indo-Pacific consists largely of the work of Savigny (1817?–1826) and Audouin (1826), Waters (1909, 1913), Hastings (1927), Cook (1966), Powell (1967a), and J. D. and D. F. Soule (1985). The reports on the South African *Meiring Naude* cruises (Hayward and Cook 1979, 1983; Cook 1982) give strong indication that there are many previously undescribed species along the eastern shelf. The publications of Seurat (1934), Salvat and Renaud-Mornant (1969), Redier (1971), and Gurgel and Vasseur (1975), as well as isolated citations by other authors on bryozoans of French Polynesia, were reviewed by d'Hondt (1985) for validity. These constitute almost the only Pacific island bryozoan papers other than those of the present authors (D. F. Soule 1973; D. F. and J. D. Soule 1967, 1968, 1970, 1972, 1973, 1975, 1976, 1979b, 1985; J. D. and D. F. Soule 1969a,b, 1970, 1974, 1975).

Extensive field work was undertaken in the Hawaiian Islands by the authors between 1966 and 1971. During that period, bryozoans were collected from 92 stations on Kauai, Oahu, Molokai, Maui, and Hawaii (Fig. 2.IV.3). Collecting methods included snorkel and scuba diving as well as settling plate exposure and scrapings from docks and boat hulls. Specimens from subtidal coral were removed by divers using hammer and chisel and rice bags attached to a truck inner tube.

The yield from the Hawaiian collecting activity far exceeded original expectations, since the scuba zone had not been explored previously for bryozoans in the tropics; collections resulted in some 3,000 lots of specimens, from which several thousand slides have been made. Publications by the present authors on the families Thalamoporellidae, Watersiporidae, Smittinidae, and the burrowing Immergentiidae, Terebriporidae, and Penetrantiidae have described 28 new species and 1 new genus; a number of potential new species remain as yet undescribed. However, based on the dearth of other Pacific island data, a strong endemic Hawaiian component has been suggested. More than 200 taxa have been tentatively identified; thus, the strongest base of information on the tropical mid-Pacific island bryozoans is that developed on the Hawaiian fauna. In the present chapter, over 150 identifications are listed, including updates of those from Busk's *Challenger* Reports and Canu and Bassler's *Albatross* publication.

Interestingly, of the 28 new species described by Soule and Soule from Hawaii, several have subsequently been found by the authors to occur elsewhere in the tropical islands south of the equator. This suggests that the shallow sublittoral Indo-Pacific bryozoan fauna is not well enough known as yet to determine the patterns of attenuation or the degree of endemism at the peripheral islands near the margins of the eastern Pacific barrier, or beyond the 27 °C isotherm.

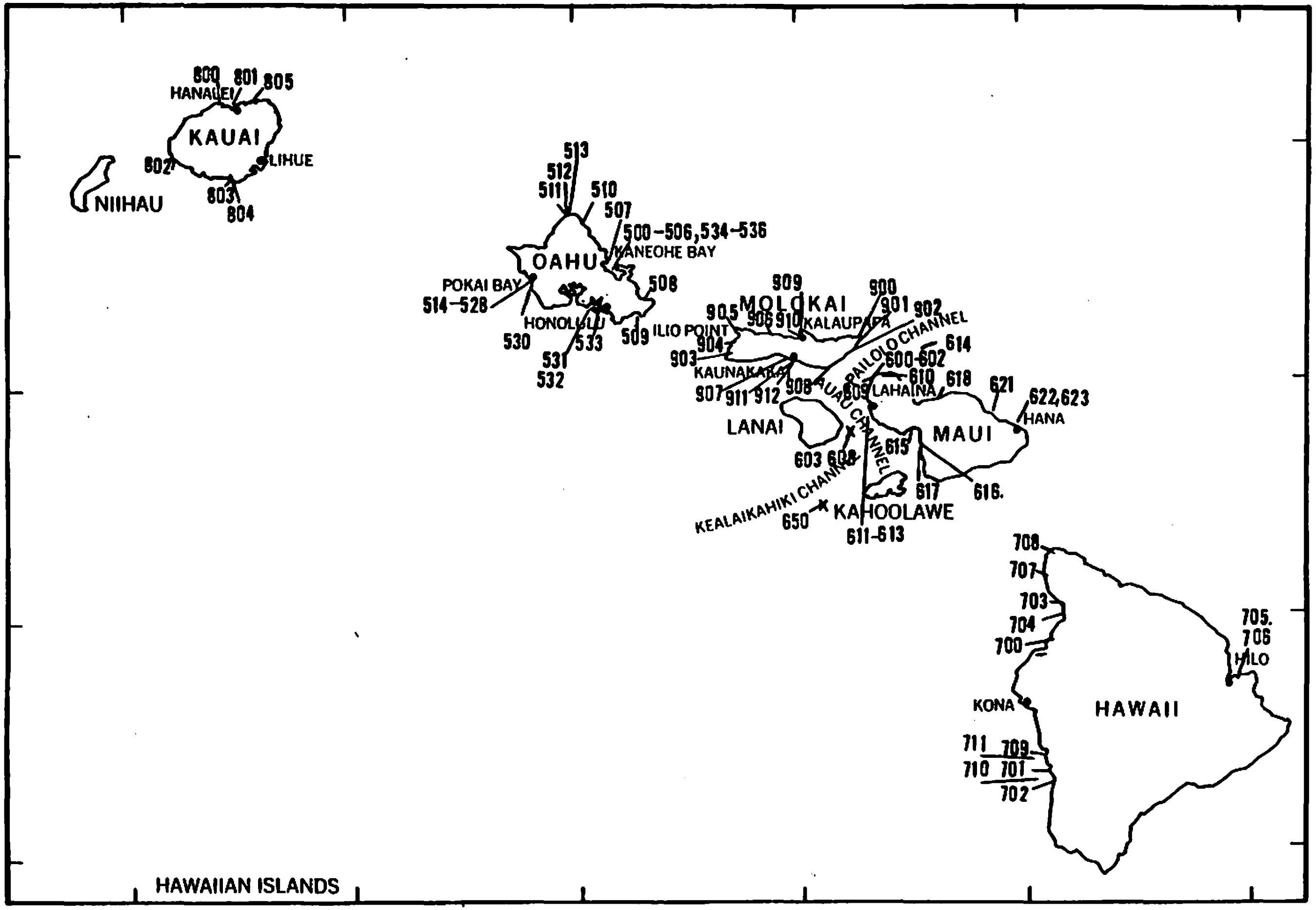


Figure 2.IV.3.—Soule and Soule collecting stations in the Hawaiian Islands, 1965–1971.

The January thermal boundaries of the tropical Pacific (Fig. 2.IV.4) may act as a filtering mechanism of more importance than either the physical boundaries of depth and light penetration or of the July isotherms which tend to be transoceanic, although it is well recognized that thermal boundaries are not static. The El Niño events off the Americas have been extensively documented (e.g., UNESCO 1980; Halpern 1983; McGowan 1984). In 1982–1983 the strong El Niño was concurrent with a disappearance of the trade winds in American Samoa; such alterations in currents and thermal structure could offer profound opportunities for developing new distributional patterns or for making formerly contiguous populations into disjunct ones (D. F. and J. D. Soule 1985). The potential for bryozoan larval transport in the Pacific hemisphere was discussed by D. F. and J. D. Soule (1979a,b) and compared to the calculations of Scheltema (1968, 1971) and others.

Gunnar Thorson (1961) first documented all the information available on marine invertebrate larval transport and noted that bryozoan larvae have been observed to persist in the plankton for many days longer than expected when conditions were not conducive to settling. P. Bougis (pers. comm.) made similar observations about the plankton off Banyuls sur Mer, France, on the Mediterranean (J. D. and D. F. Soule 1977; D. F. and J. D. Soule 1979b). Low temperature and darkness are known to retard metamorphosis in the laboratory and apparently do so in the sea. Ryland (1976b) reviewed much of the literature on larval behavior and settlement.

Colonies of some bryozoan species, especially cosmopolitan fouling ones, are repeatedly introduced on ship's hulls, but many of the reef species found in the Hawaiian Islands are not members of the fouling community. Rafting must be considered as a means of dispersal, although there is little evidence for that mode of transport for most of the Hawaiian fauna. Strong and Skolmen (1963; pers. comm. in D. F. and J. D. Soule 1973) documented the arrival of drift logs from North America, Asia, and the south Pacific. The vast majority came from North America, landing on the east coast of Kauai, the southeast coast of Oahu, and the north coast of Maui east of Kahoolawe, with the heaviest concentrations on the southeast coast of Hawaii. However, the changes in temperature from northern California or Oregon, for example, would not be conducive to introduction of temperate stenothermic species. Drifting algae also provide good substrate for a few species of bryozoans.

A surprising transport mechanism for bryozoans, on tropical sea snakes, has also been reported. Kropach and Soule (1973) reported *Membranipora tuberculata* on the eyes and head of *Pelamis platuris*, and Zann et al. (1978) reported *Membranipora savartii* and *Electra angulata* off Australia and central America. The earliest known record of such an association was from the Indian Ocean in 1840. Since tropical sea snakes are highly mobile and have a trans-Pacific range, they offer an interesting but probably not significant mechanism for introduction of species that may occur on floating *Sargassum* aggregations where sea snakes often are found.

Given the vast amount of geologic time involved since the Pacific Basin reached the present general configuration, the evidence suggests that there are sufficient mechanisms of dispersal, such as changing current patterns, fouling, and rafting to account for the introduction of many species. The Hawaiian Islands are

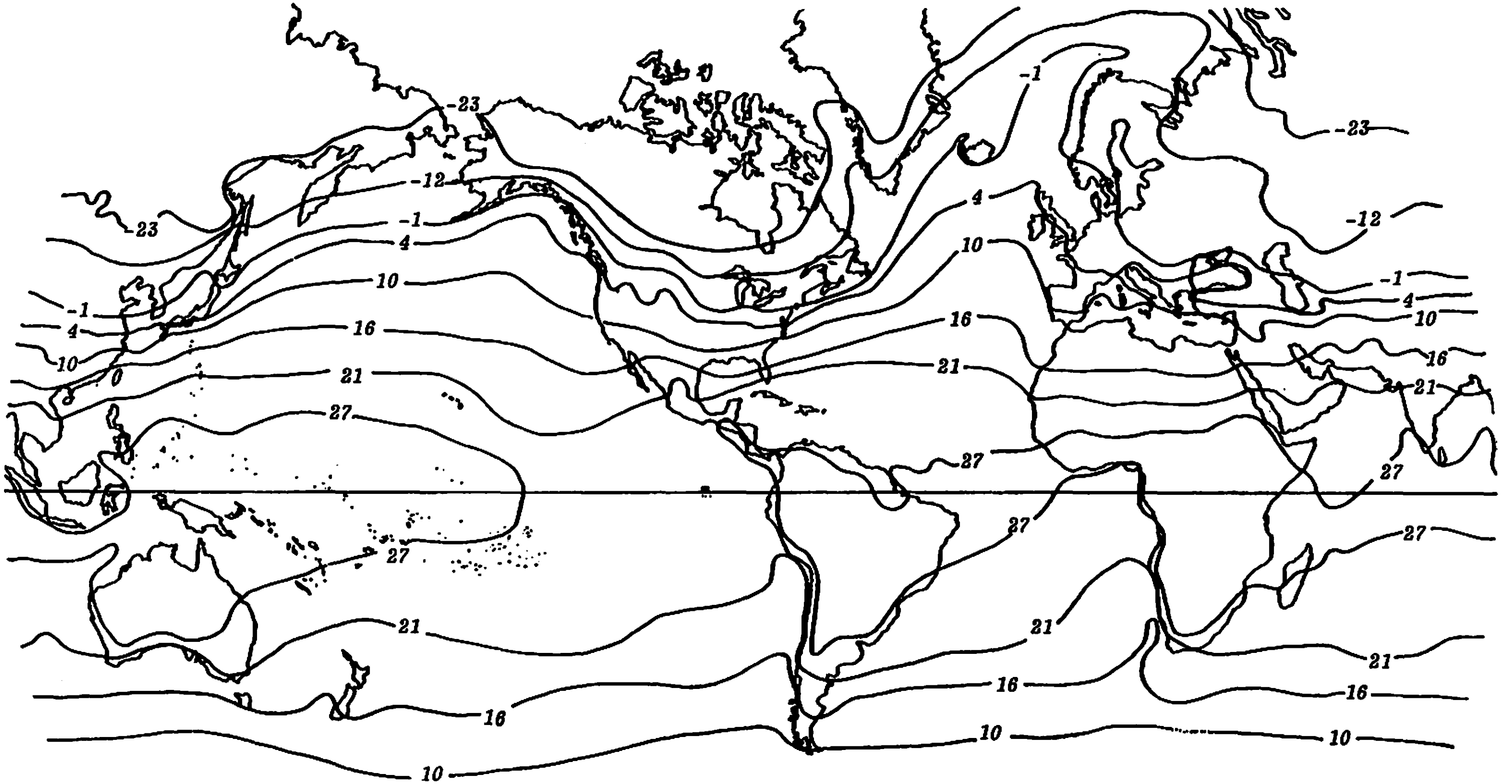


Figure 2.IV.4.—Normal isotherms for January, with the 27 °C isotherm extending past the Line Islands (Kiribati) and through part of the Tuamotu Archipelago. The 21 °C isotherm, which is generally used to define tropical boundaries, normally extends worldwide, including the Hawaiian Islands. Shifts in the isotherms to the north and south also occur. During the 1982–83 El Niño event a 28 °C isotherm extended across the Pacific through the Galápagos Islands, almost to Peru. (After D. F. and J. D. Soule 1986.)

marginally tropical and many tropical stenothermic species would not survive there. Conversely, cool temperate fauna that arrived via drift logs from northern California and Oregon would not tolerate the elevated temperatures in island waters. There is no question that the Hawaiian bryozoan fauna is an attenuated tropical one; the unanswered question is whether the majority of present species are descendents of relicts from worldwide populations that existed when the area was warmer, or whether they represent species descended from those carried into the area by dispersal from a center of origin near the Indian Ocean-Pacific Ocean boundary.

HABITATS

Shorelines and Reefs. Whereas bryozoans are common in rocky tidepools in the temperate zone, the authors have observed that in the tropics the warm, intensely lighted tidepools in dark volcanic rocks and coral rubble shores do not generally support a bryozoan fauna. The limited intertidal zone, with a range of less than 1 m, combined with intense light and insolation, offers less suitable habitat for colonization by intertidal fauna than that of the 2 m to 5 m intertidal habitats of temperate shores. However, bryozoans do occur in shallow, warm waters where they are sheltered from the intense light by docks and boat hulls, or by algae, submerged rocks, coral heads, or coral plate rubble.

Subtidally, bryozoans are most common at depths below about 8 m on the slopes of patch reefs and fringing reefs of the Hawaiian Islands and other tropical Pacific islands according to the authors' personal observations. The reef crests are too exposed to sunlight, turbulence, and desiccation to support all but the most cryptic species. Reef flats also do not support an extensive fauna, except on occasional coral boulders, probably due to the presence of unconsolidated sediments as well as to exposure.

Bryozoans are often not seen at first because they colonize the sheltered niches of the coral heads and the older coral bases rather than exposed surfaces. They proliferate on the undersides of dead coral (*Pocillopora* and *Montipora*) heads and plates that have been dislodged by storms but do not often colonize the "staghorn" forms, according to the authors' field observations. Numerous colonies can also be found on some mollusks and echinoderms. Cuffey (1978) noted that some reef flats of Enewetak and the Great Barrier Reef supported reefal bryozoan species but not those flats on shoreline beachrock tracts. At Enewetak, bryozoans were common only below 10 m, as was true on some Australian reefs, but on other Australian reefs they were prolific at all depths (Ryland 1974, 1976b). In Hawaiian waters, it is necessary to use scuba gear to reach areas of maximum diversity and richness. Dade and Honkalehto (1986a,b), in a study of bryozoans on the reefs of Kaneohe Bay, found them to be abundant. However, in diagramming that abundance, they combined the 0 to 10 m depths, giving the impression that bryozoans are equally distributed from the surface to 10 m; this is not the case.

The discoidal lichenoporan cyclostome bryozoans seem to be among the first to colonize where individual coral polyps are dying, whereas encrusting cheilostomes compete with sponges, colonial tunicates, and coralline algae for space on the older coral substrates. The extrusion of the basal wall of new zooecia creates a tight bond between the bryozoan and the coral surface (J. D. Soule 1973; J. D. and D. F. Soule 1974). Tubuliporids and reteporids also settle between polyps and extend their tubules or branches into the sheltered spaces between lobes of *Pocillopora* on reef slopes or shelves.

Of the encrusting species, the *Parasmittina* have apparently undergone extensive speculation in Hawaii (D. F. and J. D. Soule 1973). Divers often asked what species the "yellow crust" was; it can be composed of any one or several of a dozen species and that complex probably outnumbers any other genus on reefs and settling plates. *Holoporella* (*Celleporaria*) and *Parasmittina* sometimes form knobby encrustations or irregular branching colonies; *Schizoporella* may form knobs, branches, and tubes on some substrates, but in the fouling community it usually remains flattened.

Altogether some 15 genera were common on fringing and patch reefs, including *Parasmittina*, *Schizoporella*, and *Holoporella* mentioned above; *Steginoporella*, *Thalamoporella*, *Microporella*, *Exechonella*, *Cribrilina*, *Metroperiella*, *Calyptotheca*, *Schismopora*, *Hippopodina*, *Lichenopora*, *Margaretta*, and *Rynchozoon* were also found. *Bugula*, *Caberia*, *Scrupocellaria*, *Trypostega*, *Cryptosula*, and *Watersipora* were commonly found in the fouling community but also occurred on some reefs.

Dade and Honkalehto (1986a,b) found 3 distinct assemblages in Kaneohe Bay, characterized as "fringing and reef crests and slopes," "a wave-swept coral-algal flat," and "stenohaline, deeper ocean slope-bench." In contrast, all of the genera they mentioned for the reefs or the deeper ocean slopes were found by the present authors within 8 to 10 m depths, without distinct zonation on reefs and slopes, but not on coral-algal flats. However, the authors' surveys encompassed 92 stations on 5 islands over a 6-year period, so the distinctions that Dade and Honkalehto found at Kaneohe Bay may not hold true for all fringing or patch reefs in Hawaii.

Black Coral Beds. The black coral beds off Maui in the Auau Channel at depths of about 50 m supported an interesting assemblage of bryozoans. The species composition was quite uniform for the bryozoan collections made in the 1960s from coral harvests of Maui Divers, Inc. (Soule and Soule, unpubl. data). About 30 species colonized the coral bases and the mollusks attached to the lower branches of the black coral; the corals were identified by Dr. Richard Grigg as *Antipathes dichotoma*. Always present were the bryozoans *Holoporella vagans* and *Reteporellina denticulata*.

Fouling. Bryozoans usually form an important part of the biological fouling community, especially in the tropics. Edmondson and Ingram (1939) and Edmondson (1944) identified 6 species of bryozoans found in fouling community studies in Hawaii. Five of the species recorded by them were reported again by the present authors; only *Rhynchozoon nudum* was not found again. D. F. and J. D. Soule (1968) recorded 13 species that occurred repeatedly, but in varying quantities, on harbor and bay structures as well as on boat hulls around Oahu. They provided a key to those species with diagnoses and figures. Species included an entoproct, *Barentsia gracilis*, and the ectoprocts *Aetea recta*, *Bowerbankia gracilis*, *Bowerbankia imbricata*, *Bugula californica* (now identified as *B.*

stolonifera), *Bugula neritina*, *Hippopodina feegeensis*, *Savignyella lafonti*, *Schizoporella unicornis*, *Zoobotryon verticillatum*, and 2 species apparently endemic to Hawaii, *Scrupocellaria sinuosa* and *Watersipora edmondsoni*. Also present were *Cryptosula pallasiana* and *Tryptostega venusta*. At Kaneohe Bay, floating tangled masses of the flaccid *Amathia* and *Zoobotryon* were stiffened by tiny colonies of the more rigid *Savignyella* and *Caberia*.

On hulls, encrusting bryozoans provide a surface layer to which other organisms can attach. Soft-bodied ctenostomes such as *Zoobotryon* can form trailing masses 25 to 30 cm long or form a thick felt-work when mixed with firmer, branched cheilostomes. The senescent centers of some older encrusting cheilostomes such as *Schizoporella* form the settling place for ancestrulae (primary zooid formed by the metamorphosed larva) of erect anascans such as *Bugula* or *Scrupocellaria*. These growths provide shelter for numerous small crustaceans and mollusks, polychaetes, tunicates, algae, and arborescent bryozoans. This entire community can reduce the efficiency of boat operation immensely, especially in the tropics where it proliferates so rapidly. Long (1974) recorded 24 species on asbestos settling plates exposed monthly for 1 year in 30–33 m depths off Ewa Beach and the Barbers Point buoy, Oahu. He compared that data with results from panels spaced at 9 m in Pearl Harbor, where only 8 species were found. The species offshore were mostly those commonly found on the reefs as well. Bioadhesion of bryozoans to substrates were discussed in J. D. Soule (1973) and in J. D. and D. F. Soule (1977); reviews of information on fouling were presented in Ryland (1976b) and J. D. and D. F. Soule (1977).

Sand Fauna. Recently, interstitial bryozoans have been found in high energy environments elsewhere (Håkansson and Winston 1986), suggesting that these relatively unknown forms might also be found in Hawaiian waters on organically rich sandy bottoms where siltation is not so extreme as to bury them. Colonies may inhabit single sand grains, and the tiny zooids reach maturity on them, or colonies may be erect and rooted among the grains, or cap-shaped and capable of independent locomotion on vibraculae. These differ completely from fragments of bryozoan species that have been transported from elsewhere in sands and could potentially be used for analysis of shallow or deep sea sediments (Lagaaij 1968; Cook 1981).

ENVIRONMENTAL FACTORS

Sediment. A number of factors influence the occurrence of bryozoans in various locations. One of the most important is the sediment content of the waters, for bryozoans are not generally found where rapid deposition of fine sediments is taking place. Where the water is relatively clear, sediments still determine the character of the bottom flora and fauna that serve as substrates for bryozoans. In Hawaiian waters, areas typical of those apparently barren of bryozoans are the south shores of Kauai, where the Waimea and Hanapepe rivers disgorge much sediment, and the muddy, shallow south shores of Molokai inside the fringing reef. However, the river mouths have not been examined for the unique "sand fauna" mentioned above.

Salinity. Some authorities feel that reduction in salinity caused by runoff is not important to bryozoans, since fresh water forms a layer atop saline water. In shallow waters such as Kaneohe Bay (Bathen 1968) freshwater dilution caused a marked die-off of the coral, but we observed that this did not appear to affect ectoproct growth adversely on the dead coral substrate. However, subsequent development of residential subdivisions produced sediment drainage and sewage effluent which virtually eliminated coral and other fauna including bryozoans for some years by producing conditions of siltation and eutrophication. Improved flood control and sewage treatment have ameliorated some of the problems and coral reef growth has resumed.

Although some ectoproct species prefer brackish water and others are euryhaline, many bryozoans are stenohaline and do not tolerate extreme changes in the salinity of their environment. Winston (1977a) reviewed records on salinity tolerances of estuarine ectoprocts and located 22 studies on warm-temperate estuaries, 21 on boreal-antiboreal areas, and 13 on tropical estuaries. She concluded that only 7% of cyclostome genera occurred in brackish waters (from 2 of 5 suborders), while 55% of ctenostome genera, 12% of cheilostome anascan genera, and 9% of cheilostome ascophoran genera occurred there. Conversely on coral reefs, our observations are that ascophorans are most prominent, followed by cyclostomes. Relatively few soft-bodied tubular ctenostomes or anascan genera, with their uncalcified frontal walls, are found associated with coral reefs (D. F. and J. D. Soule 1979a), which might be due to the greater vulnerability to predation. Since bryozoans do not have excretory organs, lowered salinity might cause swelling and edema of soft tissues. The soft-bodied ctenostomes could probably withstand this better than ascophorans, which are encased in fixed skeletal walls.

Temperature. Temperature, and its correlation with depth, seems to be another important controlling factor. Although many species are considered cosmopolitan by virtue of having been reported at various locations around the world, they may actually occur only at the depths that present the optimum temperature, making them much less eurythermal than would first seem indicated. For example, species that occur in shallow northeastern Pacific waters have been found in deeper southern and central California waters. However, many so-called cosmopolitan species have been shown to comprise more than a single species upon more detailed investigation (e.g., D. F. and J. D. Soule 1973, 1975).

As noted earlier, the thermal boundaries of the tropical Pacific, indicated by the 27 °C isotherm, vary seasonally as well as during periodic episodes such as the El Niño events. Such variations could have considerable effect on the presence or absence of stenothermic tropical bryozoan species, even though they might be repeatedly introduced into an area.

Light. Light penetration is particularly important to bryozoan colonization. Many of the larvae are at first photopositive, becoming photonegative before metamorphosis (Ryland 1960, 1976a, 1977). Light appears to be a strong stimulus for the discharge of lecithotrophic larvae from ooecia or other gymnolaemate brood chambers. There is a firmly established preference by many species for settlement in dark places, typically underneath stones or flat coral plates, for example, a pattern that is not confined to shallow water. Light is not the only factor governing this, but, in general, if colonies are to survive the effects of insolation and dessication, they must select shaded surfaces. If they are to avoid competition with algae in the euphotic zone and smothering with sediment, they must settle on an approximately downward-facing surface. The swimming larvae are negatively geotactic, and it may be that the upward swimming response of the larvae, coupled with negative phototaxis, leads to settlement on the undersides of substrates. Increased temperature appears to increase the rapidity with which the reversal of phototaxis takes place during settling of larvae.

Turbulence and Dissolved Oxygen. Turbulence is also a controlling factor for bryozoans. Erect branching forms are too fragile to withstand wave action, and even tightly clinging, recumbent (adnate) or encrusting forms grow only on the protected surfaces of rocks and coral heads. More rigid, erect colonies such as some *Schizoporella* or *Parasmittina* are able to withstand considerable current. The reticulate or fenestrate reteporids (= Sertellidae) apparently are adapted to bottom currents, with all of the functional zooids turned in the direction away from the current and only the structural kenozooids facing into the current. Reteporids and some cyclostomes develop very different colony forms in quiet waters as compared to those with a pronounced current (Harmelin 1973). Ryland (1977) discussed rheotropism, the orientation responses of colonies, and summarized the research that he and his colleagues did on determining the directional changes in colony growth in relation to current and light. Lutaud (1961) commented on the fact that *Membranipora membranacea* colonies on *Laminaria* fronds grow toward the base of the frond where the zone of growth is, rather than toward the tip of the blade. Some species grow in the direction of the current and some away from it; however, in some species of *Bugula* the branches are positively rheotropic while the stems are negatively rheotropic.

Dissolved Oxygen and Nutrients. Most bryozoans do not tolerate stagnant water. Polyps must be provided with moving water for respiration and suspension feeding. Because ectoprocts have no circulatory or excretory systems, oxygen exchange must take place over the epithelial surfaces such as the tentacles and the frontal membrane. Some colonies apparently are capable of setting up currents by coordination of tentacle movements among individual polyps. The beating of the tentacle cilia directs food in toward the mouth and out through the tentacles, at the same time facilitating oxygen exchange.

Dissolved organic matter (DOM) as nutrients may be taken up directly by the cells in larvae and adults. Dissolved amino acids are taken up by members of most marine invertebrate phyla, as has been demonstrated by a number of investigators (e.g., Ferguson 1982; Manahan et al. 1983), based on more than 2 decades of research by Grover C. Stephens and his colleagues. Transported amino acids are utilized biochemically to synthesize proteins and in oxidative metabolism. Body walls of those invertebrates found to show uptake of DOM (Stephens and Schinske 1961) have a ciliated microvillar outer epithelium (Manahan et al. 1983), as does the bryozoan tentacle. Research on bryozoan larvae of the non-feeding types as well as on adults might demonstrate this phenomenon.

FOOD WEB

Bryozoan Feeding. Ryland (1976b) reviewed the various theories about bryozoan feeding currents in the literature, showing that colonies create incurrent and excurrent flow patterns when some groups of zooids extrude tentacles on which lateral cilia beat while other zooids remain closed (Strathman 1973). This creates "chimneys" for excurrent flow (Banta et al. 1974). Lophophores vary in size as well as in the length of tentacles among zooids, enhancing the ability to set up water currents for feeding. Winston (1977b, 1978) studied 56 species from varied habitats in Florida and Panama and concluded that polypide morphology, particularly introvert length (tentacle sheath) and lophophore symmetry, varied from species to species, with the variation linked to behavioral strategy. She concluded that feeding behavior ranged from passive filtration to tentacle feeding, to cage capture of active protistans, to mechanisms for concentration of small particles by larger individuals.

Bryozoans are suspension feeders; in laboratory experiments, various species have been reared on unicellular algae such as the chlorophyte flagellate *Dunaliella tertiolecta* and an unarmored dinoflagellate *Gymnodinium simplex*. Relatively few species have been tested in culture, and gut contents have shown mixtures of diatoms, detritus, bacteria, silicoflagellates, peridinians, coccolithophores, algal cysts, pollen grains, and a variety of flagellates. Probably only species with gizzards can digest diatoms, which may pass through the guts of other species intact. Bryozoans are able to feed selectively and will choose a preferred prey species, rejecting others and some particles (Ryland 1976b; Winston 1977b).

In shallow marine waters where phytoplankton are most likely to be available, most of the food resource apparently comes from under 50 μm in size (Winston 1977b). Concentrations of phytoplankton in inshore waters vary seasonally but are apparently adequate to support extensive bryozoan populations.

In tropical waters, bryozoans display their greatest diversity, which would assist them in taking advantage of every possible trophic resource. Phytoplankton resources are low in the tropics and feeding rates high in the warmer waters (Winston 1977b). The increasing data base on the frequent occurrence of bryozoans in deep water indicates that they may feed extensively on bacteria, as do other organisms (Jannasch 1979). Fenchel (1970) and others have documented the ingestion of fecal pellets, which contain numerous bacteria, by other invertebrate groups. The invertebrate communities around hydrothermal vents also demonstrate bacterial suspension feeding (Jannasch and Wirsten 1979). D. F. and J. D. Soule (1981) reviewed the literature on the detrital food web and presented data on estuarine waters, including microheterotrophs (bacteria, yeast, fungi, and protistans).

Predation on Bryozoans. Although bryozoans would appear to have little attraction as a food source, due to the small amount of tissue available, they do provide a significant portion of the diet of many animals. Omnivorous echinoids feed extensively on encrusting bryozoans, especially on the *Membranipora membranacea* found on *Laminaria* and *Macrocystis* kelp. Many grazing fish (e.g., labrids) browse on bryozoans as they feed on reefs. It is possible to watch some fish species bite off chunks of coral and bryozoans and spit out the calcareous debris. Other records of feeding on bryozoans include asteroids, chitons, and polyclad worms (Ryland 1976b).

By far the most notable are the nudibranchs and pycnogonids, which seem to prey quite selectively on certain species. McBeth (1971) found that the nudibranch *Triopha carpenteri* fed exclusively on 3 species of arborescent bryozoans at La Jolla, California: *Scrupocellaria diegensis*, *Crisia serrulata*, and *Cellaria mandibulata*, in that order of preference. He also found that the rose-colored nudibranch *Hopkinsia rosacea* apparently gets its pigment from feeding on the reddish *Euryostomella bilabiata*. Other species may be well camouflaged during feeding on bryozoan colonies by incorporating their host's pigment. Pycnogonids are remarkably adapted for feeding on the epizoites on the bryozoan frontal surface or on the zooids themselves. Wyer and King (1973) illustrated the insertion of the proboscis to extract the polyp as soon as an operculum opens. The supposedly dimorphic apertures of the watersiporid *Uscia* in the Gulf of California has been attributed by Soule and Soule to the reparative calcification around the aperture following damage by pycnogonid predation. Harvell (1984) demonstrated that the presence of nudibranchs on *Membranipora membranacea* stimulated the production of chitinous spines on the frontal membrane, creating the "species" *Membranipora villosa*.

GROWTH FORMS

Bryozoan growth forms can be altered extensively by environmental factors (Harmelin 1973, 1976a), whereas Jebram (1975, 1979) demonstrated that different foods could affect morphology. However, relatively little is known about the extent to which environmental factors produce the phenotypic differences used to distinguish between species.

Early ectoproct classifications were based primarily on colony forms because detailed studies of zooid structure had not yet been made. Later, it was found that colony form was not entirely species-specific. Some forms vary according to the environment. A given species growing in turbulent waters, or colder waters, may cling closely to the substrate but may rise in leafy folds when living in calmer waters or warmer waters (Harmelin 1973). Details of structure and function now provide the basis of classification, but nevertheless knowledge of typical colony forms can be of considerable help to the field collector.

Many of the growth form terms used in the literature are based on the name of the genus most typical of that form. This is most ineffective to the person unfamiliar with generic characteristics. Regardless of the names chosen for them, the following growth patterns can be recognized (J. D. Soule et al. 1975; D. F. and J. D. Soule 1979a):

I. Recumbent Forms
   A. Soft-bodied, uncalcified species
      1. Stolonate: Individuals are connected by narrow tubular structures to form colonies that float or extend over a firm substrate. Certain Ctenostomata have true stolons that are individual zooids lacking polyps (kenozooids) and modified to form the extensions (Ctenostomata: e.g., *Bowerbankia walkeria*). Some Cheilostomata are stoloni-

form, but the extensions are formed by extended portions of normal zooids (e.g., *Aetea*).
    2. Burrowing: Colonies that ramify beneath the surface of mollusk shells, showing only apertures or traces of the stolons on the surface (Ctenostomata: *Terebripora*, *Immergentia*; Cheilostomata: *Penetrantia*).
    3. Carnose (fleshy): Colonies that form gelatinous masses sometimes several centimeters in diameter (Ctenostomata: *Alcyonidium*).
  B. Encrusting, lightly or heavily calcified species
    1. Flexiform: Colonies with loosely connected or contiguous zooecia that form flat, lightly calcified crusts over soft, flexible substrates such as algal blades (Cheilostomata, Anasca: e.g., *Membranipora*, *Beania*).
    2. Rigid (escharine): Heavily calcified colonies forming unilaminar or multilaminar crusts over solid, inflexible surfaces such as shell, coral, and stone. Some species form heavy, knobby incrustations on flexible surfaces such as twigs or algae, turning them into solid, sometimes erect branching structures (most Cheilostomata, Ascophora: e.g., *Parasmittina*, *Holoporella*, *Schizoporella*).
  C. Tubular species with terminal apertures
    1. Tubules in series: Tubules recumbent, or curving to partially erect near distal ends, mostly oriented horizontally in series; colony base irregular beneath some or all tubules (Cyclostomata: *Crisina*, most Tubuliporidae).
    2. Discoidal: Colonies formed by radiate bundles of erect or partially erect tubules, surrounded by encrusting saucer-shaped basal disc; may have single center or expand to multiple centers (Cyclostomata: *Lichenopora*, *Disporella*).

II. Erect Forms
  A. Branching species
    1. Arborescent, tuftlike: Delicate colonies formed by various modes of branching, some jointed; attached to substrate loosely by rootlets; most lightly calcified, usually not able to withstand turbulent waters (Cheilostomata, Anasca: e.g., some *Thalamoporella*, *Bugula*, *Scrupocellaria*).
    2. Arborescent, fanlike: Colonies well calcified, with fewer branches, few anastomoses between branches; branching mostly in 1 plane [Cheilostomata, reteporids (Sertellidae): *Reteporella*, *Reteporellina*].
    3. Irregularly branching, heavily calcified: Thick, irregular branches and nodules arising from encrusting colony base (see also I.B.2.).
  B. Foliaceous species
    1. Leaflike: Colonies rising in folds of zooecia to form cabbagelike structures from small encrusting colony base (Cheilostomata, Anasca: e.g., some *Thalamoporella*, some *Watersipora*).
  C. Reticulate or fenestrate species
    1. Closely reticulate: Meshlike; colonies rising in frills and folds from small base, branches closely connected to give appearance of "Chex" cereal or crocheted doily [Cheilostomata, some reteporids (Sertellidae): *Iodictyum*, *Triphyllozoon*, *Phidolopora*].

  2. Fenestrate (irregularly reticulate): Branches less closely connected, or with slitlike anastomoses [Cheilostomata, some reteporids (Sertellidae): some *Triphyllozoon*, some older colonies of *Reteporella*, *Reteporellina*].

D. Tubular species
  1. Tubular individuals: Colonies of tubules with terminal apertures rising vertically in branching series (Cyclostomata: some Crissiidae).
  2. Tubular colony: Encrusting zooecia with non-terminal apertures rising from encrusting base in funnel shape (infundibuliform) (Cheilostomata: some *Schizoporella*).

METHODS OF PRESERVATION AND MICROSCOPY

Calcareous bryozoans may be preserved merely by air-drying for routine collection and identification, since gross morphological diagnostic features are not damaged. For more thorough investigation, specimens may be fixed and preserved by immersion in 70% ethanol or in 10% formalin (1 part reagent grade formaldehyde and 9 parts seawater). Seawater acts as an adequate buffer against acidity in formalin, which can cause decalcification of the exoskeleton and loss of characters for identification. Formalin is, nevertheless, the best fixative if histological studies are to be made. Calcium carbonate can be added as a buffer if distilled water is used as a diluent. Specimens should be transferred from formalin after fixation to 70% ethanol for storage.

Wet material must be examined and sorted under a dissecting microscope for Entoprocta and non-calcareous ctenostome Ectoprocta. Representative specimens should be stained, dehydrated, and mounted whole with cover slips as in conventional histological techniques, with the remainder stored in ethanol. Representative calcareous species can be air dried, but air-dried specimens will develop mold growths in the tropics if they are placed in plastic or glass before they are thoroughly dried, ruining the specimens because the mold cannot be removed.

Some bryozoans are not easily removed from the substrate without damage. Colonies encrusted on coral may be prepared for study by cutting the coral base with hammer and chisel; colonies may be cut out of large shells with a diamond abrasive disc on an electric drill. More fragile colonies may be moved to glass slides for mounting with a razor blade or damp, camel's hair brush. Use of excessive glue in mounting will obscure diagnostic features by invading the specimens. Casein (white) glue, which is non-acid, should be used since calcareous colonies mounted with balsam, household glue, or cement will disintegrate after a few years because of the acid content of the glue. Since casein glue is water soluble, it is easy to remove specimens from slides for scanning microscopy.

In the field, a hand lens will serve to identify a few of the more distinctive genera; most species identifications require higher magnification, since the individual zooids are usually less than 1.0 mm in length, their apertures about 0.1 mm in diameter, and other characters are even smaller. A low-power dissecting microscope is usually required for preliminary sorting but magnifications up to 100× are often needed for final identification of species. Scanning electron microscopy (SEM) at magnifications of 100× to 1000× is by far the best means of recognizing species differences, studying developmental morphologies, and photographing specimens. Its use has revolutionized bryozoan taxonomy and systematics.

In order to see the skeletal characteristics of heavily calcified specimens, which may be covered with a membranous cuticular outer layer or with debris, it may be necessary to place them in bleach (sodium hypochlorite) for a few minutes to remove organic material, followed by thorough rinsing in tap water. It may be desirable to bleach only part of a specimen for SEM study or control dissolution so as to remove the membrane but retain the chitinous avicularian mandibles and opercula. The specimen can be placed under the dissecting microscope and a glass rod used to apply a small spot of bleach. Action is watched carefully and the specimen is rinsed as soon as partial dissolution is observed. Bleach will disarticulate lightly calcified species. A small sonic cleaner is useful in removing debris from less delicate specimens. However, diatoms, coralline algae, fungi, and some epizoites such as the protozoan folliculinids often cannot be removed.

Living burrowing bryozoans collected in shells by dredge or divers must be fixed immediately with formalin; otherwise the tiny stolons ($<7\ \mu m$) will disintegrate. Shells are later decalcified with 4 *N* formic acid and colonies imbedded in paraffin for sectioning to determine anatomy and tentacle count. Shells that contain fossil or recent colonies may be treated with bleach to remove organic material. The burrows can then be molded with epoxy resin and the shell dissolved to obtain gross morphological characters for SEM study (Hillmer 1968; J. D. Soule and D. F. Soule 1975).

MORPHOLOGY

Individuals of ectoproct colonies are usually less than 1 mm in length, but the colonies vary greatly in size, sometimes covering 20 to 30 cm^2 of substrate. They may form discs or extensive flat crusts colored tan, yellow, red, purple, brown, or black; slender arborescent or foliaceous (flustraform, frondose) colonies can be white, yellow, or purple; thick, spiny erect branches are white, yellow, blue, brown, or gray; and crusty nodules can be gray, yellow, tan, or brown.

Each individual (zooid) has a crown of ciliated tentacles borne on a circular or crescentic ridge (the lophophore). The mouth lies within the tentacle circle, and the anus is outside; hence the name Ectoprocta ("outside anus"). The complex gastrointestinal tract includes the oral cavity, pharynx, stomach (cardia), caecum, pylorus, intestine, and anus. A gizzard is present in some ctenostome and cheilostome anascan species. The lophophore can be extended from the body to deploy the tentacles or retracted inside a tentacle sheath that completely encloses the lophophore within the body cavity. This contrasts with the entoproct body plan, in which the tentacles cannot be drawn into the body cavity and are virtually unenclosed. Ectoprocta do not have nephridia or a true circulatory system. The body cavity is considered by some to be a coelom, lined with a limited peritoneum which extends into the tentacles (Woollacott and Zimmer 1971; Zimmer 1973). A well-developed nerve plexus system is present (Lutaud 1969, 1976, 1977, 1979).

The polypide of the zooid consists of the tentacles, lophophore, gastrointestinal tract, and funiculus, a cord of tissue that functions in the transport and storage of nutrients and connects the polypide with the body wall. The funicular system also sends branches between zooecia. Included in the polypide are associated musculature, cerebral and visceral ganglia, and nerves, as well as reproductive organs. The interior soft body wall tissue of the living zooid is called the cystid; it lines the exoskeleton, contains the parietal plexus nerves, generates the polypide, and in some species can regenerate successive polypides.

Each zooid is permanently fixed within an exoskeleton (zooecium), which is formed initially by secretions from the basal epithelium of the asexual bud, followed by vertical folding to form the body walls and then deposition of calcium. The calcified frontals originate in several different ways. The patterns of body wall and frontal wall formation and calcification are complex (e.g., Cook 1973; Banta 1977; Banta and Wass 1979; Boardman et al. 1983). Calcareous vertical walls are shared by adjacent individuals (zooecia) in the colony exoskeleton (zoarium).

Bryozoan zooids may be specialized to form polymorphs, also called heterozooids or kenozooids, which generally lack a feeding polypide. Stolons, rootlets, stems, spines, and some brooding structures are considered to be modified individuals, as are whiplike vibraculae and a variety of pincerlike structures called avicularia that appear to serve in cleaning and protecting the colony or in assisting in food capture (J. D. Soule et al. 1980; Winston 1984).

REPRODUCTION

Individual bryozoans may be sequentially or simultaneously hermaphroditic, or they may be unisexual; also, a few species form permanently unisexual colonies. Bryozoans were thought to be self-fertilizing for many years because the means of fertilization by release of sperm through the tips of tentacles was unknown until fairly recently (Silén 1966; Franzên 1977). In ctenostome species, single eggs may be "brooded" by suspending them in a membranous pouch outside the tubular zooid or in the external body wall, or by holding them inside the tentacle sheath or body cavity while the polypide degenerates. Some cheilostomes brood ova internally, but most cheilostomes have developed specialized brood chambers called ovicells in which fertilized ova are sheltered during development. The very pliable egg is extruded from the body cavity through a supraneural pore into the ovicell. It is probably fertilized during the time it is exposed to ambient seawater (Ström 1977). The ovicells offer important distinctive morphological characters for species identification. The system is quite different in the Cyclostomata (Tubuliporata), wherein individuals called gonozooids may be modified for reproduction, or a colony may have an enlarged common chamber with a separate exterior opening as a brooding structure. Ström (1977) discussed the mechanisms of brooding extensively. Developing ova can sometimes be noted in the ovicells of mature colonies because the ova are bright pink or orange, giving large areas of the colony a distinctive appearance during reproduction.

Ectoproct cleavage is biradial, in contrast to the spiral cleavage in entoprocts. Cyclostome ova undergo multiple fission to form a number of larvae from a single egg in an unusual process called polyembryony, which does not occur in ctenostomes or cheilostomes. The differences in reproduction between the major groups illustrate the greater evolutionary separation between the cyclostomes (Tubuliporata) and the cheilostome-ctenostome line.

Larvae. The larval morphology was known for only about 45 genera or species of bryozoans a few years ago (Zimmer and Woollacott 1977a), but it differs greatly among the groups. One form, the cyphonautes, resembles a small triangular clam with chitinous valves and a complete digestive tract. These free-swimming, planktotrophic larvae were not recognized in the plankton as bryozoan larvae for many years. This larval type is shared by a few species of the cheilostome anascan genera *Conopeum*, *Electra*, and *Membranipora* and the ctenostomes *Alcyonidium*, *Farella*, and *Hypophorella*. Larvae of few other ctenostomes, *Flustrellidra* and *Pherusella*, resemble the cyphonautes but lack a functional digestive tract (D. F. and J. D. Soule 1979a). Cheilostome ascophoran larvae are coronate, resembling a tamoshanter cap, with a ciliary girdle or ciliary crown. They are similar in some respects to trochophore larvae, but the ciliary bands and gut are placed differently. These larvae either are not planktonic or cannot remain planktonic for extended periods of time. Some coronate larvae are oblate spheroids, almost entirely covered by cilia (e.g., *Bugula*), which settle within a few hours (Zimmer and Woollacott 1977a; D. F. and J. D. Soule 1979a). The knowledge that dissolved organic matter (DOM) can be taken up by many invertebrate larvae (Manahan et al. 1983) suggests that the non-feeding bryozoan larvae might also be nourished in that manner.

Little is known of ectoproct larvae in Hawaiian waters, but the basic body types should be similar to those described herein and found elsewhere. The *Watersipora* larvae are bright red and coronate. They can be released in the laboratory by keeping a gravid colony in slightly cooler water in the dark overnight and then turning on a bright light near the tank.

A new ectoproct colony develops when the sexually produced, free-swimming or creeping larva settles and becomes permanently attached to the substrate by extrusion of an adhesive sac. The larvae apparently exhibit considerable selectivity in choosing attachment sites. Some species settle on rock, old coral bases, mollusk shells, or other hard substrates, whereas others show preference for marine algae or wood. Metamorphosis is rapid, and radical changes occur in bryozoan larvae studied. The cellular movements are complex and can be elaborated from cytological studies by transmission electron microscopy (Zimmer and Woollacott 1977b).

When a larva settles, it forms the primary individual zooid, or ancestrula of the colony. A few species produce twin ancestrulae. All other zooids in a given colony develop by asexual budding, first from the ancestrula and then from succeeding zooids, to form an isogenous grouping. Budding patterns often are characteristic of particular species. Some produce stolons with new individuals on them while others may form new individuals that lie terminal (distal), lateral, proximal, or frontal to the ancestrula and subsequently to the existing zooids. In this way colonies of varying sizes and shapes may be formed. In some species there is a zone of change (astogeny) in which successive rows of zooecia will show morphological differences from the ancestrula and from the mature individuals. Beyond the astogenetic zone all zooecia will be virtually identical, although this includes the complete array of polymorphs (kenozooecia) such as avicularia.

Unlike the autozooids, polymorphs generally do not have polypides. Non-feeding individuals receive nutrition from funicular tissues passing between zooids through pores in lateral and transverse walls and the calcified wall where present. Coordinated activity among autozooids in the colony has been observed in capturing food and in creating a colony-wide current of water by beating of the tentacle cilia.

HAWAIIAN BRYOZOANS

The first bryozoans recorded from Hawaii consisted of 14 species collected by H.M.S. *Challenger* off Honolulu in July–August 1875 at depths from 20 to 40 fathoms. Of the 14 species, Busk (1884) described 12 as new. Canu and Bassler (1927) reported on collections dredged by the U.S. Fish Commission Steamer *Albatross* in Hawaii between 1891 and 1910. Although some of their material was from shallow water, depths also ranged below 100 m to almost 700 m, where water temperatures were recorded from 12.8 °C down to 5 °C. Canu and Bassler 43 recorded 43 species, 25 of which were newly described. They found only 3 of the 14 *Challenger* species, but this is not surprising since both surveys were brief and made at different depths and localities. Sixteen of Canu and Bassler's 18 known species were cosmopolitan or known from the eastern Pacific (J. D. Soule and D. F. Soule 1976). The fragmented condition of dredged bryozoan material made identification of some of the early dredge hauls difficult, as compared with the intact colonies collected by Scuba diving in recent years.

Material on which the present study is based included the bryozoan collections of the Bernice P. Bishop Museum and University of Hawaii made prior to 1965, which consisted primarily of shallow water, cosmopolitan, fouling community species. Subsequently, between 1965 and 1971, extensive diver collections of subtidal shores and shallow reefs were undertaken by Soule and Soule, partially supported by the National Science Foundation, in cooperation with University of Hawaii graduate students. More than 150 species have now been verified, newly recorded, or newly described, and many more specimens await detailed studies. In all, 92 stations on the islands of Kauai, Oahu, Maui, Molokai, and Hawaii were sampled (Fig. 2.IV.3).

Long-term studies are still underway to describe the many, presumably new species and verify faunal affinities of known species. A list of species found by Soule and Soule in Hawaiian waters is presented in the Appendix. Species previously identified from the *Challenger* and *Albatross* expeditions in Hawaiian waters have also been included. Possible synonymies for the species collected in the earlier surveys and references to detailed descriptions or distribution records are given. During 1983 Dade and Honkalehto (1986a,b) collected and identified 39 species from Kaneohe Bay, Oahu, 31 of which were species listed herein.

CLASSIFICATION

The ectoproct Bryozoa have traditionally been divided into 2 classes, the freshwater Phylactolaemata and the marine Gymnolaemata (Harmer 1915, 1926, 1934, 1957; Osburn 1950, 1952, 1953; Bassler 1953; Hyman 1957). The Gymnolaemata were divided into 3 orders, the uncalcified tubular Ctenostomata, the calcified tubular Cyclostomata (Tubiliporata), and the non-tubular Cheilostomata with subterminal apertures.

The higher classification still found in most of the literature is as follows:

- Phylum BRYOZOA
  - Class PHYLACTOLAEMATA (fresh water)
  - Class GYMNOLAEMATA (marine, estuarine)
    - Order CTENOSTOMATA (living; tubular zooids, uncalcified)
    - Order CHEILOSTOMATA (living; non-tubular zooids, calcified)
    - Order CYCLOSTOMATA (living; tubular zooids, calcified)
    - Order TREPOSTOMATA (fossil; tubular zooids, calcified)
    - Order CRYPTOSTOMATA (fossil; tubular zooids, calcified)

A third class, the Stenolaemata, was proposed 60 years ago by Borg (1926), in which he combined the living cyclostomes with the fossil orders. This system was followed with some modifications by Boardman et al. (1983):

- Phylum BRYOZOA
  - Class PHYLACTOLAEMATA
  - Class GYMNOLAEMATA
    - Order CTENOSTOMATA
    - Order CHEILOSTOMATA
  - Class STENOLAEMATA
    - Order TUBULIPORATA (= Cyclostomata Busk)
    - Order TREPOSTOMATA
    - Order CRYPTOSTOMATA
    - Order CYSTOPORATA
    - Order FENESTRATA

Another system that emphasizes the close relationship between the cheilostomes and ctenostomes unites them under the class Eurystomata, originated by Marcus (1938). Thus the following system can be found in some of the literature.

- Class PHYLACTOLAEMATA
- Class EURYSTOMATA
  - Subclass CTENOSTOMA
  - Subclass CHEILOSTOMATA
- Class STENOLAEMATA

The arrangement of higher categories is important to the individual attempting to locate literature. Changes that better reflect the phylogenetic relationships between groups as they become revealed by research are beneficial to taxonomists. Some recent efforts have been made to insert additional categories such as superphyla and infra-orders and to alter spellings, but we have chosen the simplest system compatible with locating information for identification of species.

The systems of classification of higher taxa do not adequately represent the overlapping of characters that exists in the bryozoans. True separations needed to construct artificial dichotomous keys may not exist in many cases. Recently Boardman et al. (1983) demonstrated the relationships between the 3 classes by use of computer cluster analysis of colonies, populations, and taxa to provide a polythetic classification (Sneath and Sokol 1973). This results in clustering of taxa on the basis of sharing a majority of character states common to a majority of members in a cluster. No single character or character state must be present for a group to be included in a taxon. The traditional system is monothetic, because all members of a group must share at least 1 character or combination of characters.

In examining the phylogeny of the 3 classes, Boardman et al. (1983) analyzed a total of 48 characteristics. This showed that the Stenolaemata were more similar to the Gymnolaemata than to the Phylactolaemata based on all characteristics. However, when they eliminated all characteristics except those related to soft parts, the Stenolaemata showed a greater similarity to the freshwater Phylactolaemata. This kind of information is of great importance to determining evolutionary relationships.

KEY TO HIGHER TAXA OF BRYOZOA

1 Tentacular crown (lophophore) horseshoe-shaped; freshwater only; forms hibernating bodies (statoblasts) .... Class PHYLACTOLAEMATA

Tentacular crown circular; marine and estuarine; no hibernating bodies 2

2(1) Zooecium a calcareous tubule with terminal circular aperture .... Class STENOLAEMATA

[The Cyclostomata (Tubuliporata) comprises the only living order of the Stenolaemata.]

Zooecium other than a calcareous tubule with terminal aperture .... Class GYMNOLAEMATA ... 3

3(2) Zooecium soft-bodied, tubular or saccate with terminal aperture closed by puckering membrane; colony stolonate or with zooecia contiguous; some with free-swimming larvae, others with brooding in internal or external membranous sac; no ovicells, no avicularia or vibraculae .... Order CTENOSTOMATA . . . 5

Zooecium lightly or heavily calcified, mostly boxlike with subterminal aperture closed by operculum; colony forms various; brooding in internal or external ovicells; avicularia, vibraculae present or not .... Order CHEILOSTOMATA . . . 4

4(3) Frontal (ventral surface) an exposed flexible membrane that performs hydrostatic function when contracted to evert tentacles; frontal may have limited calcification externally (gymnocyst), or a calcified shelf around edge of frontal or a shield (cryptocyst) originating beneath frontal membrane, or as fused spines above frontal. A mural rim around frontal margin sometimes bearing spines; operculum a hinged flap of frontal membrane; without an asc (ascus) hydrostatic sac .... Suborder ANASCA

Frontal surface calcified above or beneath frontal membrane, (gymnocyst or cryptocyst), sometimes in multiple layers with central or peripheral pores; compensation sac (ascus) between calcified frontal layers and frontal membrane with opening (ascopore) within the apertural peristome or proximal to it on the frontal .... Suborder ASCOPHORA

5(3) Colonies with 2 types of zooecia, sausage-shaped autozooids and kenozooid (polymorph) stolons; individuals separate, budding from creeping or erect stolons .... Suborder STOLONIFERA
Colonies without stolons, zooecia contiguous, gelatinous; budded directly from adjacent zooids .... Suborder CARNOSA
[Carnosa have not been found in Hawaii; they are apparently limited to cool waters.]

Class GYMNOLAEMATA

Order CTENOSTOMATA

The Ctenostomata are chitinous, forming stolonate colonies with separate tubular zooecia or fleshy encrusting gelatinous colonies. Apertures are terminal, being closed only by contraction of the tentacle sheath, which gives them a purse-string appearance. To date only the stolonate forms have been found in Hawaiian waters. The suborders and families are summarized in the following paragraphs.

Suborder STOLONIFERA

Colonies are composed of feeding autozooecia and kenozooid stolons which form floating, tangled masses or ramifying networks of creeping or partly erect individuals.

Superfamily VESICULARINA

The Vesiculariidae include fouling species of the genera *Amathia*, *Bowerbankia*, and *Zoobotryon*. The *Amathia* consist of short, erect zooecia arranged biserially in a spiral around each stolon segment. *Bowerbankia* zooecia are arranged singly or in pairs on internodes of stolons, and *Zoobotryon* forms spaghettilike tangled masses with thick stolons and small, biserially arranged zooecia. All Vesiculariidae have prominent gizzards, a trait shared with some other ctenostomes and a few cheilostome genera. Figure 2.IV.5 illustrates the anatomy of a typical ctenostome, *Bowerbankia*.

Superfamily VALKERIINA

The Valkeriidae is represented in Hawaii by the genus *Valkeria*. Zooecia are tapered at the base and attached to the stolon in clusters of short "stems."

Superfamily TEREBRIPORINA

The Terebriporina are stolonate also, but burrow primarily in the organic matrix of mollusk shells, brachiopods, or barnacles. The apertures and some of the primary stolons can be seen as minute openings and tracings on the shell exterior. Members of the family Terebriporidae have tubular zooecia connected by secondary stolons near the midsection of the body. Reproductive gonozooecia retain the developing embryo in the body cavity with a degenerated polypide.

The Immergentiidae form stolonate colonies by extensions of the distal body wall ("shoulders") flanking the aperture, which is diamond-shaped. There is no special gonozooecium. The Spathiporidae have not yet been found in Hawaiian

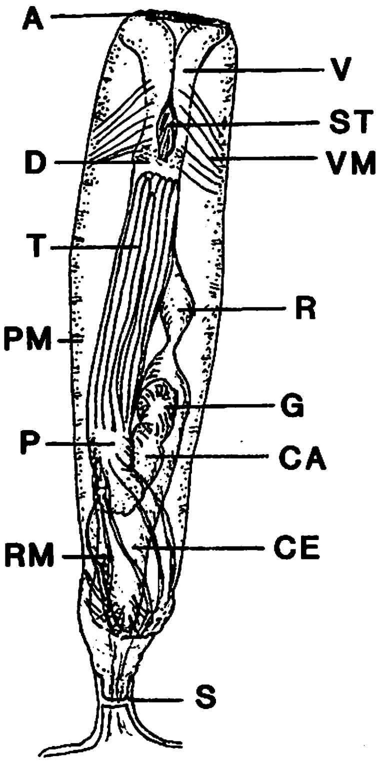


Figure 2.IV.5.—*Bowerbankia*, illustrating ctenostome morphology. (A, aperture; V, vestibule; ST, setae; VM, vestibular muscles; D, diaphragm; T, tentacles; R, rectum; PM, parietal muscles; G, gizzard; P, pharynx; CA, cardia; CE, caecum; RM, retractor muscles; S, septum.)

waters but exhibit similar tracings on shells. It is not possible to determine the genera strictly on the basis of surface tracings; either preservation and decalcification of shells or casting in epoxy resin is necessary to determine the genera. Sectioning of preserved colonies may be necessary for species identification.

Morphological studies of living species of *Terebripora* and *Spathipora* were first made by Marcus (1938b); histological studies were carried out by Silén (1946, 1947, 1956), by J. D. Soule (1950a,b), and by J. D. and D. F. Soule (1968, 1969a,b, 1975, 1976).

Suborder CARNOSA

Leathery, gelatinous, erect, foliaceous, or encrusting colonies formed by contiguous zooecia. Mostly cold-water forms, they have not been reported in Hawaiian waters.

Order CHEILOSTOMATA

One of the basic morphological characteristics of cheilostome Bryozoa is the presence of a subterminal aperture (orifice), which differentiates the species readily from the tubular non-calcareous Ctenostomata and the tubular calcareous Cyclostomata (Tubuliporata), both with terminal apertures. Beyond that characteristic, however, the Cheilostomata exhibit great diversity in modes of growth, in ornamentation and in polymorph (kenozooid, heterozooid) formation. These features have perhaps made them adaptable to many ecological habitats, since the cheilostomes are the most successful of the 3 major modern bryozoan groups in the marine environment.

Although 2 major cheilostome suborders, the Anasca and the Ascophora, are distinguished by the absence or presence of an internal hydrostatic sac (ascus) that controls the eversion and withdrawal of the lophophore, the ascus is not visible externally. A few genera have an opening to the ascus in the frontal wall, but it opens into the apertural cavity in most species. Other, more readily visible features must be utilized to determine the suborders and families and to identify the species.

Suborder ANASCA

The principal morphological feature that readily distinguishes most anascans is the uncalcified membranous frontal (ventral) wall, which includes the operculum covering the aperture (orifice) and a boxlike zooecium (Fig. 2.IV.6). The extent of the uncalcified portion of the frontal wall, called the opesia, varies

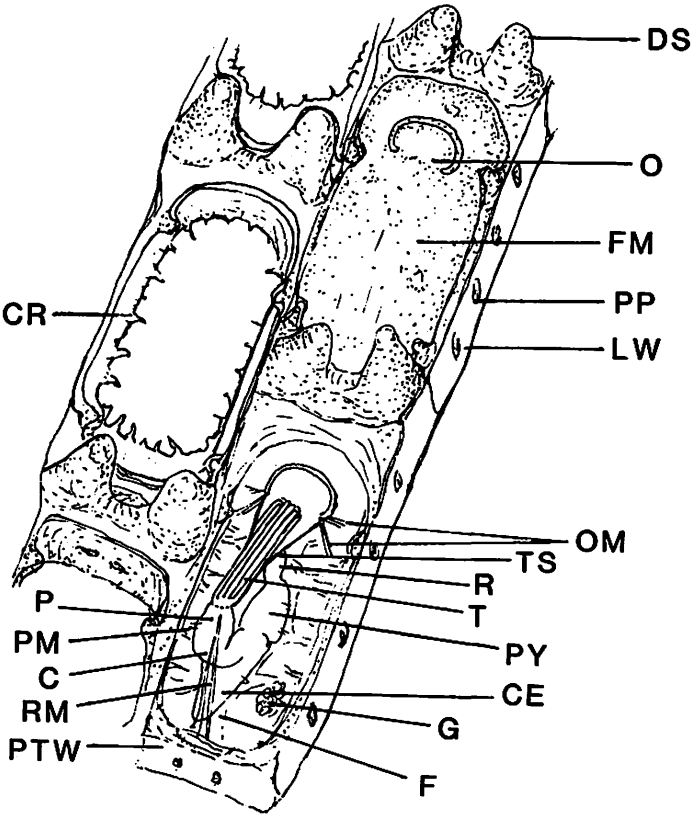


Figure 2.IV.6.—*Membranipora tuberculata*, illustrating cheilostome anascan morphology. (DS, distal spine; O, operculum; FM, frontal membrane; PP, pore plate; LW, lateral wall; OM, opercular muscles; TS, tentacle sheath; R, rectum; T, tentacle; PY, pylorus; CE, caecum; G, gonad; F, funiculus; P, pharynx; PM, parietal muscle; C, cardia; RM, retractor muscle; PTW, proximal transverse wall; CR, cryptocyst with cryptocyst spines.)

among the genera from covering virtually the entire ventral surface of the zooecium to exposure of only small areas (opesiules) around the aperture or flanking the polypide tube. The calcified frontal area may consist only of a limited mural rim around the exposed frontal wall (opesia) or may extend over much of the frontal.

The calcified frontal in anascans is most often formed by an infolding of the internal body wall epithelium to form a cryptocyst beneath the frontal membrane. The cryptocyst may be limited to a shelflike rim or may underlie most of the frontal and may be perforate or not. An external calcified layer, the gymnocyst, may be present; this is formed either by growth from the proximal margin of the zooecium as the frontal membrane develops or by folding of the external body walls (umbonuloid formation) to cover a small or large area of the frontal (Boardman et al. 1983).

Lateral and basal walls range from virtually uncalcified to moderately calcified, but generally they are not as heavily calcified as those in the cheilostome ascophorans or the cyclostomes.

Colony form among the anascans is also varied. There are those species with zooecia that are connected proximally and distally or laterally, but whose lateral walls are not contiguous, thus forming branching, stolonate, erect, or encrusting colonies. Other species form multiserial, erect, or encrusting colonies wherein all zooecia are contiguous or connected by multiple small tubules. The number and kinds of heterozooids present varies greatly. Some species have no spines, avicularia, or ovicells while others display all of these forms. Also, there are instances of dimorphic zooecia, such as the tiny male zooids in *Hippothoa aruensis* or the "B" zooids in *Steginoporella*. "B" zooids are larger zooids that contain functional polypides and have toothed opercula. They are considered to be forerunners of true avicularia, which lack feeding polypides.

Zooid and colony forms may vary considerably within the genera, making it difficult to outline clearcut separations in the taxa. This reflects probable polyphyletic origin of the cheilostomes as well as the fact that a number of the families are still not well characterized. A polythetic classification (Sneath and Sokol 1973) is essential, using a cluster of characteristics rather than the mutually exclusive characteristics generally found in dichotomous keys. A polythetic classification results from the clustering (by computer analysis) of characteristics of colonies, populations, or taxa that possess a majority of character states common to a majority of the members of a cluster (Boardman et al. 1983). At present, there is too little information in many groups to complete such analyses.

The anascan superfamilies are discussed briefly below, summarizing the general characteristics of the families known to occur in Hawaiian waters.

Superfamily INOVICELLATA

Partially erect, stoloniform species lacking ovicells and avicularia. The family Aeteidae consists of slender, tubular, vertical zooecia whose proximal portions are modified to form a horizontal stolonlike network. They are easily overlooked because of their extremely small size. The lightly calcified tubules have subterminal apertures and an uncalcified frontal area.

Superfamily SCRUPARIINA

The only genus, *Scruparia*, contains zooecia connected in uniserial chains from which erect individuals rise from recumbent zooids by frontal, distal, or lateral budding. The narrow proximal zooecial tubule is expanded distally and bears an oval opesia. While *Scruparia* are considered by some to be the most primitive anascans, they do have ovicells, formed by 2 calcified valves which fuse to form a median keel and are covered by a membranous layer.

Superfamily MALACOSTEGA

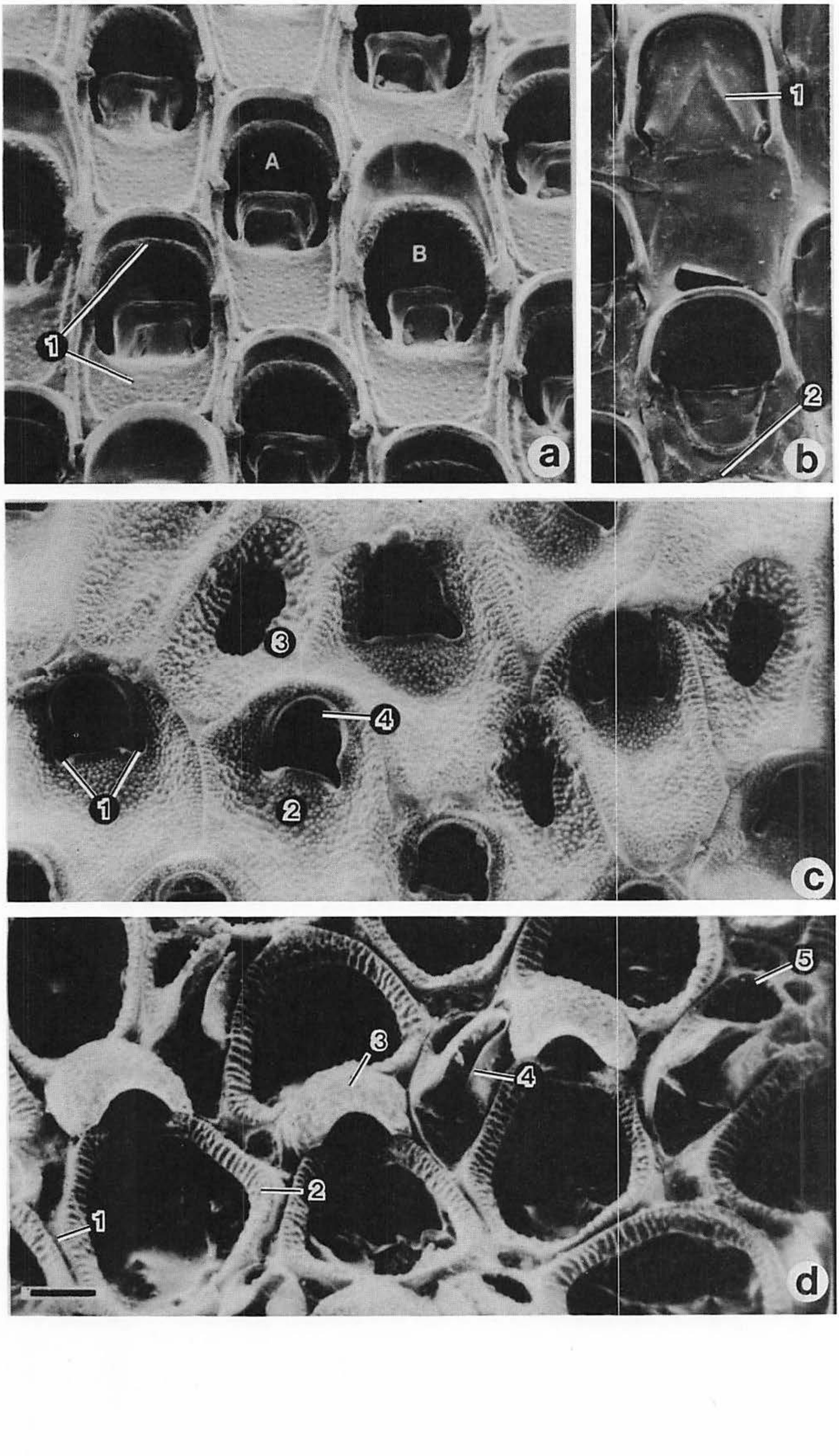
This superfamily includes encrusting species, some lacking ovicells, some with internal ovicells and still others with external ovicells. Members of the encrusting family Membraniporidae lack ovicells and avicularia. The uncalcified frontal membrane covers almost the entire ventral surface (opesia) of the rectangular zooecia and the operculum is little separated from it. The gymnocyst is absent or much restricted. The only species found in Hawaii, *Membranipora tuberculata*, has heavily calcified mounds (tubercles) at the corners of the zooecia that give the colony surface a white, toothed appearance (Fig. 2.IV.6). Not yet reported in Hawaii (so far as the authors are aware of) are the genera *Conopeum* and *Electra*. The former has oval zooecia, sometimes with spines around the opesia and with small distal kenozooecia; *Electra* has a distinct gymnocyst covering the proximal third of the zooecium with spines around the opesia.

The Calloporidae are encrusting species that have both cryptocyst and gymnocyst developed to varying degrees. The frontal membrane is usually exposed to some extent, often with many spines surrounding it. Ovicells are present; avicularia occur on the frontal wall or interzooidally, and sometimes on the ovicell. *Parellisina* (Fig. 2.IV.7d) is included in the Calloporidae by some authors and the Alderinidae by others.

The Hincksinidae differ in having an internal ovicell that is sometimes visible in the distal curve of the aperture. The cryptocyst is heavy, and paired interzooecial avicularia occur at the distal ends of zooecia.

Superfamily COILOSTEGA

The cryptocyst is highly developed underlying the membranous frontal wall layer; there is no gymnocyst. In the Steginoporellidae, the cryptocyst extends above the polypide tube, forming a flap; *Steginoporella* zooecia resemble Puritan buckle shoes with the raised flap over the tube (Figs. 2.IV.7a,b). In the Microporidae genera *Floridinella* and *Velumella* (Fig. 2.IV.7c), the cryptocystal development extends nearly to the apertural area, with lateral notches (opesiules) through which muscles extend to connect the membranous frontal wall to the dorsal wall. In the Thalamoporellidae, the cryptocyst extends dorsally around the polypide tube and opesiules and distally around the aperture so that zooecia resemble a vase with 2 handles on the neck (Figs. 2.IV.8a,b). The Thalamoporellidae are unique among bryozoans in containing minute, free calcareous spicules shaped like compasses with arms widely extended or calipers resembling old-fashioned ice tongs. In the *Micropora* opesiules are reduced to small marginal pores and the frontal wall entirely surrounds the aperture.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Most species have large avicularia, some with functional polypides, replacing autozooids. These range from the large "B" zooids with functional polypides of *Steginoporella* to the large avicularia without polypides, in *Thalamoporella*, and the winged mandible avicularia in *Velumella*. Some species have small interzooecial avicularia such as those in some *Micropora*.

Ovicells may be lacking or are placed internally as in Steginoporellidae. Brooding is in an internal sac distal to the aperture in *Steginoporella*, whereas ovicells are internal but only semi-immersed and visible externally in Microporidae. Ovicells in the *Thalamoporella* are large, hyperstomial (distal to the aperture and raised), and formed of 2 halves that fuse to form a midline suture or keel.

Superfamily PENETRANTIINA

Stolonate species of the genus *Penetrantia* (family Penetrantiidae), that burrow in mollusk shells. Externally, they are seen only as very small holes (apertures) and tracings that indicate the internal stolons (Fig. 2.IV.9c). Zooids are saccate and dimorphic, with large brood chambers formed on smaller zooids (Fig. 2.IV.9d). The method of ovicell formation is unknown. Apertures are necessarily terminal because of their burrowing habitat, as in ctenostomes, but the presence of the ovicell with a separate opening, the zooidal operculum, and the nature of the musculature places them in the cheilostome anascans.

Superfamily CELLULARINA

Most species form lightly calcified, erect, flexible or jointed, branching colonies attached by radicles (rootlets). A few species form loosely encrusting colonies, which may or may not be attached by rootlets. Avicularia are often borne on a pedicel or stalk, some with mandibles extended into whiplike vibracula. The frontal opesia is extensive, membraniporine, sometimes sur-

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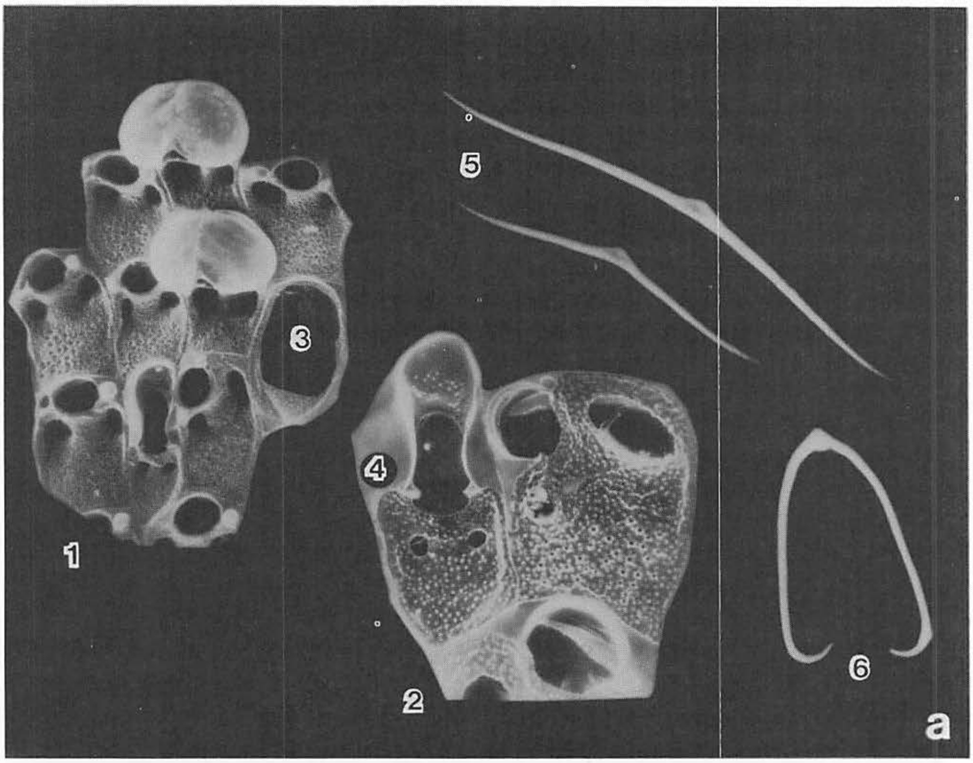
Figure 2.IV.7.—Cheilostomata Anasca.

a. *Steginoporella magnilabris*. Brick-red to orange encrusting species which can rise in foliaceous bilaminar growths. Two types of zooecia: "A" zooecia normal size and large "B" zooecia (white letters) that are thought to represent primitive incipient avicularia. Cryptocyst (1) large, descending around lightly calcified polypide tube. Distribution: Tropical worldwide, encrusting corals, shells (see Plate 2.IV.1a).

b. Ectocyst covers *Steginoporella* zooids and opercula; upper aperture of "B zooecium" (1) shows internal reinforcing sclerite with inverted Y-shape; lower "A zooecium" (autozooid) with toothed operculum open fully (2), lying on frontal showing semicircular toothed sclerite.

c. *Velumella americana*. Colony encrusting, yellowish to tan. Aperture bell-shaped, almost trifoliate where opesiules (lower corners of aperture) (1) permit muscles from the frontal to descend to the dorsal side. Zooecium with cryptocyst (2) extensive, granular. Interzooecial avicularium (3) (called an onychocellarium) has mandible with lateral winged extensions (removed by cleaning specimen for scanning microscopy). Ovicell internal (4). Distribution: West Indies, Galápagos Islands, Gulf of Panama, Hawaii.

d. *Parellisina curvirostris*. Colony encrusting, zooecia separated by grooves (1), mural rim crenulate (2), no cryptocyst or gymnocyst. Ovicells (3) small, prominent with granular surface. Avicularium interzooecial, large with incomplete hinge bar and curved rostrum (4) into which a long triangular mandible fits; a small, more or less triangular kenozooecium (5) lies distal to the avicularium. Distribution: Worldwide in warmer waters. Scale line = 200 μm.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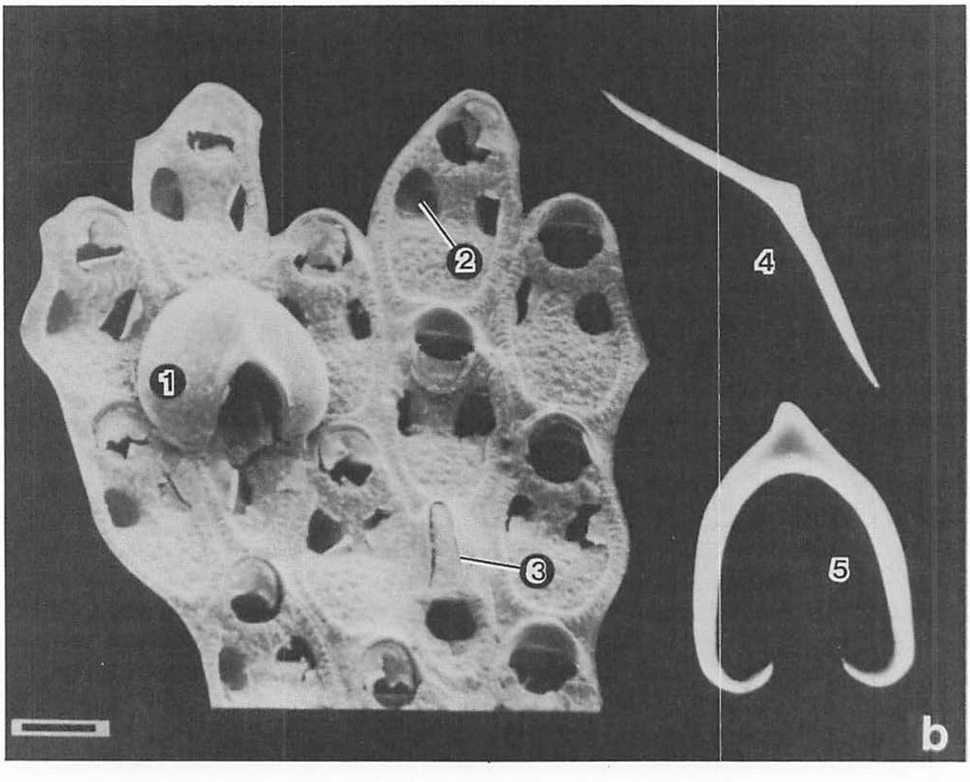
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rounded by spines or with a modified spine forming a shield over the opesia. Ovicells are usually hyperstomial.

The Beaniidae (genus *Beania*) constitute the only encrusting species in Hawaii from this superfamily. They are unusual in having the zooecia connected to each other by short lateral, proximal, and distal tubules. In *Beania discodermiae* the zooecia are connected by tubules to form a reticulate mat (Figs. 2.IV.10a,b). In other species zooecia are linked uniserially by tubules originating from the dorsal wall. Each zooecium is ovoid, wider proximally, with the entire frontal an opesia surrounded by many spines. The encrustations give the appearance of a fragile, tan, bristly mat loosely attached by short radicles. Ovicells are vestigial or absent.

The family Bugulidae contains perhaps the best known species found in fouling communities, including the bushy chitinous purple colonies of *Bugula neritina* and the lightly calcified white tufts of *B. stolonifera* (= *B. californica*) (Figs. 2.IV.11b,c). Most species form erect colonies attached by rootlets. Zooecia are biserially placed, all facing the same direction. The zooecium is elongate with an extensive opesia not separated from the operculum; the dorsal basal wall is forked, with prolongations at each proximal corner. Spines or avicularia are lacking in *B. neritina* but other species bear distal spines and pedicellate "bird's head" avicularia. Ovicells are prominent as shallow globular hoods.

Some authors combine the Beaniidae and Bugulidae in a single family, the Bicellariellidae, but the distinctions between them seem worthy of recognition (Ryland and Hayward 1977).

The Epistomiidae are represented by a single species, *Synnotum aegyptiacum*. The colonies are delicate, erect or prostrate, attached by radicles, and occur mixed with hydroids, bryozoans, and algae in fouling communities. Zooecia are arranged in pairs facing obliquely laterally; internodes are composed of portions of 6 zooecia traversed by joints. Avicularia may be raised, pedicellate (pedunculate), located at the distal ends on the frontal or dorsal side, or not raised (sessile).

The Scrupocellariidae form erect or spreading, calcareous, branched, jointed colonies. Zooecia are distinguished by the presence of an oval opesia over-arched by a modified spine that forms a raised scute or shield of varied pattern above the frontal membrane. (A few species found elsewhere lack the scute.) Zooecia are aligned in 2 or more series, all facing the same direction, while the dorsal sides bear vibraculae, avicularia, or radicles. Two genera are repre-

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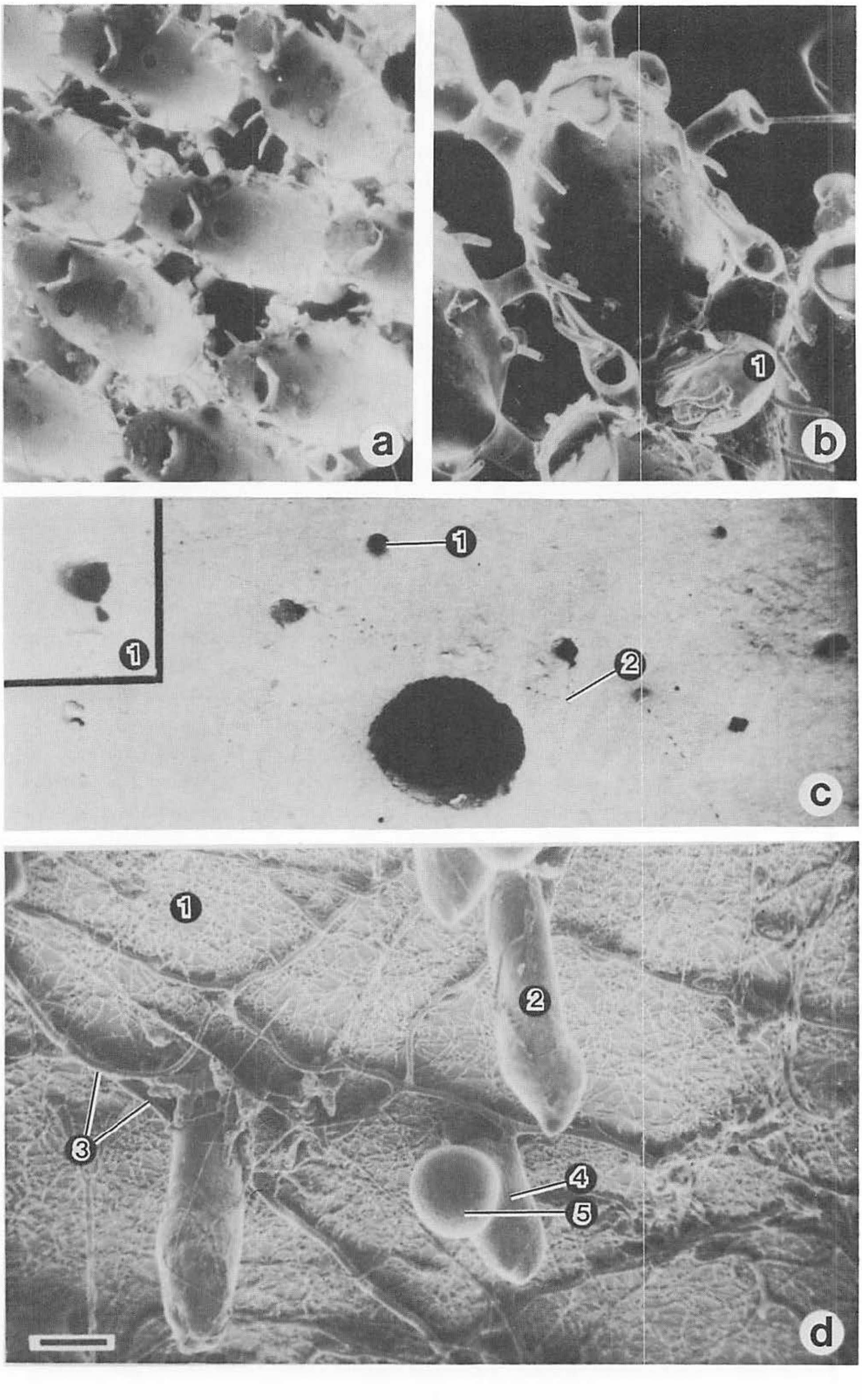
Figure 2.IV.8.—Cheilostomata, Anasca: Thalamoporellidae.

a. *Thalamoporella hawaiiana*. Colony encrusting, translucent white. Zooid types (1) include autozooids (males), gonozooids with large ovicells (females), kenozooids (undeveloped zooid) (3), and avicularia (4). The avicularium (4) in *T. hawaiiana* has 2 prominent pores on frontal; the adjacent autozooid turns toward avicularium aperture (2). Each species in the genus has characteristic calcareous spicules: compasses (5) and calipers (6). Distribution: Tropical Pacific islands. Scale line: a(1), colony = 400 μm; a(2), colony = 200 μm; a(5), compass spicule = 10 μm; a(6), caliper spicule = 10 μm.

b. *Thalamoporella stapifera*. Colony prior to cleaning. Ovicells (1) may be isolated as shown or follow in columns as in Fig. 2.IV.8a. Opesiules proximal to the aperture (2) are of unequal sizes. The avicularium shown here (3) has an intact, closed mandible. The 2 types of spicules differ in size and shape according to species: compasses (4) and calipers (5). Distribution: Hawaii and Melanesia. Scale line: b, colony = 300 μm; b(4), spicule = 5 μm; b(5), spicule = 5 μm.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sented in Hawaiian waters, *Scrupocellaria* (Fig. 2.IV.10a) and *Caberea* (Figs. 2.IV.10d–f). *Scrupocellaria* species are regularly jointed, whereas those of *Caberea* are not. Although small and delicate, species of *Caberea* are easily recognized by the numerous long vibraculae and the radicles, which pass down a groove on the dorsal midline, giving the colony a hairy appearance.

Superfamily CRIBRIMORPHA

The Cribrimorpha consist of species in which a frontal shield is formed by the fusion of riblike spines arched above the frontal membrane and fused medially, usually with pores in the interstices between the ribs (costae). The gymnocyst covers the margins of the frontal outside the ribbed area. The Cribrimorpha are considered to be a transitional group between the Anasca and Ascophora, according to Harmer (1926). The group is assigned to the Anasca by some authors and to the Ascophora by others, since there is a hydrostatic space above the frontal membrane and a coelom within the fused spines. The family Cribrilinidae includes virtually all the living species of this superfamily, but there is an extensive fossil record. *Cribrilaria* cf. *radiata* (Fig. 2.IV.11a) has been assigned to a number of genera including *Puelina*, *Coletosia*, and *Cribrilina*; *C. radiata* has been used for a wide range of variations and distribution records and may include several undescribed forms.

Suborder ASCOPHORA

The distinguishing anatomical feature for which the suborder is named is the presence of the ascus, although it cannot be seen without dissection. This hydrostatic organ for controlling the eversion and withdrawal of the lophophore is indicated externally in only a few genera where a small ascopore opens directly through the frontal wall. In all others, the opening to the ascus lies beneath the proximal border of the aperture, in a sinus or not.

The ascophoran frontal is completely calcified except for the aperture (Fig. 2.IV.12). The chitinous operculum that closes the aperture is usually articulated

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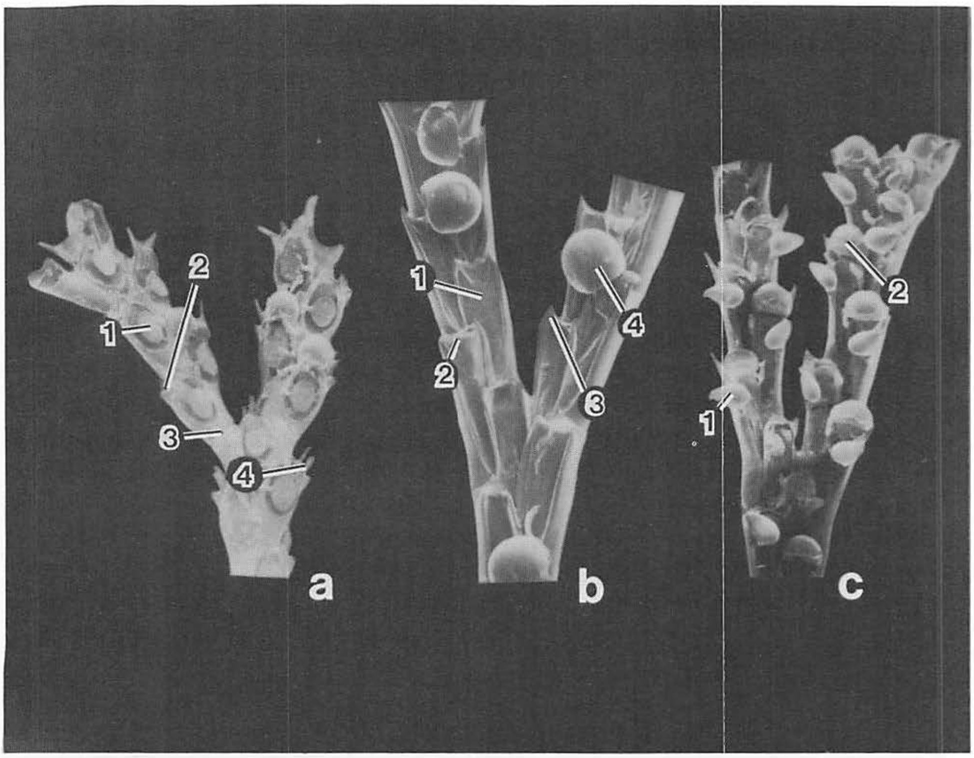
Figure 2.IV.9.—Cheilostomata, Anasca.

a. *Beania discodermiae*. Extremely delicate, encrusting species with zooids connected by short tubules, forming lightly attached reticular mats. "Pores" in basal wall are radicle evaginations; frontal membrane is dissolved by clorox. Scale line = 100 µm.

b. *Beania discodermiae*. Enlarged view showing spines, vestigial ovicell (1) flanked by avicularia. Note growing edge (upper right) where new tubules and zooids are developing. Scale line = 100 µm.

c. *Penetrantia operculata*. Shell surface of *Conus* showing small asymmetrical apertures (1, and inset), as compared with large opening of boring sponge. *Penetrantia* surface tracings (2) are often indistinct and irregular as compared with those of *Terebripora* and *Immergentia* (J. D. Soule and D. F. Soule 1969). Scale line = 100 µm.

d. Epoxy resin cast of *Penetrantia operculata* colony with interior shell matrix dissolved away. The "ceiling" is the shell surface (1), with individual autozooecia (2) lying perpendicular to the surface, connected by a network of stolons (3). Gonozooid with reduced polypide (4) has embryo within globular ovicell chamber (5); gonozooid opens into shell matrix. *Terebripora* and *Immergentia* (Ctenostomata) do not have ovicells, brooding embryos in the body cavity. The ovicell in *Penetrantia*, the presence of an operculum, and differing internal muscle development sequences are 3 of the characteristics that place the penetrantids in the Cheilostomata Anasca. Scale line = 200 µm.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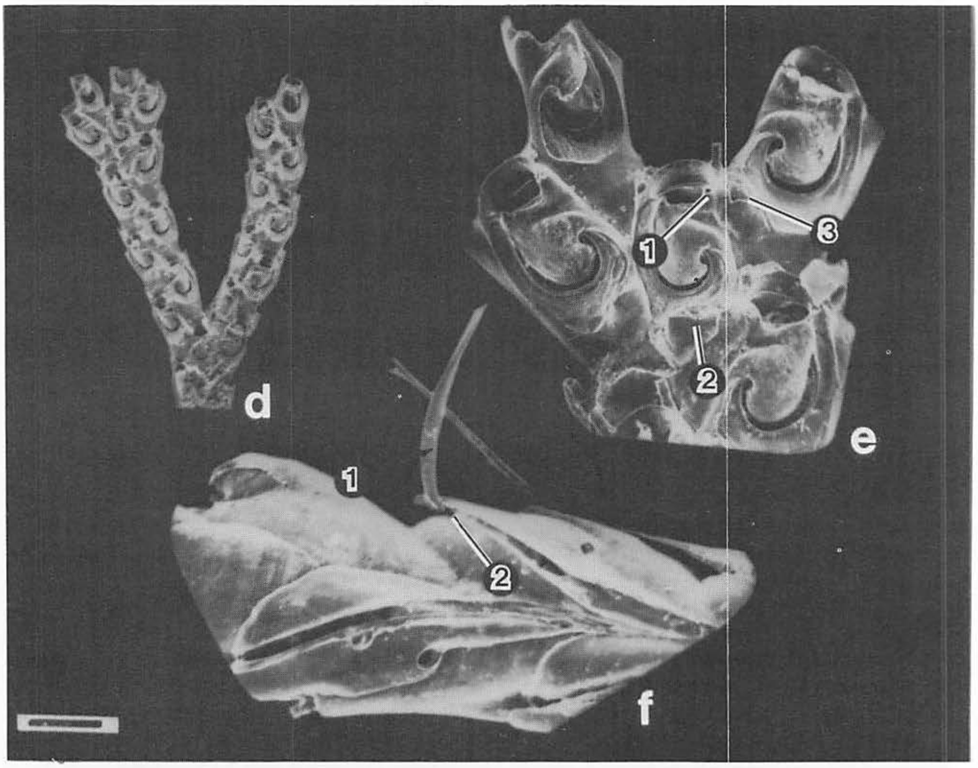
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on the sides so that the larger distal portion swings up to permit extrusion of the tentacles while the proximal portion swings down, opening the ascopore.

During development, calcification of the zooecium begins with folding upward of the basal wall of the budding area, to form lateral body walls. Proximal and distal walls may be formed by similar folding or by growth inward from lateral walls, or a combination of both modes. The calcified frontal may originate as an interior wall, the cryptocyst, below the frontal membrane (see Anasca), or as an exterior wall, the gymnocyst, growing from the exterior proximal wall as a fold (umbonuloid) or other mode. After completion of the primary layer (the olocyst of older authors) calcium continues to be deposited superficially, causing the appearance to be quite different in young colonies as compared with older ones in some species. Porous frontals (tremocyst in older terminology) may become so occluded that it is almost impossible to determine whether the frontal is normally imperforate (pleurocyst in older terminology) or not.

Spines are often present, especially on the distal rim of the aperture. Avicularia may be interzooecial or associated with the frontal, usually arising from marginal areolar pores or pores near the peristome. Ovicells are present in most species, usually hyperstomial, but a few have internal ovicells or brood in the distal body cavity. Spines, avicularia, and ovicells are all interpreted as heterozooids (polymorphs) by some authors.

Figure 2.IV.10.—Cheilostomata, Anasca.

a. *Scrupocellaria sinuosa*. Most species of *Scupocellaria* have a plate or scutum (1) attached at one side by a spinous process and arching over the opesia. Ovicells are globose with scattered minute pores. Small triangular avicularia (2) occur at the outer distal corner of the zooecia. Chitinous joints (3) occur at either side of the zooecium at the bifurcation of branches (joints do not cross an opesia in this species). There are 2 or 3 distal oral spines (4), usually on the exterior zooecia, and 1 or 2 distal oral spines on the interior zooecia of the biserial branch. Distribution: Hawaii. Scale line = 200 μm.

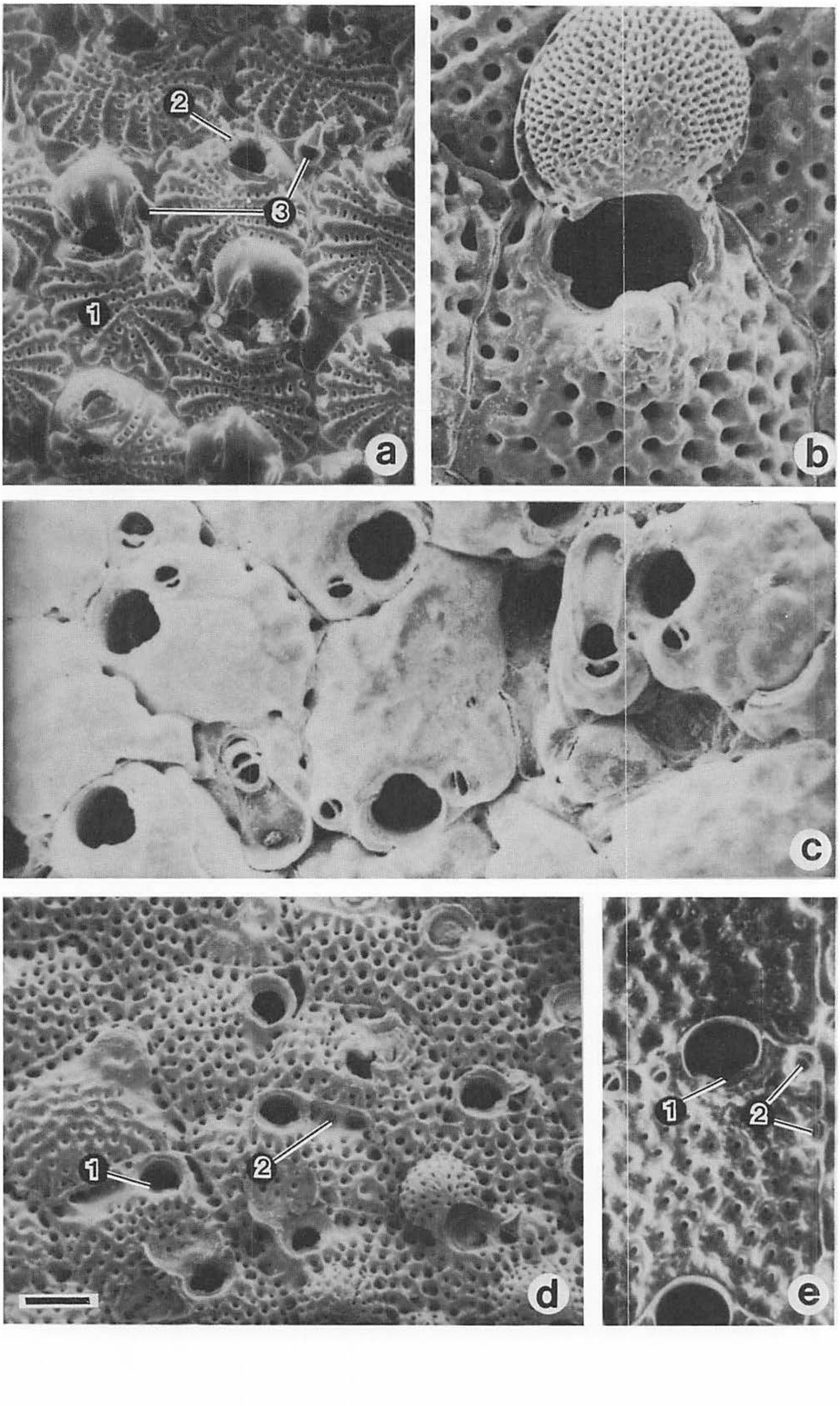
b. *Bugula neritina*. Colony biserially branching, bushy, reddish purple. Note the opesia (1), which occupies most of the frontal, with poorly differentiated operculum (2) at the distal end. Globose ovicells (4) are like shiny pearls set at an angle at the distal end of the zooecium. Spines are lacking, but outer distal corners are pointed (3). *B. neritina* has no avicularia, an exception to all other species of *Bugula*. Distribution: A common, shallow water, fouling organism in temperate and tropical seas worldwide. Scale line = 200 μm.

c. *Bugula stolonifera*. This species has been confused with *B. californica*; both species have prominent "bird's head" avicularia (1) attached to the lateral wall in the distal half of the zooecium. Colonies are bushy, with *B. californica* forming turbinate (screwshaped) colonies, while *B. stolonifera* does not. Ovicells (2) are shallow hoods, flanked on either side by spines. Distribution: Warm temperate Atlantic and Mediterranean; uncertain due to confused synonymies. *B. californica* may be limited to the eastern Pacific, north from central California. Scale line = 200 μm.

d. *Caberea* cf. *boryi*. A small, delicate biserial colony, becoming triserial at bifurcations. The scutum is distinctive (e, enlarged). Distribution: Cosmopolitan, if all records are valid; Indo-Pacific; eastern Pacific from British Columbia to the Gulf of California; Japan, East Indies, Australia, Europe, Patagonia. Scale line = 200 μm.

e. *Caberea* cf. *boryi*. Scutum curves over almost the entire opesia, merging distally to form a complete bar proximal to the aperture. There are 2 suboral spines (1) and 3 or 4 distal oral spines. Avicularia are tiny, mounted on pedestals (2) with a bulbous giant avicularium (3) at bifurcations. Scale line = 50 μm.

f. *Caberea* cf. *boryi*. Obverse (dorsal side) showing vibracula (1) extended from small circular point of setal attachment (2). Vibracular chamber has a deep groove extending diagonally to the midline of the branch where vibraculum lies when not extended. The large number of coarse vibracula give the colony a hairy appearance. Scale line = 40 μm.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The Ascophora are the most successful of the living bryozoan groups, and they exhibit great diversity in colony form and zooecial morphology. Although most ascophorans are encrusting, many of them can, under certain conditions, rise from initially encrusting colonies to form stems and branches, nodules, or elaborate foliaceous growths.

It is possible that the Ascophora are evolved from several lineages, accounting for the difficulty in determining whether families are primitive or specialized. This also makes it especially difficult to arrange the families in any phylogenetic sequence or to develop dichotomous keys to the families. There is considerable difference of opinion among bryozoan specialists as to the validity of a number of families and the genera placed within them. In the following paragraphs, classifications from several of the references cited in the species list (see Appendix) were used, in part; thus no single source of classification has been followed in its entirety. There is extensive overlap in characteristics described for the families, so that clustering of characters by polythetic classification ultimately offers the only feasible answer for reorganizing the families.

No ascophoran superfamilies are generally agreed upon in which to place seemingly related families. For a time it appeared that the mode of frontal calcification might offer the most consistent patterns, but use of a single characteristic has presented considerable difficulty and, of course, many species existing have not yet been studied sufficiently. Several authors have proposed various classification systems but no single system is generally accepted. The following summary is based on characters that will enable taxonomists unfamiliar with bryozoan groups to find identifications in the literature. It does not imply that any systematic arrangement will follow this outline.

Figure 2.IV.11.—Cheilostomata Anasca, Cribrilinidae; Cheilostomata, Ascophora.

a. *Cribrilaria* cf. *radiata*. Encrusting species with large frontal shield of fused costae (ribs, 1) and intercostal pores; aperture semicircular with oral spines or spine scars (2). Ovicells imperforate, closed by zooecial operculum. Long and short interzooecial acute avicularia (3) directed distally, sometimes flanking ovicell hood. Distribution: Cosmopolitan species, apparently with a wide range of variation if all reports are valid. Scale line = 100 μm.

b. *Mucropetraliella magnifica*. With a suboral mucro (umbo). Avicularia (not shown) scarce, usually paired beside the aperture, directed distally. Ovicells large, finely perforated. Distribution: Tropical to subtropical Pacific. Scale line = 50 μm.

c. *Schismopora* cf. *spathulata* (? = *S. redoutei*). Zooecial frontal convex, imperforate; marginal pores few, scattered; aperture sinusoid. Small avicularia adjacent to aperture. Scattered large spatulate avicularia. Distribution: Widely distributed in warm waters. Scale line = 150 μm.

d. *Schizoporella errata*. Often confused with *S. unicornis*, the orange-brown colonies are prominent fouling organisms. Heavily calcified with porous frontal, distal apertural rim semicircular with wide proximal sinus (1). Avicularia single, on right or left side of aperture sinus, directed distolaterally. (*S. unicornis* usually has paired avicularia.) Avicularia originate from 3 to 4 areolar pores (2). Ovicells porous, tending to appear costate. Distribution: Warm temperate-subtropical fouling organism prominent in harbors. Scale line = 200 μm.

e. *Schizoporella decorata*. Young colony; the species is capable of forming thick, multilaminar, erect branching colonies. Zooecia delicate, perforated by large pores; apertures small with a wide proximal sinus (1) and thin distal rim. Numerous tiny oval avicularia (2) occur along the zooecial margins. Ovicells large, globular, perforate, lying on the next distal zooecium. Occasional larger avicularia on the proximal end of the zooecium (not shown). Scale line = 100 μm.

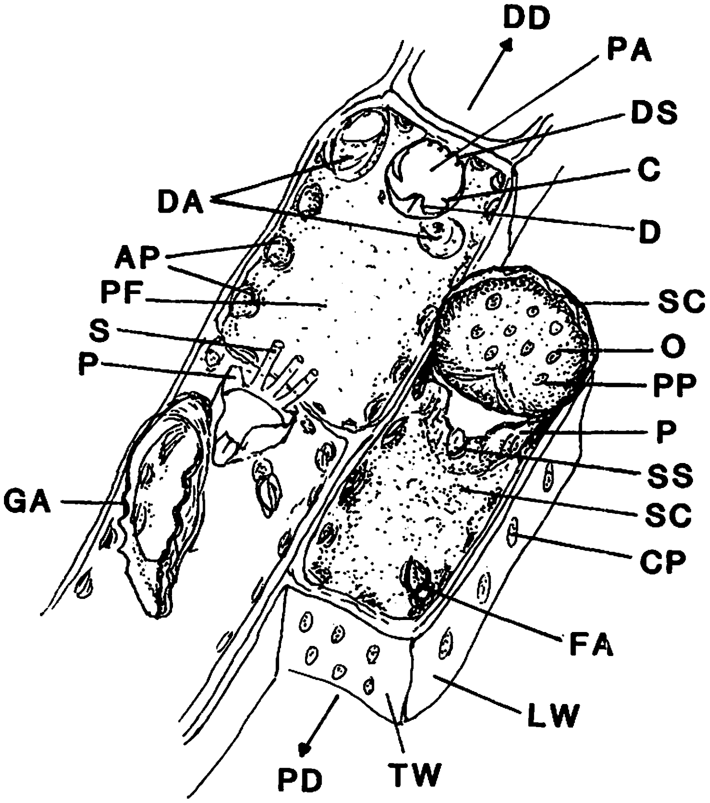


Figure 2.IV.12.—*Parasmittina*, illustrating cheilostome ascophoran morphology. (DD, distal direction; PA, primary aperture of developing autozooid; DS, spine developing from folds in distal transverse wall; C, cardelle (condyle) articular hinge tooth for operculum; D, median denticle; SC, superficial calcified layer encroaching on ovicell; O, ovicell; PP, pseudopore; P, peristomal lappet; SS, suboral sinus; SC, superficial calcification on older frontal (ventral) wall; CP, communication pore; FA, frontal avicularium; LW, lateral wall; TW, transverse wall; PD, proximal direction; GA, giant avicularium; P, peristome; S, spine; PF, primary calcified layer of frontal wall; AP, areolar pores; DA, developing avicularia.)

ASCOPHORAN FAMILIES WITHOUT EXTERNAL OVICELLS

Adeonellidae: Colonies encrusting, sometimes forming nodules or branches. Frontal wall imperforate except for marginal areolar pores and an ascopore. Apertures are subterminal, without a sinus. An avicularium is median, suboral in *Adeona*; paired lateral-oral avicularia occur in *Adeonella*.

Vittaticellidae: Delicate, erect, branching, jointed colonies sometimes with radicles for attachment. Zooecia separate, all facing the same way, 2 or 3 to an internode. Two rows of pores (vitta) in longitudinal grooves extend down lateral frontal. A tiny avicularium at each distal corner gives the appearance of "ears."

Savignyellidae: Uniserial, with delicate erect, branching, jointed colonies; zooecia brick red in the Hawaiian species *Savignyella lafontii*, with perforate frontals. The aperture is surrounded by spines; a median suboral avicularium is present on an umbo (Fig. 2.IV.14d).

Margarettidae: Colonies erect, branching, jointed, segments consisting of 2–6 zooecia placed back-to-back facing outward around the stem, in alternating positions (whorls). Frontals are porous, with a median ascopore; rounded tubular peristomes extend out from the stem. Fertile zooecia are larger proximally and the ovicells are within the peristome. There are no avicularia in species of *Margaretta*. The genus name *Tubucellaria* was used in earlier literature for many of the species now included in *Margaretta*.

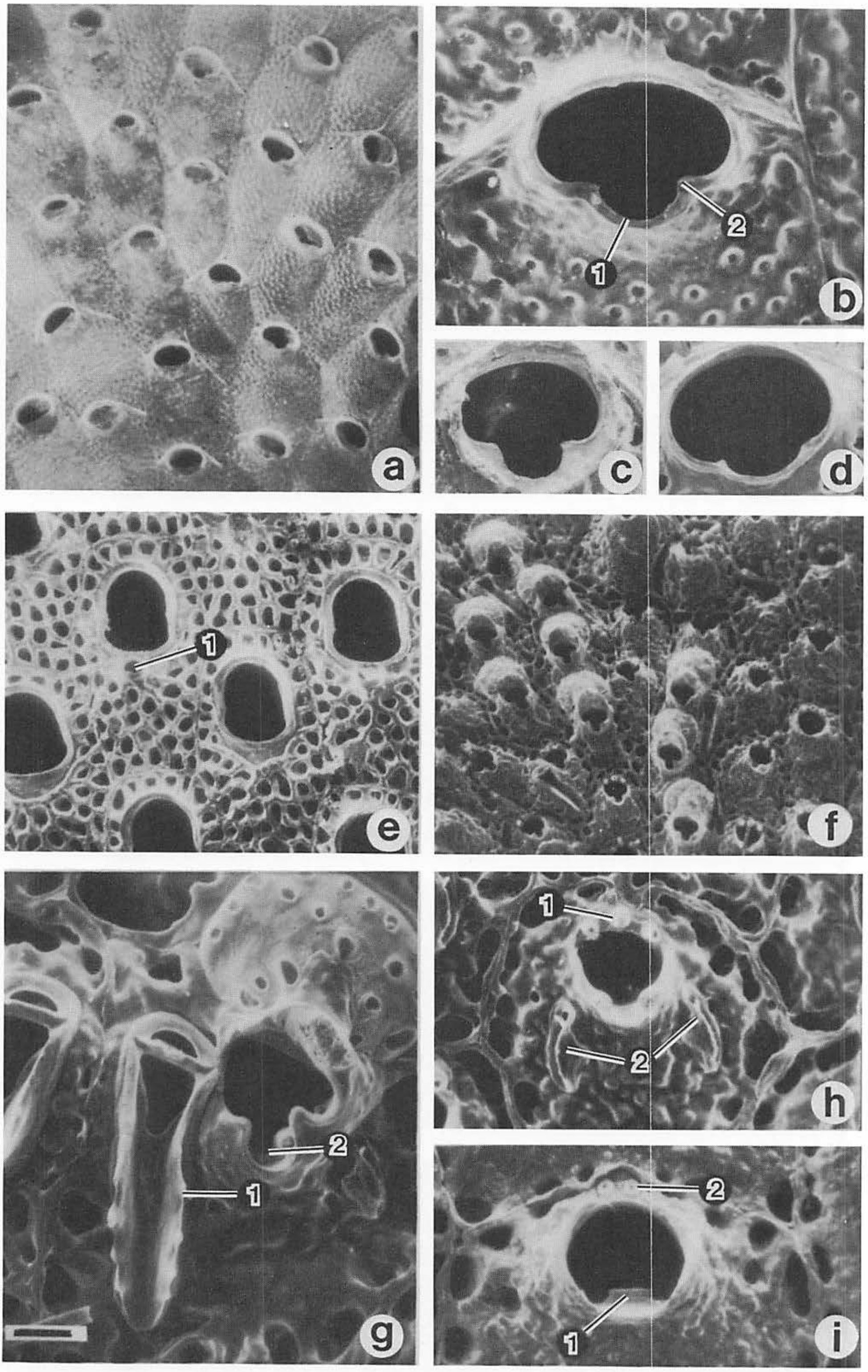
Pasytheidae: Colony jointed, erect, regularly pinnate, rising from an encrusting base. Zooecia elongate, narrow, back-to-back, with apertures torqued to face in opposite directions. Frontals with longitudinal row of pores on each side of frontal and some additional frontal pores. Ovicells and avicularia unknown; *Pasythea eburnea* is a deep-water species (to ± 3300 m); dredged off Honolulu by the *Challenger*.

Watersiporidae: The species now included in the genus *Watersipora* have been placed in various families (e.g., Cheiloporinidae, Osburn 1953; Schizoporellidae, Harmer 1957) and in various genera (*Lepralia*, Busk 1854; *Dakaria*, Harmer 1957). Colonies are encrusting, radiate in development, sometimes raised in foliaceous cabbagelike balls 3–4 inches in diameter. A black or dark brown to tan epitheca covers the colonies, with orange at the growing edge during reproduction. Zooecia are subrectangular, uniformly perforate, cryptocystidean, with or without a proximal sinus (Figs. 2.IV.13a–d). There are no spines or avicularia and the brood sac is internal distally. It is unfortunate that Harmer (1957) revived the use of *W. subovoidea*, originally an Audouin (1826) species, because there is no type and it cannot be distinguished from other species based on the illustration (Savigny 1817?).

Cheiloporinidae: Colonies are encrusting, sometimes raised, with zooecia back-to-back. Zooecia flat with numerous frontal pores covered by yellowish epitheca. Apertures without spines, large, widened proximally with a proximal lip. Fertile zooecia have a wider aperture proximally, with notches at the corners. The egg is brooded in the distal body cavity as in Watersiporidae, but a semicircular beaded band may show distally. A lateral oral avicularium extends distally, curved around the aperture in the Hawaiian species. Species of *Cheiloporina* were formerly included within the family Hippopodinidae but were removed because they lack the hyperstomial ovicell of other Hippopodinidae.

Exochonellidae: Colony encrusting; zooecia convex with long tubular peristomes. Frontal development is umbonuloid, with irregular processes originating from lateral and proximal margins and forming a shield with numerous foramina. These are not closed with tissue as in most perforate frontals but open directly into the space (epistege) above a primitive frontal membrane (the species have been classified in the Malacostega Anasca by earlier authors).

Cryptosulidae: Colony forming white, to pink-orange incrustations. Zooecia large, distinct, with bell-shaped apertures. Frontals evenly perforate, pores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become sunken with age and superficial calcification. A small suboral umbo sometimes present, sometimes with a tiny oval avicularium on the distal side of the umbo. No spines present (*Cryptosula pallasiana*, Fig. 2.IV.13e).

Tetraplariidae: Colonies attached with encrusting base or rootlets, rising in erect articulated dichotomous branches, arranged with 4 rows of alternating zooecia placed back-to-back, 3–5 per internode. Zooecia distinct, separated by grooves, frontals perforate. Tiny frontal avicularia sometimes present. Fertile zooecia larger, with larger aperture, ovicell internal (endozooecial). *Pollaploecium* was considered a synonym of *Tetraplaria* by Harmer (1957) who created the family Tetraplariidae. Bassler (1953) indicated that *Tetraplaria* differs from *Pollaploecium*, the latter having 6–8 zooecia per internode; he placed the genera in the family Cheiloporinidae. The type of *Tetraplaria*, a fossil, may have been imperforate, although later authors described it as being finely perforate.

ASCOPHORAN FAMILIES WITH EXTERNAL OVICELLS

Gigantoporidae: Encrusting colonies; distinctive zooecia with a tubular peristome and an unusual large tubular spiramen (pore) proximal to the aperture. The

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Figure 2.IV.13.—Cheilostomata, Ascophora.

a. *Watersipora edmondsoni.* Colony with orange-brown ectocyst covering porous frontal; zooecia radiating from ancestrula at colony center (not shown). Apertures abutt the transverse wall distally and are sinusoid proximally. The apertural collar (rim) may be raised in a proximal spout or into lateral-oral or distal projections. Distribution: Oahu and Kauai, Hawaii; probably in other harbors and nearby reefs. Scale line = 400 μm.

b. *Watersipora edmondsoni.* Aperture with medium width sinus (1); cardelles (2) on which the operculum articulates flank the sinus. Apertural collar thickened, somewhat raised. Scale line = 75 μm.

c. *Watersipora edmondsoni.* With narrower sinus, heavier cardelles on wide ledge; thickened frontal with papillate small pores encroaching on apertural rim to form projections. Collected from coral. Scale line = 75 μm.

d. *Watersipora "subovoidea."* Thin apertural rim with wide sinus, very small cardelles, frontal pores large, aperture not usually raised. ? = *W. aterrima* from Japan, Ceylon; ? = *W. subtorquata* from West Indies. Distribution: Pearl Harbor and Ala Wai Marina, Oahu, Hawaii. Scale line = 75 μm.

e. *Cryptosula pallasiana.* Colony with large bell-shaped apertures having heavy rims, separate from distal wall. Frontal with large pores; sometimes with tiny suboral avicularium on small umbo (1). No spines and no external ovicell (the larva develops distal to the aperture inside the zooecial chamber). Distribution: Temperate and tropical Atlantic and Pacific. Scale line = 200 μm.

f. *Parasmittina serrula.* Encrusting yellowish colony, with granular imperforate frontals; areolar pores along margins. Raised tubular peristome with sinus groove, 3-6 spines; small, paired lateral oral avicularia directed distolaterally with one occasionally replaced by giant avicularium having a serrate rostrum. Ovicells raised, perforated. Distribution: Hawaiian Islands (not *P. crosslandi* of eastern Pacific, which lacks the large serrations on the avicularium rostrum). Scale line = 300 μm.

g. *Parasmittina serrula.* Giant lateral oral avicularium with serrate rostrum (1), strong hinge bar. Aperture with raised peristome and sinus groove (2). Ovicell with fewer pores than *P. crosslandi.* Scale line = 100 μm.

h. *Parasmittina serrula.* Aperture with 3 distal oral spines (1). Small, narrow, paired lateral oral avicularia directed distolaterally (2) with serrate rostra. Scale line = 100 μm.

i. *Parasmittina delicatula.* Developing zooid with only smooth primary calcified layer before granular secondary surface layer is formed. Circular aperture with medium-wide denticle (lyrula) (1) proximally, and 2 spine bases (2) distally. Lateral oral peristomal lappets beginning to be raised. Distribution: Hawaiian Islands. Scale line = 100 μm.

bridge between the two is said to originate from the rostra of paired lateral oral avicularia. The frontal may be decorated with minute tubercles having divided, spreading tips. The ovicell is raised, globular, with pores and tubercles on the hood; it opens into the peristome.

Smittinidae: This is probably the most successful group of the Hawaiian bryozoan fauna and may represent the strongest evidence for endemism (D. F. and J. D. Soule 1973), perhaps the marine equivalent of Darwin's finches. Colonies of *Parasmittina* form extensive yellowish crusts, or thickened tubules, stems, or nodules, competing well for available substrates. Frontal budding apparently produces multiple layers rapidly to form the thickened colonies.

The common suite of smittinid characters includes the presence of a median denticle (lyrula) in the center of the proximal aperture flanked laterally by articular cardelles (condyles), the hinges of the operculum. Avicularia are present; oral spines occur in most species at least during development; and ovicells are hyperstomial.

It is possible that this large family should be taxonomically divided but further research is needed. Some genera (e.g., *Codonellina*) that lack the denticle but have similar frontals and avicularia have been placed in the family, while others have denticles but avicularia are not similar or are entirely lacking. The genera found in Hawaii are summarized as follows:

Frontal perforate

Smittina: Median denticle; median suboral avicularium a part of aperture, no other avicularia; ovicell perforate (specimens not common in Hawaii).

Codonellina: No denticle; small avicularium sometimes appearing to be median suboral or asymmetrically suboral, sometimes replaced by huge spatulate avicularium; ovicell perforate.

Frontal imperforate with marginal areolar pores

Parasmittina: Median denticle; paired lateral oral avicularia never median, other small frontal avicularia present; giant avicularia of interzooecial origin may lie on zooecial frontals; ovicells perforate (Figs. 2.IV.13f–i). One unique species, *P. marsupialis*, has abandoned the hyperstomial ovicell position, indicated by a distal crescentic space, and a fertile zooecium with ovicell is budded vertically in the middle of the frontal wall.

Smittoidea: Median denticle; median suboral avicularium originating from bilateral pores in proximal peristome; no other avicularia; ovicells perforate.

Hemismittoidea: Wide anvil-shaped median denticle; suboral avicularium originating from a median peristomal pore and a lateral areolar pore, no other avicularia; ovicells perforate.

Pleurocodonellina: No median denticle; small frontal avicularium originating from median peristomal pore and areolar pore; sometimes replaced by giant spoon-shaped avicularium with rostrum covering most of zooecia frontal; ovicell a small hood, perforate.

Rhamphostomella: Frontal imperforate with costules; aperture asymmetrical, with or without denticle, with asymmetrical suboral avicularium on large rostrum; ovicell with few small pores. Harmer (1957) synonymized *Schizoporella flexilis* Canu and Bassler, 1927, with *Rhamphostomella argentea*. The many citations of *R. argentea* probably belong, at least in part, to *Robertsonidra* Osburn, 1952, a lightly calcified group attached to the substrate by rootlets and tentatively placed in the Chorizoporidae herein (Figs. 2.IV.14a,b).

Hippothoidae: Encrusting colonies; zooecia terete (sweet potato-shaped), arranged uniserially or contiguously. Frontal non-porous, translucent, lightly calcified, a gymnocyst showing transverse striations due to successive calcification from the proximal to the distal end, imperforate; apertures pyriform or with a sinus. There are 3 kinds of zooecia: autozooecia, larger female zooecia with perforate or imperforate ovicells, and tiny club-shaped males (Fig. 2.IV.14c).

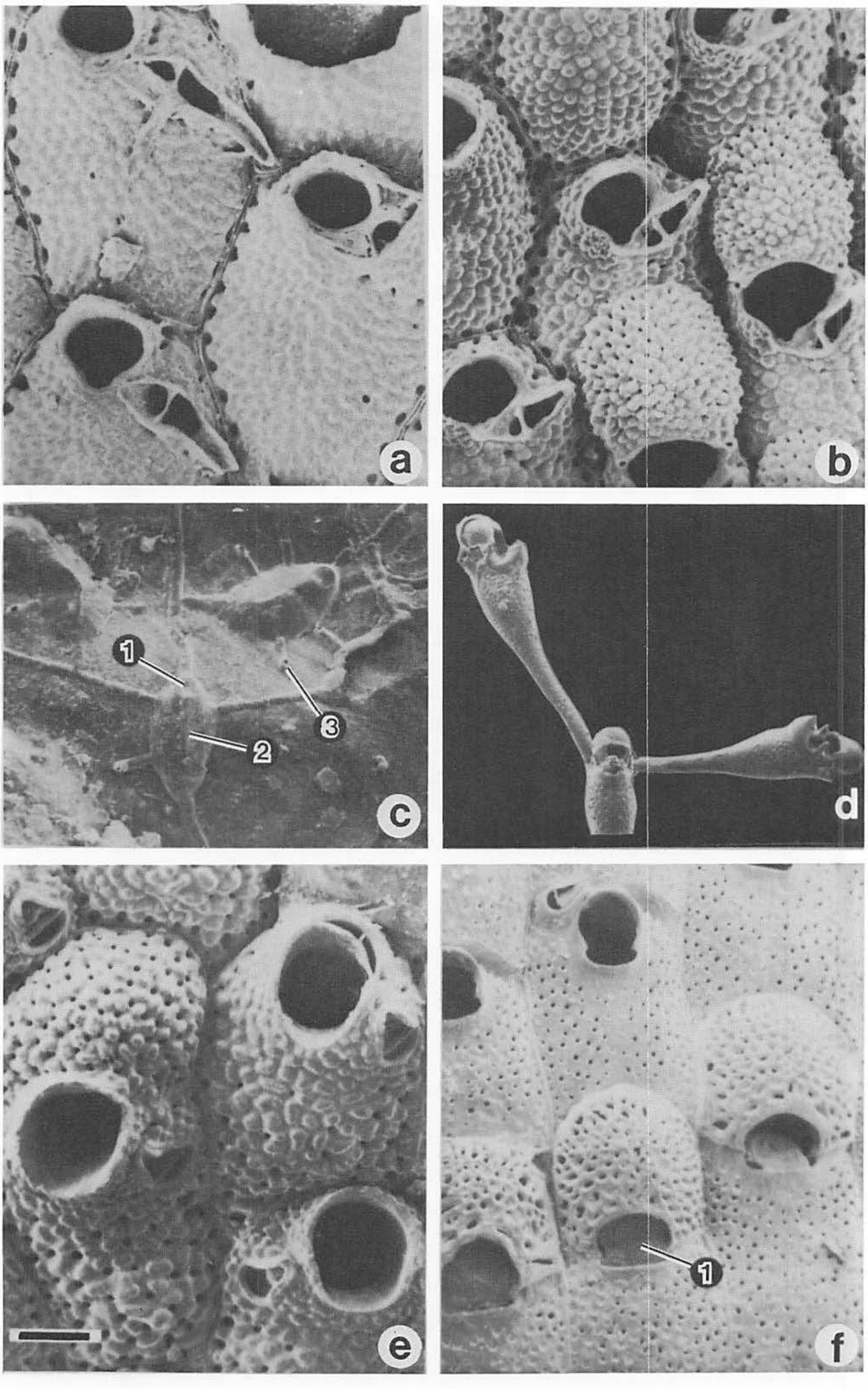
Chorizoporidae: Colonies encrusting; zooecia lightly calcified, gymnocystideal, imperforate; contiguous zooecia linked by multiple horizontal tubules. Interzooecial avicularia present distal to the zooecia in *Chorizopora*; asymmetrically suboral avicularia if *Robertsonidra* is to be included. Ovicells prominent, imperforate, granular.

Cleidochasmatidae: Encrusting colonies, white and glistening; frontals imperforate except for a few areolae and scattered pores; becoming thick, granular. Apertures keyhole-shaped (cleithridiate) with cardelles placed where the wide distal portion narrows. Small frontal avicularia present or absent; sometimes a small frontal umbo. Ovicells imperforate with a low distal rim.

Crepidacanthidae: Colonies encrusting, white, small, usually on shells. Zooecia separated by deep grooves; frontals smooth with small areolar pores. Aperture rounded distally, narrowing at cardelles and widened proximally with a straight border and overhanging lip (*Crepidacantha*) or a sinus (*Escharina*). Paired, lateral suboral avicularia with long, setigerous mandibles extend proximally the length of the frontal (*Crepidacantha*), or with duck-footed avicularia directed distally (*Escharina*, Hawaiian species). At the zooecial margin distal to the peristome rim are 6–10 slender spines. Ovicell imperforate, with a distal rim.

Hippopodinidae: Colony encrusting, frequently on oyster shells, unilaminar, covered with tan ectocyst. Zooecia rectangular, frontals with numerous small pores; apertures large, horseshoe-shaped, arcuate distally with distinct cardelles proximally and a wide straight or arcuate proximal margin. Paired (sometimes single) distolateral avicularia with long, acute mandibles, curving distally beyond the aperture to meet medially. Ovicells with large pores; fertile zooecia lack the distally curving avicularia (Figs. 2.IV.14e,f).

Celleporidae (Holoporellidae, Celleporariidae): Colony encrusting, often massive, raised in irregular accretions. Young colonies are quite regular, with imperforate frontals and small areolar pores; some species having apertures with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sinus, others without; some with 2–3 median denticles proximally; some with spines distally. Denticles, spines difficult to see in older colonies, submerged. Large or small median suboral rostrum with large or small avicularium on the oral side or laterally on rostrum; rostra may grow into tall, white conical spikes. Numerous frontal avicularia and giant interzooecial avicularia often present. Frontal budding with randomly oriented zooecia gives the colony a jumbled crustose appearance. Ovicells imperforate or with few pores, globose hoods, becoming immersed (Figs. 12.IV.12c, 15a–d).

There is no concensus on the taxonomy of this group. The identity of the type species of *Cellepora* is questioned by various authors; the family was divided by Levinsen (1909) into Celleporidae for species with a sinus and Holoporellidae for those without a sinus. Harmer (1957) placed the sinusoid forms in a new family Celleporinidae. Osburn (1952) and Hayward and Ryland (1979) retained Celleporidae. Osburn used *Holoporella* and *Trematooecia* for non-sinusoid forms, with non-porous and porous ovicells respectively. Harmer used *Celleporaria* for non-sinuate forms, in spite of the questions concerning the type species. In searching the literature, many of the tropical species are discussed and figured in Harmer (1957). The present authors regard *Holoporella* as preferable to *Celleporaria*.

Microporellidae: Small encrusting colonies; frontals with small scattered pores and a central crescentic ascopore, the latter with minute denticles projecting from the rim into opening. Apertures rounded distally, straight proximally, with oral spines distally. Avicularia absent (*Fenestrulina*) or present (*Microporella*). Ovicells prominent, perforate or imperforate, sometimes with rib indicating limit of superficial calcification.

Petralliellidae: Colonies encrusting, or raised and attached by dorsal rootlets. Zooecia very large, separated by deep grooves; frontal pores large, giving reticulate appearance beneath heavy brown ectocyst. Aperture large, variable,

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Figure 2.IV.14.—Cheilostomata, Ascophora.

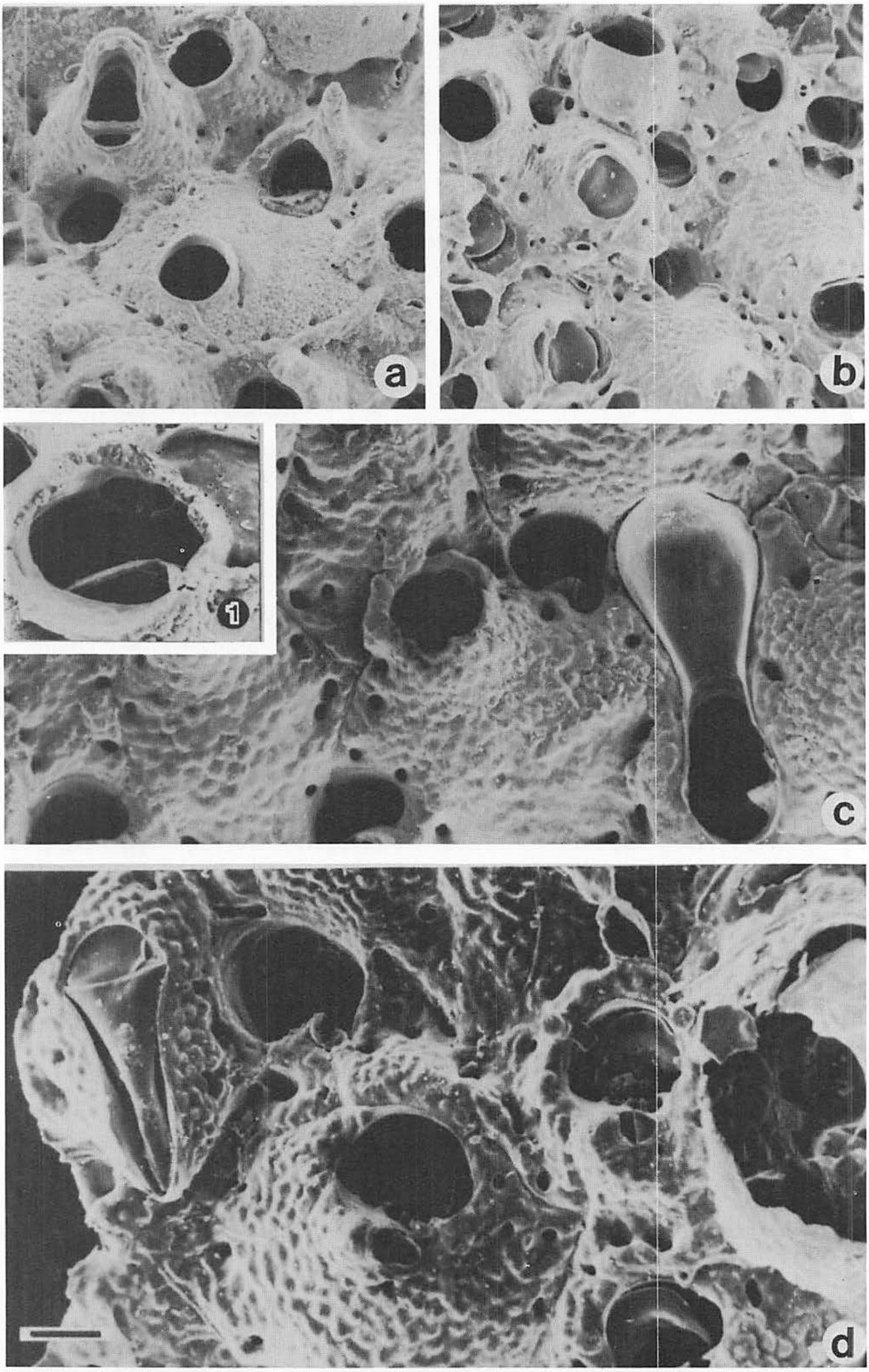
a–b. *Rhamphostomella argentea*. Note the foramina (pores) between adjacent zooecia. Avicularium on one side of aperture, usually directed distolaterally. Distribution: Warm waters off Ceylon, Tahiti, Lord Howe Island, Papua New Guinea, Red Sea, Hawaii. Scale line = 150 μm.

c. *Hippothoa aruensis* (cf. *distans*). Primitive stolonlike proximal extensions of zooecia connect colony; aperture (1) with sinus visible on autozooid (2). Female zooid larger (upper left), ovicell with disc on top. Males are tiny, starlike extensions from autozooecia (3). Distribution: Tropical eastern and mid-Pacific; *H. distans* apparently is an Indo-Pacific species. Scale line = 50 μm.

d. *Savignyella lafontii*. Bright red, delicate erect uniserial colony, frequently interwoven in fouling ctenostome colonies. Branching from distal dorsal side of vase-shaped zooecia. Tiny avicularium on prominence below aperture; frontal perforate except on tapered proximal portion of zooecium. Ovicells small. Distribution: Worldwide in warmer waters. Scale line = 150 μm.

e. *Cosciniopsis fusca*. Zooecial frontal rough, tubercular, with scattered small pores. Distally directed avicularia adjacent to the aperture. Ovicells conspicuous, perforate. Distribution: Red Sea, Fiji, Tahiti, Hawaii. Scale line = 150 μm.

f. *Hippopodina feegeensis*. Encrusting colony with large zooecia, horseshoe-shaped apertures. Ovicells imbedded, flattened, closed by zooidal operculum (1). Both frontal and ovicells with numerous pores. Distal to the aperture are single (or paired), long triangular avicularia (top center zooecium); mandibles or paired avicularia may touch distally behind aperture. Scale line = 150 μm.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some with distal spines, some proximal, with a median dental ledge with lateral projections. Sometimes a suboral avicularium on a mucro (suboral frontal projection) or paired lateral oral avicularia; some larger avicularia with toothed mandibles, many tiny oval marginal avicularia. Ovicell large with fine pores (*Mucropetraliella magnifica*, Fig. 2.IV.12b).

Phylactellidae: Colonies small, encrusting; zooecia flask-shaped, translucent, with raised peristomes composed of fused spines that give the growing tips a fluted appearance; frontals with large pores; no avicularia. Ovicell caplike, suspended from a gap in the distal peristome. Use of the genus *Lagenipora* has been confused in the literature; many species belong to *Lagenicella*, as clarified by Cheetham and Sandburg (1964).

Schizoporellidae: A large and diverse family, or an aggregation of genera all having a proximal sinus in the aperture. Colonies may be thin, flat, subcircular, or raised in frills, formed into tubular colonies or into thick, branching stems. Genera should perhaps be restricted to those with perforate frontals. Hawaiian genera include the following:

Arthropoma: Aperture with a slitlike proximal sinus filled by operculum appendage; ovicell imperforate.

Schizomavella: With a wide shallow sinus, a median frontal avicularium; ovicell very finely perforate.

Emballotheca: With a very wide, rounded proximal aperture; may not belong to the Schizoporellidae (*incertae sedis* of Harmer 1957). The deeply perforate frontal and ovicell with large pores resemble *Schizoporella*, but in some species the proximal lip may be toothed, and ovicells bear prominent sutural lines indicating that superficial calcified layers are derived from adjacent zooecia.

Metroperiella: With a pyriform aperture having a wide arcuate sinus extending to the cardelles, almost median suboral avicularium sometimes present; like *Schizomavella* except that ovicells surround the zooecial aperture.

Schizoporella: With V-shaped or U-shaped sinus, avicularia lateral-oral, not median, if present. Ovicells finely perforate, pores sometimes occluded by ridges in older colonies (Figs. 2.IV.12d,e).

Figure 2.IV.15.—Cheilostomata, Ascophora: Celleporidae.

a. *Holoporella aperta*. Zoaria often form thick tan crusts. Interzooecial avicularia large, variable in size. Distribution: Common, widely distributed in tropical and subtropical waters of the Pacific. Scale line = 150 μm

b. *Holoporella pilaefera*. Frontal pores conspicuous, aperture partially hidden by rostrum. Ovicell (top center) an open, imperforate hood. Distribution: Tropical-subtropical Pacific, Indian Ocean, Red Sea. Scale line = 150 μm.

c. *Holoporella serratorostris*. Giant avicularium with an expanded spatulate mandible. Inset (1), oriented with proximal lip at top to show delicate denticle (lyrula) separating a pair of thin cardelles. Distribution: Bass Straits, Australia, Philippine Islands, Hawaii. Scale line = 150 μm.

d. *Holoporella aperta*. Proximal apertural rostrum with small suboral avicularium. Interzooecial avicularia large, some showing marginal teeth. Distribution: Tropical and subtropical Pacific, Indian Ocean. Scale line = 100 μm.

Myriozoidae: Colonies with encrusting base, becoming erect, branching, not jointed, irregularly cylindrical, thick. Apertures longer than wide with a narrow U-shaped sinus. The frontal perforate, becoming occluded with age; apertures become sunken, zooecia indistinct. Avicularia variously placed. Ovicells hyperstomial, perforate, but imbedded in distal zooecium, becoming covered by superficial calcification.

Sertellidae (= Reteporidae): Members of the Reteporidae are easily the most attractive and eye-catching of the Hawaiian bryozoans. The family name Reteporidae has been most commonly used in the literature. However, the genus *Retepora* is no longer considered valid, requiring another family name, Sertellidae, to be used from the genus *Sertella*, which has not been reported from Hawaii. The literature will mostly be found under the older, more familiar name. The reteporids include several genera and a number of species that form large (10–15 cm), heavily calcified, erect, bilaminar, branching or reticulate, foliaceous colonies. The branches may anastomose little or form long slitlike, rhomboidal fenestrae, or may be so interconnected and reticulate that the colony resembles a crocheted doily or the "Chex" breakfast cereals (Figs. 2.IV.16a,c,e; Plates 2.IV.1b–e). The terms fenestrate and reticulate have been used interchangeably by various authors. In the present manuscript, fenestrate has been used for forms

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Figure 2.IV.16.—Cheliostomata, Ascophora, Sertellidae (Reteporidae).

a. *Triphyllozoon contortuplicata.* Fenestrate, erect, foliaceous white colony with all apertures on one side. Ovicells (1) with trifoliate suture (stigma) area on hood where the outer layer (ectooecium) remains uncalcified. Proximal oral lip, which originates as slit, closes to form suboral pore (2); occasional paired pores (retepores) occur in the lateral frontal walls. The aperture is flanked by a pair of spines. Longer spines occur at the distal corners of zooecia and flank the ovicell giving the colony a "hairy" appearance. Small, round or pointed avicularia occur along the margins, with a few larger acute avicularia. Suture lines (vibices) occur on both the smooth frontal (ventral) surface and on the granular obverse (dorsal) side. The connecting bars between branches (3) (trabeculae) are formed of zooecia and kenozooecia. Distribution: Hawaiian Islands. Scale line = 200 μm.

b. *Triphyllozoon contortuplicata.* Enlarged ovicell shown in Fig. 2.IV.16a, showing trifoliate stigma unclosed. Scale line = 50 μm.

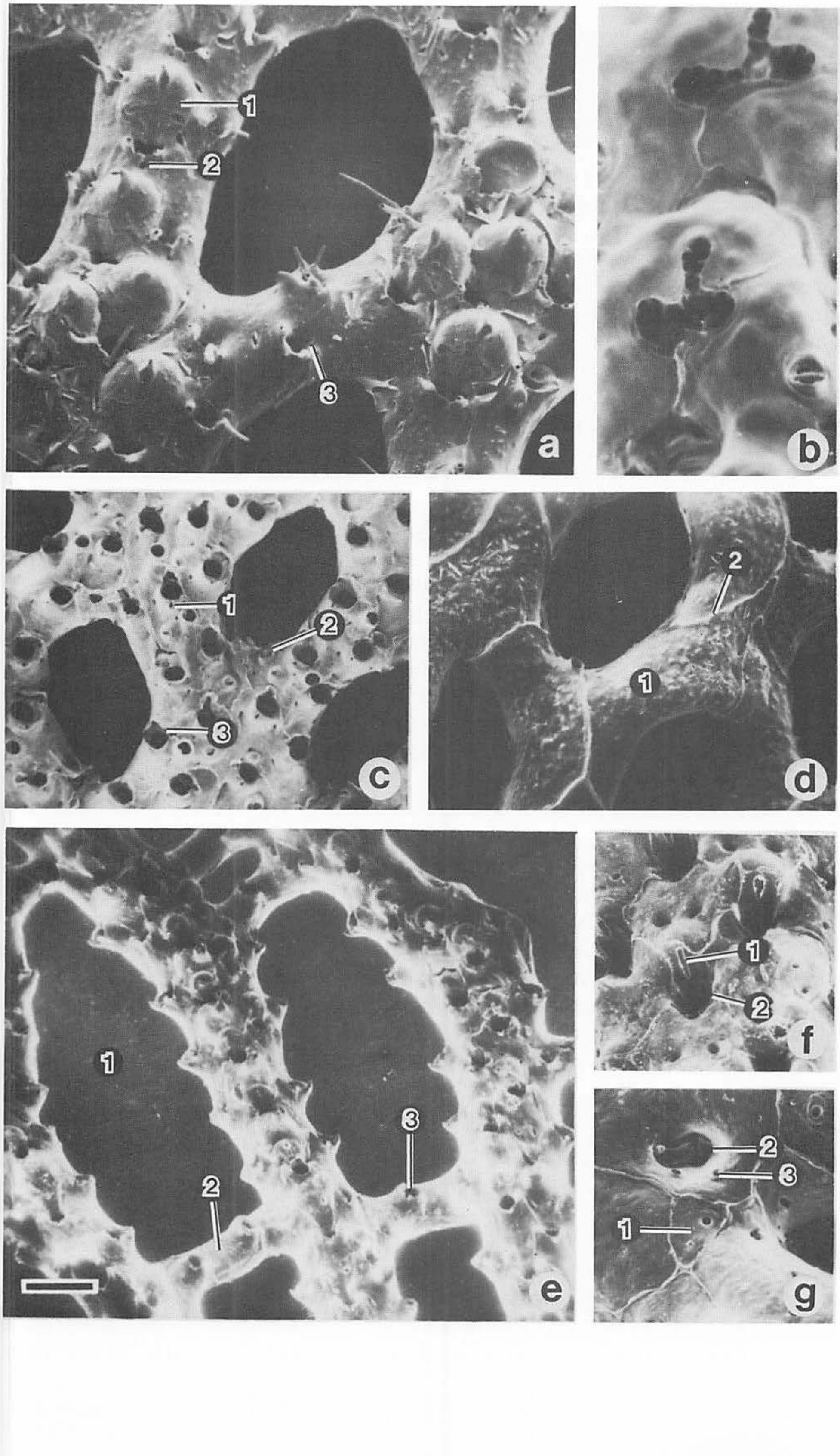
c. *Triphyllozoon* sp. Colony closely reticulate without kenozooid trabeculae. Zooecia much smaller, some with small round apertures, other zooecia with tubular peristomes, with closed suboral slit forming a median suboral pore (1). Numerous frontal round or oval avicularia (2) on raised mounds. Ovicells beginning to form as small irregularly open hoods (3). The frontal bears a pair of lateral pores. Distribution: Hawaii. Scale line = 200 μm.

d. *Triphyllozoon* sp. Obverse (dorsal) side shown in Fig. 2.IV.16c, showing granular kenozooecia (1) with vibices (lines separating kenozooecia) (2); a tiny avicularium sometimes lies where ventral zooecia fuse with kenozooecia. Scale line = 200 μm.

e. *Reteporellina denticulata.* Colony branching with slitlike fenestrae (1), trabeculae (interconnecting branches) narrow (2); peristomes at first raised, older apertures immersed, with proximal oral sinus (3) not closing to form a pore; suboral avicularia sometimes present. Ovicells becoming immersed. Distribution: Indo-Pacific, described by Busk from the *Challenger* Expedition "off Honoruru, Sandwich Islands." Scale line = 400 μm.

f. *Reteporellina denticulata.* Ovicells enlarged to show median slit in hood (1) with labellum (2), a tonguelike lightly calcified area extending into sunken peristome below the ovicell, and with flanges of ovicell extending down sides into lateral peristome area. Frontal smooth, with paired pores (retepores) and with vibices (lines separating zooecia) (see Plate 2.IV.1b). Scale line = 100 μm.

g. *Reteporellina denticulata.* Obverse side of colony showing kenozooecia (1) separated by vibices, avicularium (2), and pores (3). Scale line = 100 μm.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having somewhat longer, more irregularly shaped openings. The reticulate foliaceous colonies are common in Hawaii, found in underwater lava tubes off Kona and at depths of 25–100 m where bottom substrates are firm and currents apparently are sufficient to keep sediments swept free. The black coral *Antipathes* almost always bears 1 species of branching reteporid, *Reteporellina denticulata*, while others occur on pocilloporid corals.

All reteporid feeding zooecia (autozooecia) occur on one side of the branches while the obverse side is composed of heavily calcified non-feeding kenozooecia usually separated by distinctive ridges (Fig. 2.IV.16d). The initial colony is probably cup-shaped. In tubular colonies, all autozooecia may face the inside of the tube or the outside, depending upon the mode of fusion; folding in foliaceous colonies forms many funnellike sections with zooecia facing the interior.

Zooecial apertures generally have high peristomes that may or may not be complete distally. Proximally, there may be a vertical sinus fold, groove, or a slit that ends at a pore (retepore) at the base of the peristome. The primary aperture (orifice) is deep within the peristome and hidden by it, but the aperture may contain important diagnostic characters such as the operculum and denticles or beading on the apertural rim beneath the operculum.

Ovicells are very important for identification. Different genera may have a rounded hood, or one with a labellum (tonguelike lightly calcified area) extending from the top of the hood downward toward the orifice. In some species, ovicell hoods may be smoothly calcified or have an umbo on top. Others show a "stigma," a vertical or trifoliate slit representing incompletely calcified sutures in the external calcified hood surface (Figs. 2.IV.16b,f). Peristomes and ovicells become immersed and heavily calcified in older colonies. Avicularia of various sizes and shapes, as well as spines, may or may not be present. Frontal pores are few and are usually located near the margins of zooecia (Fig. 2.IV.16g).

Reteporid species number perhaps between 35 and 50 in the Indo-Pacific; 9 species have been identified in the shallow waters of Hawaii and fewer still occur in the eastern Pacific. There are many abyssal records of reteporids (Harmer 1934), which can perhaps be correlated with the solubility of calcium carbonate according to temperature and depth, in waters where deposition of heavily calcified exoskeletons is possible.

The systematic placement of the reteporids has been questioned; we place them in the cheilostome ascophorans. Osburn (1952) also includes the encrusting genus *Rhynchozoon* in the Reteporidae based on characters of the ovicell, orifice, and frontal. Because the reteporids are so eye-catching and difficult to identify from the literature, we have characterized the genera from Hawaii or mid-Pacific islands as follows:

Colonies mostly reticulate

Iodictyum: Live or dead colonies mostly a vivid red to purple; colonies usually closely reticulate, foliaceous, branches (trabeculae) connecting fronds formed by kenozooecia; often tabular; a few species small, white, forming cup-shaped reticulate colonies; ovicell hood at first with 2 flaps and median open pore between, becoming fused to form a central, keeled labellum (tongue-shaped area of different calcification pattern); lateral flanges extend down to peristome; zooecia with 4–6 frontal pores; small round frontal avicularia associated with pores, large interzooecial avicularia sometimes present; peristome with sinus groove, not closed to form pore, primary aperture rounded. (Members of this genus not yet found in the Hawaiian Islands but have been collected on seamounts to the south.)

Phidolopora: Colony reticulate; ovicell completely smooth but with labellum; no stigma (suture pattern) between ovicell halves present; primary aperture curved with shallow sinus, 1 or 2 long oral spines on each side; orifice becoming deeply immersed in peristome; without labial avicularium; large, long-triangular, hooked frontal avicularium directed proximally; large avicularia sometimes on trabeculae (connecting bars).

Sertella: Colony reticulate; ovicell with elongated narrow median fissure that closes in mature zooecia of some species to form a median keel on the ovicell face but not on the labellum; orifice wider than long; zooecium with smooth frontal wall and areolar pores (not yet reported from Hawaii).

Triphyllozoon: Colony reticulate or fenestrate, fenestrae large or small; ovicell not completely fused, with a trifoliate stigma (suture pattern) in the center, labellum absent; peristome usually with vertical sinus slit becoming fused, but with pore remaining at base of slit, some species with simple sinus; lateral oral spines present or absent; avicularia common, small, rounded or oval, large bicuspid.

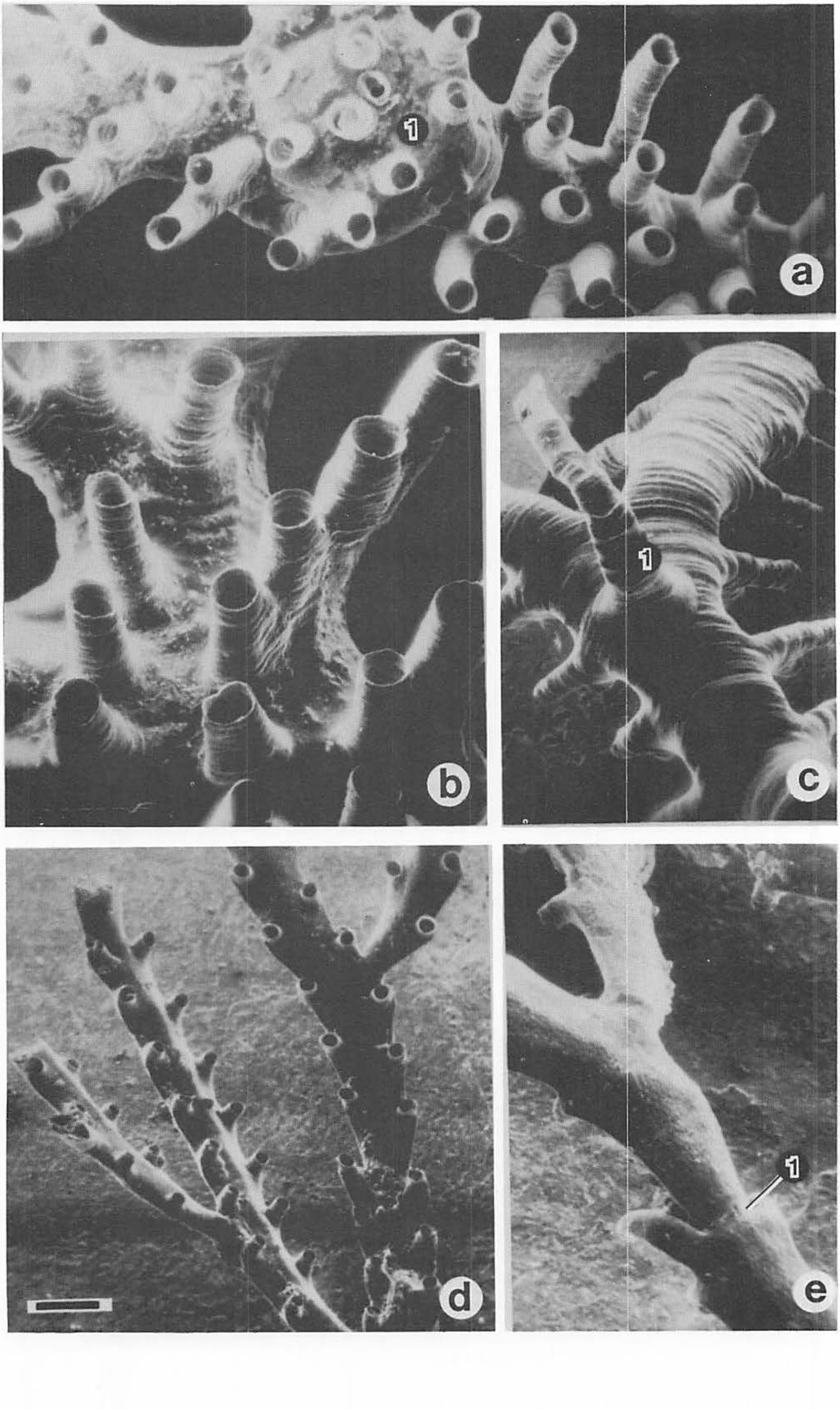
Colonies arborescent, ramose

Reteporella: Colony mostly ramose; sub-branching usually in 1 plane, with slitlike fenestrae; ovicell rounded, without labellum or lateral flanges, but with median vertical slit; peristome with closed labial pore and labial avicularium, usually with oral spines; marginal denticles on primary aperture.

Reteporellina: Colony ramose; sub-branching usually in same plane, branches not anastomosing in young colonies, slitlike fenestrae in older colonies; ovicell pear-shaped, with narrow labellum, median vertical slit, lateral flanges longer; primary orifice denticulate, without spines; peristome fluted, grooved, with sinus groove or closed to form pore; small peristomal avicularia, large, multicusped frontal and infrafenestral avicularia (sometimes rare).

Colonies encrusting

Rhynchozoon: Colony encrusting, multilayered; ovicell without a median fissure but with a semicircular, lightly calcified area above the orifice, sometimes with a labellum extending downward toward aperture; primary orifice transversely oval with a slight median proximal sinus, vestibular rim beaded, secondary orifice raised, notched, with an asymmetrical suboral avicularium on a raised, bulbous chamber; frontal smooth or with costae; few areolar pores. Osburn (1952) included the genus *Rhynchozoon* in the Reteporidae, while Harmer (1957) left them as uncertain in place (*incertae sedis*). Osburn (1952) remarked that it was one of the genera that "try men's souls," and Canu and Bassler (1927) said more emphatically "La plupart des . . . espèces . . . sont abominablement compliquées par leurs ornaments frontaux et leur organes adventifs."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Class STENOLAEMATA
Order CYCLOSTOMATA (Tubuliporata)

The living Cyclostomata (Tubuliporata) are considered to be relicts of the extensive and diverse fossil Trepostomata, now usually combined as the living and fossil class Stenolaemata (Boardman et al. 1983). The order Cyclostomata Busk, 1852, was almost universally used for the calcareous tubular bryozoans with terminal apertures in the taxonomic literature until recently. Cyclostomata Dumeril, 1806, is an order of fish, the jawless lampreys and hagfish. Although replacement of the invertebrate name is not required under the International Code of Zoological Nomenclature, Boardman et al. (1983) instituted the change to Tubuliporata Johnson, 1847, in the *Treatise on Invertebrate Paleontology*. The preponderance of the literature will be found under Cyclostomata, however.

The body plans of the diverse suborders suggest that the separate lineages are quite old and distinct. Only 1 group, the Crisiidae (suborder Articulata), has joints (nodes) between sections of tubules. Other groups lack joints, regardless of the branching patterns. The suborders Articulata and Tubuliporina generally have simple (single) body walls, and brood chambers range from simple gonozooids to complex forms surrounding tubules. The body walls of the 3 other suborders—the Cancellata, Cerioporina, and Rectangulata—are thick and complex (interpreted as being double, composed of both cryptocyst and gymnocyst). The brood chamber in the Cancellata is an enlarged gonozooid, but in the latter 2 suborders the brood chambers are zooarial, formed by fusion of zooids around the enlarged chamber.

The growth characteristics of the colonies in branching species are profoundly influenced by factors such as substrate, ambient currents, light, and competition for space. Harmelin (1973), in particular, illustrated the great variation in growth form of specimens identified by various authors from numerous locations as "*Idmonea*" *atlantica* (= *Idmodronea atlantica*). The species varies from a recumbent and little-branched colony form, to bushy, to an almost circular branching colony, depending upon the environment. Identification on the basis of colony form is therefore very difficult because characters are not constant.

So many genera and species of cyclostomes have been described from fossil material or very small fragments that the taxonomy is very confused. There is, at this time, virtually no cyclostome family or genus that can be designated without risk of disagreement among taxonomists. More work is needed on developmental and structural characteristics, such as the studies of Borg (1926) and Harmelin

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Figure 2.IV.17.—Cyclostomata (= Tubuliporata).

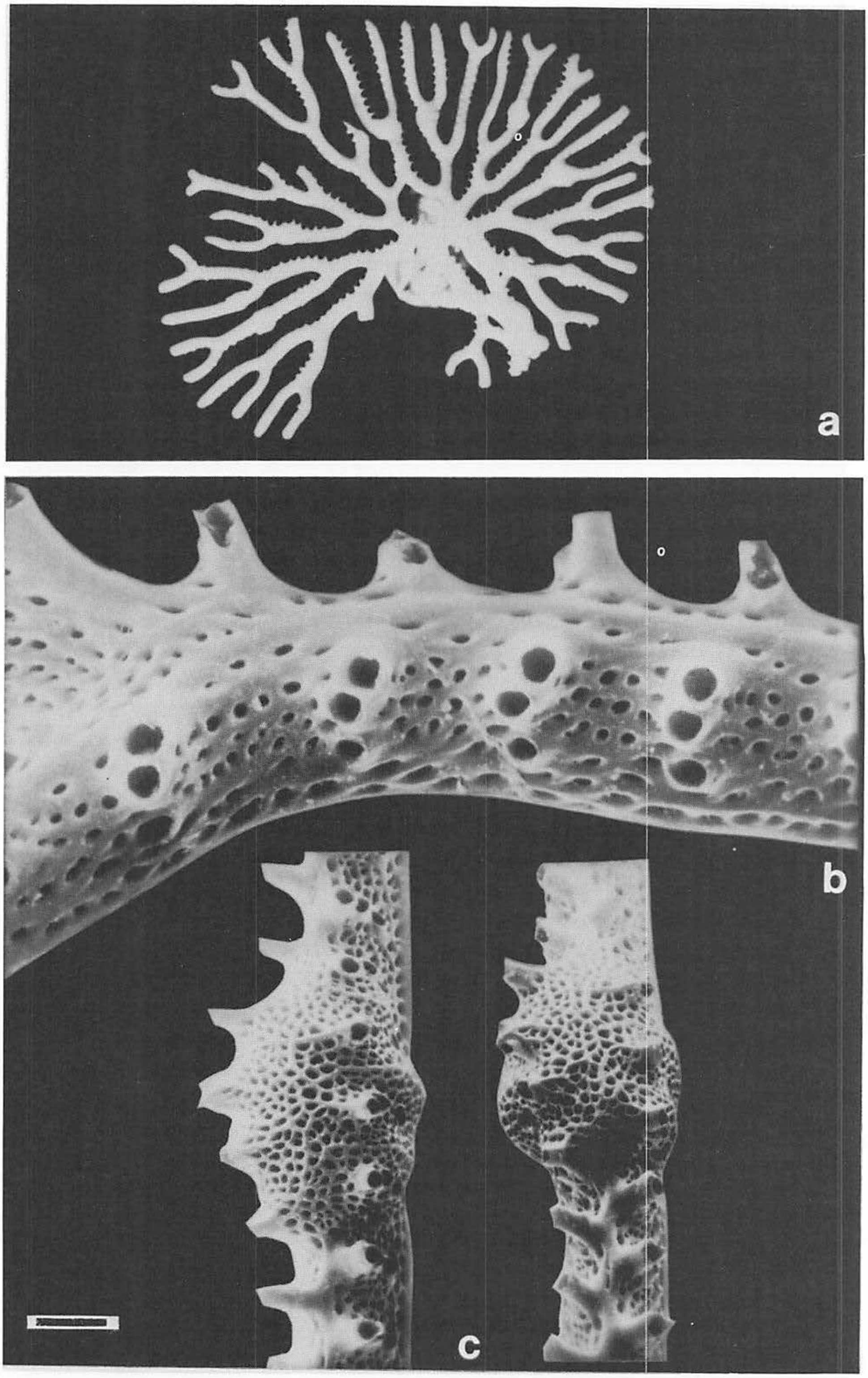
a. *Idmodronea flexuosa*. A portion of the erect colony, showing gonozooecium with small ovoid ooeciostome to the left and slightly above the numeral 1. Scale line = 400 μm.

b. *Idmodronea flexuosa*. Detail of the arrangement of the tubular peristomes. Scale line = 200 μm.

c. *Idmodronea flexuosa*. Dorsal side, showing a portion of an attachment kenozooecium (1). Scale line = 400 μm.

d. *Crisia circinata*. Erect colony, with internodes having peripheral curved alternating peristomes. Scale line = 200 μm.

e. *Crisia circinata*. Dorsal view, showing joint (1) separating the internodes. Scale line = 100 μm.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(1976a). It is possible that much of the tropical Pacific fauna is undescribed, rather than representing cosmopolitan species. However, the age of the group suggests that species with worldwide distribution might be common.

The summary of suborders and genera below is designed to permit the collector to recognize important, visible differences, and to locate references without being confused by family-level taxonomic disagreements. The studies of Harmelin (1976a) and Buge (1979) illustrate some recent generic changes. For example, one of the most commonly cited *Tubulipora* species, *T. atlantica*, is now placed in *Idmodronea*, a genus which had been virtually abandoned until the work of Harmelin (1976a). Buge (1979) redescribed the type specimen of *Lichenopora turbinata* Defrance, 1823, designated by d'Orbigny (1853), and concluded that *Lichenopora* species generally have vertical, corkscrew-type budding, whereas *Disporella* species generally bud laterally. Buge quoted Osburn (1953) in stating that the only character for differentiating the 2 genera is the presence in *Lichenopora* of secondary cancelli above the ovicell, which is covered by a thin, perforate, calcareous layer. Monographs on living cyclostomes are rare, but while works of Harmer (1915) and Osburn (1953) may be to some extent obsolete, the discussions and illustrations are still most useful for consultation.

Suborder ARTICULATA

Colonies jointed, erect; all apertures directed frontally; ovicell a simple gonozooid; body wall a single layer. Families in Hawaii: Crisiidae, Crisuliporidae (Figs. 2.IV.17d,e).

Suborder TUBULIPORINA

Colonies not jointed; first tubules adnate (attached), then recumbent or semi-erect; apertures directed frontally; ovicell a simple or expanded gonozooid; body wall a single layer. Families in Hawaii: Tubuliporidae, Diaperoeciidae, Frondiporidae, Diastoporidae, Oncousoeciidae, Mecynoeciidae (= Pustuloporidae = Entalophoridae), Terviidae (Figs. 2.IV.17a–c).

Suborder CANCELLATA

Colonies not jointed; erect, branching; apertures directed frontally; ovicell a much expanded gonozooid; body wall double (gymnocyst and cryptocyst). Family in Hawaii: Crisinidae (Figs. 2.IV.18a–c; Plate 2.IV.1f).

Suborder RECTANGULATA

Colonies discoidal, attached; tubular zooecia rising at right angles to base; tubules rising in radiate bundles, rows, or scattered around center; central area a

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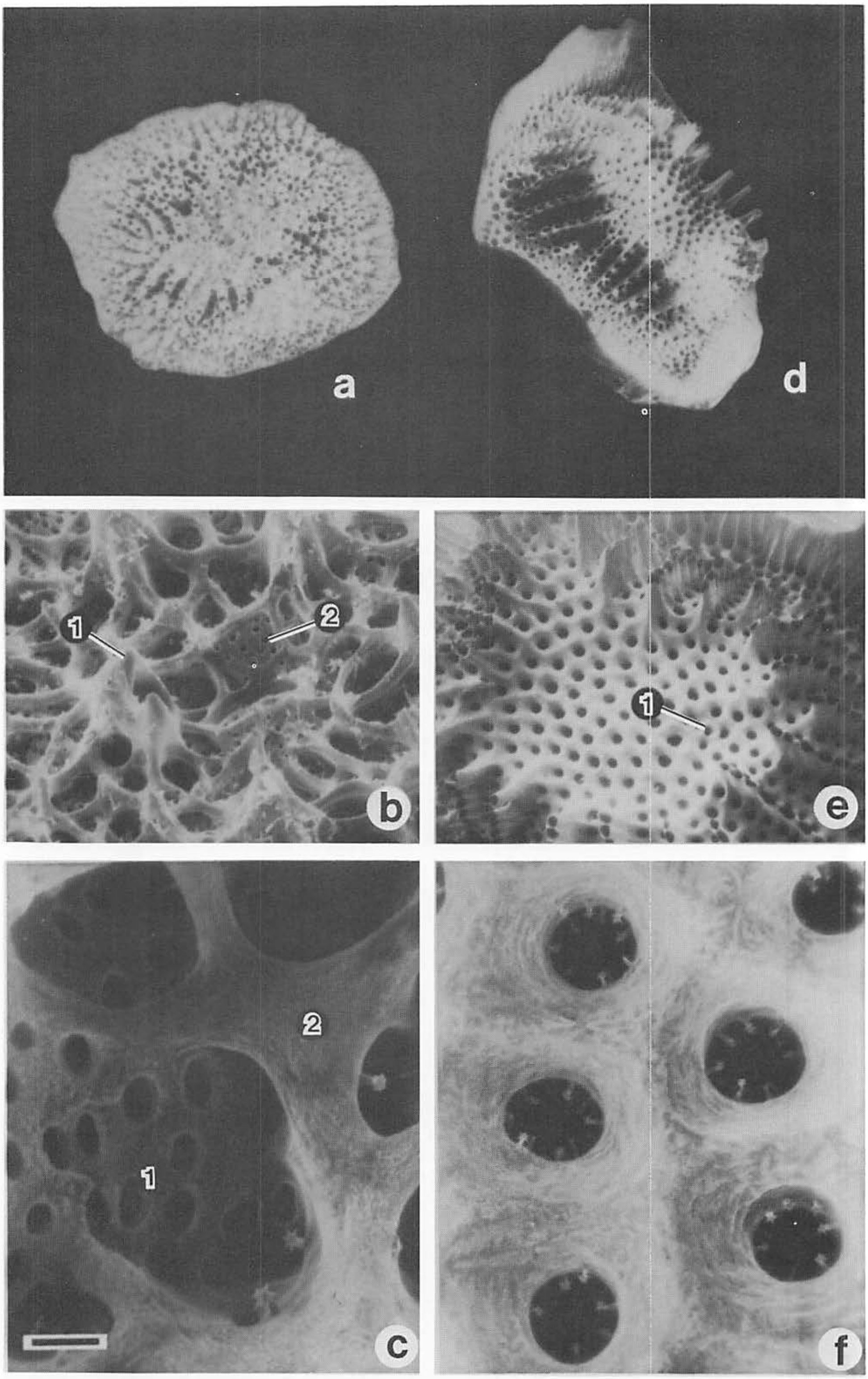
Figure 2.IV.18.—Cyclostomata (= Tubuliporata).

a. *Crisina radians*. Overall view of small colony. Note "tuning fork" branching in 1 plane. The swellings just below some of the branches mark the sites of gonozooecia. Scale line = 2 cm.

b. *Crisina radians*. Side view of a branch with obliquely placed zooecia in series of 3. Note small cancelli (pores). Scale line = 125 μm.

c. *Crisina radians*. Two gonozooecia, showing numerous small cancelli (pores). Scale line = 250 μm.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reticulum of kenozooid openings (cancelli, alveoli); ovicell a communal chamber sometimes visible through alveoli; "pinhead" spicules sometimes radiating from walls of alveoli; body wall double. Family in Hawaii: Lichenoporidae (Figs. 2.IV.19a–f).

Disporella: Budding of secondary colonies lateral on same basal disc; alveoli not covered but partly closed by irislike calcareous layer.

Lichenopora: Single colony in basal disc, secondary colonies budded vertically or outside primary disc; alveoli covered by porous calcified layer with secondary cancelli above ovicells in central colony.

Suborder CERIOPORINA

Colonies erect, branching; apertures face all directions; kenozooids more numerous than autozooids, tubules project little above surface; brood chamber a common internal chamber, not visible; body wall double. Family: Heteroporidae (not yet found in Hawaii).

ACKNOWLEDGMENTS

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The *Albatross* Hawaiian collections at the Smithsonian Institution were made available for comparative studies through the cooperation of Dr. Alan Cheetham and his staff. Miss Patricia Cook, the late Dr. Anna B. Hastings, and Mr. P. James Chimonides provided invaluable consultation and cooperation at the British Museum (Natural History) on *Siboga* and *Challenger* expedition collections and other type materials. Cyclostomes from the *Siboga* material were

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Figure 2.IV.19.—Cyclostomata (= Tubuliporata).

a. *Lichenopora* sp. Colony discoid, with rows of connate (connected) tubules interspersed with a meshwork of kenozooids forming buttressed alveoli, spaces ("pores"), called primary cancelli. Colony brood chamber beneath central area is covered by meshwork of tiny pores and irregular secondary cancelli. Scale line = 1,000 μm.

b. Enlarged central area showing pointed tips of zooecia (1); with fine pores (2) in brood chamber showing through buttresses of primary and secondary cancelli between rows of zooecia. Scale line = 200 μm.

c. Enlarged view of pores (1) in brood chamber seen through cancelli (2); cancelli bear perpendicular spicules with star-shaped terminal plates (right center) that have minute pores in the central area (much higher magnification required to see pores). Scale line = 30 μm.

d. *Disporella violacea*. Wide basal disc with radiating rows of connate zooecia, central area without tubules. Scale line = 1,000 μm.

e. *Disporella violacea*. Central area enlarged, simple low ooeciostome (entrance to brood chamber) in lower right center (1). Scale line = 600 μm.

f. *Disporella violacea*. Primary cancelli with numerous star-shaped perpendicular spicules. No secondary cancelli cover brood chambers in *Disporella* spp. Scale line = 75 μm.

examined at the Zoologisch Museum, Amsterdam, courtesy of Dr. S. Van der Spoel. Drs. Geneviève Lutaud and Geneviève Bobin provided consultation at the University of Paris, and Dr. E. Buge made d'Orbigny type material available at the Museum National d'Histoire Naturelle Paris.

Without the cooperation and assistance of these colleagues the Hawaiian bryozoan studies would not have been possible. Rita M. Bester has provided invaluable word processing assistance. Much of the photography is the work of Dr. Henry W. Chaney. The Center for Electron Microscopy, University of Southern California, through the cooperation of Dr. Robert E. Bils, provided use of equipment and facilities.

APPENDIX [HAWAIIAN BRYOZOA (ECTOPROCTA)]

The following list presents species known to occur in Hawaii, including the citations from the *Challenger* and *Albatross* expeditions, with their probable modern synonymies.

The species name, original descriptor, and date are listed first. Information may be presented after the principal entry as follows.

1. An equals sign (=) indicates a junior synonym or an obsolete or otherwise invalid name.
2. "See" refers to the currently accepted name.
3. A colon (:) after the principal citation followed by the name and date of another author indicates that the latter author identified a specimen by that name, not necessarily correctly.
4. A question mark (?) indicates the present authors' doubts about the identification or synonymy.

Pertinent references for more information or illustrations are listed in brackets following the species citations.

At the end of each citation, initials are given to indicate where the collections of Hawaiian specimens are deposited or where reference material may be consulted as follows: the Soule and Soule collections (S&S); Bernice P. Bishop Museum collection (BPBM); the *Albatross* collections at the Smithsonian Institution (SI); the *Challenger* collections at the British Museum (Natural History) (BMNH); and University of Hawaii collections (UH). The *Siboga* collections were examined by the authors at the British Museum (NH), where the monographs by Harmer were written; much of the *Siboga* material is now deposited at the Zoologisch Museum, Amsterdam.

Class GYMNOLAEMATA

Order CTENOSTOMATA Busk, 1852

Suborder STOLONIFERA Ehlers, 1876

Superfamily (= Division) VALKERIINA (J. D. and D. F. Soule 1969a)

Family **Vesiculariidae** Johnston, 1838

✓*Amathia* sp. [Edmondson and Ingram 1939]

Amathia distans Busk, 1886 [Osburn 1953]—UH, S&S

Bowerbankia cf. *gracilis* Leidy, 1855 [Emschermann 1972; Osburn 1953]—S&S

Bowerbankia cf. *imbricata* (Adams, 1800) [Emschermann 1972; Osburn 1953]—S&S

Zoobotryon verticillatum (delle Chiaje, 1828) (= *Z. pellucidus* Ehrenberg, 1831: Edmondson and Ingram 1939) [Osburn 1953]—S&S, UH, BPBM

Family **Valkeriidae** (Hincks, 1877)

Valkeria sp. [Osburn 1953]—S&S

Superfamily (= Division) TEREBRIPORINA Soule, 1953

Family **Immergentiidae** Silén, 1946

Immergentia angulata J. D. and D. F. Soule, 1969 [J. D. and D. F. Soule 1969a]—S&S

Immergentia zealandica minuta J. D. Soule, 1950 (= *Immergentia zealandica* (Silén, 1946) var. *minuta* J. D. Soule, 1950) [J. D. and D. F. Soule 1969a]—S&S

Family **Terebriporidae** Silén, 1946

Terebripora varians J. D. and D. F. Soule, 1969 [J. D. and D. F. Soule 1969a]—S&S

Order CHEILOSTOMATA Busk, 1852
Suborder ANASCA Levinsen, 1909
Superfamily INOVICELLATA Jullien, 1888
Family **Aeteidae** Smitt, 1867
✓*Aetea truncata* (Landsborough, 1852) [Harmer 1926; Osburn 1950; D. F. and J. D. Soule 1968]—S&S, BPBM
Superfamily SCRUPARIINA Silén, 1941
Family **Scrupariidae** Silén, 1941
Scruparia cf. *chelata elongata* (Lomas, 1886) [Prenant and Bobin 1966]—S&S
Superfamily MALACOSTEGA Levinsen, 1909
Family **Membraniporidae** Busk, 1854
Membranipora tuberculata (Bosc, 1802) [Osburn 1950]—S&S
Family **Calloporidae** Norman, 1903 (= Alderinidae Canu and Bassler, 1927)
Callopora (Copidozoum) curvirostris Hincks, 1862: Canu and Bassler 1927 (see *Parellisina*)
Callopora parvirostratus (Canu and Bassler, 1927) (= *Rhamphonotus parvirostratus*) [Canu and Bassler 1927; Prenant and Bobin 1966]—SI
Parellisina curvirostris (Hincks, 1862) (= *Callopora curvirostris*) [Osburn 1950]—S&S, SI, BMNH
Pyrulella corbula (Hincks, 1880) [Harmer 1915]—BMNH, S&S
Ramphonotus parvirostratus Canu and Bassler, 1927 (see *Callopora*) [Canu and Bassler 1927]—SI
Family **Hincksinidae** Canu and Bassler, 1927
Antropora granulifera (Hincks, 1880) [Osburn 1950]—S&S
Dacryonella levigata Canu and Bassler, 1927 [Canu and Bassler 1927]—SI
Superfamily COILOSTEGA Levinsen, 1909
Family **Microporidae** Hincks, 1880
Floridinella arculifera Canu and Bassler, 1927 [Canu and Bassler 1927]—SI
Micropora cf. *coriacea* (Esper, 1791): Canu and Bassler 1927 (see *Micropora* cf. *normani*) [Ryland and Hayward 1977]—SI
Micropora cf. *normani* Levinsen, 1909 (may be undescribed species, fide Soule and Soule)—S&S
Velumella americana Canu and Bassler, 1928 (= *Smittipora*, fide Bassler 1953) [Osburn 1950]—S&S
✓Family **Steginoporellidae** Bassler, 1953 (= Steganoporellidae Hincks, 1884)
Labioporella crenulata (Levinsen, 1909) [Harmer 1926]—S&S
Steginoporella lateralis MacGillivray, 1895 [Harmer 1926]—S&S
Steginoporella magnilabris (Busk, 1854) [Canu and Bassler 1927; Harmer 1926]—S&S
Family **Thalamoporellidae** Levinsen, 1902
Thalamoporella delicata D. F. and J. D. Soule, 1970 [D. F. and J. D. Soule 1970]—S&S
✓*Thalamoporella hawaiiana* D. F. and J. D. Soule, 1970 [D. F. and J. D. Soule 1970]—S&S
Thalamoporella rozieri (Audouin, 1826) (fide Blagg, UH coll., see *T. stapifera*)—UH
Thalamoporella stapifera (Levinsen, 1909) [Harmer 1926; D. F. and J. D. Soule 1970]—S&S, BMNH
Thalamoporella verrilli D. F. and J. D. Soule, 1970 [D. F. and J. D. Soule 1970]—S&S
Superfamily PENETRANTIINA J. D. and D. F. Soule, 1969
Family **Penetrantiidae** Silén, 1946
Penetrantia operculata J. D. and D. F. Soule, 1969a [J. D. and D. F. Soule 1969a]—S&S
Penetrantia parva Silén, 1946 [J. D. and D. F. Soule 1969a]—S&S
Superfamily CELLULARINA Smitt, 1867
Family **Beaniidae** Canu and Bassler, 1927
✓*Beania discodermiae* (Ortmann, 1890) [Harmer 1926]—S&S
Beania mirabilis Johnston, 1842 [Harmer 1926; Ryland and Hayward 1977]—S&S
Family **Bugulidae** Gray, 1848
✓*Bugula californica* Robertson, 1905: D. F. and J. D. Soule 1968 (*B. californica* may be limited to the eastern Pacific, cool-temp.; see *B. stolonifera*) [Osburn 1950; D. F. and J. D. Soule 1968]—S&S, BPBM

  - ✓*Bugula neritina* (Linnaeus, 1758) [Osburn 1950]—S&S, UH, BPBM
  - *Bugula stolonifera* Ryland, 1960 [Ryland and Hayward 1977]—BPBM, UH, S&S
- Family **Epistomiidae** Gregory, 1903
  - *Synnotum aegyptiacum* (Audouin, 1826) [Osburn 1950]—S&S
- Family **Scrupocellariidae** Levinsen, 1909
  - *Caberia* cf. *boryi* (Audouin, 1826) [Harmer 1926; Ryland and Hayward 1977]—S&S
  - *Canda pecten scutata* Harmer, 1926 [Harmer 1926]—S&S
  - *Scrupocellaria delilii* (Audouin, 1826) [Harmer 1926]—S&S, BMNH
  - *Scrupocellaria maderensis* Busk, 1860 [Harmer 1926]—S&S, BMNH
  - *Scrupocellaria ornithorhynchus* Wyville Thomson, 1858: Busk 1884 (not that species, see *S. delilii*, fide Harmer) [Busk 1884; Harmer 1926]—BMNH
  - ✓*Scrupocellaria sinuosa* Canu and Bassler, 1927 [Canu and Bassler 1927]—BPBM, S&S, SI, UH
  - *Scrupocellaria spatulata* (d'Orbigny, 1851) [Harmer 1926]—S&S
- Family **Cribrilinidae** Hincks, 1880
  - ✓*Cribrilaria radiata* (Moll, 1803) (= *Puellina radiata* Moll, 1803: Canu and Bassler 1927); (= *Colletosia*; = *Cribrilina radiata*) [Harmelin 1970]—BPBM, S&S, SI

Suborder ASCOPHORA Levinsen, 1909

- Family **Adeonidae** Jullien, 1903
  - *Adeona japonica* (Ortmann, 1890): Canu and Bassler 1927 (Ortman, sic) (see *Adeonella*)—SI
  - *Adeonella japonica* Ortmann, 1890 [Ortmann 1890; Canu and Bassler 1927]—SI
- ✓Family **Vittaticellidae** Harmer, 1957 (= Catenicellidae Busk, 1852)
  - *Vittaticella uberrima* Harmer, 1957 [Harmer 1957]—S&S, BMNH
- Family **Savignyellidae** Levinsen, 1909
  - ✓*Savignyella lafontii* (Audouin, 1826) (= *Catenaria lafontii*: Edmondson and Ingram 1939) [Harmer 1957; Osburn 1952]—UH, S&S, BMNH
- Family **Margarettidae** Harmer, 1957
  - *Margaretta opuntioides* (Pallas, 1766) (= *Tubucellaria fusiformis* d'Orbigny, 1852, fide Harmer 1957) [Harmer 1957]—S&S, BMNH
  - *Margaretta tenuis* Harmer, 1957 (= *Tubucellaria cereoides* var. *gracilis*: Canu and Bassler 1929) [Canu and Bassler 1929; Harmer 1957]—SI, BMNH
- Family **Pasytheidae** Davis, 1934
  - *Gemellipora eburnea* Smitt, 1873 [Harmer 1957]—S&S, BMNH
  - *Pasythea eburnea* (Smitt, 1873): Busk 1884; Canu and Bassler 1927 (see *Gemellipora*) [Busk 1884; Canu and Bassler 1927; Bassler 1953]—BMNH, SI
- Family **Watersiporidae** Vigneaux, 1949
  - *Watersipora cucullata* (Busk, 1854): Osburn, UH coll. (see *W. edmondsoni*)
  - ✓*Watersipora edmondsoni* D. F. and J. D. Soule, 1968 [D. F. and J. D. Soule 1968, 1975]—S&S
  - *Watersipora* "*subovoidea*" (Audouin, 1826) (synonymy doubtful, may be *W. atterima* Ortmann, 1889; *W. subtorquata* d'Orbigny, 1852: D. F. and J. D. Soule 1975) [D. F. and J. D. Soule 1975]
  - *Watersipora* sp. (may be undescribed sp., fide Soule and Soule)—S&S
- Family **Cheiloporinidae** Bassler, 1936
  - *Cheiloporina haddoni* (Harmer, 1902) [Harmer 1957]—S&S, BMNH
- Family **Exechonellidae** Harmer, 1957
  - *Exechonella tuberculata* (MacGillivray, 1883) [Harmer 1957]—S&S, BMNH
- Family **Cryptosulidae** Vigneaux, 1949
  - *Cryptosula pallasiana* (Moll, 1803) [Osburn 1952]—S&S
- Family **Tetraplariidae** Harmer, 1957
  - *Pollaploecium brevis* Canu and Bassler, 1927 (= *Tetraplaria*, fide Harmer 1957; doubtful, fide Soule and Soule) [Canu and Bassler 1927, 1929; Harmer 1957]—SI, S&S
  - *Tetraplaria ventricosa* (Haswell, 1880) [Harmer 1957]—S&S
- Family **Gigantoporidae** Bassler, 1935

  - *Gigantopora spiculifera* Canu and Bassler, 1927 [Canu and Bassler 1927; Harmer 1957]—SI
- Family **Smittinidae** Levinsen, 1909
  - *Codonella anatina* Canu and Bassler, 1927 (see *Codonellina anatina*)
  - *Codonellina anatina* (Canu and Bassler, 1927) (= *Codonella anatina*) [Canu and Bassler 1927]—SI
  - *Mucronella delicatula* Busk 1884 (see *Parasmittina delicatula*) [Busk 1884; D. F. and J. D. Soule 1973]—S&S, BMNH
  - *Mucronella magnifica* Busk, 1884 (see *Mucropetraliella*) [Busk 1884]—BMNH
  - *Mucronella ?quadrata* Busk, 1884: Canu and Bassler 1927 (see Schizoporellidae: *Emballotheca pacifica*) [Busk 1884; Canu and Bassler 1927]—SI, BMNH
  - *Parasmittina egyptiaca* (Waters, 1909) (? in Hawaii, see *P. parsevaliformis*)—BMNH
  - *Parasmittina alanbanneri* D. F. and J. D. Soule, 1973 [D. F. and J. D. Soule 1973]—S&S
  - *Parasmittina areolata* (Canu and Bassler, 1927) (= *Smittina areolata*) [Canu and Bassler 1927; D. F. and J. D. Soule 1973]—SI, S&S
  - *Parasmittina circularis* D. F. and J. D. Soule, 1973 [D. F. and J. D. Soule 1973]—S&S
  - *Parasmittina decorata* D. F. and J. D. Soule, 1973 [D. F. and J. D. Soule 1973]—S&S
  - *Parasmittina delicatula* (Busk 1884) (= *Mucronella delicatula*) [Busk 1884; D. F. and J. D. Soule 1973]—S&S
  - *Parasmittina emersoni* D. F. and J. D. Soule, 1973 [D. F. and J. D. Soule 1973]—S&S
  - *Parasmittina hastingsae* D. F. and J. D. Soule, 1973 [D. F. and J. D. Soule 1973]—S&S
  - *Parasmittina ilioensis* D. F. and J. D. Soule, 1973 [D. F. and J. D. Soule 1973]—S&S
  - *Parasmittina kauaiensis* D. F. and J. D. Soule, 1973 [D. F. and J. D. Soule 1973]—S&S
  - *Parasmittina leviavicularia* D. F. and J. D. Soule, 1973 [D. F. and J. D. Soule 1973]—S&S
  - *Parasmittina marsupialis* (Busk, 1884) (= *Smittia marsupialis*) [D. F. and J. D. Soule 1973]—S&S
  - *Parasmittina parsevaliformis* D. F. and J. D. Soule, 1973 [D. F. and J. D. Soule 1973]—S&S
  - *Parasmittina parviuncinata* D. F. and J. D. Soule, 1973 [D. F. and J. D. Soule, 1973]—S&S
  - *Parasmittina raigiformis* D. F. and J. D. Soule, 1973 [D. F. and J. D. Soule 1973]—S&S
  - *Parasmittina serrula* D. F. and J. D. Soule, 1973 [D. F. and J. D. Soule 1973]—S&S
  - *Parasmittina trispinosa* var. *minuta* (Hincks, 1884) (fide Osburn, UH coll.; not that species, fide Soule and Soule) [D. F. and J. D. Soule 1973]—S&S
  - *Parasmittina tropica* (Waters, 1909) (not that species, fide Soule and Soule; see *P. serrula*) [D. F. and J. D. Soule 1973]—BMNH
  - *Parasmittina uncinata* D. F. and J. D. Soule, 1973 [D. F. and J. D. Soule 1973]—S&S
  - *Hemismittoidea corallinea* D. F. and J. D. Soule, 1973 [D. F. and J. D. Soule 1973]—S&S
  - *Hemismittoidea osburni* D. F. and J. D. Soule, 1973 [D. F. and J. D. Soule 1973]—S&S
  - *Smittia marsupialis* Busk, 1884 (see *Parasmittina marsupialis*)
  - *Smittina kukuiula* D. F. and J. D. Soule, 1973 [D. F. and J. D. Soule 1973]—S&S
  - *Smittoidea pacifica* D. F. and J. D. Soule, 1973 [D. F. and J. D. Soule 1973]—S&S
  - *Pleurocodonella lahainae* D. F. and J. D. Soule, 1973 [D. F. and J. D. Soule 1973]—S&S
- Family **Hippothoidae** Levinsen, 1909
  - *Hippothoa aruensis* Morris, 1980 [Gordon 1984; Morris 1980] (? = *Hippothoa distans* (MacGillivray, 1869): Canu and Bassler 1927)—S&S, SI
  - *Trypostega venusta* (Norman, 1864)—S&S
- Family **Chorizoporidae** Vigneaux, 1949
  - *Chorizopora honolulensis* Busk, 1884 [Busk 1884] (= *Mastigophora honolulensis* Busk, 1884: Canu and Bassler 1927; Busk type not *Mastigophora*, not identifiable further, fide Soule and Soule) [Canu and Bassler 1927]—BMNH, SI
  - *Rhamphostomella ?argentea* (Hincks, 1881): Harmer 1957, Sta 399D (? = *Robertsonidra* Osburn, 1952; ? = *Schizoporella flexilis* Canu and Bassler, 1927) [Harmer 1957; Osburn 1952]—SI, BMNH
- Family **Cleidochasmatidae** Cheetham and Sandberg, 1964

Cleidochasma porcellanum (Busk, 1860) (= *Hippoporina porcellana* (Busk): Osburn 1952) [Osburn 1952; Cheetham and Sandburg 1964]—S&S, BMNH

Hippoporella calyciformis (Philipps, 1899) [Harmer 1957]—S&S, BMNH

Family **Crepidacanthidae** Levinsen, 1909

Crepidacantha poissonii (Audouin, 1826): Canu and Bassler 1927 (see *C. zelanica*) [Canu and Bassler 1927; Harmer 1957]—SI

Crepidacantha zelanica Canu and Bassler, 1929: Brown 1952 [Brown 1952]—S&S

Escharina pesanseris (Smitt, 1873) (= *Mastigophora pesanseris* Smitt, 1873): Canu and Bassler 1927 [Canu and Bassler 1927; Harmer 1957]—UH, S&S, SI

Mastigophora honolulensis (Busk, 1884): Canu and Bassler 1927 (? not *Chorizopora honolulensis* Busk, 1884, as indicated by Canu and Bassler 1927) [Canu and Bassler 1927]—BMNH

Mastigophora pesanseris (Smitt, 1873): Canu and Bassler 1927 (see *Escharina pesanseris*)

Family **Hippopodinidae** Levinsen, 1909

Hippopodina feegeensis (Busk, 1884) (= *Lepralia feegeensis* Busk, 1884) [Busk 1884; Harmer 1957; Osburn 1952]—BPBM, S&S

Cosciniopsis fusca Canu and Bassler, 1927 (? = *C. lonchaea* Busk, 1884, fide Harmer 1957; not *C. lonchaea*, fide Soule and Soule) [Canu and Bassler 1927; Harmer 1957]—S&S

Family **Celleporidae** Busk, 1852 (= Holoporellidae Levinsen, 1909; Celleporariidae plus Celleporinidae of Harmer 1957)

Cellepora (part) = *Holoporella* Waters, 1909, fide Soule and Soule; = *Celleporaria* Lamoureaux, 1821 (part), fide Harmer 1957; not so, fide Hayward and Ryland 1979 (see text for discussion)

Cellepora aperta Hincks, 1882 (= *Celleporaria aperta*, fide Harmer 1957; see *Holoporella*, fide Soule and Soule)

Cellepora fusca Busk, 1854 (= *Celleporaria fusca*, fide Harmer 1957; see *Holoporella fusca*, fide Soule and Soule)

Cellepora honolulensis Busk, 1884 (see *Holoporella honolulensis*, fide Soule and Soule)

Cellepora polymorpha Busk, 1881 (see *Holoporella polymorpha*)

Cellepora pumicosa (Linnaeus, 1767): Blagg, UH coll. (doubtful, fide Soule and Soule) [Hayward and Ryland 1979]—UH

Cellepora vagans Busk, 1881 (see *Holoporella vagans*)

Celleporaria aperta (Hincks, 1882) (= *Cellepora*; see *Holoporella*, fide Soule and Soule) [Harmer 1957]

Celleporaria erectorostris Canu and Bassler, 1929 (? = *C. tridenticulata*; see *Holoporella tridenticulata*) [Busk 1884; Canu and Bassler 1929; Harmer 1957]—SI

Celleporaria pilaefera (Canu and Bassler, 1929) (see *Holoporella pilaefera*)

Holoporella aperta (Hincks, 1882) (= *Cellepora*; = *Celleporaria*) [Harmer 1957]—S&S, BMNH

Holoporella fusca (Busk, 1854) (= *Cellepora*; = *Celleporaria*) [Harmer 1957]—S&S, BMNH

Holoporella honolulensis (Busk, 1884) (= *Cellepora honolulensis*) [Busk 1881, 1884]—BMNH, S&S

Holoporella pilaefera Canu and Bassler, 1929 [Canu and Bassler 1929; Harmer 1957]—S&S

Holoporella polymorpha (Busk, 1881) (= *Cellepora*; = *Celleporaria*; not recorded since)[Busk 1884]—BMNH

Holoporella serratorostris MacGillivray, 1884: Canu and Bassler 1929 [Canu and Bassler 1929]—SI, S&S

Holoporella tridenticulata (Busk, 1881) (= *Cellepora*; = *Celleporaria*, fide Harmer; *Holoporella*, fide Osburn, Soule and Soule) [Busk 1881, 1884; Osburn 1952; Harmer 1957]—S&S, BMNH

Holoporella vagans (Busk, 1881) (= *Holoporella* sp. of Edmondson and Ingraham 1939; = *Cellepora* Busk, 1881, 1884; = *Celleporaria*, fide Harmer 1957) [Busk 1881, 1884; Harmer 1957]—S&S, BMNH

Schismopora cf. *spathulata* (MacGillivray, 1887) (= *Costazia spathulata* MacGillivray:

Canu and Bassler 1929; ? = *Schismopora redoutei* (Audouin): Harmer 1957; ? = *Costazia avicularia* Hincks: Blagg, UH coll.) [Canu and Bassler 1929; Harmer 1957]—UH, SI, S&S

Family **Microporellidae** Hincks, 1880

Fenestrulina infundibulipora Canu and Bassler, 1929 [Canu and Bassler 1929]—S&S

Fenestrulina malusii (Audouin, 1826) (? in Hawaii, see *F. infundibulipora*) [Harmer 1957]

Microporella orientalis Harmer, 1957 [Harmer 1957]—S&S

Family **Petraliellidae** Harmer, 1957

Mucronella magnifica Busk, 1884 (see *Mucropetraliella magnifica*) [Busk 1884]

Mucropetraliella albirostris (Canu and Bassler, 1927) (? possibly *Mucropetraliella magnifica*) [Canu and Bassler 1927]—SI

Mucropetraliella magnifica (Busk, 1884) (= *Mucronella*) [Busk 1884]—S&S

Petraliella albirostris Canu and Bassler, 1927 (see *Mucropetraliella albirostris*) [Canu and Bassler 1927]—SI

Family **Phylactellidae** Canu and Bassler, 1917

Lagenicella cylindrica (Harmer, 1957) (= *Lagenipora cylindrica*) [Cheetham and Sandburg 1964]—S&S

Lagenicella spinulosa (Hincks, 1884) (= *Lagenipora spinulosa*) [Cheetham and Sandburg 1964]—S&S

Family **Schizoporellidae** Jullien, 1903

Arthropoma cf. *punctigerum* (MacGillivray, 1883) (= *Schizoporella* ? *punctigera*) [Harmer 1957]—S&S

Emballotheca pacifica Harmer, 1957 (? = *Mucronella* ?*quadrata* Busk: Canu and Bassler 1927; not *E. quadrata* (MacGillivray 1869), fide Harmer) [Busk 1884; Canu and Bassler 1927; Harmer 1957]—SI, S&S, BMNH

Metroperiella sp. (prob. undescribed, fide Soule and Soule) [Harmer 1957]—S&S

Schizomavella torquata Canu and Bassler, 1927 [Canu and Bassler 1927]—SI, S&S

Schizoporella crassomuralis Canu and Bassler, 1927 (? = *Myriozoum honolulense* Busk, 1884) [Canu and Bassler 1927]—SI

Schizoporella decorata Canu and Bassler, 1927 (not *Calyptotheca wasinensis* Waters: Harmer 1957, fide Soule and Soule) [Canu and Bassler 1927; Harmer 1957]—SI, S&S

Schizoporella errata (Waters, 1878) [Hayward and Ryland 1979]—S&S, BMNH

Schizoporella flexilis Canu and Bassler, 1927 (not *Schizoporella*; may be Chorizoporidae, *Rhamphostomella argentea* of Harmer, 1957, fide Soule and Soule) [Canu and Bassler 1927; Harmer 1957]—S&S, SI, BMNH

Schizoporella furcata (Busk, 1884) (includes *Schizoporella tenuis* (Busk, 1884); A. B. Hastings said both are described from parts of same colony) [Harmer 1957]—S&S, BMNH

Schizoporella punctigera MacGillivray, 1883 (see *Arthropoma punctigerum*)

✓ *Schizoporella unicornis* (Johnston, 1847) [Osburn 1953; Hayward and Ryland 1979]—S&S

Schizoporella cf. *violacea* Canu and Bassler, 1930 (? may be *S. errata*) [Pouyet 1971]—S&S, SI

Family **Myriozoidae** Smitt, 1867

Myriozoum honolulense Busk, 1884 (? = *Schizoporella crassomuralis* Canu and Bassler, 1927); ? = *Schizoporella furcata* or *Calyptotheca*, fide Harmer 1957 [Busk 1884; Canu and Bassler 1927; Harmer 1957]—BMNH, SI

Myriozoum superficiale Ortmann, 1890 [Ortmann 1890]—S&S

Family **Sertellidae** Jullien, 1903 (= Reteporidae Smitt, 1867)

Phidolopora robusta Canu and Bassler, 1927 [Canu and Bassler, 1927]—SI, S&S

Retepora contortuplicata Busk, 1884 (see *Triphyllozoon*)—BMNH

Retepora denticulata Busk, 1884 (see *Reteporellina*)—BMNH

Retepora fimbriata Canu and Bassler, 1927 (see *Reteporella*)—SI

Retepora gigantea Busk, 1884 (genus undetermined, not identified since) [Busk 1884]—BMNH

Retepora hirsuta Busk, 1884 (see *Triphyllozoon*)—BMNH

Retepora obtecta Buchner, 1924: Canu and Bassler 1927 (see *Reteporella*)—SI

Retepora producta Busk, 1884 (see *Reteporella graeffei* Kirchenpauer, 1869, fide Harmer 1934) [Busk 1884; Harmer 1934]—BMNH

Retepora trabeculifera Canu and Bassler, 1927 (see *Reteporellina*) [Canu and Bassler 1927]

Reteporella fimbriata (Canu and Bassler, 1927) (= *Retepora fimbriata* Canu and Bassler 1927; may = *R. graeffei*, fide Soule and Soule) [Canu and Bassler 1927]—SI

Reteporella graeffei (Kirchenpauer, 1869) [Harmer 1934]—S&S

Reteporella obtecta (Buchner, 1924): Canu and Bassler 1927 (not *R. obtecta*, fide Harmer 1934) [Canu and Bassler 1927; Harmer 1934]—SI, BMNH

Reteporellina denticulata (Busk 1884) (= *Retepora denticulata* Busk, 1884) [Busk 1884; Harmer 1934]—S&S, BMNH

Reteporellina trabeculifera (Canu and Bassler, 1927) (may be *R. denticulata*, fide Soule and Soule) [Canu and Bassler 1927]—SI

Triphyllozoon contortuplicata (Busk, 1884) (= *Retepora contortuplicata* Busk, 1884) [Busk 1884]—S&S, BMNH

Triphyllozoon hirsuta (Busk, 1884) (= *Retepora hirsuta* Busk, 1884) [Busk 1884]—BMNH

Rhynchozoon bispinosum (Johnston, 1847) [Osburn 1952]—S&S

Rhynchozoon nudum Canu and Bassler, 1927 (not recorded since) [Canu and Bassler 1927]—SI

Rhynchozoon rostratum (Busk, 1855) [Osburn 1952]—S&S

Rhynchozoon tuberosum Canu and Bassler, 1927 (? = *R. rostratum*) [Canu and Bassler 1927]—SI

Rynchozoon spp., possibly undescribed, fide Soule and Soule

Incertae Sedis

Cribella strophiae Canu and Bassler, 1927 (genus *Cribella* invalid, preoccupied, fide Harmer 1957; ? = *Calyptotheca strophiae*, fide Soule and Soule) [Canu and Bassler 1927; Harmer 1957]—SI

Lepraliella prolifica Canu and Bassler, 1927 (? = *Cigclisula prolifica*, fide Soule and Soule) [Canu and Bassler 1927]—SI

Class STENOLAEMATA Borg, 1926

Order CYCLOSTOMATA Busk, 1852 (= Tubuliporata Johnston, 1847)

Suborder ARTICULATA Busk, 1859 (= Acamptostega Borg, 1926)

Family **Crisiidae** Johnston, 1838

Crisia circinata Waters, 1914 [Harmer 1915]—S&S, BMNH

Family **Crisuliporidae** Buge, 1979

Crisulipora cf. *occidentalis* Robertson, 1910 [Buge 1979; Osburn 1953]—S&S

Suborder TUBULIPORINA Hagenow, 1851 (= Camptostega Borg, 1926)

Family **Diaperoeciidae** Canu, 1918 [Buge 1979]

Diaperoecia californica (d'Orbigny, 1852) [Osburn 1953]—S&S

Diaperoecia intricata Canu and Bassler, 1927 (= *D. californica*, fide Osburn; questionable, fide Soule and Soule) [Canu and Bassler 1927]—SI

Family **Frondiporidae** Busk, 1875

Filifascigera robusta Canu and Bassler, 1927 [Canu and Bassler 1927; Osburn 1953]—SI, S&S

Family **Diastoporidae** Gregory, 1899

Diplosolen obelium (Johnston, 1838): Canu and Bassler 1927 [Canu and Bassler 1927; Osburn 1953]—SI, S&S

Plagioecia patina (Lamarck, 1816) (= *Diastopora simplex* Busk, 1859; = *Berenicea patina*, fide Harmer 1915) [Harmer 1915]—S&S, BMNH

Family **Oncousoeciidae** Canu, 1918

Oncousoecia major (Johnston, 1847): Canu and Bassler 1927 (see *Proboscina*) [Canu and Bassler 1927]—SI

Proboscina cf. *major* (Johnston, 1847) [Osburn 1953]—S&S

Stomatopora trahens (Couch, 1841) [Lagaaij 1963]—S&S

Family **Tubuliporidae** Johnston, 1838

Idmodronea flexuosa (Pourtales, 1867) (= *Tubulipora atlantica* var. *flexuosa*; = *T. flexuosa*) [Harmer 1915; Harmelin 1976a]—S&S
✓*Tubulipora concinna* MacGillivray, 1885 [Harmer 1915; Osburn 1953]—S&S
Tubulipora atlantica var. *flexuosa*: UH coll., fide Osburn (= *T. flexuosa* (Pourtales 1867): Osburn 1953; see *Idmodronea flexuosa*) [Osburn 1953]—S&S
Tubulipora pulcherrima Kirkpatrick, 1890 [Harmer 1915]—S&S
Tubulipora spp. (may be undescribed, fide Soule and Soule)
Family **Mecynoeciidae** Canu, 1918 (= Entalophoridae Reuss, 1869; = Pustuloporidae Smitt, 1872)
Entalophora cf. *proboscideoides* Smitt, 1872 (see *Mecynoecia*) [Osburn 1953]—S&S
Mecynoecia proboscidea (Milne-Edwards, 1838): Canu and Bassler 1927 [Canu and Bassler 1927]—SI
Mecynoecia proboscideoides (Smitt, 1872) [Harmelin 1976a; Osburn 1953]—S&S
Family **Terviidae** Canu and Bassler, 1920
Tervia jellyae Harmer, 1915 [Harmer 1915]—S&S
Suborder CANCELLATA Gregory, 1896 (= Pachystega Borg, 1926)
Family **Crisinidae** d'Orbigny, 1853: Borg 1941
Crisina radians (Lamarck, 1816) [Harmer 1926]—S&S, BMNH
Suborder RECTANGULATA Waters, 1887 (= Calyptrostega Borg, 1926)
Family **Lichenoporidae** Smitt, 1866
Disporella californica (d'Orbigny, 1853) [Osburn 1953]—S&S
Disporella cf. *fimbriata* (Busk, 1875) (may be *Lichenopora*, undescribed species) [Osburn 1953]—S&S
Disporella violacea (Canu and Bassler, 1927) (= *Lichenopora*) [Canu and Bassler 1927]—S&S
✓ *Lichenopora novaezelandiae* Busk, 1875 [Harmer 1915]—S&S
Lichenopora violacea Canu and Bassler, 1927 (see *Disporella violacea*)
Lichenopora spp. (many unidentified forms, juveniles)—S&S
Incertae sedis
Crisiona baculifera Canu and Bassler, 1927 (not found again, fide Soule and Soule)—SI

GLOSSARY [ENTOPROCTA and BRYOZOA (ECTOPROCTA)]

Extensive glossaries are presented by Bassler (1953), Osburn (1950, 1952, 1953), Ryland (1970), Ryland and Hayward (1977), Hayward and Ryland (1979), and Boardman et al. (1983). Most of these present extensive diagrams with terminology. The glossary below is restricted to common terms used in identifications.

ancestrula (pl. ancestrulae): The primary individual of a colony; metamorphosed larva.
anter: Term used in older literature for the distal rim of the aperture.
aperture: The opening in the front wall through which the lophophore is extruded. The term has been used for other openings, but should be restricted to this meaning (see also **orifice**).
areolar pore: In Ascophora, 1 or more rows of pores around the margin of the zooecium frontal wall.
ascopore: In Ascophora, opening of the ascus (compensation or hydrostatic sac), either as a visible opening in the central frontal wall, or hidden inside the aperture.
ascus: In Ascophora, sac beneath the calcareous or membranous frontal wall that allows for adjustment of water pressure when tentacles are extended or retracted; also termed compensation sac.
astogeny: Development of colony by asexual budding.
autozooid: Feeding individual (zooid) in colony.
avicularium (pl. avicularia): Structure provided with beak or mandible; considered to be highly

modified individual zooid (heterozooid or polymorph), possibly for cleaning colony surface, protection, or capture of food.

basal: Attached or dorsal side of colony.

cancellus (pl. cancelli): A small space (e.g., the space in a honeycomb); in Cyclostomata (Tubuliporata), a kenozooid forming a space between zooecial tubules. Also called an alveolus (pl. alveoli).

cardelle: Lateral hinge "teeth" in the aperture to which the operculum is attached (see also denticle).

compensation sac (see **ascus**).

condyle (see **cardelle**).

costa (pl. costae): Riblike structures or ridges (paired spines) that form the calcified frontal shield, extending from the lateral walls to the center with pores between the ribs.

cryptocyst: Calcified "shelf" or frontal shield formed by epidermal fold extending inward from the lateral interior body walls. In Anasca, space between the shelf and membranous frontal wall acts as the hydrostatic chamber (hypostega) for the extension and retraction of the tentacles since anascans lack the compensation sac of the ascophorans. Source of calcified frontal in some ascophorans (see also **gymnocyst**).

cystid: Living body wall layers lining the calcareous walls of the zooecium.

denticle: Calcareous "tooth," may be median (lyrule), or paired lateral oral (cardelle, condyle).

diatellae: Small cavities in the interior zooecial side walls containing tissue with pores that communicate between adjacent zooecia.

distal: In Ectoprocta, toward the oral end of the zooecium; beyond the aperture.

ectocyst: Thin, outermost cuticular layer covering zooecia, zoarium; sometimes used to include epidermis, cuticle, and skeleton.

endozooecial: Ovicell formed by the distal wall of the zooecium, usually hidden, immersed, and pushing into the next zooecium distally. See also **hyperstomial**.

fenestra (pl. fenestrae): Opening (windows) between branching elements (trabeculae) of irregularly reticulate colony (e.g., reteporids).

frontal: In Cheilostomata, exposed side of encrusting zooecium; side bearing the aperture; also the ventral surface. Dorsal (basal) side of zooecium usually has no openings and is the attached surface for encrusting species.

frontal membrane: Soft tissue layer covering frontal area of cheilostomes.

gonozooecium: Individual zooids modified to provide a brood chamber for developing embryos; lacking a polypide.

gymnocyst: Portion of calcified frontal wall formed by epidermal folds and calcification of the outer body wall; in some anascans present as a proximal rim over opesia; in some ascophorans present as fused frontal spines or a shield that grows by exterior-wall outpocketings to cover frontal and becomes attached to interior lateral walls.

heterozooid: Zooecium other than autozooid, modified in function (e.g., avicularium) usually lacking polypide; also called polymorph (see also **kenozooid**).

hyperstomial: Ovicell rising externally, distal to the peristome, usually resting on surface of next zooecium distal.

hypostega: Coelomic space between frontal wall and cryptocyst in Anasca, between epidermis and calcified (cryptocystidean or gymnocystidean) frontal wall in Ascophora.

internode: Segment of colony between "joints" in erect, movable colonies.

kenozooid: A zooid devoid of polypide and musculature, modified for special function; e.g., a stolon, cancellus.

labellum: Central area on ovicell of lighter calcification descending from upper margin of the calcareous hood toward the orifice between the halves of the ovicell.

lophophore: Ridge of soft tissue around mouth, bearing the tentacles; can be extruded for feeding.

lyrule: Median denticle on proximal border of primary aperture. (Syn. lyrula).

mandible: Articulated part of avicularium, usually chitinous; homologous to zooecial operculum.

mucro: In Ascophora, calcified mound or projection, usually at proximal edge of peristome located on proximal side of lyrule; sometimes used for denticle or lyrule.

mural rim: In Anasca, frontal edge of side wall, often bearing spines.

ooeciopore: Aperture of ovicell.

ooeciostome: In Cyclostomata, peristome surrounding ooeciopore.

ooecium: Brood chamber (see also **ovicell**).

olocyst: In Ascophora, obsolete term used in older literature for primary calcified layer of frontal. See **pleurocyst** and **tremocyst.**

operculum: In Cheilostomata, chitinous structure closing aperture.

opesia (pl. opesiae): In Anasca, uncalcified membranous frontal; the original use of the word was by Jullien (1888) in French, *une opesie*; occasionally misused as opesium (sing.), opesia (pl.).

opesiule: Small uncalcified areas flanking polypide tube, openings in cryptocyst for passage of muscles to ectocyst.

orifice: Opening of the mouth between tentacles of the lophophore; recently used for external aperture of zooid.

ovicell: Structure serving as a brood chamber, usually containing 1 egg or larva during development; probably formed as a modified individual (kenozooid) budded from 1 or more zooids in a colony.

peristome: Raised, sometimes tubular collar surrounding the aperture. Since the derivation indicates "surrounding the mouth," perhaps apertural or orificial collar would be a better term.

pleurocyst: In Ascophora, obsolete term used in older literature for secondary calcifying layer of frontal, which begins at border of zooecium and appears to grow toward the more or less imperforate center of the frontal. See **olocyst** and **tremocyst.**

polypide: Internal living parts, movable within the zooecium; includes tentacles, tentacle sheath, mouth, pharynx, esophagus, stomach, intestine and rectum, funiculus and associated muscles, ganglia, and nerves.

poster: Obsolete term; proximal portion or rim of the aperture.

proximal: In Ectoprocta, directed toward the point of origin of the zooecium, below or away from the aperture and direction of growth.

scutum: In Anasca, modified spine overhanging frontal; may be branched or flattened into a shield (= scute).

sinus: In some Ascophora, slit or notch at proximal edge of aperture (orifice).

spiramen: Large pore or opening; in Gigantiporidae, a large opening proximal to the aperture.

stigma: In reteporids, a vertical or trifoliate slit representing incompletely calcified sutures in the external calcified ovicell hood.

trabecula (pl. trabeculae): Small kenozooid bars that connect the branches of some reteporids to form fenestrate colonies.

tremocyst: Obsolete term used in older literature for secondary calcifying layer of frontal, developed evenly around more or less uniform frontal perforations filled with tissue (pseudopores). See **olocyst** and **pleurocyst.**

umbo: Elevated or knoblike process on frontal below the aperture, sometimes also on ovicell (= umbone).

vestibular arch: Rim inside primary aperture.

vibraculum: Avicularium mandible modified into a long, whiplike structure.

zooarium: The colony (restricted to colony skeleton by some authors); formed by isogenous zooids budding from a single ancestrula.

zooecium: The individual (usually calcareous) body wall chamber or skeleton containing the living soft parts (cystid and polypide).

zooid (= zoid): Single individual; includes both zooecium and soft parts (pronounced zoo-id, zo-oid, or zo-id).

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Chapter V

Phylum BRACHIOPODA

CHRISTIAN C. EMIG

BRACHIOPODS (lamp shells) are enclosed in shells (valves) and may be mistaken at first for clams or other bivalve mollusks. However, the shells of brachiopods are dorsal and ventral in position instead of lateral as in mollusks. Most brachiopods are attached to the substrate by a cordlike stalk, the pedicle, opening through the ventral valve in the Articulata and between them in the Inarticulata. A few species are attached directly to the substrate by the surface of the ventral valve. The lophophore, a specialized structure consisting of 2 thin, coiled plates bearing ciliated tentacles, surrounds the mouth but not the anus (the latter absent in the Articulata). The lophophore mainly functions in feeding, respiration, and protection. Brachiopods are an entirely marine group found in shallow water as well as at great depths. Far more species are recorded from earlier geological periods than occur at the present time.

The brachiopods are divided into 2 classes[1]: the Articulata, in which the valves are hinged by interlocking teeth and sockets, and the Inarticulata, in which the valves are held together by muscles only. In Hawaiian shallow waters only 1 species from each class is known with certainty, although 5 others are recorded from deeper waters (Dall 1895, 1921).

Class INARTICULATA

Lingula reevei Davidson, 1880

The thin, smooth, oblong-ovate shells (dorsal and ventral valves) attain 4 cm in length and the slim whitish pedicle is from 5 cm long when contracted to more than 20 cm when extended. The valves are broadest near the posterior third and have parallel lateral edges (Fig. 2.V.1). Posteriorly, the ventral beak slightly overlaps the dorsal. The valves have a conspicuous blue-greenish or emerald color, with reddish brown and black in varying amounts marginally. The edges are surrounded by light-colored setae of various lengths (Plate 2.V.1a) (Emig 1982).

In Hawaii the animal lives in a vertical burrow in sand at depths from 30 cm

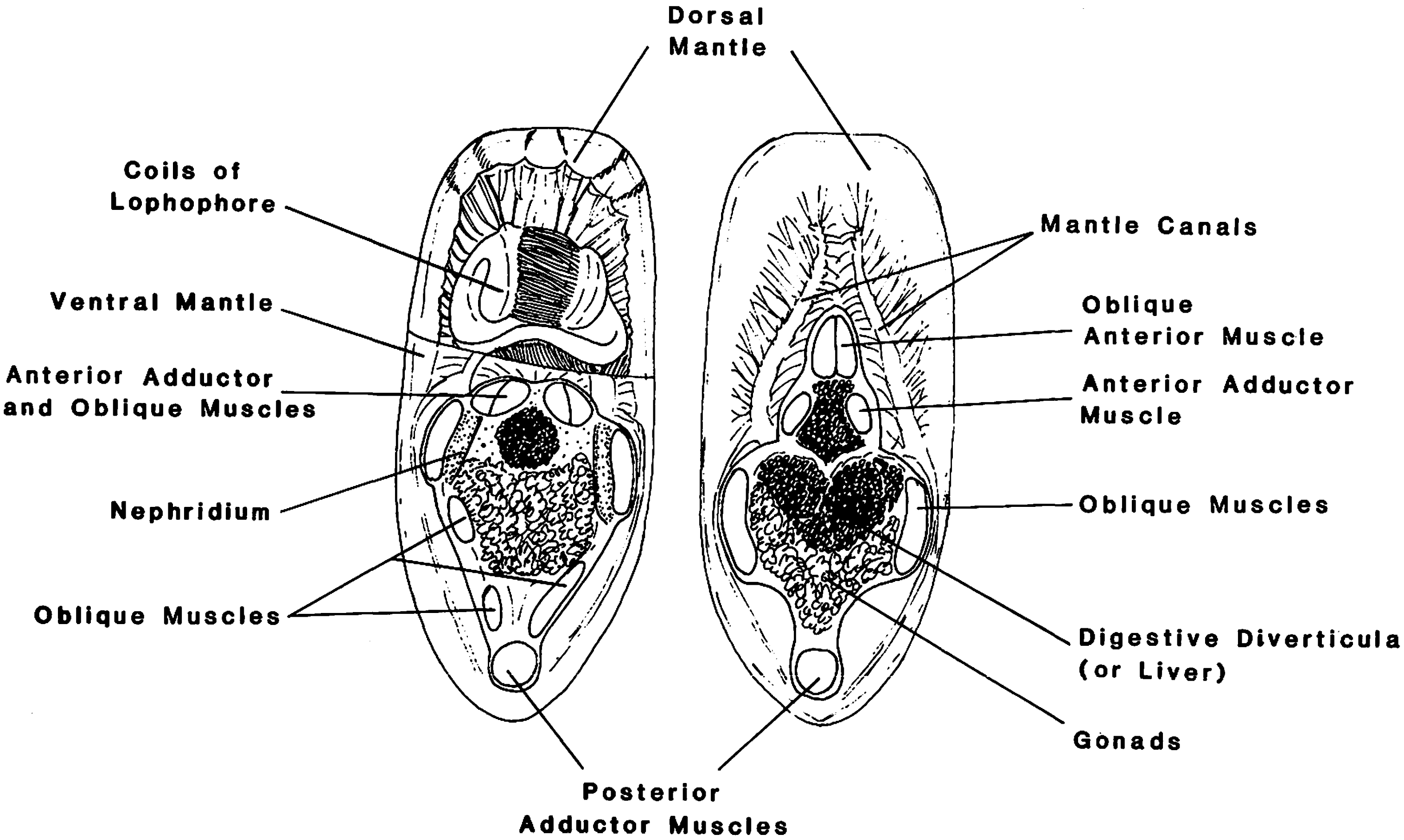

Figure 2.V.1.—*Lingula reevei:* generalized diagrammatic external views of ventral (left) side of body (with anterior part of mantle cut away to show lophophore) and dorsal (right) side of body.

Figure 2.V.2.—*Lingula reevei:* several characteristic 3-hole burrow openings in sand maintained by setae for water currents.

to 5 m. A 3–hole siphonal opening formed by the valve setae is evident at the sand surface (Fig. 2.V.2). This opening is reduced to a slit when the animal retracts. In Hawaiian waters, *L. reevei* is recorded only from Kaneohe Bay, Oahu, where it has been found most abundantly in the southeastern part of the bay in the lower intertidal and subtidal reef flats (Emig 1978, 1981, 1984). Recently Cals and Emig (1979) reported this species from Indonesian waters.

Class ARTICULATA

Frenulina sanguinolenta (Gmelin, ~~1817~~ 1791)
[syn. *Megerlia sanguinea* Chemnitz: Edmondson 1946]

This brachiopod is subcircular in outline and has inflated valves about 5 mm in diameter with an opening in the ventral valve for the pedicle (Plates 2.V.1b,c). The shell is beautifully colored with irregular, radiating blotches of red. An extensive description was given by Hatai (1940). Specimens have been collected from shallow depths in Kaneohe Bay and Honolulu Harbor and along the leeward coast of Oahu, where they have been found to depths of over 600 m. The valves are occasionally washed ashore along beaches. *Frenulina sanguinolenta* is widely distributed in the tropical Indo-West Pacific, including the Philippines as well as Japan.

NOTE

1. Editor's note: Emig (1977) has proposed that Brachiopoda, Ectoprocta, and Phoronida constitute separate classes in his newly established phylum Lophophorata. Adoption of this classification scheme has yet to be agreed upon by Anglo-American biologists working with these groups. The more conventional system that considers these 3 groups as separate phyla is retained in the present publication.

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SECTION 2

Chapter VI

Phylum PHORONIDA

CHRISTIAN C. EMIG and JULIE H. BAILEY-BROCK

PHORONIDS are exclusively marine animals living in cylindrical tubes of their own secretion. The tubes may be covered with sand grains and arranged vertically in soft sediments or the animals may encrust or burrow in hard substrates (e.g., corals, rocks, shells, barnacles). This group of small, widely distributed benthic invertebrates comprises only 2 genera, *Phoronis* and *Phoronopsis*. Three species of *Phoronis* are known from Hawaiian waters (Emig 1982).

Until recently the only evidence of phoronids in Hawaiian waters has been the presence of their actinotroch larvae in the plankton. Zooplankton samples have periodically yielded advanced actinotrochs since 1945 (A. H. Banner, pers. comm.), but the location of phoronid populations remained unknown until 1976 when 3 phoronid species were collected from shallow coral-reef habitats in Kaneohe Bay, Oahu. Two species, *Phoronis ovalis* and *Phoronis hippocrepia,* burrow into calcareous materials and were found in the course of sorting benthic carbonate samples processed by acid dissolution, a technique devised by Brock and Brock (1977). The third species, *Phoronis psammophila,* came from a subtidal sand flat where it forms vertically oriented, sand-encrusted tubes. These 3 species of phoronids from Hawaiian waters were identified by Emig (1977) and the distribution of *Phoronis hippocrepia* was included in an unpublished environmental report by Brock (1976).

Adult morphology (Fig. 2.VI.1). The phoronid body is vermiform and divided into 3 regions, each with a coelomic cavity (coel): the epistome (or protosome), with a protocoel; the lophophore (or mesosome), with a mesocoel; and the trunk (or metasome), with a divided metacoel. The lophophore is the anteriormost region and is a tentacular extension of the mesosome surrounding the mouth but not the anus. The lophophore functions in food gathering (ciliary bands on the lophophoral tentacles filter particulate organic matter from the water and convey it to the mouth), respiration, and protection (Emig 1976). A transverse mesentery,

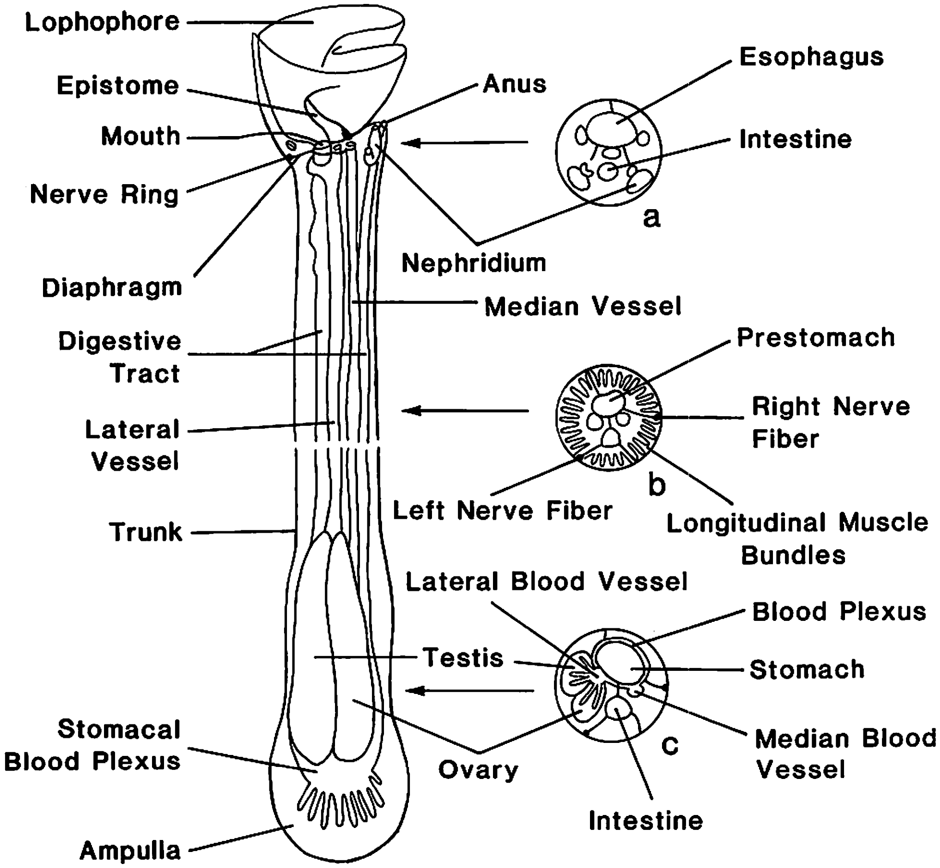

Figure 2.VI.1.—Diagram of an adult phoronid (*Phoronis psammophila*), with cross sections at 3 levels: a, nephridial; b, muscular; c, ampullary.

the diaphragm, is located at the base of the lophophore. The trunk contains the main organs and is slender and cylindrical with an end-bulb, or ampulla, which is used for burrowing and anchorage in the tube. The U-shaped digestive tract extends through the trunk. The anus lies near the mouth but is separated from it by the lophophore and the epistome. Nephridia (excretory organs) are located on both sides of the intestine near an anal papilla. The nephridia open into the trunk coelom by 1 or 2 funnels and to the exterior by a nephridiopore on either side of the anus. Ripe gametes (eggs and sperm) as well as excretory wastes pass to the exterior via the nephridia. The circulatory system contains red blood corpuscles and comprises 2 longitudinal vessels (3 in *Phoronis ovalis*) uniting in the stomacal blood plexus and in the lophophoral vessel. The nervous system is basiepithelial; a ganglion between the mouth and anus connects to a nerve ring at the level of the diaphragm, and to 1 or 2 giant nerve fibers.

Most phoronids are hermaphroditic (an individual produces both eggs and sperm), but some are dioecious (produce only eggs or sperm). The gonads are attached to the lateral blood vessel and its capillary caeca adjacent to the stomach. Accessory sex glands develop in the lophophoral cavity and may be concerned

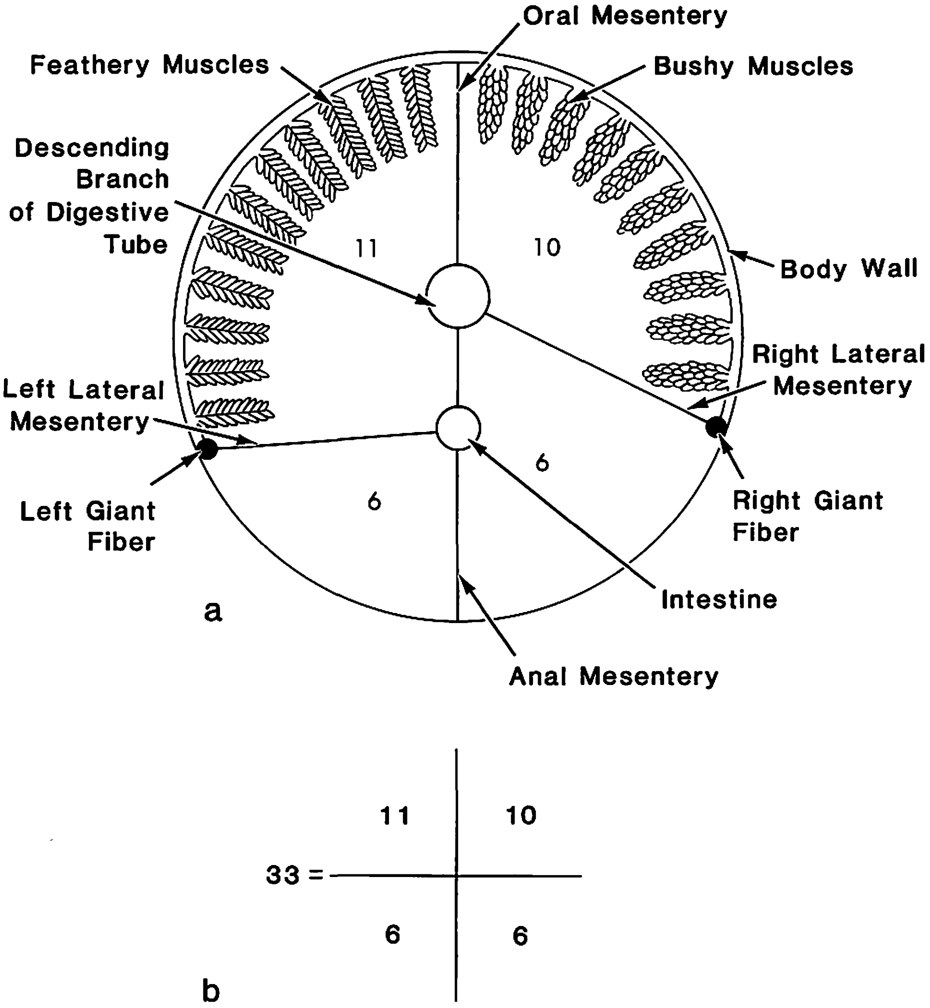

Figure 2.VI.2.—a, cross section through the trunk of a diagrammatic phoronid showing the arrangement of longitudinal mesenteries dividing the trunk into 4 unequal compartments, and the 2 types of longitudinal body-wall muscles (bushy and feathery) recognized. Muscles are all of 1 type for any given species, although the number in each quadrant varies from individual to individual and may change with age (body-wall muscles in lower compartments not shown); b, the conventional muscle formula for Figure 2.VI.2a.

with sperm distribution and, in some species, with embryo brooding. The trunk coelom is divided into 4 compartments by longitudinal mesenteries, which are used to establish the formulae describing the arrangement of the longitudinal muscle bundles of the trunk wall (Figs. 2.VI.2a,b). This formula and the shape of the longitudinal muscles in section (bushy or feathery, Fig. 2.VI.2a) are key taxonomic features.

Larval morphology (Fig. 2.VI.3). The typical phoronid larva is an actinotroch that usually has a lengthy planktonic existence, although *Phoronis ovalis* is an

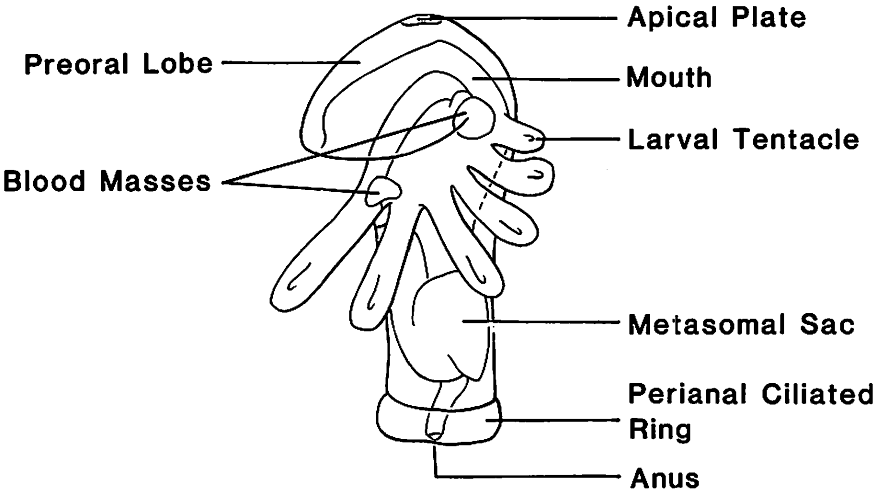

Figure 2.VI.3.—Diagram of an actinotroch larva (*Phoronis psammophila*) approaching metamorphosis.

exception (Emig 1982). The actinotroch is composed of 3 regions, each with a coelomic cavity, but the collar coelom (or incipient lophophoral coelom) appears only in later stages of development.

A preoral hood or lobe bears the apical plate, or larval neural ganglion, that is characteristic of most actinotroch larvae. The main swimming and feeding structures are an anterior circle of ciliated tentacles and a posterior ciliated ring. Larvae approaching metamorphosis develop definitive lophophoral tentacles at the bases of the larval tentacles and a metasomal pouch within the elongating metasome. At metamorphosis the metasomal pouch everts to form the trunk; burrowing and tube formation follow. The larval digestive tube is straight and lacks the prestomach but becomes U-shaped following eversion of the metasomal pouch at metamorphosis (Zimmer 1978; Emig 1979; Herrmann 1979).

Phoronis ovalis produces lecithotrophic larvae that have a short pelagic life (4 days) before developing into crawling, sluglike larvae (Figs. 2.VI.4a,b) that settle, curl up under a thin membrane (Figs. 2.VI.4c,d), and eventually burrow into the underlying carbonate substrates (Silén 1954).

PHORONID STUDY TECHNIQUES

Features of taxonomic importance used in the identification of adult phoronids include lophophoral tentacle arrangement, nephridial morphology, giant nerve fiber number, longitudinal trunk body-wall muscle formula, gonads, and accessory sex-gland characteristics (Emig 1974, 1979). Most of these features can only be determined after histological examination. At the time of collection, specimens should be placed in Bouin's fixative, dehydrated, embedded in paraffin wax, sectioned at 7 μm, and stained in Azan (Heidenhain method). Details of the embedding, sectioning, and staining techniques can be found in Galigher and Kozloff (1971). The habitat from which specimens are collected can also be useful in identification of the species.

The following key to the identification of known adult Hawaiian phoronids is based on readily visible external structures.

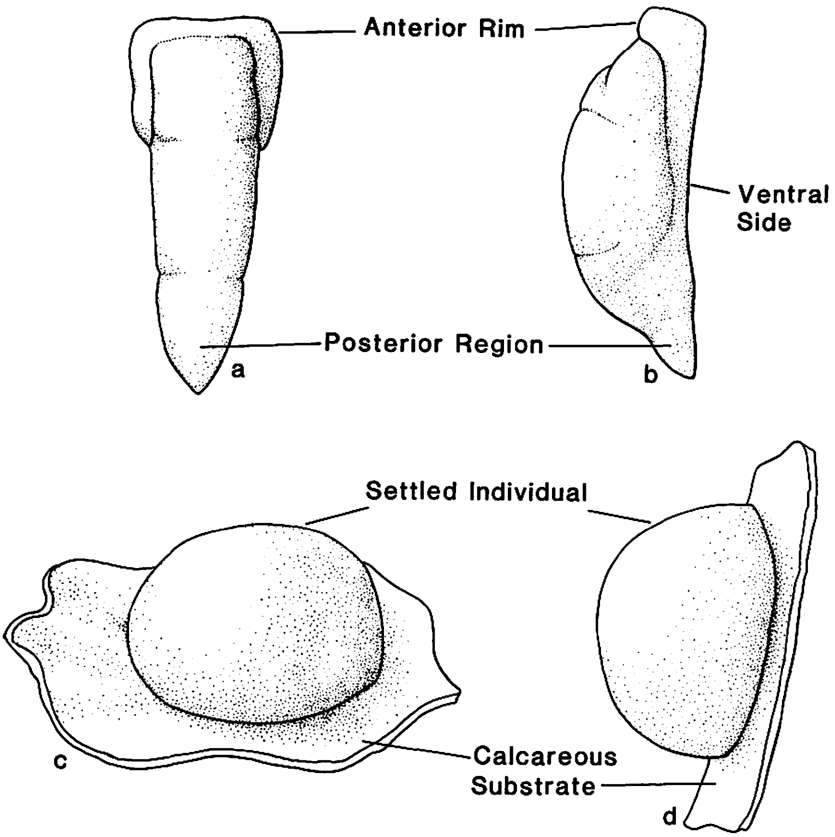

Figure 2.VI.4.—*Phoronis ovalis* larvae: a, dorsal and b, lateral view of fifth-day larva at the creeping stage; c, dorsal and d, lateral view of seventh-day larva at settlement (from Silén 1954).

KEY TO HAWAIIAN PHORONIDA

1 Tube straight, vertically oriented in sediment, and covered with attached sand grains; adults 15 to 44 mm long (contracted) .... *Phoronis psammophila*

Tube membranous, often sinuous and contained within calcareous materials (except for the aperture); adults 2 to 30 mm long........ 2

2(1) Tentacle bases form simple oval shape; adults minute, 2 to 6 mm long (contracted) .... *Phoronis ovalis*

Tentacle bases form horseshoe shape; adults 5 to 30 mm long (contracted) .... *Phoronis hippocrepia*

Phoronis hippocrepia Wright, 1856

This species (Figs. 2.VI.5a–c) is flesh-colored, about 5 to 30 mm long when contracted, and has a horseshoe-shaped lophophore composed of as many as 150 tentacles. The nephridia have a single ascending branch (Fig. 2.VI.6a) forming 2 horizontal chambers; the lower one opens by 2 coelomic funnels (the anal funnel

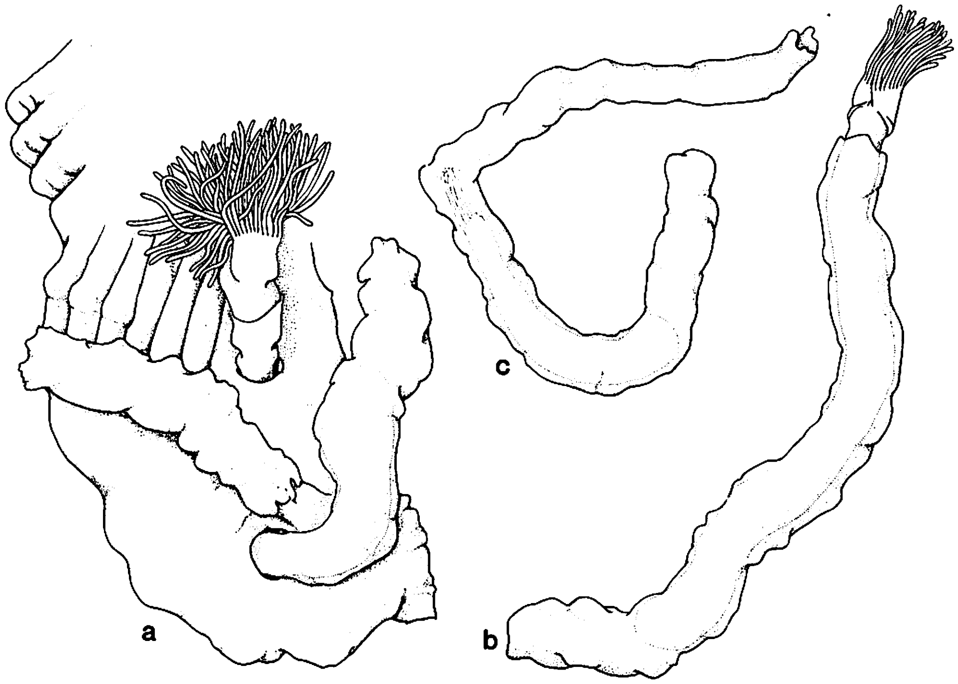

Figure 2.VI. 5.—*Phoronis hippocrepia*, whole animal: a, *in situ* within an empty barnacle shell; b, removed from the shell, an individual with the anterior region and lophophore protruding from its tube; c, the position of a retracted individual within its tube.

is larger than the oral funnel). Two giant nerve fibers are present, 1 on the left (4 to 10 μm in diameter) and 1 on the right (1 to 7 μm in diameter). The longitudinal muscles, of the bushy type, vary according to the following conventional formula (see Fig. 2.VI.2):

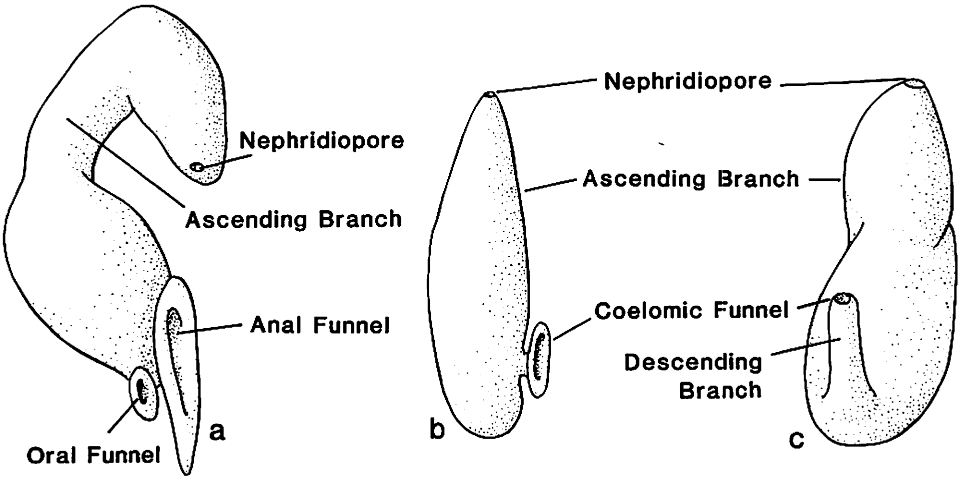

Figure 2.VI.6.—Structure of nephridia: a, *Phoronis hippocrepia*; b, *P. ovalis*; c, *P. psammophila*.

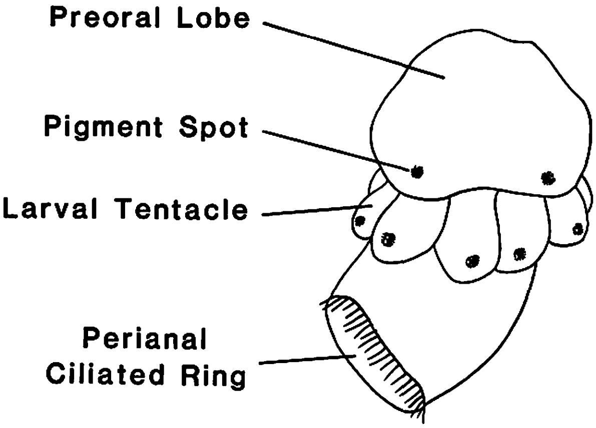

Figure 2.VI.7.—*Phoronis hippocrepia* larva: lateral view (from Silén 1954).

$$[24\text{–}43] = \begin{array}{c|c} 7\text{–}15 & 7\text{–}16 \\ \hline 3\text{–}7 & 3\text{–}10 \end{array}$$

Phoronis hippocrepia is hermaphroditic, and its embryos are brooded as paired masses in the lophophore. The larva, which was described by Silén (1954) as *Actinotrocha hippocrepia* (Fig. 2.VI.7), is characterized by an opaque body covered with patches of pigment. The larva also has 2 ventral blood masses that fuse in older larvae and 10 larval tentacles.

In Kaneohe Bay, *P. hippocrepia* burrows into coral rock, and into oyster shells and barnacles (Fig. 2.VI.5a) attached to harbor pilings to depths of 30 cm below mean tide level. The animal secretes a membranous tube that lines the burrow and that usually branches and ramifies through the carbonate matrix. Clusters of translucent white lophophores are readily visible in areas protected from excessive water motion. This species is known from the North Atlantic, North Sea, Mediterranean, southern Africa, and Brazil (Emig 1973). In the Pacific this species has been recorded only from the Hawaiian Islands (Emig 1977).

Phoronis ovalis Wright, 1856

This is the smallest known phoronid species. It is generally 2 to 6 mm long, with an oval-shaped lophophore (composed of 11 to 28 short tentacles). Specimens are usually transparent or semitransparent and some have a band of brown pigmentation where the lophophore joins the trunk (Forneris 1959). The ampulla is well developed (Fig. 2.VI.8), serving to anchor the animal within the burrow. Nephridia have a straight ascending tube and a single, small coelomic funnel (Fig. 2.VI.6b). The nervous system lacks (not visible) giant nerve fibers, and both lateral mesenteries are absent from the trunk. In addition to the typical circulatory system, an "accessory" blood vessel and a second lateral longitudinal vessel exist. There are 14 to 39 longitudinal muscles, of which 7 to 21 are in the left cavity and 7 to 19 in the right one. (There is no conventional formula for this species because of the absence of lateral mesenteries in the trunk). *Phoronis ovalis* is probably dioecious. It lacks nidamental glands (accessory sex glands) but is

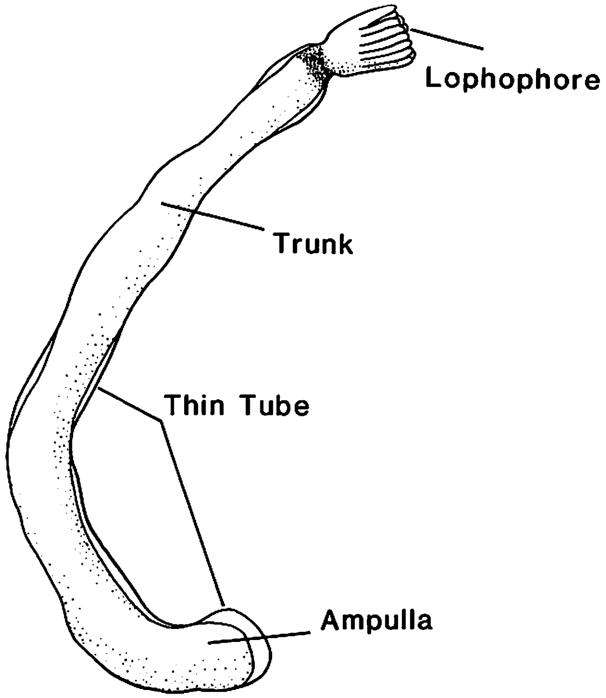

Figure 2.VI.8.—*Phoronis ovalis:* whole animal (contracted).

known to brood embryos within the parental tube (Silén 1954). In Hawaii, *P. ovalis* is found on shallow reef flats in burrows in coral rubble, where it attains estimated densities of 12,000/m^2 in Kaneohe Bay, Oahu. However, individuals are difficult to find because of their small size and cryptic habitat. This species is known from the North and South Atlantic, North Sea, Mediterranean, Chile, New Zealand, Vancouver, and the Hawaiian Islands (Emig 1973, 1977).

Phoronis psammophila Cori, 1889

Adult specimens are flesh-colored and from 15 to 40 mm long when contracted (Fig. 2.VI.9). The lophophore is horseshoe-shaped and composed of as many as 130 tentacles, which are speckled with white spots that remain after preservation. The nephridia have a descending branch opening by a single coelomic funnel and an ascending branch (Fig. 2.VI.6c). There is a single giant nerve fiber on the left side measuring 5 to 27 μm in diameter. The longitudinal muscles are of the feathery type and the formula is:

$$[25\text{–}53] = \frac{7\text{–}19 \;\big|\; 7\text{–}17}{4\text{–}11 \;\big|\; 4\text{–}11}$$

Specimens from Kaneohe Bay, Oahu, had the following muscle band formulae:

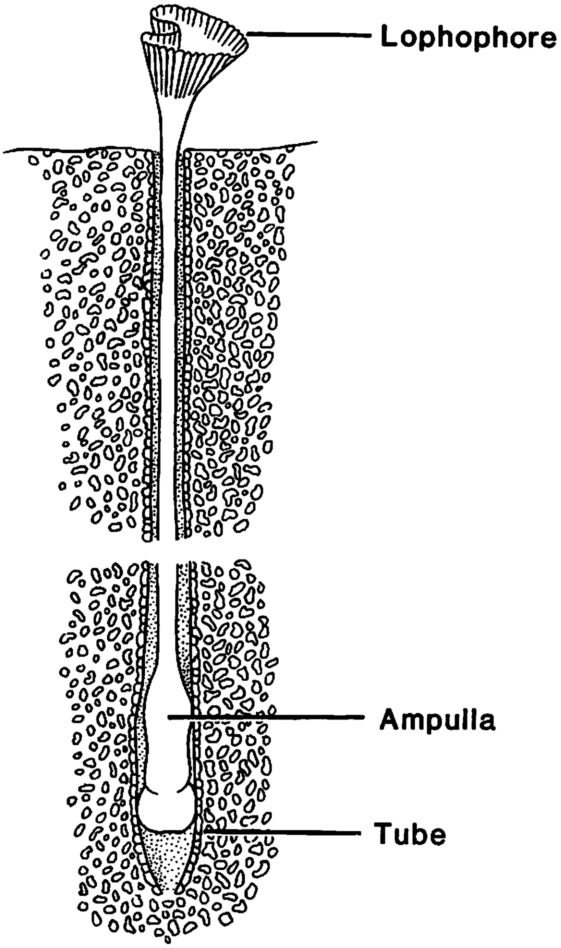

Figure 2.VI.9.—*Phoronis psammophila:* whole animal in normal position in its tube embedded in sand.

$$33 = \begin{array}{c|c} 11 & 10 \\ \hline 6 & 6 \end{array} \text{ or } 34 = \begin{array}{c|c} 10 & 10 \\ \hline 7 & 7 \end{array} .$$

Phoronis psammophila is dioecious; the females brood their embryos in a single mass in the lophophoral cavity. The pelagic larva is known as *Actinotrocha sabatieri* and was discovered by Roule (1896). The larva (Herrmann 1979) is transparent and has 3 blood masses, 1 on each side of the esophagus and the third on the ventral midline just above the tentacles. There are up to 12 larval tentacles, and presumptive adult tentacles are represented by thickenings of the larval tentacles (Fig. 2.VI.3).

Phoronis psammophila has been found subtidally to a depth of 3.5 m in an area of fine sand and coral rubble in Kaneohe Bay, Oahu. These specimens have the characteristic straight tube covered with sand grains arranged vertically in the sediment (Fig. 2.VI.9). *Phoronis psammophila* is known from cool temperate and tropical regions of world oceans; in the tropical Pacific it has been found in the Solomon Islands, Panama, and in the Hawaiian Islands (Emig 1973, 1979).

ACKNOWLEDGMENTS

We are grateful to the Director and staff of the Hawaii Institute of Marine Biology for providing laboratory space for one of us (C.C.E.). We thank the late Dr. A. H. Banner for information on phoronid larvae in Hawaiian waters, Dr. S. V. Smith for making E.P.A. data and facilities available to us (Grant No. R 803983), and Geof Grovhoug (Naval Oceans System Center) for specimens. Richard E. Brock and Linda A. Ward kindly helped with sample processing.

NOTE

1. Annotated diagrams of morphology and internal anatomy of adult and larval phoronids can also be found in Emig (1975, 1979, 1982).

GLOSSARY (PHORONIDA)[1]

basiepithelial: In the lower part of the epithelium.

capillary caecum: Small blood vessel arising from the lateral blood vessel.

epistome: Epidermal flap of tissue bordering the inner tentacle row and overlapping the mouth that contains a fluid-filled cavity, the protocoel, and is surrounded by the lophophore.

ganglion: Group of nerve cell bodies.

lecithotrophic larvae: Larvae containing stored food reserves as yolk, usually with a short pelagic phase.

lophophore: Oval or horseshoe-shaped (sometimes more complex) feeding, respiratory, and protective structure composed of 2 rows of ciliated tentacles that surround the mouth and contain extensions of the mesocoel. The lophophore contains important components of the nervous and vascular systems.

muscle formula (Fig. 2.VI.2): The number of longitudinal body-wall muscles in each quadrant of the trunk.

preoral lobe or hood: Anterior hood in the actinotroch larva that projects ventrally above the entrance to the mouth and contains the protocoel.

prestomach: Part of the descending branch of the digestive system between the esophagus and the stomach, with a ciliary groove for conveying food materials to the stomach. Not present in the larva.

stomacal blood plexus: Blood-filled sinus surrounding the stomach of the phoronid into which the lateral blood vessels flow. Blood then enters the median vessel and is transported anteriorly.

trunk: The adult phoronid is divided into 2 major body regions based on external morphological features, the lophophore anteriorly and the rest of the body (or trunk) posteriorly. The trunk contains most or all of the main organs and systems, and the swollen posterior end is referred to as the ampulla.

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SECTION

3

SECTION 3

Chapter I

Phyla SIPUNCULA and ECHIURA

S. J. EDMONDS

SIPUNCULANS (peanut worms) and echiurans (proboscis worms) are marine invertebrates whose bodies are unsegmented, unlike those of earthworms and bristle worms (polychaetes) of the phylum Annelida. Although some similarities are found in their structure and habits, annelids, sipunculans, and echiurans are each considered to belong to a different phylum. Sipunculans and echiurans are found in tropical, temperate, and polar seas.

Members of both phyla are soft-bodied animals that live in protected places, often in burrows. They are usually found in sand or mud, under or between rocks, in masses of coral or in limestone reefs, in the holdfasts of algae or the roots of seagrasses, in the empty shells of molluscs, or in the tests of echinoids and large foraminiferans. In warm water areas they can be abundant if not conspicuous inhabitants of coral reefs and other marine habitats. Sipunculans and echiurans are largely detritus feeders, ingesting large quantities of sand, mud, rock, or coral fragments and extracting the organic matter contained in them.

Most sipunculans and echiurans are cylindrical, flasklike, or saclike and vary in length from 5 to 300 mm. The body wall of both sipunculans and echiurans is muscular, and sometimes the longitudinal muscle layer is grouped into bands that may be clearly visible externally. Natural colors caused by respiratory and other pigments present in living animals are usually lost when animals are fixed and stored.

The sexes in both groups are separate. In sipunculans, eggs and sperm are shed into the sea, where fertilization takes place. The zygote rapidly develops into a trochophorelike larva. A later larval stage, the pelagosphaera, is known for some Hawaiian sipunculans (Williams 1977). After a free-swimming stage, the larva changes into an adult. Two species of sipunculans are known to reproduce asexually by budding. Reproduction and development in some echiurans, especially bonelliids, may be more complex.

SIPUNCULAN AND ECHIURAN STUDY TECHNIQUES

Species that live in sand, mud, or under rocks are usually easy to collect. When it is necessary to dig them out, it is usually best to use a fork rather than a spade. Those that are flask- or sausage-shaped can be more difficult to collect, especially if they are sipunculans that live in limestone or coral. Rarely can animals be collected by tugging at the introvert or proboscis. They are usually best collected by working or pulling at the posterior end of the trunk. If the hard substrate does not break easily, it is sometimes helpful to soak it in very weak formalin (0.5%) made up in seawater. The sheltered worms will then sometimes partly or completely dislodge themselves. The external features of living specimens are best studied by placing them in fresh seawater.

Sipunculans and echiurans can be relaxed in seawater to which a liberal amount of menthol crystals has been added. In an hour or two, carefully add (drop by drop) 80% alcohol. It may take from 30 minutes to 12 hours before the animals do not respond to touch. They should then be left 24 hours in 5% neutral formalin, washed in tap water, then stored in 70% ethyl alcohol.

To dissect a preserved specimen, place it dorsal side up (the anteriorly placed anus denotes the dorsal side of a sipunculan; the anteriorly placed setae indicate the ventral surface of an echiuran) in a dish or shallow pan containing a layer of solidified paraffin wax. Cover the animal with water. Using a scalpel and forceps, make a longitudinal incision on the dorsal surface at the posterior end of the trunk, and cut forward along the body wall. For a sipunculan, the cut should pass a little to the left of the anus; avoid cutting deeply. Pin out the flaps of the body wall, cutting away any mesenteries if necessary and exposing the internal structures. To prepare a mount of the introvert hooks or the body papillae of a sipunculan, snip off small pieces of the skin from the introvert and body and place them on a slide with a drop of glycerine. With the aid of 2 fine needles, tease the introvert tissue containing the hooks. When this preparation is examined under low power, single hooks or groups of hooks can be seen. Remove unwanted tissue and cover with a cover slip. Only hooks that lie flat should be drawn. There is no need to tease the tissue containing the papillae.

The anatomy of a "typical" sipunculan and echiuran is shown in Figs. 3.I.1,2.

Phylum SIPUNCULA

Sipunculans differ most noticeably from echiurans in possessing an anteriorly placed introvert that can be extended in front of the trunk or retracted within it. The mouth of a sipunculan is usually completely or partly surrounded by tentacles, which may be fingerlike, branched, or modified into folds of tissue. Setae are never present. The anal aperture is usually on the dorsal surface of the trunk at the base of the introvert. In oxygenated water, sipunculans are sometimes pink-red because of the respiratory pigment hemerythrin that they contain. Some species of *Phascolosoma, Aspidosiphon, Golfingia,* and *Themiste,* however, are gray, brown, or dark red-brown.

The most noticeable internal structures of a sipunculan are (1) the retractor muscles, which help to control the retraction of the introvert, and (2) the alimentary canal. The number and point of attachment of the retractors to the

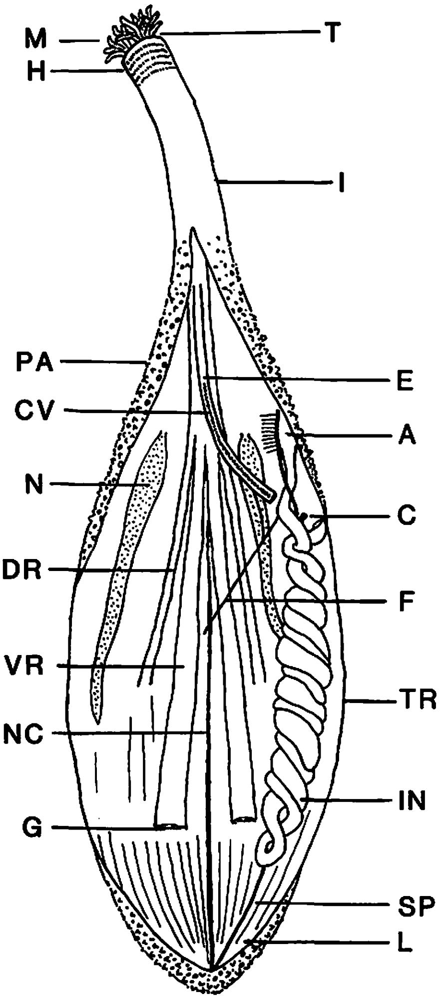

Figure 3.I.1.—A dissected sipunculan (generalized). See Fig. 3.I.2 for explanation of abbreviations.

body wall are often important in identification. Another important set of muscles in some species is the longitudinal bands. The number of longitudinal muscles is counted in the midtrunk region. Muscles lying on each side of and next to the ventral nerve cord are numbered 1; those lying more dorsally to number 1 become 2, 3, 4, etc., in succession. The alimentary canal is very long and most of it is usually wound into a spiral. Additional internal structures are also encountered. There is a contractile vessel attached to the dorsal wall of the esophagus. A pair of tubular, flasklike, or saclike nephridia is usually present on the ventral surface near the level of the anus and a nerve cord runs along the ventral surface of the body wall.

Until recently, little had been published on the habits and ecology of sipunculans. Rice (1975) reviewed the common species that inhabit beach rock and coralline limestone in the Caribbean Sea and reported on their feeding patterns and possible boring habits. Two limestone reef solution benches on the

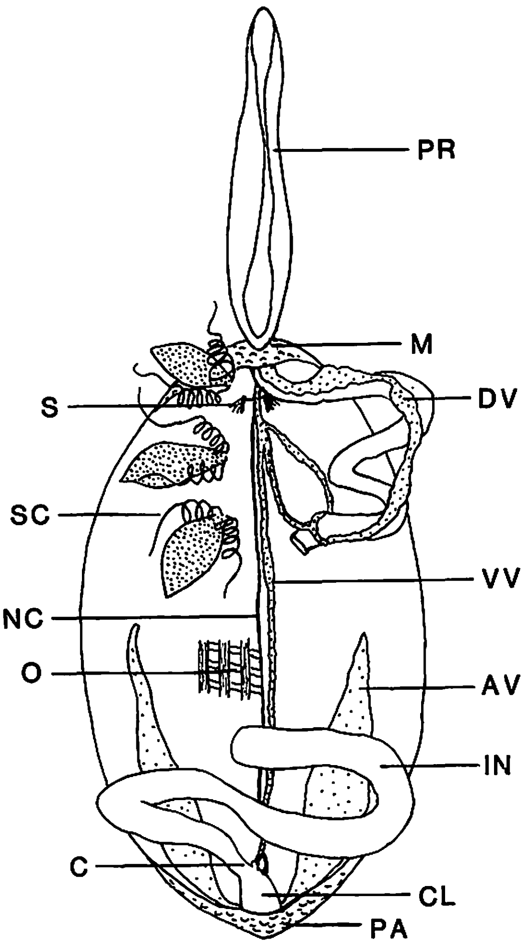

Figure 3.I.2.—A dissected echiuran (generalized). (Abbreviations for Figures 3.I.1,2: A, anus; AV, anal vesicle; C, caecum; CL, cloaca; CV, contractile vessel; DR dorsal retractor muscle; DV, dorsal blood vessel; E, esophagus; F, fixing muscle; G, gonad; H, hooks; I, introvert; IN, intestine; L, longitudinal muscle band; M, mouth; N, nephridium; NC, nerve cord; O, oblique muscle bands; PA, papillae; PR, proboscis; S, setae; SC, spirally coiled nephrostomal lips; SP, spindle muscle; T, tentacles; TR, trunk; VR, ventral retractor muscles; VV, ventral blood vessel.)

islands of Oahu and Hawaii revealed densities of burrowing sipunculans ranging from 470 to 740 worms/m^2 (Kohn 1970). In another paper, Rice (1976) dealt with sipunculans associated with coral communities. Some of the Caribbean species studied, such as *Antillesoma antillarum, Phascolosoma perlucens,* and *Themiste lageniformis,* are also present in Hawaii, and it seems likely that their habits are similar in the 2 localities.

Rice (1976) reported on the feeding methods of some rock-dwelling sipunculans and described at least 2 kinds of feeding behavior. On the one hand there are species with long, extensible introverts and short, digitiform tentacles. These animals extend their introvert from the mouth of the burrow to graze the surface of the surrounding substrate. For example, a specimen of *Phascolosoma* *perlucens* kept within burrows in the laboratory fed on sediment and detritus from the surface of the rock, scraping with the small hooks on its introvert and collecting any particles that adhered to its tentacles. The food was then directed into the mouth, presumably by ciliary activity of the tentacles. The gut contents of *P. perlucens* contained rock fragments, unidentified fine particulate matter, algal strands, diatoms, foraminiferans, and a few small crustaceans. On the other hand, rock-dwelling species, such as *Antillesoma antillarum* and *Themiste lageniformis,* with long, more threadlike tentacles and a short introvert, use a ciliary-mucus mechanism for feeding. Rice also noted that for those animals in which the tentacular crown is extended above the mouth of the burrow, particles adhere to the sticky tentacles and are directed by ciliary currents into the digestive tract. Rice (1975) reported that some rock-boring sipunculans are algal grazers.

Rice (1969), Rice and MacIntyre (1972), and Williams and Margolis (1974) have investigated how sipunculans bore into calcareous rock. Because the surface of a sipunculan is highly glandular, it has been suggested that some secretion is responsible for the dissolution of the rock. Another theory is that the burrows are formed by the abrasive action of hardened papillae, introvert hooks, and hardened terminal shields. In a discussion on the matter, Rice (1976, p. 128) said that "microscopic examination of the linings of burrows suggested that both mechanical and chemical processes could be involved in burrow formation. Indication of mechanical abrasion in burrows in coral fragments with sediment infill were found in the finely comminuted carbonate skeletal grains in pockets of the walls of the burrows. However, the source of the comminuted material was uncertain. Indication of chemical activity was found in the alteration of the microstructure of components of rock at the edge of the burrow." Williams and Margolis (1974) examined sipunculan burrows with the aid of a scanning electron microscope. They found that the crystalline structure of the lining of the burrows of *Themiste lageniformis* was etched and eroded, a condition similar to that produced when unmodified coral surfaces were treated with acid and the chemical EDTA. They considered that "initial bio-chemical activity appears to weaken intercrystalline bonds, permitting detachment of crystals by mechanical abrasion and the subsequent deposition of their fragments in spaces between the corallite walls" (p. 357).

Edmonds (1980) summarized the ecological roles of sipunculans, noting that they perform at least 5 functions. (1) They are decomposer organisms, feeding on complex substances (usually as finely divided particles, algae, diatoms, etc.) and breaking them down into simpler substances. (2) By their boring action, sipunculans assist in the disintegration of coral and limestone reefs. (3) They are eaten by other animals, especially fishes and, to a lesser extent, molluscs. Kohn (1970) reported that the gastropod *Mitra litterata* preys on 2 species of *Phascolosoma* and on *Aspidosiphon elegans* that burrow in the intertidal reef at Oahu, Hawaii, where it is believed that the sipunculans are eaten mostly during the night. (4) Sipunculans are the definitive hosts of a number of parasites, especially sporozoans, and they also act as intermediate hosts for a number of trematodes and cestodes, the adult stages of which probably occur in fishes. (5) They form symbiotic associations with other animals, especially the solitary corals *Heteropsammia* and *Heterocyathus,* the anemone-like *Cerianthus,* polychaetes, and molluscs.

A detailed account of the systematics of the phylum is given in Stephen and

Edmonds (1972). During the last several years, however, a number of important developments have occurred in sipunculan taxonomy as a result of the work of Cutler and Cutler (1982, 1983), Gibbs et al. (1983), Cutler et al. (1984), and Cutler and Gibbs (1985), the last serving to some extent as a summary of their ideas up to 1985. Attempts have been made in the present paper to bring the nomenclature of the Hawaiian sipunculans in line with the recent systematic changes within the phylum.

LIST OF SIPUNCULANS KNOWN FROM HAWAII

Specimens of the species listed below, except those marked with an asterisk (*), were sent to me for identification from the Bishop Museum, Honolulu. The species asterisked were collected and identified by Dr. and Mrs. E. B. Cutler during a visit made to Hawaii in August, 1985. I am indebted to the Cutlers for passing on the information and permitting me to use it in the present paper. Their assistance is acknowledged. Previous records of Hawaiian sipunculans are contained in Edmondson (1933, 1946), Fisher (1952), Kohn (1970), and Edmonds (1980). Fourteen species have now been recorded.

1. *Antillesoma antillarum* (Grübe and Oersted, 1858)
2. *Phascolosoma nigrescens* Keferstein, 1865
*3. *Phascolosoma pacificum* Keferstein, 1866
4. *Phascolosoma perlucens* Baird, 1868
5. *Phascolosoma scolops* Selenka, de Man, and Bülow, 1883
6. *Phascolosoma stephensoni* (Stephen, 1942)
7. *Sipunculus norvegicus* Danielssen, 1868
8. *Siphonosoma rotumanum* (Shipley, 1898)
*9. *Siphonosoma vastum* (Selenka, de Man, and Bülow, 1883)
10. *Themiste langeniformis* Baird, 1868
*11. *Aspidosiphon cumingi* Baird, 1868
12. *Aspidosiphon elegans* (Chamisso and Eysenhardt, 1821)
*13. *Aspidosiphon ochrus* Cutler and Cutler, 1979
14. *Lithacrosiphon cristatus* (Sluiter, 1902)

KEY TO SOME TROPICAL AND SUBTROPICAL SIPUNCULAN GENERA OF THE PACIFIC REGION

The following key to some of the tropical and subtropical sipunculan genera of the Pacific Region is based on the more general ones contained in Edmonds (1980) and Cutler et al. (1984). Figure 3.I.3 illustrates the body shapes and external characters of some of the common genera.

1 No horny, chitinous, or calcareous cap or cone at anterior end of trunk 2
Horny, chitinous, or calcareous shield, cap, or cone present at anterior end of trunk 13

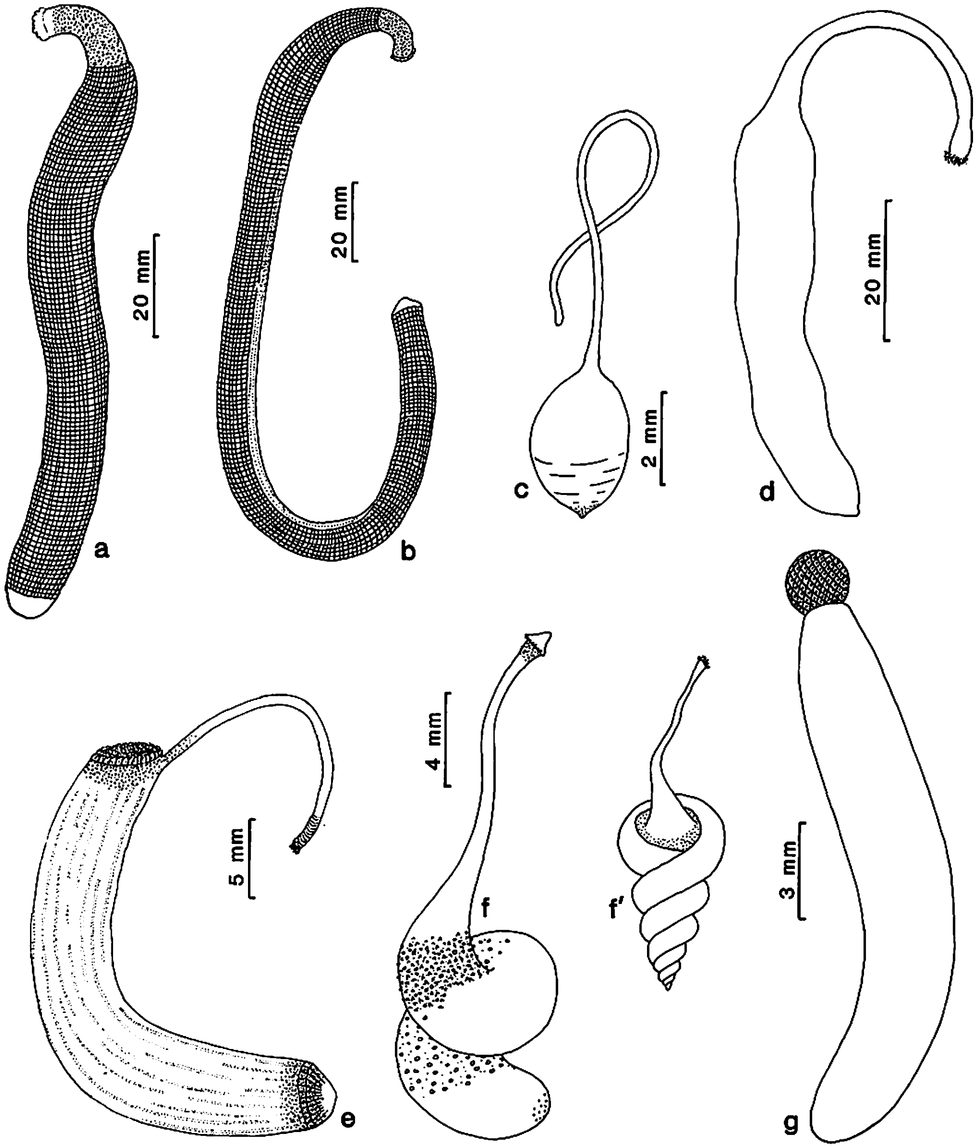

Figure 3.I.3.—Diagrams of additional genera of Pacific Ocean sipunculans (collected from non-Hawaiian regions of the Pacific Ocean): a, *Sipunculus*; b, *Xenosiphon*; c, *Onchnesoma*; d, *Golfingia*; e, *Aspidosiphon*; f, *Phascolion*, removed from shell; f′, *Phascolion*, in shell; g, *Cloeosiphon*.

2(1) Longitudinal muscle layer of body wall thickened into separate bands or bundles, which may anastomose (bands usually visible externally and always revealed on dissection) 3

Longitudinal muscle layer of body wall continuous and not thickened into separate bands 7

3(2) Complex peripheral tentacles or a tentacular fold surrounds mouth; body of adult long and cylindrical; usually found in sand or mud ... 4

Tentacles do not surround the mouth but lie in a ring dorsal to mouth; prominent, pigmented papillae usually present on anterior and posterior surfaces of trunk; usually found in firm substrates ... 6

4(3) Introvert with many triangular, scalelike papillae; body wall divided into rectangular areas by intersection of bands of longitudinal and circular muscles; spindle muscle arises anteriorly from 1 root and is not fastened posteriorly to body wall 5

Introvert without triangular, scalelike papillae; body wall not divided into rectangular areas; spindle muscle arises anteriorly usually from 3 roots and is fastened posteriorly to body wall .... *Siphonosoma*

5(4) Four retractor muscles; in addition, 2 small protractor muscles attached to introvert near brain .... *Xenosiphon*

Four retractor muscles but no protractor muscles .... *Sipunculus*

6(3) Introvert hooks present; contractile vessel without villi .... *Phascolosoma*

Introvert hooks absent; contractile vessel with villi ...... *Antillesoma*

7(2) Peripheral tentacles branching, bushlike, or dendritic; contractile vessel with villi 8

Peripheral tentacles not branching, bushlike, or dendritic; contractile vessel without villi 9

8(7) Oral tentacles arranged in double longitudinal rows ("festoons") around mouth and forming a dorsal arc that encloses nuchal organ .... *Thysanocardia*

Oral tentacles arising from 4 to 8 stems; nuchal tentacles absent .... *Themiste*

9(7) Spindle muscle attached posteriorly .... *Apionsoma*

Spindle muscle not attached posteriorly 10

10(9) Two nephridia 11

One nephridium 12

11(10) Two pairs of retractor muscles .... *Golfingia*

One pair of retractor muscles .... *Nephasoma*

12(10) Anal aperture lies on anterior surface of trunk (the usual position within the phylum); 1 or 2 retractor muscles; usually lives in empty shells of molluscs .... *Phascolion*

Anal aperture not on trunk but on introvert near mouth; 1 or 2 retractor muscles .... *Onchnesoma*

13(1) Introvert arises from center of a white, calcareous, rounded or pineapplelike knob or cap; longitudinal musculature of body wall continuous .... *Cloeosiphon*

Introvert arises ventrally to longitudinal axis of trunk 14

14(13) Cone-shaped, calcareous cap consisting of a single unit; longitudinal musculature of body wall in anastomosing bands .... *Lithacrosiphon*

Shield consists of numerous, hardened plates or units; longitudinal musculature of body wall either continuous or grouped into bundles; a second shield usually present at posterior extremity of trunk .... *Aspidosiphon*

DESCRIPTIONS OF GENERA AND SPECIES

Genus *Antillesoma* (Stephen and Edmonds, 1972)

Small to medium-sized sipunculans, rarely longer than 60 mm. Longitudinal musculature of trunk wall grouped into anastomosing bands, not always visible externally. Tentacles arranged in a near ring dorsal to mouth and surround the nuchal organ. Introvert hooks lacking. Four retractor muscles, which often fuse so that only 2 muscles may appear to be present. Spindle muscle attached posteriorly to body wall. Contractile vessel bears numerous villi, differing in this respect from the genus *Phascolosoma*. (*Antillesoma,* formerly a subgenus of *Phascolosoma,* was raised to generic level in Cutler et al. 1984, p. 289).

Antillesoma antillarum (Grübe and Oersted, 1858)
[syn. *Phascolosoma asser* (Selenka, de Man, and Bülow, 1883). *Phascolosoma pelmum* (Selenka, de Man, and Bülow, 1883): Edmondson 1933, 1946. *Phascolosoma antillarum* Grübe and Oersted, 1858]

The trunk of the Hawaiian specimens (Fig. 3.I.4) is brown, 22 to 40 mm long and 4 to 8 mm wide (maximum); the introvert is 7 to 13 mm long, straw to light brown and without hooks. Numerous threadlike tentacles present; they lie, as clearly shown in 2 specimens, in a near ring dorsal to the mouth. Numerous flat to rounded papillae are present on the trunk and introvert and are largest and most dense on the anterior and posterior regions of the trunk. The trunk papillae possess a small clear central area, which is surrounded by near circles of large, brown plates. Dark brown plates are also present on the trunk surface between the papillae and even on the introvert. The longitudinal musculature is grouped into 25 to 30 anastomosing bundles. Two ventral and 2 dorsal retractors arise at about the same level in the posterior half of the trunk. The 2 retractors on each side are separate for only a short distance and then fuse, so that when a specimen is dissected there may appear to be only 2 retractors. A spindle muscle is fixed anteriorly near the anus and posteriorly near the extremity of the trunk. A fixing muscle is attached to the rectum near the caecum. The contractile vessel bears numerous fingerlike villi. Two long, tubular nephridia extend into the posterior third of the trunk and are fixed to the body wall for most of their length.

Edmondson (1933, 1946) provisionally named one of the common boring sipunculans of Hawaii as *Phascolosoma pelmum,* a species now considered to be *Antillesoma antillarum.* The burrowing and feeding habits of the species have been described by Rice (1976). The specimens examined by me were collected from the south shore of Oahu and from Kahului, Maui. Cutler (1985, pers. comm.) collected 52 specimens from Maui. Fisher (1952) reported it from Halape, Hawaii. The species is also recorded from several other localities in the Pacific, from the Gulf of California, Panama, western Caroline Islands, Philippines, Malaysia, and Japan.

Genus *Phascolosoma* Leuckart

Small to medium-sized sipunculans, with trunk rarely longer than 60 mm; bottle or flask-shaped, sometimes subcylindrical. Longitudinal muscles of body wall always in bands, which often anastomose. Introvert hooks present. Tentacles lie in a horseshoe-shaped ring dorsal to mouth and enclose the nuchal organ.

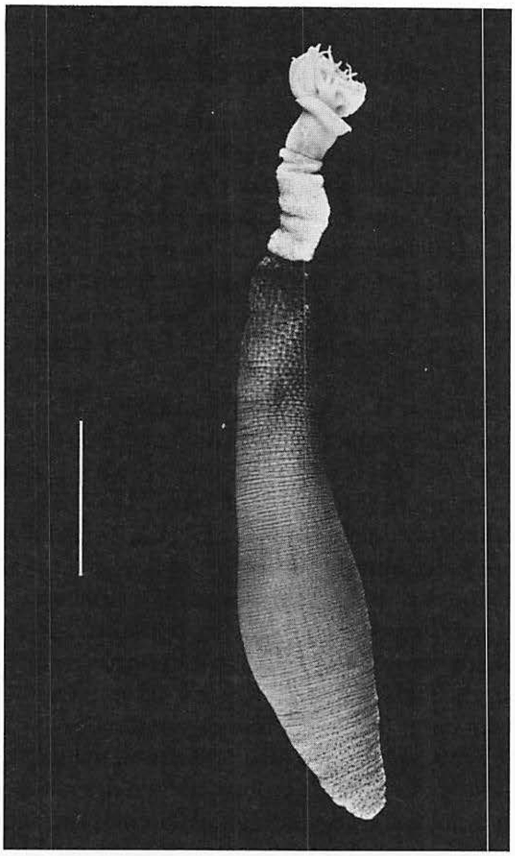

Figure 3.I.4.—*Antillesoma antillarum*: Hawaiian specimen. (Courtesy P. Kempster.) Scale line = 10 mm.

Introvert and trunk bear prominent, conical to hemispherical papillae, often darker in color than the body wall. Four retractor muscles. Contractile vessel single and without villi (differing in this aspect from the genus *Antillesoma*).

Species of *Phascolosoma* commonly occur as borers in coral and limestone reefs, among masses of serpulid worms, amongst mussels, and under rocks. Five species are known from Hawaii. The shape, structure, and markings of the introvert hooks are important in the identification of the species.

KEY TO HAWAIIAN SPECIES OF *PHASCOLOSOMA*

1 Posterior, dorsal region of introvert armed with large, prominent, red to almost black, backwardly directed, hooklike to clawlike papillae .... *P. perlucens*

Introvert without clawlike or hooklike papillae 2

2(1) Papillae on trunk tall and sharply conical, making specimen bristlelike to touch; nephridia long, extending almost to base of trunk and fixed to body wall for most of their length .... *P. pacificum*

Papillae on trunk not tall and sharply conical; nephridia less than half length of trunk 3

3(2) Introvert hooks with clear streak of almost uniform width from apex to midpoint at base 4

Introvert hooks with clear streak much widened at base and with a knob or tonguelike protrusion of streak basally .... *P. nigrescens*

4(3) Pale or clear area on each side of clear streak of hook, one area triangular and the other crescentic .... *P. stephensoni*

Pale area only on one side of clear streak, forming a pale triangular area (but no crescentic area) .... *P. scolops*

Phascolosoma nigrescens Keferstein, 1865

The introvert hooks of this species possess characteristic markings (Fig. 3.I.5), the clear streak being slightly swollen in its upper half and very much expanded posteriorly. In addition, the basal part of the expansion is indented slightly so as to form a bulge or tongue, which is directed towards the tip of the hook. The longitudinal musculature of the trunk wall is grouped into 22 to 30 anastomosing bundles. There are 4 retractor muscles. A spindle muscle is fastened posteriorly to the body wall and a fixing muscle is present. Two nephridia are attached to the trunk wall for about two-thirds of their length.

Phascolosoma nigrescens is a rock borer and is well known in all tropical and subtropical waters. The Hawaiian specimens examined are from Maui (Kahului), Oahu (Waikiki reef), and Laysan reef. The species was also reported from Hawaii by Fisher (1952).

Phascolosoma pacificum Keferstein, 1866

One specimen of *Phascolosoma pacificum* was identified by Cutler (1985, pers. comm.) from among a collection at the Bishop Museum, Honolulu. Three characters enable the species to be distinguished from related ones of the same genus: (1) its bristling appearance and feel, caused by the presence of numerous, sharply pointed or conical papillae on its trunk wall; (2) its very long nephridia, which extend almost to the base of the trunk; and (3) its sharply bent introvert hook. The trunk of some Australian specimens of *P. pacificum* is 60 to 70 mm long. The species is a rock borer and is known from the warmer waters of the Indian and West-Pacific oceans.

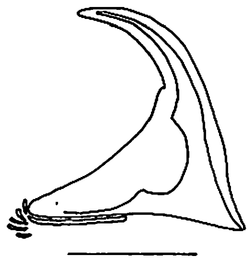

Figure 3.I.5.—*Phascolosoma nigrescens*: introvert hook. Scale line = 0.05 mm.

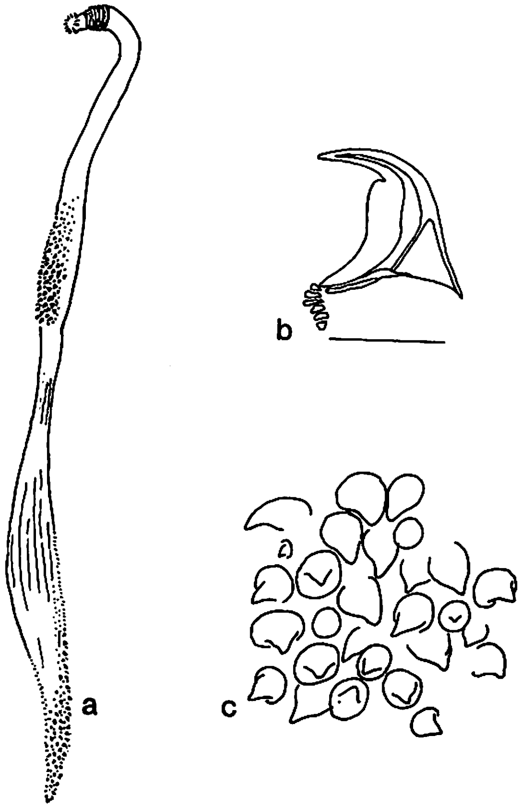

Figure 3.I.6.—*Phascolosoma perlucens*: a, entire specimen; b, introvert hook; c, spinelike papillae from introvert. (a,b after Fisher 1952; c after Selenka et al. 1883.) Scale line = 0.05 mm.

Phascolosoma perlucens Baird, 1868
[syn. *Phascolosoma dentigerum* Selenka, de Man, and Bülow, 1883: Fisher 1952]

The trunk of this species is often slender (Fig. 3.I.6a) and the introvert hook is rather sharply bent (Fig. 3.I.6b). The base of the introvert and the pre-anal region of the trunk bear conspicuously enlarged, dark brown, sharp, posteriorly directed skin papillae (Fig. 3.I.6c). Similar hooklike papillae or tubercles are also present on the posterior region of the trunk.

Phascolosoma perlucens is a rock-boring species. Rice (1976) commented on the feeding habits of the species. Fisher (1952) reported it from Laysan and Kauai. Cutler (1985, pers. comm.) found it off Ala Moana, Honolulu. It appears to be an Indo-Pacific species.

Phascolosoma scolops (Selenka, de Man, and Bülow, 1883)

This species is a typical *Phascolosoma;* the longitudinal musculature of its body wall is grouped into 20 to 30 anastomosing bands, it possesses 4 retractor muscles, introvert hooks, and prominent skin papillae. It is distinguished by the markings on its introvert hooks and the structure of its trunk papillae. There is a clear, triangular area on one side of the clear streak (Fig. 3.I.7b) of the hook and

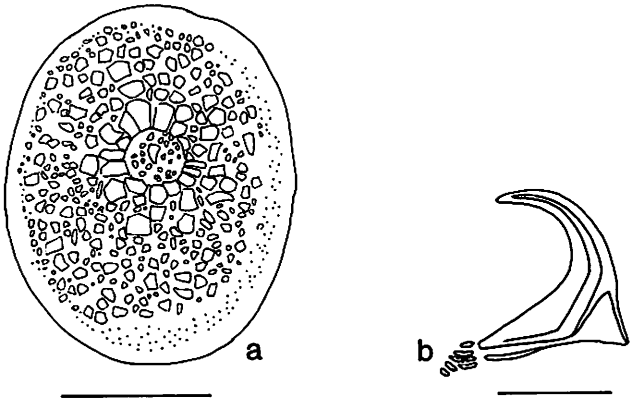

Figure 3.I.7.—*Phascolosoma scolops*: a, body papilla; b, introvert hook. (a after Selenka et al. 1883.) Scale line = 0.05 mm.

the trunk papillae (Fig. 3.I.7a) are hemispherical or rounded, covered with polygonal plates that are largest around the central pore of the papilla.

The specimens examined were collected from the intertidal reefs of Oahu. Kohn (1970) reports that *P. scolops* is eaten on these reefs by the gastropod *Mitra litterata*. Cutler (1985, pers. comm.) collected the sipunculan "from almost any station." The species is recorded from most warm-water areas, particularly of the Indian and Pacific oceans.

Phascolosoma stephensoni (Stephen, 1942)
[syn. *Phascolosoma* sp. cf. *heronis* Edmonds, 1956: Kohn 1970]

This species resembles *P. scolops* in that a variable number of darkly pigmented bands are usually present on the dorsal surface of the introvert. The markings on the hooks of *P. stephensoni,* however, are different; on one side of the clear streak of the hook there is a pale crescentic area and on the other side a clear triangular area (Fig. 3.I.9b). The shape of the trunk papillae is shown in Fig. 3.I.9a and the general appearance of a specimen in Fig. 3.I.8.

The Hawaiian specimens examined by me are from Kahului, Maui (in coral reef rock at a depth of 1 to 3 m), and Oahu (Waikiki reef). More than 100 specimens were collected by Cutler (1985, pers. comm.) from numerous stations on the islands. *Phascolosoma stephensoni* is a rock borer and is widely distributed in the Indo-West Pacific region.

Genus *Sipunculus* Linnaeus

Adult specimens usually large (70 to 260 mm long) and often stout. Trunk cylindrical and usually divided into squares or rectangles by intersection of longitudinal and circular muscles. Introvert short and carrying numerous, flat, triangular papillae. Mouth surrounded by a tentacular fold. Introvert without hooks and spines. Four retractor muscles. A postesophageal or "sipunculus" loop present in alimentary canal anterior to intestinal spiral.

Most of the species of the genus are burrowers in sand or sandy mud. Only 1 species has so far been reported from Hawaii. The undetermined *Sipunculus* reported by Edmondson (1933, 1946) from Hanauma Bay, Oahu, cannot be

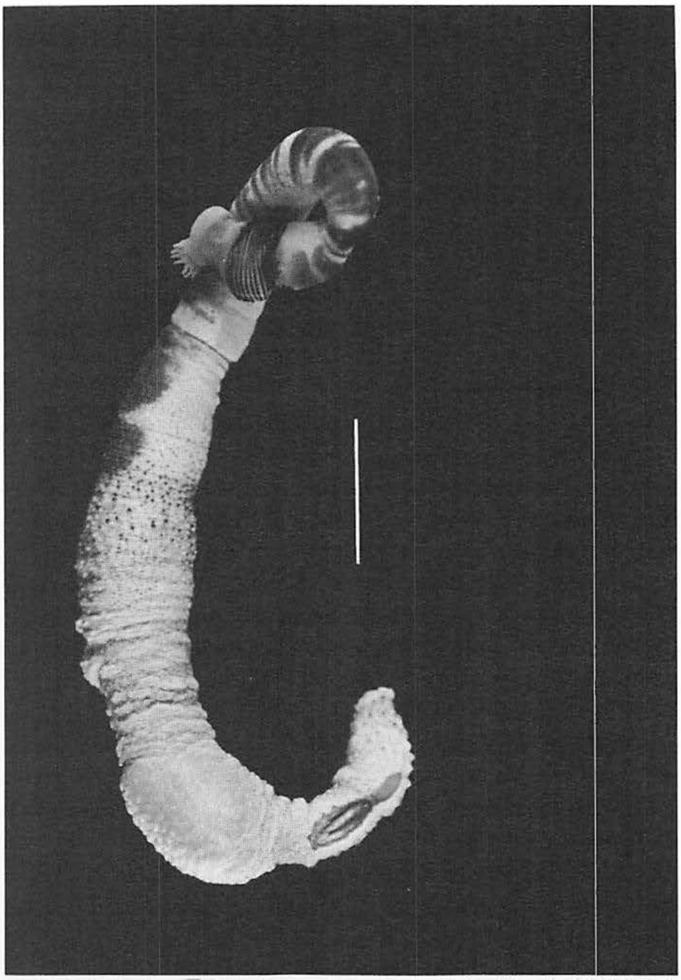

Figure 3.I.8.—*Phascolosoma stephensoni*: specimen from Hawaii (slightly damaged posteriorly). (Courtesy P. Kempster.) Scale line = 5 mm.

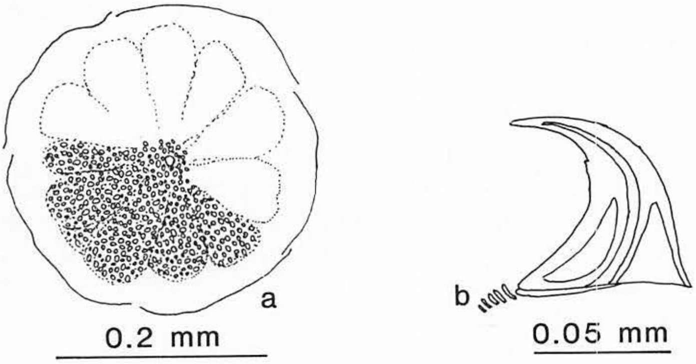

Figure 3.I.9.—*Phascolosoma stephensoni*: a, papilla from posterior trunk (a portion only outlined); b, introvert hook.

identified from the information and figure that he gave. His specimens were quite possibly *Siphonosoma rotumanum,* a species since reported from Oahu.

Sipunculus norvegicus Danielssen, 1868

Stephen and Edmonds (1972, p. 31) reported 2 specimens collected in the vicinity of Kauai that were identified by W. K. Fisher as *Sipunculus norvegicus*. Fisher, however, did not publish his finding. According to Stephen and Edmonds, the trunk of 1 specimen is about 140 mm long and the introvert about 20 mm. The longitudinal musculature of the trunk wall is grouped into 23 bands. A circular ridge or annulation marks off the posterior part of the trunk as a distinct glans. The 4 retractor muscles arise from the trunk wall at the same level. A rectal caecum and racemose glands are also present.

Sipunculus norvegicus is known mainly from the North Atlantic but also from the east coast of the USA and off West Africa. It has been recorded from the Indian Ocean, Japan, the South Pacific, and the Tasman Sea. Fisher's 2 specimens were collected in 1902 by the U.S.F.C. Steamer *Albatross* (Stn. 4132) at a depth between 470 and 571 m on a bottom of fine, gray sand and mud.

Genus *Siphonosoma* Spengel

Specimens usually large in size and cylindrical in shape. Introvert short in comparison with trunk and lacking triangular, scalelike papillae present in *Sipunculus* and *Xenosiphon*. Hooks or spines may be present on introvert. Tentacles fingerlike or threadlike. Longitudinal musculature of trunk wall grouped into bands. Four retractor muscles. The spindle muscle arises anteriorly usually from 3 roots and posteriorly it is always fixed to the body wall. The contractile vessel is always single and villi may or may not be present. Most species live in sand or sandy mud.

Siphonosoma rotumanum (Shipley, 1898)
[syn. *Siphonosoma hawaiense* Edmonds, 1966]

The trunk is 90 to 150 mm long, 3 to 6 mm wide and cylindrical (Fig. 3.I.10). The introvert, which is short relative to the trunk and not always clearly differentiated from it, bears numerous rows of blunt, slipper-shaped spines anteriorly (Fig. 3.I.11). Hemispherical papillae are present on the anterior and posterior surfaces of the trunk. The longitudinal muscles of the body wall are grouped into 14 to 17 bands. Two pairs of retractor muscles are attached to the body wall at different levels: a ventral pair to bands 2 and 3 in the middle of the trunk and a dorsal pair more anteriorly to bands 4 to 6. The spindle muscle is fastened anteriorly by 3 roots and posteriorly by one. The contractile vessel bears numerous small villi.

The species has been found on Oahu at Kualoa Point in hard, packed sand above low-water level and at Hanauma Bay. It was described originally from Rotuma, later from Guam (Edmonds 1971), and more recently from Queensland (Edmonds 1980). The synonymy of *S. rotumanum* and *S. hawaiense* was determined by Stephen and Edmonds (1972).

**Siphonosoma vastum* (Selenka, de Man, and Bülow, 1883)

One specimen was identified by Cutler (1985, pers. comm.) from among specimens in the Bishop Museum, Honolulu. Cutler found the specimen in a

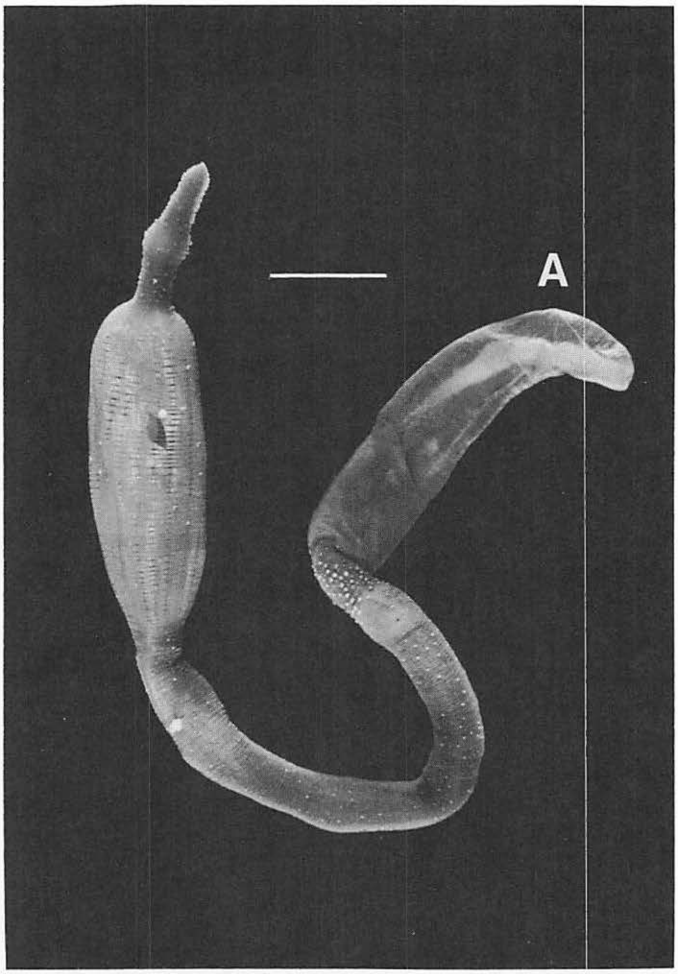

Figure 3.I.10.—*Siphonosoma rotumanum*: specimen from Hawaii (A, anterior extremity with introvert retracted). (Courtesy P. Kempster.) Scale line = 10 mm.

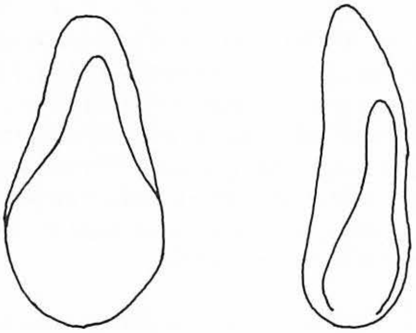

Figure 3.I.11.—*Siphonosoma rotumanum*: slipper-shaped spines from anterior region of introvert.

collection of material made by "a Navy Group" on the eastern side of Maui. The trunk of Australian specimens seen by me varies from 57 to 260 mm in length. The distinguishing feature of the species is the presence of numerous, prominent, fingerlike caeca attached to the rectum. Their function is not known. Specimens must be dissected to reveal the caeca. The contractile vessel lacks villi. The species is Indo-Pacific in distribution.

Genus *Themiste* Gray

Pear-shaped, globular, or elongate sipunculans with trunk 5 to 150 mm long. Tentacular system consists of 4 to 8 grooved stems that divide and subdivide to form numerous tentacles. The longitudinal musculature of body wall is continuous and not banded. Usually 2 retractor muscles. Contractile vessel bears few to many villi that may be short and fingerlike or long and threadlike.

Some species are rock borers, others live among sand and debris found in the roots of marine angiosperms or under rocks. Only 1 species, a rock borer, has so far been found in Hawaii.

Themiste langeniformis Baird, 1868

The trunk is pear-shaped to subglobular, 5 to 35 mm long, and its posterior region may be rounded or weakly pointed. The introvert is short (up to 10 mm long), lacking hooks and spines and often possessing anteriorly a dark blue or brown band. The tentacles arise from 4 to 8 stems, which by division and subdivision give rise to numerous small tentacles or tentacules (Fig. 3.I.12). The longitudinal musculature of the body wall is continuous and the skin appears smooth, although numerous, very small, pale papillae are present. Two strong retractors arise in the posterior half of the trunk. A contractile vessel runs along the esophagus to the base of the retractors and bears numerous, short, fingerlike villi. Two freely suspended nephridia are present.

Williams (1977) described the larval development of the species and reported that this sipunculan was one of the major rock-boring species in Hawaii. The specimens examined by me came from Kahului, Maui, and from the island of Hawaii. Cutler (1985, pers. comm.) found *T. langeniformis* widely distributed in the Hawaiian Islands. The species has a broad Indo-West Pacific distribution.

Genus *Aspidosiphon* Diesing

Usually small to medium-sized sipunculans with trunk less than 60 mm long. Anal (anterior) and caudal (posterior) shields are present on the trunk, although the latter is sometimes not well developed; the shields are usually darker than the trunk and often furrowed or grooved. The introvert is generally slender and arises ventrally just posterior to the anal shield; it usually carries both hooks and spines. The tentacles are fingerlike and lie in a near ring dorsal to the mouth. Introvert retractors 1 or 2, with a single retractor usually arising from 2 short roots. Longitudinal musculature either continuous or grouped into bundles. Most species form burrows in limestone or coral reefs. Three species are known from Hawaii.

Stephen (1964) split the genus *Aspidosiphon* into 2 genera, *Aspidosiphon* and *Paraspidosiphon,* on the basis of the condition of the longitudinal musculature of the body wall. Stephen and Edmonds (1972), Edmonds (1980), and Murina (1975)

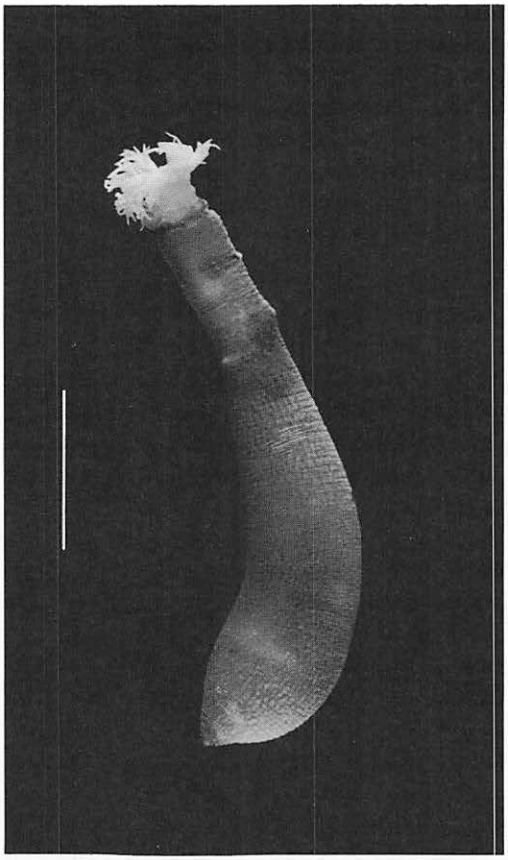

Figure 3.I.12.—*Themiste langeniformis*: specimen from Great Barrier Reef. (Courtesy P. Kempster.) Scale line = 5 mm.

followed Stephen's lead. Cutler et al. (1984, pp. 302–03), on the other hand, consider that the division is justified at subgeneric but not generic level. Cutler et al. have argued their case convincingly and I now agree that *Paraspidosiphon* is valid only at subgeneric level.

KEY TO HAWAIIAN SPECIES OF *ASPIDOSIPHON*

1	Longitudinal musculature of trunk wall continuous and not divided into bands	*A. elegans*
	Longitudinal musculature of trunk wall divided into bands	2
2(1)	Introvert hooks with single points	*A. cumingi*
	Introvert with 2 points	*A. ochrus*

Aspidosiphon elegans (Chamisso and Eysenhardt, 1821)

This is a rather slender, delicate, straw-colored species. The trunk is 8 to 30 mm long and 1.5 to 2.8 mm wide. The longitudinal musculature of the trunk wall

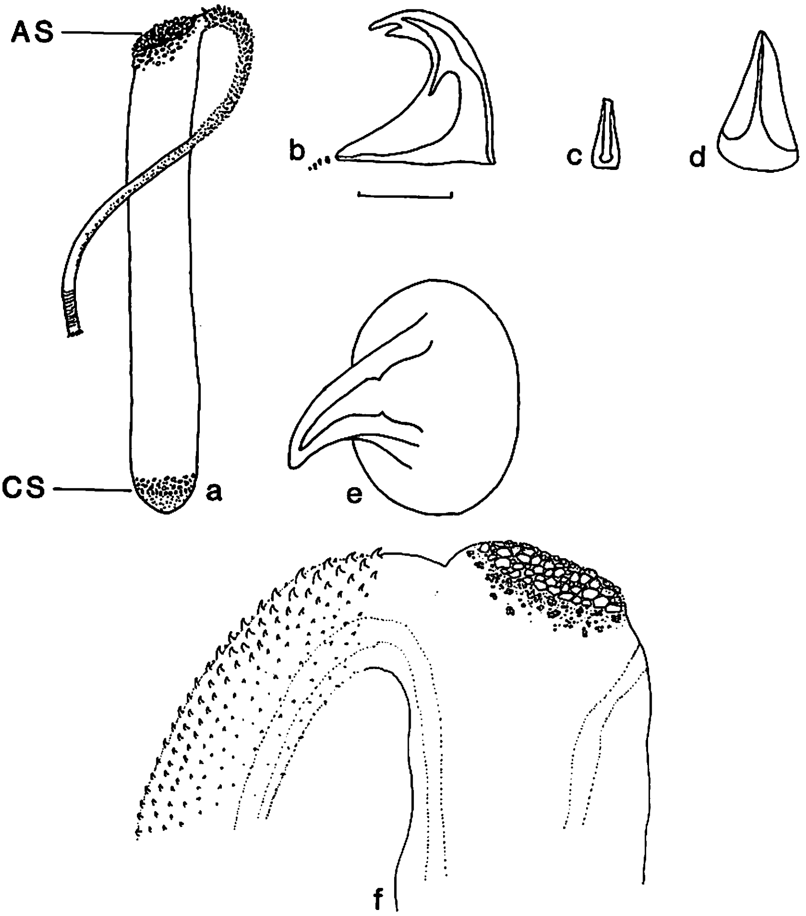

Figure 3.I.13.—*Aspidosiphon elegans*: a, entire animal; b, introvert hook; c, papilla from introvert; d, spine from anterior region of introvert; e, larger spine from posterior dorsal region of introvert; f, posterior region of introvert and anterior region of trunk. (Figs. 3.I.13b–e to same scale; scale line = 0.025 mm.) (AS, anal shield; CS, caudal shield.)

is continuous and not banded. The anal shield (Figs. 3.I.13a,f) is dark brown, subelliptical, usually wartlike in appearance and without furrows or grooves. The caudal shield is usually more weakly developed than the anal shield and has small, chitinous plates around its edges; the edges of the shield may be somewhat furrowed. When present, furrows do not extend very far radially. The central area of the caudal shield is sometimes bare.

The introvert in preserved specimens is slender and arises ventral to the anal shield (Figs. 3.I.13a,f); anteriorly it bears numerous rows of 2-pointed hooks (Fig. 3.I.13b) and posteriorly numerous spines. A clear area or streak in the hook reveals a slender almost downwardly directed tongue or extension. The field of hooks and spines extends to the base of the introvert. Small, conical papillae are also present on the introvert (Fig. 3.I.13c). The presence of dark spines of varying size and shape on the introvert posterior to the hooks is characteristic (Fig. 3.I.13d). The spines are closely set, all single pointed, more densely distributed on the dorsal surface of the introvert and becoming larger in the posterior region (Fig. 3.I.13e). Sometimes the spination may be heavy, the spines then arising from very strong roots or bases. The largest spines usually possess a central, tubular canal. The retractor muscle, consisting of 2 short roots which soon fuse to form 1 stout muscle, arises from the body wall well in front of the caudal shield. Two nephridia, about half as long as the trunk, are fixed to the body wall for most of their length.

Aspidosiphon elegans was recorded by Kohn (1970) as a dominant burrowing sipunculan in a solution bench limestone habitat. Edmonds (1980, p. 46) reported it from Kahului, Maui, from coral in shallow water. Cutler (1985, pers. comm.) collected 48 specimens from Maui. It is an Indo-West Pacific species.

**Aspidosiphon cumingi* Baird, 1868

The trunk of this species tends to be long (up to 100 mm in an Australian specimen), almost cylindrical, and about 4 to 9 mm wide. The anal shield is marked with radiating furrows, many of which are forked. The caudal shield may be conical. The longitudinal musculature of the body wall is grouped into about 30 anastomosing bundles. The body wall is thick and contains coelomic extensions, and the introvert is armed with numerous single-pointed hooks. The introvert retractor is single, strong, and attached to the body wall anterior to the caudal shield. The posterior point of attachment of the muscle spans about 18 to 20 longitudinal muscles. The rectum is long and tubular and is associated for about two-thirds of its length with numerous caeca that seem arranged in clusters. The nephridia are tubular and about half as long as the trunk.

The species is distinguished by the possession of a mass of fingerlike villi or caeca (blind tubes) attached to its rectum. Four specimens were collected by Cutler (1985, pers. comm.). The species is an inhabitant of tropical seas.

**Aspidosiphon ochrus* Cutler and Cutler, 1979

According to the type description, the trunk of this species is 9 to 20 mm long and 1.5 to 5 mm in diameter. The introvert, about as long as the trunk, is armed with 20 to 40 rings of hooks, each with 2 points. The anal shield is creamy tan in color and has distinct, sharp boundaries. The caudal shield is less distinct, with ill-defined boundaries. The longitudinal musculature of the body wall is grouped into 25 to 30 anastomosing bundles. A pair of retractor muscles arises near the posterior extremity of the trunk, each spanning 5 to 8 muscles. The 2 muscles are fused into a single muscle for about half of their length. The species, according to Cutler and Cutler (1979, p. 978), is closely related to *A. steenstrupi.*

Cutler (1985, pers. comm.) collected 74 specimens from 1 station off Ala Moana beach, Honolulu, and 31 from Maui. Cutler and Cutler (1979) also recorded the species from Madagascar, Cocos-Keeling Islands, Diego Garcia, and Solomon Islands.

Genus *Lithacrosiphon* Shipley

Anterior end of trunk surmounted by a hard, calcareous cone-shaped cap. Introvert arises on ventral side of cap and bears numerous rows of hooks. Longitudinal musculature of trunk wall forms bands which may anastomose

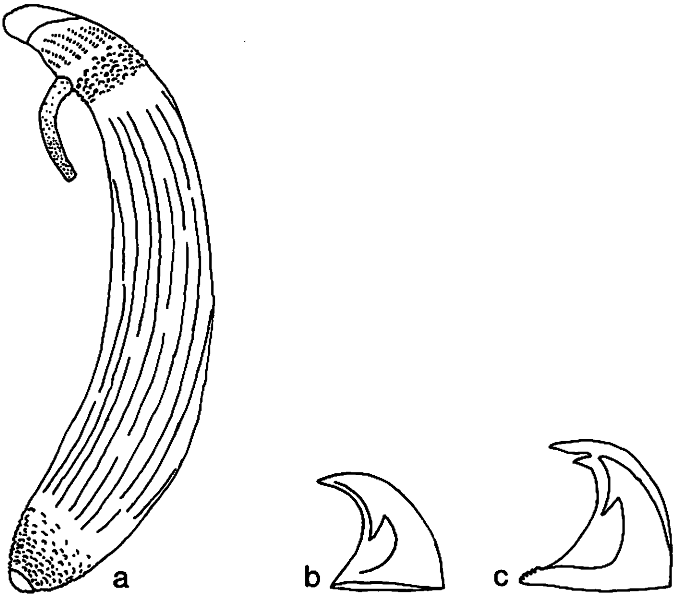

Figure 3.I.14.—*Lithacrosiphon cristatus*: a, entire animal; b, introvert hook with single point; c, introvert hook with 2 points.

freely. Two retractor muscles and 2 nephridia present. Spindle muscle attached posteriorly. Specimens known only from coral formations.

Lithacrosiphon cristatus (Sluiter, 1902)

The trunk is 8 to 22 mm long and 1.0 to 3.5 mm wide, light brown and translucent. The introvert is about as long as the trunk and arises on the ventral side of the cap (Fig. 3.I.14a). Anteriorly placed introvert hooks possess 2 points (Fig. 3.I.14c) but those placed posteriorly have only 1 point (Fig. 3.I.14b). The hard, calcareous, cone-shaped anterior cap is furrowed with numerous grooves. The longitudinal muscles of the body wall are arranged in 13 to 24 anastomosing bands. Two retractor muscles are joined for more than half their length and a spindle muscle is attached posteriorly to the body wall. Two nephridia present.

This species was recorded from Halape, Hawaii, by Cutler and Jurczak (1975) and again by Cutler (1985, pers. comm.) from Maui. The species is known from the warmer waters of the Pacific Ocean and from the Caribbean Sea.

Phylum ECHIURA

Echiurans possess an anterior proboscis that, although highly extensible, cannot be retracted within the body (Fig. 3.I.2). It is a rather fragile organ, which may in some species be easily detached from the trunk if the animal is roughly handled. The mouth is at the base of the proboscis in the anterior region of the trunk, and tentacles are lacking. A pair of setae or bristles is usually present on the ventral surface just posterior to the mouth. The anal aperture is at the posterior extremity of the worm. Echiurans are often pink because they contain hemoglobin, but species of *Thalassema, Anelassorhynchus,* and *Bonellia* may be light to dark green.

The complexly wound gut of an echiuran occupies almost all of the body cavity. Most echiurans possess 1 to 7 pairs of nephridia that lie on each side of the nerve cord in the anterior region of the body. A pair of anal vesicles empties posteriorly into the cloaca.

Most echiurans are ciliary-mucus feeders, ingesting small particles of organic matter. Some form burrows in sand and mud. It is not known whether those that live in rock are able to make burrows or whether they inhabit those vacated by other organisms.

A general account of the Echiura has been given by Fisher (1946) and Stephen and Edmonds (1972). Datta Gupta (1976) has also written on the systematics of the phylum. Records of echiurans from Hawaii have been compiled by Edmondson (1933, 1946) and more completely by Fisher (1948). Four identified and 2 unidentified species have been recorded from Hawaii. These include: *Anelassorhynchus inanensis* (Ikeda), *Anelassorhynchus porcellus* Fisher, *Ochetostoma manjuyodense* (Ikeda), *Ochetostoma erythrogrammon* Leuckart and Rüppell, ?*Echiurus* sp., and *Thalassema* sp. Hawaiian specimens of the above-mentioned species have not been examined by the author. The following key includes genera commonly found in the tropical Pacific in addition to those recorded from Hawaii. The key does not apply to deep-sea echiurans.

KEY TO SOME TROPICAL PACIFIC ECHIURAN GENERA

1	Two circles of setae present near posterior extremity of trunk	*Echiurus*
	No posterior setae present	2
2(1)	Proboscis bifid; sexually dimorphic, with male parasitic in or on female	7
	Proboscis not bifid, but may be flattened anteriorly into a spoonlike structure (may be detached from trunk if roughly handled); not sexually dimorphic	3
3(2)	Longitudinal muscles of body wall grouped into bundles	4
	Longitudinal muscles of body wall not in bundles	5
4(3)	Interval between longitudinal muscles crossed by numerous small, separate bundles of inner oblique muscle layer	*Ochetostoma*
	Interval between longitudinal muscles not crossed by numerous separate bundles of inner muscle layer	*Listriolobus*
5(3)	Nephrostomal lips of nephridia long and spirally coiled	*Anelassorhynchus*
	Nephrostomal lips of nephridia not long or spirally coiled	6
6(5)	Nephrostomal lips expanded into a leaflike structure; proboscis expanded anteriorly into a fanlike structure	*Arhynchite*
	Nephrostomal lips not expanded; proboscis not expanded anteriorly	*Thalassema*
7(2)	Only 1 nephridium; male usually lodged in nephridium	*Bonellia*
	Two nephridia; male lodged in a small blind tube that opens between the 2 nephridia of the female	*Pseudobonellia*

Genus *Anelassorhynchus* Annandale

In the genus *Anelassorhynchus,* the trunk or body is saclike or sausage-shaped and the longitudinal and oblique muscle layers are continuous, not forming bands. Nephridia occur in 1 to 3 pairs and nephrostomal lips are long and coiled.

KEY TO HAWAIIAN SPECIES OF *ANELASSORHYNCHUS*

Three pairs of nephridia	*A. inanensis*
Two pairs of nephridia	*A. porcellus*

Anelassorhynchus inanensis (Ikeda, 1904)

The trunk is up to 40 mm long and 13 mm wide. The proboscis is about 20 mm long. There are 3 pairs of nephridia, with the anterior pair attached to the trunk in front of the ventral setae. The nephrostomal lips are long and spirally coiled. Fisher (1948) reported this species from Halape, Hawaii. Extra-Hawaiian distribution includes Okinawa Island, Japan (in coral), and Vietnam.

Anelassorhynchus porcellus Fisher, 1948

The trunk is 50 to 70 mm long and of variable width (Fig. 3.I.15). The proboscis is fleshy and easily detached from the trunk. There are 2 pairs of nephridia, both attached to the trunk posterior to the setae. The nephrostomal lips are long and usually coiled. The color of Australian specimens were recorded as sandy gray when alive, with the 2 rather inconspicuous setae a golden color (Edmonds 1960). Fisher (1948) recorded *A. porcellus* from Honolulu reef tidal pools, as well as from the island of Hawaii at Halape in sand under rocks and at

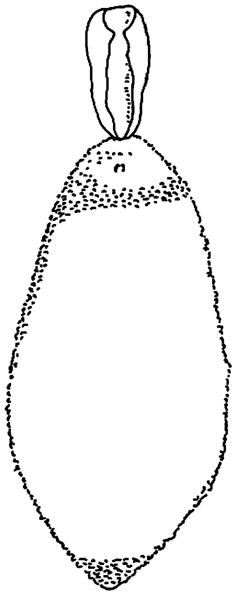

Figure 3.I.15.—*Anelassorhynchus porcellus*: entire animal. (After Fisher 1948.)

Puako Bay. It has also been recorded from tidal pools at Heron Island, Queensland, Australia (Edmonds 1960).

Genus *Ochetostoma* Leuckart and Rüppell

In this genus the trunk may be sac- or sausage-shaped or subcylindrical. The longitudinal musculature of the body wall is thickened into bands and the zone between the longitudinal bands is crossed by bands or fascicles of the inner oblique musculature. The nephridia occur in 1 to 7 pairs, and the nephrostomal lips are long and spirally coiled.

KEY TO HAWAIIAN SPECIES OF *OCHETOSTOMA*

Three pairs of nephridia	*O. erythrogrammon*
Two pairs of nephridia	*O. manjuyodense*

Ochetostoma erythrogrammon Leuckart and Rüppell, 1828

The trunk may be saclike, sausage-shaped, or even long and subcylindrical (Fig. 3.I.16). The body may be 60 to 100 mm long. The proboscis is capable of great extension but in preserved specimens may not be as long as the trunk. Longitudinal muscles are grouped into 14 to 18 well-developed bands; the body wall between the bands is crossed by numerous bands of oblique muscles. There are 3 pairs of nephridia with spirally coiled lips, the first pair opening anterior to the setae. Although the color of Hawaiian specimens has not been recorded, this species in other parts of the world is described as varying from light green to violet. The species was recorded from the islands of Kauai (at Nawiliwili) and Hawaii (at Halape) by Fisher (1948). Extra-Hawaiian distribution includes the Red Sea, Zanzibar, South Africa, Mauritius, Indonesia, Vietnam, and Japan.

Ochetostoma manjuyodense (Ikeda, 1905)

The trunk is spindle-shaped and up to 18 mm long. Longitudinal muscles occur in 14 broad bands. Two pairs of nephridia with long, spirally coiled lips open posteriorly to the setae. The skin is gray-green, and the ventral setae are golden yellow. Fisher (1948) recorded this species from Halape, Hawaii. Extra-Hawaiian distribution includes Manjuyodi in the Philippines.

?*Echiurus* sp.

Edmondson (1933, 1946) tentatively considered some grayish white echiurans from Hawaii as *Echiurus* sp. The record needs confirmation.

Members of this genus are distinguished by the presence of 2 rings of anal setae circling the posterior end of the trunk and by 1 to 3 pairs of nephridia without spirally coiled nephrostomal lips.

?*Thalassema* sp.

Although Edmondson (1933, 1946) mentioned the occurrence of *Thalassema* in Hawaii, Fisher (1948) stated that no true *Thalassema* had been recorded from the Islands. Edmondson's record, therefore, needs confirmation.

In the genus *Thalassema,* the body is saclike and lacks rings of anal setae.

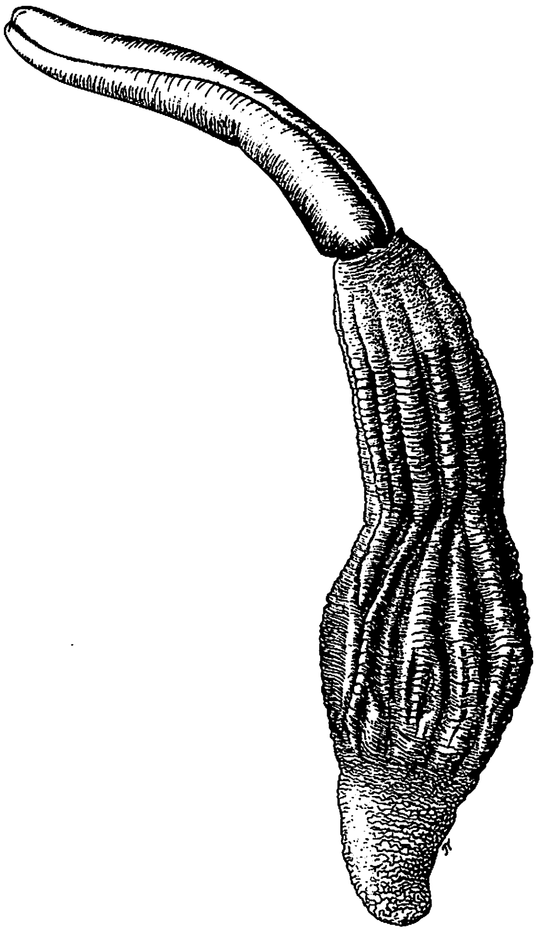

Figure 3.I.16.—*Ochetostoma erythrogrammon*: specimen from Singapore, trunk length = 80 mm. (J. Thurmer artist.)

Musculature of the body wall is continuous and not divided into longitudinal bands. The lips of the nephrostomes are neither spirally coiled nor leaflike.

GLOSSARY (SIPUNCULA and ECHIURA)

anal shield: Hardened elliptical, circular, or horseshoe-shaped modification of the skin near the anterior end of the trunk of the sipunculan genus *Aspidosiphon*. Usually it is darker than the trunk and may be rough or wartlike. In some species it is furrowed or grooved.

anal vesicles: A pair of tubular or saclike excretory organs lying in the body cavity of an echiuran; they empty into the cloaca.

anastomosing: Running together with cross connections.

anterior cap: Knoblike, usually calcified, rounded or conical structure at the anterior end of the trunk of the sipunculan genera *Cloeosiphon* and *Lithacrosiphon*. In *Cloeosiphon* it resembles a pineapple. In *Lithacrosiphon* it is conical or subtruncate.

bifid: Forked.

caecum: Small, blind tubule arising on the rectal section of the gut of some sipunculans and echiurans.

caudal shield: Hardened cap or modification of the skin at the posterior region of sipunculans of the genus *Aspidosiphon;* it is usually flat or subconical and is often grooved.

circular muscles: Outer muscular layer of the body wall of both sipunculans and echiurans. It usually forms a continuous sheath but in some genera it is grouped into well-defined bands or bundles.

cloaca: Posterior region of the gut of an echiuran.

coelom: Body cavity.

coelomic canals: Extensions of the body cavity into the body wall of some sipunculans of genera *Sipunculus, Xenosiphon,* and *Siphonosoma.*

contractile vessel: Single tube or pair of tubes attached to the dorsal wall of the esophagus of sipunculans; the vessel may be simple or it may bear anywhere from a few to many tubules or villi that extend into the coelom. Fluid contained in the vessel closely resembles that in the body cavity and is known to have a respiratory function in some species (Manwell 1960); the vessel is also regarded as a compensatory sac acting as a reservoir for the fluid in the tentacles when these contract (Hyman 1959).

dendritic: Branching or treelike.

fascicles: Small bundles.

fixing or fastening muscles: Thin strands of muscular tissue attached at one end to the body wall and at the other to some part of the gut, usually the esophagus and/or the rectal region.

introvert: The anterior, retractable region of a sipunculan.

longitudinal muscle: One of the inner muscle layers of sipunculans and echiurans. In some genera it may be thickened to form bands.

nephridium (pl. -dia): Tubular to saclike organs that hang in the body cavity of sipunculans and echiurans, usually occurring in pairs. The coelomic opening of a nephridium is a nephrostome.

nephrostomal lips: Tissue lying on each side of the nephrostome of an echiuran; sometimes inconspicuous, at other times expanded and leaflike or drawn out into long threads that may or may not be spirally coiled.

oblique muscles: One of the inner, muscular layers of the body wall of sipunculans and echiurans; these muscles form bands in the echiuran genus *Ochetostoma.*

papillae: External tubercles or swellings, often prominent structures, on sipunculans and echiurans; may be almost flat, conical, hemispherical, or wartlike.

pelagosphaera: Post-trochophore larva of some sipunculans that swims by means of a prominent ciliated band (metatroch) and in which the anterior ciliated band (prototroch) has been lost or has regressed.

proboscis: Anteriormost portion of an echiuran that cannot be retracted into the body cavity of the animal.

protractor muscles: Small, ribbonlike muscles that arise from the internal body wall of the trunk of some sipunculans and connect with the introvert near the brain. They are additional to the retractor muscles and are present in the genus *Xenosiphon.*

racemose glands: Glandular structures of unknown function, usually paired, found on each side of the rectum of some species of *Sipunculus.*

retractor muscles: Longitudinal bands of muscles fixed at one end to the coelomic body wall and at the other end to the introvert. They function in the withdrawal of the introvert in sipunculans.

setae: Bristlelike structures of echiurans that project from the ventral surface in 1 pair just posterior to the mouth; 2 genera have 1 or 2 rings of anal setae encircling the posterior regions.

shield (see **anal shield** and **caudal shield**).

spindle muscle: Threadlike strand of muscle that helps to fasten the coils of the gut of a sipunculan. It arises anteriorly near the anus and may or may not be fastened posteriorly to the body wall.

tentacles: Fingerlike, threadlike, or dendritic extensions of the body wall that arise at the anterior end of a sipunculan and function in feeding and respiration.

trochophore: Free-swimming larval stage of many sipunculans that is characterized by bands of cilia.

trunk: The body, as distinct from either the introvert of a sipunculan or the proboscis of an echiuran. It is much wider than the introvert and proboscis.

villi: Tubular branches that arise from the contractile vessel of some sipunculans. They may be few or many, short or long.

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SECTION 3

Chapter II

Phylum ANNELIDA

JULIE H. BAILEY-BROCK

THE ANNELIDS (segmented round worms) include many familiar forms, among which are the earthworms and the leeches, as well as a great many other terrestrial, freshwater, and marine species. The annelids are separated into 3 classes: Polychaeta (marine bristle worms), Oligochaeta (earthworms and blood worms), and Hirudinea (leeches). The oligochaetes and leeches are often grouped together in the Clitellata (Meglitsch 1972), since both possess a clitellum and have the reproductive organs restricted to a few anterior segments. The polychaetes do not develop a clitellum and have segmentally arranged gonads. While all 3 classes have marine representatives, the polychaetes are the most numerous in marine habitats.

The annelids are annulated in appearance; generally, each annulus corresponds to a segment, except in the leeches in which each segment bears a number of annuli. The segments are serially repeated units, often called metameres, that have essentially the same elements. Each contains excretory organs, muscles, gonads, blood vessels, and nerves. Segments are separated from each other by thin septa. The digestive tract, nerve cord, and longitudinal blood vessels are arranged along the anterior-posterior axis and pass through perforations in the septa. The coelom forms a cavity within each segment and serves as the receiving area for developing gametes, waste products, and soluble food materials. Excretory organs remove nitrogenous wastes from the coelomic fluid, and gametes are spawned through modified coelomoducts.

The polychaetes are the largest and most primitive annelidan class in the marine environment. Leeches and oligochaetes are evolutionarily more advanced, and most species are specialized for freshwater and terrestrial habitats. The highly specialized Myzostomidae (considered Polychaetes) are not known from Hawaiian waters but are well represented in the Marshall Islands and western Pacific. The Archiannelida are now considered polychaetes (Fauchald 1977a) and are discussed here in a separate section, Archiannelidan Group. Worms that may be oligochaetes were recorded from Hawaiian sandy reefs and are tentatively placed in the family Questidae, which Fauchald (1977a) included in the polychaetes. He does say that they may be more appropriately placed in the Oligochaeta, and M. Pettibone (pers. comm.) makes the same suggestion. Questids have the gonads restricted to a discrete number of anterior segments in true oligochaete fashion, yet bear more than 1 type of seta, which is a polychaete characteristic (Fauchald 1977a).

Class HIRUDINEA

Leeches, the most specialized group of annelids, evolved from freshwater oligochaete stock. Many aquatic forms are ectoparasites; however, some are free-living. Other species are terrestrial. The body is dorsoventrally flattened, with suckers at both the anterior and posterior ends. The segments always number 34, but secondary annulation gives the appearance of many more segments. Even though several Hawaiian forms have been observed, only 1 species, from a fish, has been positively identified. Large sharks often have a number of leeches attached around the gills or on the fins. A key to the marine leech genera of the world, along with notes on each genus, is found in Knight-Jones (1962).

Aestabdella abditovesiculata (Moore, 1946)
[syn. *Johanssonia abditovesiculata* Moore]

The body may be as long as 15 mm, and the cephalic (anterior) sucker is eccentric. Only imperfect ocelli are present; eyes are absent. The general color pattern of alternating dark and light bands varies in intensity among individuals. On the cephalic sucker the pigment roughly forms a cross, and the darker transverse bar includes dark spots ("eyes"). The ventral surface is mostly colorless medially, through which the nerve cord can be seen, thus serving as a good guide to the basic segmentation of the form. The first records of *A. abditovesiculata* were specimens taken from the pufferfish *Arothron hispidus* at the Waikiki Aquarium in Honolulu. Burreson (1976) presented a revised diagnosis of this leech and recorded it from several fishes collected along the Oregon and California coasts.

Class OLIGOCHAETA

Marine oligochaetes have received little attention from zoologists in Hawaii. Members of the Questidae represent the only family recorded from the Hawaiian Islands that can be placed in this annelid class because the gonads are restricted to a few segments (Fauchald 1977a).

*Family **Questidae** → CLASS: POLYCHAETA

Two genera have been collected from the reef flat at Fort Kamehameha, Oahu (Bailey-Brock 1979), and were identified to the generic level by Dr. M. Pettibone. Both are small, fragile worms that resemble earthworms in having a rounded, cone-shaped prostomium and an anterior region with segments that are broader than those of the posterior region. The gonads can be seen as a pale, creamy area in the anterior portion, which resembles the clitellum of earthworms. The 2 genera recorded from the reef are separated by the presence or absence of gills and anal cirri, as well as by the nature of the setae. The presence of different

* Questidae family has been placed into the Polychaeta Class,
Source: Glasby, C.J. (2000). Family Questidae. Pp. 84-86 "Poly's & Allies, Vol 4A"

kinds of setae is a polychaete characteristic, and recent work suggest that questids are modified polychaetes and not oligochaetes. However, cocoon formation and sperm transfer have not been observed; without this information the taxonomic argument remains unsettled (Griere and Riser 1981).

KEY TO HAWAIIAN QUESTID GENERA

Posterior gills and anal cirri present; setae are capillaries and bidentate hooks	*Questa*
Posterior gills and anal cirri absent; setae are capillaries, bidentate and tridentate hooks	*Novaquesta*

Novaquesta sp.

These are threadlike worms with finely serrated capillary setae and bidentate and trifurcate hooked setae. Worms belonging to this genus reach densities of 27,240/m^2 in the chaetopterid mounds on a south shore fringing reef on Oahu (Bailey-Brock 1979).

Questa sp.

These threadlike worms have finely serrated capillary setae and bidentate hooked setae. The posterior region bears cirriform branchiae and anal cirri. Worms belonging to this genus reached densities of 7,320/m^2 in the same chaetopterid mounds at Fort Kamehameha, Oahu (Bailey-Brock 1979).

Group ARCHIANNELIDAN

These small, interstitial worms have generally been overlooked or unremarked by researchers. Bailey-Brock (1979) recorded a species of *Saccocirrus* from the Fort Kamehameha reef flat, Oahu. More recently, Emig (1981) recorded archiannelids as members of the community associated with *Lingula reevei* in Kaneohe Bay, Oahu, but he did not identify them.

Current research on Hawaiian interstitial fauna has revealed the genus *Protodrilus*, which is rare compared with the commonly occurring *Saccocirrus* (M. M. Khan, pers. comm., 1982). Jouin (1966, 1971) gives the fullest descriptions and keys to these genera.

KEY TO HAWAIIAN ARCHIANNELIDAN FAMILIES

Uniramous parapodia present; setae chisel-shaped	**Saccocirridae**
Uniramous parapodia absent; setae may or may not be present	**Protodrilidae**

Protodrilus sp.

The prostomium bears eyes and a pair of antennae that may be hollow or solid. The pharynx is muscular but not eversible. Segmentation is poorly developed and parapodia are absent. Worms belonging to this genus have been collected on Oahu's south and east shores (M. M. Khan, pers. comm.).

Saccocirrus sp.

The prostomium bears eyes and a pair of hollow antennae. The proboscis is a muscular pad. The parapodia are uniramous with simple, chisel-shaped setae. The density of this unidentified species was estimated to reach 9,660/m^2 on the reef at Fort Kamehameha, Oahu (Bailey-Brock 1979).

Class POLYCHAETA

JULIE H. BAILEY-BROCK and OLGA HARTMAN

Polychaetes are typically marine worms that occur in abundance throughout the Hawaiian Islands on reefs, in estuaries and shallow coastal regions, and at great depths in offshore waters. Species included in this revision are found at depths ranging from the intertidal region to approximately 100 m (55 fm), although some with broad bathymetric distributions may extend below that depth.

The taxonomy of Hawaiian polychaetes was not well known until Hartman (1966) reviewed all species. Up to that time, *Reef and shore fauna of Hawaii* by C. H. Edmondson (1933, 1946) was the most useful manual for the identification of Hawaiian invertebrates, including some polychaetes. Hartman's publication included the results of 3 scientific voyages: the Swedish frigate *Eugenies* in 1852 (Kinberg 1855, 1857, 1865, 1866, 1867), the H.M.S. *Challenger* in 1875 (McIntosh 1885), and the U.S.S. *Albatross* in 1902 (Treadwell 1906). Her review also included Holly's (1935) new species of Nereididae based on epitokous stages, 2 new amphinomids (Holly 1939), and several species recorded by Treadwell (1943). It also updated Edmondson's review of the polychaetes, and Hartman was also able to include Hartmann-Schröder's 1965 work based on reef polychaetes from Hawaii, Palmyra, and Samoa. Hartman (1966) covered 168 species belonging to 32 families, including several records from depths below 100 m. Since then various groups have been revised, including the Serpulidae (Straughan 1969a) and the Spirorbidae (Vine 1972a; Vine et al. 1972). Sedentary polychaete assemblages characteristic of specific shallow and deeper water habitats around the Hawaiian Islands have also been described (Bailey-Brock 1972, 1976, 1979). Following the untimely death of Dr. Hartman in 1974, her illustrated manuscript for the revision of C. H. Edmondson's *Reef and shore fauna of Hawaii* was sent to the senior author by the editors for subsequent updating and further illustration.

This treatment of polychaete worms includes descriptions of, and keys to, 243 species belonging to 43 families. Approximately 25% of the species are endemic to the Hawaiian Islands; 25% are also known from the Indo-West Pacific, 5% are from the eastern Pacific, and the remaining 45% are considered cosmopolitan. This inventory is by no means complete, as unrecorded species are being found with continued collecting effort.

The class Polychaeta is renowned for diversity of life style and body structure. Free-moving, active worms tend to be elongate and cephalized, have powerful mouthparts, and possess well-developed parapodia for efficient locomotion. Burrowers are vermiform but cephalization is much reduced, mouthparts are modified as a protrusible proboscis for excavating sediments, parapodial lobes are reduced to bundles of setae that aid in burrowing, and parapodia usually bear vascularized branchiae. Tube-dwellers build tubes from environmental materials or from their own secretions that harden to provide a durable protective covering. These worms are conspicuously divided into anterior and posterior body regions and they possess specialized structures for food gathering that can be protruded through the tube opening. Tubicolous worms also have modified parapodia for locomotion and anchorage within the tube, and ciliary pathways for ventilating branchiae and voiding feces. Parasitic polychaetes and some commensal species bear little resemblance to free-living forms, but close examination reveals such characteristic structures as setae or modified parapodia.

Polychaetes are important constituents of marine and estuarine communities in the Hawaiian Islands. Coral reefs are composed of a range of habitats, including living and dead corals, algal turf and pavement, sand and mud flats, seagrass beds, caves, ledges, and crevices, all of which provide cover for polychaetes. Manmade coastal structures such as fish ponds, harbors, lagoons, piers, and revetments also support diverse polychaete assemblages. Some species are important foulers of ships and harbor structures and as such have received attention in Hawaii (Edmondson and Ingram 1939; Edmondson 1944; Long 1974).

The contribution of polychaetes to the diet of reef invertebrates and fishes is quite well understood for some species (Kohn 1959; Hiatt and Strasburg 1960; Hobson 1974; Porter 1974; Leviten 1978; Brock 1979). Polychaetes contribute to the diet of 15 species of the gastropod genus *Conus* in Hawaii (Kohn 1959). Sand-dwelling forms are eaten by goatfishes and wrasses, and worms associated with coral rubble and live coral are eaten by species of chaetodontid fishes (Hobson 1974; Motta 1980). Larval polychaetes are consumed by planktivorous fishes, and large numbers of *Polydora websteri* larvae have been found in the guts of the pomacentrid *Abudefduf abdominalis* (Smith et al. 1977).

The diverse feeding methods and diets of polychaetes have recently been reviewed (Fauchald and Jumars 1979). Predatory species feed on corals, molluscs, hydroids, and other worms; scavengers consume carrion, algae, and decaying vegetable material; detritivores may select specific types or sizes of particulate matter, or engulf sediments and associated organic materials. Suspension feeders use a variety of palps and feeding appendages to remove materials from the water column, while still other worms are commensals living with sponges and other invertebrates.

Evidence suggests that polychaetes must be numerically important in a variety of habitats. Studies in Kaneohe Bay, Oahu, have shown that densities of polychaetes can reach 127,900/m^2 on shallow reefs subjected to sewage enrichment for approximately 20 years (Brock and Brock 1977). The minute size of most polychaetes points to their small contribution to the total standing crop of organisms on Hawaiian reefs; however, these attributes of small size, abundance, and apparent rapid recruitment to coralline surfaces (White 1980) suggest a notable contribution to the energy flow and turnover on reefs. Furthermore, their effect on the stability of sediments and erosion of coral rock is considerable. Fossil and recent evidence indicates that polychaetes affect the geological framework of coral reefs. Some species are efficient bioeroders, removing calcium carbonate as they excavate burrows in dead coral or coralline algae (White 1979, 1980). Others contribute to reef stability by forming tubes of cemented sand grains (Bailey-Brock 1979) or calcium carbonate secreted by specialized glands (Scoffin and Garrett 1974). These are a few of the reasons why further work on polychaete systematics and ecology would be a valuable contribution to coral reef management in the Hawaiian Islands and in the Pacific Basin.

There has been little work on the reproductive biology and larval ecology of Hawaiian polychaetes. Thus, we remain largely ignorant about reproductive cycles, seasonality, spawning, length of time larvae spend in the plankton, and factors that stimulate metamorphosis and settlement. However, Ward (1978) has presented information on pelagic stages and larval development of 12 Hawaiian polychaete species. Casual observations over the years indicate that our common spirorbid species are incubating embryos almost continuously. Other polychaetes may spawn seasonally or with some periodicity (Bailey-Brock 1984b): the nereidid *Platynereis dumerilii* has been seen swimming actively at the sea's surface prior to mass spawning (E. Guinther, R. Brock, and J. Bailey-Brock, pers. observ.); *Sabellastarte sanctijosephi* (a large sabellid) spawned en masse one morning, coinciding with a full moon (R. Brock, pers. observ.); and windrows of the amphinomid *Chloeia flava*, some still swollen with gametes, have been seen on windward beaches following swarming (L. Taylor, pers. comm., 1974). Recruitment rates of metamorphosing and settling polychaete larvae upon plates and blocks of coral are known for some species (Rastetter and Cooke 1979; White 1980). Such information indicates that polychaete larvae are plentiful in nearshore plankton and must compete for space with other coral reef invertebrates.

A number of polychaetes are cosmopolitan in their distribution, with many species found circumtropically. This is partially brought about by their long history through geological time, with representatives known at least since the Cambrian (500 to 600 million years ago) and possibly the Precambrian. The fossil records of some groups (e.g., the Spirorbidae) are quite well known (Pillai 1970). Likewise, the broad distribution of species is attributable to the long-range dispersal of pelagic larvae and rafting of adults (Knight-Jones et al. 1975).

Some polychaetes may be important for medical research. Antitumor properties have been demonstrated for 2 species of terebellids; one of these, *Lanice conchilega*, is a cosmopolitan species that occurs on Hawaiian reefs. Extracts of the retractile tentacles and adhered food particles have proved effective against Erhlich ascites cell tumor (Tabrah et al. 1970).

Ecology. The importance of polychaetes in coral reef environments has been recognized by many researchers since the beginning of the 20th century. Fauchald (1976) discusses the need for quantitative and qualitative sampling of polychaetes from various habitat types in tropical areas to include soft sedimentary materials as well as coralline substrates.

The Hawaiian polychaetes included in this revision are from many different habitats, extending from the intertidal region to the deep channels between the islands. Habitats of the intertidal region include surf-washed limestone platforms, coral rubble reef flats, algal patches and turfs, sand and mud deposits, and estuaries and stream mouths. Hard substrates (notably coral rubble) support a more diverse polychaete assemblage than soft sediments (Brock and Smith 1982). Presumably the opportunity for borers, cryptic crevice dwellers, and encrusting sedentary species to occupy coral rock outweighs the less heterogeneous habitat offered by sand and mud. Sandy areas quite often support a dense polychaete fauna, as exemplified by the sediment-trapping chaetopterids that form mounds on reef flats (Bailey-Brock 1979).

Frondose algae and encrusting corallines provide cover for mobile and burrowing polychaetes. Worms living among thalloid algae may feed on other components of the community or on the detritus that becomes trapped among the thalli. The cirratulid *Dodecaceria laddi* lives in burrows within coralline algae and can be abundant in intertidal regions.

The polychaete fauna of brackish waters includes estuarine forms and some of the more euryhaline reef dwellers such as *Eurythoe complanata* (the common fire worm), *Neanthes succinea* (Mangum et al. 1980), and the serpulid *Hydroides elegans* (Bailey-Brock 1976).

Subtidally the polychaete fauna is more strictly marine, consisting of species less tolerant to reduced salinity conditions. Three basic habitat types are distinguished: live coral; dead coral, as rocks or rubble; and sand, with variable amounts of associated algal material. Live coral is remarkably devoid of polychaetes, although the association between *Spirobranchus giganteus* (the Christmas tree worm) and *Porites lobata* is a conspicuous and well-known example of such an association in Hawaiian waters (Bailey-Brock 1976). Polynoids, amphinomids, eunicids, chaetopterids, serpulids, and terebellids are typically represented in the other 2 habitats.

Deep waters between the islands have a benthic polychaete fauna associated with fine sand, mudlike oozes, and basalt rocks that cover the bottom near the islands and in the channels (Treadwell 1906). Tubicolous worms from such depths frequently have tubes formed of radiolarian tests (Hartman 1966), while serpulids are found on all hard substrates, including gastropod shells (Bailey-Brock 1972, 1976).

Planktonic polychaetes are less well represented than benthic forms, but 2 families, the Tomopteridae and Alciopidae, are caught in surface tows among the islands. Another group of worms is found attached to floating debris and on glass balls; the amphinomid *Amphinome rostrata* is a representative of this floating community. Entire worms or epitokes of nereidids and eunicids become temporarily planktonic prior to spawning.

Commensal polychaetes are known from the Hawaiian Islands. Species of polynoids are associated with brittle stars and starfish (Devaney 1967), spintherids with sponges, and spionids with oysters.

Human activities have variously modified coastal regions, but the construction of boat harbors and canals and the addition of sewage to the water are 2 of the perturbations most important to polychaetes. The protected waters of harbors are suitable environments for sessile tube worms and mud-dwelling species. Fouling communities on docks, buoys, and floating structures are usually made up of many sedentary and mobile polychaete species, in addition to hydroids, molluscs, amphipods, barnacles, sponges, and tunicates. Sewage enrichment has contributed to diverse communities of deposit- and filter-feeding species in hard substrates and sedimentary materials (Brock and Smith 1982). Other perturbations that have influenced the composition of polychaete assemblages include sedimentation caused by housing construction near shores, and the dredging of channels and stream mouths.

Some polychaete species serve as indicators of polluted or altered environmental conditions. The capitellid *Capitella capitata* occurs in waters with considerable organic enrichment (Reish 1973) and some freshwater influence, while the serpulid *Ficopomatus enigmaticus* is seen only in brackish areas in natural or altered environments (Bailey-Brock 1976). The walls of dredged channels in shallow or intertidal waters are frequently populated by the large fan worm *Sabellastarte sanctijosephi.*

In summary, polychaetes are found in all marine habitats around the Hawaiian Islands, forming abundant and diverse communities in many of them. Their small size, cryptic behavior, and usually subdued coloration make them less conspicuous on reefs than corals, crustaceans, and molluscs; however, the importance of the impact of polychaetes on reef ecosystems is just beginning to be realized.

POLYCHAETE STUDY TECHNIQUES

Preservation. Most polychaetes have soft, unprotected bodies from which accessory structures (e.g., cirri, tentacles, and scales) are easily lost. Worms should be treated with care, handled as little as possible, and kept covered with water prior to preservation. Polychaetes can be collected by any of the conventional methods for taking benthic or planktonic samples. Extraction of worms from the samples, whether coral rock, sand, mud, or algae, should be done with caution, either allowing the worms to leave the substrate as conditions become anoxic or removing them by gentle sieving. Worms may be relaxed in propylene-phynoxotol or in a 7% solution of $MgCl_2$ prior to formalin fixation. Coral rock can be dissolved in an acid bath following formalin fixation (Brock and Brock 1977). Polychaetes remain in good condition and the technique allows for quantitative analyses. Once removed from the sample, polychaetes must be fixed in a 10% formalin solution in seawater for approximately 48 hours. After fixation worms should be rinsed in tap water, put into screw-cap jars or vials with a solution of 70% ethyl alcohol, and labelled. Reference collections must be checked periodically to ensure that containers are full of alcohol. Any vials with discolored liquid should be emptied and refilled with fresh alcohol.

Examination of jaws and setae. Identification of polychaetes requires the examination of setae, and in those families equipped with biting mouthparts the jaw must also be studied. The jaw apparatus can be seen most easily if the proboscis is everted at the time of preservation. Relaxation prior to fixation sometimes causes the proboscis to evert. If the mouthparts remain inside the worm, the proboscis should be dissected using fine scissors or a sharp scalpel and forceps; make a longitudinal cut on the dorsolateral aspect, then pin back the cut edge to expose paragnaths or maxillae and mandibles. Syllids are generally so small and transparent that the pharyngeal structures can be seen when the specimen is prepared as a whole-mount and examined with a compound microscope.

Parapodia can be removed with forceps from most worms above 5 mm in length and made into a slide for examination of setae. For a permanent record, the parapodia should be dehydrated then mounted (with a commercial mountant). Tap water or a mixture of 5% formalin and glycerol makes adequate temporary mounts. Tiny worms can be preserved as whole-mounts on slides. Polyvinyllactophenol renders the tissue completely transparent, leaving the setae clearly visible and eventually hardens to preserve the specimen. Prior to polyvinyllactophenol treatment, tissue or specimens should be thoroughly dehydrated in ethanol, as water clouds the medium; any calcareous structures should be removed, since they will dissolve. Spirorbid opercula and other diagnostic structures containing calcium carbonate may be stored separately in clove oil. Amphinomid setae are also calcareous and should be mounted in Canada balsam or some other medium that will not dissolve the setae.

Polychaete morphology. The variations of body shape and types of appendages seen in the polychaetes can be bewildering for the nonspecialist, and the same can be said for the terminology used to describe them. A glossary of terms used in this revision begins on page 438, and the reader is also referred to excellent keys and glossaries given in Fauchald (1977a) and Day (1967). The diversity in body structure is shown in the figures illustrating the species in the present volume, but Day's key is useful because it includes illustrations of a whole worm, the head, parapodia, and setae representative of each family. The color, structure, and number of setae in each fascicle may vary according to the age of the worm. For example, juvenile stages of some nereidids and chaetopterids may have fewer, pale setae and acicula than older individuals. To facilitate recognition of the main morphological features necessary for taxonomic work herein, diagrams of stylized free-living and tubicolous worms are included (Figs. 3.II.1,2).

HAWAIIAN POLYCHAETA

- **Aphroditidae** (p. 232)
  - *Aphrodita* sp.
  - *Laetmonice producta wyvillei* McIntosh, 1885
- **Polynoidae** (p. 233)
  - *Hololepidella nigropunctata* (Horst, 1915)
  - *Iphione muricata* (Savigny, 1818)
  - *Lepidasthenia alba* (Treadwell, 1906)
  - *Lepidasthenia lucida* (Treadwell, 1906)
  - *Lepidonotus havaicus* Kinberg, 1855
  - *Paralepidonotus ampulliferus* (Grube, 1878)
  - *Thormora atrata* (Treadwell, 1940)
- **Polyodontidae** (p. 239)
  - *Panthalis mutilata* (Treadwell, 1906)
- **Sigalionidae** (p. 239)
  - *Euthalenessa chacei* Pettibone, 1970
  - *Psammolyce fijiensis* McIntosh, 1885
- **Chrysopetalidae** (p. 242)
  - *Paleanotus* sp.
- **Spintheridae** (p. 242)
  - *Spinther japonicus* Imajima and Hartman, 1964

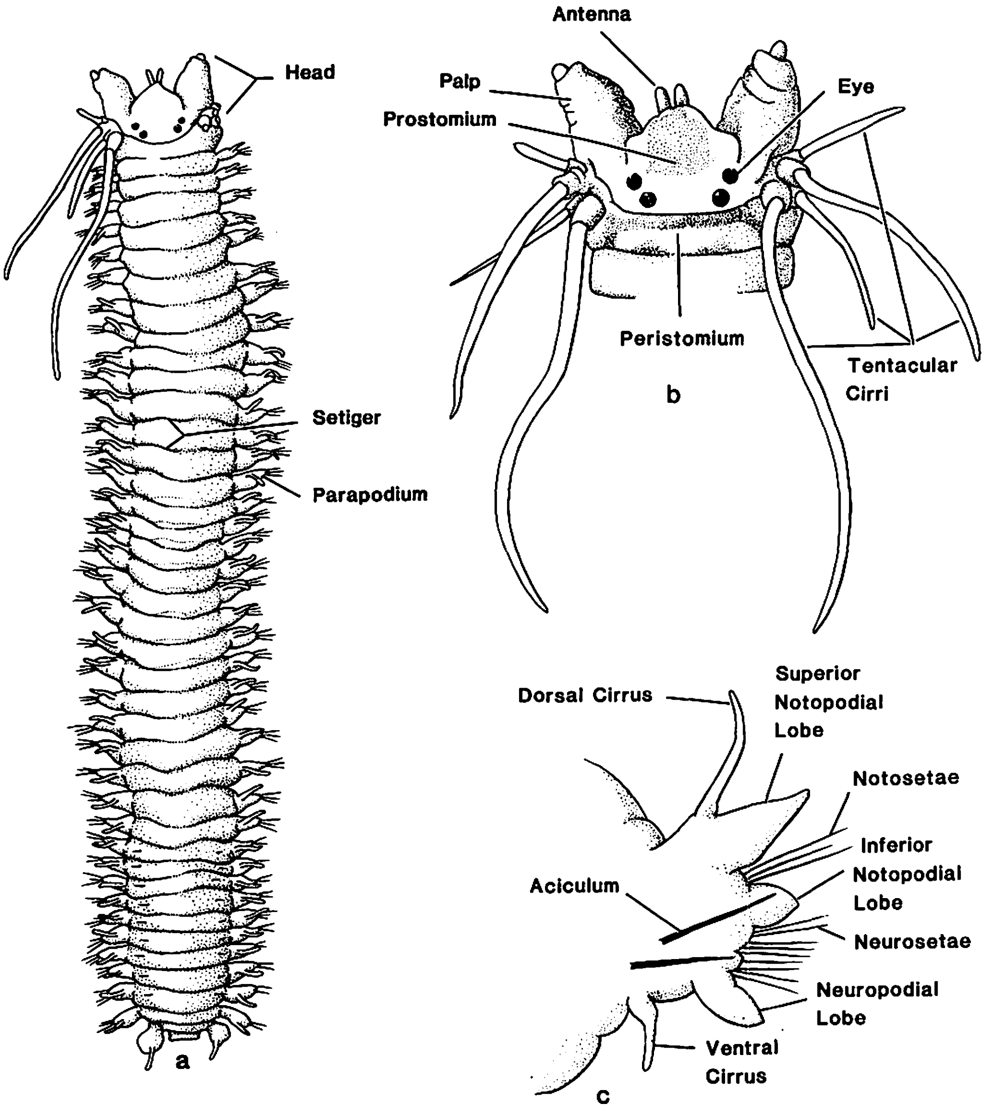

Figure 3.II.1.—Morphology of a generalized, free-living polychaete: a, anterior end (dorsal view); b, head structure and appendages; c, parapodium.

Amphinomidae (p. 244)
Amphinome rostrata (Pallas, 1766)
Chloeia flava (Pallas, 1766)
Eurythoe complanata (Pallas, 1766)
Hipponoe gaudichaudi Audouin and Milne Edwards, 1830
Notopygos albiseta Holly, 1939
Notopygos gregoryi Holly, 1939
Pareurythoe sp.
Pherecardia striata (Kinberg, 1857)

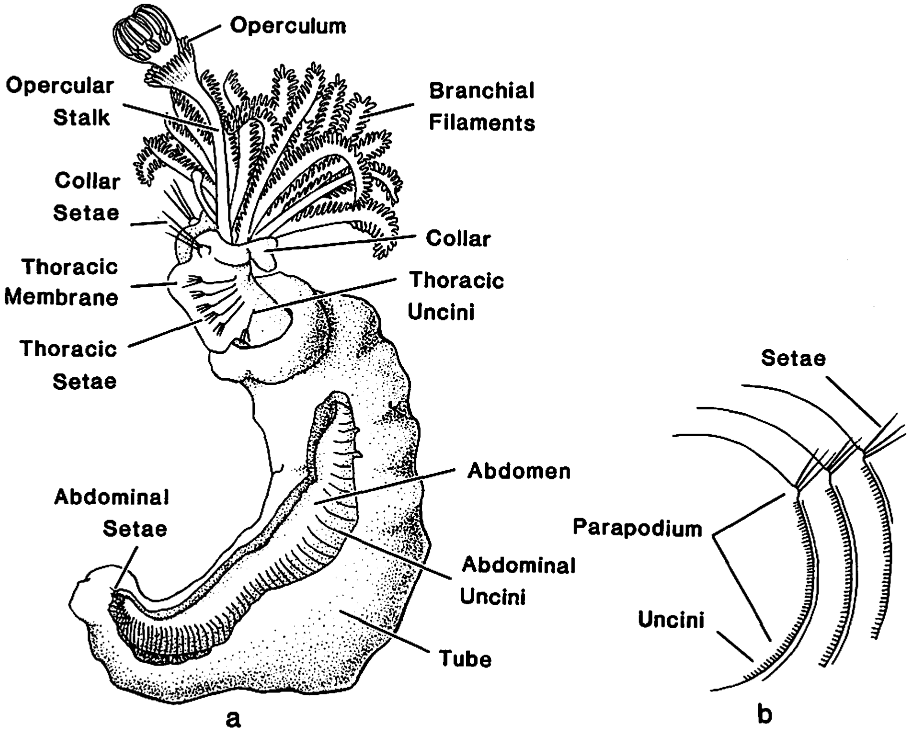

Figure 3.II.2.—Morphology of a generalized tubicolous polychaete: a, entire worm *in situ* (tube wall removed to show abdominal features); b, parapodium.

Pisionidae (p. 250)
- *Pisione africana* Day, 1963
- *Pisionidens indica* (Aiyar and Alikunhi, 1940)

Phyllodocidae (p. 252)
- *Eulalia havaica* Kinberg, 1866
- *Eulalia sanguinea* Oersted, 1843
- *Eumida caspersi* Hartmann-Schröder, 1965
- *Phyllodoce (Anaitides) madeirensis* (Langerhans, 1880)
- *Phyllodoce (Anaitides) parva* (Hartmann-Schröder, 1965)
- *Phyllodoce (Phyllodoce) hiatti* Hartman, 1966
- *Phyllodoce (Phyllodoce) tenera* Grube, 1878
- *Prophyllodoce hawaiia* Hartman, 1966

Alciopidae (p. 257)
- *Alciopa reynaudii* Audouin and Milne Edwards, 1833
- *Naiades cantrainii* delle Chiaje, 1830
- *Vanadis minuta* Treadwell, 1906

Tomopteridae (p. 259)
- *Tomopteris* sp.

Pilargidae (p. 260)
- *Sigambra parva* (Day, 1963)

Hesionidae (p. 261)
Hesione splendida Savigny, 1818
Leocrates chinensis Kinberg, 1866
Leocrates giardi Gravier, 1900a
Podarke pugettensis Johnson, 1901
Syllidia armata Quatrefages, 1865
Syllidae (p. 265)
Amblyosyllis sp.
Brachiosyllis exilis (Gravier, 1900b)
Brania rhopalohphora (Ehlers, 1897)
Brania sp.
Eusyllis sp.
Exogone verugera (Claparède, 1868)
Exogone sp.
Haplosyllis spongicola (Grube, 1855)
Langerhansia cornuta (Rathke, 1843)
Myrianida crassicirrata Hartmann-Schröder, 1965
Odontosyllis ctenostoma Claparède, 1868
Opisthosyllis brunnea Langerhans, 1879
Opisthosyllis corallicola Hartmann-Schröder, 1965
Opisthosyllis papillosa Hartmann-Schröder, 1960
Parasphaerosyllis indica Monro, 1937
Pionosyllis sp.
Sphaerosyllis capensis serrata Hartmann-Schröder, 1960
Sphaerosyllis centroamericana Hartmann-Schröder, 1959
Sphaerosyllis sublaevis Ehlers, 1913
Syllis gracilis
Trypanosyllis hawaiiensis Hartmann-Schröder, 1978
Trypanosyllis zebra (Grube, 1860)
Typosyllis crassicirrata Treadwell, 1925
Typosyllis hyalina (Grube, 1863)
Typosyllis hawaiiensis Hartmann-Schröder, 1965
Typosyllis microoculata Hartmann-Schröder, 1965
Typosyllis ornata Hartmann-Schröder, 1965
Typosyllis prolifera Krohn, 1852
Typosyllis variegata (Grube, 1860)
Typosyllis sp. A
Typosyllis sp. B
Nereididae (p. 292)
Ceratonereis pietschmanni Holly, 1935
Ceratonereis tentaculata Kinberg, 1866
Ceratonereis vulgata Kinberg, 1866
Micronereis bansei (Paxton, 1983)
Namalycastis abiuma (Müller, in Grube, 1872)
Neanthes arenaceodonta Moore, 1903b
Neanthes succinea Frey and Leuckart, 1847
Nereis abbreviata Holly, 1935
Nereis corallina Kinberg, 1866
Nereis hawaiiensis Holly, 1935

Nereis jacksoni Kinberg, 1866
Nereis mariae Holly, 1935
Nereis myersi Holly, 1935
Nereis nigroaciculata Holly, 1935
Nereis unica Holly, 1935
Nereis waikikiensis Holly, 1935
Perinereis curvata Holly, 1935
Perinereis helleri Grube, 1878
Perinereis nigropunctata (Horst, 1889)
Platynereis abnormis Horst, 1924
Platynereis bicanaliculata (Baird, 1863)
Platynereis dumerilii (Audouin and Milne Edwards, 1833)
Platynereis pulchella Gravier, 1901
Pseudonereis anomala Gravier, 1901
Pseudonereis gallapagensis Kinberg, 1866
Pseudonereis sp.

Glyceridae (p. 313)
Glycera tesselata Grube, 1863

Goniadidae (p. 314)
Goniada brunnea Treadwell, 1906

Eunicidae (p. 315)
Eunice afra Peters, 1854
Eunice antennata (Savigny, 1820)
Eunice australis Quatrefages, 1865
Eunice bilobata Treadwell, 1906
Eunice cariboea (Grube, 1856)
Eunice filamentosa Grube, 1856
Eunice hawaiensis Treadwell, 1906
Eunice nicidioformis Treadwell, 1906
Eunice vittata (delle Chiaje, 1828)
Lysidice ninetta Audouin and Milne Edwards, 1833
Marphysa corallina Kinberg, 1865
Marphysa macintoshi Crossland, 1903
Marphysa sanguinea Montagu, 1815
Nematonereis unicornis Schmarda, 1861
Palola siciliensis (Grube, 1840)

Onuphidae (p. 326)
Diopatra leuckarti Kinberg, 1865
Diopatra, undescribed species
Nothria hawaiiensis Pettibone, 1970
Onuphis holobranchiata Marenzeller, 1879

Lumbrineridae (p. 328)
Lumbrineris dentata Hartmann-Schröder, 1965
Lumbrineris heteropoda (Marenzeller, 1879)
Lumbrineris inflata (Moore, 1911)
Lumbrineris latreilli Audouin and Milne Edwards, 1834
Lumbrineris minuscula (Moore, 1911)
Lumbrineris sarsi (Kinberg, 1865)

Lumbrineris sphaerocephala (Schmarda, 1861)

Arabellidae (p. 333)

Arabella iricolor (Montagu, 1804)
Arabella iridescens Treadwell, 1906

Dorvilleidae (p. 336)

Apophryotrocha sp.
Dorvillea ?angolana (Augener, 1918)
Dorvillea moniloceras (Moore, 1909)
Ophryotrocha sp.
Schistomeringos rudolphi (delle Chiaje, 1828)

Spionidae (p. 340)

Aonides oxycephala (Sars, 1862)
Australospio mokapu Ward, 1981a
Boccardiella sp.
Carazziella reishi (Woodwick, 1964)
Dispio uncinata Hartman, 1951
Laonice papillibranchiae Ward, 1981a
Malacoceros sp.
Microspio granulata Blake and Kudenov, 1978
Minuspio sp.
Polydora armata Langerhans, 1880
Polydora kaneohe Ward, 1981a
Polydora pilikia Ward, 1981a
Polydora tridenticulata Woodwick, 1964
Polydora websteri Hartman, 1943
Prionospio sp.
Pseudopolydora antennata (Claparède, 1870)
Pseudopolydora corallicola Woodwick, 1964
Pseudopolydora sp.
Pygospio muscularis Ward, 1981a
Rhynchospio sp.
Scolelepis squamata (Müller, 1806)
Scolelepis sp.
Spio filicornis (Müller, 1776)
Spio pettiboneae Foster, 1971
Spiophanes berkeleyorum Pettibone, 1962
Spiophanes bombyx (Claparède, 1870)
Spiophanes wigleyi Pettibone, 1962
Streblospio benedicti Webster, 1879
Tripolydora spinosa Woodwick, 1964

Magelonidae (p. 369)

Magelona sp.

Cirratulidae (p. 370)

Cirratulus zebuensis McIntosh, 1885
?Cirriformia capensis (Schmarda, 1861)
Cirriformia crassicollis (Kinberg, 1866)
Cirriformia hawaiensis (Hartman, 1956)
Cirriformia punctata (Grube, 1856)

Cirriformia semicincta (Ehlers, 1905)
Dodecaceria laddi Hartman, 1954a
Chaetopteridae (p. 374)
Chaetopterus variopedatus (Renier, 1804)
Mesochaetopterus sagittarius (Claparède, 1870)
Phyllochaetopterus socialis (Claparède, 1870)
Phyllochaetopterus verrilli Treadwell, 1943
Orbiniidae (p. 378)
Naineris bicornis minuta Hartmann-Schröder, 1965
Naineris laevigata (Grube, 1855)
Paraonidae (p. 380)
Paraonis sp.
Opheliidae (p. 381)
Armandia intermedia Fauvel, 1902
Ophelina sp.
Polyophthalmus pictus Dujardin, 1839a

amily:
Questidae
(see p,214)

Cossuridae (p. 383)
Cossura coasta Kitamori, 1960
Scalibregmidae (p. 385)
Hyboscolex longiseta Schmarda, 1861
Capitellidae (p. 386)
Capitella capitata (Fabricius, 1780)
Dasybranchus ?lumbricoides Grube, 1878
Notomastus (Clistomastus) anoculatus Hartmann-Schröder, 1965
Scyphoproctus djiboutiensis Gravier, 1906
Arenicolidae (p. 389)
Arenicola brasiliensis (Nonato, 1958)
Maldanidae (p. 390)
?Praxillella sp.
Sternaspidae (p. 390)
Sternaspis sp.
Oweniidae (p. 390)
Myriochele hiruensis Gibbs, 1971
Flabelligeridae (p. 392)
Pherusa havaica (Kinberg, 1867)
Sabellariidae (p. 393)
Lygdamis nesiotes (Chamberlain, 1919)
Monorchos varians Hartman and Fauchald, 1971
Phalacrostemma setosa (Treadwell, 1906)
Phragmatopoma moerchi Kinberg, 1867
Trichobranchidae (p. 397)
Trichobranchus sp.
Terebellidae (p. 398)
Lanice conchilega (Pallas, 1766)
Lanice expansa Treadwell, 1906
Loimia medusa (Savigny, 1818)
Lysilla ubianensis Caullery, 1944
Neoamphitrite sp.

Nicolea gracilibranchis (Grube, 1878)
Pista dibranchis Gibbs, 1971
Polycirrus sp.
Terebella lapidaria Linnaeus, 1767
Thelepus branchiatus Treadwell, 1906
Thelepus setosus (Quatrefages, 1865)

Sabellidae (p. 408)
Augeneriella dubia Hartmann-Schröder, 1965
Branchiomma nigromaculata (Baird, 1865)
Demonax leucaspis Kinberg, 1867
Hypsicomus phaeotaenia (Schmarda, 1861)
Megalomma intermedium (Beddard, 1888)
Potamethus elongatus (Treadwell, 1906)
Potamilla sp.
=*Sabellastarte sanctijosephi* (Gravier, 1906b) S. spectabilis

Serpulidae (p. 416)
Ficopomatus enigmaticus (Fauvel, 1923)
Hydroides brachyacantha Rioja, 1941
Hydroides crucigera (Mörch, 1863)
Hydroides dirampha (Mörch, 1863) - ns
Hydroides elegans (Haswell, 1883)
Pomatoleios kraussii (Baird, 1865)
Protula atypha Bush, 1904
Pseudovermilia occidentalis McIntosh, 1885
Salmacina dysteri (Huxley, 1855)
Semivermilia pomatostegoides (Zibrowius, 1969)
Serpula vermicularis Linnaeus, 1767
Spirobranchus giganteus corniculatus (Grube, 1862)
Spirobranchus latiscapus Marenzeller, 1885
Vermiliopsis infundibulum (Philippi, 1844)
Vermiliopsis torquata Treadwell, 1943

Spirorbidae (p. 426)
Eulaeospira orientalis (Pillai, 1960)
Janua pagenstecheri Quatrefages, 1865
Leodora knightjonesi (de Silva, 1965)
Neodexiospira foraminosa (Moore and Bush, 1904)
Neodexiospira nipponica Okuda, 1934
Neodexiospira preacuta Vine, 1972b
Neodexiospira pseudocorrugata (Bush, 1904)
Nidificaria dalestraughanae (Vine, 1972a)
Pileolaria militaris Claparède, 1868
Pileolaria pseudoclavus Vine, 1972b
Protolaeospira capensis (Day, 1961)
Simplicaria pseudomilitaris (Thiriot-Quiévreux, 1965)
Spirorbis marioni (Caullery and Mesnil, 1897)
Vinearia koehleri Caullery and Mesnil, 1897

KEY TO HAWAIIAN POLYCHAETE FAMILIES

1 Body oval or elongate; segmented or apparently so; may be covered with long setae or elytra (scales) 2

Body round and flattened; segmentation indistinct; covered with membraneous ridges, each supported by a few short setae (Figs. 3.II.13a,b,c) .... **Spintheridae** (p. 242)

2(1) Head a distinct region, often with sensory antennae, 1 or 2 pairs of eyes, and a protrusible pharynx that may have jaws, teeth, or papillae; parapodial lobes well-developed, each supported by an aciculum and bearing a tuft of setae; compound setae generally present 3

Head lacks jaws and sensory appendages; head usually modified for feeding as buccal cirri, palps, or a feathery branchial crown; parapodia reduced, compound setae generally absent 21

3(2) Dorsum entirely or partially covered by a layer of feltlike setae and/or elytra (Fig. 3.II.4a) 4

Dorsum not covered by felt or elytra 7

4(3) Dorsum may be covered by a felt; harpoon setae often present; no jaws .... **Aphroditidae** (p. 232)

Dorsum entirely or partially covered by elytra, feltlike setae absent; harpoon setae absent; 4 horny jaws 5

5(4) Compound neurosetae present (Figs. 3.II.11g–j); elytra and dorsal cirri borne on alternate segments anteriorly, but elytra present on all posterior segments .... **Sigalionidae** (p. 239)

No compound neurosetae; elytra and dorsal cirri alternate regularly or irregularly along entire length, or anteriorly 6

6(5) Eyes sessile; notopodial spinning glands absent; neurosetae not in groups (Figs. 3.II.5a,b, 6a,c, 7a,b, 8a,b) .... **Polynoidae** (p. 233)

Eyes stalked or sessile; notopodial spinning glands present (Fig. 3.II.10a); neurosetae in 3 distinct groups .... **Polyodontidae** (p. 239)

7(3) Dorsum entirely or partially covered by fans of flattened notosetae (paleae) (Figs. 3.II.12a,b) .... **Chrysopetalidae** (p. 242)

Dorsum not covered by setae 8

8(7) A sensory lobe (caruncle) usually present behind the head (Figs. 3.II.15a, 16, 19, 20, 21); biramous parapodia with simple calcareous setae .... **Amphinomidae** (p. 244)

No sensory lobe; parapodia uniramous or biramous with chitinous setae 9

9(8) Parapodia uniramous with lamellar dorsal cirri (Figs. 3.II.22a,b, 23a,b, 24a,b, 25a,b, 26a,b, 27a,b) 10

Parapodia not uniramous and without lamellar dorsal cirri 11

10(9) One pair of small eyes; body pigmented in benthic animals, transparent in pelagic forms; setae all compound spinigers (Fig. 3.II.22c) .... **Phyllodocidae** (p. 252)

One pair of extremely large-lensed eyes (Figs. 3.II.28a, 29a, 30a); all transparent and planktonic; setae of 3 types: simple capillary, acicular, and compound spinigers .... **Alciopidae** (p. 257)

11(9) Biramous parapodia without setae (Fig. 3.II.31c); body transparent; eyes small; planktonic .... **Tomopteridae** (p. 259)

Biramous or uniramous parapodia with setae; body pigmented; iridescent or transparent; benthic 12

12(11) First 3 to 4 segments short and fused to the prostomium, lacking parapodia but with 2 to 8 pairs of tentacular cirri with acicula .... **Hesionidae** (p. 261)

Parapodial structures of anterior segments otherwise 13

13(12) Proboscis a muscular pharynx with a proventriculus; no jaws (Fig. 3.II.37a) .... **Syllidae** (p. 265)

Jaws and an eversible proboscis present 14

14(13) Proboscis with distal jaws and paragnaths or soft papillae; prostomium with a pair of biarticulate palps (Fig. 3.II.68a) .... **Nereididae** (p. 292)

Arrangement of jaws otherwise; palps not biarticulate; paragnaths and soft papillae absent 15

15(14) Prostomium a long, annulated cone with 4 small frontal antennae at the tip (Fig. 3.II.93a); jaws simple 16

Prostomium rounded or conical but never annulated; elaborate jaws of maxillary plates and mandibles 17

16(15) Proboscis with 4 terminal jaws, each with a V-shaped support (Fig. 3.II.92c); parapodia either all uniramous or all biramous .... **Glyceridae** (p. 313)

Proboscis with 2 large terminal jaws and a ring of smaller ones; parapodia uniramous anteriorly and biramous posteriorly (Fig. 3.II.93e).................................. **Goniadidae** (p. 314)

17(15) Prostomium with antennae (Fig. 3.II.94a) 18

Prostomium without antennae (Fig. 3.II.108a) 20

18(17) Tubicolous worms with 7 antennae, 2 frontals and 5 long occipitals, on ringed ceratophores (Fig. 3.II.106b) .... **Onuphidae** (p. 326)

Fewer than 7 antennae, no ringed ceratophores 19

19(18) One, 3, or 5 antennae (Figs. 3.II.100a, 103a, 104a) with or without short peristomial cirri; 4 or 5 pairs of maxillae, without a middle piece .... **Eunicidae** (p. 315)

One pair of antennae and palps (Fig. 3.II.116a); maxillae of numerous small elements (denticles) in 2 or 4 longitudinal rows .... **Dorvilleidae** (p. 336)

20(17) No eyes; maxillary plates with 2 short supports, without a median piece, mandibles well-developed; setae include winged capillaries and simple or compound hooded hooks (Figs. 3.II.113b,c,d) .... **Lumbrineridae** (p. 328)

With or without eyes; maxillary supports with a median piece; setae are winged capillaries, no hooded hooks (Fig. 3.II.114c) .... **Arabellidae** (p. 333)

21(2) Body short, dumbbell-shaped, anterior end narrower than posterior, which bears filamentous anal gills and shield-shaped plates (Fig. 3.II.166a) .... **Sternaspidae** (p. 390)

Body elongate, without anal gills and plates 22

22(21) Anterior end with or without a pair of palps, grooved tentacles, and/or an eversible proboscis; surface sediment dwellers and burrowers ... 23

Anterior end modified to form a branchial crown, tentacles, or a crown of setae; tubicolous ... 35

23(22) A pair of palps present ... 24

A pair of palps absent ... 27

24(23) Anterior part of worm retractable, concealing branchial filaments and palps (Fig. 3.II.167a); anteriormost setae may form a cephalic cage over the head ... **Flabelligeridae** (p. 392)

Head structures exposed ... 25

25(24) Anterior segments rounded, frequently with dorsal cirriform or pinnate gills (Fig. 3.II.121a); body not divided into distinct regions ... **Spionidae** (p. 340)

Head or anterior segments flattened dorsoventrally, gills absent; body divided into 2 to 3 distinct regions ... 26

26(25) Head shovel-shaped for burrowing; body divided into 2 regions; setiger 4 with capillary setae; palps bear numerous small papillae ... **Magelonidae** (p. 369)

Tubicolous; body divided into 3 regions (Figs. 3.II.154a,b); setiger 4 with heavy acicular setae; middle region with parapodia modified as paddles ... **Chaetopteridae** (p. 374)

27(23) Anterior segments with extensile tentacles and numerous filamentous branchiae ... **Cirratulidae** (p. 370)

Anterior segments without extensile tentacles and filamentous branchiae ... 28

28(27) A single long, filiform branchia present on the dorsum of an anterior setiger; capillary setae with finely spinulose margins (Fig. 3.II.161c) ... **Cossuridae** (p. 383)

Branchiae and capillary setae otherwise ... 29

29(28) Branchiae are notopodial structures (Fig. 3.II.158b), present on a variable number of anterior setigers; anterior setigers with smooth capillaries; specialized setae may be present in either ramus posteriorly; a single antenna may be present ... **Paraonidae** (p. 380)

Branchiae and capillary setae otherwise; no antenna ... 30

30(29) Branchiae arranged over the dorsum; setae all simple, crenulate capillaries or hooks (Fig. 3.II.157d) ... **Orbiniidae** (p. 378)

Branchiae (when present) are notopodial; setae otherwise ... 31

31(30) Body elongate, tapered, and may be grooved ventrally; lateral segmental eyespots often present (Figs. 3.II.159a,b, 160a); setae simple capillaries ... **Opheliidae** (p. 381)

Body short and stout, bamboolike, earthwormlike, or arenicoliform (anterior segments wider than posterior ones); usually without lateral segmental eyespots; with or without branchiae ... 32

32(31) Earthwormlike body; setae are tooth-crested hooks with hoods (Fig. 3.II.164) ... **Capitellidae** (p. 386)

Body not like an earthworm; setae are tooth-crested hooks without hoods, forked acicular, or capillary setae ... 33

33(32) Prostomium bilobed or broadly V-shaped (Fig. 3.II.162a), with or without eyes; branchiae (when present) on anterior segments only .... **Scalibregmidae** (p. 385)
Prostomium and body otherwise; with or without branchiae 34

34(33) Body arenicoliform, with annulated middle segments; tufted branchiae always present (Fig. 3.II.165) .... **Arenicolidae** (p. 389)
Body with elongate middle segments that are not annulated; branchiae usually absent .... **Maldanidae** (p. 390)

35(22) Anterior end with a crown of golden, flattened setae forming an operculum (Figs. 3.II.168a,b) .... **Sabellariidae** (p. 393)
Anterior region with branchiae and/or filamentous structures for food gathering 36

36(35) Thoracic uncini long-shafted hooks (Fig. 3.II.172c); abdominal uncini (Fig. 3.II.172d) short-handled .... **Trichobranchidae** (p. 397)
Thoracic uncini otherwise, abdominal uncini short- or long-handled 37

37(36) Thoracic uncini short-handled (Fig. 3.II.180d); filamentous tentacles and branched branchiae anteriorly; tubes of sand and shell fragments (Figs. 3.II.173a,c) .... **Terebellidae** (p. 398)
Thoracic uncini with or without companion setae; anterior region with a crown of bipinnulate branchiae forming a funnel around the mouth; tubes calcareous or of fine sand, mud, or mucus 38

38(37) Tubes covered with fine sand or mud, or formed of mucus; no operculum .... **Sabellidae** (p. 408)
Tubes calcareous; operculum usually present 39

39(38) Tubes sinuous, attached or erect (Figs. 3.II.188a,b, 195, 199a); more than 5 thoracic setigers .... **Serpulidae** (p. 416)
Tubes spirally coiled (Figs. 3.II.202a, 204a, 205a, 206a, 207a, 213a), mostly attached (mouth may be erect); 5 or fewer thoracic setigers .... **Spirorbidae** (p. 426)

Since going to press 3 other polychaete families have been collected in Hawaiian waters: 2 pisionid species (p. 251) from Midway Island (NWHI), an oweniid (p. 390), and a pilargid (p. 260) from Oahu.

Family **Aphroditidae** — inc. Polyodontidae

Aphroditids are oval scale worms that burrow in soft sediments and feed on sessile or slow-moving invertebrates (Fauchald and Jumars 1979). The elytra are usually covered by a felt of silky setae that keep them free of sediment, allowing the elytra to serve as respiratory surfaces. The 2 species known from Hawaii, *Aphrodita* sp. (as *A. echidna* by Treadwell 1906) and *Laetmonice producta wyvillei* McIntosh, 1885, occur at great depths and so will not be further described here. Hartman (1966) and Treadwell (1906) give brief diagnoses of these 2 species, and Hartman indicates that *A. echidna* described by Treadwell may not be the same as *A. echidna* Quatrefages described originally from South America. General features of aphroditids are given in Day (1967).

Family **Polynoidae**

Polynoids are short or long worms, flattened dorsoventrally, with the dorsum more or less covered by pairs of overlapping elytra (scales) that give this family the colloquial name of scale worms. These worms are predaceous, catching and swallowing their prey with a proboscis armed with stout jaws (Fauchald and Jumars 1979). Many species are free-living and cryptic, lodging under rocks and in crevices; others are commensal with tubicolous polychaetes and echinoderms. Seven species belonging to 6 genera are known from Hawaii.

Elytra are borne on specific segments. The segments lacking elytra bear dorsal cirri. Elytra are easily dislodged when living or preserved material is handled. The button-shaped points of attachment (elytrophores) must be observed to determine the number and arrangement of the elytra. The shape, ornamentation, and number of pairs of elytra are diagnostic characters, as are the head appendages, parapodial lobes, setae, and cirri. Pelagic larval stages of polynoids are easily recognized, since they have a few pairs of delicate elytra (Ward 1978).

KEY TO HAWAIIAN POLYNOID GENERA

1	Body with fewer than 30 segments; elytra 12 or 13 pairs	2
	Body with 30 segments; elytra 15 or more pairs	4
2(1)	Body elongate or oval, composed of 29 segments; elytra 13 pairs, on segments 2, 4, 5, 7, alternate segments to 23, and 27; elytral surface divided into polygonal areas with lateral fringes of papillae; prostomium with 2 lateral antennae inserted terminally, without median antenna (Fig. 3.II.4)	*Iphione*
	Body subrectangular, composed of 26 segments; elytra 12 pairs, on segments 2, 4, 5, 7, alternate segments to 23; elytral surface covered with tubercles, with or without marginal fringes; prostomium with 3 antennae; lateral antennae inserted terminally	3
3(2)	Notosetae of 1 type, with spinous rows	*Lepidonotus*
	Notosetae of 2 distinct types: few short, with spinous rows and blunt tips, and numerous long, smooth, spear-shaped, with tapered tips (Figs. 3.II.9a,b)	*Thormora*
4(1)	Lateral antennae inserted terminally on anterior extensions of prostomium (Figs. 3.II.5a, 6a); parapodia sub-biramous, notopodia with acicula only, without notosetae (Fig. 3.II.5b); neuropodia deeply cut dorsally and ventrally, forming anterior and posterior rounded lips	*Lepidasthenia*
	Lateral antennae with distinct ceratophores, inserted ventral to median antenna (Figs. 3.II.3c, 8a); parapodia biramous, with notosetae; neuropodia with subconical presetal and shorter, rounded postsetal lobes (Figs. 3.II.3b,d, 8b)	5
5(4)	Elytra 15 pairs, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32; elytra with numerous microtubercles, some globular vesicles, and lateral fringe of papillae (Fig. 3.II.8f); paired ventral lamellae medial to ventral cirri; notosetae with numerous rows of fine spines (Fig. 3.II.8c)	*Paralepidonotus*

Elytra up to 26 or more pairs, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 31, 34, alternate segments to end of body; elytra with few scattered microtubercles, without fringe of papilla (Fig. 3.II.3a); without paired lamellae; notosetae coarsely serrated along 1 border (Fig. 3.II.3e) .... *Hololepidella*

Hololepidella nigropunctata (Horst, 1915)
[syn. near *Acanthicolepis*: Hartman 1966]

Specimens may be as long as 18 mm and up to 4.8 mm wide including setae. The dorsum may be colorless, tan, or dark brown; darker specimens have triangular patches of dark pigmentation. The body is composed of up to 55 segments, with up to 26 pairs of elytra that overlap and cover the dorsum. Elytra are round or slightly oval and are smooth except for a few microtubercles on the anterior part (Fig. 3.II.3a). The prostomium bears 2 pairs of eyes (the anterior pair

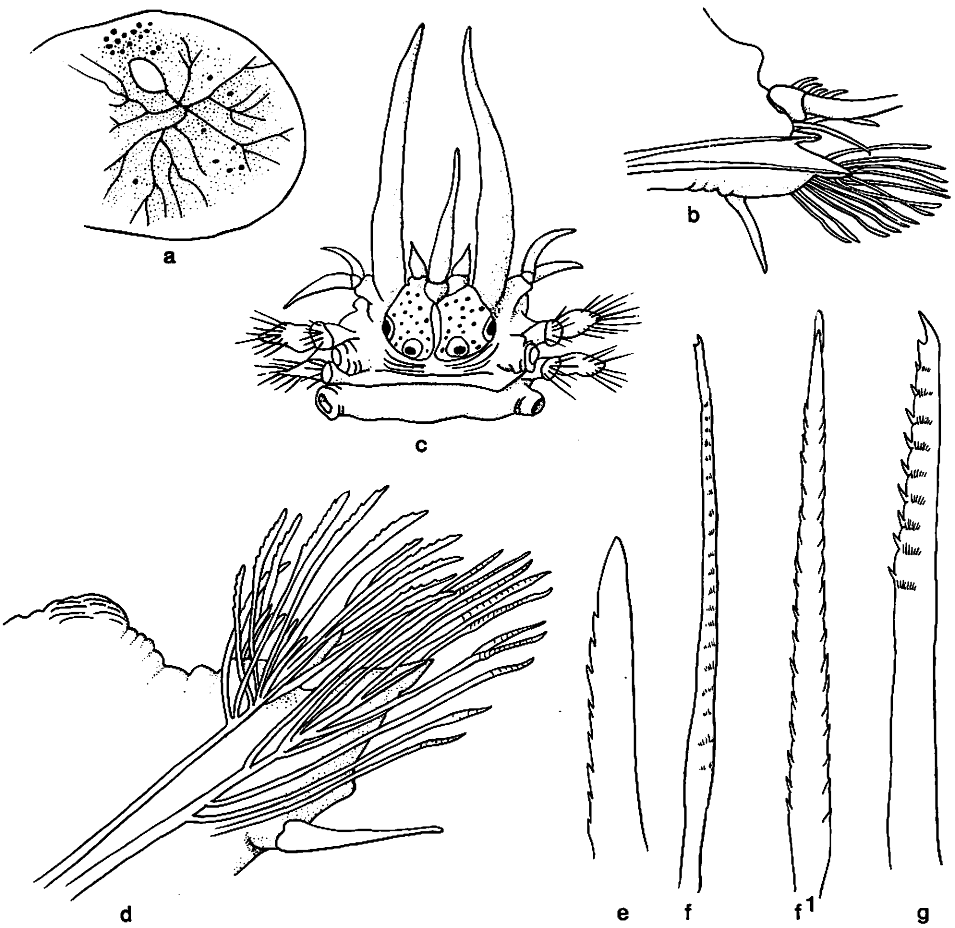

Figure 3.II.3.—*Hololepidella nigropunctata*: a, elytron; b, parapodium with dorsal cirrus; c, anterior region with head appendages and 2 pairs of round elytrophores; d, parapodium with elytrophore; e, notoseta; f,f^1, middle neurosetae; g, lower neuroseta. (After Devaney 1967.)

on the widest part of the prostomium) a pair of long palps, a long median antenna, and a pair of short lateral antennae with distinct ceratophores inserted ventral to the median antenna (Fig. 3.II.3c). The parapodia are biramous and bear dorsal cirri (Fig. 3.II.3b) or elytra (Fig. 3.II.3d). Notosetae have 8 to 14 widely spaced spines along the convex edge (Fig. 3.II.3e). Uppermost neurosetae are slender and spinous with slightly bifid tips; middle neurosetae have distinctly bifid tips (Figs. 3.II.3f, f^1); and lower neurosetae have shorter spinous regions and entire or indistinctly bifid tips (Fig. 3.II.3g). These polynoids are ectocommensal with the brittle star *Ophiocoma dentata*, or less frequently with other ophiocomid brittle stars or even *Acanthaster planci* (crown-of-thorns sea star). They are found, usually singly, on the oral surface of the arms or central disc, with the head oriented towards the mouth of the brittle star (Devaney 1967). *Hololepidella nigropunctata* has a tropical Indo-West Pacific distribution (Gibbs 1971). See Pettibone (1969) for a review of the genus.

Iphione muricata (Savigny, 1818)

Specimens are up to 25 mm long, 10 mm wide, and are composed of 29 segments. These worms are flat, elongate-oval, red in life, and reddish brown or orange when preserved (Plate 3.II.2a). There are 13 pairs of firmly attached, overlapping elytra covering the dorsum (Fig. 3.II.4a). The prostomium is deeply incised medially, with a pair of long antennae inserted terminally and a pair of stout palps (Fig. 3.II.4b). Elytra are broadly reniform, marginally fringed with papillae, with their surfaces divided into polygonal areas (Fig. 3.II.4c). The species is common intertidally among coral rubble, clinging to the undersides of stones and other hard surfaces (Hartman 1966), and has been collected on the Ulupau bench, Kaneohe Bay, Oahu, in water less than 1 m deep. *Iphione muricata* has an extensive Indo-West Pacific distribution (Day 1967).

Lepidasthenia alba (Treadwell, 1906)
[syn. *Polynoe alba* Treadwell, 1906]

The body is elongate, with up to 100 or more segments. The prostomium appears bilobed and has 2 pairs of eyes and 3 smooth antennae. The ceratophore of the median antenna is in the anterior notch between the 2 lateral antennae,

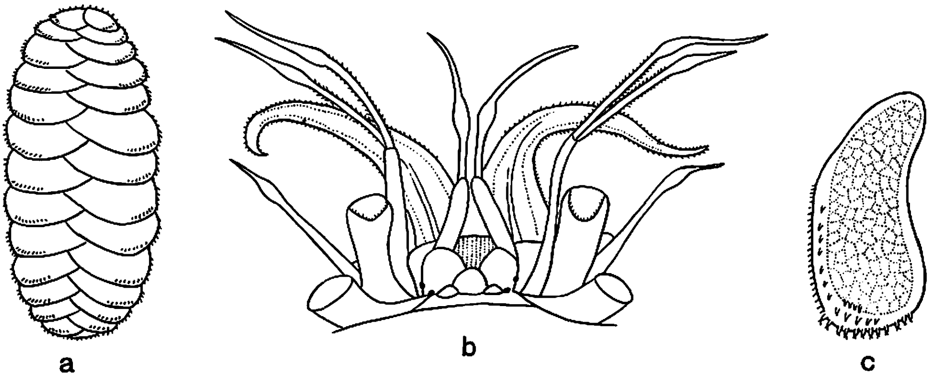

Figure 3.II.4.—*Iphione muricata*: a, entire worm; b, anterior region with head appendages and 2 pairs of round elytrophores; c, elytron. (After Gravier 1901.)

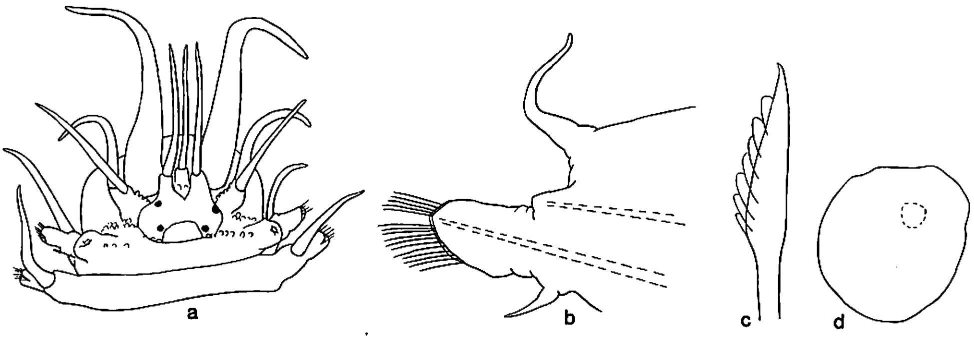

Figure 3.II.5.—*Lepidasthenia alba*: a, anterior region with head appendages and 1 pair of elytrophores; b, parapodium; c, neuroseta; d, elytron.

which are inserted terminally on anterior extensions of the prostomium (Fig. 3.II.5a). The lst segment lacks setae; parapodia lie on both sides of the prostomium. The 2nd segment bears setae, lies behind the prostomium, and bears a semilunar papillate nuchal fold (Fig. 3.II.5a) that slightly overlaps the prostomium. The 1st and 2nd segments, median ceratophore, and nuchal fold area bear dorsal transverse rows of papillae (Fig. 3.II.5a). Parapodia are long, sub-biramous, with the notopodia in the form of small digitiform lobes with an internal aciculum; notosetae are lacking (Fig. 3.II.5b). The neuropodia are well developed, with an aciculum and fan-shaped bundles of neurosetae. Distally the neuropodia are deeply cut dorsally and ventrally, forming anterior and posterior rounded lips. The dorsal cirri are long, tapered, and borne on distinct ceratophores; the ventral cirri are short (Fig. 3.II.5b). Neurosetae are all of one kind, with 2 rows of delicate plates continuing distally to their tips (Fig. 3.II.5c). There are numerous pairs of elytra arranged on segments 2, 4, 5, 7, and on alternate segments to 23, 26, 29, 32, 35, continuing on every 3rd segment to the end of the body. Elytra have white patches, are oval, smooth, without tubercles or fringes of papillae (Fig. 3.II.5d), and leave the mid-dorsum uncovered. *Lepidasthenia alba* has been collected from the bench at Ulupau, Kaneohe Bay, Oahu, in water less than 1 m deep, and was originally reported from Honolulu, Oahu, reefs by Treadwell (1906).

Lepidasthenia lucida (Treadwell, 1906)
[syn. *Polynoe lucida* Treadwell, 1906]

An incomplete specimen measures 37 mm long and 7.5 mm wide (including the setae), and is composed of 60 segments or more. The prostomium is similar to that of *L. alba*, with 2 lateral and 1 median antenna, each with a subterminal swelling and pointed tip (Fig. 3.II.6a). The head region is iridescent after preservation in alcohol. Elytra are oval, leaving the mid-dorsum uncovered, and are smooth, lacking tubercles and fringes of papillae (Fig. 3.II.6b). Elytra are arranged on segments 2, 4, 5, 7, on alternate segments to 23, 26, 29, 32, 35, continuing on every 3rd segment. Except for patches of brown pigment, elytra appear transparent. Parapodia are similar to *L. alba*, with only a notoaciculum (no notosetae), a fan of neurosetae, an elongate dorsal cirrus, and a short ventral cirrus (Fig. 3.II.6c). Neurosetae are more numerous than in *L. alba*, the upper

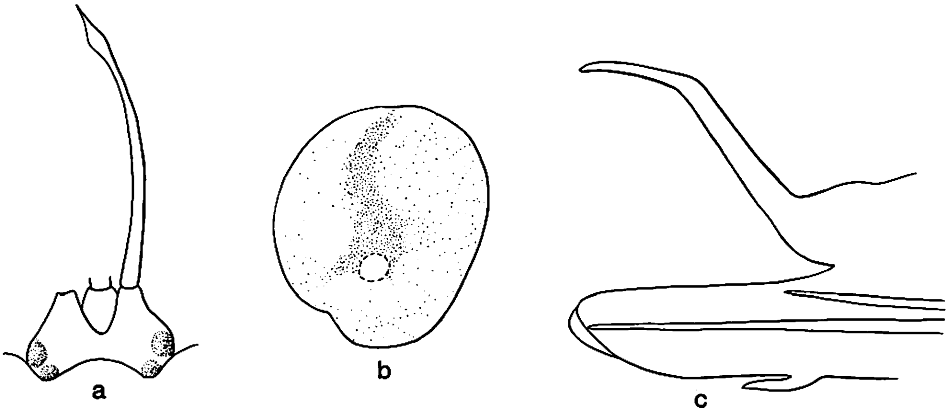

Figure 3.II.6.—*Lepidasthenia lucida*: a, head, 1 antenna shown; b, elytron; c, parapodium, setae omitted. (After Treadwell 1906.)

ones having longer spinous regions than the lower ones and extend to their distal tips. This species was reported off Hawaii at a depth of 152 to 207 m (83 to 113 fm) from a sand bottom of volcanic and coralline sand and shells.

Lepidonotus havaicus Kinberg, 1855

The body is up to 12 mm long. The prostomium has 2 pairs of eyes, 3 frontal antennae, and a pair of tapering palps; the lst or tentacular segment is achaetous, with 2 pairs of tentacular cirri (Fig. 3.II.7a). Parapodia are sub-biramous, with short notopodia and small bundles of notosetae (Fig. 3.II.7b). Some notosetae are short and curved with blunt tips, while others are longer, tapering to fine tips. The neuropodia are much larger, with the presetal acicular lobe subconical and a shorter truncate postsetal fleshy lobe. Neurosetae are distally bifid in the superiormost series and gradually become entire in the inferiormost part (Figs. 4, 5 in Hartman 1948a). The elytra are oval and covered with small, blunt, simple tubercles; some have lateral fringes of papillae (Fig. 3.II.7c). This species was originally described from the intertidal region of Oahu and was reviewed by Hartman (1948a).

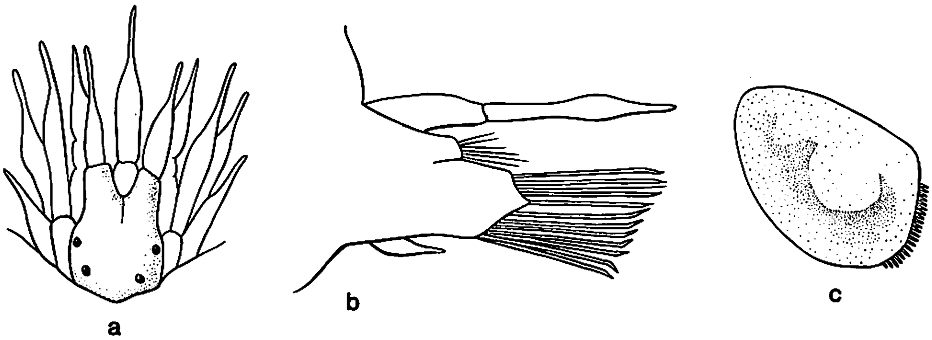

Figure 3.II.7.—*Lepidonotus havaicus*: a, head and appendages; b, parapodium; c, elytron. (After Kinberg 1910.)

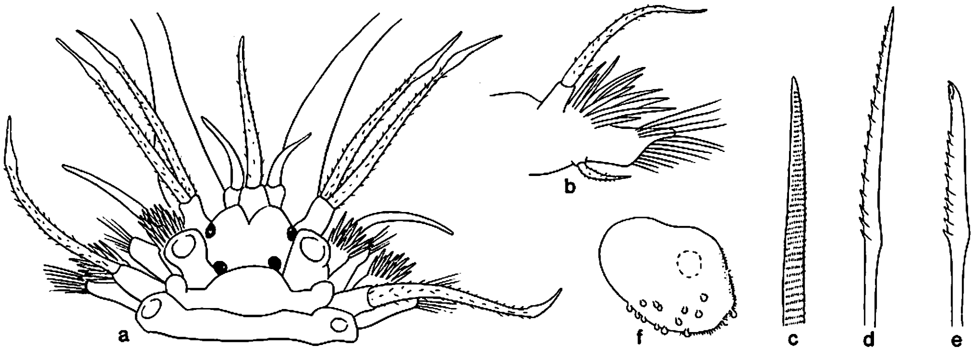

Figure 3.II.8.—*Paralepidonotus ampulliferus*: a, anterior region with head appendages and 2 pairs of elytrophores; b, parapodium; c, notoseta; d,e, neurosetae; f, elytron.

Paralepidonotus ampulliferus (Grube, 1878)

A specimen with 38 segments covered by 15 pairs of elytra is 20 mm long. The prostomium (Fig. 3.II.8a) bears 4 eyes, 3 antennae, and a pair of long, stout, tapering palps; the short lateral antennae are inserted on distinct ceratophores ventral to the longer median antenna. The achaetous tentacular (1st) segment has 2 pairs of tentacular cirri lateral to the prostomium. Antennae and tentacular cirri are densely covered with fine papillae (Fig. 3.II.8a). Elytra are oval, their surface covered with microtubercles appearing as brown specks, and have some flask-shaped vesicles and a marginal fringe of fine papillae (Fig. 3.II.8f). The notopodia are provided with thick brown notosetae, coarsely serrated and unidentate (Fig. 3.II.8c). The neurosetae are slender, pale yellow, with a few rows of spinules, some with entire tips (Fig. 3.II.8d) but most with bidentate tips (Fig. 3.II.8e). Dorsal cirri are long and easily detached, ventral cirri are much shorter; all are covered with fine papillae (Fig. 3.II.8b). *Paralepidonotus ampulliferus* is an Indo-West Pacific species (Day 1967; Gibbs 1971). Specimens have been collected from coral rubble in waters less than 2 m deep in southern Kaneohe Bay, Oahu.

Thormora atrata (Treadwell, 1940)
[syn. *Lepidonotus atratus* Treadwell, 1940. *Thormora socialis* (Kinberg, 1855): Hartman 1966]

Worms are up to 24 mm long and are composed of 26 segments with 12 pairs of elytra. The prostomium has 3 antennae, a pair of stout palps, and 2 pairs of eyes in trapezoidal arrangement. The achaetous tentacular (1st) segment bears 2 pairs of tentacular cirri. Elytra are oval, tough, without a marginal fringe, but with scattered rounded tubercles and pigmented brown patches (after preservation). Parapodia are biramous; the notopodia are shorter than the neuropodia and bear notosetae of 2 kinds: few short, spinous, with blunt tips (Fig. 3.II.9b) and numerous smooth, short to longer, dorsal setae with tapering tips (Fig. 3.II.9a). Neurosetae are stouter, with rows of spinules, slightly hooked unidentate tips, and are golden in color (Fig. 3.II.9c). According to Pettibone (pers. comm.), Kinberg's species as *T. socialis* is indeterminable, since the original description and types are deficient. The identification was made by Pettibone on specimens in the Bishop Museum from Halape, Hawaii, recorded by Hartman (1966) as *T.*

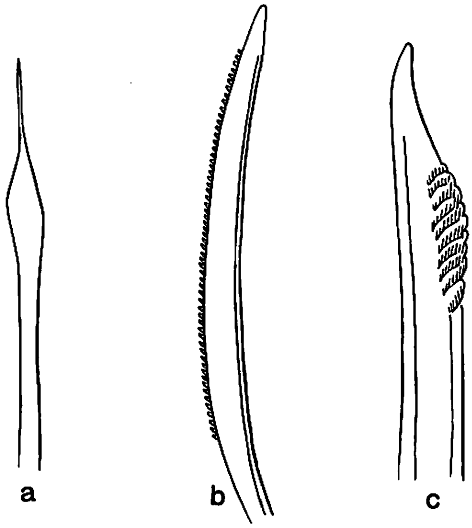

Figure 3.II.9.—*Thormora atrata*: a, sagittate notoseta; b, blunt, spinous notoseta; c, neuroseta. (After Hartman 1948.)

socialis. Recently specimens have been collected on the bench at Ulupau, Kaneohe Bay, Oahu, in water less than 1 m deep and at Johnston Atoll among coral rubble. *Thormora atrata* was originally collected in the Philippine Islands.

Family ~~**Polyodontidae**~~ Acoetidae (G. Read, 1996)

Polyodontids are large, tube-dwelling scale worms with powerful jaws, indicating carnivorous or omnivorous feeding behavior (Fauchald and Jumars 1979). These worms are frequent components of deep-sea benthic communities, and the only species known from Hawaii was dredged from deep water. Parapodial spinning glands are characteristic of this family.

Panthalis mutilata (Treadwell, 1906)
[syn. *Polynoe mutilata* Treadwell, 1906. *Eupanthalis mutilata* (Treadwell): Hartman 1966]

The length of 28 anterior segments is 17 mm; the total number of segments exceeds 78. Parapodia are sub-biramous, distally blunt, with embedded, coiled spinning glands (Fig. 3.II.10a). Neuropodia have 3 kinds of setae: a few are penicillate with a brush top (Fig. 3.II.10b); more are thicker, spinelike, with a long arista (Fig. 3.II.10c); and others are geniculate, with a curved subdistal region. There are also a few slender capillary notosetae. Elytra are pale, translucent, orbicular, smooth-surfaced, and have a postlateral pouch. Individuals construct thick, mud-walled tubes that are difficult to tear or break. This species has been found in mud dredged from a depth of 584 to 600 m (320 to 328 fm) around Molokai and Kauai (Treadwell 1906).

Family **Sigalionidae**

This family includes scale worms that are considered active predators and that live on soft sediments or among coral rubble. Elytra in some species are

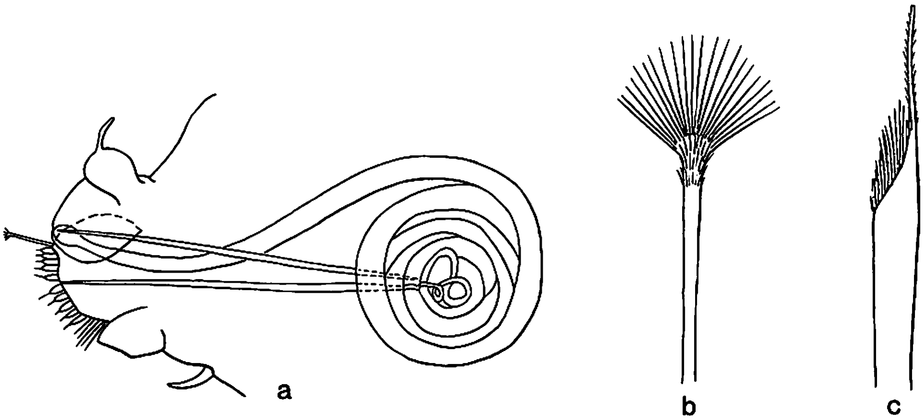

Figure 3.II.10.—*Panthalis mutilata*: a, coiled spinning gland of 10th parapodium; b, penicillate neuroseta; c, aristate neuroseta. (After Hartman 1938.)

raised off the body to allow water to circulate over the gills, which are attached to the elytrophores (Day 1967).

KEY TO HAWAIIAN SIGALIONID GENERA

Surface of dorsum and elytra sand-incrusted; prostomium having a single median antenna with large ceratophore .... *Psammolyce*

Surface of elytra free of sand; prostomium having 3 small antennae with small ceratophores .... *Euthalenessa*

Euthalenessa chacei Pettibone, 1970

[syn. *Thalenessa oculata* not McIntosh, 1885: misident. by Treadwell 1906. *T. digitata* McIntosh, 1885: record of *T. digitata* by Hartman 1966, based on Treadwell's record]

A complete specimen is 33 mm long and 2 mm wide. The prostomium (Fig. 3.II.11a) bears 2 pairs of eyes; the anterior pair is oval, larger and less pigmented than the posterior pair, which lie immediately behind them. Eyes are well separated to the left and right sides. There are 3 short antennae on the anterior margin of the head between the eyes. A pair of triangular palps with paired, short cirri project anteriorly. A conspicuous pair of long tentacular cirri attached ventrally under the head extends back to setiger 12 or 13. The proboscis is 2 mm long when fully extended, somewhat trumpet-shaped, with a frilly lip formed of a number of rounded, flattened papillae. There are small dark specks at the base of each papilla, and a pair of bipartite, curved brown jaws occupy the trumpet opening (Fig. 3.II.11b). Elytra are delicate (wrinkled in alcohol), translucent, and reniform with digitately branched papillae on their posterior margins (Figs. 3.II.11d,e,f). Each parapodium bears a swollen dorsal cirrus that curves ventrally, forming an open chamber against the dorsal aspect of the notopodium. The lower surface of the cirrus is thickly ciliated and there are 2 cup-shaped ctenidia and 1 ciliated process in the chamber (Fig. 3.II.11c). The notopodia have simple capillary setae, and the neuropodia have compound setae that appear to be

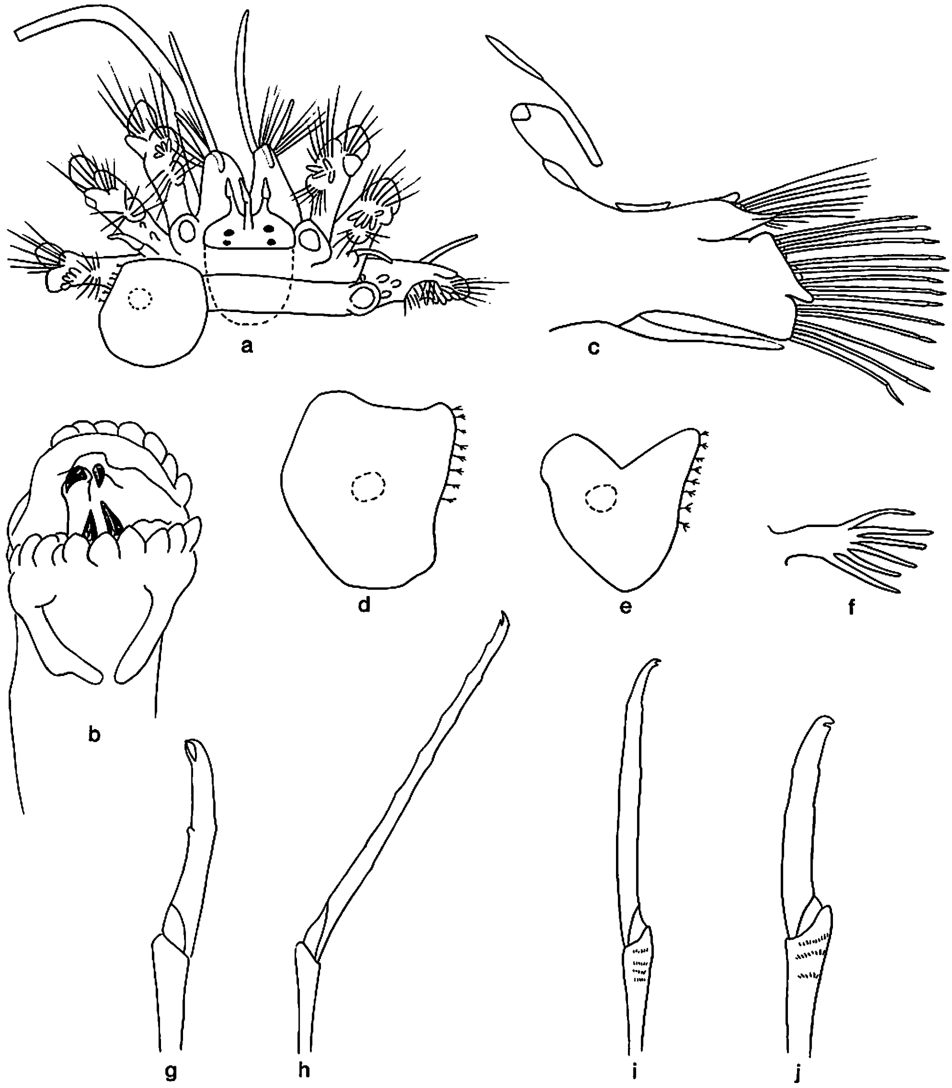

Figure 3.II.11.—*Euthalenessa chacei*: a, anterior region with head appendages and 2 pairs of elytrophores, 1 with an attached elytron; b, proboscis and jaws; c, parapodium of segment 14, posterior view; d, elytron from right side of anterior region; e, elytron from right side of middle region; f, branched papilla of elytron; g,h, neurosetae from anterior region; i,j, neurosetae from middle region. (a,c–j after Pettibone 1970.)

multiarticulated, with rounded or bidentate tips (Figs. 3.II.11g,h,i,j). The top of the shaft of compound setae from middle and posterior regions bears rows of short spines. Three specimens were collected in airlift samples from coarse and fine sand patches near Sampan Channel, Kaneohe Bay, Oahu, at depths of 3.7 and 2.5 m, respectively. In addition, *E. chacei,* as yet known only from the Hawaiian Islands, has been collected from depths of 37 to 260 m (20 to 142 fm) with the original specimens coming from Laysan Island.

Pottsipelogenia Treadwelli Pettibone, 1997

[*Psammolyce fijiensis* McIntosh, 1885]

Treadwell (1906) described a single damaged specimen measuring 11 mm long for the anterior 38 segments. The elytra cover less than half of the dorsum, exposing a broad median strip; this and the inner third of each elytron are coated with sand grains. The prostomium has a median antenna with large ceratophore, a pair of long, tapering, smooth palps, and 2 pairs of eyes. The proboscis, when protruded, is as long as the first 4 segments and contains 2 pairs of jaws. Parapodia are biramous; notopodia bear numerous capillary notosetae; neuropodia have compound neurosetae, some with transverse rows of minute serrations on the basal joint. The Hawaiian specimen was dredged from 45 to 50 m (25 to 27 fm) off Molokai; the species was originally reported from Fiji.

Family **Chrysopetalidae**

The chrysopetalids are small worms that are rare; they are especially hard to find because of their cryptic behavior. The dorsum is covered by broad, flattened notosetae (paleae) that form fans across the body of the worm, meeting or slightly overlapping at the midline. The head may be obscured by paleae but has 2 pairs of eyes, an antenna, and a facial tubercle in front of the prostomium. Neurosetae are all compound, with spinigers and unidentate falcigers; notosetae are all paleae. Very little is known about the habits of these worms, but they are known from coral reefs in the Indo-West Pacific.

Paleanotus sp.

Several specimens of an elongate, flattened worm, rather brittle and fragile, are assigned to this genus. The worms are approximately 2 mm long. The head is sunk between notopodial fans of the 1st setiger and bears 2 pairs of dark eyes, a median antenna, and a tubercle in front of the prostomium that is more conspicuous than the antenna. Notopodia bear setae modified as flattened, slightly curved paleae arising from a raised tubercle. Fans of paleae overlap each other towards the posterior (Fig. 3.II.12a) and meet or slightly overlap at the midline of the dorsum. The striae of the paleae (Fig. 3.II.12b) impart an iridescent appearance to the dorsal surface of the worm. Paleae near the dorsum are broader and a little shorter than those at the lateral edge of the fan. Each notopodium has a short, 4-jointed cirrus at the lateral extremity (Fig. 3.II.12c). Neuropodia are well developed, having laterally projecting lobes with a bundle of compound setae. More dorsally situated setae are spinigerous-like falcigers (Fig. 3.II.12d), more ventral ones are shorter, terminally unidentate falcigers (Fig. 3.II.12e). A few specimens have been found in Kaneohe Bay and Pearl Harbor, Oahu, and at Johnston Atoll.

Family **Spintheridae**

Spintherids are small, oval, flattened worms that are convex dorsally. The prostomium is inconspicuous, bearing a median, globular antenna and usually 2 pairs of eyes. The mouth is ventral and has an unarmed eversible proboscis. Notopodia form membraneous ridges supported by simple or furcate setae. Neuropodia have composite, strongly curved hooks. Branchiae are absent. Species in this family are ectoparasitic on sponges.

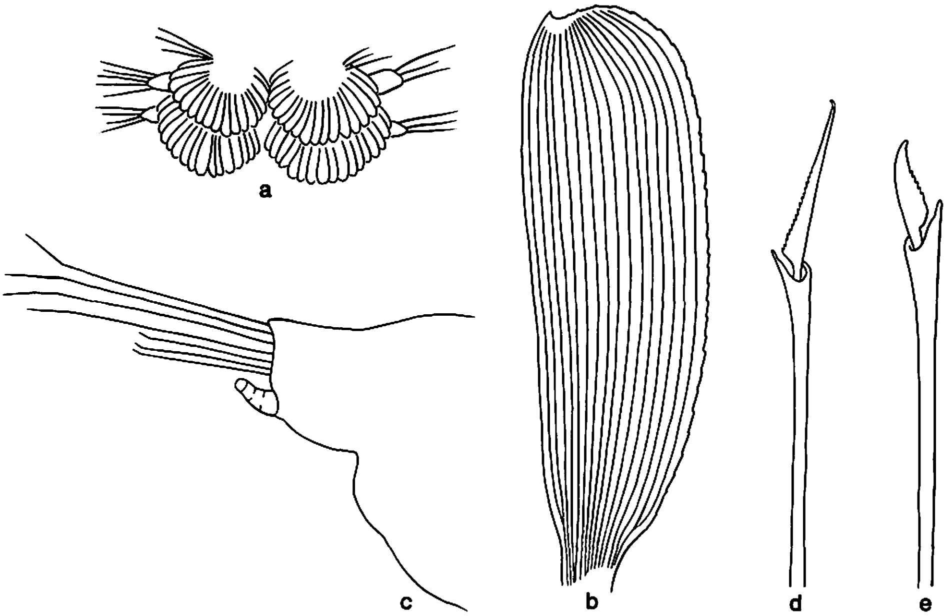

Figure 3.II.12.—*Paleanotus* sp.: a, fans of notopodial paleae on 2 adjacent setigers; b, palea; c, parapodium; d, superior falcigerous neuroseta with long spinigerous-type blade; e, inferior falcigerous neuroseta.

Spinther japonicus Imajima and Hartman, 1964

The ovate body of this worm is 2.5 mm long, 2 mm wide at its broadest point, and has 13 setigers (Fig. 3.II.13a). The dorsum is convex, covered with membraneous notopodial lamellae (Fig. 3.II.13b) except for a narrow mid-dorsal stripe. The ventral surface is smooth. The prostomium is a small spherical lobe visible dorsally. Imajima and Hartman (1964) report the presence of 4 small brown eyes in a quadrate arrangement at the lateral bases of the prostomium. The mouth is ventral. Notopodia (Figs. 3.II.13b,c) have well-developed folds that consist of double membranes separated from each other at their distal ends. The lamellae are supported by 2 types of notosetae: straight or sinuous simple acicular (Fig.

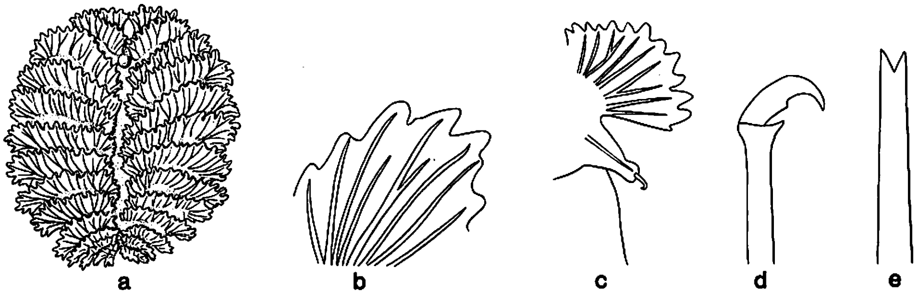

Figure 3.II.13.—*Spinther japonicus*: a, whole worm, dorsal view; b, notopodial lamella; c, parapodium; d, neuropodial hooked acicular seta; e, notopodial acicular seta. (After Imajima and Hartman 1964.)

3.II.13b), and bifurcate setae (Figs. 3.II.13b,c,e). Those of the anterior notopodia are longer than the posterior notosetae. Neuropodia are long, cylindrical, and have a thick conical postsetal lobe and a single, projecting compound seta. Each hooked acicular seta has a strongly curved and sharply pointed appendage; the shaft has a distal tubercle (Fig. 3.II.13d). Developing neurosetae are visible in the embedded portion of the setal bundle. The pygidium is conical, with 2 lateral, glandular, cone-shaped projections. A few specimens of this species, which was reported originally from Japan, have been collected among sponges from Pearl Harbor and southern Kaneohe Bay, Oahu.

Family **Amphinomidae**

Amphinomids are stout worms oval in cross section or vermiform worms subrectangular in cross section, usually with a dorsal sensory lobe (the caruncle) just behind the head that may be smooth or pleated. The muscular pharynx is protrusible but unarmed, and members of this family may be carrion feeders, browsers on corals and other cnidarians, or associated with stalked barnacles on which they feed (Fauchald and Jumars 1979). At least 1 species, *Pherecardia striata,* is an active predator that will swallow pieces of fish and live prey such as small crabs, shelled gastropods, and other worms. Amphinomids are called fire worms, because of their brittle, harpoonlike notosetae that break off in the skin if the worms are touched with bare hands. The embedded tips of the setae introduce a toxin to the wound, which causes itching and discomfort in some people and may severely incapacitate others. The local fire worm, *Eurythoe complanata,* is found commonly under stones on reef flats, and the superficially similar *P. striata* can be found in the same rubble habitat and sublittorally. A vividly colored species, *Chloeia flava,* has been taken in dredge hauls between 200 and 600 m (109 and 328 fm) and found stranded on windward Oahu beaches after spawning. Floating driftwood and other debris with attached stalked barnacles are the known habitats of *Amphinome rostrata* and *Hipponoe gaudichaudi.*

KEY TO HAWAIIAN AMPHINOMID GENERA

1	Body short, oval or spindle-shaped	2
	Body long and vermiform	4
2(1)	Prostomium without caruncle; commensal with *Lepas* (stalked barnacle) on floating debris	*Hipponoe*
	Prostomium with caruncle (Fig. 3.II.16); free-living	3
3(2)	Notopodial branchiae dendritically branched	*Notopygos*
	Notopodial branchiae pinnately branched (Fig. 3.II.15b)	*Chloeia*
4(1)	Caruncle large, with broad, pleated lateral lobes (Fig. 3.II.21)	*Pherecardia*
	Caruncle with 1 or 3 simple lobes (Figs. 3.II.16,20)	5
5(4)	Benthic worms; square to oblong in cross section	6
	Associated with floating debris; pentagonal in cross section	*Amphinome*
6(5)	Caruncle with 2 narrow, lateral lobes partially obscured by a median lobe	*Eurythoe*
	Caruncle a slender, sinuous lobe	*Pareurythoe*

Amphinome rostrata (Pallas, 1766)

This is a large worm, 15 to 25 cm long and 2.5 cm wide (Fig. 3.II.14a), dark gray to black in preservative, and pentagonal in cross section. The caruncle is a U-shaped lobe extending to the 2nd setiger (Fig. 3.II.14b). Tufted branched gills start on the 3rd setiger (Fig. 3.II.14c) and notopodia have capillary setae and a dorsal cirrus. Neuropodia are widely separated from the notopodia (Fig. 3.II.14c) and bear stout recurved setae (Fig. 3.II.14d) and acicular setae (Fig. 3.II.14e). These worms are found on driftwood and colonies of stalked barnacles (*Lepas*) in tropical and subtropical seas (Day 1967). Specimens have been collected from fishing floats washed up on windward Oahu beaches at Waimanalo and Kaneohe Bay, and on floating debris at Kilauea, Kauai.

Chloeia flava (Pallas, 1766)

The body of this species is short (about 45 mm), oval, and depressed, with conspicuous tufts of white, laterally directed setae. The dorsum of each segment has longitudinally arranged markings of a central dark pink spot and 2 continuous paler pink to brown lines. Dorsal cirri are long and deep pink, ventral cirri are shorter and white. Notosetae include harpoon setae that are serrated on one side and forked setae; neurosetae are forked and may be smooth, or serrated on the outer side of the longer prong. Serrated setae are yellow at the tips. The caruncle has a median ridge with pleated lateral folds and covers about 5 segments (Fig. 3.II.15a). Pinnately branched branchiae are present from the 5th segment (Fig. 3.II.15b). Pygidium with a pair of anal cirri. This species is cosmopolitan in tropical regions; stranded specimens have been collected from sandy beaches after spawning and by dredging from 200 to 600 m (109 to 328 fm) around the Hawaiian Islands. The color pattern on the dorsum is variable and fades in preservative.

Eurythoe complanata (Pallas, 1766)
[syn. *E. kamehameha* Kinberg, 1857: Hartman 1966. *E. corallina* Kinberg, 1857. *E. pacifica* Treadwell, 1906: Edmondson 1946]

Individuals may be large, reaching 240 mm long and 10 mm wide. The body is long and is rectangular in cross section. The color in life is pale gray or green to reddish brown, with an iridescent cuticle and red branchiae (Plate 3.II.2b). The caruncle (Fig. 3.II.16) extends above 3 segments and consists of a sinuous keel lobe partially obscuring 2 narrow lateral lobes. Tufted branchiae begin on the 2nd segment and continue through most of the body. This species is commonly called the fire worm and occurs under stones and among coral rubble on fringing reefs. *Eurythoe complanata* is known throughout the Hawaiian Islands from the littoral zone (including estuarine waters) to depths of 60 m (28 fm) and is cosmopolitan in tropical and subtropical regions.

red eyes
in alcohol

Hipponoe gaudichaudi Audouin and Milne Edwards, 1830

The body of this worm is short and spindle-shaped (Fig. 3.II.17a), about 25 mm long, with as many as 35 segments. The color in life is bright orange to red. The prostomium (Fig. 3.II.17b) is diamond-shaped, bears 4 eyes, 5 antennae (4 on the anterior margin and 1 on the top of the head), and lacks a caruncle. Bushy branchiae (Fig. 3.II.17c) begin on the notopodium of the 3rd segment and continue posteriorly. Neurosetae are much thicker than notosetae, with few in each fascicle. Each neuroseta is distally bifid, bearing a large curved fang and a slender

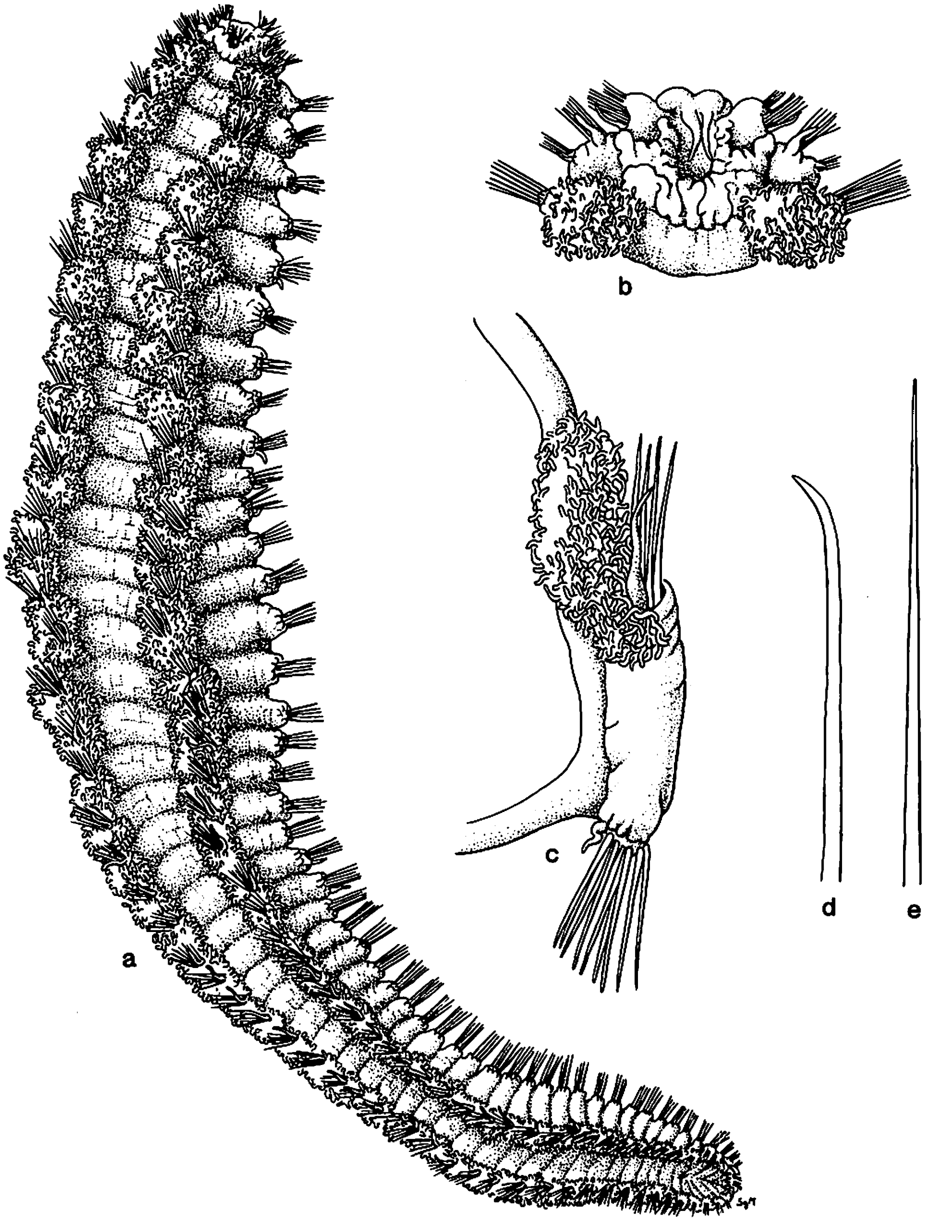

Figure 3.II.14.—*Amphinome rostrata*: a, entire worm, dorsolateral view; b, head with frilly caruncle lobe and first pair of branchiae; c, branchiferous parapodium; d, curved seta; e, acicular seta.

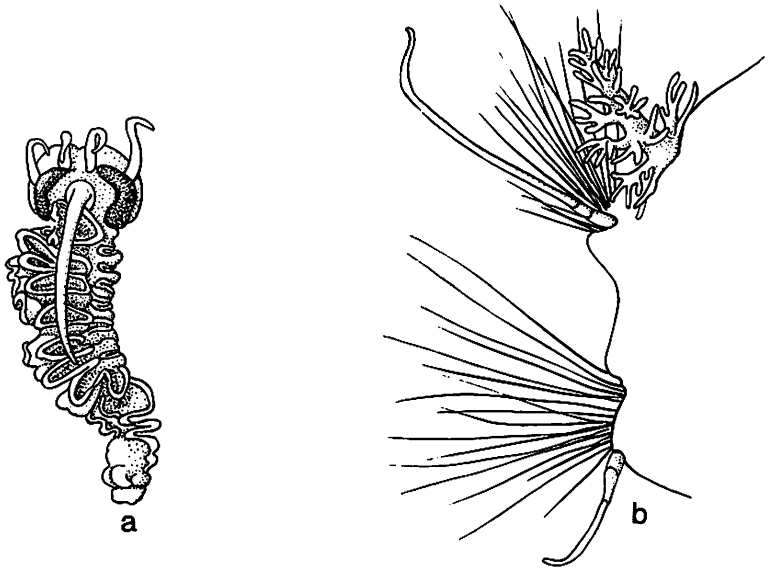

Figure 3.II.15.—*Chloeia flava*: a, head and elongate, frilly caruncle lobe; b, parapodium with notopodial gill.

lateral tooth (Fig. 3.II.17d). These worms live in close association with *Lepas* colonies (stalked barnacles) on drifting logs. They are protandric hermaphrodites and exhibit brooding behavior (Kudenov 1977). Cosmopolitan in tropical seas, *H. gaudichaudi* is often found on the windward sides of the Hawaiian Islands (Hartman 1966) and in Kaneohe Bay, Oahu.

KEY TO HAWAIIAN *NOTOPYGOS* SPECIES

Anal pore between setigers 22 and 23............................ *N. albiseta*
Anal pore between setigers 28 and 29 .... *N. gregoryi*

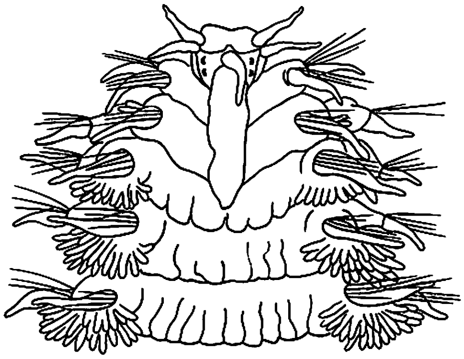

Figure 3.II.16.—*Eurythoe complanata*: anterior region with mid-dorsal caruncle and tufted branchiae. (After Hartman 1951.)

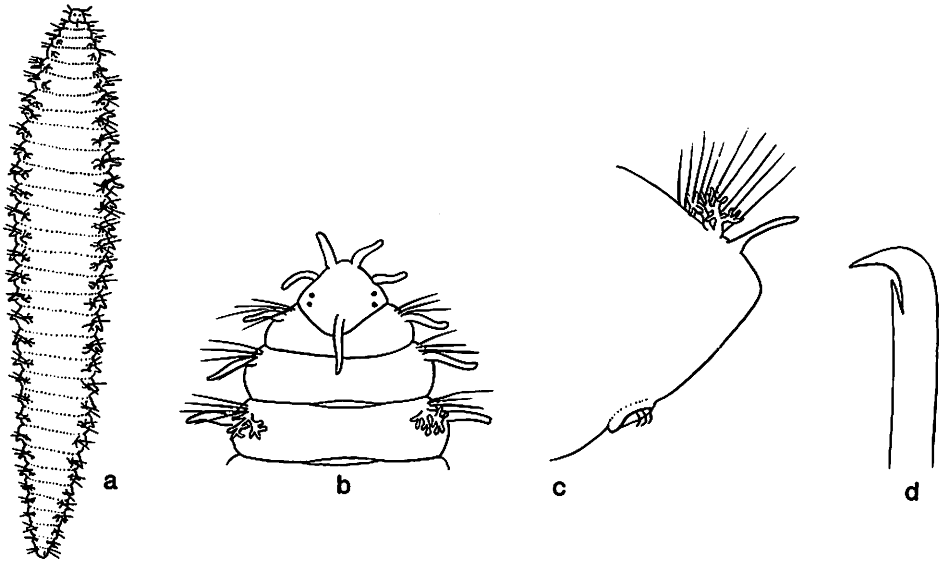

Figure 3.II.17.—*Hipponoe gaudichaudi*: a, entire worm; b, anterior region; c, parapodium with gill; d, neuroseta. (a,c,d after Fauvel 1923; b after Pettibone 1963.)

Although 4 species of *Notopygos* have been reported from the Hawaiian Islands, *N. megalops* and *N. labiata* are omitted from this revision as they may only represent juvenile stages of *N. albiseta* and *N. gregoryi* (Hartman 1966; J. Kudenov, pers. comm.).

Notopygos albiseta Holly, 1939

This species has an ovate body up to 90 mm long. Living specimens have an overall color of pale purple with dark purple patches on the dorsum of each segment and around the bases of the notopodia (Frontispiece). The head bears 4 large eyes and a median antenna, which projects posteriorly. The caruncle has a high central ridge and 2 lateral lobes flattened against the dorsum. There is a thin purple line along the crest of the central lobe. Lateral lobes are complexly pleated and there is a deep purple band where each lobe meets the central lobe. Bushy branchiae, orange to red in life, are dendritically branched and begin on the 5th setiger. Notopodia and neuropodia are widely separated at their bases (Fig. 3.II.18a). A dark purple ring surrounds the notopodium, which bears 2 types of cirri. True dorsal cirri are short and slender, each situated at the base of the notosetae, adjacent to the branchiae. The accessory cirri (Fig. 3.II.18b) are on the ventral side of the notopodia and are longer than the notosetae. These extensible cirri are orange with white tips in live worms. The anal pore is on the dorsum at the junction of setigers 22 and 23 (Plate 3.II.1). Notosetae are yellowish white with opaque white flecks, and neurosetae are silvery white. Setae are all furcate (Figs. 3.II.18c,d); shaft and barb are basically straight in posterior setae, although the shaft curves out slightly in anterior setae (Fig. 3.II.18c). *Notopygos albiseta* has been collected under a dead coral boulder at Maile Point, Oahu, at a depth of 18

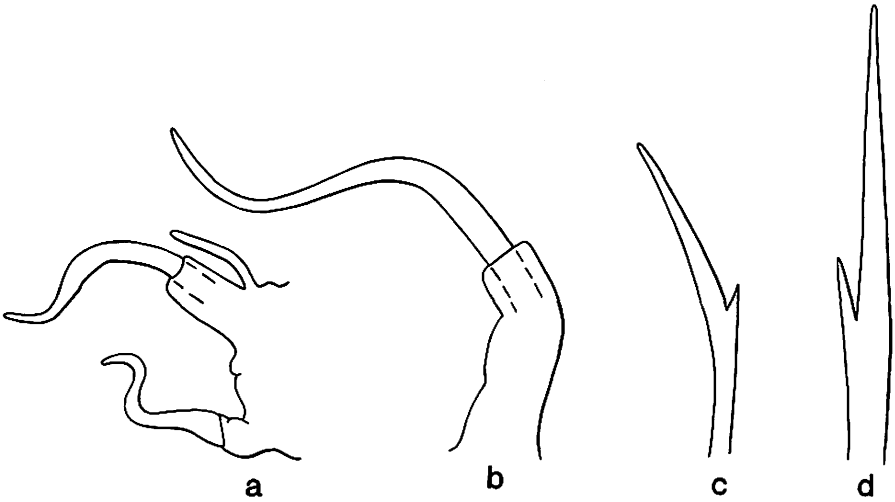

Figure 3.II.18.—*Notopygos albiseta*: a, parapodium; b, accessory cirrus; c, anterior forked seta; d, posterior forked seta. (After Holly 1939.)

m (10 fm). This species is also known from other parts of the Hawaiian Islands and Johnston Atoll (Hartman 1966).

Notopygos gregoryi Holly, 1939

This is a large worm composed of 47 segments, and it attains a length of 109 mm and a width of 18 mm. The anal pore lies dorsally between segments 28 and 29. The prostomial caruncle is large, trilobed, with many fine folds, and extends back to the 5th segment (Fig. 3.II.19a). Dendritic branchiae (Fig. 3.II.19b) begin on the 5th segment. Setae are bifurcate and smooth or denticulate (Fig. 3.II.19c). This amphinomid was originally described from Midway Island (Holly 1939; Hartman 1966) in the Northwestern Hawaiian Islands and has since been collected from Lisianski Island, which is also in the Northwestern Hawaiian Islands.

Pareurythoe sp.

The prostomium of this worm is depressed and oval, with 1 median and 4 anterior antennae. The caruncle is a simple, sinuous lobe (Fig. 3.II.20), which extends back to setiger 3. Branchiae begin on the 2nd setiger and continue to the posterior end; they are small throughout. This undetermined species was found at Halape, Hawaii, in tide pools (Hartman 1966), which were subsequently submerged following earthquakes along this coastline in 1977.

Pherecardia striata (Kinberg, 1857)
[syn. *Hermodice pennata* Treadwell, 1906]

The body is as long as 200 mm and up to 7 mm wide. Segments number up to 100 or more. The prostomial caruncle is broad and large, extending back to segment 4, and its free edges are deeply lobed and directed laterally (Fig. 3.II.21, Plate 3.II.2c). Branchiae are present from the 1st setiger onward; each is

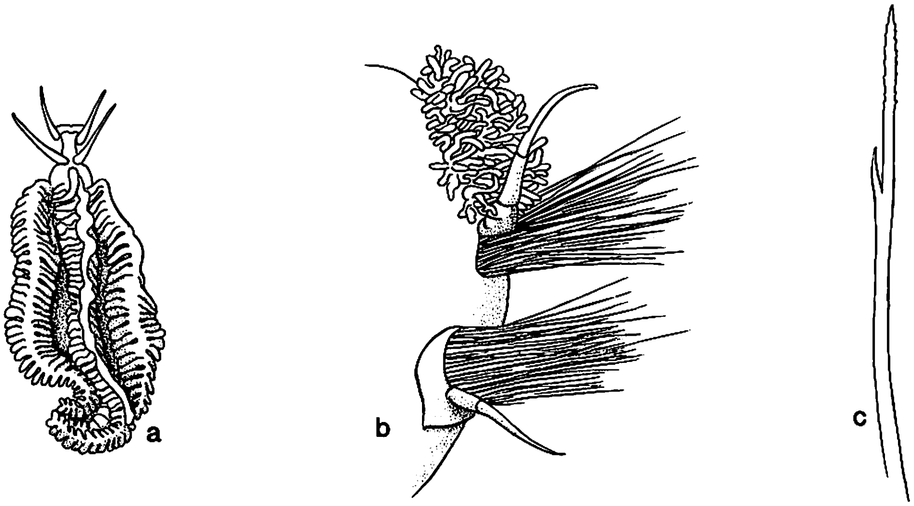

Figure 3.II.19.—*Notopygos gregoryi*: a, anterior region and 3 ridged, pleated caruncles; b, parapodium with gill; c, bifurcate, denticulate seta.

dendritically branched and bushy. The oral aperture is on the ventral side of the 3rd segment. Dorsal cirri have long bases, and cirrostyles extend distally beyond the branchiae. Notosetae and neurosetae are glistening white, numerous, and slender. This Indo-West Pacific species has been collected as atokous and epitokous individuals from among corals and coral rubble in intertidal and subtidal regions at Waikiki and Pearl Harbor, Oahu; Halape and Honokohau, Hawaii; and on Molokai.

Family **Pisionidae**

Small, elongate worms with flattened heads that burrow in sand and silt. Prostomium with paired antennae and palps, peristomium with 2 pairs of tentacular cirri. There are 2 pairs of subdermal eyes. The pharynx is eversible with 2 pairs of curved chitinous jaws. Parapodia are uniramous with small dorsal and ventral cirri. The genus *Pisione* is characterized by the pair of anteriorly directed acicula of the peristomium that serve as additional jaws and parapodia with setae. *Pisione africana* is known from subtidal, soft sediment locations.

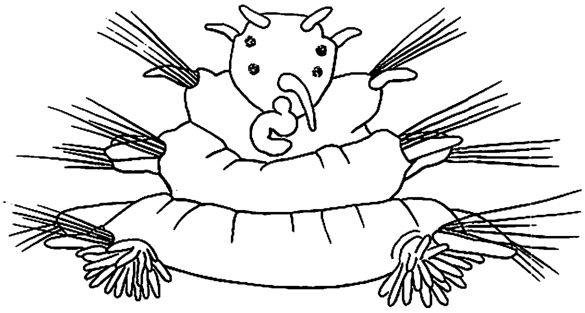

Figure 3.II.20.—*Pareurythoe* sp.: anterior region with sinuous caruncle. (After Hartman 1951.)

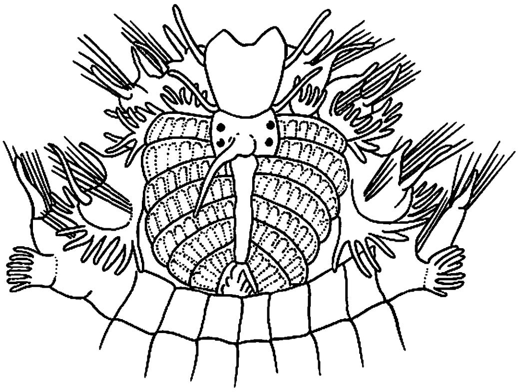

Figure 3.II.21.—*Pherecardia striata*: anterior region with dendritically branched branchiae and caruncle with lamellate lateral lobes. (After Hartman 1951.)

Pisionidens lacks the anteriorly directed acicula, parapodia are without setae, and there is a row of segmentally arranged ventral suckers. The males have copulatory organs and sperm are stored in the seminal receptacles of the females. The only known species, *Pisionidens indica*, was collected from surf-washed beaches. The suckers and lack of setae may be adaptations to a burrowing life style in this high energy habitat.

KEY TO HAWAIIAN PISIONID GENERA

Parapodia with setae	*Pisione*
Parapodia without setae	*Pisionidens*

Pisione africana Day, 1963

Small worms less than 20 mm in length with numerous segments. Prostomium and peristomium fused, peristomium with 1 pair of long palps and 2 pairs of small biarticulate tentacular cirri. Acicula of peristomial segment enlarged and directed forwards, emerging at the bases of the palps. The dorsal cirrus of setiger 2 is enlarged. Parapodia uniramous each with a small, biarticulate dorsal and ventral cirrus, 1 aciculum, and 5 long setae. Setae are simple stout blades with obliquely pointed tips, compound falcigers, and compound spinigers. Finlike blades are evident on all setae. Specimens agree with the description in Day (1967) except that only 1 aciculum could be seen in the parapodia. Collected from coral sand at a depth of 7 m at Midway Island (NWHI). This species is known from the type locality in South Africa (Day 1967).

Pisionidens indica (Aiyar and Alikunhi, 1940)

Slender worms less than 25 mm in length. Prostomium flattened and tapered anteriorly with paired antennae and lateral palps and 2 pairs of dark eyes close together. Peristomium fused to prostomium with 2 pairs of tentacular cirri. Mouth a longitudinal ventral slit just behind the eyes and between the peristomial cirri. Parapodia with short, biarticulate dorsal and ventral cirri and a long aciculum. Separate sexes. Males have cirriform copulatory organs, and females have ovaries and seminal receptacles. A genital sucker on the midventrum of reproductive segments is round or D-shaped. Pygidium with a pair of long anal cirri. Specimens from coral sand at a depth of 7 m at Midway Island (NWHI). This species is known from surf beaches of India and South Africa (Day 1967).

Family **Phyllodocidae**

Phyllodocids have an unarmed, eversible proboscis that is often covered with knoblike papillae and are thought to be hunting predators on other polychaetes and small invertebrates (Fauchald and Jumars 1979). The prostomium may be oval or heart-shaped and bears 2 pairs of antennae and often a median antenna, a nuchal papilla, and a pair of eyes. The parapodia are typically uniramous, with dorsal and often ventral cirri expanded to form leaflike paddles.

Members of this family are active worms found among coral rubble and under rocks on reef flats, in the algal turf of intertidal benches, and subtidally. They may be iridescent and shades of yellow, brown, green, or violet. Seven species in 4 genera are known from the Hawaiian Islands.

KEY TO HAWAIIAN PHYLLODOCID GENERA

1 Short, spindle-shaped worms; prostomium with 5 antennae; nuchal papilla may be present or absent 2
Long, linear worms; prostomium with 4 antennae; nuchal papilla usually present 3
2(1) First tentacular segment fused to the 2nd; nuchal papilla indistinct .... *Eumida*
Tentacular segments free of each other; no nuchal papilla .... *Eulalia*
3(1) First segment with a pair of dorsal papillae .... *Prophyllodoce*
First segment lacks dorsal papillae .... *Phyllodoce*

KEY TO HAWAIIAN *EULALIA* SPECIES

Everted proboscis diffusely papillated............................ *E. havaica*
Everted proboscis smooth .... *E. sanguinea*

Eulalia havaica Kinberg, 1866

Specimens attain 6 mm in length, and have a semiglobular prostomium. The everted proboscis is diffusely papillated. Dorsal cirri are foliaceous, longer than wide, and pinnately veined at the 10th parapodium. Farther back, the cirrophores become longer than wide. Setae are composite spinigers with their shafts distally crenulated; the setal blade is 3 to 4 times as long as wide. This species is only

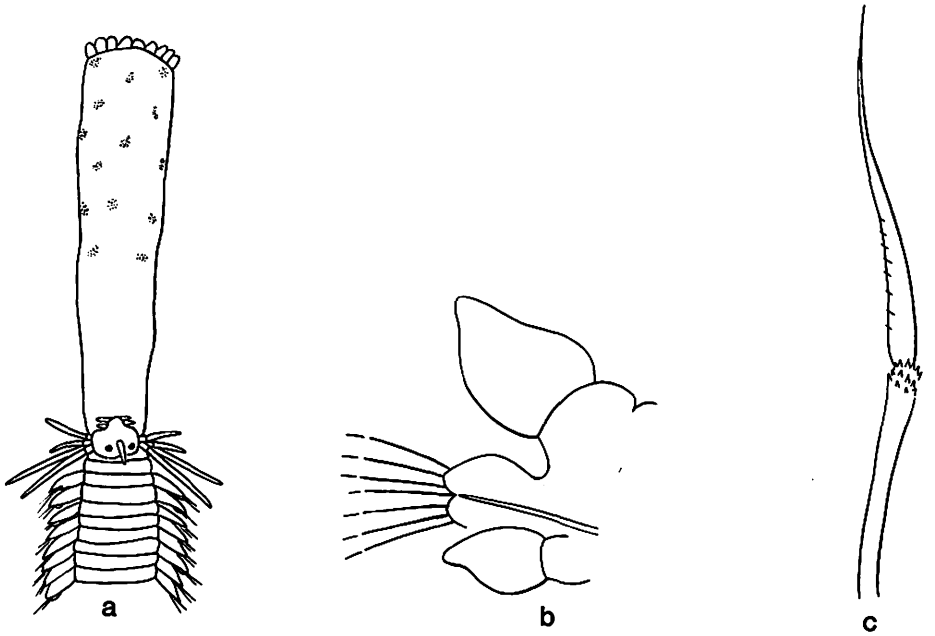

Figure 3.II.22.—*Eulalia sanguinea*: a, anterior region with everted proboscis; b, parapodium with cordate dorsal cirrus; c, composite seta. (After Fauvel 1923.)

known from specimens originally collected along the south shore of Oahu among coral rubble.

Eulalia sanguinea Oersted, 1843 – 30-60 mm

Worms attain about 20 mm in length and 0.9 mm in width (including parapodia). Segments number about 100. The body is spindlelike and is dark olive-green when preserved. The everted proboscis is smooth (Fig. 3.II.22a). Dorsal cirri are foliaceous and distally pointed (Fig. 3.II.22b). Setae are composite spinigers (Fig. 3.II.22c), each with a dentate edge. This species, found intertidally around Oahu, is cosmopolitan in warm seas (Hartman 1966).

Eumida caspersi Hartmann-Schröder, 1965
[syn. *Eumida* (*Sige*) *caspersi* Hartmann-Schröder, 1965. ?*Sige caspersi* Hartmann-Schröder: Hartman 1966]

Worms are up to 3.5 mm long and 0.8 mm wide (including parapodia). There are about 25 segments. The body is pale yellow, and the cirri are brownish. The prostomium (Fig. 3.II.23a) is broadly heart-shaped and has a pair of large eyes at the sides of the base of the median antenna. Four pairs of tentacular cirri occur, the 1st pair somewhat flattened and foliose, the other 3 pairs cirriform. Normal parapodia have obliquely heart-shaped dorsal cirri (Fig. 3.II.23b) and similar, though smaller, ventral cirri. *Eumida caspersi* has been found in the algal turf on rocks at Hilo, Hawaii, and is not recorded elsewhere.

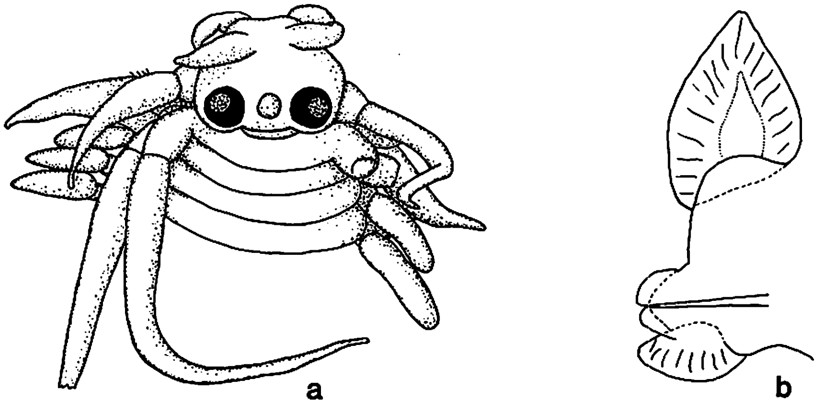

Figure 3.II.23.—*Eumida caspersi*: a, anterior region; b, parapodium. (After Hartmann-Schröder 1965.)

KEY TO HAWAIIAN *PHYLLODOCE* SPECIES

1 Prostomium not incised, with a small nuchal papilla at the posterior margin 2
Prostomium incised, without a nuchal papilla at the posterior margin .... *P.* (*Phyllodoce*) *tenera*
2(1) Prostomium oval, longer than wide 3
Prostomium broad and heart-shaped .... *P.* (*Anaitides*) *madeirensis*
3(2) Middle segment with rhomboidal dorsal cirri, uniformly pigmented .... *P.* (*A.*) *parva*
More posterior segments with broadly oval dorsal cirri, each with 2 pigmented diagonal bars .... *P.* (*P.*) *hiatti*

Phyllodoce (*Anaitides*) *madeirensis* (Langerhans, 1880)

This species may reach 60 mm long and 3 mm wide. This is a long, linear worm, highly iridescent, especially on the dorsum, but virtually colorless when preserved. Individuals in some populations have a white pigment pattern. The prostomium is heart-shaped and has a pair of eyes and a nuchal papilla (Fig. 3.II.24a). The distal end of the proboscis has a circlet of 16 papillae, and the proximal end has 6 longitudinal rows on each side with 6 to 11 papillae in a row. The anterior region has 4 pairs of tentacular cirri. Dorsal and ventral cirri are foliaceous and taper to a point (Fig. 3.II.24b), but ventral cirri are smaller and extend laterally beyond the acicular lobes. The 3rd tentacular segment lacks setae. This species has been found in shallow waters and at moderate depths around Oahu and Maui. It is cosmopolitan in temperate and tropical seas, with a Pacific distribution that includes the Solomon Islands (Gibbs 1971) and Panama (Fauchald 1977b).

Phyllodoce (*Anaitides*) *parva* (Hartmann-Schröder, 1965)

These small worms attain about 7 mm in length, 0.5 mm in width (including parapodia) and are uniformly greenish brown. The prostomium is oval (Fig. 3.II.25a), longer than wide, and has a straight posterior margin; a pair of large eyes and a small nuchal papilla are on the posterior half. There are 4 pairs of long,

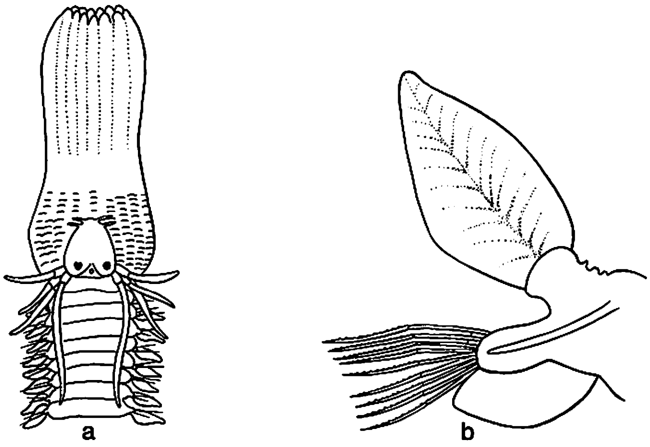

Figure 3.II.24.—*Phyllodoce (A.) madeirensis*: a, anterior region with proboscis extended; b, parapodium with foliaceous dorsal cirrus. (After Rioja 1918.)

tentacular cirri on the anterior region. Dorsal cirri of anterior segments are oval and symmetrical; those of middle segments are rhomboidal (Fig. 3.II.25b) and longer than wide. The structure of the proboscis is not known. *Phyllodoce parva* has been found at Kahana Bay, Oahu, in the algal turf growing on rocks intertidally. Gibbs (1971) also records this species from a sandy habitat in the Solomon Islands.

Phyllodoce (Phyllodoce) hiatti Hartman, 1966

These linear worms attain about 220 mm in length and 1.7 mm in width. Preserved specimens are dark violet on ventral and lateral surfaces, and there is a violet dorsal longitudinal stripe running the length of the worm, with bands of

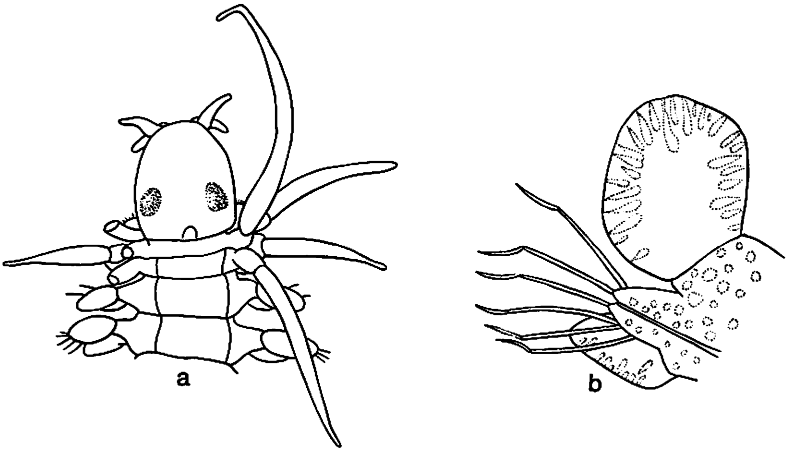

Figure 3.II.25.—*Phyllodoce (A.) parva*: a, anterior region; b, parapodium of middle segment with rounded dorsal cirrus. (After Hartmann-Schröder 1965.)

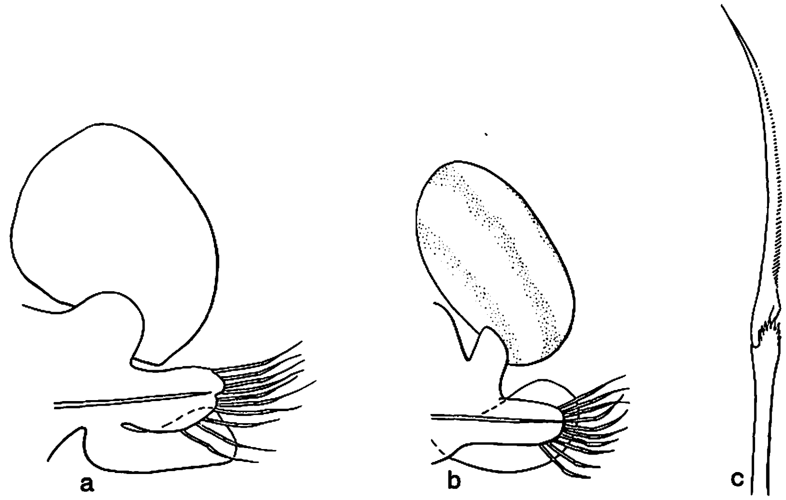

Figure 3.II.26.—*Phyllodoce* (*P.*) *hiatti*: a, parapodium of the anterior region; b, parapodium from a posterior setiger, dorsal cirrus with diagonal pigmented bars; c, composite spiniger. (After Hartman 1966.)

the same color on the dorsal cirri. The prostomium is broadly oval, widest posteriorly; it has a small nuchal papilla and 2 eyes on the posterior half. The proboscis is diffusely covered with small papillae. Parapodia have broadly foliaceous dorsal cirri in the anterior region (Fig. 3.II.26a) that are distally rounded, as are the much smaller ventral cirri. Posterior dorsal cirri are proportionately longer and narrower (Fig. 3.II.26b) than those in front and bear 2 pigmented diagonal bars. Setae are composite spinigers, each with a distally spinous shaft and crenulated appendage (Fig. 3.II.26c). This species is recorded only intertidally at Halape, Hawaii, in the interstices of coral and coral rubble.

Phyllodoce (*Phyllodoce*) *tenera* Grube, 1878

This species is at least 105 mm long, 2.4 mm wide, and has up to 230 segments. The prostomium is oval, longer than wide, incised at its postmedial margin, and bears 2 eyes. Dorsal cirri are lanceolate and distally pointed. *Phyllodoce* (*P.*) *tenera* is recorded from the south coast of Oahu (Treadwell 1906) and originally from the Philippine Islands.

Prophyllodoce hawaiia Hartman, 1966

Specimens are very long and slender, attaining about 260 mm in length, 2 mm or less in width, and having more than 800 segments. The prostomium is broadly heart-shaped (Fig. 3.II.27a), widest posteriorly, with 2 large, circular eyes and a small nuchal papilla in the postmedian emargination. The everted proboscis terminates distally in a complete circlet of 17 small, oval papillae; the basal quarter of the proboscis has many dark, disclike papillae in a dispersed arrangement; the distal part is transversely wrinkled. There are 4 pairs of tentacular cirri: the 1st pair is composed of a knoblike dorsal cirrus and a cirriform ventral cirrus; the 2nd pair is long and cirriform; the 3rd pair is composed of a long dorsal cirrus

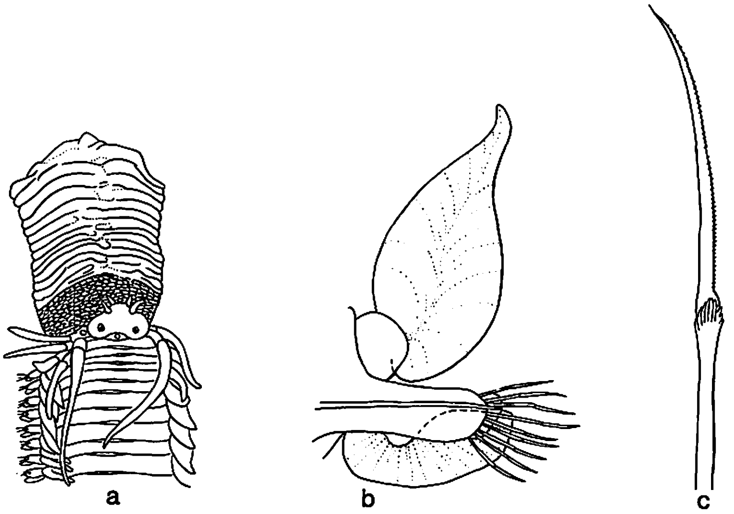

Figure 3.II.27.—*Prophyllodoce hawaiia*: a, anterior region with extended proboscis, left parapodia with dorsal cirri moved to one side; b, parapodium with elongate dorsal cirrus showing pinnate venation and ovoid ventral cirrus; c, composite spiniger. (After Hartman 1966.)

and a foliaceous ventral cirrus; the 4th segment bears a pair of foliaceous cirri and setae. Parapodia have large, erect, foliaceous, distally pointed dorsal cirri with pinnate venation (Fig. 3.II.27b). Ventral cirri are similar but smaller. Setae are composite spinigers in fan-shaped fascicles, each with a tapered, serrated blade on a toothed shaft (Fig. 3.II.27c). This species has been collected only in the Hawaiian Islands at Halape, Hawaii, and at Waikiki and Kaneohe Bay, Oahu, among coral rubble, under rocks, and swimming near the surface of the sea.

Family **Alciopidae**

Worms in this family are transparent, planktonic polychaetes with well-developed eyes, including both a lens and a retina. They are active swimmers, using an eversible proboscis to catch and eat copepods, euphausiids, thaliaceans, and other zooplankters (Fauchald and Jumars 1979). The proboscis is equipped with a pair of long papillae for grasping prey (Fig. 3.II.30a), but these papillae are not chitinous as are the "jaws" of other predaceous worms. The parapodia bear setae and the cirri are expanded to form flattened paddles for swimming. Three wide-ranging tropical species are known from waters around Hawaii. A comprehensive review of the taxonomy of pelagic polychaetes is given by Dales and Peter (1972).

KEY TO HAWAIIAN ALCIOPID SPECIES

1	Setae all compound	2
	Setae all simple capillaries	*Naiades cantrainii*
2(1)	Parapodium with 1 slender distal lobe	*Vanadis minuta*
	Parapodium with 2 slender distal lobes	*Alciopa reynaudii*

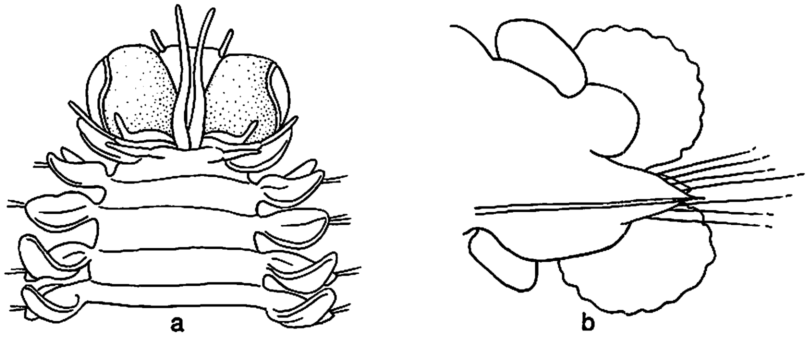

Figure 3.II.28.—*Alciopa reynaudii*: a, ventral view of anterior region showing prostomium with large laterally directed eyes, and the lateral horns of the proboscis protruding through the mouth; b, parapodium with large oval dorsal and ventral cirri. (After McIntosh 1885.)

Alciopa reynaudii Audouin and Milne Edwards, 1833
[syn. *Alciopa ?quadrioculata* McIntosh, 1885: Hartman 1966. *Greefia quadrioculata* (McIntosh): Treadwell 1906. *Greefia oahuensis* McIntosh, 1885: Treadwell 1906]

This species attains 33 mm in length and 6.5 mm in width. The body is translucent, but the eyes are pigmented. The enormous eyes are directed laterally (Fig. 3.II.28a), and the prostomium bears 2 pairs of lateral antennae and a median antenna inserted basally that may be reduced to a ridge. Parapodia are uniramous (Fig. 3.II.28b) and have only slender compound setae. This cosmopolitan species has been found swimming at the surface of the sea and has been collected between Oahu and Kauai.

Naiades cantrainii delle Chiaje, 1830
[syn. *Alciopa distorta* Treadwell, 1943]

Large individuals measure to 100 mm or more. The prostomium has a pair of large eyes (Fig. 3.II.29a) and 5 small antennae. Parapodia have only simple capillary setae (Fig. 3.II.29b). This pelagic species is cosmopolitan in tropical seas and has been found east of Hawaii at depths of 50 m (27 fm) (Hartman 1956; Tebble 1962).

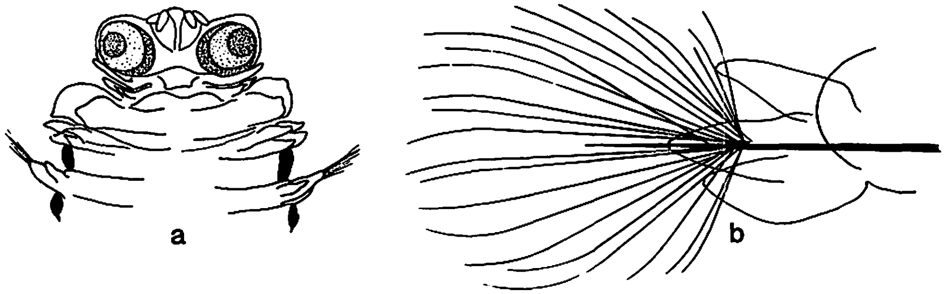

Figure 3.II.29.—*Naiades cantrainii*: a, head with large eyes; b, parapodium with numerous slender capillary setae. (After Dales 1957.)

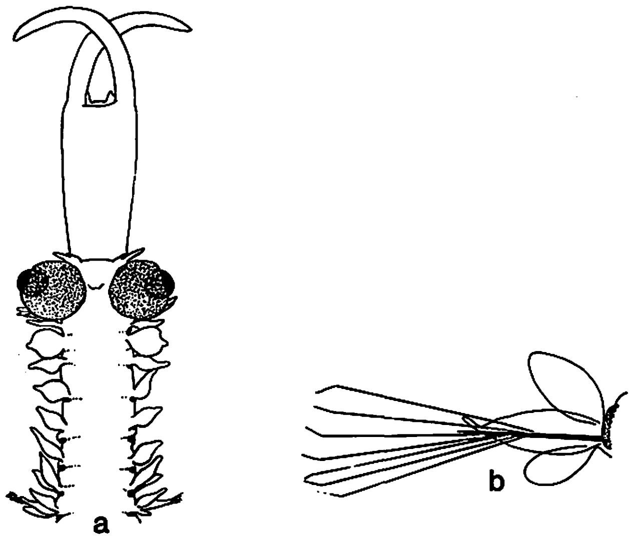

Figure 3.II.30.—*Vanadis minuta*: a, head region with everted proboscis bearing terminal horns; b, parapodium with spinigerous setae. (After Dales 1957.)

Vanadis minuta Treadwell, 1906

The body of this species is long and cylindrical, measuring about 12.5 mm for 14 segments. The prostomium has 2 large eyes (Fig. 3.II.30a) and 4 antennae at the frontal margin. The everted proboscis has a pair of terminal horns. There are 3 pairs of tentacular cirri, 1 pair on each of 3 successive anterior segments. Parapodia have single, long, cirriform distal lobes, with slender compound setae starting on segment 9 or 10 which is the first setiger (Figs. 3.II.30a,b). The dorsal and ventral cirri are ovate (Fig. 3.II.30b). The species is known from surface waters to depths of 475 m (260 fm) from Indo-West Pacific seas and from the Erben Bank to the Kaiwi Channel, Molokai, and Maui (Hartman 1966).

Family **Tomopteridae**

This is a group of transparent, planktonic worms having a pair of peristomial cirri almost as long or longer than the entire worm that are broad basally, taper distally, and contain acicula. Setae are absent from the parapodia, and the notopodia and neuropodia bear paddlelike swimming appendages. Tomopterids are carnivorous, feeding on fish eggs and larvae, pelagic tunicates, and chaetognaths in the plankton (Fauchald and Jumars 1979). As a family they are widely distributed in world oceans; they are included in an analysis of the zoogeography of pelagic polychaetes of the North Pacific Ocean prepared by Tebble (1962).

Tomopteris sp.

An undetermined species measures up to 24 mm long, composed of a body region of 17 segments 14 mm long, and a smooth, tapered tail region about 10 mm long (Fig. 3.II.31a). The anterior end has a pair of slender cirri just posterior to the antennae and equalling them in length. The 2nd pair of cirri are exceedingly long and slender, extending well back along parapodial segments (Fig. 3.II.31a). Parapodia

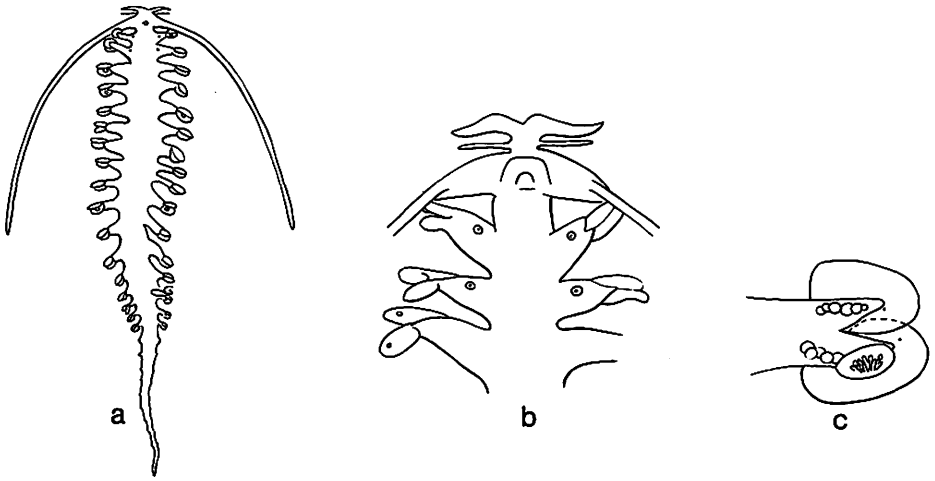

Figure 3.II.31.—*Tomopteris* sp.: a, entire worm, dorsal view, showing the pair of long cirri and tail region; b, anterior region; c, parapodium. (After Izuka 1914.)

lack setae but have thin foliose lobes (Figs. 3.II.31b,c) at the end of the parapodial rami. These worms are known from surface waters between Erben Bank and the Kaiwi Channel, and from the west coast of Hawaii (Treadwell 1906; Hartman 1966).

Family **Pilargidae**

Long worms with flattened bodies composed of many segments. Prostomium and peristomium fused, the prostomium with 2 or 3 antennae and a pair of biarticulate palps, the peristomium with 2 pairs of tentacular cirri. The proboscis is eversible and usually lacks jaws. Parapodia appear uniramous as the notopodium is reduced to a small lobe with a projecting acicular spine or stout hook. Setae are simple serrated blades. Dorsal and ventral cirri are present. Pygidium with a pair of anal cirri or a papillose plate. Pilargids are thought to be carnivores or omnivores living in soft sediment habitats. The acicular hooks may anchor the worms to appropriate substrates in the habitat (Day 1967).

Sigambra parva (Day 1963)
[syn. *Ancistrosyllis parva* Day, 1963]

A small worm measuring 6 mm in length and less than 0.5 mm in width with 47 setigers. The prostomium has a pair of short biarticulate palps and a pair of slender antennae. A median antenna may be present but is difficult to distinguish from peristomial and parapodial cirri. The peristomium has 2 pairs of long, tentacular cirri, and fuses with the prostomium and first setiger. The pharynx is muscular and unarmed. Parapodia are subbiramous, each with a long, slender dorsal cirrus and a slightly shorter ventral cirrus. Setiger 1 has a pair of extra-long dorsal cirri. Notopodial hooks start on setiger 7 and are on all setigers except the last four. A notoaciculum is present in all parapodia. Setae are simple long capillaries and shorter serrated blades. The pygidium has 2 long anal cirri. The integument is wrinkled or areolated in texture. Collected from a depth of 75 m in coral sand off the south and west shores of Oahu. A review of the family and keys to genera and species are given in Pettibone (1966). This species has been recorded from southern Africa (Day 1967).

Family **Hesionidae**

Hesionids are short-bodied, iridescent, errant worms with 2 pairs of eyes, 2 or 3 short prostomial antennae, and a pair of biarticulate palps. Clusters of 2 to 8 pairs of tentacular cirri on either side of the head represent the dorsal and ventral cirri of the reduced parapodia of fused anterior segments. There is a large muscular pharynx, which is usually papillate and sometimes bears jaws used for capturing and swallowing prey. Parapodia are either biramous or subbiramous, with the reduction of the notopodium to a dorsal cirrus and a notoaciculum in species with subbiramous parapodia. Cirri are long, jointed, and supported by a notopodial aciculum. Neurosetae are compound and usually falcigerous. Five Hawaiian representatives of this family are known.

KEY TO HAWAIIAN HESIONID GENERA

1 Body vermiform, with 16 setigers; 6 pairs of tentacular cirri anteriorly .. 2
Body short and stout, with 16 setigers; 8 pairs of tentacular cirri anteriorly 3
2(1) Head with 3 antennae; parapodia subbiramous; setae beginning on the 4th segment .... *Podarke*
Head with 2 antennae; parapodia uniramous; setae beginning on the 2nd segment .... *Syllidia*
3(1) Prostomium with 2 antennae (without median antenna or palps); parapodia subbiramous, with notoaciculum but without notosetae .... *Hesione*
Prostomium with 3 antennae (including a median antenna) and a pair of biarticulate palps; parapodia clearly biramous, with numerous notosetae .... *Leocrates*

Hesione splendida Savigny, 1818
[syn. *Hesione pacifica* McIntosh, 1885: Treadwell 1906]

The body of this species is short, approaching 23 mm long and 4 mm wide; it is broad, smooth, and has only few widely spaced segments. The cuticle is iridescent and a thick reddish brown band crosses the 2nd setigerous segment, bands become fainter posteriorly. The pair of laterofrontal antenna are short, less than the length of the prostomium which is deeply notched posteriorly. The eversible pharynx (Fig. 3.II.32a) is wide and smooth except for a dorsal tubercle just in front of the prostomium. There are 16 setigerous segments and 8 pairs of tentacular cirri (Fig. 3.II.32a). Parapodia are without distinct notopodia or notosetae, but each has a long dorsal cirrus with a narrow notoaciculum (Fig. 3.II.32b). Setae are composite falcigers with bifid tips and a fine straight accessory tooth (Fig. 3.II.32c). This cosmopolitan species has been found at French Frigate Shoals, on Maui and Hawaii, and between Maui and Lanai islands at depths of 30 to 170 m (16 to 93 fm) in a variety of carbonate sediments ranging from coarse sand with coral and shell fragments to coralline muds (Hartman 1966).

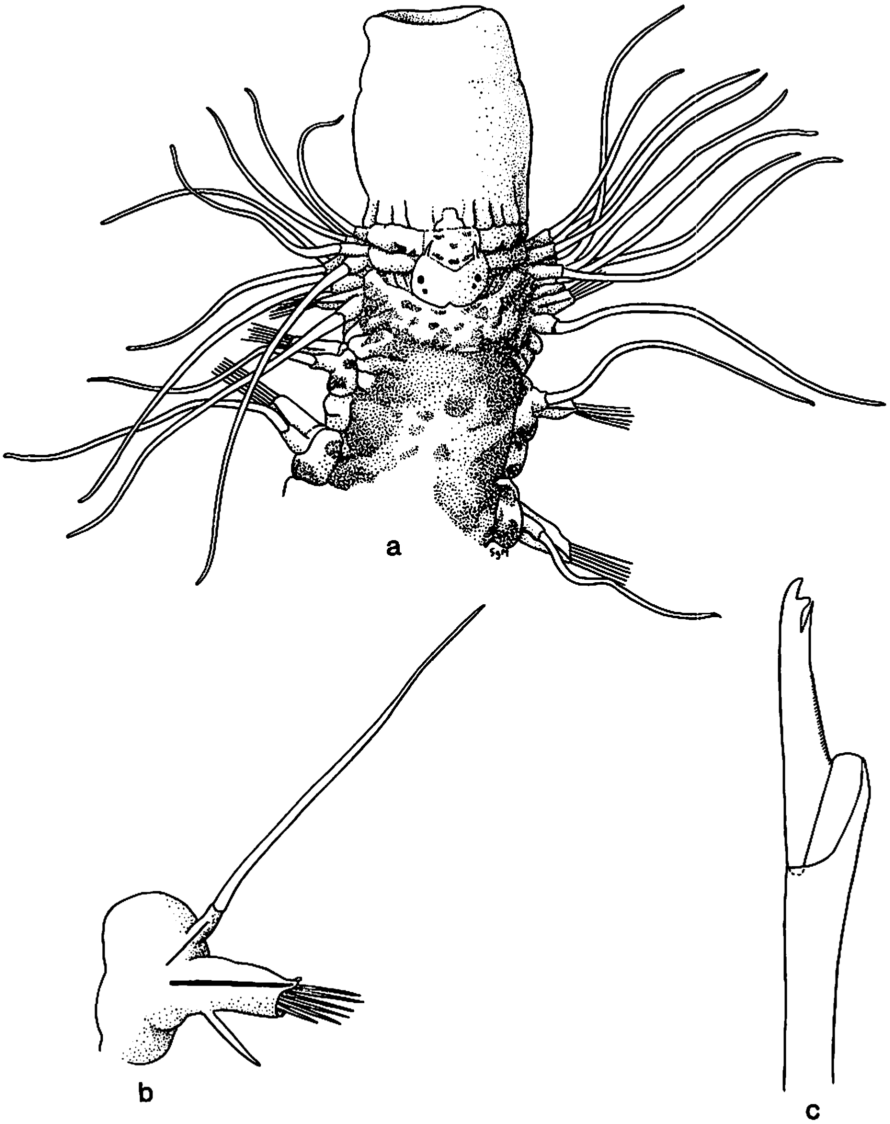

Figure 3.II.32.—*Hesione splendida*: a, anterior region with smooth proboscis extruded; b, parapodium with long dorsal cirrus; c, bifid falcigerous seta with accessory tooth.

Leocrates chinensis Kinberg, 1866

The body of this worm is 15 to 22 mm long, and there are 16 setigerous segments. The prostomium is subquadrate and has 4 small reddish brown eyes on the posterior half; the anterior pair of eyes are slightly larger than the posterior pair (Fig. 3.II.33a). There is a large subconical facial tubercle at the midfront of the prostomium, a pair of thick biarticulate palps at the sides, and a pair of slender antennae between the palps and the facial tubercle. A small occipital median antenna is present between the posterior eyes. Parapodia (Fig. 3.II.33b) are subbiramous; notopodia have fascicles of slender capillary setae; neuropodia are larger and, distally, obliquely truncate. Neuropodia have long, distally bifid,

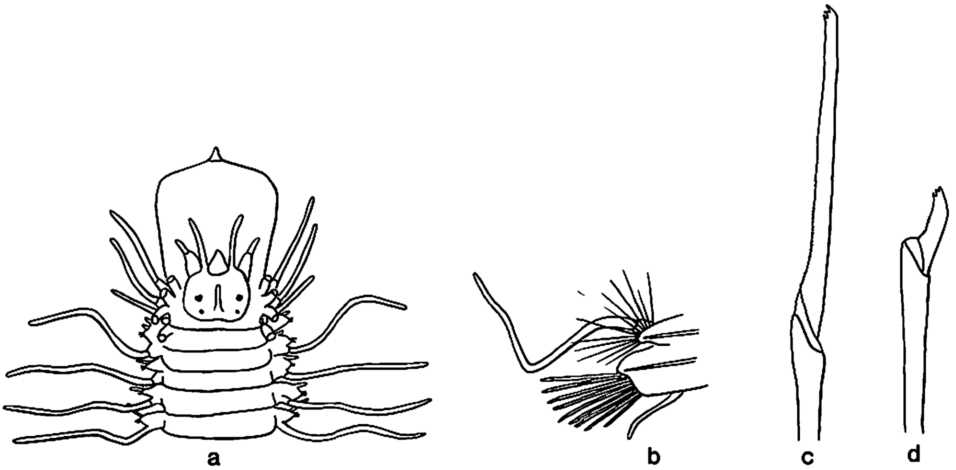

Figure 3.II.33.—*Leocrates chinensis*: a, anterior region with extruded proboscis and dorsal tooth (some tentacular cirri cut near head); b, parapodium; c, falcigerous neuroseta with accessory tooth from the upper part of the neuropodium; d, falcigerous neuroseta with accessory tooth from the lower part of the neuropodium. (After Kinberg 1910.)

composite falcigers with blades longer in the upper part and shorter in the lower part of the bundle (Figs. 3.II.33c,d). The species is known from Hong Kong, West Africa, the Mediterranean, Solomon Islands, and the Caribbean; in the Hawaiian Islands it occurs in shallow waters to a depth of 36 m (20 fm) (Hartman 1966; Pettibone 1970).

Leocrates giardi Gravier, 1900a
[syn. *Castalia oculata* Treadwell, 1906. *Leocrates oculatus* (Treadwell): Hartman 1966]

The body of this worm is short, up to 15 mm long and 4 to 5 mm wide including the parapodia; it consists of 4 anterior tentacular segments and 16 parapodial segments. The prostomium (Fig. 3.II.34a) is trapezoidal, widest in

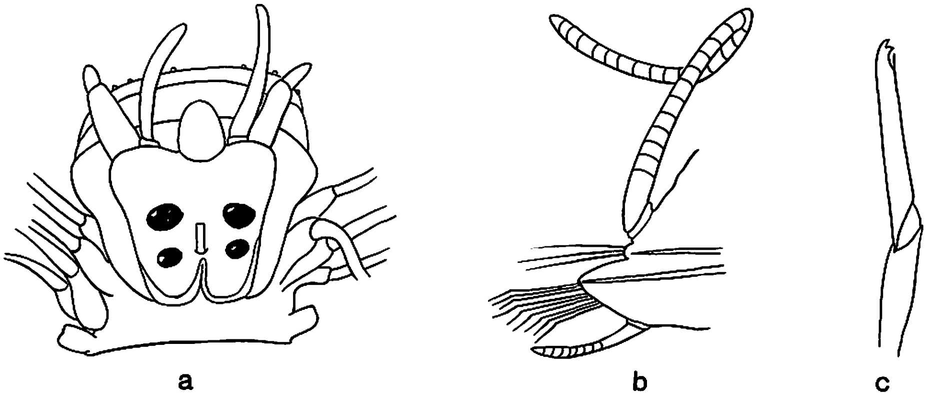

Figure 3.II.34.—*Leocrates giardi*: a, head with pharynx partially extruded showing buttonlike papillae; b, parapodium; c, falcigerous neuroseta with accessory tooth. (After Pettibone 1970.)

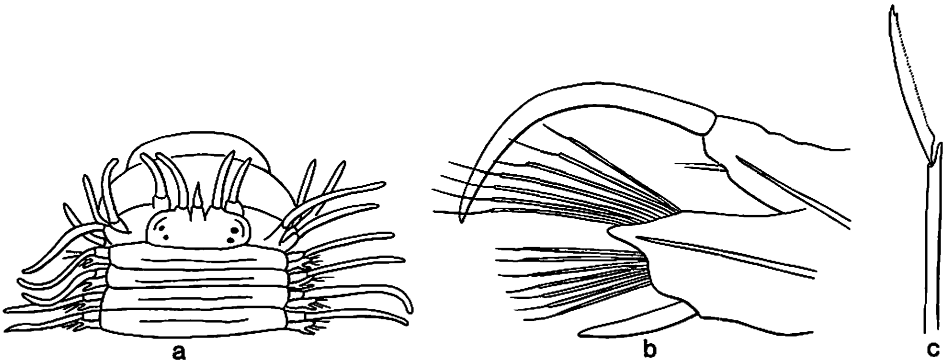

Figure 3.II.35.—*Podarke pugettensis*: a, anterior region with smooth proboscis extruded; b, sub-biramous parapodium with 2 capillary notosetae; c, falcigerous neuroseta. (After Johnson 1901.)

front, and has 2 pairs of eyes; the anterior pair is much the larger. The subconical facial tubercle lies between a pair of slender antennae on the frontal margin. A pair of frontolateral palps are biarticulate. There is a single, median antenna between the eyes. Parapodia are subbiramous (Fig. 3.II.34b), with notopodia represented by an embedded aciculum and a few simple setae. Neuropodia are large, each having composite falcigers in which the appendage is distally bifid with an additional subdistal short spine (Fig. 3.II.34c). This Indo-West Pacific species has been found in the Alenuihaha Channel between Hawaii and Maui at 100 to 350 m (55 to 164 fm) on a rocky bottom (Pettibone 1970).

Podarke pugettensis Johnson, 1901
[syn. *Ophiodromus pugettensis* (Johnson): Hartman 1966]

This species reaches 18 mm in length, 2 mm in width, and has numerous segments. The color in life is reddish brown to purple or almost black; the prostomium is pale and has 4 red eyes; the dorsum is crossed by pale, transverse lines, and the cirri and antennae are pale brown to white. The prostomium (Fig. 3.II.35a) is subquadrate, wider than long, and has a pair of biarticulate palps lateral to a pair of slender antennae and a median antenna. The everted proboscis is smooth laterally and closely fimbriated distally. Parapodia (Fig. 3.II.35b) are subbiramous, each with a large dorsal cirrus penetrated by straight acicula and 1 or 2 capillary notosetae. Neuropodia are much larger, each terminating in a projecting acicular lobe with composite falcigers having bifid tips (Fig. 3.II.35c). This species is known from intertidal waters at Oahu, where it lives commensally with sea urchins; it is also found intertidally along both sides of the North Pacific Ocean.

Syllidia armata Quatrefages, 1865

This species has a short, broad body measuring less than 10 mm long; there are 26 or more setigers. The prostomium (Fig. 3.II.36a) is square with 4 eyes, 2 antennae slightly longer than the prostomium, and 2 biarticulate palps. The proboscis bears a pair of lateral, serrated jaws, a median ventral stylet, and a margin with 10 to 15 papillae (Fig. 3.II.36c). Uniramous parapodia bear

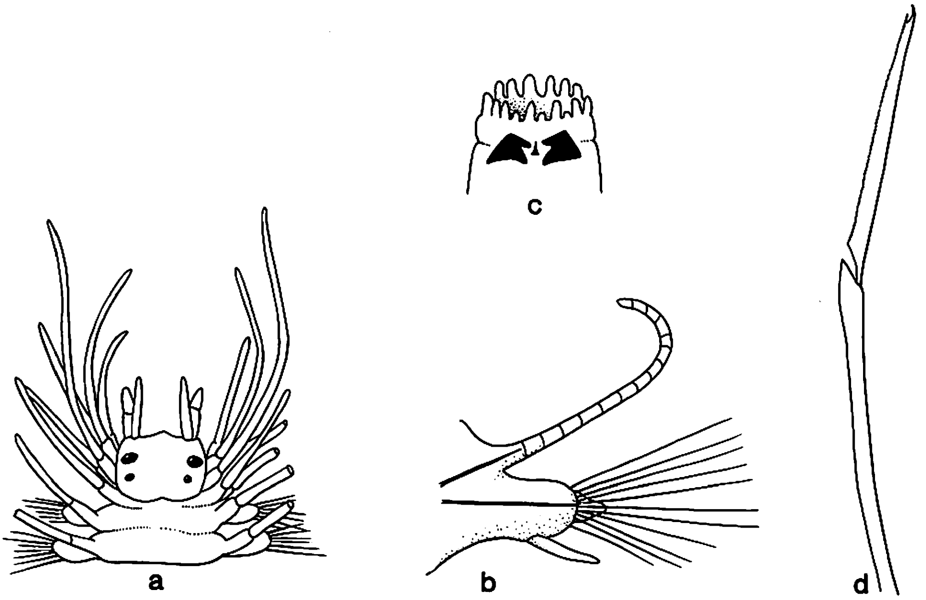

Figure 3.II.36.—*Syllidia armata*: a, anterior region; b, uniramous parapodium; c, proboscis with jaws, stylet, and papillose margin; d, falcigerous neuroseta with terminal hook and secondary tooth. (After Day 1967.)

notoacicula in the dorsal cirri, while the neuropodia have triangular presetal lobes and rounded postsetal lamellae (Fig. 3.II.36b). Each falcigerous seta has a terminal hook and a very fine subterminal tooth (Fig. 3.II.36d). Previously recorded from the North and South Atlantic (Day 1967), this species also occurs sublittorally among coral rubble in Kaneohe Bay, Oahu.

Family **Syllidae**

JANET K. FRIEND

Syllids are small, errant polychaetes living in a variety of marine habitats in Hawaii. While a few species are brightly colored and have stripes or obvious color patterns, most species are pale beige, green, brown, or transparent in life. With few exceptions syllids have a clearly visible muscular proventriculus, long, articulated antennae and cirri, 2 pairs of eyes (often with large lenses), obvious palps, 3 antennae, 2 pairs of tentacular cirri, 1 or more teeth in an eversible pharynx (Fig. 3.II.37a), uniramous parapodia (Fig. 3.II.37b) on all but the tentacular segment, and a combination of compound and simple setae (Fig. 3.II.37c). Sexual and asexual phases occur in syllid life cycles. Some species spawn at the surface, while others carry eggs and embryos on their body or attach them to the substrate in a cocoon. Little is known about the diet and feeding habits of these worms, but Fauchald and Jumars (1979) summarize available information.

The family is divided into 4 subfamilies. Most genera of Hawaiian syllids belong to the subfamily Syllinae. The main diagnostic characteristics of this group

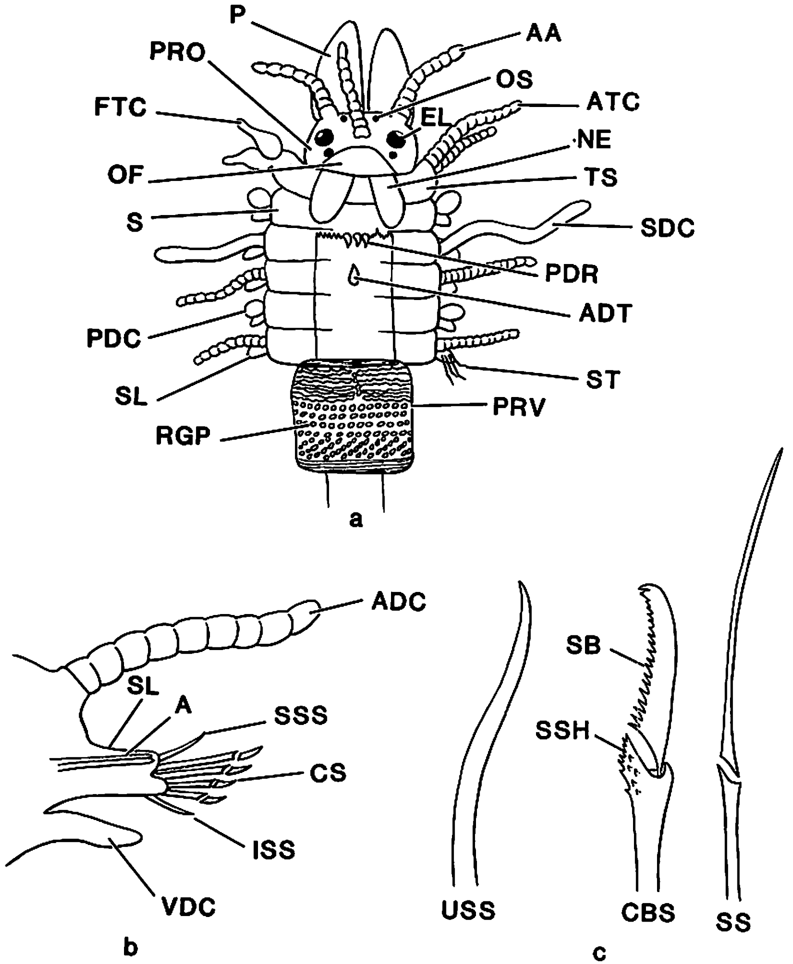

Figure 3.II.37.—Composite illustrations of a syllid to show various anatomical features: a, head features and anterior region of the digestive system; b, parapodium; c, uniramous and compound setae.

a. AA, articulated antenna; ADT, anterior dorsal tooth; ATC, articulated tentacular cirrus; EL, eye with a lens; FTC, flask-shaped tentacular cirrus; NE, nuchal epaulette; OF, occipital flap; OS, ocular speck; P, palp; PDC, papilliform dorsal cirrus; PDR, pharynx with denticulate rim or trepan; PRO, prostomium; PRV, proventriculus showing various arrangements of the underlying radial muscles; RGP, rows of radial muscle points; S, first setiger; SDC, smooth dorsal cirrus; SL, setigerous lobe; ST, setae; TS, tentacular segment.

b. A, aciculum; ADC, articulated dorsal cirrus; CS, compound seta; ISS, inferior simple seta; SL, setigerous lobe; SSS, superior simple seta; VDC, ventral digitate cirrus.

c. CBS, compound bifid seta (falcigerous); SB, serrated blade; SSH, spinous shaft head; SS, spinigerous compound seta; USS, unidentate simple seta.

include articulated antennae and dorsal cirri, 2 pairs of tentacular cirri, separate palps, and a pharynx with 1 or more teeth (Figs. 3.II.42a,b). The genera *Langerhansia*, *Haplosyllis*, *Parasphaerosyllis*, *Opisthosyllis*, *Branchiosyllis*, *Trypanosyllis*, and *Typosyllis* belong to the subfamily Syllinae and are present in Hawaii. The genera *Pionosyllis*, *Amblyosyllis*, *Odontosyllis*, and *Eusyllis*, also present in Hawaii, belong to the subfamily Eusyllinae. This group is characterized by the presence of basally fused palps, a straight or coiled pharynx with teeth and often a denticulate rim, 2 pairs of tentacular cirri, weakly articulated or smooth antennae, and dorsal cirri (Figs. 3.II.38a, 41a,b). The subfamily Exogoninae is represented in Hawaii by the genera *Exogone*, *Brania*, and *Sphaerosyllis*. These very small worms are characterized by having partially fused palps (Fig. 3.II.45a), smooth antennae and dorsal cirri, and a coiled or S-shaped pharynx with a denticulate rim. The subfamily Autolytinae, represented by the genus *Myrianida*, is characterized by the lack of ventral cirri (Fig. 3.II.47b), a pharynx that is often S-shaped with a toothed margin, and palps partially or entirely fused.

Thirty species of syllids are known from Hawaii. Five of these are endemic, 18 have been recorded from other areas, and 7 unidentified species are being studied. Since these worms are small (0.1 to 2.5 cm in length) and inconspicuous, it is quite probable that more species will be found. The species described here have been collected from a variety of habitats including mud, sand, coral rock, algal turf, sponges, artificial substrates, fouling communities, and dredged material. Syllids often constitute the majority of individual organisms in tropical benthic samples, but because of their small size they contribute little to the biomass.

Syllids are fragile and their identification is dependent upon intact cirri and antennae; therefore, care must be taken in handling the specimens. Preserved specimens usually lack their natural coloration and may lose stripe or bar patterns entirely.

KEY TO HAWAIIAN SYLLID GENERA

1 Ventral cirri absent (subfamily Autolytinae) .... *Myrianida*
Ventral cirri present 2
2(1) Palps separate; 2 pairs of tentacular cirri; antennae and dorsal cirri clearly articulated (subfamily Syllinae) 3
Palps partially or completely fused; 1 or 2 pairs of tentacular cirri; antennae and dorsal cirri weakly articulated or smooth 9
3(2) Pharynx with only a single large dorsal tooth; body cylindrical 4
Pharynx with a single large dorsal tooth and denticulate rim; body usually flattened .... *Trypanosyllis*
4(3) Single tooth anteriorly placed 5
Single tooth posteriorly placed .... *Opisthosyllis*
5(4) Many compound and simple setae present 6
No compound setae, only a few simple setae present ...... *Haplosyllis*
6(5) Compound setae with normal, straight blades that are either long and slender or sharply recurved 7
Compound setae with only normal, straight blades that decrease in length posteriorly 8
7(6) Some superior compound setae with extremely long, slender blades .... *Langerhansia*
Some inferior compound setae with sharply recurved blades .... *Branchiosyllis*
8(6) Antennae and dorsal cirri all articulated .... *Typosyllis*

Articulated dorsal cirri alternate posteriorly with short, nonarticulated bulbous cirri (Fig. 3.II.52b) .... *Parasphaerosyllis*

9(2) Palps fused basally; 2 pairs of tentacular cirri; dorsal antennae and cirri long and weakly articulated or smooth; pharynx with 1 or many teeth (subfamily Eusyllinae) 10

Palps fused for at least half their length; 1 or 2 pairs of tentacular cirri; dorsal antennae and cirri very short and smooth; pharynx with a single tooth (subfamily Exogoninae) 13

10(9) Rim of pharynx smooth .... *Pionosyllis*

Rim of pharynx denticulate 11

11(10) Without nuchal organs at posterior end of prostomium .... *Eusyllis*

With nuchal organs at posterior end of prostomium 12

12(11) A pair of oblong nuchal organs dorsolaterally (Fig. 3.II.38a); pharyngeal rim bearing fine multidentate teeth .... *Amblyosyllis*

A hemispherical nuchal flap at posterior end of prostomium (Fig. 3.II.48a); pharynx bearing a row of large ventral teeth near rim .... *Odontosyllis*

13(9) One pair of tentacular cirri 14

Two pairs of tentacular cirri.................................. *Brania*

14(13) Antennae and dorsal cirri papilliform; body elongate and linear .... *Exogone*

Antennae and dorsal cirri pear-shaped; body short and ovoid .... *Sphaerosyllis*

Amblyosyllis sp.

The length of 2 incomplete specimens with 9 and 11 setigers are 2 and 3 mm, respectively. Preserved, the specimens lack pigmentation. These specimens are in very poor condition, lacking antennae and most of their dorsal cirri. The prostomium has 4 very large eyes with lenses and a pair of nuchal organs (Fig. 3.II.38a). The palps are short and fused basally. The pharynx is long and looped upon itself, having a denticulate rim with multidentate teeth. The proventriculus is barrel-shaped and approximately 2 setigers long (Fig. 3.II.38a). Both specimens lack antennae and the dorsal cirri are weakly annulate, slender, and long (Fig. 3.II.38a). Ventral cirri are leaf-shaped and extend as far as the setigerous lobes (Fig. 3.II.38b). The body segments are markedly triangular in side view. There are approximately 15 to 17 compound bifid setae (Fig. 3.II.38c) with equal shaft lengths and 1 or 2 with extremely long shafts per parapodium. The 2 specimens were collected at Kewalo, Oahu, on a near-shore reef flat.

Branchiosyllis exilis (Gravier, 1900b)
[syn. *B. uncinigera* Hartmann-Schröder, 1965] ↗ 20-30mm (Fauvel 1953)

Body length of this syllid is up to 4.5 mm, 45mm? with 56 setigers in the largest specimen. There is no color pattern in preserved specimens. The prostomium has 4 large eyes with lenses (Fig. 3.II.39a). Palps are broad and project forward. The pharynx is 7 setigers long and has an anterior dorsal tooth. The proventriculus has approximately 30 rows of points and is 9 setigers long. The median antenna is 28 articles long and inserted between the anterior pair of eyes. Lateral antennae have

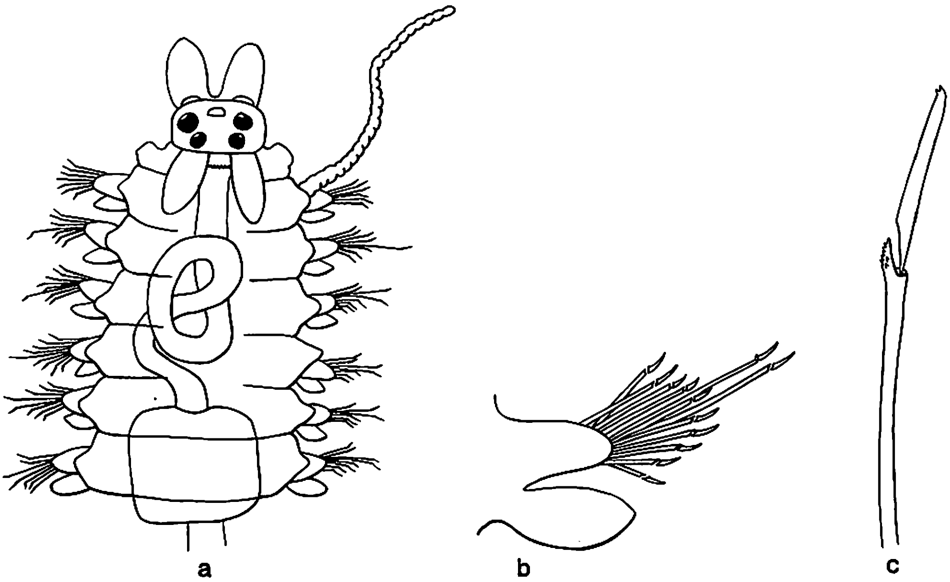

Figure 3.II.38.—*Amblyosyllis* sp.: a, anterior region; b, parapodium with foliaceous ventral cirrus; c, compound, bifid seta.

18 to 20 articles and are inserted on the anterior margin of the prostomium. The tentacular cirri differ in length, the dorsal pair with 30 articles and the ventral pair with 20. The dorsal cirri are alternately long and short. On anterior setigers the short cirri have 24 articles and long cirri have 37 articles, while on midbody setigers the short cirri have 40 and long cirri have 50 articles. Setae are compound, with unidentate blades anteriorly (Figs. 3.II.39b,c,d); starting midbody, some of the inferior compound setae have deeply hooked or recurved blades (Figs. 3.II.39e,f). The aciculum is blunt (Figs. 3.II.39g,h). A ciliated pad is present at the base of each dorsal cirrus (Fig. 3.II.39h). This circumtropical species has been collected at Kewalo and Kaneohe Bay, Oahu, and at Kahului, Maui.

KEY TO HAWAIIAN *BRANIA* SPECIES

Preserved specimens lack pigmentation; antennae and dorsal cirri flask-shaped and not as long as the body is wide; compound setae unidentate .... *B. rhopalophora*

Dorsum of preserved specimens with black stripes and black markings on the prostomium; antennae and dorsal cirri cylindrical and often as long as the body is wide; compound setae bidentate .... *Brania* sp.

Brania rhopalophora (Ehlers, 1897)

The length of this worm is 1 to 4 mm, with up to 35 setigers in the largest specimen. Preserved specimens lack pigmentation. The prostomium has 2 pairs of eyes and 1 pair of ocular specks anteriorly (Fig. 3.II.40a, 1 ocular speck visible in

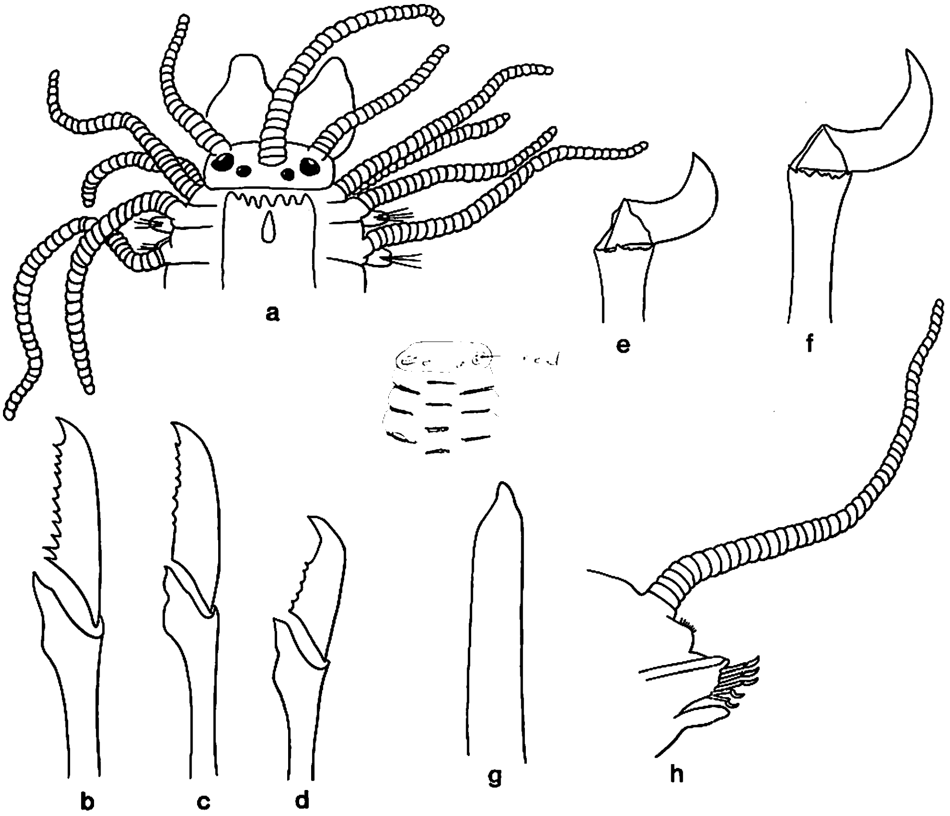

Figure 3.II.39.—*Branchiosyllis exilis*: a, anterior region; b,c,d, compound unidentate setae of anterior setigers; e,f, hooked, compound setae of middle and posterior setigers; g, aciculum; h, parapodium with long dorsal and short ventral cirri.

figure). The palps are fused basally and project forward. The pharynx is 4 to 5 setigers long and has an anterior dorsal tooth. The proventriculus is barrel-shaped, 2 setigers long, and has 13 rows of points. Antennae, tentacular cirri (2 pairs), and dorsal cirri are flask-shaped. Ventral cirri are digitate and nearly as

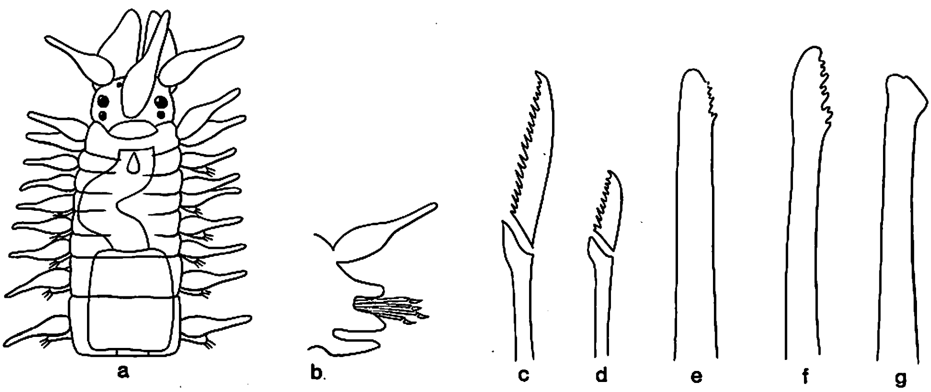

Figure 3.II.40.—*Brania rhopalophora*: a, anterior region; b, parapodium; c,d, compound setae with serrated blades; e,f, simple, serrated setae; g, knobbed aciculum.

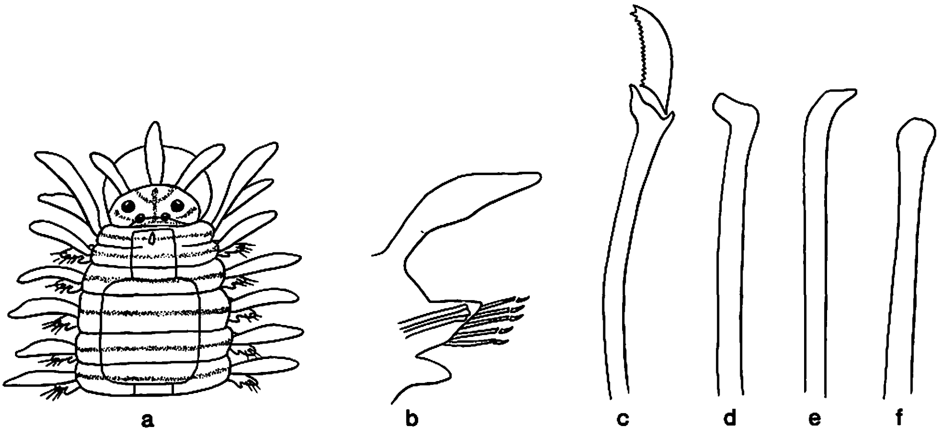

Figure 3.II.41.—*Brania* sp.: a, anterior region; b, parapodium; c, compound seta with finely serrated blade; d,e,f, acicula.

long as the setigerous lobe (Fig. 3.II.40b). Compound setae are unidentate and have strongly serrated blades (Figs. 3.II.40c,d). Simple setae with blunt ends and irregularly serrated edges begin between setigers 7 and 13 (Figs. 3.II.40e,f). The aciculum is knobbed (Fig. 3.II.40g).

This is a cosmopolitan species (Day 1967) commonly found in algal mats, coral rubble, sand, and on settling plates in Hawaii; it has been collected at Kaneohe Bay and Kewalo on Oahu.

Brania sp.

The length of the largest specimen with 34 setigers is 2 to 3 mm. Preserved specimens have black markings on the prostomium and black stripes on the dorsum. There are 2 pairs of red eyes with lenses (often coalesced) and a pair of ocular specks on the prostomium (Fig. 3.II.41a, ocular specks not visible in figure). A small occipital flap is present. The palps are short and fused for half their length. The pharynx is 1 to 2 setigers long with a small anterior dorsal tooth. A short barrel-shaped proventriculus with 50 rows of points is present. Antennae, dorsal cirri, and tentacular cirri are cylindrical and not articulated. The antennae are slightly shorter than the dorsal cirri. The median antenna originates posteriorly to the laterals. There are 2 pairs of tentacular cirri. Ventral cirri are digitate and nearly as long as the setigerous lobes (Fig. 3.II.41b). Compound bidentate setae are present (Fig. 3.II.41c) and there are no simple setae. Acicula have blunt or knobbed ends (Figs. 3.II.41d,e,f). Specimens have been collected from Barbers Point, Oahu, and Kapoho, Hawaii.

Langerhansia cornuta (Rathke, 1843)
[syn. *Ehlersia cornuta* Langerhans, 1879. *Typosyllis* (*Langerhansia*) *cornuta* (Rathke, 1843) in Hartmann-Schröder 1965] 10-15 mm (Fauvel 1953)

The length of this species is 2 to 7 mm, with up to 60 setigers in the largest specimens. Color in life is beige to brown without pigment patterns; preserved specimens lack pigmentation. The prostomium has 2 pairs of eyes and 2 ocular specks (Fig. 3.II.42a). The median antenna is inserted centrally among the 4 eyes and all antennae have 8 to 15 articles. The palps are short and separate. The

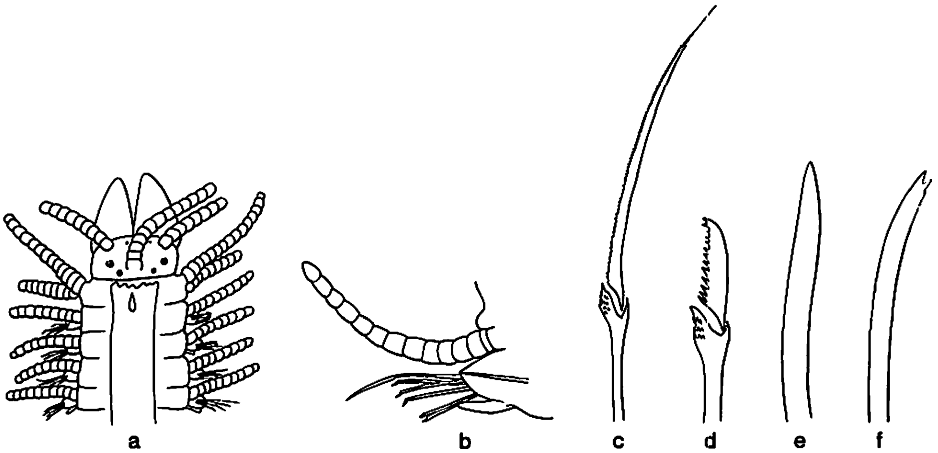

Figure 3.II.42.—*Langerhansia cornuta*: a, anterior region; b, parapodium with articulated dorsal cirrus; c, "langerhansia"-type seta; d, compound seta with short bifid blade; e, acicular seta; f, bifid simple seta.

pharynx is 7 to 9 setigers long, with an anterior dorsal tooth. The proventriculus is 3 to 4 setigers long, with 30 to 40 rows of points. Dorsal and tentacular cirri have 8 to 15 articles and the ventral cirri are digitate and as long as the setigerous lobe (Fig. 3.II.42b). Each setal bundle has 1 or 2 "langerhansia"-type superior, compound, entire or minutely bifid setae, as well as 6 to 8 compound setae with short bifid blades (Figs. 3.II.42c,d). Posteriorly there are simple entire or bifid setae (Fig. 3.II.42f). The acicular setae are tapered with blunt tips (Fig. 3.II.42e). This cosmopolitan species is common in a variety of habitats in Hawaii, including sand, coral rubble, algal mats, fouling communities, and artificial substrates. It has been collected from Kaneohe Bay and Kewalo, Oahu, Halape and Kailua, Hawaii, and Paia, Maui.

Eusyllis sp.

The length of this syllid is 3 mm with 36 setigers in the largest specimens. Preserved specimens lack pigmentation. There are 3 pairs of eyes on the prostomium (Fig. 3.II.43a). The palps are fused basally and project forward. The

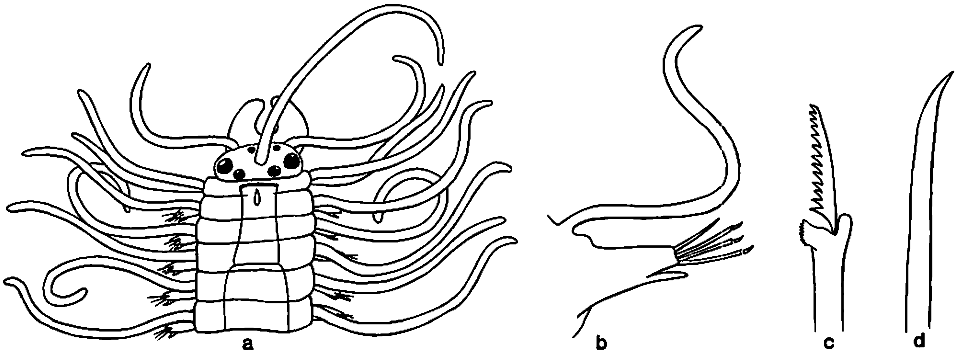

Figure 3.II.43.—*Eusyllis* sp: a, anterior region, prostomium with 3 pairs of eyes; b, parapodium; c, compound seta with strongly serrated blade; d, simple seta.

pharynx has an anterior dorsal tooth, a denticulate rim, and is 3 setigers long. The proventriculus is 4 setigers long. Antennae, tentacular cirri, and dorsal cirri are long and smooth. The dorsal cirri are more slender than the antennae or tentacular cirri. Thin, digitate ventral cirri extend beyond the long setigerous lobes (Fig. 3.II.43b). There are 3 compound unidentate setae with strongly serrated blades per parapodium (Fig. 3.II.43c). Setal blade lengths decrease markedly posteriorly. A simple superior seta is present on all setigers (Fig. 3.II.43d). This species has been collected from Kaneohe Bay and Barbers Point, Oahu.

KEY TO HAWAIIAN *EXOGONE* SPECIES

Three subequal antennae inserted between anterior pair of eyes; compound setae with short falcigerous blades and long, narrow, spinigerous serrated blades; a simple sharp, curved seta present from setiger 3 posteriorly .... *E. verugera*

Antennae inserted behind the posterior pair of eyes, the median larger than the laterals; compound setae with broad, serrated falcigerous blades anteriorly and shorter, nonserrated unidentate blades posteriorly; simple blunt setae present from midbody posteriorly .... *Exogone* sp.

Exogone verugera (Claparède, 1868)

The length of this worm is 2 to 4 mm, with up to 35 setigers in the largest specimens. The color is pale yellow to white in life, without any pigment pattern. The broad prostomium bears 2 pairs of red eyes and 3 short antennae in a parallel row between the anterior pair of eyes (Fig. 3.II.44a). Palps are fused, twice the length of the prostomium, and project forward. The pharynx is 3 to 4 setigers long,

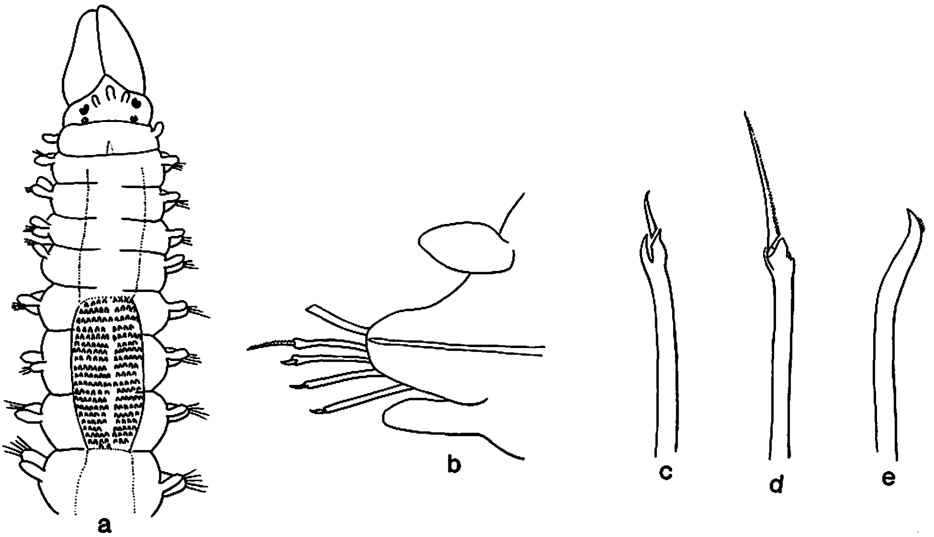

Figure 3.II.44.—*Exogone verugera*: a, anterior region; b, parapodium; c, compound falcigerous seta; d, compound spinigerous seta; e, simple seta.

ending in a ring of soft papillae and having a single middorsal tooth. The proventriculus has 15 to 20 rows of points and is 2 to 3 setigers long. Antennae, the pair of tentacular cirri, and dorsal cirri are short and papilliform. Anal cirri are long and tapered. Ventral cirri are digitate and do not extend beyond the setigerous lobe (Fig. 3.II.44b). Compound setae are of 2 types, one having a short falcigerous blade (Fig. 3.II.44c) and the other a long, narrow serrated blade (Fig. 3.II.44d). Simple setae are present from setiger 3 (Fig. 3.II.44e). Eggs and embryos are carried on the dorsum. This cosmopolitan species (Day 1967) is common in many habitats in Hawaii, including algal mats, coral rubble, sand, settling plates, and fouling communities. It has been collected from Kaneohe Bay, Kewalo, and Fort Kamehameha, Oahu, and from Paia, Maui (Hartmann-Schröder 1965; Hartman 1966).

Exogone sp.

The body of this worm is 2 mm long, with 29 setigers in the largest specimen. Preserved specimens lack pigmentation. The prostomium has 2 pairs of eyes and a pair of ocular specks (Fig. 3.II.45a). The palps are fused for at least half their length, are long and project forward. The pharynx is 5 setigers long, with a small anterior dorsal tooth. The proventriculus is 5 setigers long and slender. Antennae, tentacular cirri (a single pair), and dorsal cirri are papilliform. The antennae are small and inserted closely together in a row just behind the posterior pair of eyes. The ventral cirri are digitate and not as long as the setigerous lobes (Fig. 3.II.45b). The compound setae are unidentate, with short serrated or smooth blades (Figs. 3.II.45c,d). A simple seta is present from the midbody posteriorly (Fig. 3.II.45e). This unidentified species was collected from the intertidal zone at Kewalo, Oahu.

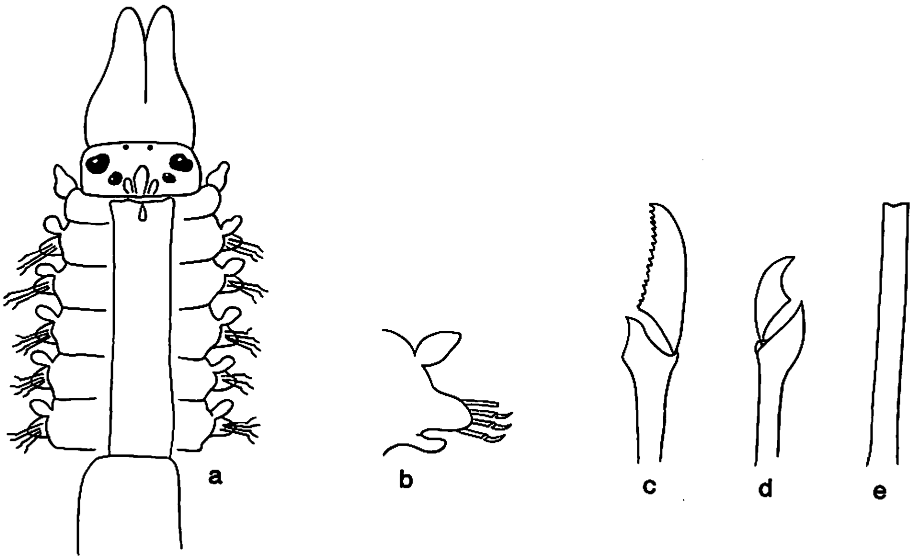

Figure 3.II.45.—*Exogone* sp.: a, anterior region; b, parapodium with papilliform dorsal cirrus; c,d, compound setae; e, simple seta.

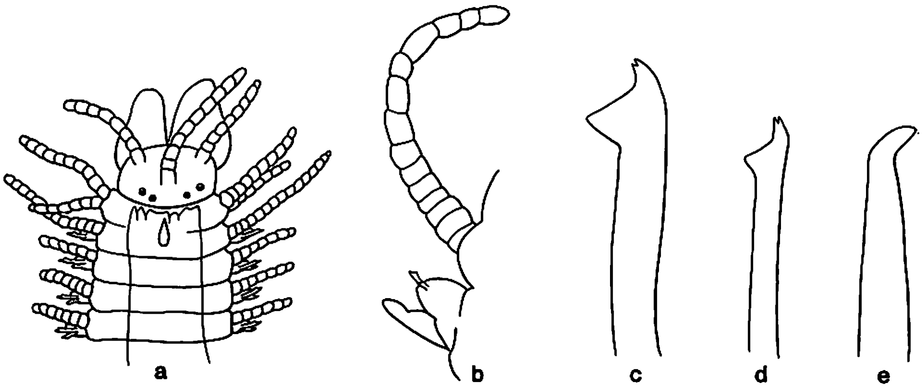

Figure 3.II.46.—*Haplosyllis spongicola*: a, anterior region; b, parapodium; c,d, bifid, simple, "boat-hook"-shaped setae; e, aciculum.

Haplosyllis spongicola (Grube, 1855) 20-50 mm (Fauvel 1953)

The length of this species is 5 to 9 mm, with up to 45 setigers in the largest specimens. The prostomium has 4 eyes and 2 ocular specks (Fig. 3.II.46a, ocular specks not visible). Pigmentation is lacking in preserved specimens. The palps are short and separate. The pharynx is long (8 setigers) and has a large anterior dorsal tooth. The proventriculus is also long, extending 7 to 9 setigers with 32 rows of points. The median antenna is inserted between the anterior pair of eyes and all antennae are slender with 6 to 10 articles. Ventral cirri are digitate and extend farther than the setigerous lobes (Fig. 3.II.46b). Setae are all "boat-hook"-shaped and most have a clearly bifid distal tooth (Figs. 3.II.46c,d). The aciculum is bent at the tip (Fig. 3.II.46e). Some preserved specimens have small, clear vesicles under the dermis after setiger 15. This cosmopolitan species (Westheide 1974) is common in algal mats and sponge colonies in Hawaii and has been collected from Kaneohe Bay and Kewalo, Oahu, and at Halape, Hawaii (Hartmann-Schröder 1965; Hartman 1966).

Myrianida crassicirrata Hartmann-Schröder, 1965

A stolon-producing adult of this species may be up to 10 mm long, with 30 segments in the largest specimens and 24 to 30 stolons. The body is wide and brightly colored yellow-brown in life, with blue cirri and antennae, and a row of blue dots surrounded by white patches edged in yellow-brown on the dorsum (Plate 3.II.2d). The prostomium has 2 pairs of large eyes, a thick median antenna and a smaller pair of lateral antennae (Fig. 3.II.47a). Palps are of medium length, often bent ventrally. The pharynx is 4 to 5 setigers long and has a finely toothed margin. The proventriculus is 3 to 4 setigers long, with 20 to 25 rows of points. Antennae, tentacular cirri, and dorsal cirri are short, stout, and not articulated. Ventral cirri are lacking (Fig. 3.II.47b). Setae are compound with short bifid blades and a spinous shaft head (Fig. 3.II.47c). This endemic species is common in Kaneohe Bay, Oahu, and has been collected from coral rubble, mud, algae, and living sponges (Hartmann-Schröder 1965; Hartman 1966).

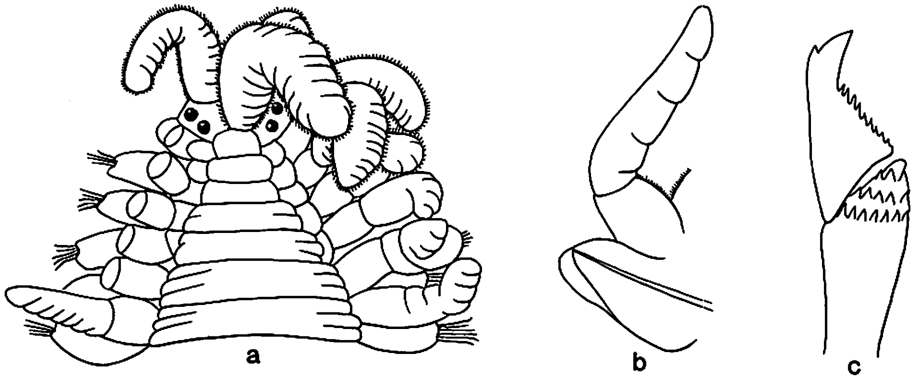

Figure 3.II.47.—*Myrianida crassicirrata*: a, anterior region; b, parapodium (setae not shown); c, compound seta. (After Hartmann-Schröder 1965.)

Odontosyllis ctenostoma Claparède, 1868

The length of this worm is 4 to 13 mm, with up to 75 setigers in the largest specimens. The body in life is yellow to light brown with faint brown dorsal segmental lines. Preserved specimens lack pigmentation. The prostomium has 2 pairs of large red eyes with lenses (Fig. 3.II.48a). The palps are short, basally fused, and bent ventrally. At the posterior end of the prostomium there is a hemispherical nuchal flap. The pharynx is 3 setigers long, with a large anterior dorsal tooth and a toothed margin with 10 large teeth (Fig. 3.II.48a). The proventriculus is disproportionately wide and 8 to 10 setigers long. The antennae, tentacular cirri, and dorsal cirri are more than twice the length of the prostomium, not articulated, but slightly wrinkled. The ventral cirri are flattened pads (Fig. 3.II.48b). The setae are compound with short unidentate blades and there may be up to 18 per parapodium (Fig. 3.II.48c). Acicular setae have a knobbed end and there are 1 to 2 per parapodium (Fig. 3.II.48d). This species, known from the

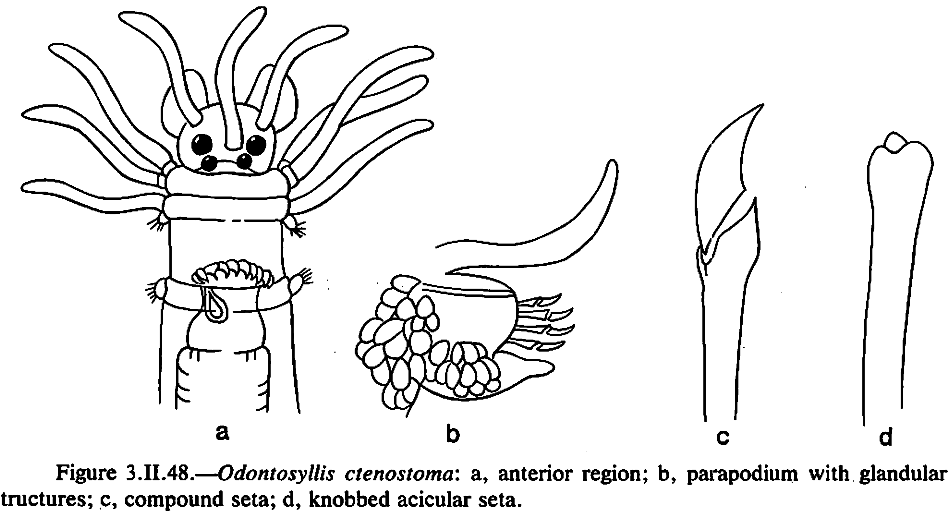

Figure 3.II.48.—*Odontosyllis ctenostoma*: a, anterior region; b, parapodium with glandular structures; c, compound seta; d, knobbed acicular seta.

Atlantic and Mediterranean (Day 1967), has been collected in Hawaii on fouling panels at Barbers Point, Oahu.

KEY TO HAWAIIAN *OPISTHOSYLLIS* SPECIES

1 Dorsum papillate; compound setae distally bifid .... *O. papillosa*
Dorsum smooth; compound setae unidentate 2
2(1) Palps tapered and bent ventrally; proventriculus 8 to 9 setigers long; dorsal cirri slender (width to length ratio 1:15) and tapered with approximately 20 to 30 articles; compound setae with short unidentate blades .... *O. brunnea*
Palps short and bent ventrally; proventriculus 6 to 7 setigers long; dorsal cirri of normal width (width to length ratio 1:10) with 11 to 24 articles; compound setae with short, deeply serrated unidentate blades .... *O. corallicola*

Opisthosyllis brunnea Langerhans, 1879

This syllid is up to 20 mm long, with 72 setigers in the largest specimens. The color in life is creamy yellow with a red pharynx. Preserved specimens retain the red coloration of the pharynx. The prostomium bears 2 pairs of red eyes and a small occipital flap (Fig. 3.II.49a). The palps are fused basally, tapered, and often bent ventrally. The pharynx is 8 to 9 setigers long, with a posterior tooth and a soft papillate anterior margin. The proventriculus is wider than the pharynx, 8 setigers long, and has 75 to 85 rows of points. The median antenna, with 20 to 25 articles, is inserted between the posterior pair of eyes; the lateral antennae, with 13 to 15 articles, are inserted anteriorly. The superior tentacular cirri are approximately 20 articles long and the inferior cirri have 10 to 12 articles. The 1st pair of dorsal cirri are up to 30 articles long and posteriorly alternate in length between 23 and 30 articles. The long cirri are approximately as long as the body is wide. Ventral cirri

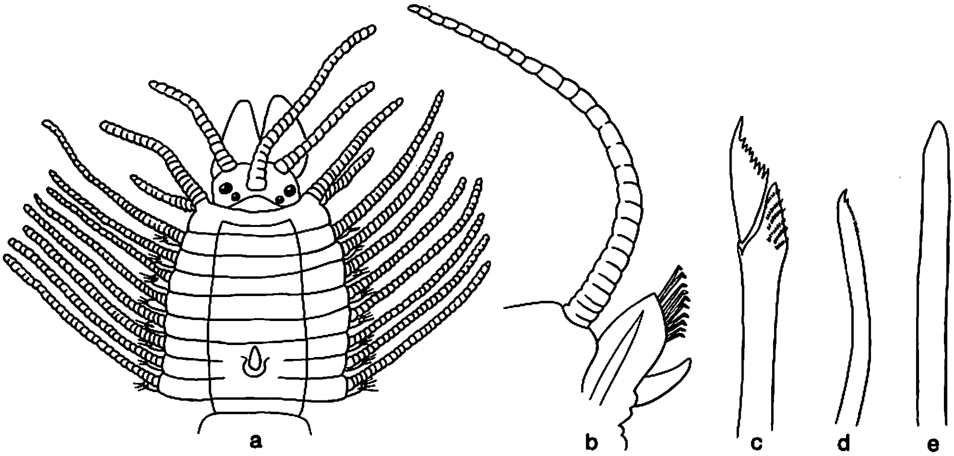

Figure 3.II.49.—*Opisthosyllis brunnea*: a, anterior region; b, parapodium with long articulated dorsal cirrus; c, compound seta with serrated blade; d, simple bifid seta; e, acicular seta. (After Imajima 1966.)

are digitate and as long as the setigerous lobes (Fig. 3.II.49b). Setae are compound with short, unidentate or minutely bidentate, serrated blades (Fig. 3.II.49c). Simple bifid, finely serrate setae are present posteriorly (Fig. 3.II.49d). Acicular setae are blunt (Fig. 3.II.49e). This species has been commonly found budding new individuals posteriorly, with the newly formed antennae and eyes clearly visible. This cosmopolitan species (Day 1967) has been collected intertidally at Halape, Hawaii, and in coral rubble at Kaneohe Bay, Oahu (Hartman 1966).

Opisthosyllis corallicola Hartmann-Schröder, 1965

This species is 1 to 9 mm long, with up to 80 setigers in the largest specimens. Preserved specimens lack pigmentation, except the pharynx is often red. The prostomium bears 4 eyes (Fig. 3.II.50a). The palps are as broad as the prostomium, fused basally, and bent ventrally. The pharynx is 6 to 10 setigers long, with a posterior dorsal tooth, and is followed by the proventriculus, which is 6 to 7 setigers long. The median antenna is 25 articles long and inserted between the posterior pair of eyes. The lateral antennae are composed of 15 articles and are inserted forward of the anterior pair of eyes. There are 2 pairs of tentacular cirri with 12 to 16 articles. The dorsal cirri have 15 to 25 articles. Ventral cirri are digitate and much shorter than the setigerous lobes (Fig. 3.II.50b). The compound setae are unidentate with short, deeply serrated blades (Figs. 3.II.50c,d). Simple superior, serrated setae (Fig. 3.II.50e) occur anteriorly; posteriorly the simple setae are inferior and not serrated. Acicula are bluntly tapered (Fig. 3.II.50f). This species is known from the Galapagos Islands (Westheide 1974) and is commonly found intertidally in algal mats in Hawaii. Specimens have been collected from

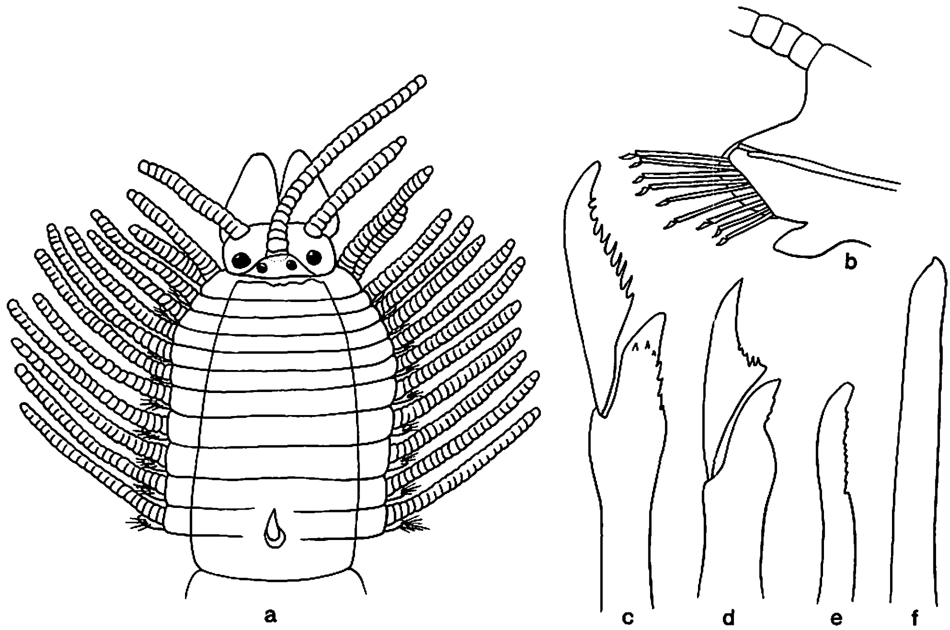

Figure 3.II.50.—*Opisthosyllis corallicola*: a, anterior region; b, parapodium; c,d, compound setae; e, simple, serrated seta from an anterior setiger; f, aciculum. (After Hartmann-Schröder 1965.)

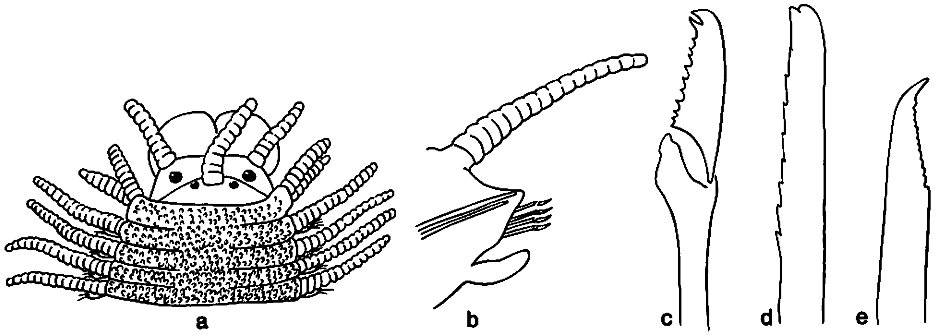

Figure 3.II.51.—*Opisthosyllis papillosa*: a, anterior region with papillate dorsum; b, parapodium; c, compound seta with bifid tip; d, inferior simple seta; e, superior simple seta. (c,d,e after Hartmann-Schröder 1965.)

Kailua Bay, Kaneohe Bay, and Kewalo, Oahu (Hartmann-Schröder 1965; Hartman 1966).

Opisthosyllis papillosa Hartmann-Schröder, 1960

The length of this species is 6 mm, with 54 segments in the largest specimens. Preserved specimens lack pigmentation. The prostomium is broad and has 2 pairs of red eyes and an occipital flap (Fig. 3.II.51a). The palps are short and bent ventrally. The dorsum is thickly covered with small papillae. The pharynx is 7 to 8 setigers long with a posterior dorsal tooth, and the proventriculus is approximately 7 setigers long with 30 rows of points. The median antenna is inserted between the posterior pair of eyes, and the lateral antennae are inserted on the anterior margin of the prostomium. All antennae have 6 to 9 articles. Tentacular and dorsal cirri have 8 to 15 articles. Ventral cirri are digitate and as long as the setigerous lobes (Fig. 3.II.51b). The compound setae are bifid, and both inferior and superior simple setae are present (Figs. 3.II.51c,d,e). This species is known from the Red Sea and from the intertidal zone, in and among rocks and algae, at Waimea Bay, Oahu, and Paia, Maui (Hartmann-Schröder 1965; Hartman 1966).

Parasphaerosyllis indica Monro, 1937

These worms are usually 3 to 5 mm long, but individuals of 18 mm having 90 setigers have been collected in Hawaii. In preserved specimens, the pharynx is usually reddish brown, but the body wall lacks pigmentation. The prostomium has 4 small red eyes. The median antenna has 45 to 50 articles and is inserted between the anterior pair (Fig. 3.II.52a). The lateral antennae have 22 to 24 articles. The palps are separate and rounded. The pharynx is up to 6 setigers long and has a single anterior dorsal tooth. The proventriculus is 4 setigers long, with approximately 30 rows of points. Antennae and tentacular and dorsal cirri are slender and tapered with many articles. The dorsal tentacular cirri have 40 to 44 articles and the ventral tentacular cirri have 18 to 21. The dorsal cirri of the 1st setiger have 55 to 60 articles, after which the cirri are alternately short and long, with 25 and approximately 40 articles, respectively. At the midbody the dorsal cirri begin to regularly alternate between slender articulated cirri, with approximately 30

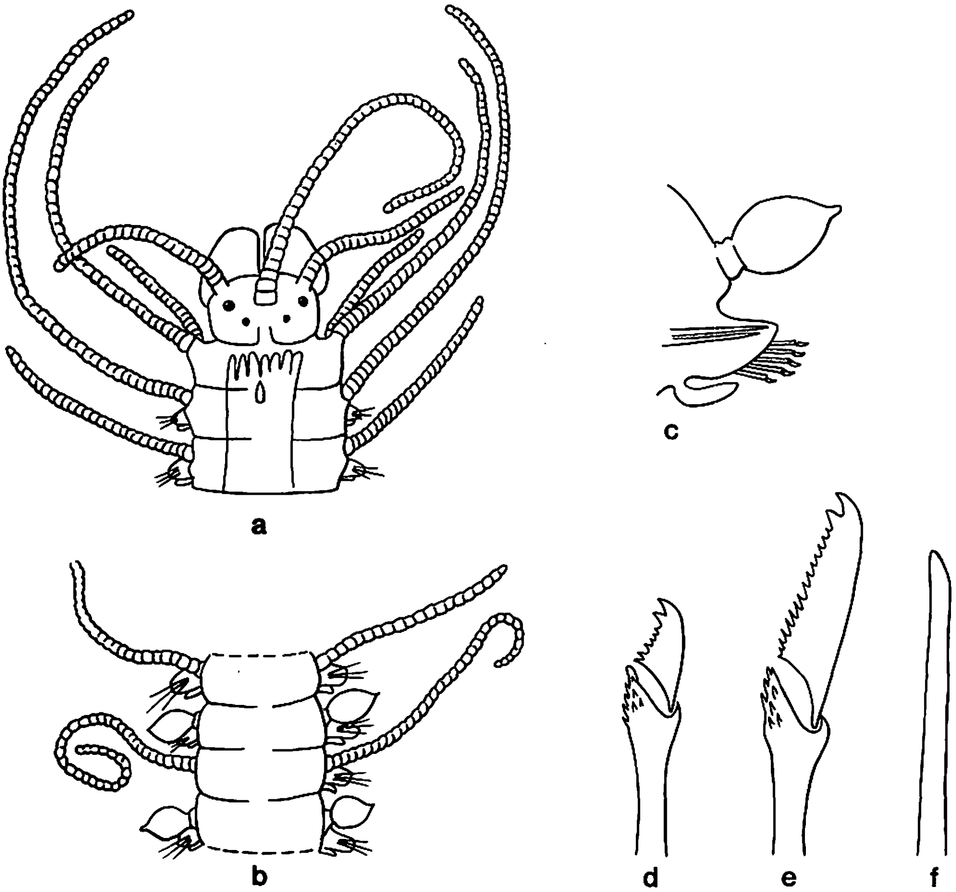

Figure 3.II.52.—*Parasphaerosyllis indica*: a, anterior region; b, dorsal view of midbody setigers showing 2 forms of dorsal cirrus; c, parapodium with short, non-articulated dorsal cirrus; d,e, compound bifid setae with serrated blades; f, tapered aciculum.

articles, and short, bulbous, nonarticulated cirri (Fig. 3.II.52b). The ventral cirri are short and thick (Fig. 3.II.52c). Setae are compound with bifid blades and serrated edges (Figs. 3.II.52d,e). The acicula are tapered (Fig. 3.II.52f). This circumtropical species (Westheide 1974) has been found commonly in algal mats, coral rubble, and on settling plates in Kaneohe Bay, Oahu, and Paia, Maui (Hartmann-Schröder 1965).

Pionosyllis sp.

This species is 2 to 3 mm long, with up to 22 setigers in the largest specimens. Preserved specimens lack pigmentation. The prostomium has 2 pairs of eyes with lenses (Fig. 3.II.53a). Palps are broad, short, fused basally, and bent ventrally. The pharynx is 2 setigers long and has an anterior dorsal tooth. The proventriculus is 3 to 4 setigers long and barrel-shaped. Antennae, tentacular cirri, and dorsal cirri are long and smooth. The antennae are inserted on the anterior margin of the prostomium. There are 2 pairs of tentacular cirri. Digitate ventral

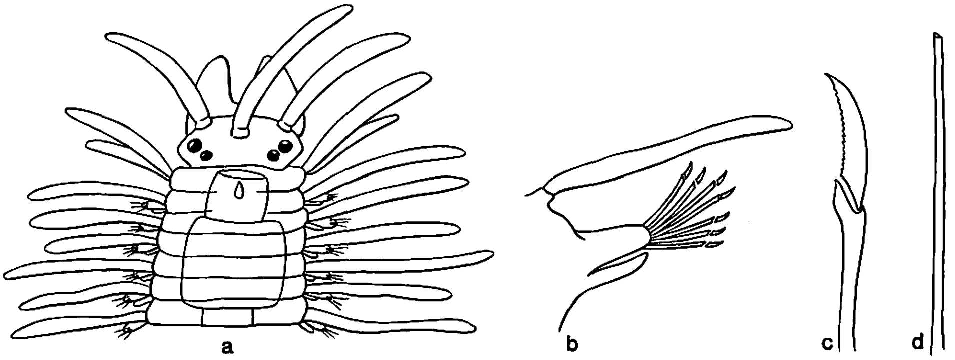

Figure 3.II.53.—*Pionosyllis* sp.: a, anterior region with long, smooth cirri; b, parapodium; c, compound seta; d, simple seta from most posterior setiger.

cirri extend as far as the setigerous lobes (Fig. 3.II.53b). There are 7 to 9 compound setae per parapodium (Fig. 3.II.53c), and a simple seta is present in the last posterior setiger (Fig. 3.II.53d). Specimens have been collected at Barbers Point, Oahu.

KEY TO HAWAIIAN *SPHAEROSYLLIS* SPECIES

1 Dorsum lacks papillae .... *S. sublaevis*
Dorsum papillate 2
2(1) Dorsum lightly papillate; 2 pairs of large, partially coalesced eyes; simple seta present from setiger 1 .... *S. capensis serrata*
Dorsum covered with small, uniformly dispersed papillae; 3 pairs of small, separated eyes; simple seta present from setiger 4 .... *S. centroamericana*

Sphaerosyllis capensis serrata Hartmann-Schröder, 1960

This syllid is 1 to 2 mm long, with up to 20 setigers in the largest specimens. Preserved specimens lack pigmentation. The prostomium has 2 pairs of large, partially coalesced eyes (Fig. 3.II.54a). The palps are fused. The dorsum is lightly papillate. The pharynx is 2 setigers long and has a small anterior dorsal tooth. The proventriculus is barrel-shaped and 2 setigers long with 12 rows of points. Antennae, tentacular cirri (a single pair), and dorsal cirri are all small and pear-shaped. Setiger 2 lacks dorsal cirri. Ventral cirri are digitate and as long as the setigerous lobes (Fig. 3.II.54b). The compound setae are unidentate and serrated, with straight to hooked blades (Fig. 3.II.54c). A simple superior seta is present from setiger 1 (Fig. 3.II.54d). There is a simple inferior seta posteriorly. This Indo-West Pacific subspecies has been collected from Barbers Point and Kaneohe Bay, Oahu (Hartmann-Schröder 1965, 1978; Hartman 1966).

Sphaerosyllis centroamericana Hartmann-Schröder, 1959

The length of this worm is 1 to 2 mm, with up to 25 setigers in the largest specimens. Preserved specimens lack pigmentation. The prostomium has 3 pairs

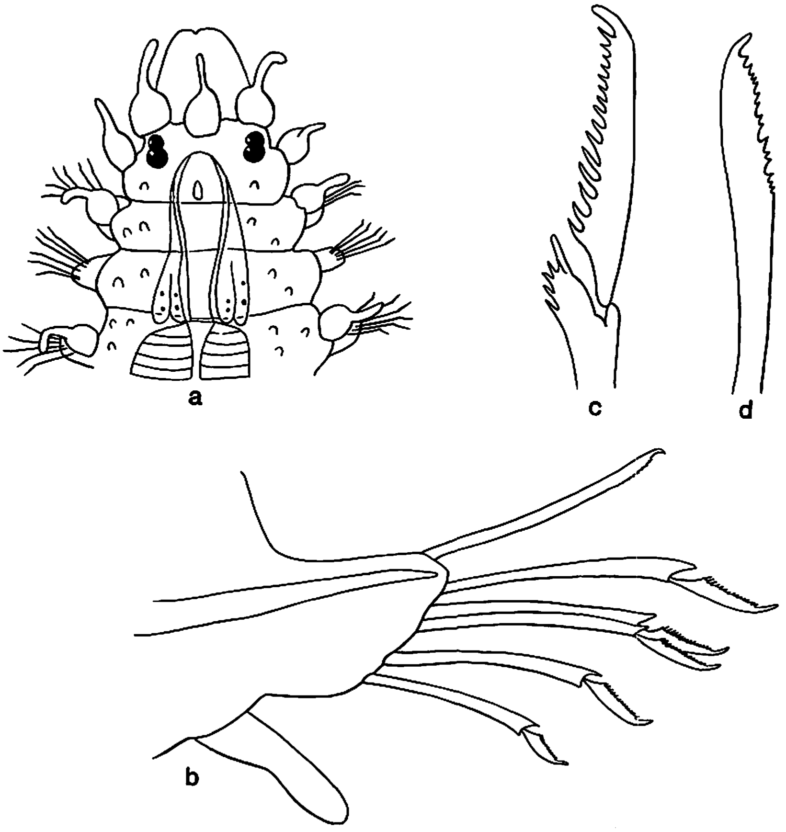

Figure 3.II.54.—*Sphaerosyllis capensis serrata*: a, anterior region; b, parapodium of setiger 2; c, compound unidentate serrated seta; d, simple superior seta. (After Hartmann-Schröder 1960.)

of eyes and 3 anteriorly inserted, pear-shaped antennae (Fig. 3.II.55a). The dorsum is covered with small, uniformly dispersed papillae. The pharynx is 3 to 4 setigers long, with an anterior dorsal tooth. The proventriculus is barrel-shaped, 2 setigers long, and has 10 rows of points. There is a single pair of tentacular cirri and the dorsal cirri are present on all but the 2nd setiger. The length of the dorsal cirri increases posteriorly. The ventral cirri are digitate. Compound setae are unidentate with a serrated edge, and a simple superior seta is present from setiger 4 (Figs. 3.II.55b,c). This cosmopolitan species (Westheide 1974) has been collected from algal turf in Hanauma Bay, Oahu (Hartmann-Schröder 1965; Hartman 1966).

Sphaerosyllis sublaevis Ehlers, 1913

This species is 1 mm long, with up to 40 setigers in the largest specimens. Pigmentation is lacking in preserved specimens. The prostomium has 2 pairs of eyes and a pair of ocular specks (Fig. 3.II.56a). The palps are fused for most of their length. The pharynx is 3 setigers long, with an anterior dorsal tooth; the proventriculus is 2 to 3 setigers long and has 17 rows of points. Antennae, tentacular cirri (a single pair), and dorsal cirri are pear-shaped. Dorsal cirri are lacking on setiger 2. Ventral cirri are conical and not as long as the setigerous

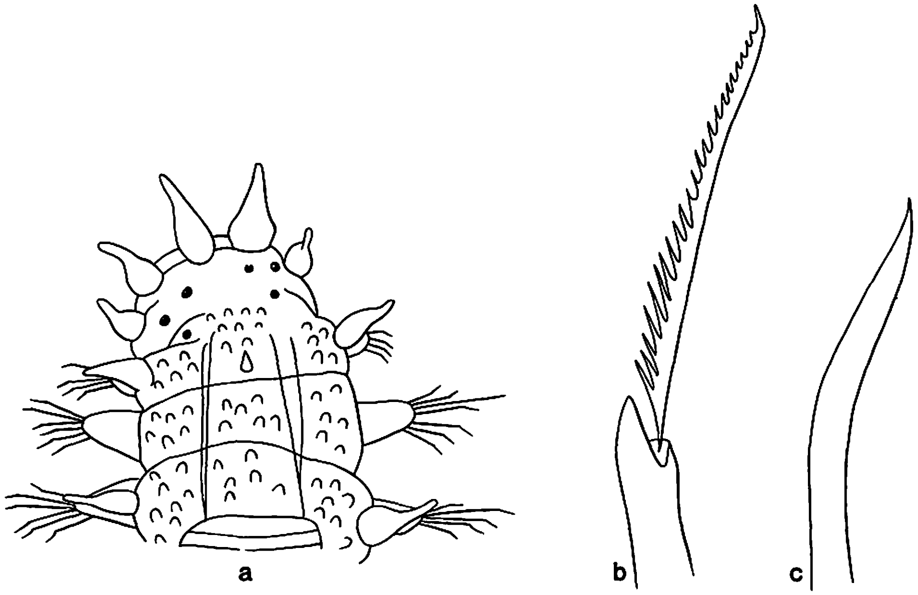

Figure 3.II.55.—*Sphaerosyllis centroamericana*: a, anterior region; b, compound seta with unidentate serrated blade; c, simple superior seta. (a after Hartmann-Schröder 1959.)

lobes (Fig. 3.II.56b). Compound setae are unidentate with a serrated edge (Figs. 3.II.56c,d), and a simple superior seta (Fig. 3.II.56e) is present in all setigers. This species has been collected from South Africa, Chile (Day 1967), Enewetak (Bailey-Brock et al. 1980), and Hawaii. In Hawaii it was collected from Barbers Point, Oahu.

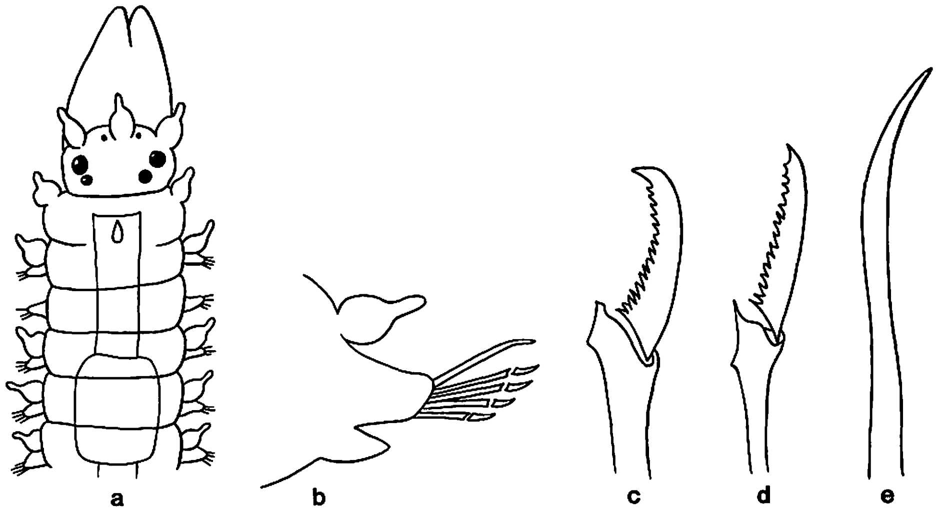

Figure 3.II.56.—*Sphaerosyllis sublaevis*: a, anterior region; b, parapodium; c,d, compound setae with serrated blades; e, simple superior seta.

KEY TO HAWAIIAN *TRYPANOSYLLIS* SPECIES

Prostomium square; anterior segments narrow; body wide and conspicuously depressed; 2 red lines per segment anteriorly .... *T. zebra*

Prostomium heart-shaped and medially indented; anterior segments not narrow; body of normal width and not conspicuously depressed; 1 red line per segment anteriorly .... *T. hawaiiensis*

Trypanosyllis hawaiiensis Hartmann-Schröder, 1978

These worms are 15 to 18 mm long, with up to 126 setigers in the largest specimens. Preserved specimens have faint red-brown bands anteriorly on the dorsum that become progressively darker posteriorly and end at approximately setiger 30. The prostomium is indented medially and has 4 large eyes with lenses (Fig. 3.II.57a). The palps are separate, longer than the prostomium, and project forward. The pharynx is up to 14 setigers long and has a large anterior dorsal tooth and a trepan of 10 to 12 smaller teeth. A long, slender proventriculus up to 11 setigers long is present. Antennae, tentacular cirri, and dorsal cirri may be clearly articulated, or more commonly, weakly or irregularly articulated (Figs. 3.II.57a,b). The ventral cirri are digitate and extend beyond the setigerous lobes (Fig. 3.II.57b). The setae are compound and bidentate, with medium-length serrated blades anteriorly (Fig. 3.II.57c) and a short blade with separated teeth posteriorly (Fig. 3.II.5d). The shaft head is spinous. This species has been collected from Kaneohe Bay and Waikiki, Oahu, and from Kahului, Maui. No other records are known.

Trypanosyllis zebra Grube, 1860

Y The length of the largest specimens collected in Hawaii is up to 2 cm, with 153 setigers. Pigmentation in preserved specimens consisted of a pair of red bands per segment anteriorly. The prostomium is small and square, bearing 4 large eyes (Fig. 3.II.58a). Antennae are inserted anteriorly, the median antenna having 18 articles and the laterals 10. The pharynx is 12 setigers long and has a single large anterior dorsal tooth and a trepan of 10 teeth. The proventriculus is 10 to 11

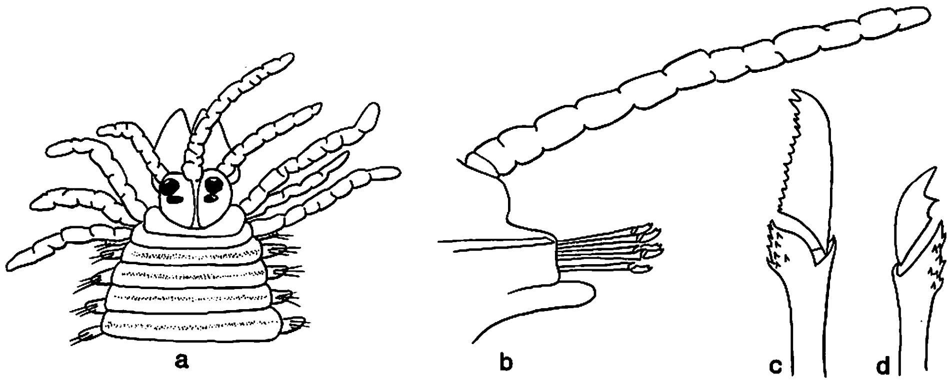

Figure 3.II.57.—*Trypanosyllis hawaiiensis*: a, anterior region; b, parapodium with weakly articulated dorsal cirrus; c, compound seta from an anterior setiger; d, compound seta from a posterior setiger. (After Hartmann-Schröder 1978.)

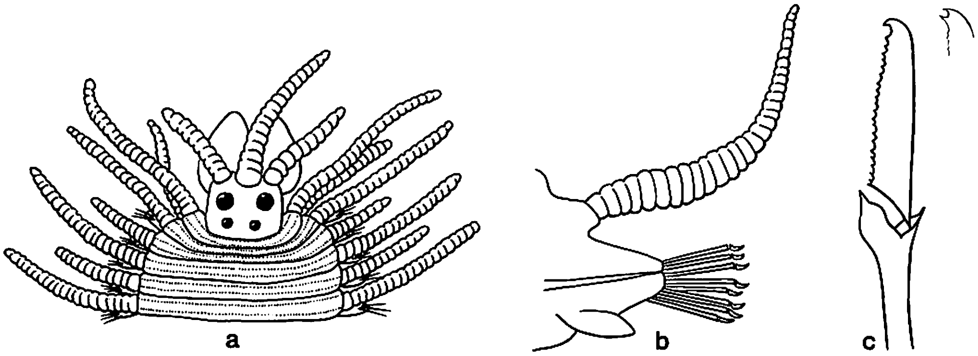

Figure 3.II.58.—*Trypanosyllis zebra*: a, anterior region; b, parapodium; c, bifid compound seta with hooked distal tooth. (After Fauvel 1923.)

setigers long, with 30 rows of points. Tentacular cirri are 15 and 23 articles long. Dorsal cirri alternate with 18 to 20 and 9 to 13 articles. The ventral cirri are digitate and not as long as the setigerous lobes (Fig. 3.II.58b). The compound setae are bifid, with a hooked distal tooth (Fig. 3.II.58c). This cosmopolitan species has been collected from Kaneohe Bay, Oahu, and Halape, Hawaii (Hartman 1966).

KEY TO HAWAIIAN *TYPOSYLLIS* SPECIES

1 Dorsum papillate .... *T. microoculata*
Dorsum smooth 2
2(1) Some or all compound setae unidentate 3
All compound setae distally bifid 4
3(2) All compound setae unidentate; brown band on prostomium .... *Typosyllis* sp. B
Compound setae unidentate anteriorly and minutely bifid posteriorly; no brown band on prostomium; dorsum with brown spots in live specimens .... *T. crassicirrata*
4(2) Dorsal cirri with 7 to 10 articles 8
Many dorsal cirri with more than 10 articles 5
5(4) Anterior segments not clearly defined; dorsal cirri alternate in length between 13 to 16 and 7 to 10 articles .... *T. hawaiiensis*
Anterior segments clearly defined; dorsal cirri otherwise 6
6(5) Dorsum and prostomium dark brown, with a pale bar across peristomium .... *T. ornata*
Dorsum pale with dark bars or bands, or lacking pigmentation 7
7(6) Dorsum colorless or with a pattern of broken brown bars; all dorsal cirri with 30 to 45 articles; pharynx up to 12 setigers long and proventriculus 9 to 16 setigers long .... *T. variegata*
Dorsum colorless or with a pattern of 2 continuous brown-to-purple stripes across each anterior segment; dorsal cirri alternate in length between 20 to 25 and 27 to 30 articles; pharynx 8 to 9 setigers long and proventriculus 4 to 5 setigers long .... *T. prolifera*

8(4) Pharynx 8 setigers long without purple band posteriorly; proventriculus 9 to 12 setigers long, not barrel-shaped .... *T. hyalina*

Pharynx 3 setigers long with dark purple band posteriorly; proventriculus 3 or 4 setigers long and barrel-shaped .... *Typosyllis* sp. A

Typosyllis crassicirrata Treadwell, 1925

[syn. *Typosyllis (T.) magnapalpa* Hartmann-Schröder, 1965. *Typosyllis magnapalpa*: Hartman 1966]

The length of this worm is up to 20 mm, with 77 setigers in the largest specimens. The dorsum has brown spots in life; preserved specimens lack pigmentation. The prostomium is broad and has 4 eyes (Fig. 3.II.59a). The palps are broad, long, and project forward. The pharynx is up to 13 setigers long, with an anterior dorsal tooth. There are 34 rows of points in the proventriculus, which is 5 to 6 setigers long. Antennae have 19 to 22 articles and the median antenna is inserted posterior to the laterals. Tentacular cirri have 15 to 17 articles. Dorsal cirri alternate between 18 to 20 and 35 to 40 articles, but some large specimens may have up to 70 articles in the longest dorsal cirri. Ventral cirri are digitate and do not extend as far as the setigerous lobes (Fig. 3.II.59b). Compound setae have bifid serrated blades (Figs. 3.II.59c,d). The acicula are tapered (Fig. 3.II.59e). This species has been collected intertidally at Laysan Island; Kewalo, Oahu; Halape, Hawaii; and Kahului, Maui (Hartmann-Schröder 1978).

Typosyllis hawaiiensis Hartmann-Schröder, 1965

[syn. *Typosyllis (T.) luteoides hawaiiensis* Hartmann-Schröder, 1965. *Typosyllis luteoides hawaiiensis*: Hartman, 1966]

The length of this species is 2.8 mm, with up to 36 setigers in the largest specimens. Preserved specimens lack pigmentation. The prostomium is narrow and has 2 pairs of reddish brown eyes (Fig. 3.II.60a). The palps are short and bent ventrally. The pharynx is 5 setigers long, with an anterior dorsal tooth; the proventriculus is 3 to 5 setigers long, with 28 rows of points. The tentacular segment is short and anterior segments are not clearly defined. The antennae have 10 to 12 articles and the tentacular cirri have 8 to 12 articles. Dorsal cirri alternate

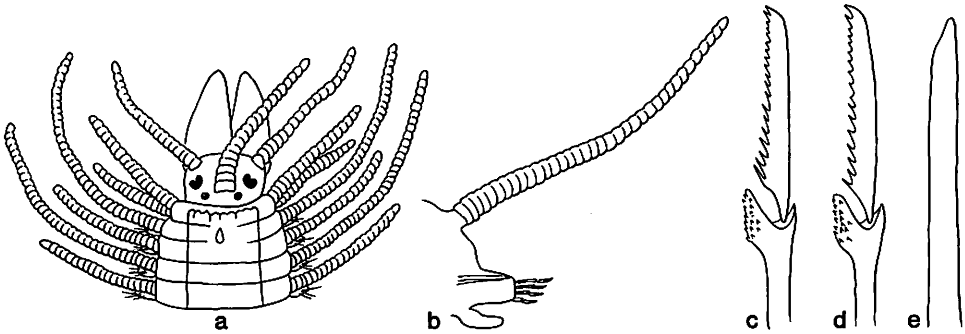

Figure 3.II.59.—*Typosyllis crassicirrata*: a, anterior region; b, parapodium with long, articulated dorsal cirrus; c,d, compound setae; e, aciculum. (After Treadwell 1925.)

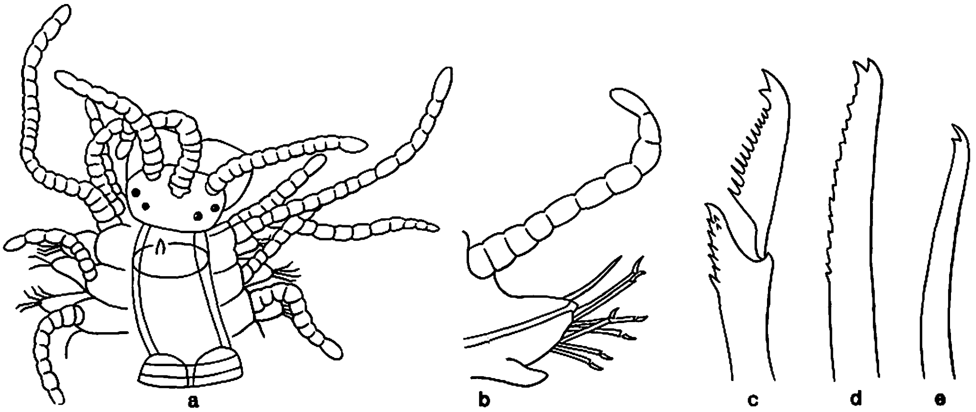

Figure 3.II.60.—*Typosyllis hawaiiensis*: a, anterior region; b, parapodium; c, bifid compound seta with serrated blade; d,e, simple setae of posterior setigers. (After Hartmann-Schröder 1965.)

between 13 to 16 and 7 to 10 articles. Ventral cirri are short and digitate (Fig. 3.II.60b). The compound setae are bifid and serrated, with a spinous shaft head (Fig. 3.II.60c). Superior and inferior simple bifid setae are present posteriorly (Figs. 3.II.60d,e). This species has been collected from settling plates and sediment at Barbers Point and Kaneohe Bay, Oahu; Hilo, Hawaii; and Kauai (Hartman 1966).

35 mm (Day 1967) long & slender

Typosyllis hyalina (Grube, 1863)
[syn. *Typosyllis* (*T.*) *hyalina*: Hartmann-Schröder 1965]

This species is up to 9 mm long with 70 to 80 setigers in the largest specimens. Some specimens have brown bands anteriorly, but many preserved individuals lack pigmentation. The prostomium is hemispherical with 2 pairs of eyes (Fig. 3.II.61a) and sometimes 2 ocular specks. The median antenna has 10 to 13 articles and originates between the posterior pair of eyes. The lateral antennae are anterior with 8 to 10 articles. The palps are long, not fused, and taper

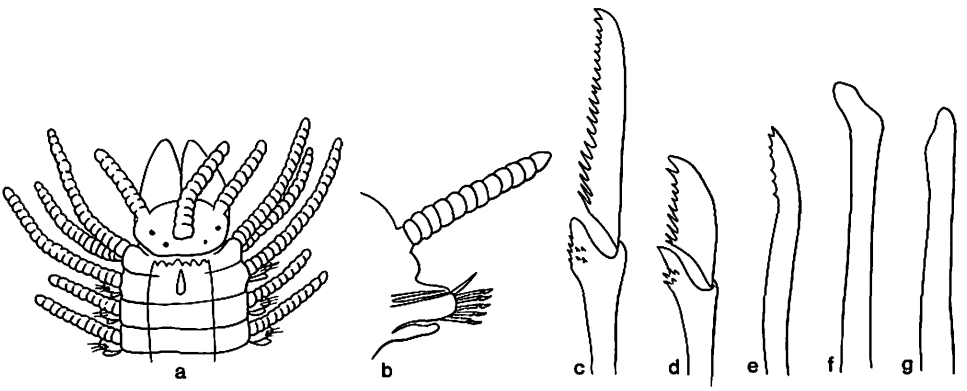

Figure 3.II.61.—*Typosyllis hyalina*: a, anterior region; b, parapodium; c,d, bifid compound setae; e, simple superior seta from posterior setigers; f,g, acicula. (After Imajima 1966.)

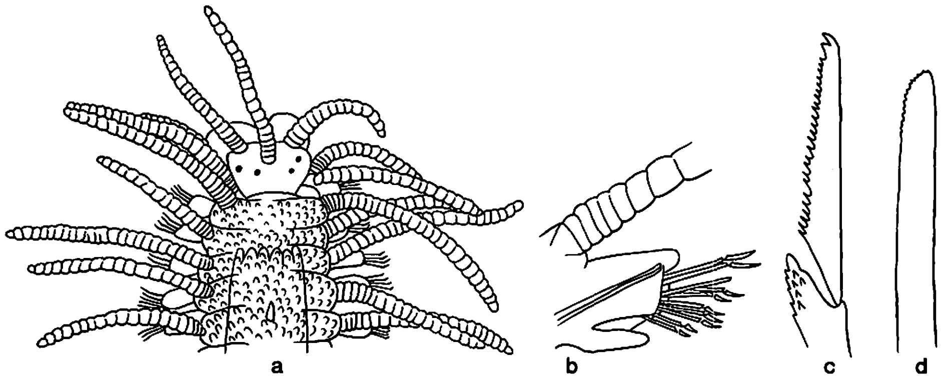

Figure 3.II.62.—*Typosyllis microoculata*: a, anterior region; b, parapodium; c, bifid compound seta with serrated blade; d, simple seta from posterior setiger. (After Hartmann-Schröder 1965.)

anteriorly. The pharynx is long, with a single anterior dorsal tooth; the margin is circled with 10 soft papillae. The proventriculus is 9 to 12 setigers long, with 30 to 40 rows of points. There are 2 pairs of tentacular cirri, each with 15 to 17 articles. The lst pair of dorsal cirri, longer than the rest, has 19 articles. Posteriorly the dorsal cirri irregularly alternate, with some cirri having 7 to 8 articles and others 9 to 12. The ventral digitate cirri may extend slightly beyond the setigerous lobe, which is quite blunt (Fig. 3.II.61b). There are approximately 10 bifid compound setae per parapodium (Figs. 3.II.61c,d) and a superior simple seta posteriorly (Fig. 3.II.61e). The acicula are tapered or knobbed (Figs. 3.II.61f,g). This cosmopolitan species (Westheide 1974) has been found in algae, coral rubble, sand, and on settling plates in Hawaii. Specimens have been collected from many sites in Kaneohe Bay and from Kewalo, Oahu; Paia, Maui; and Kauai (Hartmann-Schröder 1965; Hartman 1966).

Typosyllis microoculata Hartmann-Schröder, 1965
[syn. *Typosyllis* (*T.*) *microoculata* Hartmann-Schröder, 1965]

This worm is 7 mm long, with 40 segments; there is sometimes an additional short stolon bud. The anterior segments are pale or banded with red-brown bars. The prostomium has 2 pairs of small eyes and the antennae, with 18 to 20 articles, are inserted anteriorly (Fig. 3.II.62a). The dorsum is thickly covered with small papillae. The pharynx extends 8 setigers and has 22 rows of points. The palps are short and bent ventrally. Dorsal and tentacular cirri have 20 to 26 articles. The dorsal cirri may have brown markings, especially anteriorly. The ventral cirri are digitate and extend as far as the setigerous lobe (Fig. 3.II.62b). The setae are compound with bifid serrated blades (Fig. 3.II.62c). Posteriorly there is a superior and an inferior simple seta (Fig. 3.II.62d). This species has been found in algal mats at Paia, Maui; Kailua, Hawaii; Kahana Bay, Oahu; and Kauai (Hartman 1966).

Typosyllis ornata Hartmann-Schröder, 1965
[syn. *Typosyllis* (*T.*) *ornata* Hartmann-Schröder, 1965]

This syllid is 3.3 mm long, with 52 setigers in the largest specimens. The anterior dorsum is dark brown or transversely striped, and the peristomium is

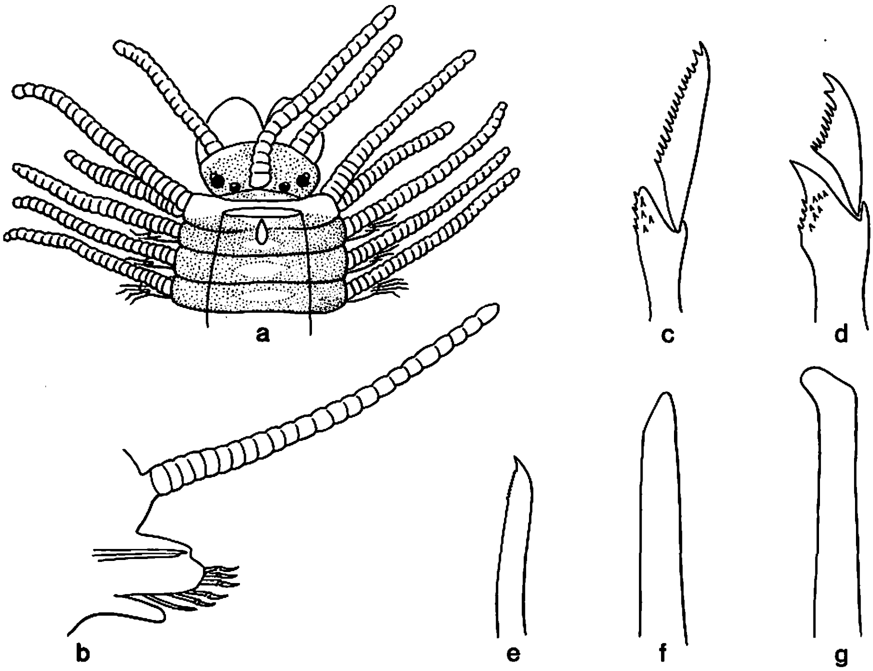

Figure 3.II.63.—*Typosyllis ornata*: a, anterior region; b, parapodium with long, articulated dorsal cirrus; c,d, bifid compound setae with serrated blades; e, simple inferior seta from a posterior setiger; f,g, acicula. (After Hartmann-Schröder 1965.)

pale. The prostomium has 2 pairs of reddish brown eyes (Fig. 3.II.63a). The median antenna is inserted between the posterior pair of eyes, and the lateral antennae are inserted anteriorly. The palps are short and bent ventrally. The pharynx is 6 to 7 setigers long, with an anterior dorsal tooth; the proventriculus is 7 setigers long, with 25 rows of points. Tentacular and dorsal cirri are 13 to 26 articles long. Ventral cirri are digitate and do not extend as far as the setigerous lobes (Fig. 3.II.63b). Compound setae are bifid and an inferior simple seta is present posteriorly (Figs. 3.II.63c–e). Acicula are tapered or knobbed (Figs. 3.II.63f,g). This species was described from algal turf at Kailua, Hawaii, and at Hanauma Bay and Kaneohe Bay, Oahu.

Typosyllis prolifera Krohn, 1852 10-25mm (Fauvel 1953)

brown & prostomium

Worms range from 3 to 12 mm long, with up to 40 setigers in the largest specimens. Coloration in life varies from purplish brown to yellow-beige. Two dark lines are present on the anterior segments but these are often lacking in preserved specimens. The prostomium bears 2 pairs of red eyes and 3 antennae; the median antenna has 30 articles and the laterals 15 to 20 (Fig. 3.II.64a). The palps are stout and not fused. The pharynx is 8 to 9 setigers long, with a soft papillate margin and a single anterior dorsal tooth. The proventriculus is 4 to 5 setigers long, with approximately 30 rows of points. There are 2 pairs of tentacular cirri having 30 to 35 articles. The slender dorsal cirri irregularly alternate between 20 to 25 and 27 to 30 articles. The ventral cirri are digitate and as long as the setigerous lobes (Fig. 3.II.64b). Bifid compound setae have the blade length

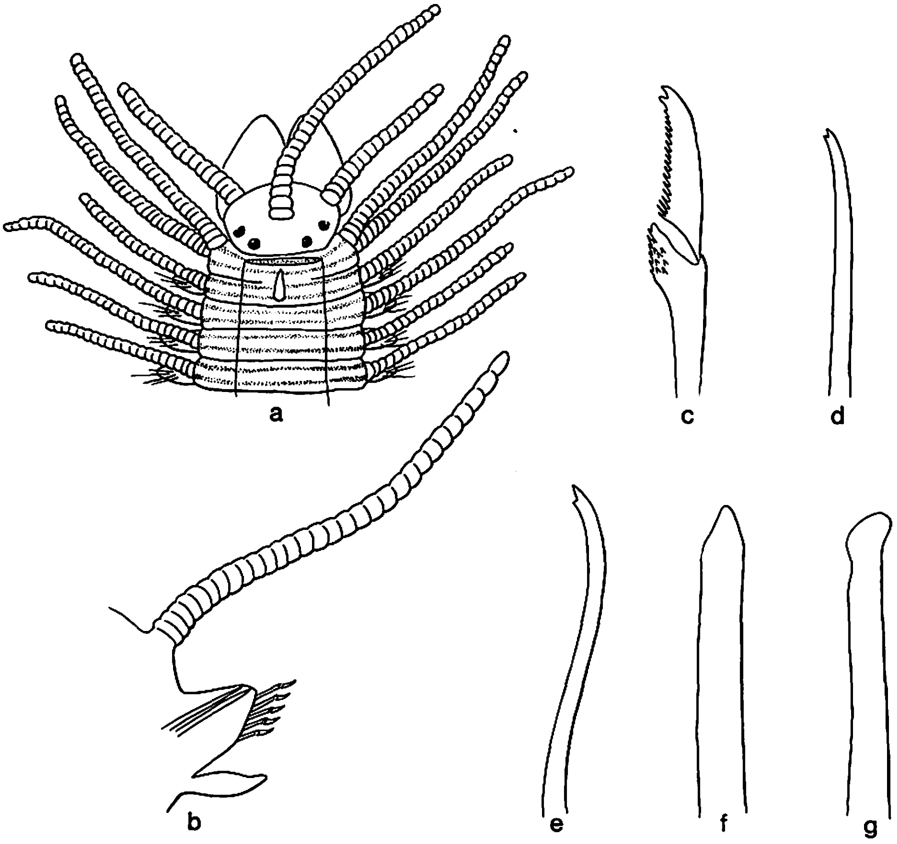

Figure 3.II.64.—*Typosyllis prolifera*: a, anterior region; b, parapodium with long articulated dorsal cirrus; c, compound seta; d,e, superior and inferior simple setae; f,g, acicula.

decreasing posteriorly (Fig. 3.II.64c). A superior bifid simple seta and an inferior simple curved seta with a subdistal tooth are also present (Figs. 3.II.64d,e). There are 3 acicula per parapodium (Figs. 3.II.64f,g). This cosmopolitan species (Day 1967) is commonly found in intertidal algal mats nearshore in Hawaii. It has also been collected from Kaneohe Bay, Kewalo, and Kailua Bay, Oahu.

Typosyllis variegata (Grube, 1860)
[syn. *Typosyllis* (*T.*) *variegata*: Hartmann-Schröder 1965]

This syllid is 2 to 40 mm long, with up to 100 setigers in the largest specimens. Some specimens have a dark brown pattern of broken bars on the anterior dorsum, while others lack this pigmentation. The prostomium has 2 pairs of eyes and 2 ocular specks (Fig. 3.II.65a). The median antenna has 28 to 32 articles and is inserted between the posterior pair of eyes, while the lateral antennae have 18 to 20 articles and are inserted far forward. Palps are long, separated, and project forward. The pharynx is up to 12 setigers long, with a large, sharp anterior dorsal tooth. The proventriculus is 9 to 16 setigers long, with 30 rows of points. There are 2 pairs of tentacular cirri with 26 to 30 articles. Dorsal cirri are long, with 30 to 45 articles in the midbody, decreasing to 15 to 20

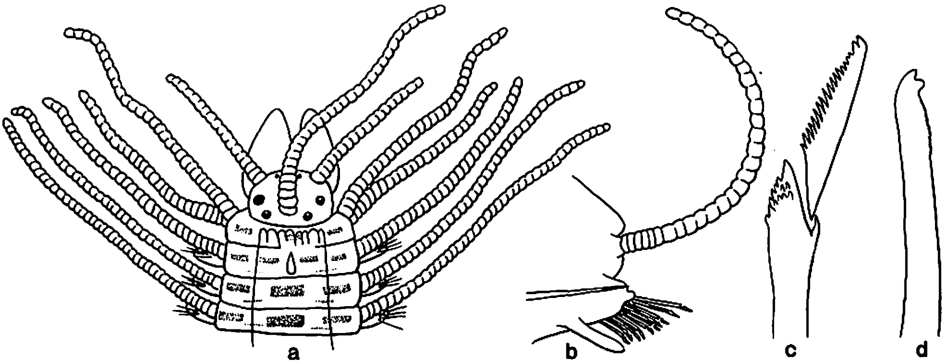

Figure 3.II.65.—*Typosyllis variegata*: a, anterior region; b, parapodium; c, bifid compound seta with serrated blade; d, bifid, simple seta from a posterior setiger. (After Imajima and Hartman 1964.)

posteriorly. Ventral cirri are digitate and as long as, or longer than, the setigerous lobe (Fig. 3.II.65b). There are 6 to 10 bifid compound setae per parapodium (Fig. 3.II.65c). Posteriorly a simple bifid seta is present (Fig. 3.II.65d) and there are 2 acicula per parapodium. This cosmopolitan species (Westheide 1974) is common in algal mats in Hawaii and has been collected at Paia, Maui, and at Kewalo and Kaneohe Bay, Oahu (Hartmann-Schröder 1965).

Typosyllis sp. A

These worms are 3 to 6 mm long, with up to 32 setigers in the largest specimens. Except for the purple band in the pharynx, preserved specimens lack pigmentation. The prostomium has 2 pairs of eyes (Fig. 3.II.66a). The palps are bent ventrally. Antennae and dorsal cirri are composed of 6 to 10 articles. The pharynx is 3 setigers long and has a large anterior dorsal tooth and a dark purple band near the proventriculus. The proventriculus is 3 to 4 setigers long with 15 to 22 rows of points. The ventral cirri are leaf-shaped and extend almost as far as the setigerous lobes (Fig. 3.II.66b). The compound setae are bifid and have a serrated blade; there are 8 to 10 per parapodium (Fig. 3.II.66c). A superior simple seta is

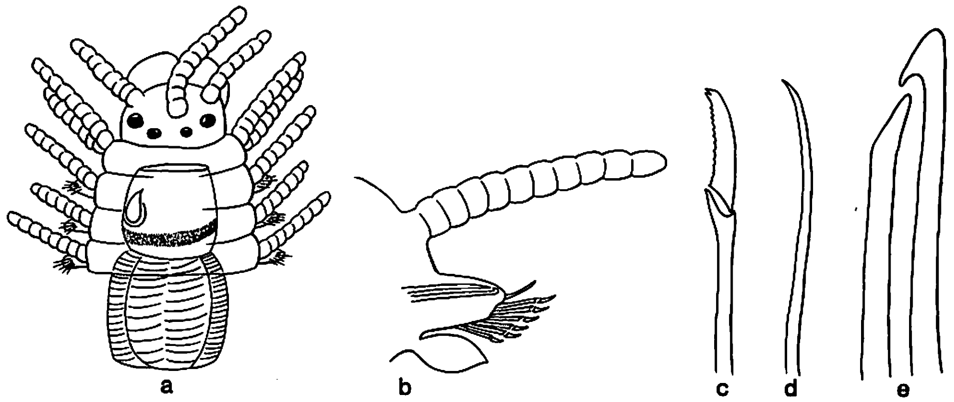

Figure 3.II.66.—*Typosyllis* sp. A: a, anterior region; b, parapodium; c, bifid compound seta with serrated blade; d, superior simple seta; e, interlocking acicula.

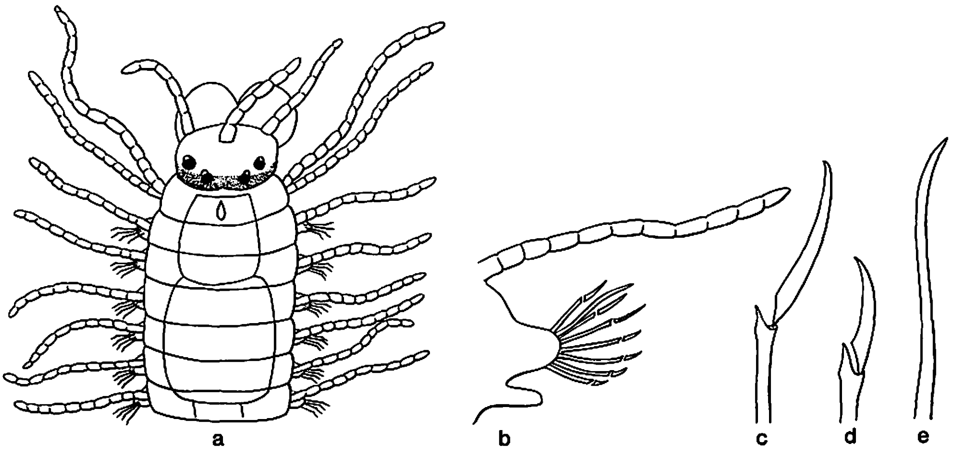

Figure 3.II.67.—*Typosyllis* sp. B: a, anterior region; b, parapodium; c,d, compound setae with curved, unidentate blades; e, simple seta.

present (Fig. 3.II.66d). The acicula are fitted together, one bent over the other (Fig. 3.II.66e). A number of specimens were collected from settling plates at Barbers Point, Oahu.

Typosyllis sp. B

This species is up to 8 mm long, in the largest specimens. A dark band occurs on the prostomium. The prostomium has 2 pairs of eyes with lenses and a brown-to-purple pigmented band that obscures the posterior pair of eyes (Fig. 3.II.67a). Palps are bent ventrally. The dorsum is distinctly arched. The pharynx is 2 setigers long and has a small anterior dorsal tooth. The proventriculus is 3 setigers long. Antennae, tentacular cirri, and dorsal cirri have long, slender articles; the antennae have 5 to 6, the tentacular cirri 15, and the dorsal cirri 10 to 12 articles. Ventral cirri are bluntly conical (Fig. 3.II.67b). Five to 7 compound unidentate setae are present per parapodium (Figs. 3.II.67c,d). The setal blades are very fine and slightly curved; some of the blades are 2 to 3 times longer than others in the same fascicle. A simple unidentate seta is also present (Fig. 3.II.67e). Often the posterior segments are bulbous with gametes. Specimens have been collected commonly from coral rubble and coral settling plates in Kaneohe Bay, Oahu.

Family Nereididae

Nereidids are benthic worms frequently illustrated in textbooks to represent the typical polychaete. They can be found in all types of shallow, coastal habitats in marine and brackish waters around the Hawaiian Islands. The head (Figs. 3.II.68a,b) has a pair of short antennae and a pair of 2-jointed, lobed palps. The proboscis is in 2 parts, a distal maxillary ring bearing the hooklike jaws and smaller paragnaths (teeth), and a proximal oral ring with paragnaths only. The structure and arrangement of chitinous jaws, paragnaths, and soft papillae (nonchitinous paragnaths) on the eversible proboscis (Figs. 3.II.69e,f) are of taxonomic importance. Sometimes the proboscis completely lacks paragnaths. The shape and arrangement of paragnaths on the 2 regions of the proboscis are described by the dental formula in Table 3.II.1, which is illustrated in Figs. 3.II.68a,b.

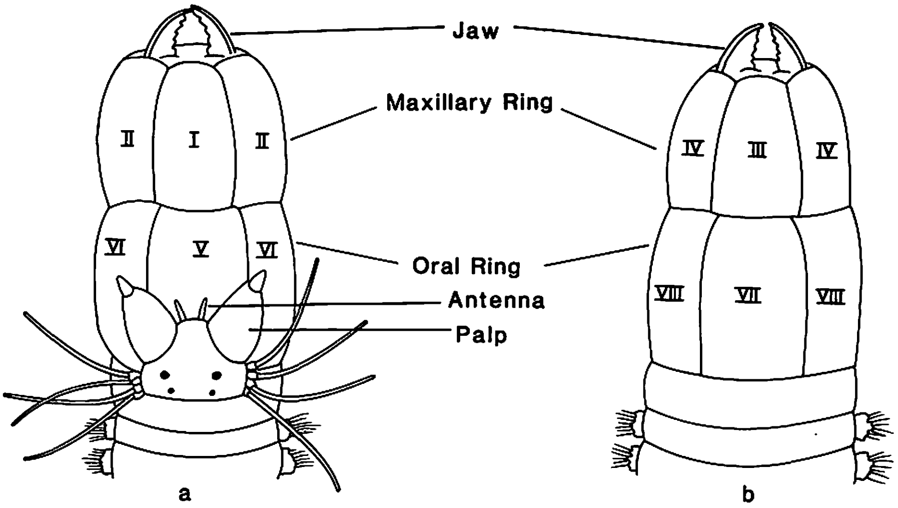

Figure 3.II.68.—Diagrams of head regions of nereidids with extended proboscis: a, dorsal view; b, ventral view. (After Fauchald 1977a.)

The number and shape of the paragnaths on each of these areas are species specific and are used in the key. Paragnaths may be cones, pectinae (combs), or transverse bars. Counts of paragnaths of areas VII and VIII are usually combined, since the boundaries between them are often indistinguishable.

Nereidid feeding strategies are quite varied. Many species are described as omnivores; others are herbivores, feeding on thalloid algae (Brostoff 1985) and benthic diatoms, and *Neanthes succinea* is known to be a surface-deposit feeder (Fauchald and Jumars 1979). The proboscis is used not only for procuring food but also in aggressive behavior. Proboscis extrusion is characteristic of both interspecific and intraspecific agonistic displays associated with territoriality (Evans 1973).

The parapodia are mostly biramous, with dorsal and ventral cirri and either homogomph or heterogomph compound setae with hooked or tapered blades. Some species develop an epitokous stage at the time of sexual reproduction, allowing them to swim to the surface waters for spawning. Epitokes have paddlelike parapodia suitable for swimming and well-developed sense organs,

Table 3.II.1. Shape and arrangemant of paragnaths on the maxillary ring (bears the jaws) and the oral ring (surrounds the mouth) of the proboscis.*

	Area	No. of areas	Location
Maxillary ring	I	1	Median, dorsal
	II	2	Lateral, dorsal
	III	1	Median, ventral
	IV	2	Lateral, ventral
Oral ring	V	1	Median, dorsal
	VI	2	Lateral, dorsal
	VII	1	Median, ventral
	VIII	2	Lateral, ventral

* See Figs. 3.II.68a,b.

which enable them to reach the surface and spawn. The epitokous or "heteronereid" forms are morphologically so different from the benthic individuals that they have been mistakenly identified as different species. The genus *Nereis* includes 7 Hawaiian species described only from epitokous forms—*Nereis abbreviata, N. hawaiiensis, N. mariae, N. myersi, N. nigroaciculata, N. unica,* and *N. waikikiensis*—all described by Holly (1935). The status of these species must still be correlated with benthic "atokous" stages; some may belong to the subgenus *Neanthes,* since they lack notopodial homogomph falcigers (Hartman 1966). One species, *Micronereis bansei*, shows sexual dimorphism (Paxton 1983). The epitokous males have copulatory hooks on the ventral surface of setiger 3; epitokous females have enlarged dorsal cirri with lamellar extensions. *Platynereis tongatabuensis* McIntosh, 1885, is omitted from this revision because the identification is still in doubt. The species was recorded from 2 incomplete specimens, one from French Frigate Shoals and the other from Pearl Harbor, Oahu (Hartman 1966).

KEY TO HAWAIIAN NEREIDID GENERA

1 Prostomium with antennae; pharynx eversible 2
Prostomium without antennae; pharynx not eversible .... *Micronereis*
2(1) Parapodia subbiramous, appearing uniramous (Fig. 3.II.71b) .... *Namalycastis*
Parapodia clearly biramous from the third segment (Figs. 3.II.70b, 84c) 3
3(2) Oral ring of proboscis lacks paragnaths.................... *Ceratonereis*
Oral and maxillary rings of pharynx with paragnaths 4
4(3) Oral and maxillary rings with conical paragnaths only 5
Maxillary ring with conical, pectinate, and/or transverse bar paragnaths; oral ring otherwise 6
5(4) Notosetae are all homogomph spinigers .... *Neanthes*
Notosetae of median and posterior segments include homogomph spinigers and falcigers .... *Nereis*
6(4) Area IV of oral ring with transverse bar or conical paragnaths 7
Pectinate paragnaths on all areas of proboscis except I and V .... *Platynereis*
7(6) Superior notopodial lobe expanded in posterior segments; pectinate bars usually present; notosetae are spinigers and falcigers..... *Pseudonereis*
Superior notopodial lobe not expanded anywhere; pectinate bars absent except on area IV; notosetae are homogomph spinigers .... *Perinereis*

KEY TO HAWAIIAN *CERATONEREIS* SPECIES

1 Notopodia with homogomph falcigers from setigers 15 to 20 .... *C. tentaculata*
Notopodia without homogomph falcigers 2
2(1) Proboscis area III has 5 to 8 cones .... *C. vulgata*
Proboscis area III has 3 to 4 cones .... *C. pietschmanni*

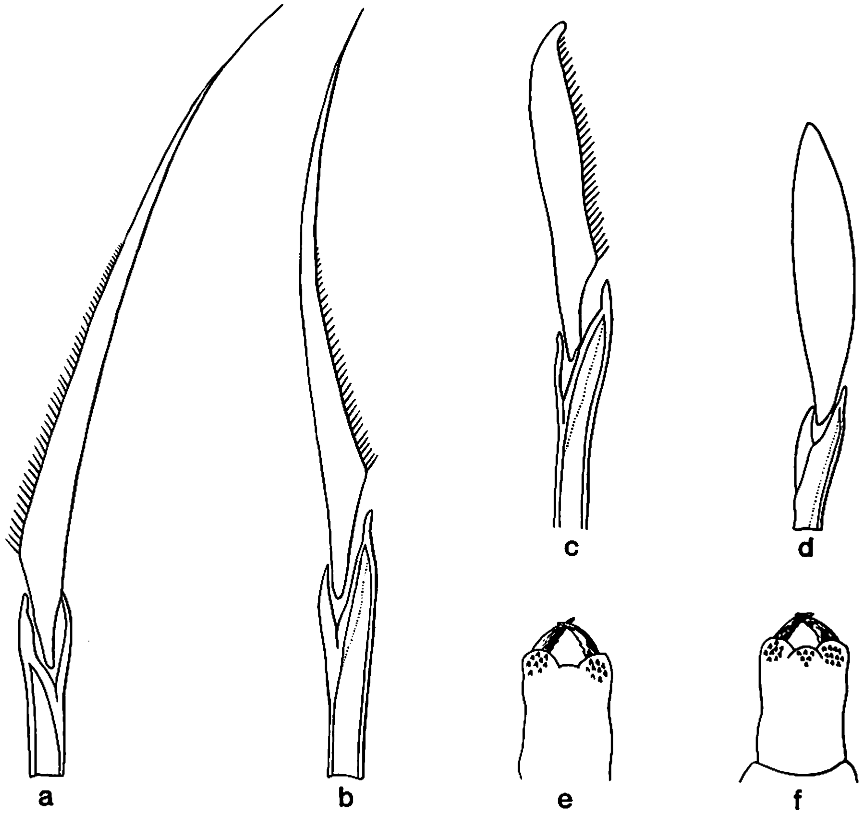

Figure 3.II.69.—*Ceratonereis pietschmanni*: a, homogomph spiniger from an anterior notopodium; b, neuropodial heterogomph spiniger; c, neuropodial heterogomph falciger; d, natatory seta; e, dorsal view of proboscis; f, ventral view of proboscis. (After Holly 1935.)

Ceratonereis pietschmanni Holly, 1935
[syn. *Nereis* (*Ceratonereis*) *pietschmanni*: Holly 1935]

This form is known only from epitokous individuals 6 to 12 mm long. The pre-epitokal region has 16 segments, the epitokal 19 to 26, and the post-epitokal 24 to 31. Anterior notopodia have only homogomph spinigers (Fig. 3.II.69a); neuropodia have heterogomph spinigers (Fig. 3.II.69b) and falcigers (Fig. 3.II. 69c). Epitokous parapodia have special paddles or natatory setae (Fig. 3.II.69d). Proboscis area I is bare, II has 6 to 9 cones, III has 5 to 8 cones, IV has 10 to 12 cones in a patch (Figs. 3.II.69e,f), and each of the jaws is dark brown with 7 or 8 teeth. This pelagic form is known only from the Northwestern Hawaiian Islands (Pearl and Hermes Reef and Lisianski Island).

Ceratonereis tentaculata Kinberg, 1866
[syn. *Ceratonereis mirabilis* Kinberg, 1866: Hartman 1966. ?*Nereis* sp. Treadwell, 1906]

The body length of this nereidid is 12 to 20 mm, the width 2.5 to 3 mm, and segments number 40 or more. The color is usually pale, with the dorsum crossed by dark brown transverse lines. The prostomium (Fig. 3.II.70a) is deeply cleft and has 4 large eyes, a pair of long, cylindrical palps that are directed forward, a pair

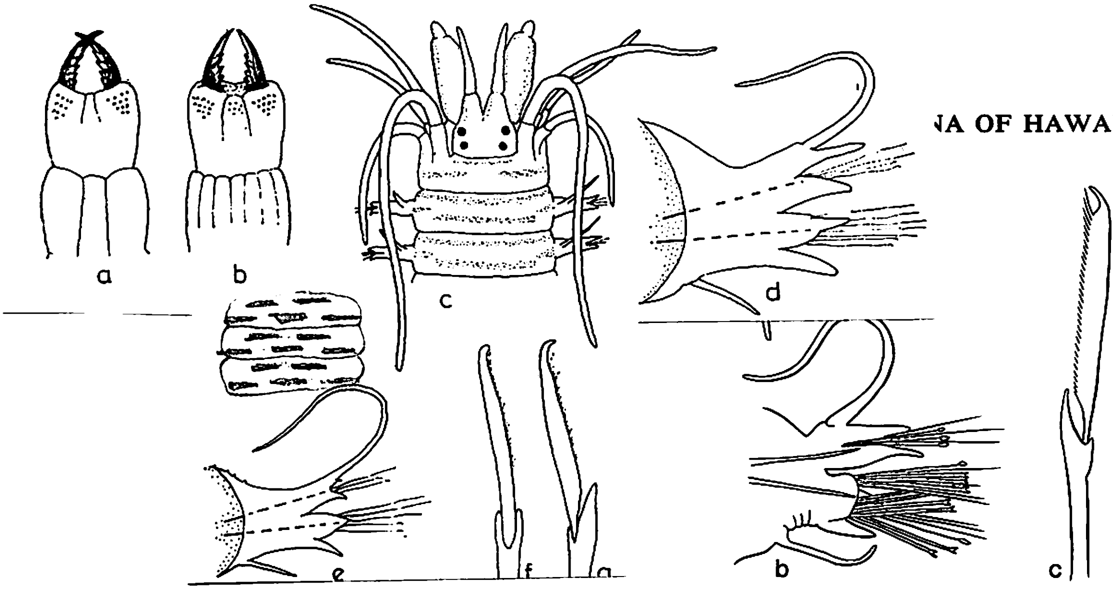

Figure 3.II.70.—*Ceratonereis tentaculata*: a, anterior region; b, parapodium; c, heterogomph composite falciger of a posterior neuropodium. (After Ehlers 1887.)

of slender frontal antennae, and 4 pairs of long tentacular cirri. The eversible proboscis lacks paragnaths on the oral ring; the maxillary ring lacks paragnaths on area I, and there are 8 or 9 conical paragnaths on II, 5 or 6 cones on III, and about 11 cones on IV. The golden brown jaws are translucent, each with about 7 oblique teeth. Parapodia (Fig. 3.II.70b) have long dorsal, middle, and ventral lobes. Posterior notopodia have homogomph composite falcigers. Neuropodia have heterogomph composite falcigers (Fig. 3.II.70c). Large numbers of this species have been collected from Kaneohe Bay and the south shore of Oahu. This Indo-West Pacific species has also been recorded from Japan and western Australia and was until recently confused with *C. mirabilis* (Perkins 1980).

Ceratonereis vulgata Kinberg, 1866

In this species, the length of the body reaches 20 to 30 mm and the prostomium is pale with 4 dark eyes. Parapodial lobes are long and triangular. Notopodia have only composite spinigers, and neuropodia have spinigers and falcigers. Proboscis area I lacks cones, II has 4 to 6 cones, III has 3 to 4 cones, and IV has about 6 cones. This species is known only questionably from Honolulu (entered in ship's log as Brazil), having been collected only once more than 100 years ago (Hartman 1966).

Micronereis bansei (Hartmann-Schröder, 1979)
[syn. *Quadricirra bansei* Hartmann-Schröder, 1979]

The length of male specimens examined reached 2.1 mm × 0.30 mm in width with up to 17 setigers. Female length reached 2.1 mm and width 0.34 mm with up to 18 setigers. The body color, after preservation in formalin and storage in alcohol, is creamy white with a slight brown tinge, especially concentrated in the parapodial lobes. In all specimens, the midventral surface had 2 creamy white longitudinal stripes running parallel from the 1st setiger to the pygidium. The prostomium is broadly rounded, longer than wide with a pair of small palps, lacking palpostyles, at the anterior margin. Two pairs of lensed eyes are present, usually arranged in a trapezoid. The anterior pair of eyes is larger and more widely spaced than the posterior pair. The 2 pairs are sometimes arranged in a linear fashion. (May be correlated with epitokous condition.) Four pairs of tentacular cirri are present on the peristomium. The anterior 2 pairs inserted just dorsolateral to the anterior pair of eyes. The 2nd pair of tentacular cirri is inserted laterally just beneath the prostomium. A bulbous pharynx with a pair of jaws extends through the 1st 4 setigers. The jaws do not show sexual dimorphism as in some species of this genus. They are triangular in shape with 4 teeth along the cutting edge. The parapodia of setigers 1 and 2 are uniramous, possessing the neuropodium only, and directed forward. The remaining setigers are biramous, the noto- and neuropodia being roughly rectangular in shape, widely spaced, and each supported by 1 aciculum. The dorsal and ventral cirri extend beyond the parapodial lobes in both male and female. The epitokous males possess accessory cirri on the ventral side of the notopodia and the dorsal side of the neuropodia. Epitokous females possess enlarged dorsal cirri with lamellar extensions and a swollen base. There are 8–10 compound homogomph spinigers with finely serrated blades in both noto- and neuropodia. In epitokous males, compound spinigers and simple fine capillary setae are seen along with these compound spinigers. Two to 3 copulatory hooks, with 4–6 spines present on the head are also seen on the ventral surface of setiger 3 of the males. The pygidium is broadly rounded with 2 lateral anal cirri. This species has been described from Australia from sandy substrates with algae and from dead coral fragments (Paxton 1983). A total of 173 specimens were collected from 21 dead *Porites compressa* coral heads at a depth of 12–15 meters on the seaward edge of a fringing reef at Puako, Hawaii. These specimens agree with Paxton's description in a review of the diagnostic characters of the genus *Micronereis* and subfamily Notophycinae (Paxton 1983).

Namalycastis abiuma (Müller in Grube, 1872)
[syn. *Lycastis hawaiiensis* Johnson, 1903]

An individual with 190 segments may be as long as 105 mm and 3.5 mm wide. The color is flesh pink in life and green in formalin. The prostomium is blunt (Fig. 3.II.71a), medially incised, and has 4 small eyes at the outer posterior edges. The proboscis lacks paragnaths; each of the dark brown jaws has about 10 teeth along

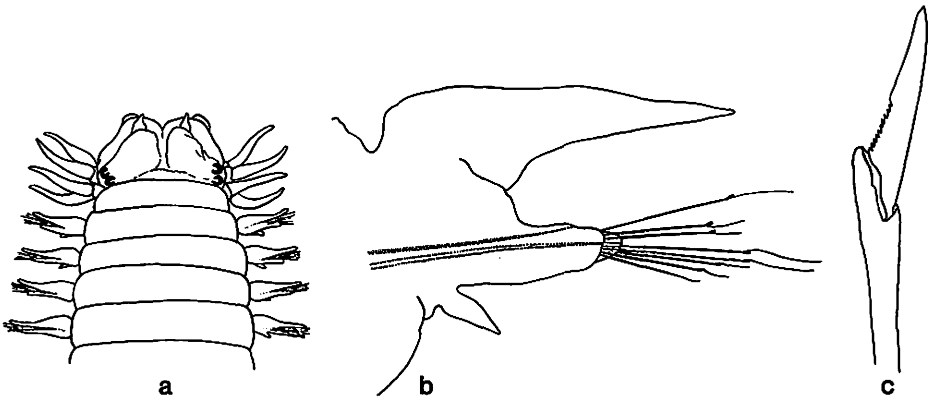

Figure 3.II.71.—*Namalycastis abiuma*: a, anterior region; b, parapodium with notoaciculum and foliaceous dorsal cirrus; c, neuropodial heterogomph seta, proximally dentate, distally smooth. (After Hartman 1959.)

the cutting edge. Parapodia are seemingly uniramous (Fig. 3.II.71b) but have a notopodial-embedded aciculum. Setae are composite, with heterogomph spinigers and falcigers (Fig. 3.II.71c) in each of which the appendage is distally smooth and proximally dentate. This species has been recorded from Brazil (Hartman 1966) and is found on Oahu, Kauai, and Hawaii in estuarine (mixohaline) and limnetic waters.

KEY TO HAWAIIAN *NEANTHES* SPECIES

Proboscis areas VII-VIII with 8 rows of paragnaths that merge with areas V and VI, which also have 8 rows .... *N. arenaceodonta*

Proboscis areas VII-VIII with 3 rows of paragnaths not merging with areas V and VI, which have 3 and 9 paragnaths, respectively ...... *N. succinea*

Neanthes arenaceodonta Moore, 1903b
[syn. *Neanthes caudata* (delle Chiaje, 1828): Hartman 1966]

The length of the 32 anterior segments of a specimen is 10.5 mm. The prostomium is pentagonal, with 4 eyes, large palps, and a pair of small frontal antennae (Fig. 3.II.72a). The everted proboscis has many small paragnaths on the oral and maxillary rings, distributed on all areas. The proboscis formula is: I, 17; II, about 36; III, 56; IV, about 50 in a wedge shape; V and VI, 4 rows of numerous paragnaths that merge with areas VII-VIII, which have 8 rows. Parapodia (Fig. 3.II.72b) are clearly biramous and have large dorsal, middle, and posterior ligules

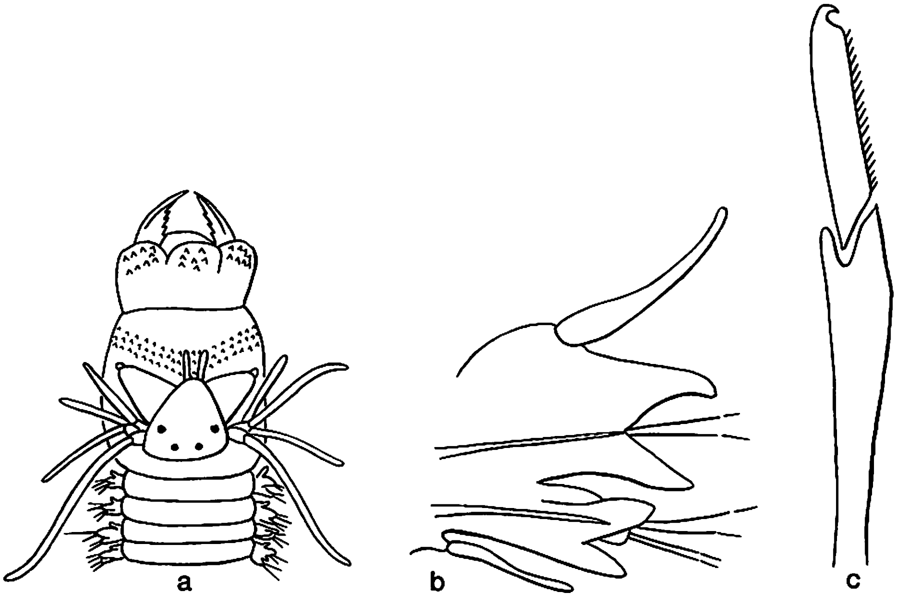

Figure 3.II.72.—*Neanthes arenaceodonta*: a, anterior region with proboscis extruded; b, parapodium; c, neuropodial heterogomph seta with hooked tip.

and short dorsal and ventral cirri. Neuropodia have prolonged preacicular and postacicular lobes. Notopodia have only composite spinigers; neuropodia have similar spinigers and long-appendaged falcigers (Fig. 3.II.72c). *Neanthes arenaceodonta* is recorded from temperate and tropical seas of the Northern Hemisphere (Day 1967; Gardiner 1975). This species may have been introduced to Kaneohe Bay, Oahu, where it occurs in coral sand.

Neanthes succinea Frey and Leuckart, 1847

The overall body length of this worm is about 80 mm. The head has conspicuous bilobed palps (Fig. 3.II.73a). The proboscis formula is I, 5; II, 26 in a double row; III, 45; IV, 9 in a wedge-shaped group; V, 3; VI, a group of 9; VII-VIII, a broad band of 63 paragnaths in 3 irregular rows. The number and arrangement of paragnaths differs slightly from the description in Day (1967). The parapodia of anterior segments have 3 notopodial lobes (Fig. 3.II.73b), and the superior notopodial lobe of posterior segments is enlarged and leaflike (Fig. 3.II.73c). Setae include homogomph compound spinigers but there are no notopodial falcigers, only neuropodial falcigers with long, straight blades and blunt tips (Fig. 3.II.73d). This is a new distributional record for this estuarine species, which is abundant in the mud along the banks of the Ala Wai Canal on Oahu. It is a widely distributed species that lives in intertidal regions of the Atlantic and Pacific oceans (Day 1967; Gardiner 1975).

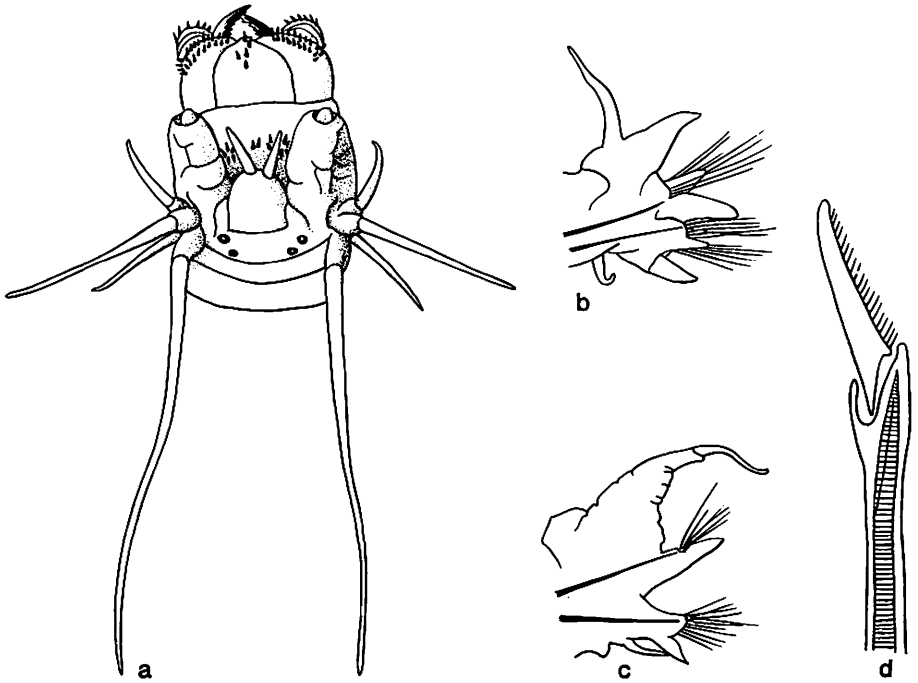

Figure 3.II.73.—*Neanthes succinea*: a, anterior region with proboscis extruded; b, anterior parapodium; c, posterior parapodium; d, neuropodial falciger. (a,b,c after Day 1967.)

KEY TO HAWAIIAN *NEREIS* SPECIES

1	Proboscis with paragnaths on all areas	4
	Proboscis otherwise	2
2(1)	Proboscis lacks paragnaths on areas I, V, and VI	3
	Proboscis lacks paragnaths on areas I, II, III, and V	*N. waikikiensis*
3(2)	Pre-epitokal region with 14 setigerous segments	*N. hawaiiensis*
	Pre-epitokal region with 18 setigerous segments	*N. nigroaciculata*
4(1)	Notopodial homogomph falcigers each with a short, coarsely bifid appendage	*N. jacksoni*
	Notopodial homogomph falcigers not coarsely bifid	5
5(4)	Proboscis with many paragnaths, of which areas VII-VIII have 3 to 5 irregular rows of large cones	*N. corallina*
	Proboscis with relatively few paragnaths, of which areas VII-VIII together have a single row of cones	6
6(5)	Epitokous stage with 14 anterior (pre-epitokal) setigerous segments	7
	Epitokous stage with 16 anterior (pre-epitokal) setigerous segments	*N. myersi*
7(6)	Body consists of 3 regions in epitokous stage, each with 14 anterior, 29 to 37 median epitokal, and 9 to 11 posterior segments; jaws with 9 to 10 teeth	*N. abbreviata*
	Body consists of only 2 regions in epitokous stage, each with 14 anterior and 41 epitokal segments; jaws with fewer than 9 teeth	8
8(7)	Pharyngeal jaw with 6 teeth	*N. unica*
	Pharyngeal jaw with 7 or 8 teeth	*N. mariae*

Nereis abbreviata Holly, 1935

The length of an epitokous worm is 9 mm. The body consists of 3 regions, the first composed of 14 anterior or pre-epitokal segments, the second of 29 to 37 epitokal segments, and the third of 9 or 10 posterior or post-epitokal segments. The prostomium has 4 large, dark eyes; the longest of the tentacular cirri extends back to setiger 8 to 9, and each is slightly annulated. The proboscis lacks paragnaths on areas I and V; II has 6 to 8 cones in 2 rows; III has 4 to 5 cones; IV has a group of 4 to 6 cones; V has none; VI has 1 cone; and VII-VIII share 8 to 12 cones in 1 row (Figs. 3.II.74a,b). Each of the jaws has 9 to 10 teeth along the cutting edge. Parapodia of the third (posterior) region either lack setae or the neuropodia have a few heterogomph falcigers. Notopodia of anterior segments bear homogomph spinigers (Fig. 3.II.74c) and neuropodia bear both homogomph and heterogomph spinigers (Fig. 3.II.74d) and heterogomph falcigers (Fig. 3.II.74e). This pelagic form has been collected from surface waters at Pearl and Hermes Reef.

Nereis corallina Kinberg, 1866

Worms attain about 35 mm in length. The dorsum is diffusely pigmented with a distinct dark brown band across the peristomium. The proboscis has many paragnaths: area I has 2 to 9 large, pointed cones; II, III, and IV have many similar cones; V has a single large cone or is bare; VI has 4 cones in a quadrate

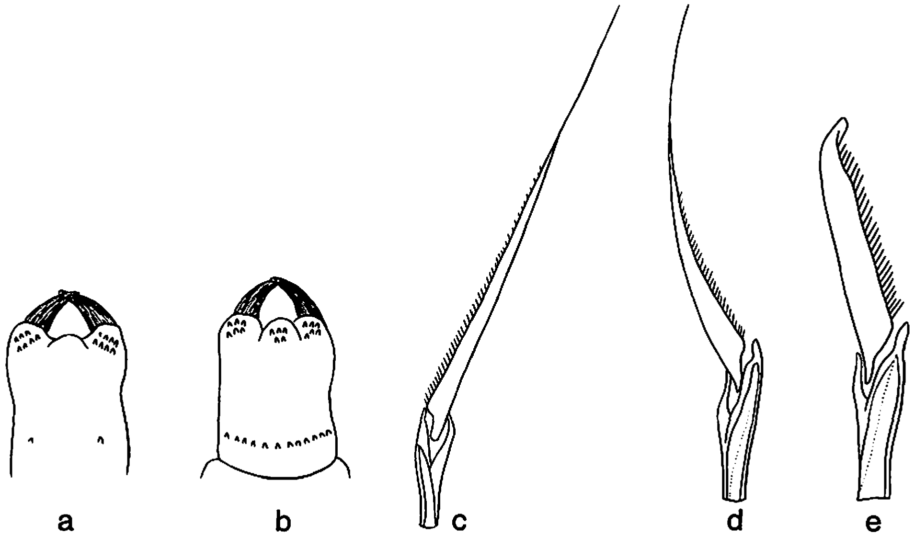

Figure 3.II.74.—*Nereis abbreviata*: a, proboscis, dorsal view; b, proboscis, ventral view; c, notopodial homogomph spiniger; d, neuropodial heterogomph spiniger; e, neuropodial heterogomph falciger.

patch; and VII-VIII have a continuous band of many large cones in 3 to 5 irregular rows. The jaws are thin and translucent, each with 9 teeth along the cutting edge. Parapodia have long dorsal, middle, and ventral lobes (Fig. 3.II.75a), each with a dark pigment patch. Notosetae include spinigers and homogomph falcigers (Fig. 3.II.75b). Neurosetae are heterogomph spinigers and falcigers (Fig. 3.II.75c). This species is known from the intertidal region of Oahu and was recorded by Hartman (1966) from Pearl Harbor, Oahu, in oyster blisters with *Polydora websteri* (a spionid polychaete).

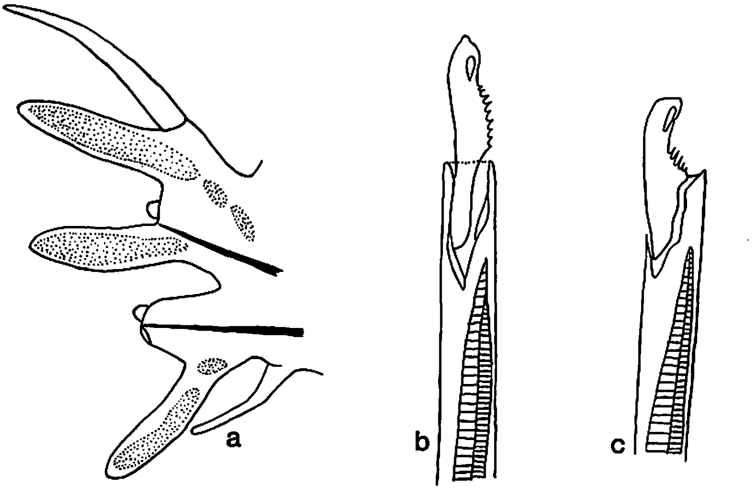

Figure 3.II.75.—*Nereis corallina*: a, parapodium; b, notopodial homogomph falciger; c, neuropodial heterogomph falciger. (After Hartman 1948.)

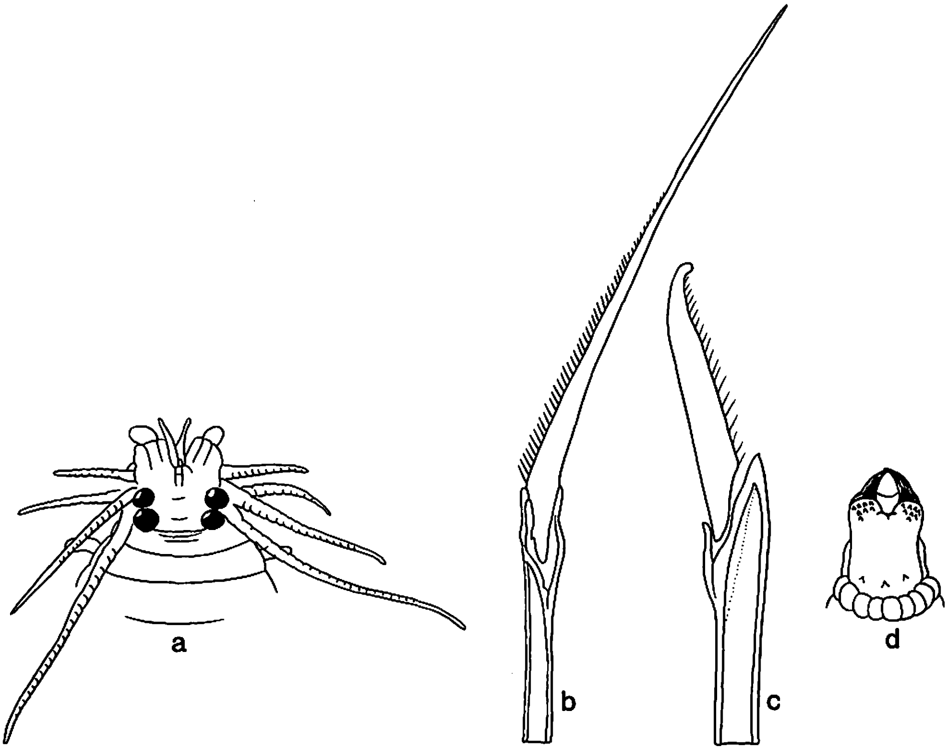

Figure 3.II.76.—*Nereis hawaiiensis*: a, anterior region; b, neuropodial homogomph spiniger; c, neuropodial heterogomph falciger; d, proboscis, ventral view. (a,b after Holly 1935.)

Nereis hawaiiensis Holly, 1935

Epitokous worms are 7.25 to 19.5 mm long and consist of 14 pre-epitokal and 41 to 57 epitokal segments. The prostomium has 2 pairs of very large, dark eyes, with the 2 on each side in contact (Fig. 3.II.76a). The longest of 4 pairs of tentacular cirri extends back to segments 9 to 12. On the proboscis, areas I, V, and VI are bare; II has 5 to 8 cones in 2 to 3 rows; III has 1 to 3 cones; IV has 7 to 10 cones in 2 rows; and VII-VIII share 3 cones in 1 row (Fig. 3.II.76d). Jaws are dark brown, each with 6 to 7 teeth at the cutting edge. Notopodia of anterior segments have only homogomph spinigers. Neuropodia have spinigers (Fig. 3.II.76b) and heterogomph falcigers (Fig. 3.II.76c). Specimens have been collected from the sea surface at Pearl and Hermes Reef and Lisianski Island.

Nereis jacksoni Kinberg, 1866

An individual with 50 segments is 12 mm long. On the proboscis, areas I and V are bare; each of II, III, IV has a few cones; VI has 1 to 4 cones; and VII-VIII share 1 row of 2 to 7 cones. Each of the parapodia (Fig. 3.II.77a) has a reduced dorsal lobe, a larger middle lobe, and a ventral lobe resembling the middle one. Notopodia have composite homogomph falcigers. The appendage of each notopodium is short, and either distally trifid (Fig. 3.II.77b) and seen as a small knob in frontal view (Fig. 3.II.77c), or bifid (Fig. 3.II.77d), the degree of bifurcation diminishing posteriorly so that posterior falcigers have simple, curved

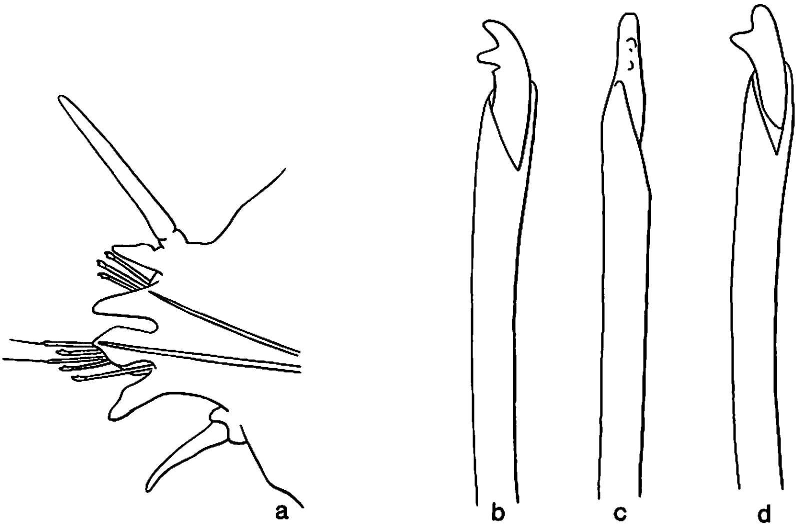

Figure 3.II.77.—*Nereis jacksoni*: a, parapodium; b, trifid, homogomph falciger, side view; c, the same, face view; d, bifid homogomph falciger. (After Hartman 1954b.)

fangs. This species attains densities of 112 to 4720/m^2 intertidally (Kohn 1959) and has been found in algal mats on rocks at Paia, Maui; Haleolono Pt., Molokai; and Spouting Horn, Kauai; otherwise, it has an Indo-West Pacific distribution (Hartmann-Schröder 1965).

Nereis mariae Holly, 1935

Epitokous, mature worms vary in length from 6.9 to 8 mm and have 14 pre-epitokal and 44 to 49 epitokal segments. The prostomium is rounded and bears 2 large eyes. The longest of 4 pairs of tentacular cirri reaches back to segment 5 or 6; each is slightly annulated. On the proboscis, areas I and V are bare; II has 3 to 4 cones; III has 3; IV has a group of 4 to 5; VI has 3 small cones; and VII-VIII support a row of 9 to 11 paragnaths (Figs. 3.II.78a,b). All cones are very light and difficult to distinguish. Jaws have 7 to 8 serrated teeth. Notopodia of anterior segments have homogomph spinigers (Fig. 3.II.78c) and neuropodia have heterogomph spinigers and heterogomph falcigers (Figs. 3.II.78d,e). This form is pelagic and has been collected in the Hawaiian Islands at Oahu, and Pearl and Hermes Reef.

Nereis myersi Holly, 1935

An epitokous individual is 8.2 mm long and has 16 pre-epitokal and 44 epitokal segments. The prostomium is rounded and has 2 pairs of large, dark eyes. Palps are short and thick, with small tips. The longest of 4 pairs of tentacular cirri extends back to segment 6 and each is slightly annulated. On the proboscis, areas I and V are bare; II has 3 cones in a slanting row; III has 1 cone; IV has a group of 4; VI has 2; and VII-VIII have a row of 10 paragnaths (Figs. 3.II.79a,b). Each of the jaws has 7 serrated teeth. Parapodia bear notopodia with homogomph spinigers, while neuropodia bear both homogomph and heterogomph spinigers as well as stout heterogomph falcigers (Fig. 3.II.79c). This species is planktonic and has been collected at Pearl and Hermes Reef in the Northwestern Hawaiian Islands.

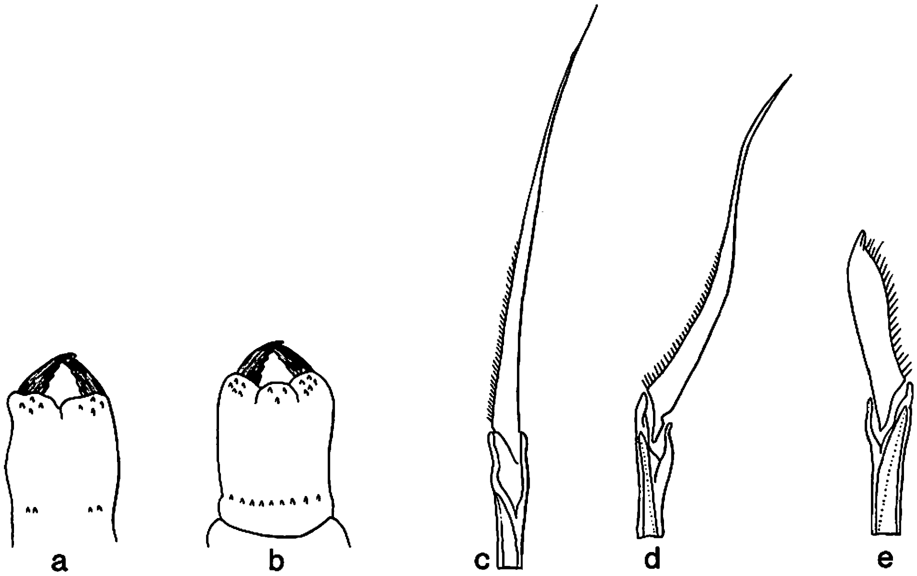

Figure 3.II.78.—*Nereis mariae*: a, proboscis, dorsal view; b, proboscis, ventral view; c, notopodial homogomph spiniger of an anterior setiger; d, neuropodial heterogomph spiniger; e, neuropodial heterogomph falciger. (After Holly 1935.)

Nereis nigroaciculata Holly, 1935
[syn. *Nereis* (*Neonereis*) *nigroaciculata* Holly, 1935]

Epitokous worms consisting of 18 pre-epitokal and 58 to 71 epitokal segments are 12.3 to 17.5 mm long. The prostomium is quadrate and has 2 pairs of black eyes. The longest of 4 pairs of tentacular cirri extends back to segment 13 or 14. Conical paragnaths are distributed as follows: area I lacks paragnaths; area II has 4 to 9 in 2 rows (Fig. 3.II.80a); area III has 3, with 2 anterior to the third (Fig. 3.II.80b); area IV has a group of 9 to 11; areas V and VI lack paragnaths; and areas VII-VIII have 3 or 4 distributed in a row. [Holly (1935) reversed the illustrations of paragnath arrangement, i.e., his fig. 9k is the ventral view and fig. 91 is the dorsal view.] Each jaw has 9 teeth. Notopodia of anterior segments have homogomph spinigers; neuropodia have homogomph spinigers (occasionally 1 heterogomph spiniger) and heterogomph falcigers (Fig. 3.II.80c). The last pre-

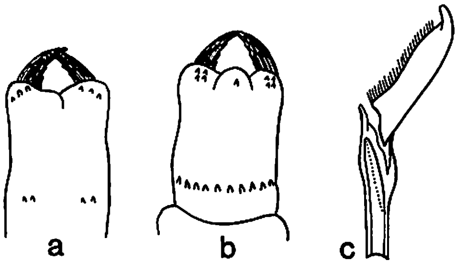

Figure 3.II.79.—*Nereis myersi*: a, proboscis, dorsal view; b, proboscis, ventral view; c, neuropodial heterogomph falciger. (After Holly 1935.)

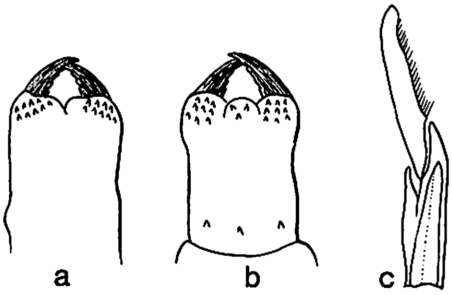

Figure 3.II.80.—*Nereis nigroaciculata*: a, proboscis, dorsal view; b, proboscis, ventral view; c, neuropodial heterogomph falciger. (After Holly 1935.)

epitokal segment lacks setae. This species is planktonic and was collected at Pearl and Hermes Reef, Northwestern Hawaiian Islands.

Nereis unica Holly, 1935

An epitokous worm 8.75 mm long has 14 pre-epitokal and 41 epitokal segments. The prostomium is widest posteriorly, with 2 pairs of large, dark eyes. The longest of 4 pairs of tentacular cirri extends back to segment 7. On the proboscis, areas I and V are bare; II has 4 cones in 2 diagonal rows; III has 1 large and 1 small cone; IV has a group of 6 to 7 cones; VI has 1 cone; and VII-VIII have 6 cones in 1 row (Figs. 3.II.81a,b). Each of the jaws has 6 serrated teeth. Anterior notopodia have homogomph spinigers; neuropodia have homogomph spinigers and heterogomph falcigers; all other parapodia have natatory setae (see Fig. 3.II.69d). This is a pelagic form taken in plankton at Pearl and Hermes Reef, Northwestern Hawaiian Islands.

Nereis waikikiensis Holly, 1935
[syn. *Nereis* (*Herfriedia*) *waikikiensis* Holly, 1935]

Epitokous worms are 3 to 6.2 mm long. The body consists of a pre-epitokal region of 13 segments, an epitokal region with 16 to 17, and a post-epitokal region with 11 to 13. The prostomium is rounded and has 2 pairs of large, black eyes. The longest of the 4 pairs of tentacular cirri extends back to the 4th parapodial segment. On the proboscis, areas I, II, III, V, and VI lack paragnaths; IV has 3 or 4; and VII-VIII have 7 to 9 paragnaths in 1 row (Figs. 3.II.82a,b). Anterior

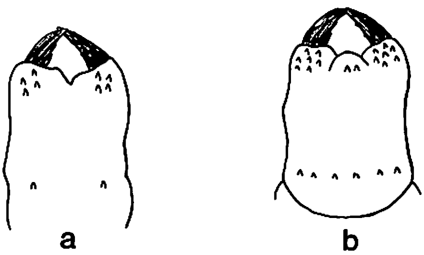

Figure 3.II.81.—*Nereis unica*: a, proboscis, dorsal view; b, proboscis, ventral view. (After Holly 1935.)

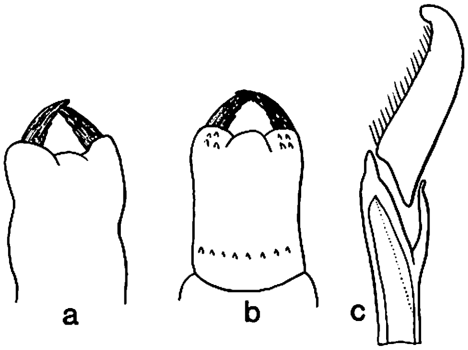

Figure 3.II.82.—*Nereis waikikiensis*: a, proboscis, dorsal view; b, proboscis, ventral view; c, neuropodial heterogomph falciger. (After Holly 1935.)

notopodia have a single homogomph spiniger; neuropodia have homogomph and heterogomph spinigers and heterogomph falcigers (Fig. 3.II.82c). This species is known from plankton samples taken at Waikiki, Oahu, and in the Northwestern Hawaiian Islands, at Pearl and Hermes Reef and French Frigate Shoals.

KEY TO HAWAIIAN *PERINEREIS* SPECIES

1 Area V of the proboscis with 1 conical paragnath............. *P. curvata*
Area V of the proboscis with more than 1 conical paragnath 2
2(1) Areas VII-VIII with 17 paragnaths in a double row .... *P. helleri*
Areas VII-VIII with 33 paragnaths in a double row ..... *P. nigropunctata*

Perinereis curvata Holly, 1935

Epitokous worms are 9 to 14 mm long, have 15 pre-epitokal and 43 to 56 epitokal segments. The prostomium is rounded and has 2 pairs of large, dark eyes. The longest of the 4 pairs of tentacular cirri extends back to parapodial segment 4 or 5. On the proboscis (Figs. 3.II.83a,b), area I has 2 or 3 conical paragnaths; II

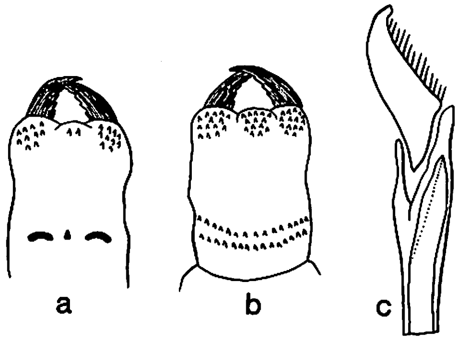

Figure 3.II.83.—*Perinereis curvata*: a, proboscis, dorsal view; b, proboscis, ventral view; c, heterogomph falciger. (After Holly 1935.)

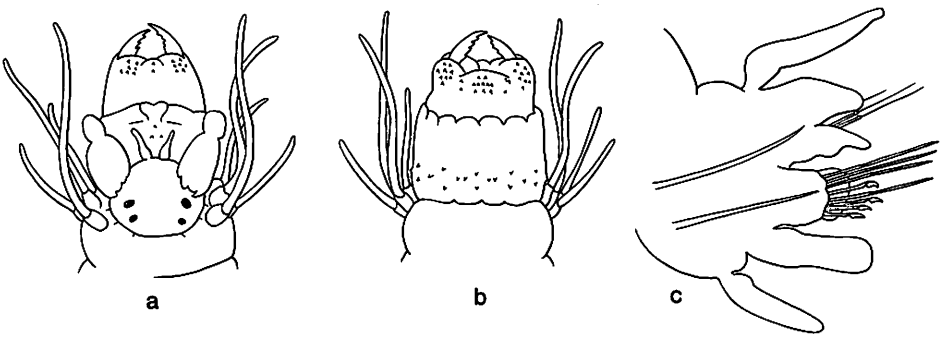

Figure 3.II.84.—*Perinereis helleri*: a, dorsal view of head and proboscis; b, ventral view of proboscis; c, parapodium. (After Monro 1931.)

has 8 to 12; III has 16 to 20; IV has 14 to 20; V has 1; VI has 1 bar-shaped paragnath; and VII-VIII have 34 to 36 conical paragnaths in 2 rows. Setae include homogomph and heterogomph spinigers and heterogomph falcigers (Fig. 3.II.83c). This pelagic form is known from Pearl and Hermes Reef and Lisianski Island in the Northwestern Hawaiian Islands.

Imajima (1972) describes an epitokous form, *Perinereis cultifera* var. *floridana* new to Japan. This variety resembles *P. curvata* except in the number of paragnaths on area I, which may be 1, 2, or 3 in Hawaiian specimens and 2 in Japanese specimens. Examination of Holly's specimens is required to determine if these species are synonymous.

Perinereis helleri Grube, 1878

The body of this species is large, dark, and iridescent, and it is 70 mm long. The prostomium is suboval with 4 conspicuous eyes and palps. Tentacular cirri extend back 4 to 6 segments. On the proboscis (Figs. 3.II.84a,b), area I has 2 cones; II has a patch of about 7; III has 3 small groups (a median group with 9 and 2 lateral groups with 2 cones each); IV has about 10 in a mass; V has 2 or 3 cones; VI has a broad transverse ridge on each side of V; and VII-VIII have about 17 paragnaths in an irregular double row. Parapodia (Fig. 3.II.84c) have only spinigers in the notopodia; neuropodia have spinigers and composite falcigers. This widespread Indo-West Pacific species has been found throughout the Hawaiian Islands on coral reefs (Hartman 1966).

Perinereis nigropunctata (Horst, 1889)

These worms are about 50 to 60 mm long and are marked with 3 rows of dark brown bands and a brown inverted V on the prostomium. The head (Fig. 3.II.85a) bears short, tentacular cirri. Paragnaths are all conical except for transverse bars on area VI (Figs. 3.II.85b,c); area I has 4; II has 11; III has a patch of 15; IV has a crescentic group of 14; V has 3 in a triangle; VI has a transverse bar on each side of V; VII-VIII have 2 rows of 33 cones. Anterior parapodia have 2 notopodial lobes (Fig. 3.II.85d), while posterior parapodia have an enlarged dorsal lobe bearing the dorsal cirrus (Fig. 3.II.85e). Notosetae are spinigers; neurosetae include spinigers and falcigers; acicula are black. Middle and posterior segments

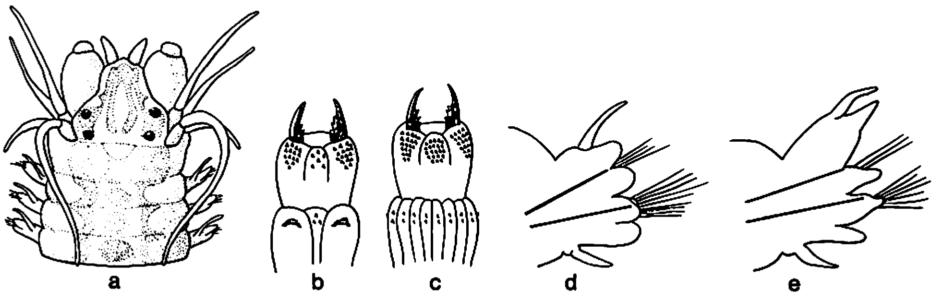

Figure 3.II.85.—*Perinereis nigropunctata*: a, anterior region; b, proboscis, dorsal view; c, proboscis, ventral view; d, anterior parapodium; e, posterior parapodium. (After Day 1967.)

of 1 specimen were full of eggs. This Indo-West Pacific species (Fauvel 1953; Day 1967) has been found living among coral rubble at shallow depths in Kaneohe Bay, Oahu, and in mud in Suva Harbor, Fiji (Bailey-Brock 1985).

KEY TO HAWAIIAN *PLATYNEREIS* SPECIES

1 Median and posterior notopodia with conspicuous simple falcigers (Fig. 3.II.87c) .... *P. bicanaliculata*
Median and posterior notopodia with compound falcigers (Fig. 3.II.88c) 2
2(1) Peristomium medially prolonged as a triangular lobe covering posterior part of prostomium .... *P. abnormis*
Peristomium not medially prolonged 3
3(2) Prostomium more than one half times longer than broad ..... *P. pulchella*
Prostomium slightly longer than broad .... *P. dumerilii*

Platynereis abnormis (Horst, 1924)

A male epitokous specimen consists of 15 pre-epitokal and 52 epitokal segments and is about 10 mm long. There are no measurements for female epitokes. The prostomium is broader than wide, with 4 enormous eyes (Fig. 3.II.86a) and a pair of frontal antennae directed ventrally (Fig. 3.II.86b). Tentacular cirri are moderately short. Anterior parapodia have short lobes and a long dorsal cirrus (Fig. 3.II.86c). Epitokal parapodia are modified with a crenulated dorsal cirrus and thin, foliaceous lobes; the largest are the middle and neuropodial lobes (Fig. 3.II.86d). On the pharynx, areas I, II, III, and V are bare; IV has 3 transverse rows of pectinae; VI has 2 short rows of pectinae; and VII-VIII have 5 short, transverse rows of pectinae. Jaws are yellowish brown, each with 5 teeth. Notopodia include homogomph spinigers; neuropodia have heterogomph spinigers and falcigers. *Platynereis abnormis* has been found in coral, mud, and in sponges from Kaneohe Bay, Oahu; otherwise it has a broad Indo-West Pacific distribution (Hartmann-Schröder 1965).

Platynereis bicanaliculata (Baird, 1863)
[syn. *Nereis kobiensis* McIntosh, 1885: Edmondson 1946]

Atokous worms are as long as 50 mm; male epitokes are only about 25 mm long, and female epitokes are slightly larger. The prostomium is pentagonal and

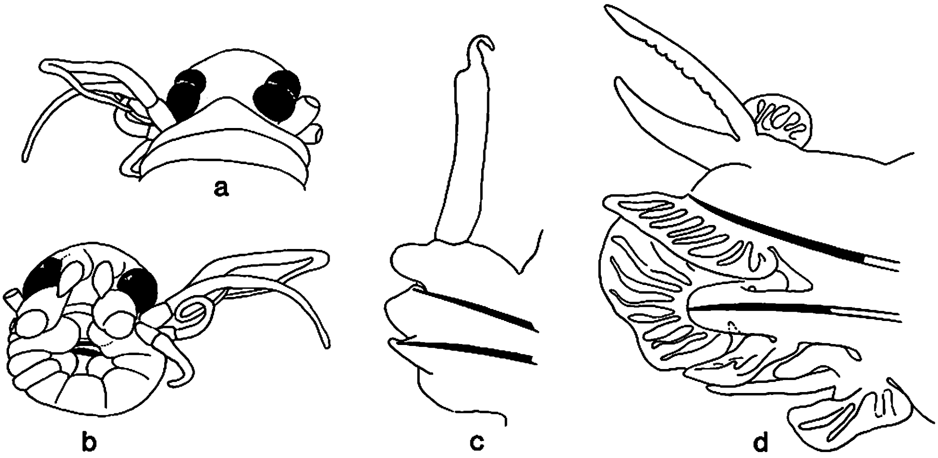

Figure 3.II.86.—*Platynereis abnormis*: a, head, dorsal view; b, head, ventral view; c, anterior parapodium; d, posterior parapodium. (After Hartmann-Schröder 1965.)

has 4 eyes. Tentacular cirri are prolonged (Fig. 3.II.87a). The proboscis lacks processes on areas I, II, and V; area III has an oval patch of cones; other areas have inconspicuous rows of pectinae. Parapodia of atokes are marked with saddles of dark pigment (Fig. 3.II.87b). Notopodia have homogomph spinigers (tapered setae) and simple, thick, recurved falcigers (Fig. 3.II.87c) on the middle and posterior segments. Worms live among tufts of algae where they build tubes in which epitokes develop. The epitokous stage swims to the surface for mass

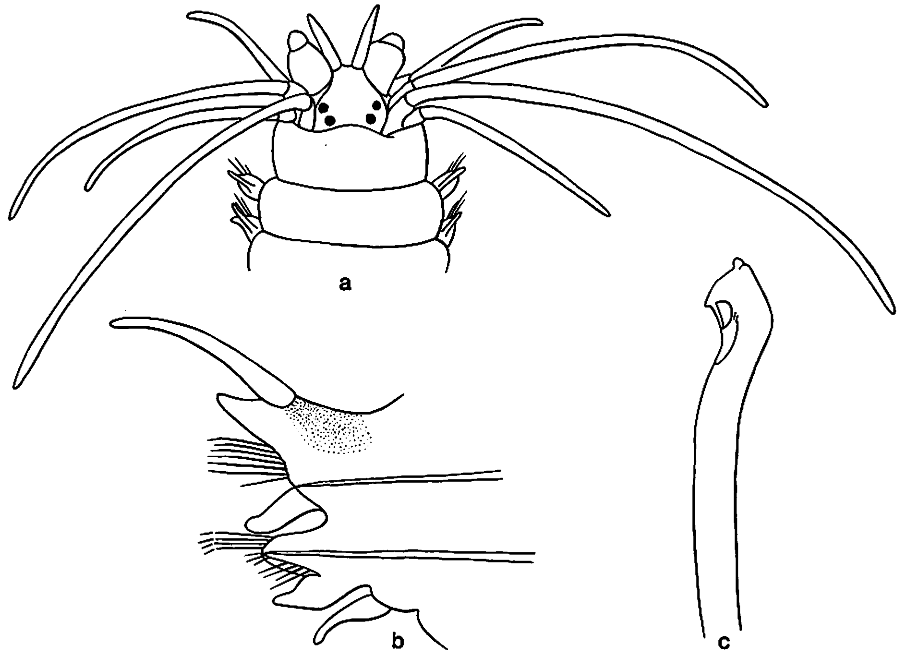

Figure 3.II.87.—*Platynereis bicanaliculata*: a, anterior region; b, parapodium; c, notopodial falciger. (After Johnson 1901.)

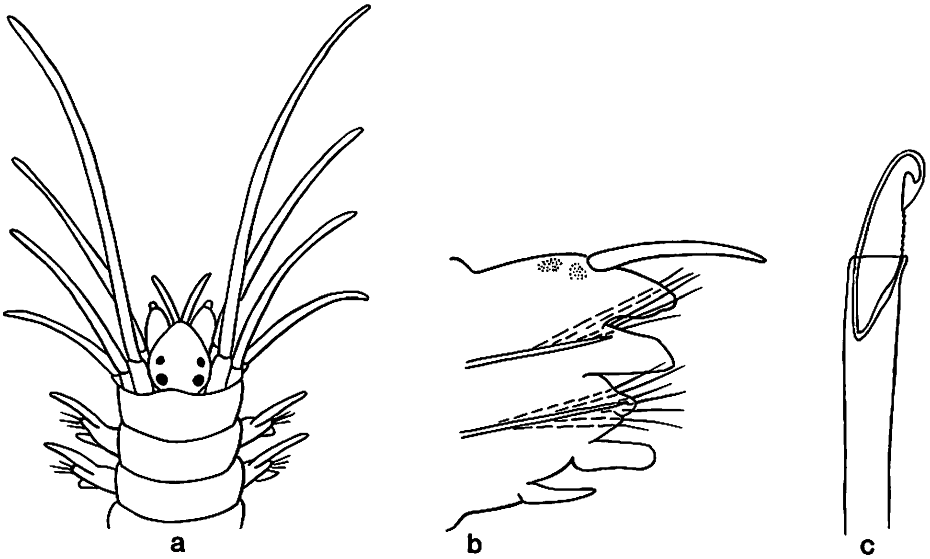

Figure 3.II.88.—*Platynereis dumerilii*: a, head; b, parapodium from middle region; c, notopodial falciger. (After Pettibone 1963.)

spawning. This species has been found throughout the Hawaiian Islands and from the North and South Pacific (Hartman 1966).

Platynereis dumerilii (Audouin and Milne Edwards, 1833)
[syn. *Platynereis jacunda* Kinberg, 1866. *Nereis kobiensis* McIntosh, 1885 (pt.): Treadwell 1906. *Platynereis massiliensis* (Moquin-Tandon, 1869): Hartman 1966]

The length of atokous worms is 40 to 50 mm; maturity is attained without epitoky. The prostomium is roughly pentagonal and has 4 small eyes on the posterior half (Fig. 3.II.88a). Tentacular cirri are long and slender, the longest extending back from 10 to 15 segments. On the proboscis, areas I, II, and V are bare; all other areas have small, short, inconspicuous rows of pectinae. Parapodia (Fig. 3.II.88b) have patches of dark pigment over the notopodial ridge and equally long dorsal, middle, and ventral lobes. Notopodia in the middle and posterior segments have homogomph, composite falcigers with curved tips (Fig. 3.II.88c). Widely known from circumtropical areas in littoral zones, this species feeds on algae in Kaneohe Bay and has been found in algal mats on stones at Halape and Hilo, Hawaii, and at Kaaawa and Kahana, Oahu (Hartmann-Schröder 1965). *Platynereis dumerilii* and *P. massiliensis* are considered to be sibling species (H.-D. Pfannenstiel, pers. comm.).

Platynereis pulchella Gravier, 1901
[syn. *Nereis kobiensis* McIntosh, 1885 (pt.): Treadwell 1906. *Platynereis pestai* Holly, 1935]

Epitokous adults are nearly 19 mm long, and their width without parapodia is 2 mm. The anterior or pre-epitokal region consists of 14 segments in the male and 19 in the female; epitokal segments number 64 to 78. The prostomium has 4

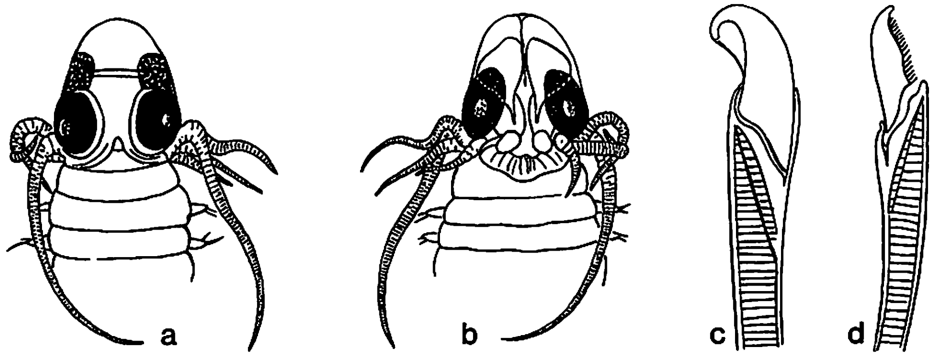

Figure 3.II.89.—*Platynereis pulchella*: a, male, dorsal view of head showing posterior eyes; b, ventral view of head showing anterior eyes; c, notopodial falciger; d, neuropodial falciger. (After Holly 1935.)

very conspicuous lenticulated eyes: the posterior pair is best seen in dorsal view (Fig. 3.II.89a), while the anterior pair far forward are best seen in ventral view (Fig. 3.II.89b). The frontal antennae are turned back, and tentacular cirri are short and transversely wrinkled. The proboscis terminates in a pair of thick, brown jaws. Paragnaths are very small, absent from areas I, II, and V, and occur as pectinae on other areas. Notopodia have homogomph falcigers (Fig. 3.II.89c), and neuropodia have heterogomph falcigers (Fig. 3.II.89d). This species has been collected from Molokai and Oahu, as well as from several of the Northwestern Hawaiian Islands. Atokes were found at shallow depths and epitokes at the surface. *Platynereis pulchella* is widely distributed in the Indo-West Pacific as far as the Red Sea (Hartman 1966).

KEY TO HAWAIIAN *PSEUDONEREIS* SPECIES

1 Area VI of proboscis with 6 to 12 short bar paragnaths in a curved row 2
Area VI of proboscis with a single large, transverse bar paragnath .... *P. gallapagensis*
2(1) Area V of proboscis lacks paragnaths .... *P. anomala*
Area V of proboscis with a large, rectangular paragnath .... *Pseudonereis* sp.

Pseudonereis anomala Gravier, 1901

Worms are as long as 65 mm. The prostomium (Fig. 3.II.90a) is a broad, inverted T-shaped structure with 2 pairs of eyes, a pair of conspicuous antennae, and paired elongate palps. The proboscis has 1 to 2 cones on area I; 4 rows of cones on II; 4 comblike rows on III; a series of comblike rows on IV; paragnaths absent on V; 6 short bars in a curved row on VI; and about 14 paragnaths in a single row on VII-VIII. Parapodial lobes of anterior setigers are equal (Fig. 3.II.90b); posterior parapodia (Fig. 3.II.90c) have elongate dorsal lobes, each with a cirrus at the tip, and rounded ventral lobes. Neuropodial falcigers all have short

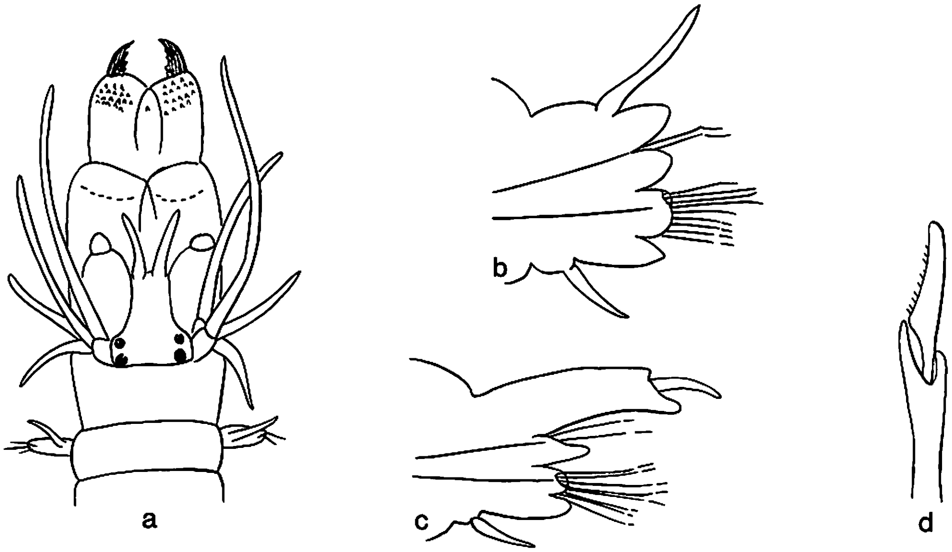

Figure 3.II.90.—*Pseudonereis anomala*: a, anterior region, dorsal view; b, anterior parapodium; c, parapodium from posterior region; d, neuropodial falciger. (After Day 1967.)

blades (Fig. 3.II.90d). *Pseudonereis anomala* has a broad distribution in the Indian Ocean and Red Sea (Fauvel 1953; Day 1967) and is also known from the Marshall Islands (Hartman 1954a). Hartman (1966) included *P. anomala* in a key to this genus but did not give a description.

Pseudonereis gallapagensis Kinberg, 1866
[syn. *Pseudonereis formosa* Kinberg, 1866]

Worms are as long as 45 mm; the dorsal surface tends to be dark and iridescent. The prostomium is pentagonal, bearing 4 eyes and a pair of thick palps (Fig. 3.II.91a). Tentacular cirri are short and blunt. The everted proboscis has

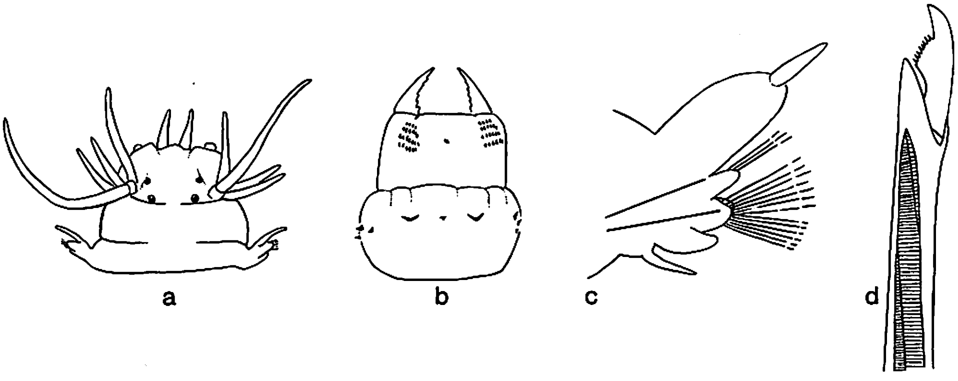

Figure 3.II.91.—*Pseudonereis gallapagensis*: a, dorsal view of head; b, dorsal view of everted proboscis; c, parapodium from posterior region; d, neuropodial falciger. [a,b,d after Imajima 1972; c after Day 1967 (as *P. variegata*).]

paragnaths on the oral ring and pectinae on the maxillary ring (Fig. 3.II.91b): area I has 1 cone; II has 3 rows of pectinae; III and IV each have rows of pectinae; V has a dark cone; VI has a single transverse bar; and VII-VIII share a continuous band of 18 to 19 cones in 2 or 3 rows. Parapodia increase in size in median segments, the base of the dorsal cirrus becoming foliaceous and pigmented, with a style inserted at the distal end of the lobe (Fig. 3.II.91c). Notopodia have only composite spinigers; neuropodia are unmodified and have spinigers and composite falcigers (Fig. 3.II.91d). This species is known from intertidal shores where it occupies burrows in dead coral (Hartman 1954a). It has a circumtropical distribution.

Pseudonereis sp.

An undetermined species of *Pseudonereis*, of unknown size, has been recorded (Hartman 1966). The proboscis has a large, rectangular paragnath on area V, a transverse row of small paragnaths on either side of VI, and pectinae on the maxillary ring. The posterior parapodia have long, rectangular notopodial lobes. This undetermined species is known from the algal turf of intertidal regions on Hawaii and Oahu.

Family **Glyceridae**

Glycerids are burrowing worms with a pointed, conical prostomium bearing 4 small antennae. The eversible proboscis is very long, covered with papillae, and bears 4 chitinous jaws at the tip. Each jaw is associated with a V-shaped support (aileron) (Fig. 3.II.92c). The structure of this armed proboscis, and the absence of sand in the gut of some species, has led to the conclusion that some glycerids may be predaceous carnivores, while other species are regarded as detritivores (Fauchald and Jumars 1979). Parapodia are either all biramous or all uniramous (as in the genus *Hemipodus*) (Fauchald 1977a).

Glycera tesselata Grube, 1863
[syn. *Glycera sagittariae* Treadwell, 1906]

These slender worms reach 30 mm in length. The prostomium is a long, depressed cone with 12 to 14 annuli, and terminates in 4 minute antennae (Fig. 3.II.92a). The eversible proboscis, covered with tall, slender papillar processes

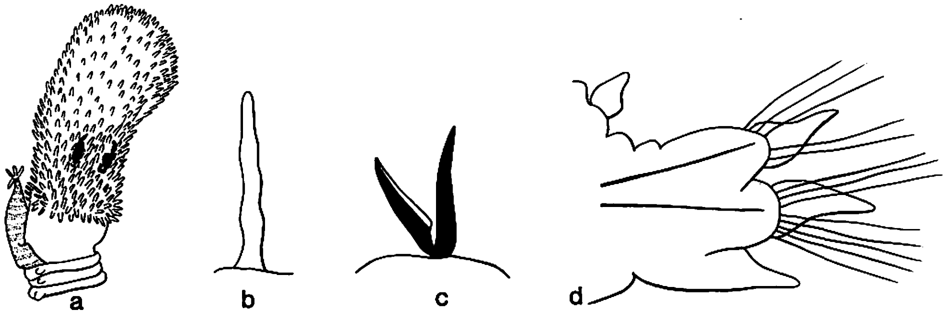

Figure 3.II.92.—*Glycera tesselata*: a, lateral view of anterior region with proboscis partly extended, 2 jaws visible through proboscis wall; b, proboscis papillar process; c, jaw support; d, parapodium. (c,d after Day 1967.)

(Fig. 3.II.92b), terminates in a circlet of papillae and 4 hard, dark processes, each consisting of a curved jaw and an attached aileron with diverging, chitinized wings (Fig. 3.II.92c). Parapodia (Fig. 3.II.92d) are biramous; each has 2 short presetal and 2 longer postsetal lobes. Notosetae are simple capillaries; neurosetae are composite spinigers. This circumtropical species is associated with sand, pebbles, rocks, or mixed sediments and has been found on Maui and Molokai from shallow water to moderate depths of 143 to 463 m (78 to 253 fm) (Hartman 1966).

Family **Goniadidae**

The goniadids are burrowing worms that are morphologically very similar to the Glyceridae. They differ in the number and arrangement of jaws and in the structure of parapodia. There are only 2 chitinous jaws at the tip of the conical proboscis, as well as a ring of small paragnaths. Near the base of the proboscis there are 2 short, lateral rows of V-shaped chevrons in most taxa. The widespread genus *Glycinde* lacks chevrons on the proboscis. Anterior parapodia are uniramous; posterior parapodia are biramous. Representatives of this genus have yet to be found in Hawaiian waters. Goniadids are all thought to be predaceous carnivores (Fauchald and Jumars 1979).

Goniada brunnea Treadwell, 1906

The body of this species reaches 36 mm in length and 2 mm in width; segments number about 100. The preserved color is dark or drab olive-brown, mostly concentrated dorsally. The elongate prostomium is an annulated, depressed cone, terminating in 4 small frontal antennae (Figs. 3.II.93a,b). The eversible proboscis is 3.5 times the length of the prostomium and covered with small papillae, each hoodlike with a terminal pore (Fig. 3.II.93c). Paired rows of chevrons occur laterally near the base of the proboscis (Fig. 3.II.93b); each has 7

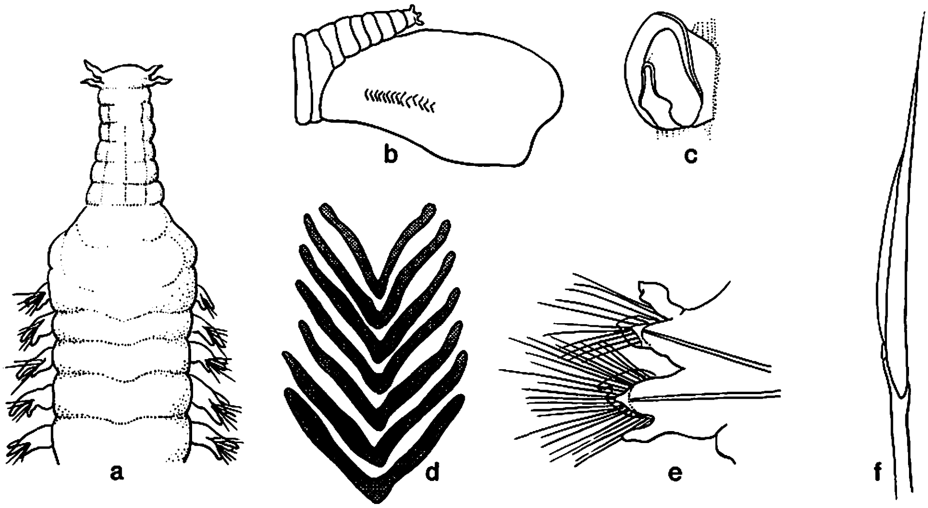

Figure 3.II.93.—*Goniada brunnea*: a, anterior region and prostomium; b, lateral view of head with everted proboscis; c, proboscis papilla; d, row of chevrons; e, posterior parapodium; f, neuropodial spiniger. (a,c–e after Hartman 1950; b,f after Treadwell 1906.)

to 14 V-shaped, dark pieces (Fig. 3.II.93d). Anterior parapodia are uniramous, becoming biramous at about segment 50. Biramous parapodia (Fig. 3.II.93e) have foliaceous dorsal cirri, simple capillary notosetae, and large neuropodia with composite spinigers (Fig. 3.II.93f). Known from California and the northeastern Pacific Ocean at shallow to moderate depths, this species was originally described from Maui at a depth of more than 365m (200 fm).

Family **Eunicidae**

This family is composed of typically free-living, mobile worms and includes some species that may become tube-dwellers or burrowers as adults. The head is well-defined and composed of a prostomium with 2 stout, rounded palps and 1 to 5 short antennae, a peristomium, and 2 apodous segments. The eversible proboscis is armed with well-developed chitinous mandibles and 4 to 5 pairs of toothed maxillary plates (maxillae) operated by powerful muscles. The jaw apparatus is used for a variety of feeding methods; some species feed on invertebrates, others rasp algae, and coral borers use the platelike mandibles in burrow formation (Fauchald and Jumars 1979). Some species display the mouthparts during aggressive behavior in captivity and may severely injure other worms (pers. observ.). Parapodia are typically uniramous, but the aciculum of the notopodium may be present. Setae include capillaries, compound setae, comb setae, and subacicular hooks. The structure and number of segments with branchiae are diagnostic features. Branchiae are simple cirriform or pectinate structures and are borne on the dorsolateral aspect of setigerous segments. Juvenile eunicids may lack 2 of the 5 occipital antennae which develop later.

KEY TO HAWAIIAN EUNICID GENERA

1 Prostomium with 5 occipital antennae; peristomial ring with a pair of dorsal cirri (Fig. 3.II.94a) 2
Prostomium with 1, 3, or 5 occipital antennae; peristomial ring lacks dorsal cirri 3
2(1) Subacicular hooked setae present (Fig. 3.II.101d) .... *Eunice*
Subacicular hooked setae absent .... *Palola*
3(1) Peristomium with 5 occipital antennae .... *Marphysa*
Peristomium with 1 or 3 occipital antennae 4
4(3) Prostomium with a single median antenna, palps fused and rounded .... *Nematonereis*
Prostomium with 3 antennae, palps well separated .... *Lysidice*

KEY TO HAWAIIAN *EUNICE* SPECIES

1 Anterior and/or middle-region segments with pectinate branchiae, each with few to many filaments 2
Branchiae absent or limited to a few simple filaments on the most posterior segments .... *E. cariboea*
2(1) Branchiae start on setiger 2, with as many as 30 filaments at greatest development .... *E. hawaiensis*

Branchiae start behind setiger 2, with fewer than 20 filaments at greatest development 3

3(2) Branchiae shorter than dorsal cirri and represented by a single filament .... *E. nicidioformis*

Branchiae conspicuous structures with 3 or more filaments at greatest development 4

4(3) Acicula and subacicular hooks dark brown or black 5

Acicula and subacicular hooks pale 7

5(4) Branchiae begin on setiger 7, with 9 to 18 filaments at greatest development .... *E. bilobata*

Branchiae begin on or behind setiger 17, with 3 to 9 filaments at greatest development 6

6(5) Acicula terminate in 3 blunt knobs; subacicular hooks strongly beaked and bidentate (Fig. 3.II.96a) .... *E. filamentosa*

Acicula bluntly pointed; subacicular hooks terminate in 2 short prongs (Fig. 3.II.94e) .... *E. afra*

7(4) Branchiae begin on setiger 5 or 6, with up to 9 filaments in anterior segments, middle region with branchiae as single filaments, posterior region with up to 5 filaments .... *E. antennata*

Branchiae begin on setiger 3 to 7, with number of filaments gradually increasing then decreasing posteriorly 8

8(7) Branchiae begin on setiger 3; prostomial antennae with long, cylindrical articles .... *E. vittata*

Branchiae begin on setiger 6 or 7; prostomial antennae with long, distinctly beaded articles .... *E. australis*

Eunice afra Peters, 1854

[syn. *Eunice collaris* (Grube, 1870): Treadwell 1906. *Leodice collaris* Grube: Edmondson 1946. *Eunice paupera* Holly, 1935. *Eunice* (*Eunice*) ?*aphroditois* (Pallas, 1788): Hartmann-Schröder 1965]

The body of this eunicid is 80 to 100 mm long and is up to 6.5 mm wide. Living worms are red with small white punctations (in ethanol, brown with white punctations); occipital antennae and tentacular cirri are pale. Prostomial antennae are short and smooth (Figs. 3.II.94a,b). Branchiae, never large, begin on about setiger 17 to 20; the number of branchial filaments in some populations of *E. afra* never exceeds 4, while in others it may reach 9; each filament is larger than the dorsal cirrus (Fig. 3.II.94c). Acicula are dark and have straight, blunt tips (Fig. 3.II.94d). Acicular setae are subacicular hooks, beginning on about segment 24; each is dark except for 2 blunt teeth, which are pale at the tip (Fig. 3.II.94e), and each seta occurs singly in a fascicle. First parapodia have few setae; the second and all other segments have more numerous setae, which are simple lanceolate capillaries (Fig. 3.II.94g), comblike setae (Fig. 3.II.94h), and bifid compound falcigers (Fig. 3.II.94f), in addition to the subacicular simple hooks. *Eunice afra* is a circumtropical species (Fauchald 1970) and has been collected with algal material from Waikiki, Oahu; Hilo and Halape, Hawaii; Paia, Maui; and the Northwestern Hawaiian Islands (Hartman 1966).

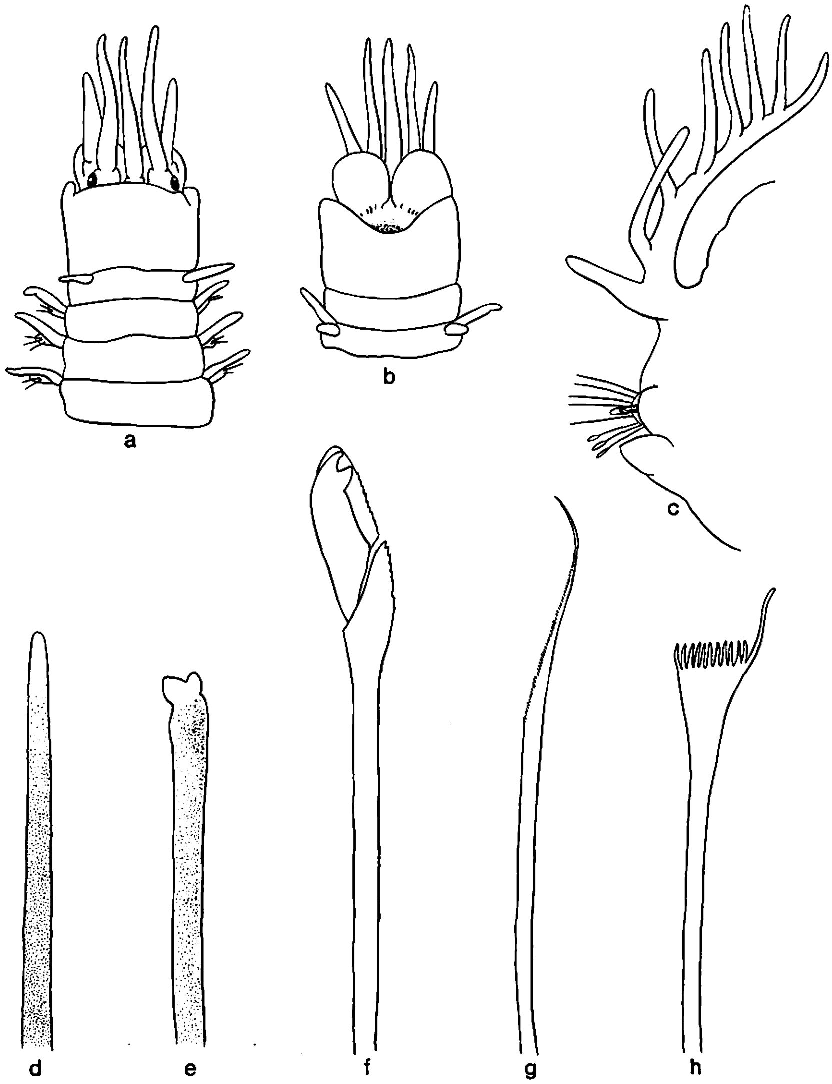

Figure 3.II.94.—*Eunice afra*: a, dorsal anterior region; b, ventral anterior region; c, parapodium; d, aciculum; e, subacicular hook; f, bifid compound seta; g, capillary seta; h, comb seta.

Eunice antennata (Savigny, 1820)

[syn. *Eunice havaica* Kinberg, 1865. *E. interrupta* Treadwell, 1906. *Leodice interrupta* (Treadwell): Edmondson 1946]

The body of this worm may be up to 55 mm long. Occipital antennae and dorsal cirri are strongly moniliform; buccal (peristomial) tentacles are smooth to moniliform (Fig. 3.II.95a). Branchiae begin on setiger 5 or 6 and have 3 to 4 or as many as 9 filaments (Fig. 3.II.95b) on setigers 15 to 25 at maximum development; these decrease in number in the middle of the body and increase again farther back to a maximum of 5. Acicula and subacicular hooks are yellow. Acicula terminate in 2 blunt knobs. Subacicular hooks are simple and distally tridentate, and there

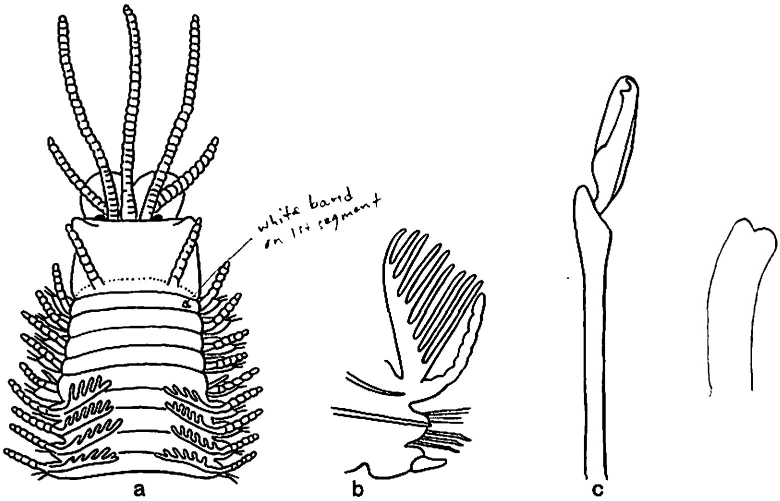

Figure 3.II.95.—*Eunice antennata*: a, anterior region; b, parapodium; c, composite falciger. (After McIntosh 1885.)

are usually 1 or 2 in a fascicle. Compound falcigers have slender, bifid appendages (Fig. 3.II.95c), and comb setae are present. This widespread tropical species (Fauchald 1970) has been collected from marine benches and shallow reefs around the high Hawaiian Islands and found among coarse coral sediments dredged off Laysan at depths of 140 m (77 fm) (Hartman 1966).

Eunice australis Quatrefages, 1865

Worms with up to 130 segments are 80 mm long. The prostomium is medially incised, and the occipital antennae are long and moniliform. The buccal segment is as long as the 4 following segments. Dorsal cirri are annulated. Branchiae begin on setiger 6 or 7, with up to 10 filaments at maximum development, and are absent from posterior segments. Acicula are yellow with curved tips; subacicular hooks are yellow and tridentate with guards. Comb setae and bidentate compound falcigers are also present. This Indo-West Pacific species (Fauvel 1953) is known from Waikiki, Oahu (Holly 1935), and was originally described from New Zealand.

iridescent

Eunice bilobata Treadwell, 1906

A specimen with 35 segments is 18 mm long and about 5.5 mm wide including parapodia. The color is an iridescent gray, and the tips of the dorsal cirri are white, each with a subterminal band of dark brown. The prostomium is deeply bilobed anteriorly and occipital antennae and dorsal cirri are smooth. Branchiae begin on setiger 7, with 9 to 18 filaments at greatest development. Acicula are black with blunt tips. Subacicular hooks have slightly curved, pointed tips and compound falcigers have small guards. This species is known from a single specimen dredged from sand at 30 m (16 fm) depth in the Auau Channel between Maui and Lanai.

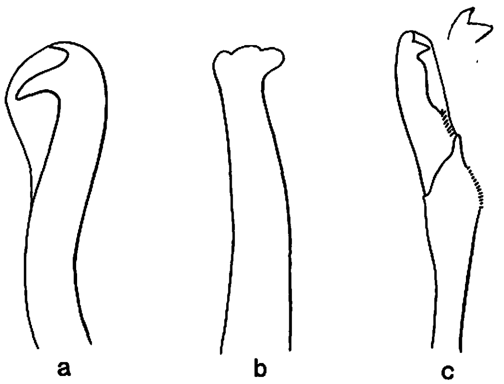

Figure 3.II.96.—*Eunice filamentosa*: a, subacicular hook; b, aciculum; c, composite falciger. (After Hartman 1944.)

Eunice cariboea (Grube, 1856)
[syn. *Nicidion longicirrata* Kinberg, 1865. *Nicidion cariboea* Grube: Hartman 1966]

Specimens of undetermined size have branchiae lacking or limited to a few simple filaments in the most posterior segments. Acicula are black, slightly curved distally, and occur singly in a fascicle. Black, bidentate subacicular hooks are present on setigers of the middle region. Simple capillaries and bidentate compound falcigers are also present. Found at shallow depths in tropical seas (Fauchald 1970), specimens have been collected at Waikiki, Oahu, and Halape, Hawaii (Kohn 1959; Hartman 1966).

#16

Eunice filamentosa Grube, 1856

Specimens are about 120 mm long (Day 1967). Occipital antennae are short, smooth, or irregularly ringed but are not moniliform. Branchiae begin on about segment 26 and have 3 filaments at greatest development. Subacicular hooks (Fig. 3.II.96a) are brown, distally beaked, and bidentate with guards. Acicula are dark brown; their tips, formed of 3 blunt knobs, are somewhat hammer-shaped or truncate (Fig. 3.II.96b). Compound falcigers are distally bifid and hooded (Fig. 3.II.96c). This species is known from eastern and western tropical America (Day 1973) and is found at shallow depths around the Hawaiian Islands (Kohn 1959).

Eunice hawaiensis Treadwell, 1906

These large worms have 125 segments, are 115 mm long, and are 7 mm wide at segment 50. The prostomium is deeply incised anteriorly and occipital antennae and tentacular cirri are long and smooth (Fig. 3.II.97a). Branchiae begin on the second setigerous segment; the first has an axis and 3 lateral branches; the second has 12 branches and reaches across the dorsum to the mid-dorsal line. Branchiae may have as many as 30 filaments (Fig. 3.II.97b) at greatest development but fewer in posterior segments. Branchiae overlap across the dorsum from the fourth setiger. Acicula and acicular setae are present; composite falcigers each have a

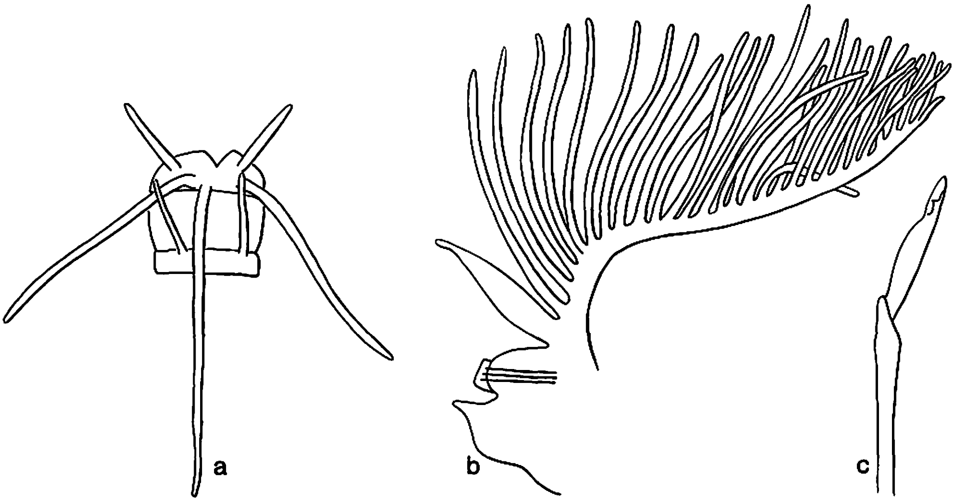

Figure 3.II.97.—*Eunice hawaiensis*: a, dorsal view of anterior region; b, parapodium with filamentous branchia; c, composite falciger with hooded, bifid tip. (After Treadwell 1906.)

pointed hood and slender bifid tip (Fig. 3.II.97c). This species was described from specimens dredged at a depth of 412 to 730 m (225 to 399 fm) off Kauai.

Eunice nicidioformis Treadwell, 1906

The length of a worm with about 100 segments is 43 to 47 mm. The color in alcohol is light brownish yellow with iridescence. The prostomium has a deep median cleft. Occipital antennae are moniliform, the longest one extending back to segment 15. Tentacular cirri are annulated, each with 4 articles (Fig. 3.II.98a). Branchiae are small, inconspicuous, simple filaments present on segments 7 to 37 and are shorter than the dorsal cirri, which are long and smooth. Acicular setae have gently curving, pointed tips; compound setae have bifid tips and a small guard (Fig. 3.II.98b). This species was described from specimens collected at depths of 200 to 300 m (109 to 164 fm) off the northern coast of Maui and from the Pailolo Channel between Maui and Molokai.

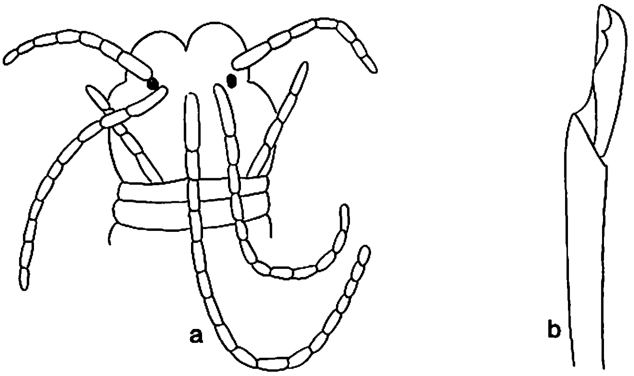

Figure 3.II.98.—*Eunice nicidioformis*: a, dorsal view of anterior region; b, compound falcigerous seta. (After Treadwell 1906.)

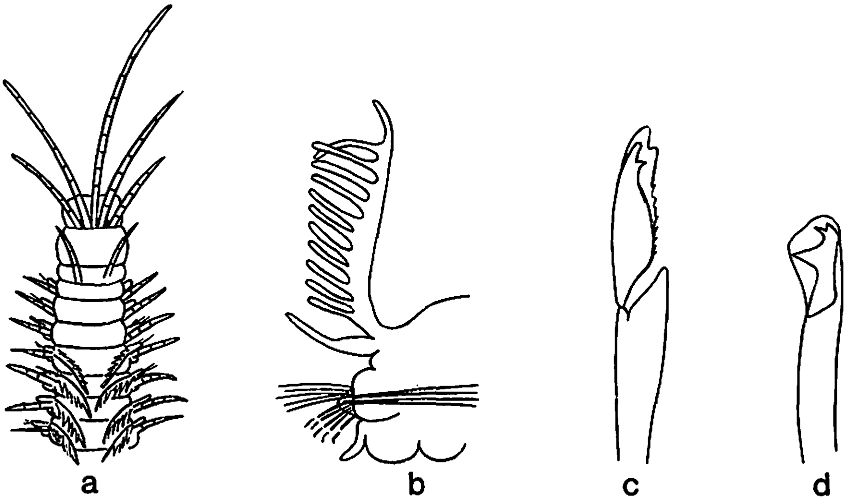

Figure 3.II.99.—*Eunice vittata*: a, dorsal view of anterior region; b, branchiferous parapodium; c, compound falciger; d, subacicular hook. (After Fauvel 1923.)

Eunice vittata (delle Chiaje, 1828)

Worms measure about 40 mm or more in length. The dorsum has transverse lines of red pigment. Occipital antennae and tentacular cirri are lightly annulated, the articles cylindrical and tapering (Fig. 3.II.99a). Branchiae begin on setiger 3 to 5, with as many as 12 filaments (Fig. 3.II.99b) at greatest development, and continue through the midregion, but are absent from the most posterior segments. Compound falcigers are bifid and have pointed hoods (Fig. 3.II.99c). Subacicular hooks are yellow and distally tridentate (Fig. 3.II.99d); acicula are yellow with slightly curved tips. *Eunice vittata* is known from tropical and subtropical regions of the world (Fauchald 1970) and has been collected off Kauai in fine coral sand at depths of 523 to 547 m (286 to 299 fm). - also shallow 1m

Lysidice ninetta Audouin and Milne Edwards, 1833
[syn. *Lysidice pectinifera* Kinberg, 1865. *L. fusca* Treadwell, 1922: Edmondson 1946. *L. collaris* Grube, 1870: Hartman 1966]

This worm attains a length of 150 mm (Day 1967). The prostomium is deeply cleft anteriorly and has 2 small, oval to reniform eyes and 3 simple, white occipital antennae (Fig. 3.II.100a). The peristomium consists of 2 smooth rings, followed by the first setigerous segment. The dorsum of the peristomium is brown with small white punctations. Acicula are thick, straight, black, embedded rods. Subacicular hooks are simple, distally hooded, and terminate in a bifid tip (Fig. 3.II.100c). Each compound falciger has a short appendage terminating in a bifid tip (Fig. 3.II.100b). Mandibles are gougelike, partly calcified, and have dark jaw supports. This Indo-West Pacific species (Fauchald 1970) occurs at shallow depths in coral rubble and algal turf. It has been found on the south and west coasts and at Kaneohe Bay, Oahu; Haleolono Pt., Molokai; and Halape, Hawaii (Hartmann-Schröder 1965; Hartman 1966).

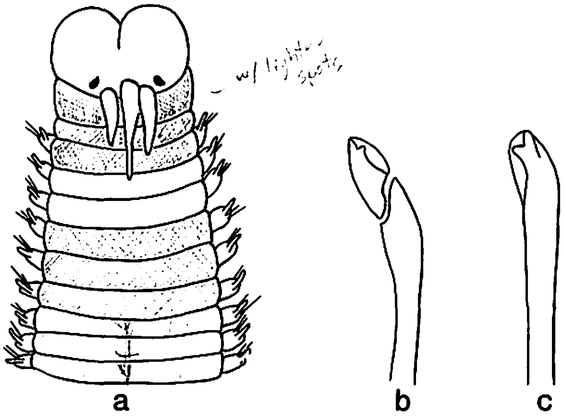

Figure 3.II.100.—*Lysidice ninetta*: a, dorsal view of anterior region; b, compound falciger; c, subacicular hook. (After Okuda 1937.)

KEY TO HAWAIIAN *MARPHYSA* SPECIES

1 Compound setae all spinigers with tapered tips 2
Compound setae all falcigers with bidentate tips .... *M. corallina*
2(1) Subacicular hooks unidentate without guards; prostomium rounded .... *M. macintoshi*
Subacicular hooks bidentate with small guards; prostomium incised .... *M. sanguinea*

Marphysa corallina Kinberg, 1865

This species attains a length of 300 mm (Day 1967). The prostomium is deeply incised in front, with 5 smooth, short occipital tentacles (Fig. 3.II.101a). Branchiae begin on about segment 18 and have as many as 5 filaments where best developed; each is accompanied by a short dorsal cirrus (Figs. 3.II.101b,c). Acicula are dark brown and taper distally; there are as many as 3 in a fascicle.

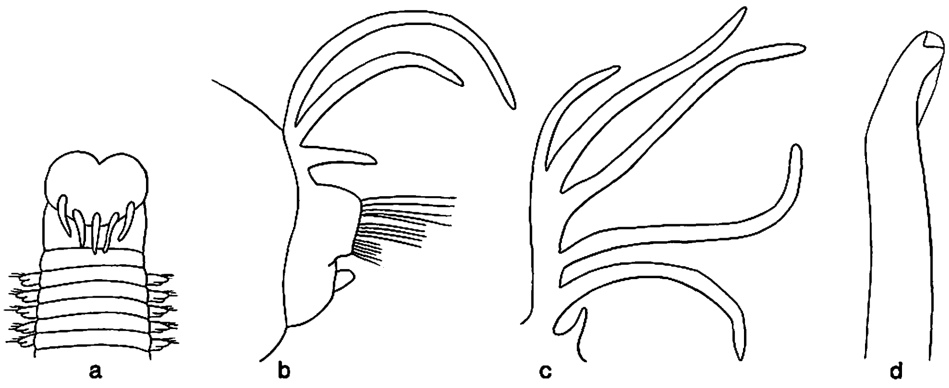

Figure 3.II.101.—*Marphysa corallina*: a, dorsal view of anterior region; b, branchiferous parapodium; c, 5 filament branchia and dorsal cirrus; d, hooded subacicular hook. (a after Kinberg 1910; c,d after Hartman 1948.)

Subacicular hooks are pale, simple, distally obliquely bifid, covered with a rounded hood (Fig. 3.II.101d), and number about 3 in a fascicle. Compound falcigers are distally bifid and covered with a rounded hood. Comb setae and slender capillaries are present. This species has an Indo-West Pacific distribution and has been found on south shore reefs on Oahu (Hartman 1966).

Marphysa macintoshi Crossland, 1903

This is a large worm reaching more than 200 mm in length, rounded in cross section, and slightly narrower at the anterior end. The prostomium (Fig. 3.II.102a) is rounded, bearing 5 smooth antennae as long as, or slightly longer than the

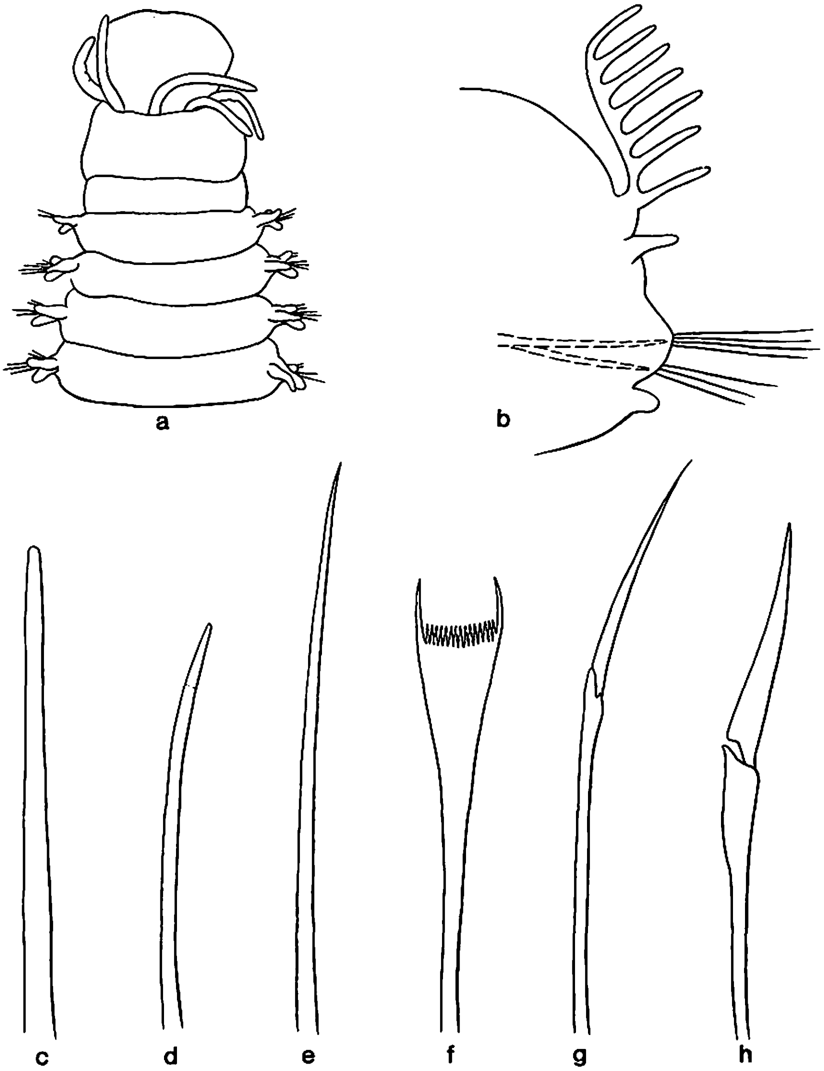

Figure 3.II.102.—*Marphysa macintoshi*: a, anterior region; b, branchiferous parapodium; c, aciculum; d, acicular seta; e, capillary seta; f, comb seta; g, anterior spiniger with long blade; h, anterior spiniger with short blade.

prostomium. The eyes are small and difficult to distinguish; the peristomium is slightly longer than the first segment and lacks tentacular cirri. Branchiae begin on the 37th setiger with 1 or 2 filaments and reach a maximum of 6 filaments (Fig. 3.II.102b) in the middle to posterior region. Parapodia each have a short but pointed dorsal cirrus and a round, lobate ventral cirrus. Anterior parapodia have 3 or 4 brown acicular setae; posterior parapodia have 1 aciculum and 1 acicular seta. Acicula have blunt, rounded tips (Fig. 3.II.102c); acicular setae (1 on each parapodium) have slightly narrower and paler tips that are unidentate (Fig. 3.II.102d). Parapodia also have capillary setae (Fig. 3.II.102e), comb setae (Fig. 3.II.102f), and compound spinigers with straight tips. The blades of anterior spinigers appear to be of 2 lengths (Figs. 3.II.102g,h), some very long and tapered, and others shorter with tapered tips. This Indo-West Pacific species (Day 1967; Fauvel 1953) has been found among coral rubble in Kaneohe Bay and on the Niu Valley reef, Oahu, in water less than 1 m deep (Bailey-Brock 1984a).

Marphysa sanguinea (Montagu, 1815)

Large specimens with about 200 segments are 75 to 150 mm long and 4 mm wide (Plate 3.II.3a). The prostomium (Fig. 3.II.103a) is incised in front and bears 5 short, smooth occipital tentacles in addition to paired eyes. The peristomium is a long, smooth ring without cirri. Branchiae begin on about segment 33 and have as many as 3 to 5 filaments in palmate arrangement (Fig. 3.II.103b). Acicula and subacicular hooks are light brown to dark yellow; the latter are distally hooded and bifid (Fig. 3.II.103c). Notosetae are capillaries, while neurosetae are com-

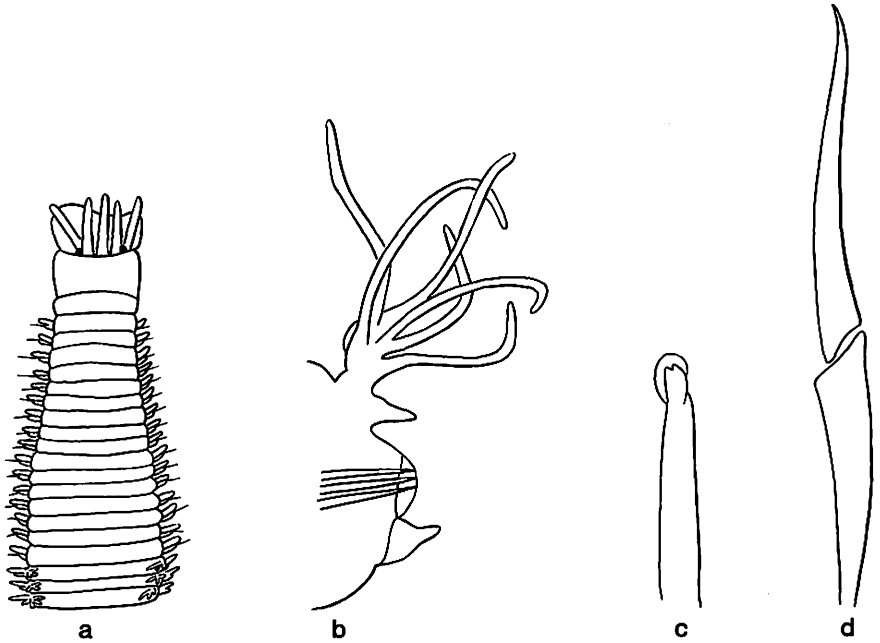

Figure 3.II.103.—*Marphysa sanguinea*: a, anterior region; b, branchiferous parapodium; c, bifid subacicular hook; d, neuroseta. (After Fauvel 1923.)

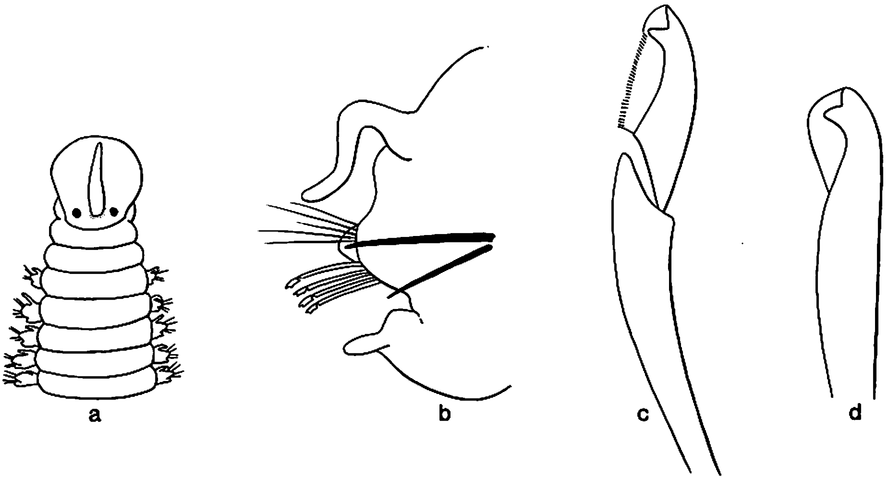

Figure 3.II.104.—*Nematonereis unicornis*: a, anterior region; b, parapodium; c, composite falciger; d, subacicular hook. (After Fauvel 1923.)

posite spinigers, each with a long, pointed blade (Fig. 3.II.103d). *Marphysa sanguinea* is a cosmopolitan warm-water species living on shallow coral reefs (Day 1967). This species has been collected from sand pockets on reef flats on Oahu's south shore and in Kaneohe Bay (Hartman 1966).

Nematonereis unicornis Schmarda, 1861

This is a small and slender species; the anterior end of 1 specimen has 37 segments and is 5.5 mm long. The prostomium is broadly conical, with a pair of dark eyes and a single occipital antenna (Fig. 3.II.104a). The first 2 segments are smooth rings without cirri. Parapodia (Fig. 3.II.104b) are short and uniramous, with slender dorsal cirri and padlike ventral cirri. Setae include dark acicula, limbate capillaries, pectinate setae, compound falcigers with bifid appendages (Fig. 3.II.104c), and subacicular hooks that are distally bifid and hooded (Fig. 3.II.104d). There are no branchiae. Mandibles are gougelike and partly calcified, with dark jaw supports. Tropical and subtropical in distribution, this species is found in coral rubble and among algal turf on reef flats (Hartmann-Schröder 1965), at shallow depths around the high Hawaiian Islands, and at French Frigate Shoals in the Northwestern Hawaiian Islands.

Palola siciliensis (Grube, 1840)
[syn. *Eunice siciliensis* Grube: Treadwell 1906]

This species may exceed 100 mm in length. The prostomium is medially incised, with 5 short, smooth occipital antennae (Fig. 3.II.105a) and a pair of dark eyes. Peristomial cirri are short and smooth, occurring on the second of 2 smooth rings that precede the 1st parapodial segment. Massive, calcified mandibles are usually seen extending from the oral aperture (Fig. 3.II.105b). (Calcified structures may dissolve during storage in formalin.) Branchiae are absent from a long

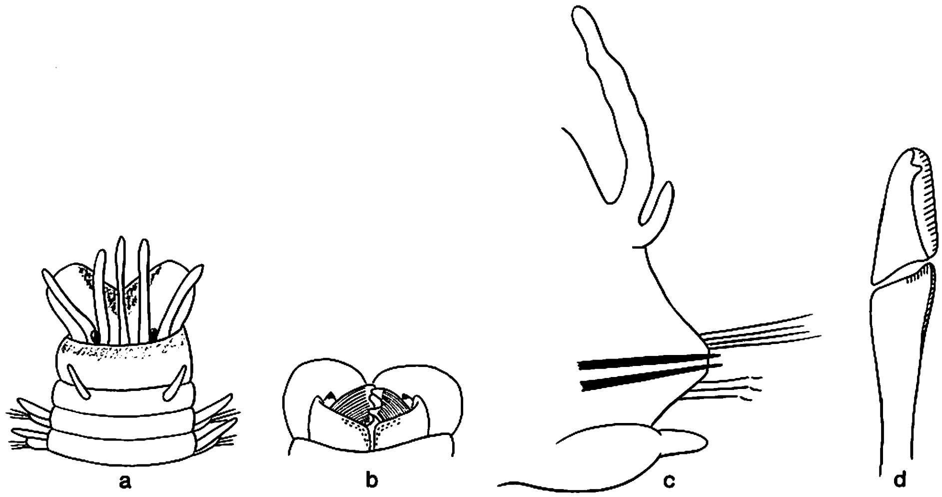

Figure 3.II.105.—*Palola siciliensis*: a, dorsal view of anterior region; b, ventral view with mandibles; c, branchiferous parapodium; d, composite falciger. (After Fauvel 1923.)

anterior region of 60 to 100 segments; they then appear as a single long filament above the short dorsal cirrus (Fig. 3.II.105c). Acicula are black with blunt, slightly rounded tips, while subacicular hooks and pectinate setae are totally lacking. Parapodia have simple slender setae and compound, distally bifid falcigers (Fig. 3.II.105d). This circumtropical species occurs throughout the Hawaiian Islands (Kohn 1959; Hartman 1966) and Indo-West Pacific region (Fauvel 1953), where it burrows into calcareous rocks, contributing to the erosion of coral reefs.

Palola siciliensis is the "palolo" worm collected by South Pacific islanders when it is swarming at the surface of the sea prior to spawning. Epitokal swarming is predictable and follows specific lunar phases in October and November, or November and December. In Fiji the worm is called "mbalolo" and vast numbers of it are scooped up and eaten raw or cooked. The nutritive value is high and the flavor of "palolo" soup is said to rival or surpass oyster and lobster soups (Miller and Pen 1959). Even today the collection of swarming "palolo" worms at Suva, Fiji, and in American Samoa is an important event that local residents look forward to and participate in with enthusiasm (R. Brock and D. Devaney, pers. comm.). "Palolo" worms also swarm in Vanuatu (New Hebrides), Samoa, Tonga, Rarotonga (Miller and Pen 1959), and the Solomon Islands (Gibbs 1971), and they have been given different local names in each island group. Gibbs also listed 4 other polychaete species collected as epitokes with *P. siciliensis* in the Solomons, and a fifth species, *Notopygos gregoryi* (Amphinomidae), that he concluded was feeding on the epitokes as they emerged. Such mass swarming by *P. siciliensis* is not known to occur in the Hawaiian Islands.

Family **Onuphidae**

Onuphids are tubicolous worms that construct tubes of sand and pieces of vegetation. They are scavengers, feeding on rotting vegetation, algae, and small invertebrates that are caught on protruding portions of the tubes (Fauchald and Jumars 1979). The intertidal species *Diopatra dexiognatha* feeds by extending partially out of the tube to forage near the tube mouth on pieces of algae attached to or trapped between tubes. Onuphids resemble the eunicids but are characterized by ringed ceratophores at the bases of the prostomial cirri, and stalked, spiral, pectinate or single filament branchiae on anterior parapodia. The shallow-water Hawaiian species is found in coarse sand on a south-shore fringing reef on Oahu. Two deep-water species, *Nothria hawaiiensis* Pettibone, 1970 [syn. *Nothria macrobranchiata* Treadwell, 1906: Hartman 1966], and *Onuphis (Nothria) holobranchiata* Marenzeller, 1879 (see Day 1967; Bailey-Brock, unpubl.), have been found at depths of 560 to 1115 m (280 to 557 fm) between the high Hawaiian Islands (Bailey-Brock, unpubl.).

Diopatra leuckarti Kinberg, 1865

Worms have a rounded anterior region with large, bushy branchiae and flattened posterior end. Branchiae from setiger 5 acquiring maximum development through the next 4 setigers and decreasing to setiger 33 where they are shorter than the dorsal cirri and comprised of a stalk and 3 filaments. Ventral cirri are largest on setiger 3 and cirriform through setiger 6, and as low padlike structures after that. Dorsal cirri are longer than the ventral cirri, the postsetal lobe is simple, the presetal lobe is unequally bifid (Fig. 3.II.216a). A single heavy acicular seta is present in parapodia from setiger 22 (Fig. 3.II.216b) and occur 2 in a fascicle from setiger 28. Comb setae are strongly asymmetrical and terminate in about 12 delicate teeth. *Diopatra leuckarti* is known from coral rubble habitats on south-shore reefs of Oahu (Hartman 1948, 1966).

Diopatra undescribed species

These worms are 15 to 31 mm long, 1.5 mm wide, and are rounded anteriorly and flattened posteriorly. The prostomium bears 5 tentacular cirri dorsally, with ringed ceratophores (Fig. 3.II.106b). Ventrally there is a pair of bilobed palps just in front of the mouth (Fig. 3.II.106c). The prostomium also bears a pair of short, squat antennae on the anterior margin. The peristomium has a pair of short tentacular cirri that are easily detached and may be missing, especially in juvenile specimens. Large, spiralled, stalked branchiae begin on setiger 4 and may partially cover the dorsum of anterior setigers (Fig. 3.II.106d). Branchiae are less well developed from setigers 21 to 33 and in posterior setigers are reduced to 1, 2 or 3 filaments that are shorter than the accompanying dorsal cirri (Fig. 3.II.106e). Parapodia of the 5 most anterior setigers are larger than the others, with long dorsal and ventral cirri, and single presetal and double postsetal lobes (Fig. 3.II.106d). Parapodia posterior to segment 7 have shorter dorsal cirri and padlike ventral cirri. Setae are broad blade capillaries (Fig. 3.II.106f) and comb setae (Fig. 3.II.106g). Setigers 1 to 6 have bifid, pseudocompound, hooked setae (Fig. 3.II.106h).

In recent years this species has been found along the inner part of the reef flat at Wailupe and Niu Valley Beach Park, Oahu, where the packed tubes (Plate 3.II.3b) form low, domed mounds near the beach (as *Diopatra leuckarti* Kinberg in Bailey-Brock 1980, 1984a). Worms build vertically oriented tubes (45 to 75 mm long) from shell and coral fragments and may attach pieces of frondose algae near

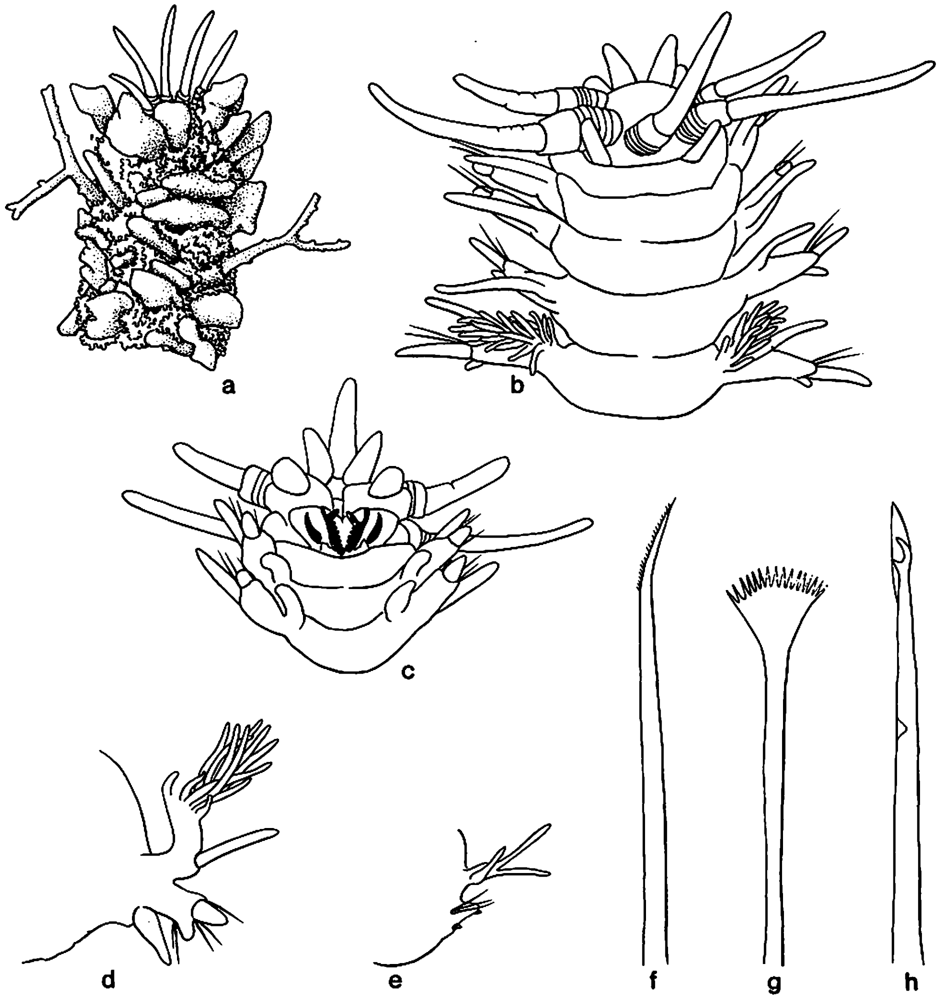

Figure 3.II.106.—*Diopatra* undescribed species: a, portion of a tube with tentacular cirri of worm protruding; b, anterior region, dorsal view; c, anterior region, ventral view; d, branchiferous parapodium from an anterior (1–4) setiger; e, branchiferous parapodium from a posterior setiger; f, limbate seta; g, comb seta; h, pseudocompound hooked seta.

the mouth (Fig. 3.II.106a). The Niu Valley site receives freshwater inundation following heavy rains from a nearby channelized stream and the sediments are anoxic below the upper 2 to 4 cm (Paxton and Bailey-Brock, in press).

Family **Lumbrineridae**

Lumbrinerids are cylindrical worms with inconspicuous uniramous parapodia. The prostomium is conical or rounded and globular and usually lacks eyes, antennae, and palps; nuchal papillae, when present, are minute. The mouthparts are well developed, with powerful jaws and musculature for predaceous and scavenging feeding or herbivory (Fauchald and Jumars 1979). The mouthparts are composed of paired mandibles and 4 pairs of toothed, platelike maxillae with a pair of maxillary supports. A diagnostic feature of many species in this family is the number of teeth on each pair of maxillae (maxillary plates). Maxillae I are closest to the maxillary supports (thus most posterior in position), resemble curved forceps with a terminal tooth on each plate, and are designated I = 1 + 1 to indicate 1 tooth on each plate. Maxillae II have 3 to 5 teeth along the inner (cutting) edge of each plate; when there are 4 or 5 teeth on each plate, the designation is II = (4–5) + (4–5). Maxillae III are smaller than II and have 1 to 4 teeth on each plate; when there are 4 teeth on each plate, the designation is III = 4 + 4. Maxillae IV are most anterior in position and usually have only 1 or 2 teeth on each plate; when there is only 1 tooth on a plate, the designation is IV = 1 + 1. A maxillary tooth formula for a species comprises the number of teeth on each plate of all 4 maxillae. The uniramous parapodia may have small dorsal cirri but lack ventral cirri. Setae include both capillaries and simple or compound hooded hooks. The presence of hooks readily distinguishes lumbrinerids from arabellids, which look superficially similar. Lumbrinerids burrow in soft or compacted sediments and in coral rock; they are prominent components of coral rubble and algal-mat communities (Bailey-Brock 1979). Species reported from Hawaiian waters are members of the genus *Lumbrineris*.

KEY TO HAWAIIAN *LUMBRINERIS* SPECIES

1 Anterior parapodia with hooded hooks and capillary setae 2
Anterior parapodia with winged capillaries only — error? .... *L. heteropoda*
2(1) Anterior parapodia with simple hooks 3
Anterior parapodia with composite hooks 4
3(2) Parapodia short and similar throughout .... *L. dentata*
Posterior parapodia with elongated postsetal lobes .... *L. sarsi*
4(2) Postsetal lobes of posterior parapodia only slightly longer than anterior lobes 5
Postsetal lobes of posterior parapodia distinctly longer than anterior lobes 6
5(4) Prostomium globular (Fig. 3.II.113a)................. *L. sphaerocephala*
Prostomium conical (Fig. 3.II.110a) .... *L. latreilli*
6(4) Prostomium globular; maxilla III with 3 or 4 teeth .... *L. inflata*
Prostomium conical; maxilla III with 1 tooth .... *L. minuscula*

Lumbrineris dentata Hartmann-Schröder, 1965

Specimens examined ranged from 16 to 30 mm long, and from 0.8 to 1.3 mm wide; segments number up to 88. The prostomium is subspherical (Fig. 3.II.107a) and is about as long as broad. The first 2 segments are smooth rings; others are smooth or indistinctly biannulate. Parapodia are short; each is supported by 2 yellow acicula (Fig. 3.II.107b). Simple hooded hooks and winged capillary setae (Fig. 3.II.107c) begin on the first parapodia; hooded hooks completely replace the capillaries by segments 19 to 30. Each hook terminates in a multidentate tip (Fig. 3.II.107d) and is covered by a rounded, dentate hood. Mandibles (ventral jaw plates) have long, slender bases fused anteriorly and flaring posteriorly. The

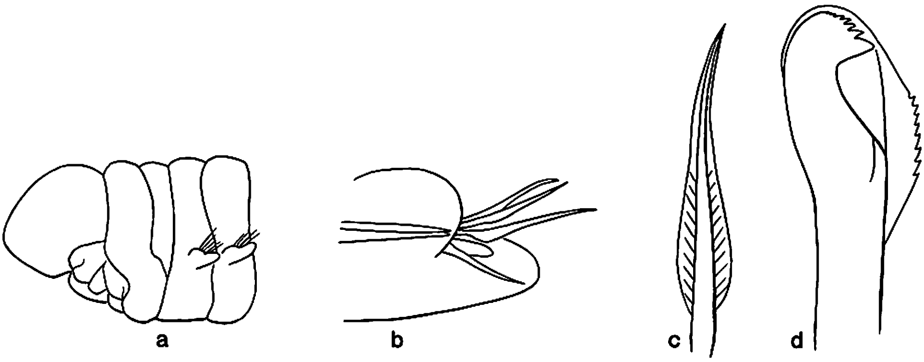

Figure 3.II.107.—*Lumbrineris dentata*: a, anterior region, lateral view; b, parapodium; c, winged capillary seta; d, hooded hook seta. (After Hartmann-Schröder 1965.)

maxillary tooth formula is I = 1 + 1; II = 4 + 4; III = 2 + 2; and IV = 1 + 1. This endemic species is known from Kahuku, where it was found in association with the ascidian *Styela* from Coconut Island in Kaneohe Bay and Kahana Bay, Oahu; Haleolono Pt., Molokai; and Paia, Maui (Kohn 1959; Hartmann-Schröder 1965; Hartman 1966).

Lumbrineris heteropoda (Marenzeller, 1879)

These long worms have 240 setigers; they are 120 mm long and are covered with an iridescent cuticle. The prostomium is a short cone (Fig. 3.II.108a). Mandibles have straight, broad shafts and calcareous cutting edges. The maxillary tooth formula is: I = 1 + 1; II = (4–5) + (4–5); III = 2 + 2; IV = 1 + 1. Parapodia have unequal lobes, presetal lobes are low and rounded (Fig. 3.II.108b); postsetal lobes are elongated and conical (Fig. 3.II.108c) and increase slightly in length posteriorly. Setae of setigers 1 to 35 are all winged capillaries (Fig. 3.II.108e), with simple hooded hooks present from setiger 36 (Fig.

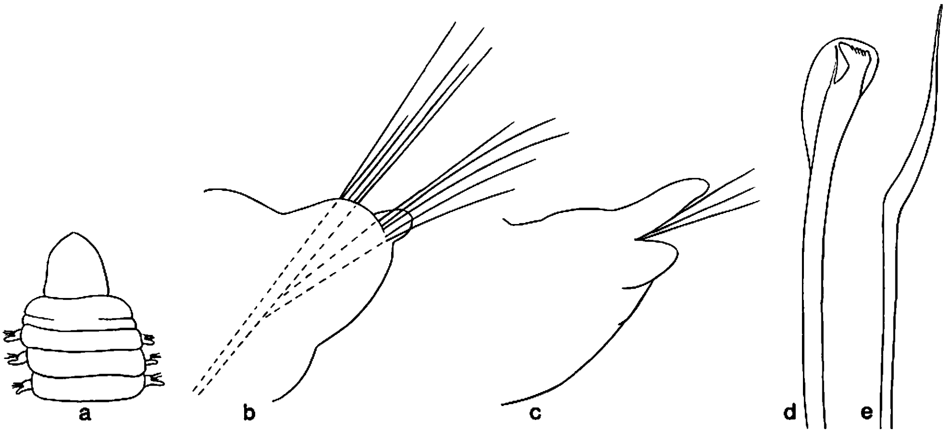

Figure 3.II.108.—*Lumbrineris heteropoda*: a, anterior region; b, anterior parapodium; c, posterior parapodium; d, simple, hooked seta; e, winged capillary seta. (After Day 1967.)

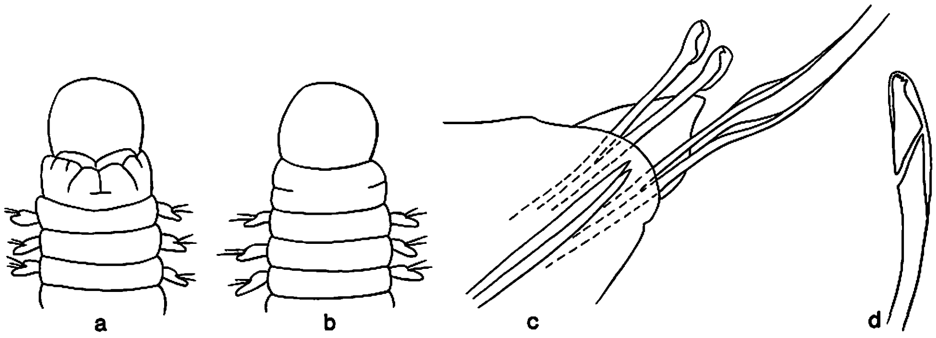

Figure 3.II.109.—*Lumbrineris inflata*: a, ventral and b, dorsal view of anterior region; c, parapodium of posterior region; d, hooded hook seta. (After Crossland 1924.)

3.II.108d); these posterior setigers also include 1 or 2 capillaries. Setae are all golden brown, and acicula are clear. This species has been found in benthic samples from Honolulu Harbor and Hawaii Kai, Oahu. *Lumbrineris heteropoda* has an Indo-West Pacific distribution (Imajima and Hartman 1964; Day 1967).

Lumbrineris inflata (Moore, 1911)

This orange worm reaches about 20 mm in length and has a white, depressed, globular prostomium (Figs. 3.II.109a,b), followed by a long peristomial ring that is weakly biannulate at the sides. Ventrally, this ring forms a crenulated lower lip (Fig. 3.II.109a). Composite, hooded hooks (Fig. 3.II.109d) and limbate capillaries are present from the 1st parapodium. More posteriorly, parapodia have simple hooks and capillary setae together with yellow embedded acicula (Fig. 3.II.109c). Posterior parapodia have prolonged postsetal lobes directed laterally or obliquely upward. The maxillary tooth formula is: I = 1 + 1; II = 5 + 5; III = (3–4) + (3–4); IV = 2 + 2. This species is known from intertidal areas in Hawaii and California and from the tropical eastern Pacific (Hartman 1966; Day 1967).

Lumbrineris latreilli Audouin and Milne Edwards, 1834
[syn. *Lumbriconereis grandis* Treadwell, 1906]

The body of a specimen consisting of 50 segments is up to 15 mm long. The prostomium is thick, conical, and bluntly pointed in front (Fig. 3.II.110a). Parapodia (Fig. 3.II.110b) are small and inconspicuous throughout. Composite hooded hooks (Fig. 3.II.110c) with dentate tips as well as capillary setae are found in anterior segments; more posteriorly, the composite hooks are replaced by simple hooks, with or without capillary setae. The maxillary tooth formula is: I = 1 + 1; II = 4 + 4; III = 2 + 2; IV = 1 + 1. Acicula are yellow. *Lumbrineris latreilli* has been found off Kauai and Honolulu in fine sand at depths of 300 to 500 m (164 to 274 fm). This species is cosmopolitan in warm seas.

Lumbrineris minuscula (Moore, 1911)
[syn. *Lumbriconereis minuta* Treadwell, 1906]

A specimen with 87 segments is about 20 mm long and 2 mm wide. Each postsetal lobe of the anterior parapodia (Fig. 3.II.111a) is broadly rounded.

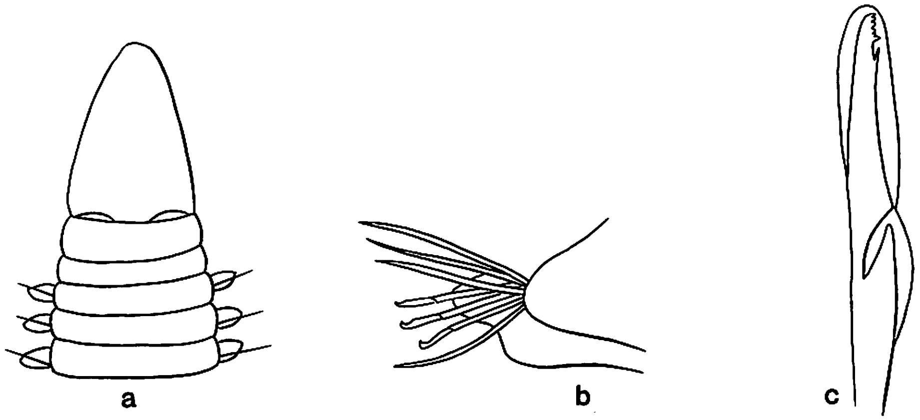

Figure 3.II.110.—*Lumbrineris latreilli*: a, anterior region; b, parapodium; c, composite, hooked seta. (After Fauvel 1923.)

Anterior setae include winged capillaries and composite hooks in vertical series. Each composite hook is covered by a rounded hood, the distal end of which is multidentate (Fig. 3.II.111b). Median and posterior parapodia have simple hooded hooks, together with some simple capillary setae in posterior parapodia. The maxillary tooth formula is incompletely described except for II = 5 + 4. This species is known only from Maui and was found at a depth of 500 m (274 fm) in sand (Hartman 1966).

Lumbrineris sarsi (Kinberg, 1865)
[syn. *Lumbriconereis havaica* Kinberg, 1865]

The length of the body of a specimen is more than 55 mm. Anterior parapodia have simple, winged capillary setae and hooded hooks without articulation. In median and posterior parapodia, winged setae are replaced by hooded

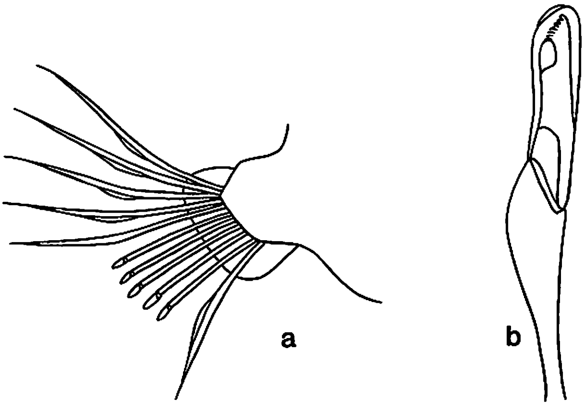

Figure 3.II.111.—*Lumbrineris minuscula*: a, anterior parapodium; b, composite, hooked seta. (After Hartman 1942.)

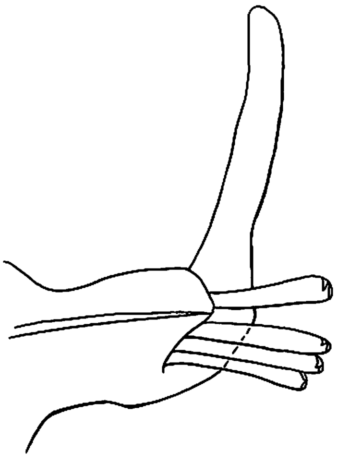

Figure 3.II.112.—*Lumbrineris sarsi*: anterior view of parapodium typical of middle and posterior setigers showing erect postsetal lobe. (After Hartman 1948.)

hooks, and the postsetal lobe elongates to form an erect lobe (Fig. 3.II.112). The maxillary tooth formula is incompletely known except for III = 2 + 2, and IV = 1 + 1. This species was first found near Honolulu (Hartman 1948a) at 40 to 60 m (22 to 33 fm) but subsequently at lesser depths from shallow coral reefs and intertidal benches on Oahu and Maui (Kohn 1959).

Lumbrineris sphaerocephala (Schmarda, 1861)

A specimen with a body 5 mm long has 26 segments. The dorsum of each segment bears a faint purplish brown transverse stripe and these are more conspicuous anteriorly. The prostomium is round, slightly depressed dorsoventrally (Fig. 3.II.113a), and marked with 2 triangular patches of purplish brown pigmentation. Presetal lobes are low and rounded; postsetal lobes are slightly longer and conical, especially in posterior parapodia. Anterior setae are winged capillaries (Fig. 3.II.113c) and composite hooded hooks (Fig. 3.II.113b). Posteriorly only simple hooded hooks are present (Fig. 3.II.113d). The maxillary tooth formula is: I = 1 + 1; II = 5 + 5; III = 3 + 3; and IV = 2 + 2. The mandibles are lightly calcified and fused basally. This species has been found commonly among fouling communities in Kaneohe Bay, Oahu. It has an Indo-West Pacific distribution (Fauvel 1953; Gibbs 1971).

Family **Arabellidae** — now Oenonidae

Arabellids are free-living, burrowing worms or endoparasites lacking prostomial appendages; they are superficially similar to the lumbrinerids. Typically, jaws are composed of a pair of mandibles and a series of paired maxillary plates supported by 1 paddle-shaped and 2 long, slender supporting rods. In contrast, lumbrinerids have only 2 maxillary supports, which are shorter and stouter. The parasitic genera may have maxillae reduced to a slender rod. The only genus known from the Hawaiian Islands is *Arabella*, having the character-

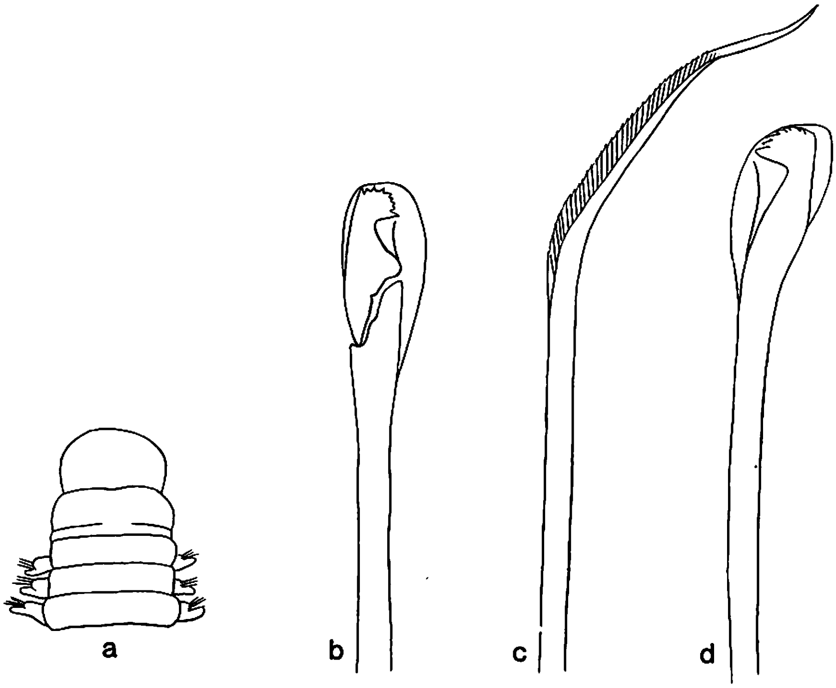

Figure 3.II.113.—*Lumbrineris sphaerocephala*: a, anterior region; b, composite, hooked seta of anterior setiger; c, winged capillary seta; d, simple, hooked seta of posterior setigers.

istic jaw structure of free-living arabellids with toothed maxillary plates and 3 long supporting rods. Parapodia are uniramous, with rudimentary dorsal cirri and winged capillary setae. Arabellids have no setae with hooded hooks, while lumbrinerids may have both simple and compound setae with hooded hooks. The free-living arabellids form part of the benthic community of coral reefs and algal turf developments on reef flats. The parasitic forms in this family, as yet unrecorded from Hawaii, parasitize other polychaetes and echiuran worms (Fauchald 1977a).

KEY TO HAWAIIAN *ARABELLA* SPECIES

Prostomium with 4 eyes in a transverse row	*A. iricolor*
Prostomium without eyes	*A. iridescens*

Arabella iricolor (Montagu, 1804)

These cylindrical worms reach approximately 40 mm in length and have a highly iridescent cuticle covering the entire body. The conical prostomium bears 4 dark eyes in a crescentic row near the junction with the 1st segment (Fig. 3.II.114a). Care should be taken to push back the projecting fold of tissue from the peristomium that may obscure the eyes; failure to do so could lead to an erroneous

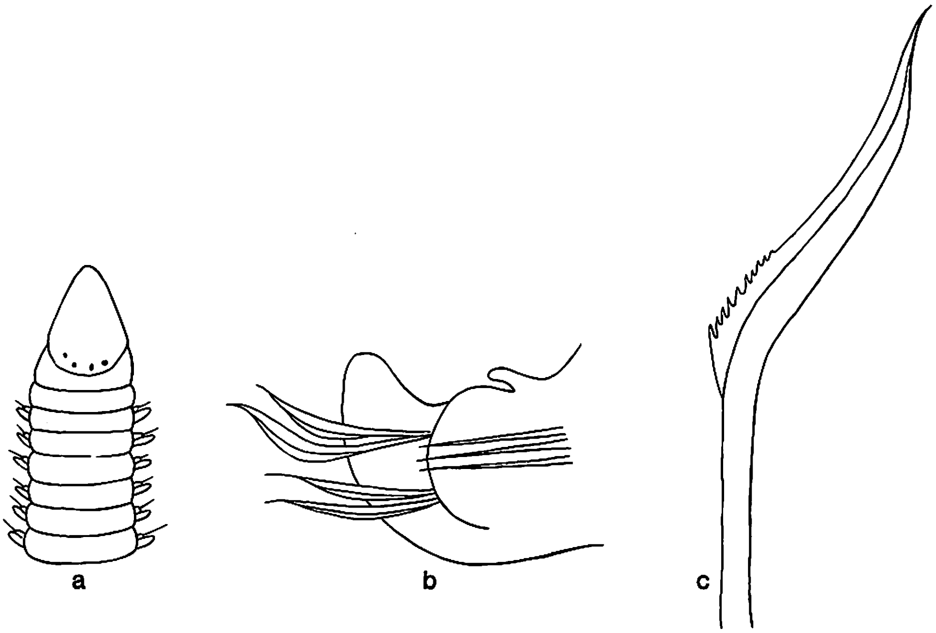

Figure 3.II.114.—*Arabella iricolor*: a, anterior region showing four eyes; b, anterior view of parapodium showing conical postsetal lobe and papilliform dorsal cirrus; c, dentate, limbate seta. (After Fauvel 1923.)

diagnosis as *A. iridescens*, which lacks prostomial eyes. The peristomial rings are smooth. The uniramous parapodia (Fig. 3.II.114b) have several embedded acicula and limbate setae of 2 kinds, some marginally smooth and others dentate (Fig. 3.II.114c). The middle maxillary support is long; the 1st pair of maxillary plates is falcate and the others are all multidentate. This species has a cosmopolitan distribution in shallow warm waters and has been recorded in Hawaiian waters from the algal mat at Paia, Maui, from coral rubble at Kaneohe Bay, Oahu, and from among the branches of a *Pocillopora* coral at Halape, Hawaii (Kohn 1959; Hartmann-Schröder 1965; Hartman 1966).

Arabella iridescens Treadwell, 1906

These cylindrical worms reach 75 mm or more in length, 4 mm in width, and are covered by a highly iridescent cuticle. The prostomium is bluntly conical, almost as broad as the first segment, and equal to the length of 3 segments (Fig. 3.II.115a). There are no eyes or other prostomial structures. Anterior parapodia are two-thirds the length of more posterior parapodia; the latter attain greatest development at segment 16. Parapodia are composed of a median lobe and a very small dorsal cirrus (Fig. 3.II.115b); there is no ventral cirrus. Setae are limbate, with toothed margins (Fig. 3.II.115c). This species has been found in coral rubble, among fouling communities, and associated with masses of *Chaetopterus*

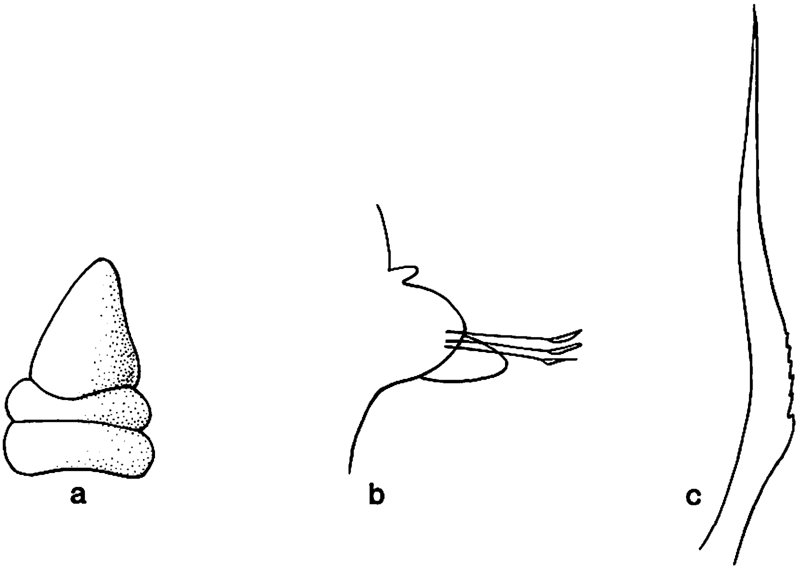

Figure 3.II.115.—*Arabella iridescens*: a, dorsal view of anterior region; b, parapodium; c, denticulate limbate seta. (After Treadwell 1906.)

variopedatus tubes on reef flats in Kaneohe Bay, Oahu, and also from the Pailolo Channel between Molokai and Maui at 232 m (127 fm) in muddy sand.

Family **Dorvilleidae**

Members of this family are eunicid-like worms with a rounded head bearing a pair of palps, 2 articulated antennae, and often a nuchal papilla. The jaw apparatus, considered primitive, consists of a pair of toothed mandibles and maxillae, the latter bearing 2 or 4 rows of many small-toothed denticles. Parapodia are uniramous, although a notoaciculum is present in the dorsal cirrus of some genera. Neurosetae include superior capillaries and often forked setae; inferior setae are compound falcigers with blades of varying length. In Hawaii, dorvilleids are common cryptofaunal components of shallow reefs (Bailey-Brock 1979). Fauchald and Jumars (1979) suggest that all dorvilleids are probably carnivores, but that they could feed on plant materials if necessary. The structure of the jaws would allow for such generalized feeding habits. Revisions of the family by Pettibone (1961) and Jumars (1974) were used to prepare the key and for identification of the 4 Hawaiian genera, only 1 of which had previously been recorded here.

KEY TO HAWAIIAN DORVILLEID GENERA

1 Notoacicula present 2
Notoacicula absent 3
2(1) Forked setae present .... *Schistomeringos*
Forked setae absent .... *Dorvillea*

3(2) Antennae and palps reduced to short papillae .... *Ophryotrocha*
Antennae and palps tentacular structures .... *Apophryotrocha*

Apophryotrocha sp.

These are small worms, 7 to 10 mm long. The prostomium is rounded, bearing a pair of antennae each having 4 to 8 articles (Figs. 3.II.116a,b). Bases of the palps appear somewhat swollen and each has an oval cirrostyle at the tip. There is no nuchal papilla, but 2 pairs of eyes are present. Dorsal cirri are absent from the first setiger and all are without notoacicula (Fig. 3.II.116c). Superior setae of 2 types occur: simple serrated capillaries (Fig. 3.II.116f) and simple, round-tipped, serrated capillaries (Fig. 3.II.116e). Inferior setae are heterogomph falcigers with bifid tips (Fig. 3.II.116d). Forked setae are absent. Setae of the first setiger are the same as in all other setigers. This as yet undetermined form has been collected from the reef flats at Coconut Island and Fort Kamehameha, Oahu. For a discussion of this genus see Jumars (1974).

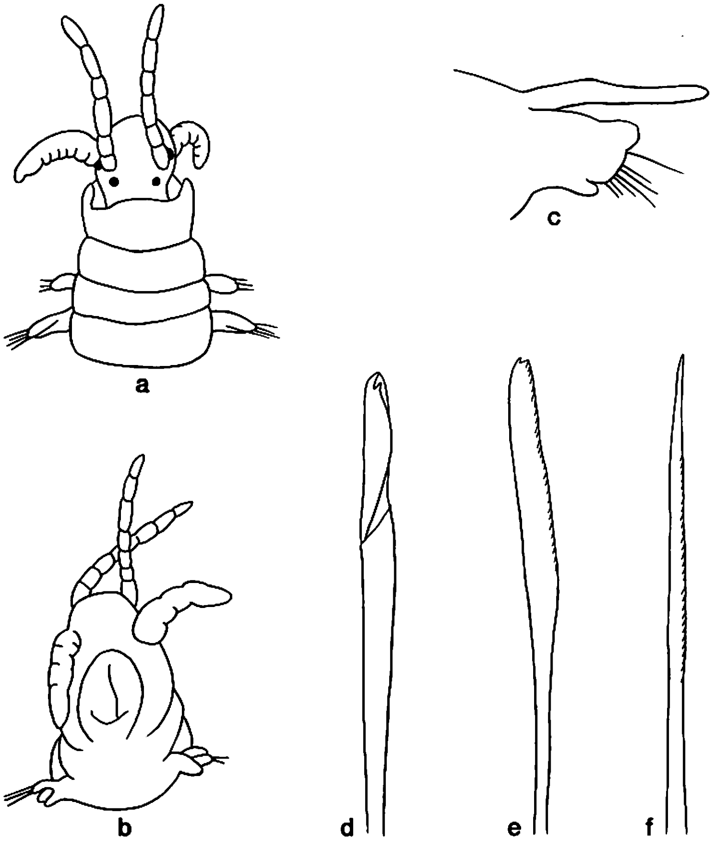

Figure 3.II.116.—*Apophryotrocha* sp.: a, anterior region, dorsal view; b, anterior region, ventral view; c, parapodium; d, falcigerous seta; e, round-tipped, serrated capillary seta; f, serrated slender capillary seta.

Dorvillea ?angolana (Augener, 1918)

This dorvilleid, up to 9 mm long, has 36 segments. The prostomium is rounded and bears 2 pairs of dark eyes, of which the most anterior pair is the largest and may be obscured by the bases of the antennae. A pair of long, slender antennae, each with 19 short articles is present (Figs. 3.II.117a,b). The paired palps are broad basally and appear wrinkled. Dorsal cirri have the notoacicula (Fig. 3.II.117c) in the basal portion of the cirrus and have conspicuous cirrostyles; dorsal cirri are absent from the first setiger. Ventral cirri are shorter than the notopodial cirrostyles. Parapodia have an anterior rounded and a posterior triangular lobe. Superior setae are long, serrated capillaries (Fig. 3.II.117e); inferior setae are bidentate heterogomph setae (Fig. 3.II.117d). Forked setae are absent. A number of specimens were found in a circulating holding tank at the Hawaii Institute of Marine Biology, Kaneohe Bay, Oahu. The questionable identification as *D. angolana* is based on close similarity with this species, which has been recorded only from West Africa (Day 1967).

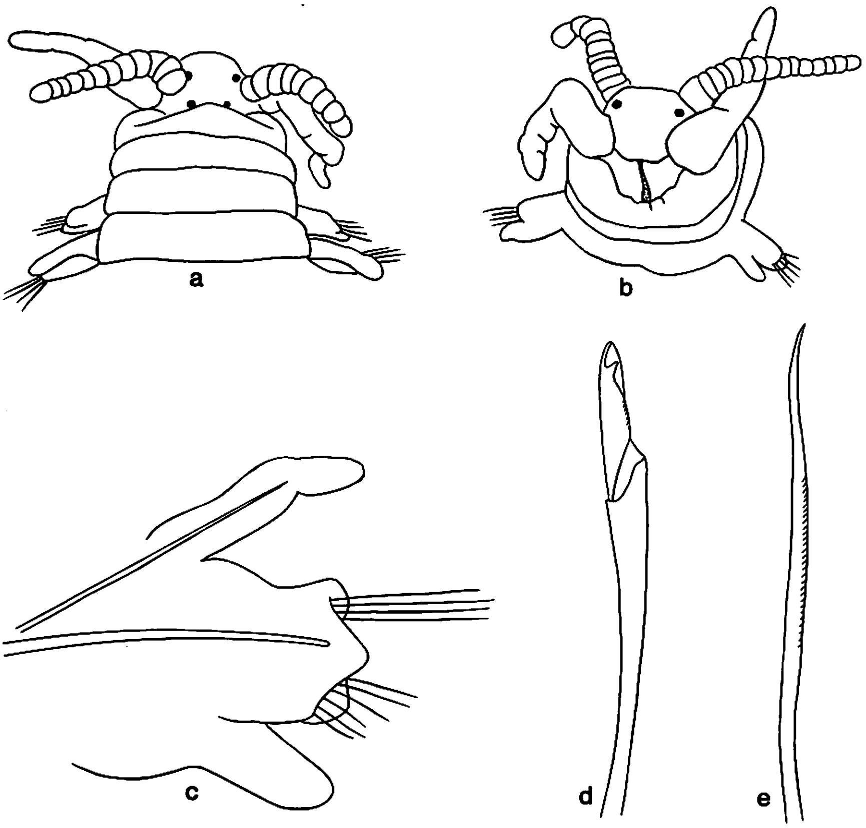

Figure 3.II.117.—*Dorvillea ?angolana*: a, anterior region, dorsal view; b, frontal view of head and first setiger; c, parapodium with notoaciculum in the dorsal cirrus; d, inferior falcigerous seta; e, superior serrated capillary seta.

Dorvillea moniloceras (Moore, 1909)
[syn. ?*Staurocephalus australiensis* Treadwell, 1906]

These worms are about 100 mm long. The prostomium is rounded, has a short nuchal papilla, a pair of dorsal antennae, and a pair of anterior palps (Figs. 3.II.118a,b). The nuchal papilla is between the antennal bases and may be partially obscured by a fold of the peristomium (Fig. 3.II.118a). The antennae are smooth (or slightly wrinkled after preservation), slender, and about the same length as the palps, which are broader basally (Fig. 3.II.118b). There are 4 red eyes, an anterior pair located at the bases of the palps and a posterior pair, with 1 eye at each side of the nuchal papilla (Fig. 3.II.118a). The parapodia are uniramous, with a long dorsal cirrus terminating in a cirrostyle and supported by a slender transparent notoaciculum (Fig. 3.II.118c). The ventral cirrus is short and projects ventrally. Setae are compound heterogomph falcigers with bifid tips (Fig.

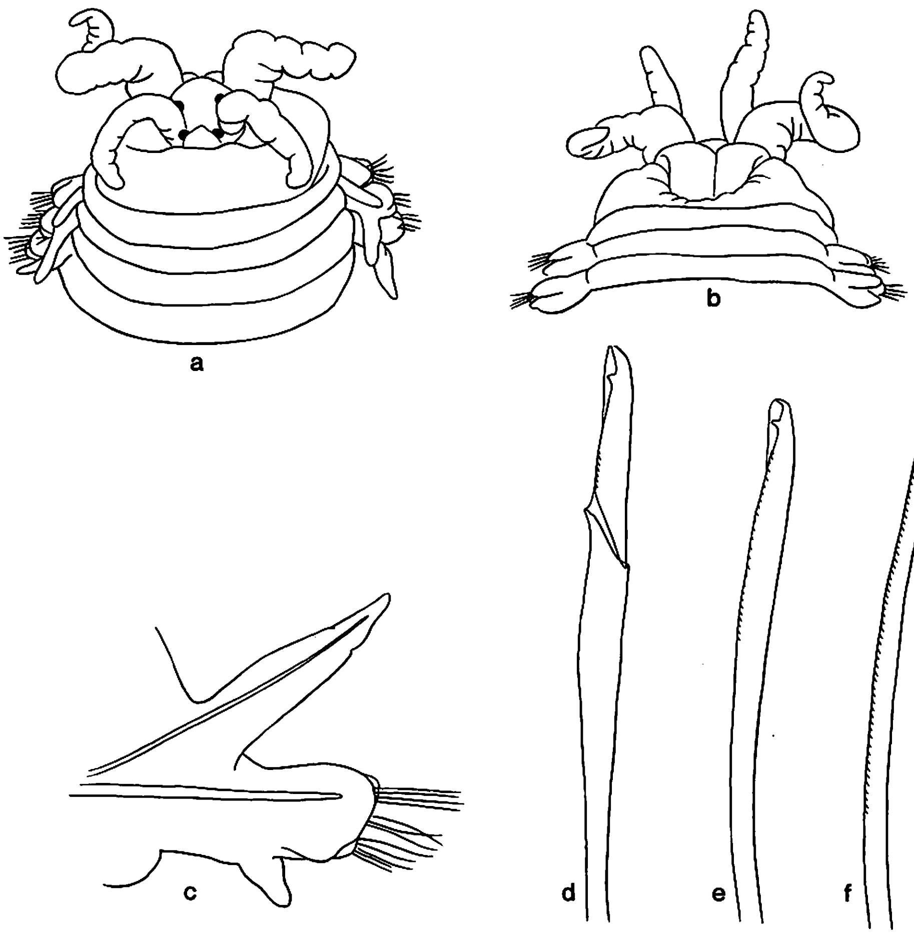

Figure 3.II.118.—*Dorvillea moniloceras*: a, anterior region, dorsal view; b, anterior region, ventral view; c, parapodium with notoaciculum in the dorsal cirrus; d, compound falciger; e, simple bidentate spiniger; f, serrated capillary seta.

3.II.118d), simple spinigers with bifid tips (Fig. 3.II.118e), and narrow capillaries (Fig. 3.II.118f). This species has been found in the Auau Channel between Maui and Lanai, off the south shore of Oahu at depths of 26 to 67 m (14 to 37 fm), and intertidally in dead coral heads. *Dorvillea moniloceras* otherwise has an Indo-West Pacific distribution.

Ophryotrocha sp.

A very small specimen, 2 mm long, composed of 16 segments has been found. The prostomium is hemispherical, with antennae absent and palps reduced to a pair of round papillae. Dorsal cirri are absent from the first setiger and all dorsal cirri are without notoacicula. Superior setae are serrated capillaries; inferior setae are bidentate compound falcigers. Forked setae are absent. This undetermined species was collected from sand and coral rubble on the reef flat at Fort Kamehameha, Oahu. For a discussion of this genus see Jumars (1974).

Schistomeringos rudolphi (delle Chiaje, 1828)

Specimens of this species with 80 segments are 15 to 20 mm long. The prostomium is broadly conical but blunt, and bears 2 pairs of eyes. Each long palp has a cirrostyle (Figs. 3.II.119a,b); the 2 antennae are jointed with 4 articles and are shorter than the palps (Fig. 3.II.119a). The first 2 segments lack parapodia and the multidentate maxillary teeth are often visible through the ventrum in this region (Fig. 3.II.119b, teeth not shown). Parapodia are uniramous. Each dorsal cirrus contains a notoaciculum and has a cirrostyle about half the length of the cirrus (Fig 3.II.119c). Dorsal cirri are missing from the first setiger. Superior setae include serrated capillaries (Fig. 3.II.119g), compound setae with slender blades (Figs. 3.II.119d,e), and 1 or 2 forked simple setae with unequal prongs and serrated shafts (Fig. 3.II.119f). Numerous specimens have been collected from coral settlement plates in Kaneohe Bay, Oahu. This widely distributed species is known from both sides of the North Atlantic, the Mediterranean, and western Mexico (Fauchald 1970; Jumars 1974; Gardiner 1975).

Family **Spionidae**

LINDA A. WARD

Spionids are tube-dwelling, boring, or free-living worms that inhabit coral reefs, sand banks, muddy estuaries, and waters of high sediment content. Two species of *Polydora* bore into calcareous substrates: *P. armata* in coralline algae (Blake and Evans 1973) and in the coral *Leptastrea purpurea* (Okuda 1937); *P. websteri* in oyster shells (Blake and Evans 1973). Sediment dwellers include *Pygospio muscularis*, which lives in shifting sand, *Minuspio* sp. and *Prionospio* sp., which form tubes in sediments on reef flats, and *Malacoceros* sp. and *Streblospio benedicti*, which live in muddy estuaries. *Polydora websteri* is of economic importance because it forms mud-filled burrows (mud-blisters) in the shells of cultured oysters, often making them unmarketable.

Spionids are predominantly surface-deposit feeders (Fauchald and Jumars 1979), using their extensible palps to gather and convey food particles to the mouth. The palps are also used to select and manipulate tube-building materials. Reproduction and larval development are varied in this family, but the tube-

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Plate 3.II.1

Notopygos albiseta (Amphinomidae). Dorsal view of live specimen showing the pleated sensory lobe behind the head, paired orange branchiae, and anal pore between setigers 22 and 23. (Courtesy S. A. Reed.)

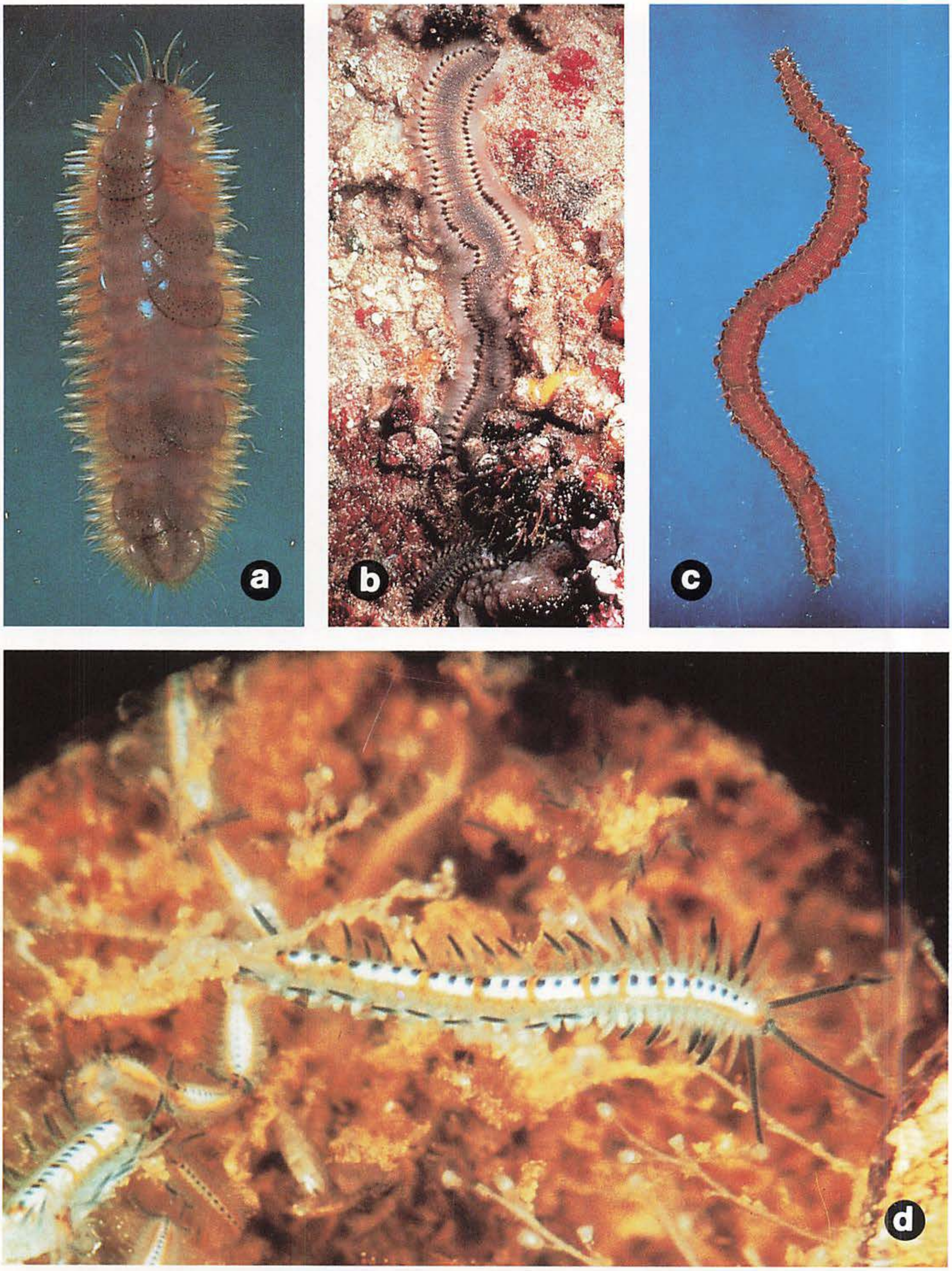


Plate 3.II.2

a. *Paralepidonotus ampulliferus* (Polynoidae). Dorsum covered by 15 pairs of overlapping scales; 4 scales missing from right side. (Courtesy S. A. Reed.) *Photo substituted for* Iphione muricata *photograph cited.*

b. *Eurythoe complanata* (Amphinomidae). Commonly called the fire worm, this species is found among coral rubble in shallow waters. (Courtesy Waikiki Aquarium.)

c. *Pherecardia striata* (Amphinomidae). A carnivorous fire worm from subtidal habitats. (Courtesy S. A. Reed.)

d. *Myrianida crassicirrata* (Syllidae). Brightly colored worms swimming over fouling community in Pearl Harbor. (Courtesy J. Grovhoug.)

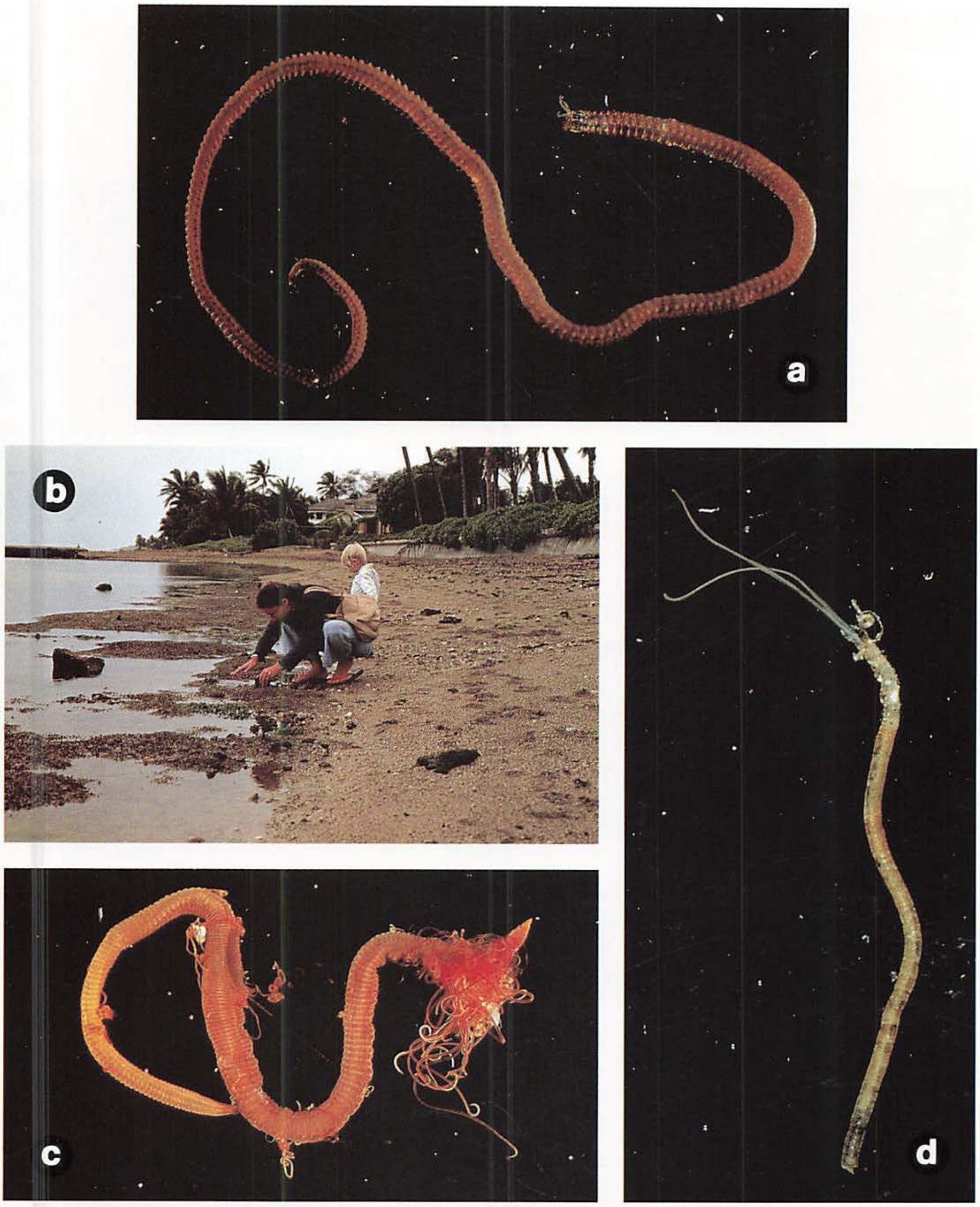


Plate 3.II.3

a. *Marphysa sanguinea* (Eunicidae). Entire worm showing segmentally arranged filamentous branchiae and the iridescent cuticle in the anterior region. (Courtesy S. A. Reed.)

b. *Diopatra dexiognatha* (Onuphidae). Mounds formed of closely packed tubes of *Diopatra dexiognatha* exposed at low tide at Kawainui Beach Park, Oahu. (Courtesy R. Brock.)

c. *Cirriformia hawaiensis* (Cirratulidae). A burrowing worm with numerous filamentous branchiae in the anterior region. (Courtesy S. A. Reed.)

d. *Phyllochaetopterus socialis* (Chaetopteridae). Paired extensile palps project from the translucent tube of this species. (Courtesy S. A. Reed.)

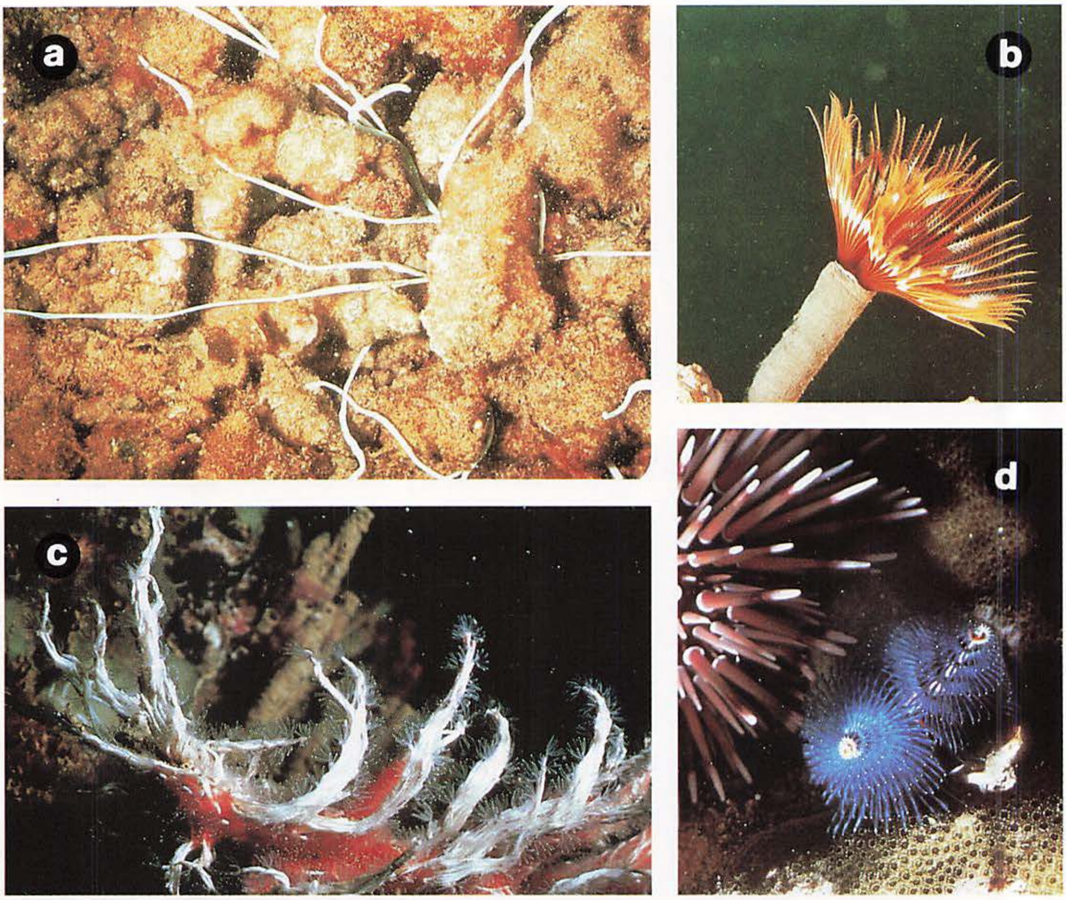


Plate 3.II.4

a. *Loimia medusa* (Terebellidae). Feeding tentacles extended over algal-covered coral rubble. (Courtesy S. A. Reed.)

b. *Sabellastarte sanctijosephi* (Sabellidae). Fan of colored radioles extend from the fine-grain mud tube. (Courtesy S. A. Reed.)

c. *Salmacina dysteri* (Serpulidae). Interwined white tubes and extended branchial crowns of this serpulid growing on a pier piling in Pearl Harbor. (Courtesy J. Grovhoug.)

d. *Spirobranchus giganteus corniculatus* (Serpulidae). The orange branchial crown and operculum project from the tube surrounded by the coral *Porites lobata*. (Courtesy J. Grovhoug.)

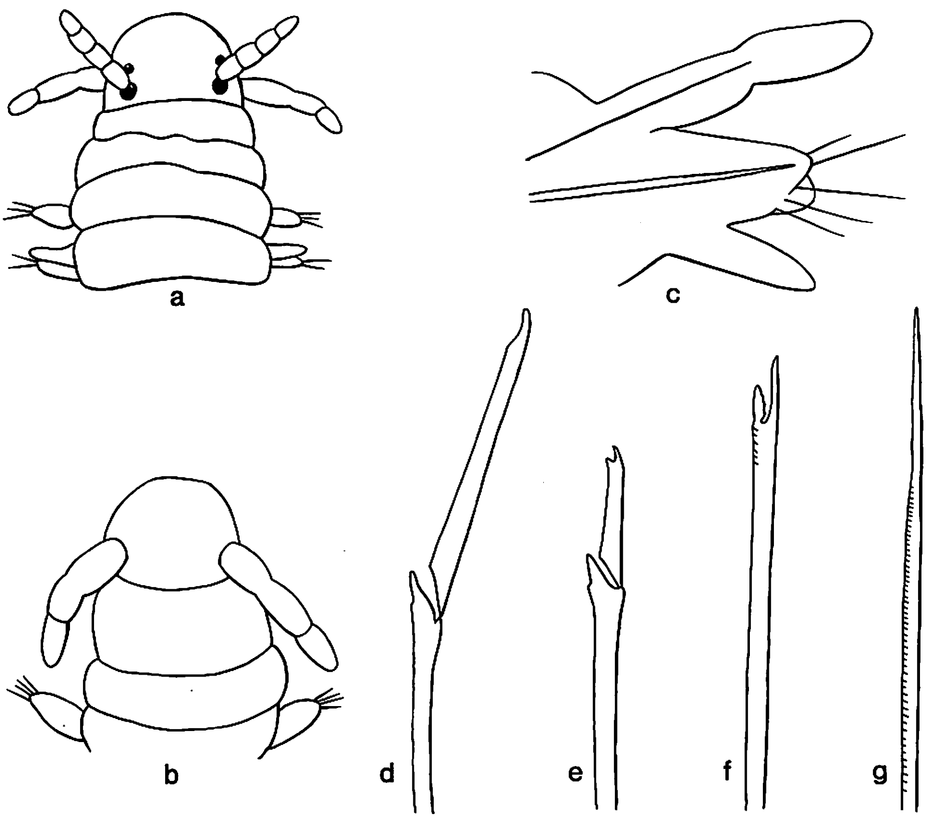


Figure 3.II.119.—*Schistomeringos rudolphi*: a, anterior region, dorsal view showing jointed antennae and palps with terminal palpostyle; b, anterior region, ventral view; c, parapodium with notoaciculum; d,e, compound setae; f, forked seta; g, serrated capillary seta.

dweller *Polydora websteri* is known to lay egg capsules and brood developing larvae within its burrows.

Spionid worms are elongate, taper posteriorly, and often have a conspicuous pygidium. The prostomium may be anteriorly rounded, incised, pointed, or with frontal horns, and often extends posteriorly as a low caruncle. Eyes and an occipital tentacle may or may not be present. A pair of long, grooved peristomial palps is characteristic of the family, but they are easily lost, sometimes leaving circular scars (see stippled circles on Figs. 3.II.135a, 136a, 137a). Parapodia are biramous, but the notopodial lobe may be absent or reduced in some anterior setigers. Most setae are simple capillaries, although some genera have modified spines on the fifth setiger. Hooks with 1 to many teeth, with and without hoods, are present in posterior neuropodia of all genera, and in the notopodia of genera such as *Prionospio* and *Scolelepis*. Dorsal branchiae, present in all genera except *Spiophanes*, may be straplike, cirriform, or pinnate. Branchiae are free or partially attached to notopodial lamellae. Pygidia vary in shape; they are cup- or saucer-shaped in *Polydora*, and they bear anal cirri in *Prionospio*, *Microspio*, and *Spio*.

The spionid fauna of Hawaii is incompletely known, but at least 29 species in 19 genera have been recognized (Ward 1981a). Hartman's review (1966) included only *Polydora websteri* and *Pseudopolydora antennata*.

KEY TO HAWAIIAN SPIONID GENERA

1 Branchiae absent; neuropodium 1 with a stout, hooked seta .... *Spiophanes*
Branchiae present; neuropodium 1 without a stout, hooked seta 2
2(1) Setiger 5 with modified spinelike setae 3
Setiger 5 without modified spinelike setae 7
3(2) Branchiae present from setiger 2 4
Branchiae present from setiger 5 5
4(3) Neuropodial hooded hooks tridentate, beginning on setiger 9 .... *Tripolydora*
Neuropodial hooded hooks bidentate, beginning on setiger 7 .... *Boccardiella*
5(3) Modified spines on setiger 5 of 1 type; bidentate neuropodial hooded hooks usually begin on setiger 7 (occasionally from 6 to 17) .... *Polydora*
Modified spines of setiger 5 of 2 types in 2 rows; bidentate neuropodial hooded hooks begin on setiger 7 to 14 6
6(5) Neuropodial hooded hooks with constriction on the shaft begin on setiger 8 .... *Pseudopolydora*
Neuropodial hooded hooks without constriction on the shaft begin on setiger 7 to 14 .... *Carazziella*
7(2) Branchiae present for most of body length 8
Branchiae limited to less than half of body length........ 16
8(7) Branchiae begin on setiger 1 9
Branchiae begin on setiger 2 12
9(8) Digitate accessory branchiae present on some setigers .... *Dispio*
Digitate accessory branchiae absent 10
10(9) Prostomium not T-shaped, rounded anteriorly........ *Spio*
Prostomium anteriorly T-shaped and blunt, or pointed and trilobed 11
11(10) Anterior margin of prostomium wide and blunt (Fig. 3.II.126a) .... *Malacoceros*
Anterior margin of prostomium trilobed (Fig. 3.II.121a) .... *Australospio*
12(8) Posterior notosetae are hooded hooks and capillaries 13
Posterior notosetae are capillaries 14
13(12) Branchiae free of notopodial lamellae .... *Aonides*
Branchiae fused to notopodial lamellae (Fig. 3.II.140c) ..... *Scolelepis*
14(12) Prostomium with frontolateral horns (Fig. 3.II.139a) ..... *Rhynchospio*
Prostomium without frontolateral horns 15
15(14) Prostomium anteriorly blunt, 1 pair of eyes (Fig. 3.II.125a); branchiae with pinnules .... *Laonice*

Prostomium anteriorly incised, 2 pairs of eyes; branchiae smooth .... *Microspio*
16(7) A single pair of branchiae present .... *Streblospio*
At least 2 pairs of branchiae present 17
17(16) Branchiae begin on setiger 7, restricted to medioposterior region .... *Pygospio*
Branchiae begin on setiger 2, restricted to anterior region 18
18(17) Branchiae all cirriform (Fig. 3.II.128a) .... *Minuspio*
Branchiae cirriform and pinnate (Fig. 3.II.134a) .... *Prionospio*

Aonides oxycephala (Sars, 1862)

A complete specimen is approximately 20 mm long and is composed of more than 100 setigers. The prostomium is anteriorly pointed, continuing back as a caruncle to setiger 1; an occipital tentacle and 2 pairs of eyes are present. The anterior pair of eyes are straight, the posterior pair are circular (Fig. 3.II.120a). The peristomium is inconspicuous and the palps are missing. Setiger 1 is reduced, with capillary setae in both parapodial lobes. Anterior notosetae and neurosetae are alimbate capillaries. Bidentate hooded hooks (Fig. 3.II.120b) begin on setiger 35 in the notopodium and on setiger 34 in the neuropodium and continue with a few capillaries to the end of the body. According to Day (1967) notopodial hooded hooks can occur from setiger 35 to 42 and neuropodial hooks from setiger 32 to 35. Cirriform branchiae, free of the notopodial lamellae, begin on setiger 2 and continue for about 25 setigers. Notopodial lamellae are large, and triangular anteriorly; they decrease in size in postbranchial setigers. Neuropodial lamellae are small and triangular throughout. The pygidium usually has 6 anal cirri, but there may be from 4 to 8 (Day 1967). This cosmopolitan species was collected from silt in a marine microcosm tank at Mokapu Peninsula and from Kaneohe Bay, Oahu.

Australospio mokapu Ward, 1981a

No entire specimens have been collected. The length of the largest anterior fragment, which has 64 setigers, is 20 mm. The prostomium is anteriorly trilobed

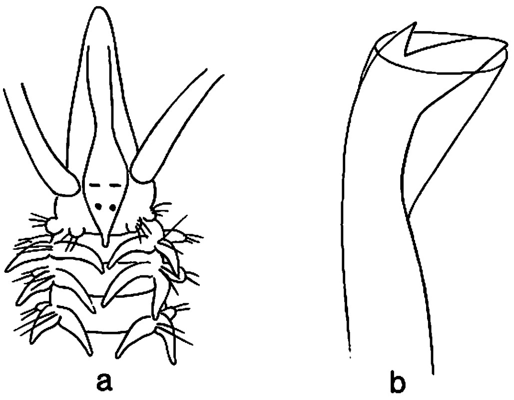


Figure 3.II.120.—*Aonides oxycephala*: a, anterior region, dorsal view showing 4 eyes and incompletely figured prostomial palps; b, neuropodial hooded hook.

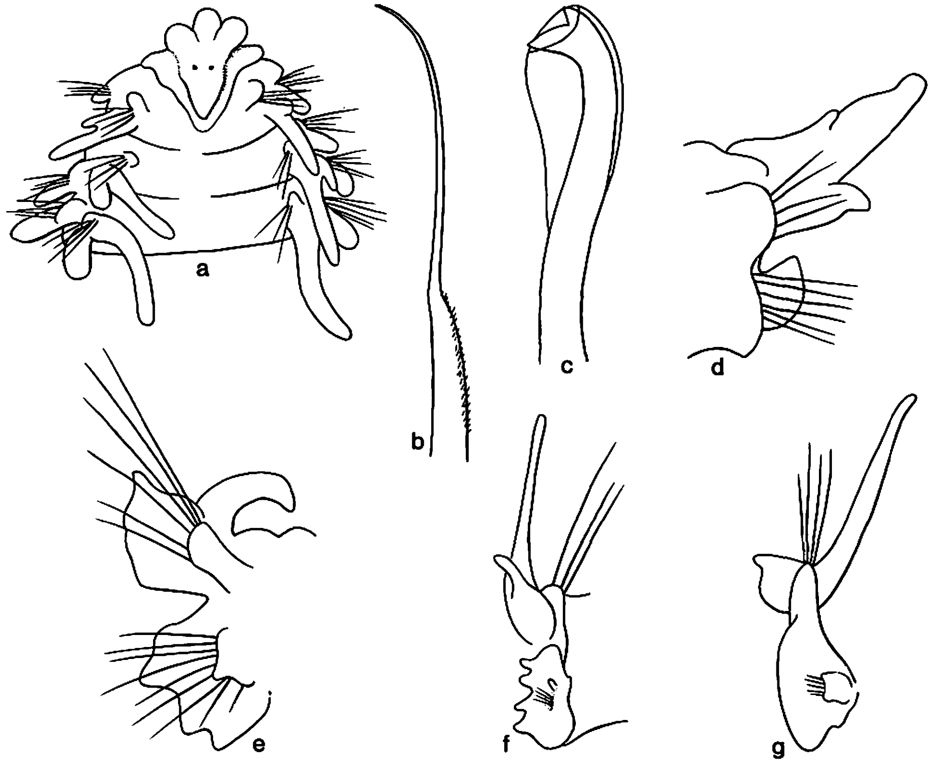


Figure 3.II.121.—*Australospio mokapu*: a, anterior region showing trilobed margin of the head; b, neuropodial geniculate seta; c, neuropodial hooked seta; d, parapodium, setiger 1; e, parapodium, setiger 13; f, parapodium, setiger 19; g, parapodium, setiger 40.

(Fig. 3.II.121a) and tapers as a caruncle to the posterior margin of setiger 1. One to 3 pairs of small, circular eyes are present; occipital tentacles are absent. The peristomium is reduced, forming small lateral wings. Setiger 1 is also reduced but bears capillary notosetae and neurosetae. Notosetae are winged capillaries in 2 tiers on setigers 1 to 5, followed by 4 tiers of heavy, granular, winged capillaries on setigers 6 to 9, and reverting to 2 tiers of finer, winged capillaries from setiger 10. Neurosetae form 2 tiers of winged capillaries on setigers 1 to 5, 4 tiers of heavy, granular, winged capillaries and geniculate setae with fine hairs (Fig. 3.II.121b) on setigers 6 to 9, 2 tiers of winged capillaries on setigers 10 to 14, 2 to 3 granular saber setae from setiger 15, and bidentate hooded hooks (Fig. 3.II.121c) from setiger 25. Tridentate neuropodial hooded hooks may be found on various posterior setigers of some specimens. Cirriform branchiae begin on setiger 1 and continue throughout the fragment. Basally these branchiae are attached firmly to the notopodial lamellae in the anterior portion of the fragment but they are connected by an easily detachable thin membrane in some posterior setigers. Notopodial lamellae are short and rounded on setigers 1 to 3 (Fig. 3.II.121d), becoming broader and leaflike from setiger 4, and increasing somewhat in size towards the rear of the fragment (Figs. 3.II.121e,g). Neuropodial lamellae are small and subtriangular on setigers 1 to 3 (Fig. 3.II.121d). The lamellae become

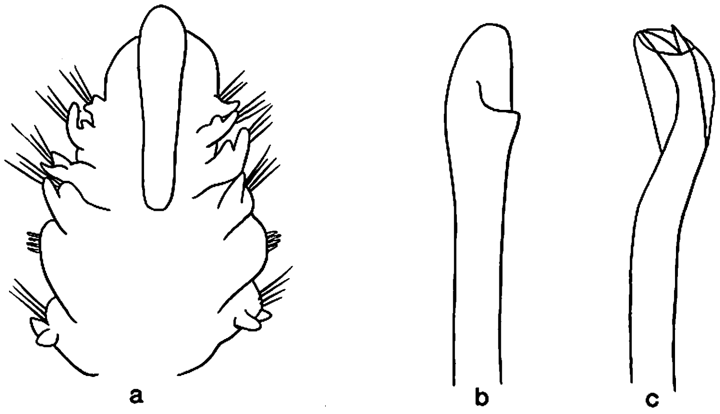


Figure 3.II.122.—*Boccardiella* sp.: a, anterior region; b, major spine, setiger 5; c, neuropodial hooked seta.

larger and broader from setiger 4, divide into 4 lateral lobes from setigers 10 to 14 (Fig. 3.II.121e), are produced into 4 papilla-shaped projections from setigers 16 to about 23 in some specimens (Fig. 3.II.121f), and finally are single elongate lobes on posterior setigers (Fig. 3.II.121g). The shape of the pygidium is unknown. Incomplete specimens were collected from silt at Sweep Pier Lagoon, Kaneohe Bay, and from sediment and coral rubble in marine microcosm experiment tanks at Mokapu Peninsula, Oahu (Ward 1981b).

Boccardiella sp.

The length of an anterior fragment of 48 setigers is 8 mm. The prostomium is damaged but appears to be bifid and it extends posteriorly as a caruncle to the middle of setiger 3 (Fig. 3.II.122a). Eyes and an occipital tentacle are absent, and the peristomium is inconspicuous. Setiger 1 is reduced, with the digitate notopodial lobe displaced dorsally; notosetae are absent; neurosetae are capillaries. Setigers 2, 3, 4, and 6 have notopodial and neuropodial capillaries. Setiger 5 appears uniramous, with dorsal and ventral fascicles of capillaries and a curved row of modified spines alternating with pennoned setae. Spines are simple and falcate, with a weak subterminal concavity (Fig. 3.II.122b). Bidentate neuropodial hooded hooks (Fig. 3.II.122c), without a constriction on the shaft, begin on setiger 7 and continue throughout the fragment along with a few capillary setae. There are no modified notosetae in the posterior portion of the fragment, thus preventing positive identification beyond the generic level (Blake and Kudenov 1978). Straplike branchiae begin on setiger 2, are absent on setiger 5, and reach full size on setiger 7. The shape of the pygidium is unknown. A single incomplete specimen was collected from coral rock at the reef crest in northern Kaneohe Bay, Oahu (Ward 1981b).

Carazziella reishi (Woodwick, 1964)

A complete specimen with 31 setigers is 3.5 mm long. The prostomium, slightly incised anteriorly, extends as a caruncle to the posterior margin of setiger 1 (Fig. 3.II.123a). The peristomium is inconspicuous; occipital tentacles and eyes are absent. Setigers 1 through 4 and 6 to 7 have capillary setae in the notopodium

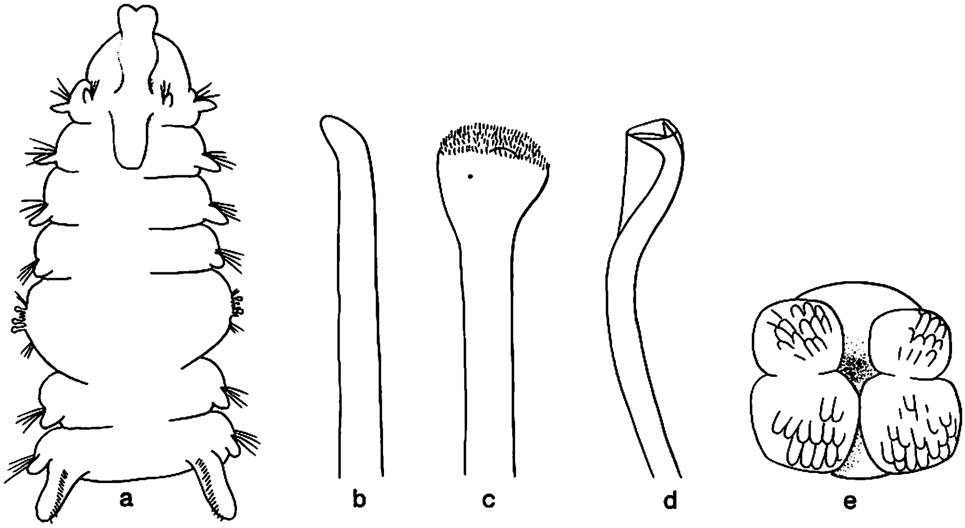


Figure 3.II.123.—*Carazziella reishi*: a, anterior region; b, simple falcate spine of setiger 5; c, bristle-topped spine of setiger 5; d, neuropodial hooked seta; e, pygidium.

and neuropodium. Setiger 5 appears uniramous, with dorsal and ventral fascicles of capillary setae and 2 curved rows of modified spines of 2 types: an outer row of simple falcate spines curved distally (Fig. 3.II.123b) and an inner row of falcate, bristle-topped spines with expanded distal ends arising from a small apical cone (Fig. 3.II.123c). Bidentate neuropodial hooded hooks (Fig. 3.II.123d), without a constriction on the shaft, begin on setiger 8 and continue to the end of the body along with a few capillary setae. Posterior notosetae are all capillaries. Small, straplike branchiae occur from setiger 7 until near the end of the body. The pygidium is quadrilobate (Fig. 3.II.123e). This species is a bioeroder and specimens have been collected in carbonate materials from the reefs in Kaneohe Bay and on the south shore of Oahu. It has also been reported from Enewetak, Marshall Islands (Woodwick 1964), Indonesia (Blake 1979), and Johnston Atoll (Ward 1981b).

Dispio uncinata Hartman, 1951

A single incomplete specimen with 70 setigers has been collected in Hawaii. The length of this anterior fragment is 30 mm. A pointed prostomium extends to the posterior margin of setiger 1 (Fig. 3.II.124a). An occipital tentacle and eyes are absent. There may be up to 4 eyes or none according to Foster (1971). The peristomium forms a collar laterally and ventrally. The notopodial lamellae on setigers 1 and 2 have serrate outer margins (Fig. 3.II.124a). Anterior notopodial lamellae are subrectangular and attached to the branchiae throughout their length. Posterior notopodial lamellae in the region of setiger 18 are distally free from the branchiae. Neuropodial lamellae are elliptical to rounded. Notosetae on setiger 1 are long capillaries. Anterior setae on the notopodium and neuropodium are granular, winged capillaries. Unidentate neuropodial hooded hooks (Fig. 3.II.124b) with companion capillary setae begin on setiger 19 in the Hawaiian

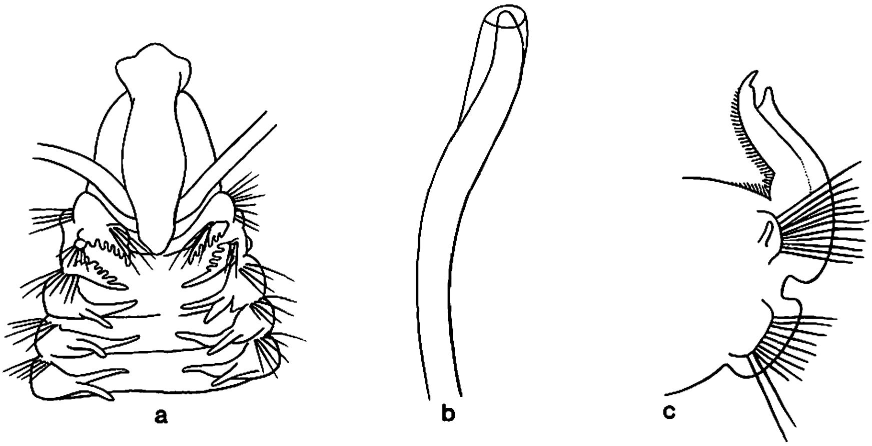


Figure 3.II.124.—*Dispio uncinata*: a, anterior region; b, neuropodial hooked seta; c, posterior parapodium showing accessory branchia attached to the dorsal lamella.

specimen, but these can range from setiger 16 to 37 (Foster 1971). Cirriform branchiae begin on setiger 1 and continue to the end of the fragment; they are attached basally to the notopodial lamellae. Accessory branchiae (Fig. 3.II.124c) consisting of 1 to 2 digitate lobes occur on the posterior portion of the neuropodial lobe from setiger 24. According to Foster (1971) the accessory branchiae in this species begin on setiger 18 to 28 and have up to 8 digitate lobes in the posterior setigers. The pygidium, missing in the Hawaiian specimen, has been described by Foster (1971) as having a midventral flap and 4 lateral anal cirri. The Hawaiian specimen was collected from sand on the southern portion of the barrier reef in Kaneohe Bay, Oahu (Ward 1981b). This species has been reported from the North Atlantic, Caribbean, Central America, and California (Foster 1971).

Laonice papillibranchiae Ward, 1981a

A complete specimen with 87 setigers is 12 mm long. The prostomium is anteriorly blunt, tapers posteriorly to the middle of setiger 1, and bears a long, thin occipital tentacle and a pair of large lightly pigmented eyes (Figs. 3.II.125a,b). The peristomium is inconspicuous. Setiger 1 is reduced and bears capillary notosetae and neurosetae. All notosetae and anterior neurosetae consist of 2 tiers of winged capillaries without granulations. The anterior row of capillaries is shorter than the posterior row. Bidentate neuropodial hooded hooks (Fig. 3.II.125c) begin on setiger 16 to 19 and continue posteriorly with a few fine capillaries. Two granular saber neurosetae (Fig. 3.II.125d) are present from setiger 9 or 12 posteriorly. Branchiae are free of notopodial lamellae and begin on setiger 2; they are absent on the posterior third of the body. The first pair is small and digitiform; they become longer and thinner from setiger 3, and reach full size on setiger 6. The branchiae (Fig. 3.II.125e) have pinnules or papillae on 1 side, giving them an appearance similar to the pinnate branchiae of *Prionospio*. Low ridges extend across the dorsum of each segment from setiger 17. Notopodial lamellae are small and digitate on setiger 1 (Fig. 3.II.125b), become foliose and large from setiger 2 (Fig. 3.II.125e), and decrease in size on posterior setigers. Neuropodial lamellae are smaller than notopodial lamellae; they are subtriangular on setigers 1 and 2

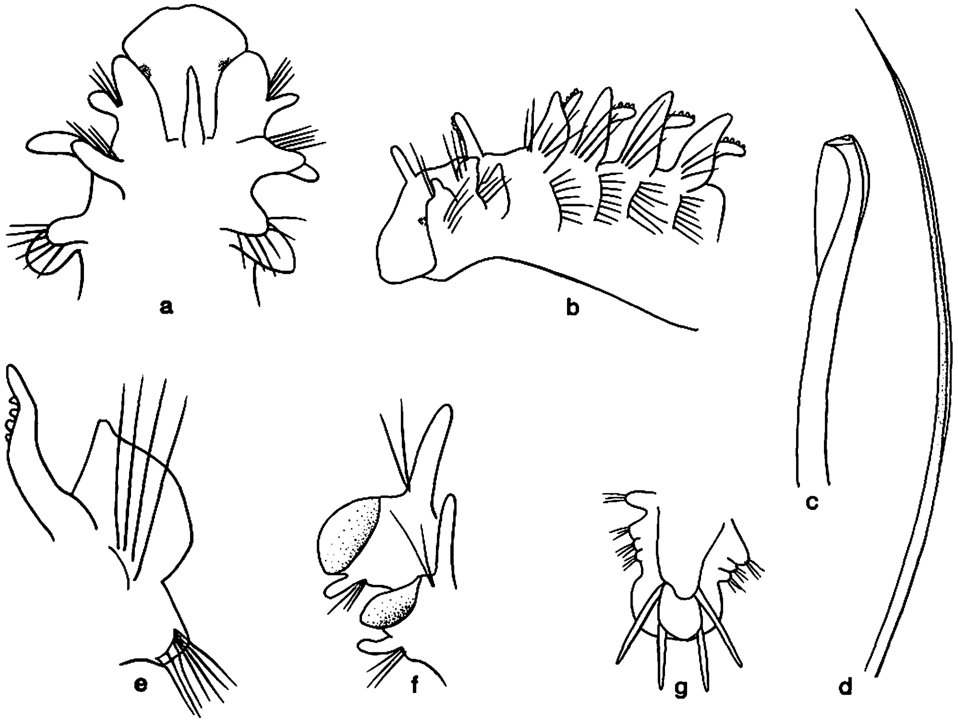


Figure 3.II.125.—*Laonice papillibranchiae*: a, anterior region, dorsal view showing prostomial occipital tentacle and pair of eyes; b, anterior region, lateral view; c, neuropodial hooked seta; d, neuropodial saber seta; e, anterior parapodium; f, dorsolateral view of 2 posterior setigers showing interramal pouches (stippled); g, trilobed pygidium with 4 slender dorsolateral anal cirri.

(Fig. 3.II.125b) and become subquadrate thereafter (Fig. 3.II.125e). Interramal pouches (Fig. 3.II.125f) are present between the notopodial lamellae from setiger 12 and 13. The pygidium (Fig. 3.II.125g) consists of 3 lobes with 4 elongate dorsolateral cirri, which are easily lost. This species has been reported from the south shore of Oahu in sand, at Barbers Point, and from Kaneohe Bay with coral rock and in mud.

Malacoceros sp.
[syn. *Malacoceros* cf. *M. vanderhorsti* Ward, 1981b]

This species is the largest of the Hawaiian spionids, with an anterior fragment of 175 setigers measuring 45 mm. The prostomium is T-shaped, with a pair of frontal lobes and a broad, slightly convex anterior margin (Fig. 3.II.126a). The prostomium tapers posteriorly, forming a raised caruncle from the anterior to the posterior margin of setiger 1 (Fig. 3.II.126a). An occipital tentacle is absent and eyes are small, circular, and numerous, forming 2 irregularly shaped groups. The peristomium is inconspicuous. Setiger 1 is reduced, with notopodia and neuropodia shifted dorsally. All notopodia and anterior neuropodia have capillaries. Neurosetae include a ventral group of 7 to 8 granular acicular setae. Neuropodial hooded hooks (Figs. 3.II.126b,c) begin from setiger 77 to 106. The hooks are tridentate (Fig. 3.II.126b) in anterior setigers and quadridentate in posterior setigers. Branchiae begin on setiger 1 and continue to the end of the

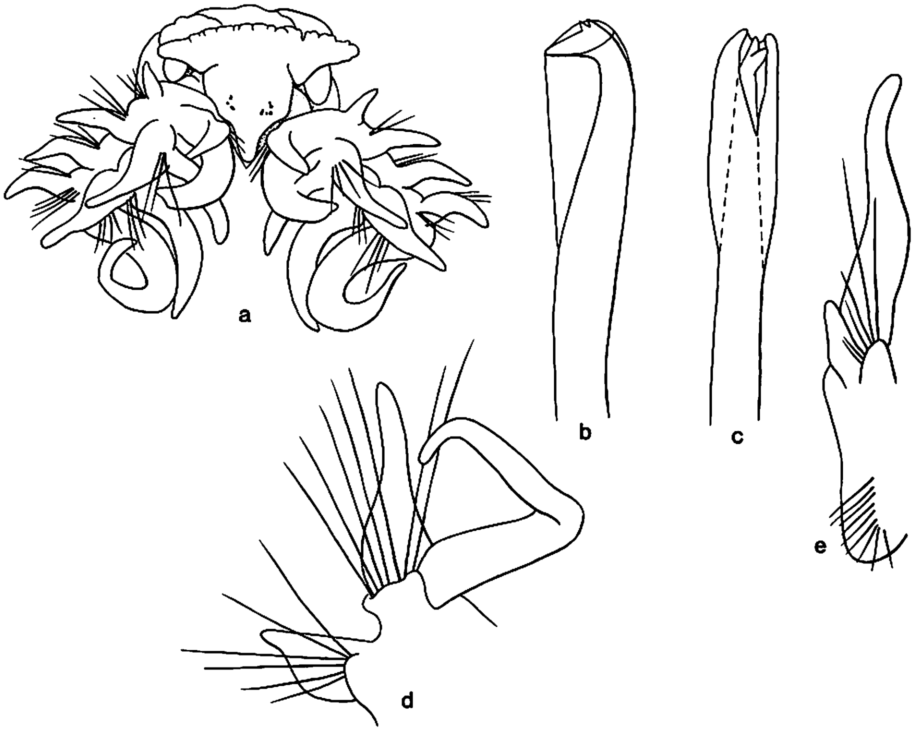


Figure 3.II.126.—*Malacoceros* sp.: a, anterior region showing T-shaped prostomium; b, neuropodial hooked seta, lateral view; c, neuropodial hooked seta, face view; d, anterior parapodium; e, posterior parapodium.

fragment; they are attached basally to the notopodial lamellae and taper distally. Branchiae extend over the dorsum and are longest in the anterior half of the fragment. Anterior notopodial lamellae are long, tapering distally (Fig. 3.II.126d); posterior lamellae are shorter and broader (Fig. 3.II.126e). Neuropodial lamellae are long and tapered on setiger 1, becoming more rounded in posterior setigers (Fig. 3.II.126e). Interramal glandular swellings start on setigers 1 to 2; they appear to continue as notopodial presetal lamellae. The shape of the pygidium is unknown for Hawaiian specimens. Specimens of *Malacoceros* sp. have been collected from mud banks in the eastern end of the Ala Wai Canal, an estuarine environment on the south shore of Oahu.

Microspio granulata Blake and Kudenov, 1978

A complete specimen with 34 setigers is 7 mm long. Brown pigment occurs dorsally on the prostomium as a band between the anterior pair of eyes and along the anterior margin of the prostomium. There are also patches of pigment on the dorsal surface of the first few setigers, on the outer margins of the branchiae, and laterally between the notopodia and neuropodia off the anterior setigers. The prostomium is anteriorly incised to form 2 lobes (Fig. 3.II.127a). An elevated prostomial caruncle extends posteriorly to the middle of setiger 2. A large occipital tentacle is present on the caruncle in the region of setiger 1 and extends forward between the eyes (Figs. 3.II.127a,b). Four round, black eyes are present

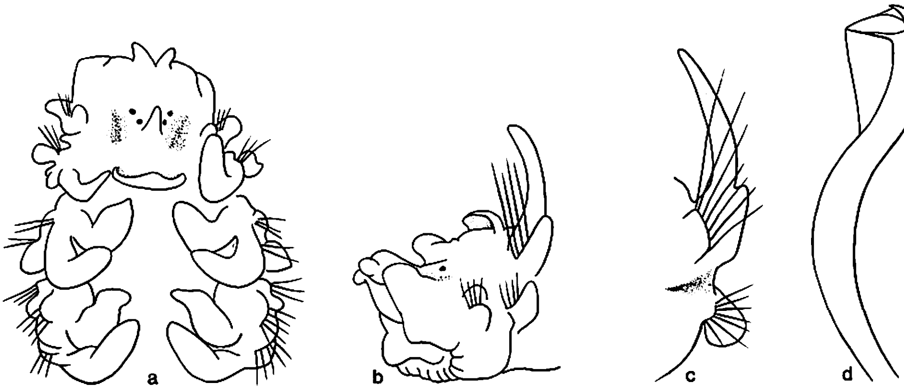


Figure 3.II.127.—*Microspio granulata*: a, anterior region, dorsal view (scars from prostomial palps are stippled); b, anterior region, lateral view; c, anterior setiger; d, neuropodial hooked seta.

in a trapezoidal arrangement; the posterior pair of eyes are close together on the caruncle and may be obscured by the occipital tentacle when viewed dorsally. A transverse dorsal hood is located directly posterior to the caruncle between the branchiae of setiger 2 (Fig. 3.II.127b). The peristomium is reduced laterally, and inflated ventrally. Setiger 1 has a small notopodial lobe lacking setae and a slightly larger neuropodial lobe with a few capillary setae. All notosetae consist of 2 tiers of granular, winged capillaries and a few longer superior capillaries. Anterior neurosetae are granular, winged capillaries in 2 tiers. The posterior tier of capillaries is replaced by fascicles of tridentate neuropodial hooded hooks (Fig. 3.II.127d) on setiger 9, with 4 to 5 hooks per fascicle, accompanied by an anterior row of granular, winged capillaries and a few very small, fine capillaries between the hooded hooks. Saber setae start in the neuropodium of setiger 15, and continue throughout the worm with 1 per fascicle. Branchiae begin on setiger 2 and continue throughout. They are attached basally to the notopodial lamellae and are connected dorsally by a low, ciliated ridge. The branchiae are longest on setiger 2 where they are erect. Branchiae on setigers 3 through 7 are approximately twice as long as the notopodial lamellae, and meet mid-dorsally; posterior to setiger 7 the branchiae are shorter. Notopodial lamellae are small and digitate on setiger 1, broadly triangular on setiger 2, and become shorter and narrower on setiger 7. Neuropodial lamellae on setigers 1 and 2 are long and narrow, becoming broadly rounded from setiger 3 (Fig. 3.II.127c). Interramal pouches are not visible in the Hawaiian specimens but reportedly start on setiger 12 in Australian specimens (Blake and Kudenov 1978). The pygidium has 4 anal cirri.

Hawaiian specimens of *M. granulata* build sand-grain and mucus tubes, which are attached to pieces of coral rock embedded in an algal-sand matrix on the reef bench. Specimens have been collected from Kaneohe Bay, Mokapu Peninsula, and the south shore of Oahu (Ward 1981b). This species is otherwise known from Botany Bay, New South Wales, Australia (Blake and Kudenov 1978), and Johnston Atoll (Ward 1981b).

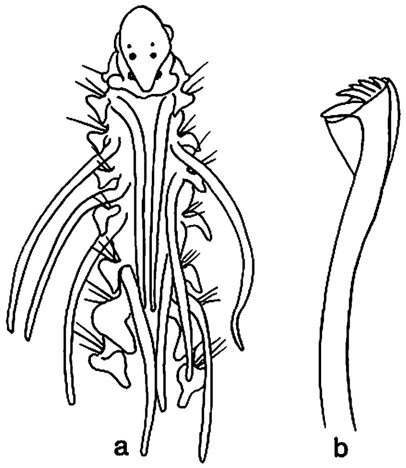


Figure 3.II.128.—*Minuspio* sp.: a, anterior region showing long cirriform branchiae (scars from prostomial palps are stippled); b, neuropodial hooked seta.

Minuspio sp.

The body length of a specimen with 80 setigers is 14.5 mm. Anteriorly the prostomium is rounded and it tapers as a caruncle to the posterior margin of setiger 1 or 2 (Fig. 3.II.128a). An occipital tentacle is absent. Two pairs of eyes are present; the anterior pair is small and round, and the posterior pair is larger. The peristomium, with low lateral wings, is closely affixed to the prostomium. Setiger 1 is reduced, fused with the peristomium, and has capillary notosetae and neurosetae. Branchiae begin on setigers 2 through 10; they are cirriform (Fig. 3.II.128a), of variable length, and there may be 6 to 12 pairs. Notopodial lamellae are triangular, smallest on setiger 1, increasing in size to setigers 7 to 8, then decreasing in size. Neuropodial lamellae are triangular, smaller than notopodial lamellae, and become low and rounded on postbranchial setigers. Faint dorsal ridges are present on postbranchial setigers. Interramal pouches are absent. Anterior setae are capillaries. Multidentate hooded hooks (Fig. 3.II.128b) occur in neuropodia beginning on setigers 15 to 16 and in notopodia from setiger 22. Granular saber neurosetae begin on setiger 12. The pygidium of Hawaiian specimens has a long, lateral anal cirrus on either the left or right side that is fragile and easily lost. This species has been found in sediment collected from the lagoon floor in Kaneohe Bay, from Barbers Point and Pearl Harbor, and from sediment and coral rubble in experimental microcosm tanks, Mokapu Peninsula, Oahu (Ward 1981b).

KEY TO HAWAIIAN *POLYDORA* SPECIES

1 Setiger 1 with notosetae; neuropodial hooded hooks without a constriction on the shaft 2

Setiger 1 without notosetae; neuropodial hooded hooks with a constriction on the shaft (Fig. 3.II.133c) 4

2(1) Posterior notosetae include capillaries and modified setae 3
Posterior notosetae are capillaries only .... *P. tridenticulata*
3(2) Posterior notosetae are heavy spines forming an inverted cone when extended; pygidium collar-shaped with a dorsal and ventral notch .... *P. armata*
Posterior notosetae are capillaries with a few short acicular spines; pygidium cup-shaped with a dorsal notch .... *P. pilikia*
4(1) Occipital tentacle present; posterior notosetae capillaries with acicular spines .... *P. kaneohe*
Occipital tentacle absent; posterior notosetae all capillaries .... *P. websteri*

Polydora armata Langerhans, 1880

A complete specimen with 28 setigers is 3 mm long. The prostomium is anteriorly rounded or incised and extends posteriorly as a caruncle to setiger 1 or 2 (Fig. 3.II.129a). Eyes and an occipital tentacle are absent, and the peristomium is inconspicuous. Setigers 1 through 4 and 6 have capillary setae on both rami. Setiger 5 appears uniramous, with dorsal and ventral fascicles of winged capillaries as well as a straight row of 2 to 4 modified spines. The spines are bluntly hooked distally, with a transverse flange (Fig. 3.II.129b) making them look tridentate. The appearance of the spines varies depending on the viewing angle and amount of wear. Bidentate neuropodial hooded hooks (Fig. 3.II.129c), without a constriction on the shaft, begin on setiger 7 and continue together with a few capillaries to the last setiger. Notopodial capillaries are replaced in posterior setigers by bundles of large golden spines that may be distally curved (Fig. 3.II.129d) or straight and form an inverted cone when protruded (Fig. 3.II.129e). Small straplike branchiae occur on setigers 7 through 12. The pygidium (Fig. 3.II.129e) is collar-shaped, with a dorsal and a ventral notch. *Polydora armata* is

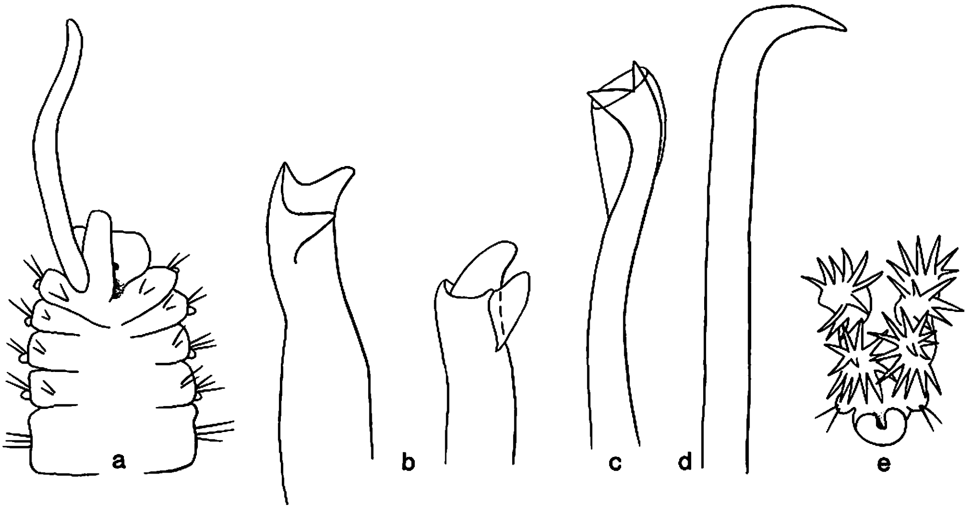


Figure 3.II.129.—*Polydora armata*: a, anterior region (left palp shown); b, major spine of setiger 5, 2 views; c, neuropodial hooked seta; d, curved posterior notopodial spine; e, clusters of straight posterior notopodial spines and notched pygidium.

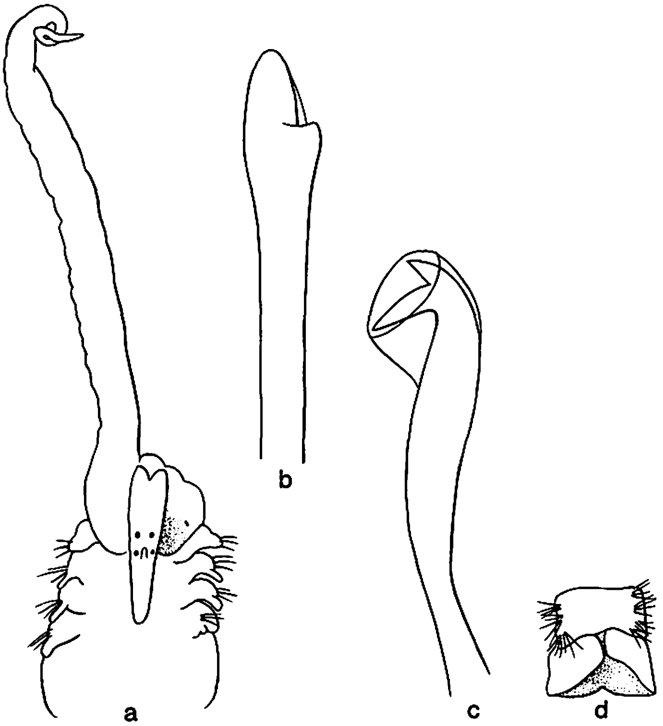


Figure 3.II.130.—*Polydora kaneohe*: a, anterior region (left palp shown); b, major spine of setiger 5; c, neuropodial hooked seta; d, pygidium.

a cosmopolitan species and is the most frequently encountered spionid on Hawaiian reefs, with densities reaching 36,600 worms/m^2. It is an important bioeroder of coral rock and coralline algae (Ward 1979).

Polydora kaneohe Ward, 1981a

A complete specimen with about 61 setigers is 9 mm long. The prostomium is incised, tapering as a raised caruncle to the posterior margin of setiger 2 or 3 (Fig. 3.II.130a). A small occipital tentacle is present on the caruncle, as are 2 pairs of round eyes. The peristomium is inconspicuous, and setiger 1 is reduced, lacking notopodia and notosetae; neurosetae are winged capillaries. Setiger 5 appears uniramous, with dorsal and ventral fascicles of winged capillaries and a curved row of modified spines alternating with pennoned setae. Spines are simple and falcate, with a broad shelf having a lateral sheath and a subterminal concavity (Fig. 3.II.130b). Bidentate neuropodial hooded hooks (Fig. 3.II.130c) with a constriction on the shaft begin on setiger 6 or 7. Straplike branchiae begin on setiger 7, reaching full size on setiger 10. Posterior notosetae include capillaries and short acicular spines. The pygidium is cup-shaped, with a dorsal notch and a portion missing from the ventral section, giving the ventral surface of the pygidium an indented appearance (Fig. 3.II.130d). Specimens were collected from Checker Reef and from settlement blocks in Kaneohe Bay, Oahu (Ward 1981b). This species was also collected at Suva Harbor, Fiji (Bailey-Brock 1985).

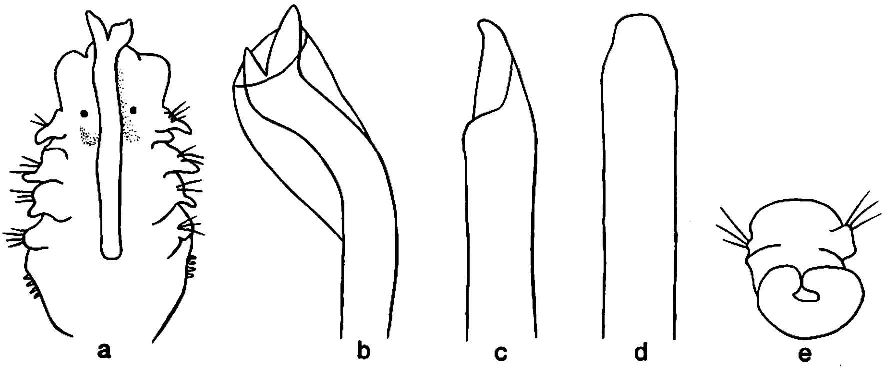


Figure 3.II.131.—*Polydora pilikia*: a, anterior region with long caruncle extending to setiger 5 (scars from prostomial palps are stippled); b, neuropodial hooked seta; c–d, major spine of setiger 5, 2 views; e, pygidium.

Polydora pilikia Ward, 1981a
[syn. *Polydora socialis* (Schmarda, 1861): White 1979]

A complete specimen with 70 setigers is 8.7 mm long and about 0.5 mm wide. The prostomium is anteriorly incised and the caruncle extends posteriorly through setiger 4 (Fig. 3.II.131a). Eyes are absent or there may be up to 3 circular pairs, some of which may be fused. The occipital tentacle is absent and the peristomium is inconspicuous. Setigers 1 through 4 and 6 have capillary setae in both the notopodia and neuropodia. Setiger 5 appears uniramous and bears a dorsal fascicle of geniculate setae, a ventral fascicle of winged capillaries, and a curved row of modified spines alternating with pennoned setae. The spines of setiger 5 vary in appearance depending on the viewing angle and amount of wear. Spines (Fig. 3.II.131c,d) are simple falcate, with a subterminal protuberance and a shelf that forms a concavity; the shelf extends laterally as a flange. The apical ends of the spines may be pointed or blunt (Fig. 3.II.131c,d). Bidentate neuropodial hooded hooks (Fig. 3.II.131b), which lack a constriction on the shaft, begin on setiger 7 and continue together with a few capillaries to the end of the body. Posterior notosetae include capillaries and acicular spines. Straplike branchiae begin on setigers 8 to 9 and continue to the end of the body. The pygidium is cup-shaped, with a dorsal notch (Fig. 3.II.131e). This very common bioeroder in coral rock (White 1979) has been collected from coral rock, coral settlement blocks, and sediment in Kaneohe Bay, from sand and rubble on the reef flat at Fort Kamehameha, and from sediment in Pearl Harbor, Oahu.

Polydora tridenticulata Woodwick, 1964

A complete specimen with approximately 115 setigers is 14 mm long. The prostomium is anteriorly incised and tapers as a caruncle to the posterior margin of setiger 3 (Fig. 3.II.132a). An occipital tentacle and eyes are absent. The peristomium is inconspicuous. Setiger 1 is reduced, with capillary setae on both notopodia and neuropodia. Setiger 5 appears uniramous, with dorsal and ventral fascicles of capillary setae and a curved row of modified spines, each of which is simple and falcate with 2 lateral teeth (Fig. 3.II.132b). The appearance of the modified setae of setiger 5 varies depending on the viewing angle and the amount

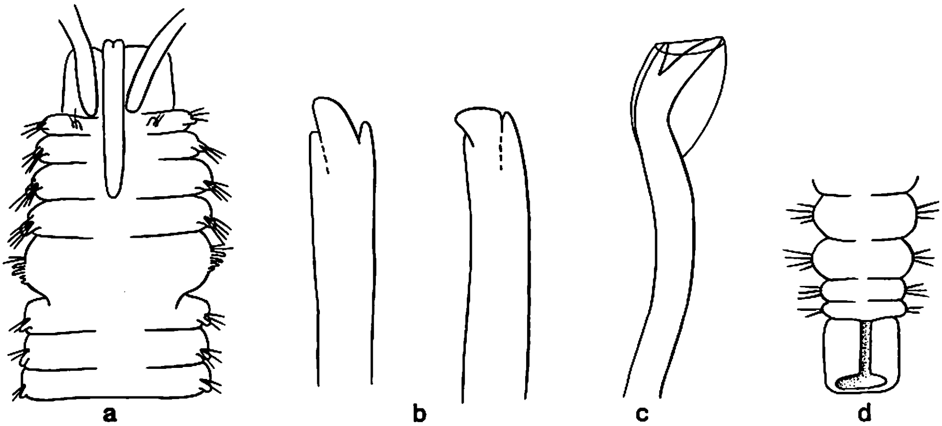


Figure 3.II.132.—*Polydora tridenticulata*: a, anterior region; b, major spine of setiger 5, 2 views; c, neuropodial hooked seta; d, pygidium.

of wear of the lateral teeth. Neuropodial hooded hooks (Fig. 3.II.132c), without a constriction on the shaft, begin on setiger 7 and continue with a few small capillary setae to the end of the body. Notosetae are capillaries throughout. Branchiae begin on setiger 7 to 10 as small papillae and reach full size on setiger 11. The pygidium is cuff-shaped and has a dorsal notch (Fig. 3.II.132d). Specimens have been collected in coral rock from reef flats in Kaneohe Bay and at Kewalo, and from muddy sediments in Kaneohe Bay and Pearl Harbor, Oahu (Ward 1981b). This species is also known from a coral rock habitat at Enewetak, Marshall Islands (Woodwick 1964).

Polydora websteri Hartman, 1943
[syn. *Polydora ciliata* (Johnston, 1838): Abbott 1946]

A complete specimen with 87 setigers is 9 mm long. The prostomium may be anteriorly notched or rounded and the caruncle extends posteriorly to setiger 2 (Fig. 3.II.133a). The occipital tentacle is absent, while eyes may be absent or may occur as 2 circular pairs. The peristomium is inconspicuous. The achaetous

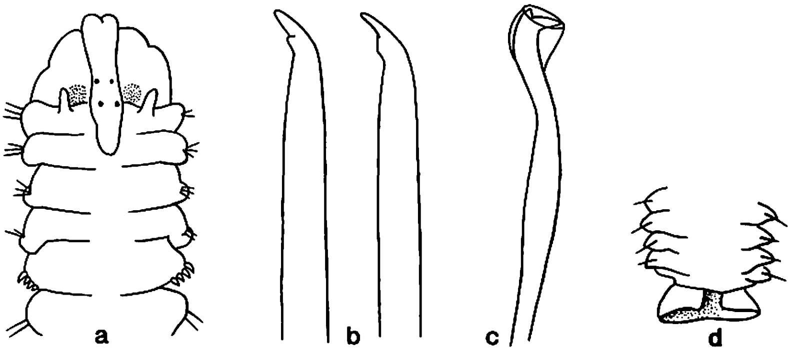


Figure 3.II.133.—*Polydora websteri*: a, anterior region (scars from prostomial palps are stippled); b, major spine of setiger 5, 2 views; c, neuropodial hooked seta; d, pygidium.

notopodial lobe of setiger 1 is displaced dorsally and the neuropodial lobe has capillaries. Setigers 2 through 4 and 6 have capillary notosetae and neurosetae. Setiger 5 appears uniramous, with 1 to 2 superior dorsal winged capillaries, a row of spines alternating with pennoned setae, and a ventral fascicle of short, winged capillaries. Each spine is simple and falcate with a lateral flange (Fig. 3.II.133b). Bidentate neuropodial hooded hooks (Fig. 3.II.133c) with a constriction on the shaft begin on setiger 7 and continue to the end of the body, replacing the capillaries. Posterior notopodia have capillaries only. Straplike branchiae begin on setiger 7 and are absent from posterior setigers. The pygidium is cup-shaped (Fig. 3.II.133d) and has a dorsal notch. Larval stages are pigmented with bar-shaped melanophores anteriorly and stellate melanophores on posterior setigers (Ward 1978).

Polydora websteri was reported from Wailupe Pond (Abbott 1946) and Pearl Harbor, Oahu (Hartman 1966), in muddy substrates and boring in oyster shells (*Crassostrea virginica*). This species has been found in commercially raised oysters from mariculture ponds near Kaneohe Bay and Kahuku, Oahu, and is detrimental to the oyster mariculture industry in Hawaii. Bailey-Brock and Ringwood (1982) discuss methods to control this pest in Hawaiian culture systems. Specimens have also been collected from coral rock in Kaneohe Bay and the Ala Wai Canal, as well as from mud in Nuupia Ponds, Oahu. Planktonic larvae were found in both Kaneohe Bay and the Ala Wai Canal (Ward 1978). This species has been reported from the east coast of North America, the Gulf of Mexico, and Oregon (Blake 1971).

Prionospio sp.

The body length of a complete specimen with 52 setigers is 10 mm. The prostomium is wedge-shaped, with the anterior margin bluntly rounded without an incision, and the posterior margin extending back as a caruncle to setiger 2 (Fig. 3.II.134a). Although an occipital tentacle is absent, 2 pairs of eyes are present; the anterior pair is small, circular, and sometimes obscured by the much larger, crescent-shaped posterior pair. The peristomium forms a collar laterally and ventrally and lacks lateral wings. Setiger 1, which is fused with the peristomium,

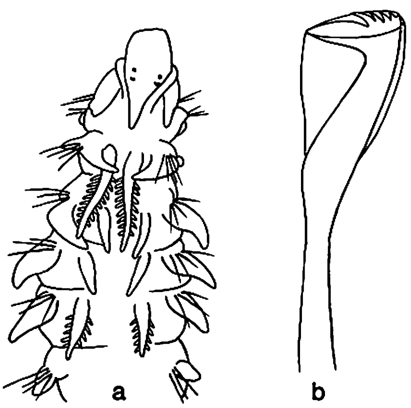


Figure 3.II.134.—*Prionospio* sp.: a, anterior region showing pinnate and cirriform branchiae; b, neuropodial hooked seta.

is reduced and bears capillary notosetae and neurosetae. Four pairs of branchiae are present on setigers 2 through 5; the first and fourth pairs are pinnate, the second and third pairs are cirriform (Fig. 3.II.134a), and all are approximately the same length. Notopodial lamellae on setiger 1 are small and rounded, becoming triangular with the distal end drawn out to a point on setiger 2 and increasing in size on setiger 3. Notopodial lamellae on setigers 4, 5, and postbranchial setigers are subquadrate, with rounded ventral edges, connected by a dorsal ridge beginning from setiger 7, and decreasing in size from setiger 12. Neuropodial lamellae are rounded on setigers 1 through 6, become larger and more foliose from setiger 7, and then decrease in size on posterior setigers. Anterior setae are all granular, winged capillaries, with those of the notopodia longer than those of the neuropodia. Heavy, granular saber setae start on setigers 10 or 11. Multidentate hooded hooks (Fig. 3.II.134b) begin in the neuropodia of setigers 10 to 17 and in the notopodia of setigers 20 to 29. The pygidium has 3 lobes and a single anal cirrus projecting from the medial lobe. Specimens have been collected from sediment in Kaneohe Bay, and among sand and coral rock at Kewalo, on the south shore of Oahu (Ward 1981b).

KEY TO HAWAIIAN *PSEUDOPOLYDORA* SPECIES

1 Occipital tentacle present; setiger 1 lacking notosetae 2
Occipital tentacle absent; setiger 1 with notosetae.... *Pseudopolydora* sp.
2(1) Posterior notosetae all capillaries; pygidium cup-shaped, with dorsal notch .... *P. antennata*
Posterior notosetae are bundles of attenuated spines; pygidium flared, with dorsal and smaller ventral notch .... *P. corallicola*

Pseudopolydora antennata (Claparède, 1870)

The length of an anterior fragment with 28 setigers is 3.5 mm. The prostomium is anteriorly incised and a caruncle extends posteriorly to setiger 2 or 3 (Fig. 3.II.135a). An occipital tentacle is present at the level of setiger 1. One to 2 pairs of eyes are present. The peristomium forms a collar laterally and ventrally. Setiger 1 lacks notosetae; its neurosetae are capillaries. Setigers 2, 3, 4, 6, and 7 have capillaries in both notopodia and neuropodia. Setiger 5 has dorsal and ventral fascicles of capillaries and modified spines in horseshoe-shaped rows. Spines are of 2 types: an outer row of spoon-shaped setae (Fig. 3.II.135b) whose distal ends are either drawn into a point or blunt from wear, and an inner row of simple falcate setae (Fig. 3.II.135c). Bidentate neuropodial hooded hooks, each with a constriction on the shaft (Fig. 3.II.135d), begin on setiger 8 and continue with a few capillaries to the end of the body. Straplike branchiae begin on setiger 7 and vary in number. The pygidium is cup-shaped and has a dorsal notch. This species has been collected on Oahu in coral rock from the Kewalo reef flat, in silt-covered coral rubble from the Ala Wai Canal, and from an experimental microcosm tank, Mokapu Peninsula. *Pseudopolydora antennata* has been reported from Japan (Okuda 1937), South Africa (Day 1955), the Indian and Atlantic

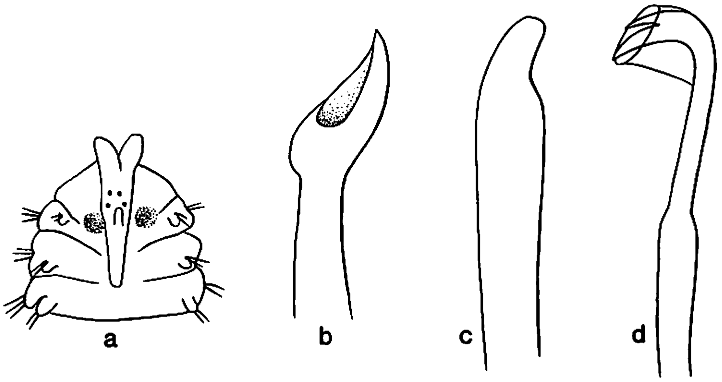


Figure 3.II.135.—*Pseudopolydora antennata*: a, anterior region (scars from prostomial palps are stippled); b, spoon-shaped spine of setiger 5; c, falcate seta of setiger 5; d, neuropodial hooked seta.

oceans, the Mediterranean Sea (Fauvel 1953), the Marshall Islands (Woodwick 1964), and Fiji (Bailey-Brock 1985).

Pseudopolydora corallicola Woodwick, 1964

The body length of an anterior fragment with 25 setigers is 3 mm. The prostomium is anteriorly incised and a caruncle extends posteriorly to setiger 6. A small occipital tentacle and 2 pairs of eyes are present (Fig. 3.II.136a), although the posterior pair may be fused. The peristomium forms a collar laterally and ventrally. Setiger 1 is reduced, without notosetae but with capillary neurosetae. Setigers 2, 3, 4, 6, and 7 have capillaries in both notopodia and neuropodia. Setiger 5 has dorsal and ventral fascicles of capillaries and 2 types of modified spines in horseshoe-shaped rows. Spines in the outer row are spoon-shaped, with their distal ends blunt from wear or drawn into points (Fig. 3.II.136b). The inner row is composed of simple falcate setae with an angled distal end terminating in a rounded tip (Fig. 3.II.136c). Bidentate neuropodial hooded hooks (Fig.

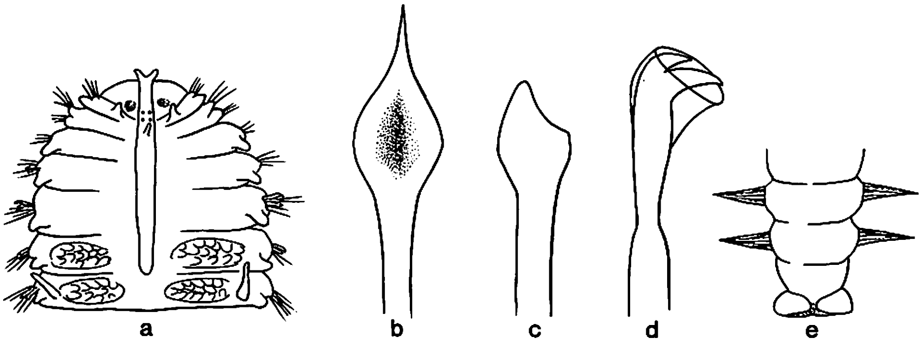


Figure 3.II.136.—*Pseudopolydora corallicola*: a, anterior region showing long slender caruncle (scars from prostomial palps are stippled); b, spoon-shaped spine of setiger 5; c, falcate seta of setiger 5; d, neuropodial hooked seta; e, notopodial spines and pygidium. (a,b,e after Woodwick 1964.)

3.II.136d) with a constriction on the shaft begin on setiger 8. Fenestrations on the teeth of the neuropodial hooded hooks as described originally were not seen in the Hawaiian specimens. Posterior notosetae are long, thin, attenuated spines (Fig. 3.II.136e), which form a distally pointed bundle. Straplike branchiae begin on setiger 7 and continue for several setigers; Woodwick (1964) reported branchiae continuing to setiger 21. The pygidium is unknown for Hawaiian specimens but was originally described as flaring, with a well-developed dorsal notch and a smaller ventral notch (Fig. 3.II.136e). This species has been collected from coral rubble in marine microcosm tanks in Kaneohe Bay and from the Kewalo reef flat, Oahu. The species is also known from a coral habitat at Enewetak, Marshall Islands (Woodwick 1964).

Pseudopolydora sp.

The body of a worm with 33 setigers is 4.5 mm long. The prostomium is slightly incised anteriorly and extends posteriorly as a caruncle through setiger 5 or occasionally only to setiger 2 (Fig. 3.II.137a). An occipital tentacle is absent, there is a well-developed pair of palps (base of one shown on Fig. 3.II.137a), and eyes occur as 2 to 3 circular pairs. The peristomium forms a collar laterally and ventrally. Setiger 1 is reduced, without notosetae but with capillary neurosetae. Setigers 2, 3, 4, 6, and 7 have winged capillary notosetae and neurosetae. Setiger 5 appears uniramous, with dorsal and ventral fascicles of winged capillaries and 2 curved rows of modified setae. The outer row is made up of lanceolate setae with a constriction on the shaft (Fig. 3.II.137b), while setae of the inner row are simple and falcate (Fig. 3.II.137c). Bidentate neuropodial hooded hooks (Fig. 3.II.137d), with a constriction on the shaft, begin on setiger 8. Posterior notosetae are mostly capillaries, but a few short spines are also present. Straplike branchiae are present on setigers 7 through 15. The pygidium (Fig. 3.II.137e) is cup-shaped and has a dorsal notch. This undetermined species was collected on Oahu from a muddy environment in coral rock at the Ala Wai Canal, a sandy coral rubble substrate at Kewalo, and from an oyster shell at Kahuku (Ward 1981b).

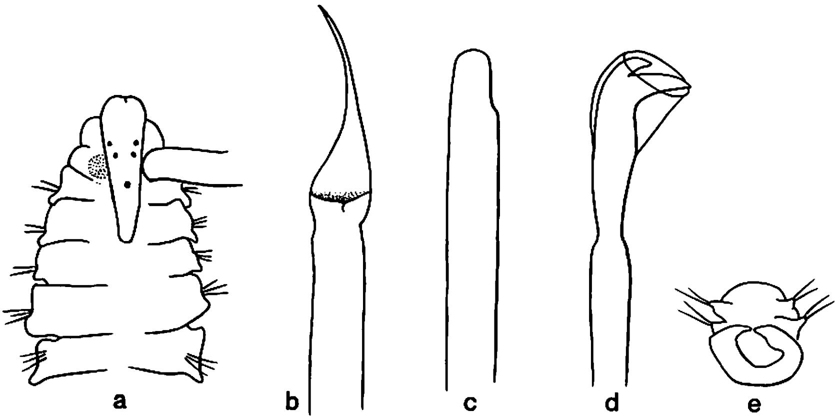


Figure 3.II.137.—*Pseudopolydora* sp.: a, anterior region (scar of missing palp stippled); b, major spine of setiger 5; c, falcate seta of setiger 5; d, neuropodial hooked seta; e, pygidium.

Pygospio muscularis Ward, 1981a

The body of a worm with 35 setigers is 3.8 mm long. The prostomium is subconical, has an entire anterior margin, and tapers as a caruncle to the posterior margin of setiger 2. An occipital tentacle is present, and there are 2 pairs of round to crescent-shaped eyes (Fig. 3.II.138a). The peristomium forms a collar laterally and ventrally. Setiger 1 is reduced and has only a single parapodial lobe, which is shifted dorsally; setae are short, granular, winged capillaries. Both notopodia and neuropodia of setigers 2 to 7 have granular, winged capillaries. The notosetae are of 2 types: abundant, short, stout capillaries in the anterior portion of the fascicle and longer, thinner capillaries posteriorly. Neurosetae are short and stout. Notosetae from setiger 8 to the end of the body are all long, thin, winged capillaries. Bidentate neuropodial hooded hooks, without a constriction on the shaft and with a closely applied apical tooth (Fig. 3.II.138b), begin on setiger 8 and continue to the posterior end. Setiger 8 is enlarged and about twice the length of adjacent setigers; it has a very muscular appearance owing to a gizzardlike structure as in *Polydora socialis* and *Carazziella reishi*. Straplike branchiae are attached basally to notopodial lamellae; they occur on setigers 7 through 17. Branchiae are absent from setigers 2 to 3 (where they may occur in male specimens of other *Pygospio* species) and they are also absent from posterior setigers. Notopodial lamellae are narrow and elongate on setiger 1, subtriangular on setigers 2 to 7, and become smaller and narrower posteriorly. Neuropodial lamellae are quadrate, smaller than the notopodial lamellae of setigers 2 to 7, and are small and rounded from setiger 8. The pygidium is cup-shaped, with a large ventral lobe and a dorsal notch (Fig. 3.II.138c). Numerous specimens were collected from sand in shallow water at Kahana Bay, sand and coral rock at Fort Kamehameha, and on the Kewalo reef flat, Oahu.

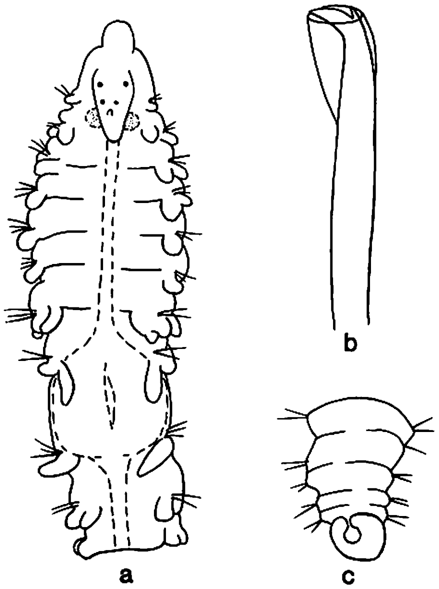


Figure 3.II.138.—*Pygospio muscularis*: a, anterior region (scars of prostomial palps are stippled); b, neuropodial hooked seta; c, pygidium.

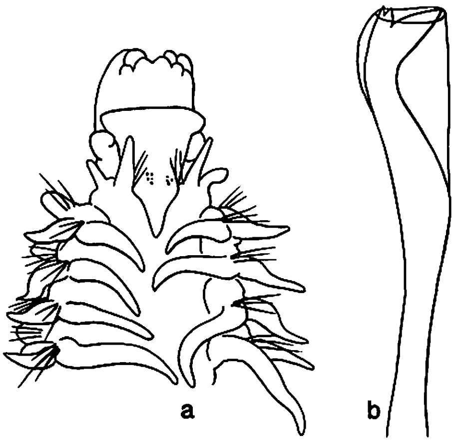


Figure 3.II.139.—*Rhynchospio* sp.: a, anterior region; b, tridentate neuropodial hooked seta.

Rhynchospio sp.

An anterior fragment of approximately 100 setigers is 18 mm long. The prostomium extends posteriorly as a tapering caruncle to setiger 2 (Fig. 3.II.139a) and may be straight or incised on the anterior margin, with a pair of frontolateral horns. An occipital tentacle is absent; eyes are round and arranged in irregularly shaped groups. The peristomium is inflated ventrally. Setiger 1 is reduced and its notopodia and neuropodia are shifted dorsally. Granular, winged capillary notosetae form 2 tiers, with the anterior tier shorter than the posterior tier. Anterior neurosetae are granular, winged capillaries in 2 tiers. Tridentate neuropodial hooded hooks (Fig. 3.II.139b) occur from setiger 28 to 47 and are accompanied by capillary setae and 2 ventral granular saber setae. Notopodial lamellae of setiger 1 are long and digitiform, but from setiger 2 they are subtriangular, taper distally, and become shorter in posterior setigers. Neuropodial lamellae are digitiform on setiger 1 and smaller than notopodial lamellae; from setiger 2 they are rounded, becoming smaller and closer to the body wall posteriorly. Branchiae start on setiger 2 and continue to near the end of the body. They are long, slender, distally tapering, and attached basally to the notopodiallamellae. The shape of the pygidium is unknown. Two specimens were collected from sediment in shallow water on a reef flat in northern Kaneohe Bay, Oahu.

KEY TO HAWAIIAN *SCOLELEPIS* SPECIES

Multidentate neuropodial hooded hooks present	*Scolelepis* sp.
Bidentate neuropodial hooded hooks present	*S. squamata*

Scolelepis squamata (Müller, 1806)

The body length of an anterior fragment with 27 setigers is 18 mm. The prostomium is pointed anteriorly and posteriorly, extending to the anterior margin of setiger 2 (Fig. 3.II.140a). An occipital tentacle is absent and 2 pairs of round

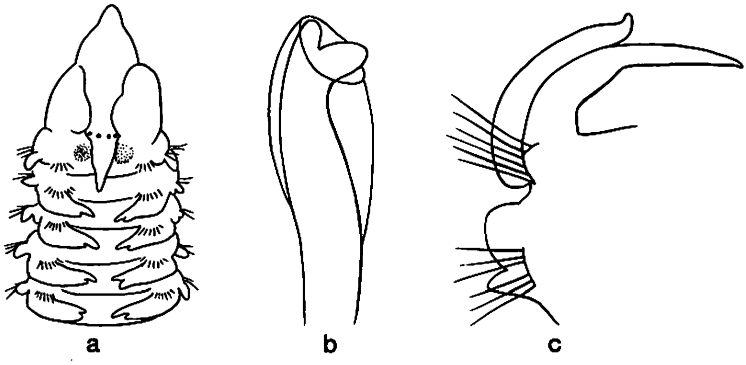


Figure 3.II.140.—*Scolelepis squamata*: a, anterior region (scars of prostomial palps are stippled); b, neuropodial hooked seta; c, posterior parapodium.

eyes are present. The peristomium forms a collar laterally and ventrally with elevated dorsal wings. Setiger 1 is reduced, with capillaries in notopodia and neuropodia. Anterior notosetae and neurosetae are granular, winged capillaries. Bidentate neuropodial hooded hooks (Fig. 3.II.140b) begin on setiger 24 (or may occur from setigers 26 to 40) and are accompanied by a few capillary setae. The Hawaiian fragment lacks notopodial hooded hooks, but they reportedly begin on setiger 60 (Day 1967). Notopodial lamellae of setiger 1 are small and digitiform; they become longer on setiger 2, with the distal tip of the lamellae becoming pointed from setiger 7. Dorsal ridges occur on all setigers after the first. Neuropodial lamellae are low and rounded from setiger 1; a notch starts to develop on the lateral surface of the lamellae from setiger 2, with lamellae dividing into 2 separate lobes by setiger 22 (Fig. 3.II.140c). The dorsal lobe of the neuropodial lamellae is round and larger than the digitiform ventral lobe. Cirriform branchiae begin on setiger 2 and continue to the end of the fragment; they are fused for most of their length to the notopodial lamellae. The pygidium (missing from the Hawaiian specimen examined) has been recorded as a small cushion that is broader than long. The single, incomplete specimen was collected from sand and coral rock in a marine microcosm tank at Mokapu Peninsula, Oahu (Ward 1981b). This species is distributed in the North Atlantic, Mediterranean, and North Pacific (Day 1967; Foster 1971).

Scolelepis sp.

The largest anterior fragment, with 43 setigers, is 10 mm long. The prostomium is anteriorly pointed, and extends as a caruncle to the posterior margin of setiger 1 (Fig. 3.II.141a). An occipital tentacle is absent, but 2 pairs of small, oval eyes are present. The peristomium forms a collar laterally and ventrally; palps are missing. Setiger 1 is reduced in size, with a small digitate notopodial lobe without setae and a larger neuropodial lobe with capillary setae. Anterior notopodia and neuropodia bear granular, winged capillaries; multidentate hooded hooks (Figs. 3.II.141b,c) begin on the neuropodium of setiger 16 and the notopodium of setiger 45. Straplike branchiae begin on setiger 2 and are attached to the notopodial lamellae; they are absent from the posterior third of the fragment. Notopodial lamellae are rounded in anterior setigers, becoming smaller

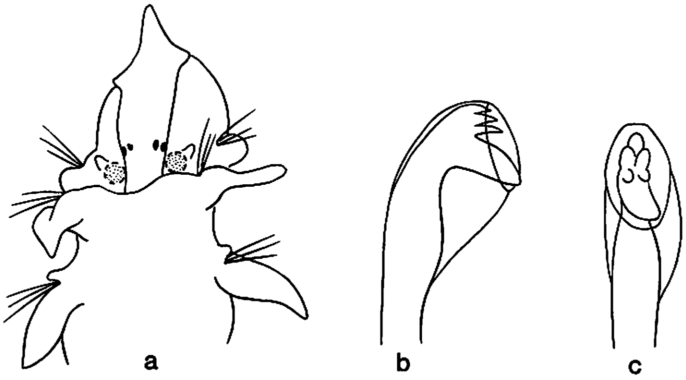


Figure 3.II.141.—*Scolelepis* sp.: a, anterior region (scars of prostomial palps are stippled); b, neuropodial hooded hook, lateral view; c, neuropodial hooded hook, frontal view.

and triangular in postbranchial setigers. Neuropodial lamellae are rounded and entire anteriorly, becoming smaller and closer to the body wall in posterior setigers. The shape of the pygidium is unknown. Specimens were collected from silt held in marine microcosm tanks in Kaneohe Bay and at Mokapu Peninsula, Oahu.

KEY TO HAWAIIAN *SPIO* SPECIES

Pygidial cirri foliose; neuropodial hooded hook setae bidentate .... *S. filicornis*
Pygidial cirri inflated, distally rounded; neuropodial hooded hook setae
tridentate .... *S. pettiboneae*

Spio filicornis (Müller, 1776)

A complete specimen with 51 setigers is 9.5 mm long. The prostomium is anteriorly rounded and extends posteriorly as a raised caruncle to setiger 2 or 3 (Fig. 3.II.142a). An occipital tentacle is absent, while 2 pairs of eyes are present

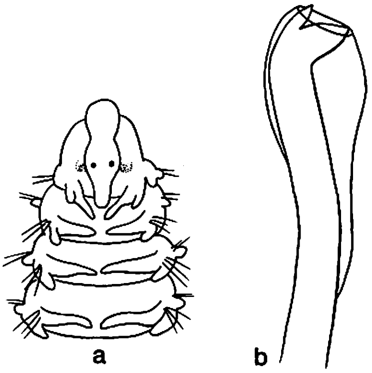


Figure 3.II.142.—*Spio filicornis*: a, anterior region (scars of prostomial palps are stippled); b, neuropodial hooked seta.

(1 pair sometimes obscured as in Fig. 3.II.142a). Setiger 1 is reduced, with parapodia shifted dorsally; its notosetae and neurosetae are granular, winged capillaries. All notopodia have 2 tiers of granular, winged capillaries, the anterior tier shorter than the posterior tier. Bidentate neuropodial hooded hooks (Fig. 3.II. 142b) begin on setiger 10 or 11 and continue to the pygidium accompanied by winged capillaries. Granular saber setae begin in the neuropodium of setiger 11. Straplike branchiae begin on setiger 1 and are attached basally to the notopodial lamellae. Notopodial lamellae are small and elliptical on setiger 1, becoming subquadrate on setiger 2 and subtriangular and distally free of branchiae on posterior setigers. Neuropodial lamellae are elliptical to round throughout. The pygidium has 5 foliose anal cirri. Specimens have been collected on Oahu from sand at Fort Kamehameha and Barbers Point on the south shore, as well as from coral rock on the reef crest and sediment on the reef flat in Kaneohe Bay. Day (1967) reported this species from the Arctic, North Atlantic, and North Pacific.

Spio pettiboneae Foster, 1971

A complete specimen with 70 setigers is 30 mm long. The prostomium is anteriorly rounded and tapers posteriorly as an elevated caruncle to setiger 1 (Fig. 3.II.143a). An occipital tentacle is absent and 3 round eyes are visible [Foster (1971) reported 4]. The peristomium forms a collar laterally and ventrally around the prostomium. Setiger 1 is well developed and bears capillary notosetae and neurosetae. Anterior notosetae and neurosetae are granular, winged capillaries arranged in 2 tiers. Tridentate hooded hooks (Fig. 3.II.143b) alternate with winged capillaries, and a ventral group of 3 to 4 granular, winged capillaries begin on the neuropodium of setiger 12. Branchiae beginning on setiger 1 are long and straplike on anterior and middle setigers, where they extend to the midline of the body; they become shorter and inflated on posterior setigers. Anterior notopodial lamellae are subquadrate and are attached to the branchiae for most of their length. The notopodial lamellae become progressively more triangular and separated from the branchiae posteriorly. Neuropodial lamellae are low and rounded anteriorly; in posterior setigers they are round and project from the body wall. The pygidium bears 4 inflated, distally rounded anal cirri (Fig. 3.II.143c). A single specimen was collected from sand and coral rock in a marine microcosm tank at

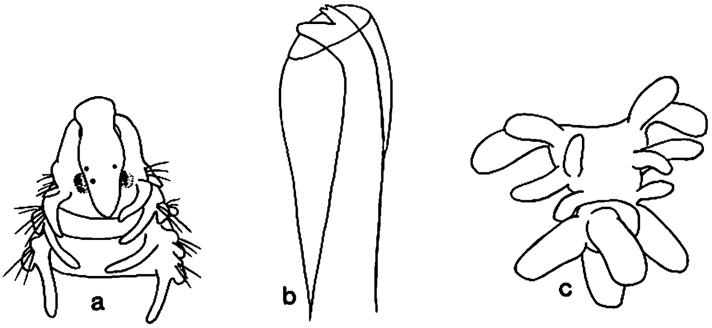


Figure 3.II.143.—*Spio pettiboneae*: a, anterior region (scars of prostomial palps are stippled); b, neuropodial hooked seta; c, pygidium with inflated anal cirri.

Mokapu Peninsula, Oahu. This species has previously been reported from the Gulf of Mexico (Foster 1971).

KEY TO HAWAIIAN *SPIOPHANES* SPECIES

1 Prostomium T-shaped, with frontolateral horns; neuropodial hooded hooks bidentate .... *S. bombyx*

Prostomium rounded or bell-shaped, lacking frontolateral horns; neuropodial hooded hooks tridentate 2

2(1) Occipital tentacle present; 2 parallel sensory grooves on setigers 1 to 4 (Fig. 3.II.144a) .... *S. berkeleyorum*

Occipital tentacle present; sensory grooves on setigers 1 to 4 W-shaped (Fig. 3.II.146a) .... *S. wigleyi*

Spiophanes berkeleyorum Pettibone, 1962

An anterior fragment with 35 setigers is 7 mm long. The prostomium is bell-shaped, widest anteriorly and tapering to the anterior margin of setiger 1 (Fig. 3.II.144a). An occipital tentacle is present. Hawaiian specimens lack eyes, but Pettibone (1962) reported 4 inconspicuous eyes. The peristomium is enlarged laterally and ventrally. The dorsal parallel grooves begin on setiger 1 and extend to setiger 4 in Hawaiian specimens but extend farther back in specimens from other areas (Pettibone 1962). Branchiae are absent. Setiger 1 is biramous, notosetae are capillaries, and neurosetae are capillaries and a single stout, hooked seta. On all setigers notosetae are alimbate capillaries without granulations. Neurosetae have 1 to 2 stout, granular capillaries anteriorly (Fig. 3.II.144b), and have hooked setae that appear tridentate in lateral view (Fig. 3.II.144c) with 4 teeth in face view that begin on setiger 15. The notopodial lamellae are elongate and tapering on setigers 1 to 4, low and rounded on setigers 5 to 9, and triangular from setiger 10 to the end of the fragment. The neuropodial lamellae are elongate and tapering on setigers 1 to 4 and low and rounded from setiger 5. The pygidium

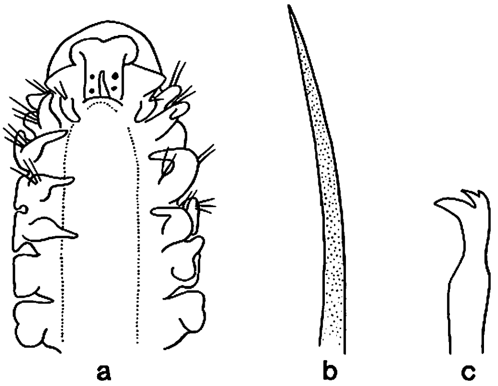


Figure 3.II.144.—*Spiophanes berkeleyorum*: a, anterior region; b, granular neuroseta; c, tridentate neuropodial hook.

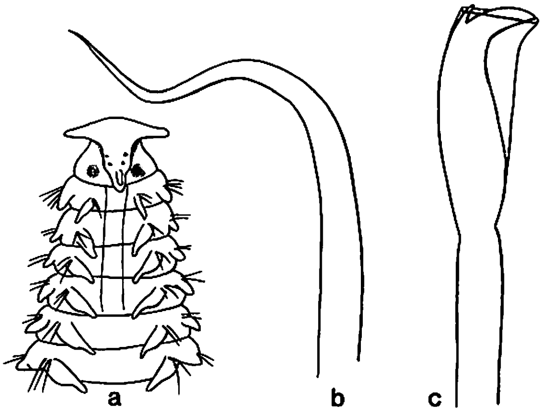


Figure 3.II.145.—*Spiophanes bombyx*: a, anterior region (scars of prostomial palps are stippled); b, neuroseta of setiger 1; c, neuropodial hooked seta.

is cylindrical, with a fringe of 8 to 12 delicate anal cirri (Pettibone 1962). *Spiophanes berkeleyorum* has an Indo-West Pacific distribution and Hawaiian specimens were collected with silty sand from depths of 400 to 450 m (219 to 246 fm) off Honolulu Harbor (Ward 1981a).

Spiophanes bombyx (Claparède, 1870)

The length of a 24-setiger anterior fragment is 5.5 mm. The prostomium is T-shaped, with a blunt anterior margin and a pair of frontolateral horns or lobes (Fig. 3.II.145a). The prostomium tapers posteriorly to setiger 1. An occipital tentacle is absent, but there are 2 pairs of eyes in most specimens. The peristomium surrounds the prostomium laterally and ventrally. Two parallel sensory grooves are present from the posterior end of the prostomium through setiger 4 (Fig. 3.II.145a). Branchiae are absent. Setiger 1 is well developed and bears capillary notosetae and neurosetae (Fig. 3.II.145b) as well as a single, heavy, hooked neuroseta. Notosetae are long, winged capillaries throughout the fragment. Neurosetae are capillaries anteriorly, with bidentate hooded hooks (Fig. 3.II.145c) and heavy, granular saber setae from setiger 15. The shape of the notopodial and neuropodial lamellae and the pygidium are unknown for the incomplete Hawaiian specimen. The notopodial lamellae on setiger 1 are reportedly long, thin, and tapered, becoming wider and basally thicker on the next few setigers and more attenuated in posterior setigers. Anterior neuropodial lamellae are foliaceous, becoming reduced and cushion- or padlike; posterior neuropodial lamellae are low and rounded. The pygidium bears 2 anal cirri (Foster 1971). This cosmopolitan species has been collected from mud in anchialine lava ponds at Anaehoomalu, Hawaii (Bailey-Brock 1976).

Spiophanes wigleyi Pettibone, 1962

An anterior fragment with 65 setigers is 27 mm long. The prostomium is anteriorly rounded, lacks frontolateral horns, and tapers posteriorly to setiger 1 (Fig. 3.II.146a). An occipital tentacle is absent. There are 3 eyes in Hawaiian specimens, but up to 5 eyes have been recorded for this species (Foster 1971). The peristomium extends laterally and ventrally around the prostomium and the

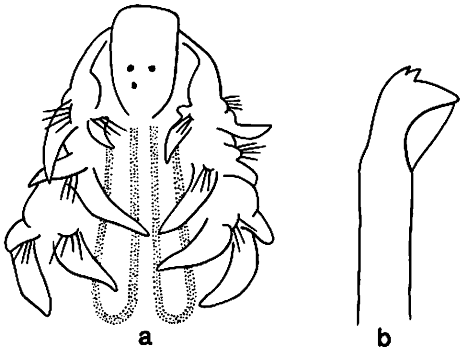


Figure 3.II.146.—*Spiophanes wigleyi*: a, anterior region showing pigmented sensory grooves; b, tridentate neuropodial hook.

proboscis may be everted and project beyond the prostomium. Two parallel sensory grooves, W-shaped and pigmented with brown, are visible on the dorsum of setigers 1 to 4. Branchiae are absent. Setigers 1 to 3 are well developed, with notopodial lobes shifted dorsally. All notosetae are alimbate, granular capillaries arranged in 2 tiers. Neurosetae are alimbate, granular capillaries arranged in 2 tiers on setigers 1 to 8, with 1 stout, hooked seta on setiger 1. These capillaries are arranged in a single tier with 1 inferior capillary seta from setiger 9. The tridentate hooded hooks (Fig. 3.II.146b) begin on setiger 15 and continue to the end of fragment without accompanying capillaries. Notopodial lamellae are long and tapered on setigers 1 to 4, short and round on setigers 5 to 8, and become elongate and tapered on the posterior setigers. Neuropodial lamellae are long and tapered on setigers 1 to 4 and short and round on setigers 5 to the end of the fragment. Transverse dorsal ciliated ridges are visible from setiger 17. Parapodial thread glands are present on setigers 5 to 14. Interramal pouches are absent. The pygidium reportedly has 4 to 6 delicate anal cirri (Pettibone 1962). Specimens were collected with silty sand from depths of 400 to 450 m (219 to 246 fm) off Honolulu Harbor (Ward 1981a). *Spiophanes wigleyi* probably has a cosmopolitan distribution (Ward 1981b).

Streblospio benedicti Webster, 1879

A complete specimen with 50 setigers is 8 mm long. The prostomium is anteriorly rounded, extending posteriorly to the anterior margin of setiger 1. An occipital tentacle is absent and 2 pairs of round eyes are present. The peristomium is closely affixed to the prostomium, forming a collar laterally and ventrally. The proboscis (often everted) may be round or incised. Setiger 1 is reduced, has capillary notosetae and neurosetae, and is fused with the peristomium. A single pair of long, cirriform branchiae occurs on setiger 1 posterior to the palps and is connected basally by a low transverse dorsal ridge (Fig. 3.II.147a showing a branchia above a palp). Notopodial lamellae, absent on setiger 1, are fused across the dorsum on setiger 2, forming the characteristic "hood" (Fig. 3.II.147a). Notopodial lamellae on setigers 2 to 7 are low and rounded, becoming inconspicuous papillae thereafter. Neuropodial lamellae are small, low, and rounded on setigers 1 to 7, becoming inconspicuous swellings from setiger 8. Anterior notosetae and neurosetae are capillaries both with and without wings. Posterior

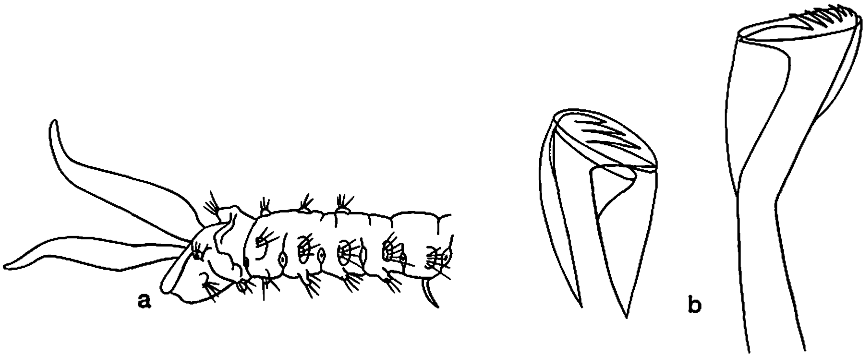


Figure 3.II.147.—*Streblospio benedicti*: a, anterior region, lateral view; b, neuropodial hooked seta, 2 views.

notosetae are long capillaries without wings. Faintly granular, inferior saber setae begin in the neuropodium of setiger 6 or 7 and continue to the end of the body. Multidentate neuropodial hooded hooks (Fig. 3.II.147b) begin on setiger 7, 8, or 9, and continue to the end of the body. Specimens have been collected from mud in Halawa Stream, which drains into Pearl Harbor, Oahu (Ward 1981b). This species has been reported from the east and west coasts of North America, as well as European and South American coastal regions (Foster 1971; Light 1978).

Tripolydora spinosa Woodwick, 1964

Complete specimens with 32 to 34 setigers are 3 to 4 mm long. The prostomium is anteriorly rounded and extends posteriorly as a caruncle to setiger 3 (Fig. 3.II.148a). An occipital tentacle and eyes are absent. The peristomium surrounds the prostomium laterally and ventrally, giving the anterior margin of the worm a trilobed appearance (Fig. 3.II.148a). Setiger 1 is reduced and lacks notopodia and notosetae; neurosetae are capillaries. Setigers 2, 3, 4, 6, 7, and 8 have capillary notosetae and neurosetae. Setiger 5 has dorsal and ventral fascicles of capillaries and a bundle of modified spines. The spines are distally expanded

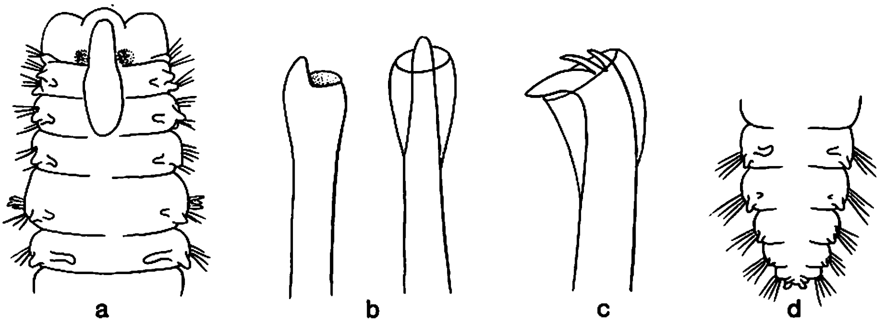


Figure 3.II.148.—*Tripolydora spinosa*: a, anterior region (scars of prostomial palps are stippled); b, major spine of setiger 5, 2 views; c, neuropodial hooked seta; d, pygidium.

and have a small concavity, with a tooth extending from the rim of the indentation (Fig. 3.II.148b). Tridentate neuropodial hooded hooks (Fig. 3.II.148c), without a constriction on the shaft, begin on setiger 9 and continue together with a few capillary setae to the end of the body. Posterior notosetae are bundles of fine needles. Small, straplike branchiae begin on setiger 2, reach full size on setiger 6, and continue to within a few setigers of the pygidium. Branchiae lie close to the dorsum, making them easily overlooked. The pygidium has 2 ventral lappets and 2 smaller dorsal lappets (Fig. 3.II.148d). Specimens have been collected from coral rock in Kaneohe Bay and at Kewalo, Oahu. This species was also found within coarse, sandlike rock and beach rock at Enewetak, Marshall Islands (Woodwick 1964), and Johnston Atoll (Ward 1981b).

Family **Magelonidae**

This family includes burrowing worms inhabiting muddy sand or silt-laden sediments. The head (Fig. 3.II.149a), an ideal burrowing organ, is flattened and shovel-shaped. It bears a pair of delicate papillose palps (Jones 1968), which frequently break off when sediment samples are washed through sieves. The rest of the body is cylindrical, with biramous parapodia bearing leaflike lobes (Figs. 3.II.149b,c). Thoracic setae are capillaries, and abdominal setae are hooded hooks (Figs. 3.II.149d,e) (Day 1967).

Magelona sp.

These worms are approximately 35 mm long, with a flattened, shovel-shaped head lacking eyes but bearing lateral expansions and a pair of distinct horns on the anterior margin. Although the anterior region (first 9 setigers) is distinctly rosy pink, the overall body color is a semitranslucent white; gonads can be seen through the body wall as opaque, cream-colored patches. The proboscis is a protrusible, transparent, unarmed sac. Palps are missing but the bases are evident on the dorsal surface of the head. Capillary setae occur on setigers 1 to 9 and

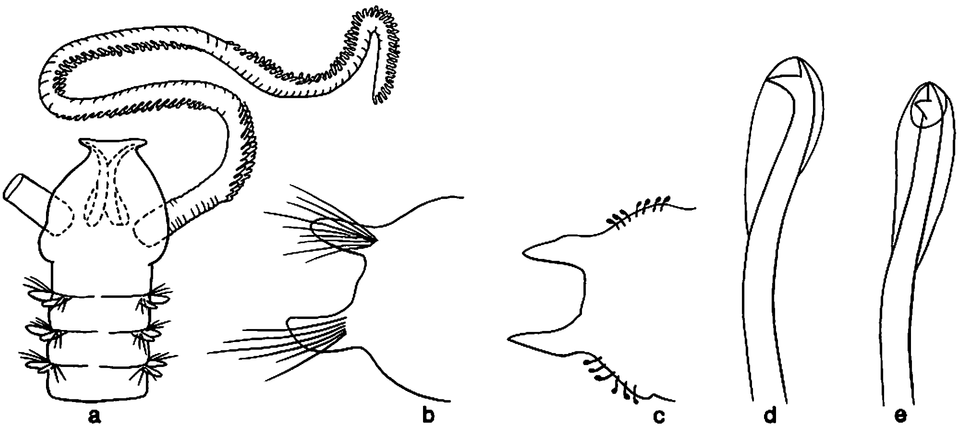


Figure 3.II.149.—A stylized magelonid illustrating the morphology: a, head with papillose palps (only 1 shown) and muscular strands ending at anterio-lateral projections; b,c, parapodia of anterior and posterior regions, respectively; d,e, lateral and face views of abdominal hooded hook setae, respectively. (a,b,c after Day 1967; d,e after Jones 1963.)

tridentate hooded hooks from setiger 10. Cirri are pointed on setigers 1 to 9 but are lobate from setiger 10 onward. Gut contents include detritus and green-colored material. Ten specimens came from muddy sand collected from a depth of 7 m in Honolulu Harbor and 3 from a depth of 3 m in Kaneohe Bay, Oahu. This family was previously unrecorded from the Hawaiian Islands, and the species is as yet undescribed (M. Jones, pers. comm.).

Family **Cirratulidae**

Typical members of this family are brightly colored, soft-bodied worms with numerous extensible, tentacular filaments for gathering food materials. They lack parapodial lobes but have 2 bundles of setae and long branchiae. Individuals are usually buried in sand or mud (although *Dodecaceria* inhabits calcareous algae or coral rock) with only branchiae and cirri protruding. The conical prostomium typically lacks conspicuous eyes and appendages. The peristomium (buccal segment) may bear tentacular filaments that closely resemble the branchiae, except that they are grooved and each has a single blood vessel, or there may be a pair of stout, grooved palps such as those in *Dodecaceria*. There is generally 1 branchial filament associated with each parapodium on some or all segments. The filaments are distinguished from tentacular cirri, since they lack grooves and each has 2 blood vessels. Setae are either simple acicular hooks or capillaries.

KEY TO HAWAIIAN CIRRATULID GENERA

1 One pair of grooved palps (Fig. 3.II.152a) and 3 or 4 tentacular cirri; acicular setae spoon-shaped; worms dark .... *Dodecaceria*
Several grooved, tentacular cirri; acicular setae with curved tips; worms dark or brightly colored 2
2(1) Branchial filaments appear to begin anterior to tentacular cirri .... *Cirriformia*
Branchial filaments appear to begin on same segment as tentacular cirri .... *Cirratulus* ?
~ not in here!

Cirratulus zebuensis McIntosh, 1885
Individuals are as long as 25 mm and are red. Acicular setae are absent from anterior parapodia but are present in middle and posterior parapodia; each seta is long, slender, and only slightly curved. Notosetae are smaller and less flattened than neurosetae. This species is known from the waters off Erben Bank to Kauai Channel (Treadwell 1906; Hartman 1966).

KEY TO HAWAIIAN *CIRRIFORMIA* SPECIES

1 Body dark violet or yellowish (in life and preserved) 2
Body color otherwise 3
2(1) Body dark violet, branchiae orange; tentacular cirri inserted between setigers 3 and 4 .... *C. ?capensis*

Body yellowish, speckled with black, branchiae and tentacles barred; tentacular cirri inserted on setiger 4 .... *C. punctata*

3(1) Acicular spines first present in neuropodia from segment 4 to 6, and in notopodia from segment 10 to 11 .... *C. crassicollis*

Acicular spines first present in neuropodia from more posterior segments, and in notopodia beyond segment 23 4

4(3) Acicular spines first present in neuropodia from segment 9 to 10, and in notopodia from about segment 50 .... *C. semicincta*

Acicular spines first present in neuropodia from segment 23 and in notopodia much farther back .... *C. hawaiensis*

Cirriformia ?capensis (Schmarda, 1861)
[syn. *Cirratulus capensis* Schmarda: Treadwell 1906, Edmondson 1946]

The size of Hawaiian specimens is unrecorded. The prostomium is rounded and depressed. The color in life is brown or dark violet, and the branchiae are orange. Tentacular cirri are inserted between the third and fourth setigerous segments. Lateral branchiae are inserted some distance above each notopodium of the median and posterior segments. Thick, acicular spines occur in both notopodia and neuropodia. According to Hartman (1966), the record of this species by Treadwell from the Honolulu reef may refer to *C. crassicollis* (Kinberg 1866) described below. *Cirriformia capensis* was originally described from South Africa.

Cirriformia crassicollis (Kinberg, 1866)
[syn. *Labranda crassicola* Kinberg, 1866]

The length of the body of a Hawaiian specimen is about 19 mm. Thick, yellow, acicular spines, slightly curved distally, are first present in neuropodia beginning on segment 4 to 6, occurring singly and accompanied by slender, pointed setae; their number increases to 4 or 5 on more posterior neuropodia, where they alternate with notopodial spines. Tentacular cirri are inserted on setiger 4. Lateral branchiae, inserted well above the notopodia, are abundant on the anterior third of the body but are sparse in the middle and posterior segments. This species was recorded from dead coral near Honolulu, Oahu (Kinberg 1866), and Halape, Hawaii (Hartman 1966).

Cirriformia hawaiensis Hartman, 1956
[syn. *Audouinia branchiata* Treadwell, 1943]

The length of the body of this worm is about 40 mm. Tentacular cirri and branchiae are numerous and form a dense mass over the anterior end of the body (Plate 3.II.3c). The frontal margin of the prostomium is dusky and has a pair of ocular patches above the oral groove. Anterior parapodia have only slender, pointed setae. Curved acicular spines occur in neuropodia from segment 23 and in notopodia farther back. Spines number 5 to 6 in a row where best developed and alternate with more slender, pointed setae. Branchiae are inserted well above the notopodial base in posterior segments. This species was originally described from Pearl Harbor and has been found in Paiko Lagoon, Oahu.

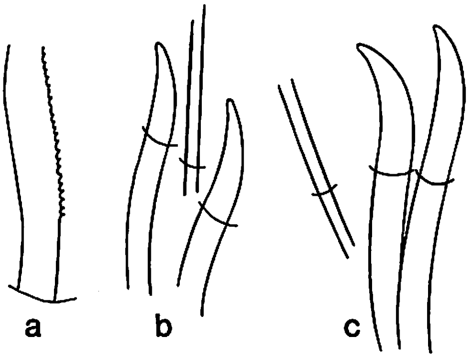


Figure 3.II.150.—*Cirriformia punctata*: a, portion of seta with serrated edge; b, acicular spines with part of a capillary seta from anterior setiger; c, acicular spines with part of a capillary seta from posterior setiger. (After Hartmann-Schröder 1965.)

Cirriformia punctata (Grube, 1856)

The body of this species, from 15 to 32 mm long, is composed of 85 or more segments. Live worms are grayish yellow to brown, with black flecks on the body, branchiae, and tentacular cirri. The prostomium is broadly rounded in front and is much broader than long. The third buccal segment is abruptly broader than the first 2. The first parapodium occurs on segment 4 and bears a pair of long branchiae and 3 to 4 pairs of tentacular cirri. The first 6 to 8 setigerous segments have only simple setae, which are laterally serrated (Fig. 3.II.150a). Thereafter, notopodia and neuropodia have 3 to 4 acicular spines, distally curved (Fig. 3.II.150b) and accompanied by more slender capillary setae. Posterior spines increase in thickness and are also accompanied by more slender capillary setae (Fig. 3.II.150c). This species is circumtropical and subtropical in distribution and is known from algal mats at Paia, Maui, and in coral sand from rubble at Kaneohe Bay, Oahu (Hartmann-Schröder 1965).

Cirriformia semicinta (Ehlers, 1905)
[syn. *Audouinia semicintus* Ehlers: Abbott 1946]

Worms with 100 to 231 segments are 20 to 62 mm long and 1 to 2.5 mm wide. The color in life is dull red or crimson, with branchiae of a lighter shade. The prostomium is bluntly conical (Fig. 3.II.151a) and lacks eyes. Paired branchiae begin on the first setigerous segment and continue posteriorly. Tentacular cirri form a clustered pair on the fourth setigerous segment. By the tenth parapodia (Fig. 3.II.151b), neuropodia are ventral and bear acicular spines and capillary setae. Farther back, by segment 100, the body is more slender, and acicular spines occur in notopodia and neuropodia (Fig. 3.II.151c). Acicular spines are clear brown, distally curved, and are thicker distally in neuropodia (Fig. 3.II.151d) than in notopodia (Fig. 3.II.151e). Known from Indo-West Pacific waters, specimens of *C. semicincta* have been collected from soft, vertical burrows or tubes in mud on the south shore of Oahu (Abbott 1946; Hartman 1966).

Dodecaceria laddi Hartman, 1954a

These are small worms from 5 to 10 mm long and 0.5 mm or less wide; they have 60 to 70 segments. Preserved worms are dark green, gray, brown, or purplish

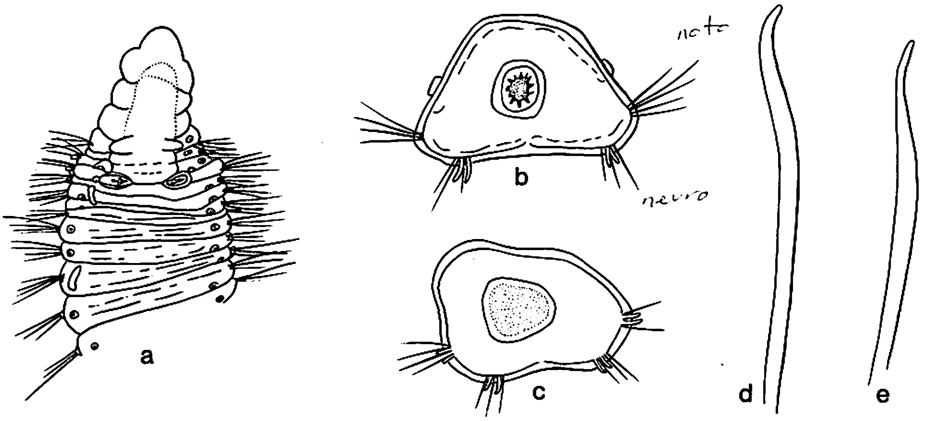


Figure 3.II.151.—*Cirriformia semicincta*: a, anterior end; b, cross section through segment 10; c, cross section through segment 100; d, neuropodial acicular spine; e, notopodial acicular spine. (After Abbott 1946.)

brown; they appear more reddish brown when alive. The prostomium is a flattened, conical lobe without eyes (Fig. 3.II.152a) and the mouth forms a triangular depression on the ventral side between the prostomium and buccal region. The first segment behind the buccal ring has a pair of thick, grooved palps in a ventrolateral position and a pair of short, more slender tentacles attached just above the palps; the next segment (the first setigerous) has 1 or 2 filamentous tentacles (Fig. 3.II.152a) and inconspicuous biramous parapodial lobes. There are no tentacles. The first 7 setigers have 3 to 4 slender, capillary setae (Fig. 3 II.152b)

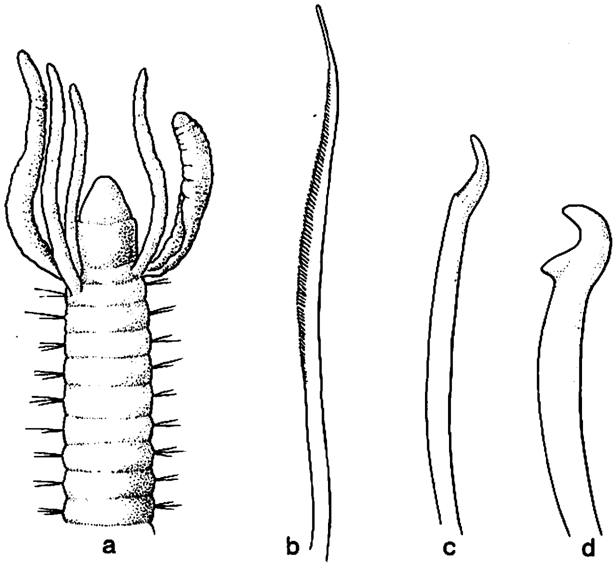


Figure 3.II.152.—*Dodecaceria laddi*: a, anterior region; b, capillary seta; c, notopodial spoon-shaped seta; d, neuropodial spoon-shaped seta. (After Hartman 1954a.)

in each fascicle. From setiger 8, notopodia bear simple, yellow, spoon-shaped setae (Fig. 3.II.152c), and neuropodia have simple, spoon-shaped and capillary setae. Each posterior neuropodial seta has a laterally projecting blunt spine below the spoon-shaped tip (Fig. 3.II.152d). This gregarious worm is very abundant and bores into calcareous algae and corals on shallow reefs (Hartman 1954a). Densities of 500 worms/100 cm^2 were recorded on a windward reef bench at Enewetak, Marshall Islands (Bailey-Brock et al. 1980). This species is known from the Hawaiian Islands at Kaneohe Bay and the south shore of Oahu (Bailey-Brock 1979), and at Kahului, Maui.

Family **Chaetopteridae**

Species of this family are tubicolous worms divided into distinct anterior, middle, and posterior regions. The prostomium bears a pair of grooved, extensible palps (long in *Phyllochaetopterus* and *Mesochaetopterus*, short in *Chaetopterus*) and may have a pair of eyes and occipital tentacles, which lack grooves. The fourth segment of the anterior region has heavily chitinized acicular setae. The notopodia of the middle region are important diagnostic structures and may be joined to form fanlike paddles in the genus *Chaetopterus*, or separate bilobed structures in *Phyllochaetopterus* and *Mesochaetopterus*. One or more of the midregion notopodia secrete a mucus filter-net, which traps food particles drawn through the tube by the pumping effect of the fanlike paddles of *Chaetopterus variopedatus* or by ciliary currents in the other genera. The mucus net with its trapped food particles is then rolled up and transported to the mouth along a mid-dorsal ciliated groove (Barnes 1965). The long prostomial palps obtain food from the sediment surface, remove fecal material from the anterior end of the tube, and select and manipulate sand grains in tube-building species that attach sand to the tube. Gregarious chaetopterids may form extensive mounds of sand-grain tubes of 1 m^2 or more in area. These worms appear to stabilize sand in shallow waters that receive considerable surf or water motion (Bailey-Brock 1979). Three genera comprising 4 species with rather wide distribution beyond Hawaii are presently recognized.

KEY TO HAWAIIAN CHAETOPTERID SPECIES

1 Middle region with fanlike and fused notopodia .... *Chaetopterus variopedatus*
Middle region with bilobed notopodia, without fans or paddles 2
2(1) Worms with sand-covered tubes; middle region composed of 2 segments 3
Worms with semitranslucent, ringed tubes; middle region composed of 7 or more segments .... *Phyllochaetopterus socialis*
3(2) Eyes lacking; a pair of short occipital tentacles present .... *Phyllochaetopterus verrilli*
Eyes present; occipital tentacles absent .... *Mesochaetopterus sagittarius*

Chaetopterus variopedatus (Renier, 1804)

The body of this species is divided into 3 regions. The anterior region, with 1 pair of short, tapered palps and a pair of eyes, is composed of 8 to 12 uniramous segments. The middle region is made up of 5 biramous segments, the second of which has 1 pair of winglike notopodia and a cupule; the third, fourth and fifth have notopodia fused dorsally to form fan-shaped paddles (Fig. 3.II.153a). The posterior region has 9 to 20 or more segments bearing sticklike notopodia with knobbed ends and bilobed neuropodia. The fourth setiger of the anterior region has modified cutting setae (Fig. 3.II.153b). The middle and posterior regions are black. Tubes are irregularly curved, open at both ends, and are approximately 8 to 12 cm long and 0.5 cm to 1 cm wide; they are tough (often described as

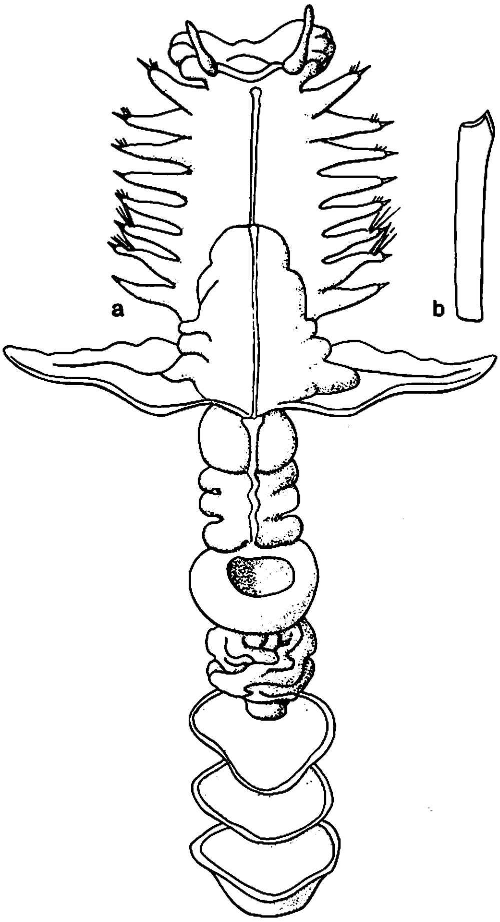


Figure 3.II.153.—*Chaetopterus variopedatus*: a, anterior and middle regions showing modified parapodia and pair of short prostomial palps; b, cutting seta of 4th setiger.

parchmentlike) and covered with fine mud. Aggregations of individuals occur in shallow, silty water attached to coral rubble, pier pilings, and thalloid algae. This cosmopolitan species is abundant in Kaneohe Bay, Oahu, on the green alga *Dictyosphaeria cavernosa* and is a frequent component of fouling communities (Bailey-Brock 1976).

Mesochaetopterus sagittarius (Claparède, 1870)
[syn. *M. minuta* Potts, 1914: Hartman 1966]

This worm is 9 to 10 mm long (excluding palps) and 1.3 to 1.9 mm wide, and is white except for a black middle region. The prostomium is ovoid (Fig. 3.II.154a), with a pair of small eyes at the bases of the long, grooved palps. The anterior region has 13 to 14 segments, the middle region has 2, and the posterior region (Fig 3.II.154b) has numerous segments. Modified acicular setae of the fourth setiger are thick and distally oblique, with serrated tips (Fig. 3.II.154c).

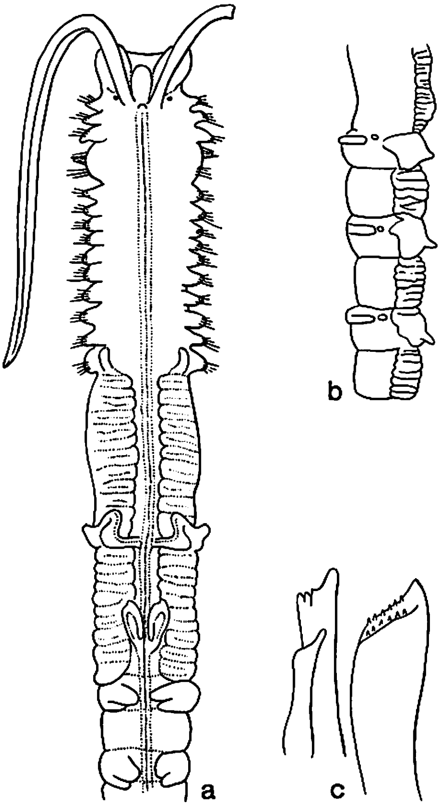


Figure 3.II.154.—*Mesochaetopterus sagittarius*: a, anterior region with paired eyes and grooved palps, and middle region of 2 setigers with bilobed notopodial lobes; b, posterior end, lateral view; c, acicular setae of 4th setiger.

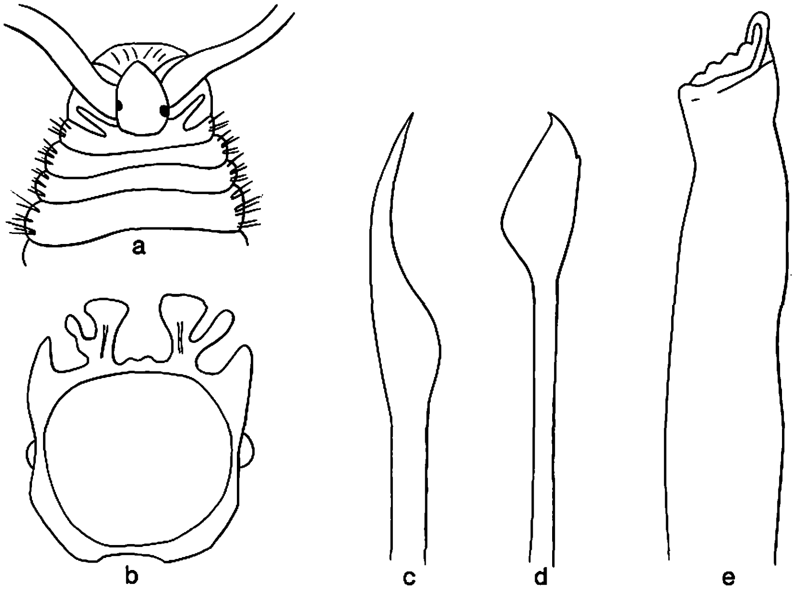


Figure 3.II.155.—*Phyllochaetopterus socialis*: a, anterior region showing paired palps, eyes and tentacular cirri; b, cross section of middle region setiger with bilobed notopodia; c,d, notopodial setae; e, cutting seta of 4th setiger. (After Fauvel 1927.)

This species forms tufts of sand-covered tubes in shallow water and on reef flats. Known from the Mediterranean (Bhaud 1969) and throughout the Indo-West Pacific region in the littoral zone, this gregarious worm has been found forming aggregations on reef flats in Kaneohe Bay and on south shore reefs of Oahu (Bailey-Brock 1979), as well as on Hawaii at Halape and along the Kona coast.

Phyllochaetopterus socialis (Claparède, 1870)

This worm is up to 20 mm long (including palps) and approximately 1 mm wide. Tubes are translucent (Plate 3.II.3d), irregularly sinuous, and may branch; they are 40 to 65 mm long and 1.5 to 2.0 mm wide. On close inspection, rings or bands of thicker material can be seen in the wall of the tube, which probably add to its strength and prevent collapse (Barnes 1965). The anterior region, composed of 12 to 13 segments, bears a pair of long, grooved palps, 2 short tentacular cirri, and a pair of small eyes (Fig. 3.II.155a). Notosetae have broad, flattened blades (Figs 3.II.155c,d) except for the fourth setiger, which has a pair of modified setae with coarsely serrated edges (Fig. 3.II.155e). The middle region has 7 or more segments with bilobed notopodial lobes (Fig. 3.II.155b) and neuropodia bearing uncini. The posterior region has numerous segments and bears digitiform notopodia, each with 1 or 2 spear-headed setae and ventral, uncinigerous neuropodia. This cosmopolitan chaetopterid has been found on shallow reef flats in fine sand or on mud flats of Oahu and Hawaii.

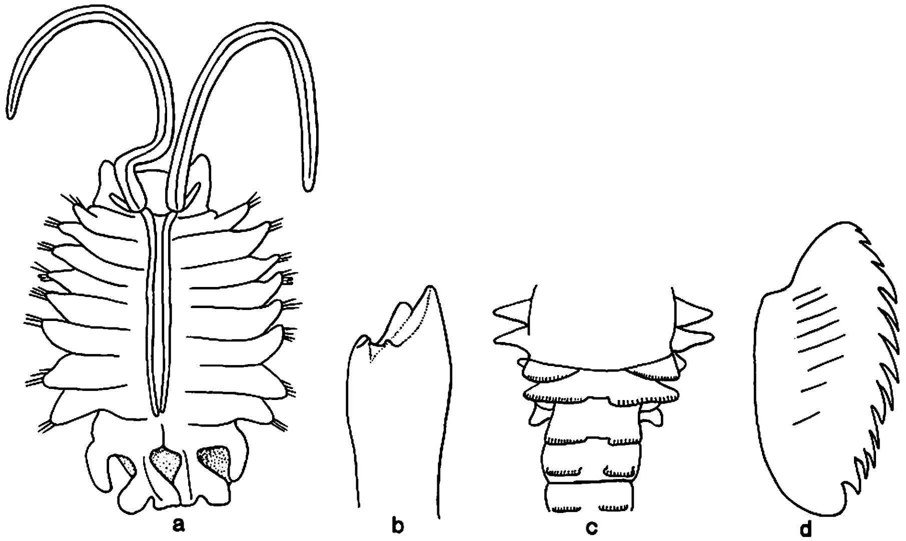


Figure 3.II.156.—*Phyllochaetopterus verrilli*: a, anterior region with paired palps and tentacular cirri, and lst segment of middle region; b, cutting seta of 4th setiger; c, middle and proximal portion of posterior region, ventral view; d, abdominal uncinus. (After Hartmann-Schröder 1965.)

Phyllochaetopterus verrilli Treadwell, 1943
[syn. *P. brevitentaculata* Hartmann-Schröder, 1965]

These worms form sand-grain tubes that may reach 46 mm in length. Preserved worms are 11 to 14 mm long (excluding palps) and 0.06 to 1.00 mm wide. The anterior and middle regions are white; the posterior section is orange or dark olive green. The anterior region is composed of 9 segments (Fig. 3.II.156a), the prostomium, a pair of long, grooved palps, and short tentacular cirri; the middle region has 2 segments, and the posterior region 20 to 28 segments. The anterior region has uniramous parapodia and the 4th setiger bears slender setae with toothed edges (Fig. 3.II.156b); all other setae are oarlike. The middle region has 2 biramous segments with frilled notopodial lobes (Fig. 3.II.156a). Segments of the posterior region appear square in cross section and have broadly transverse neuropodia on the ventral surface on each side of the midline (Fig. 3.II.156c). Abdominal uncini number about 40 per row and each has a dentate margin (Fig. 3.II.156d). Tubes are covered with fine sand and are slightly wider than those of *Mesochaetopterus sagittarius*. This species was originally described from Oahu, where it is found on sandy reef flats. It is known from other Hawaiian Islands, including Maui (Hartman 1966), and more recently it has been recorded from the Cook Islands (Gibbs 1972) and Easter Island (Kohn and Lloyd 1973).

Family **Orbiniidae**

Members of this family are long, cylindrical worms with a thorax of slightly flattened segments and a longer abdomen of rounded segments. The prostomium lacks any sensory appendages or palps and may be a rounded or sharply conical lobe. The proboscis is protrusible, unarmed, and may be used for burrowing. The muscular thorax has neuropodia reduced to ridges bearing acicular hooked setae and usually crenulate capillaries, as well as 1 to 3 conical, postsetal lobes or foot papillae. Branchiae may be entirely absent from the thorax and begin on the anterior abdominal segments. Notosetae are crenulate capillaries with convex margins (Fig. 3.II.157d). In many genera the abdomen is distinguished from the thorax by the abrupt change in location of the neurosetae to a dorsal position and the notosetae to a ventral one. Presetal and postsetal lobes are present, and the size of these structures is diagnostic. In addition to crenulate capillaries, there may be forked setae or whiplike flail setae; various coarse hooks may also be present. Only 1 genus is known from Hawaiian waters.

KEY TO HAWAIIAN *NAINERIS* SPECIES

Prostomium straight in front, with eyes; thoracic, acicular neurosetae transversely spinous .... *N. bicornis minuta*

Prostomium rounded in front, without eyes; thoracic, acicular neurosetae marginally smooth or weakly crenulate .... *N. laevigata*

Naineris bicornis minuta Hartmann-Schröder, 1965

The length of the body reaches about 40 mm and the width 1.7 mm. The anterior margin of the prostomium is straight or weakly bilobed; small eyes are nearly indiscernible at the posterior margin. The thorax has 20 to 24 segments followed by 3 transitional segments where the neuropodia become dorsal in position, a characteristic of the numerous abdominal segments. The pygidium is cylindrical and ringed, and the anus is bounded by 4 small cirriform processes. This subspecies has been described only from specimens collected in coral sand on Oahu.

Figure 3.II.157.—*Naineris laevigata*: a, anterior region showing head and everted multilobed proboscis; b, 10th parapodium; c, 50th parapodium; d, crenulate capillary seta. (b–d after Abbott 1946.)

Naineris laevigata (Grube, 1855)
[syn. *Lacydes havaicus* Kinberg, 1866]

Large specimens are 75 to 150 mm long, 4 to 5.5 mm wide, and have more than 325 segments. The division of the body into thoracic and abdominal regions is easily discerned. The prostomium is broad and flattened, with a pair of subdermal eyes that may be obscured between folds of the prostomial epithelium, and the everted proboscis is multilobed (Fig. 3.II.157a). The thorax has 24 to 26 setigers, which are flattened dorsoventrally. Branchiae (Fig. 3.II.157b) begin on setiger 6 as small straplike structures and continue throughout the body, becoming longest in the abdomen. These branchiae give the worms a ragged appearance (Fig. 3.II.157a). Thoracic neuropodia have slender, distally pointed setae, crenulate capillary setae (Fig. 3.II.157d), and thicker, acicular spines arranged transversely in rows. Abdominal parapodia (Fig. 3.II.157c) have more slender notopodia and neuropodia, and branchiae exceed the other lobes in length and width. This cosmopolitan form inhabits shallow waters and has been collected from Kaneohe Bay, and from fishponds near Honolulu (since filled in for housing developments) (Abbott 1946; Hartman 1966); it is the largest polychaete in the community dominated by *Diopatra* undescribed species at Niu on the south shore of Oahu (Bailey-Brock 1984, in press).

Family **Paraonidae**

Paraonids are small (less than 40 mm long), threadlike worms with a conical or rounded prostomium that may or may not bear a short antenna and eyespots. The antenna is easily broken off, which can be misleading when trying to assign a specimen to a genus. Similarly, eyespots are inconspicuous and fade in preservative. Nuchal slits are present on the prostomium but may be hard to distinguish on small specimens. Cirriform branchiae begin on setiger 4. Parapodia are biramous, with dorsal postsetal lobes and 2 distinct bundles of setae. Setae are

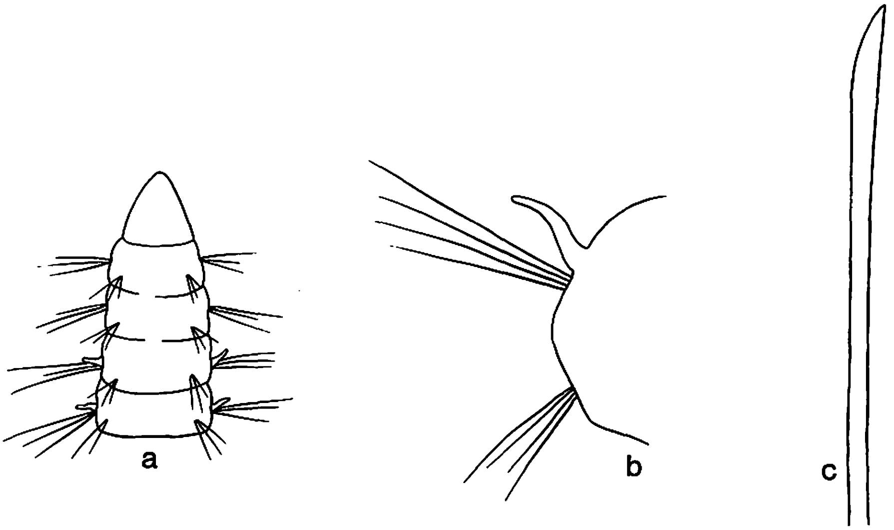


Figure 3.II.158.—*Paraonis* sp.: a, anterior region; b, parapodium with cirriform branchia; c, stout neuroseta.

predominately long capillaries, but modified setae are present in posterior segments as curved, hooked setae, aristate setae, or forked setae in either notopodial or neuropodial falcigers. Paraonids are thought to be burrowers in surface sediments, where they feed on diatoms, foraminiferans, and other small invertebrates (Fauchald and Jumars 1979).

Paraonis sp.

Specimens of *Paraonis* sp. are 3 to 5 mm long. The prostomium is a rounded cone (Fig. 3.II.158a) with a barely distinguishable button at the tip (not evident on Fig. 3.II.158a). The peristomium appears to join with the prostomium and slight grooves are visible laterally. All setigers bear dorsally directed postsetal lobes, which become longer and swollen basally in posterior segments. Cirriform branchiae (Fig. 3.II.158b) are present on setigers 4 to 9, where they lie against the dorsum and are directed posteriorly. Notosetae are all slender capillaries, while neurosetae include capillaries and short, stout setae (Fig. 3.II.158c) in posterior segments. The pygidium is rounded, with 4 short cirri about the same length as the posterior setal lobes, which are two-thirds to three-quarters the length of anterior setal lobes. This undetermined species reached densities of 227 worms/m^2 on a fringing reef flat at Fort Kamehameha, Oahu (Bailey-Brock 1979).

Family **Opheliidae**

These are fusiform worms that burrow head-down in the sand or mud, feeding on organic material in the sediments. The ventrum may be grooved along the length of the worm to convey a respiratory current that is generated by body-wall constrictions. Water is returned to the sediment surface along lateral grooves that accommodate parapodial branchiae (when present). Parapodia are small, with uniformly distributed simple capillary setae. Some genera have paired lateral eyespots located between segments. Three species are known from Hawaii: 2 widely distributed Indo-West Pacific species and an *Ophelina* sp., the last tentatively identified from juvenile specimens.

KEY TO HAWAIIAN OPHELIID GENERA

1	Cirriform branchiae present	2
	Branchiae absent	*Polyophthalmus*
2(1)	Lateral eyespots present	*Armandia*
	Lateral eyespots absent	*Ophelina*

Armandia intermedia Fauvel, 1902

These small, slender worms are about 8 to 10 mm long and have grooves along the ventral and lateral surfaces. The anterior end is conical, with a small tubercle on the tip. The posterior end is truncate and has a delicate anal funnel surrounded by 10 to 20 small dorsal papillae (Fig. 3.II.159a), and a long internal ventral cirrus. There are 27 to 28 biramous setigers and a pair of cirriform gills (Fig. 3.II.159b) is present on all setigers except the first and the last 3. Paired lateral eyespots (red-brown after preservation) are located from setigers 6 to 17

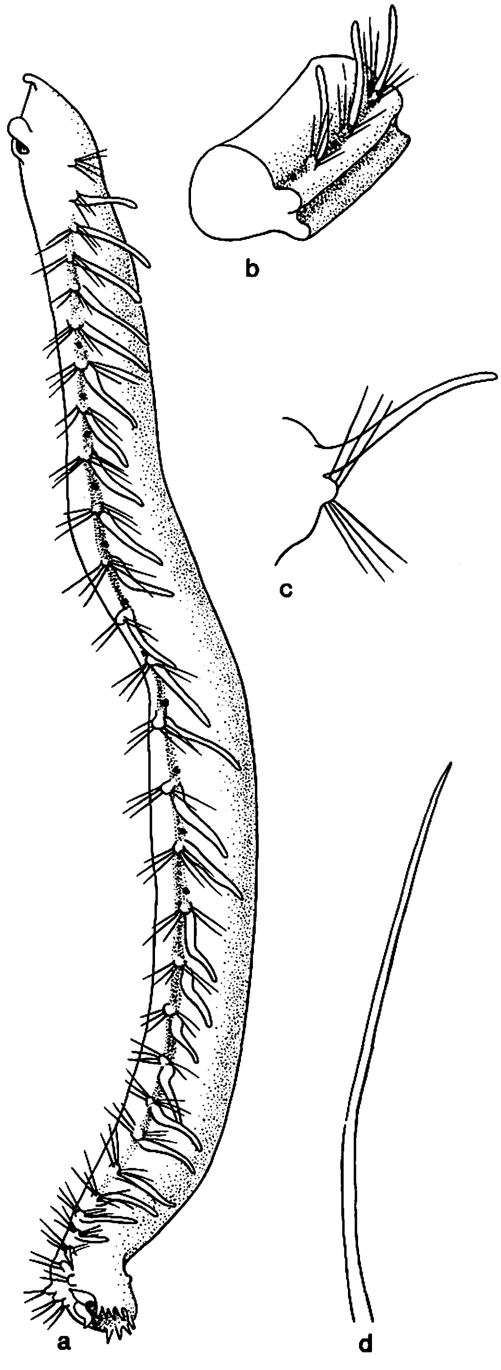


Figure 3.II.159.—*Armandia intermedia*: a, whole specimen showing parapodia with eyespots and cirriform branchiae, lateral view; b, biramous, cirriform setigers and lateral groove, lateral view; c, parapodium; d, capillary seta.

between the parapodia (Figs. 3.II.159a,b). Simple capillary setae, of a uniform length throughout, are the only kinds present (Figs. 3.II.159c,d). *Armandia intermedia* has been collected on Oahu in bottom samples from Honolulu Harbor, among mangrove roots on a south shore fringing reef where densities reach 589/m^2 (Bailey-Brock 1979), and in plankton from Kaneohe Bay. This species has a broad Indo-West Pacific and Atlantic distribution.

Ophelina sp.

This undetermined form is represented by a small specimen that closely resembles *Armandia intermedia* except that it lacks lateral eyespots. It was collected with sand samples from shallow water off Kahe, Oahu (L. A. Ward, pers. comm.).

Polyophthalmus pictus (Dujardin, 1839a)

These are small, slender worms, 8 to 13 mm long and 1 mm wide, that are composed of 27 segments. The body surface is smooth (Fig. 3.II.160a) except for the ventral groove. Biramous parapodia are inconspicuous and branchiae are absent. The head is rounded, with a ventral mouth (Fig. 3.II.160b) and a pair of subdermal eyespots. Paired lateral eyes are present between parapodia of middle segments. The dorsum is often crossed by iridescent bars following a segmental pattern. The posterior end bears an anal funnel with a few marginal papillae (Fig. 3.II.160c). Widely distributed in warm seas, this species occurs intertidally in sediments and among algal turf associated with coral rubble on Oahu, Maui, Hawaii (Holly 1935; Hartmann-Schröder 1965; Hartman 1966), and on the windward bench at Enewetak, Marshall Islands (Bailey-Brock et al. 1980).

Family **Cossuridae**

Cossurids are small, linear worms having a conical prostomium without appendages and a single median tentacle on the dorsum of an anterior setiger. The threadlike tentacle is the most conspicuous diagnostic feature, but it is easily detached and lost. Cossurids are described as burrowers, feeding by engulfing sedimentary detritus with an eversible proboscis (Day 1967). The genus *Cossura* is the best known of the family, but a second genus has been distinguished and 15 species of cossurids have been identified (Fauchald 1977a).

Cossura coasta Kitamori, 1960

A complete specimen is 8 mm long, less than 1 mm wide, and has approximately 80 setigers. It is threadlike and cylindrical, with a long tentacle attached to the dorsum (Fig. 3.II.161a) between setigers 2 and 3. The prostomium is an elongate cone without eyes or appendages. The mouth is ventral, with a protrusible pharynx that is soft and unarmed. Parapodia are reduced to 2 bundles of setae (Fig. 3.II.161b); notosetae are transparent narrow capillaries (Fig. 3.II.161c); neurosetae are pale yellow broad-blade capillaries. Setigers 2 to 22 appear to have more setae in both lobes than more posterior setigers. The pygidium has 2 or 3 short anal cirri (Fig. 3.II.161d). This new Hawaiian record is based on specimens collected from microcosm tanks at Ulupau and adjacent Kaneohe Bay, and from coral rock at Kahe, Oahu. *Cossura coasta* has a broad

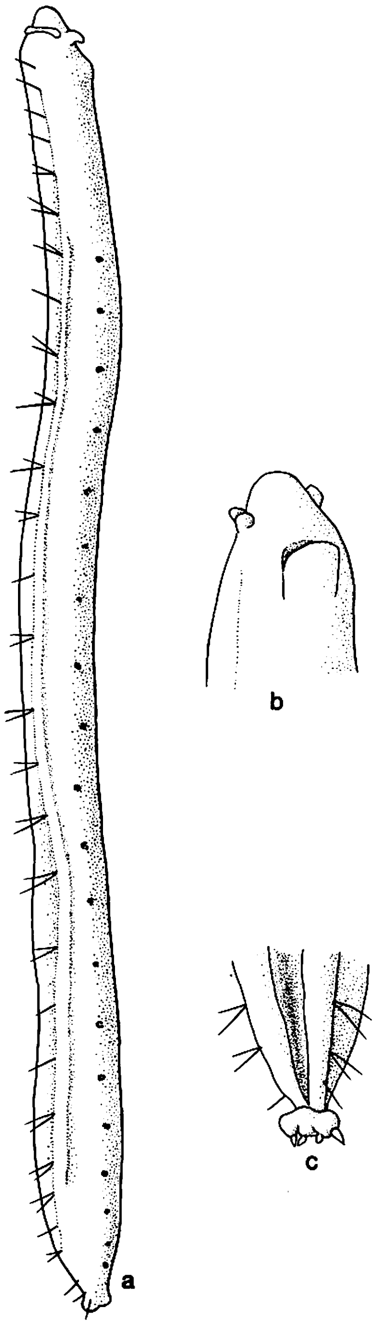


Figure 3.II.160.—*Polyophthalmus pictus*: a, whole specimen showing lateral eyespots and setae, ventrolateral view; b, ventral view of mouth; c, pygidium and part of the ventral groove.

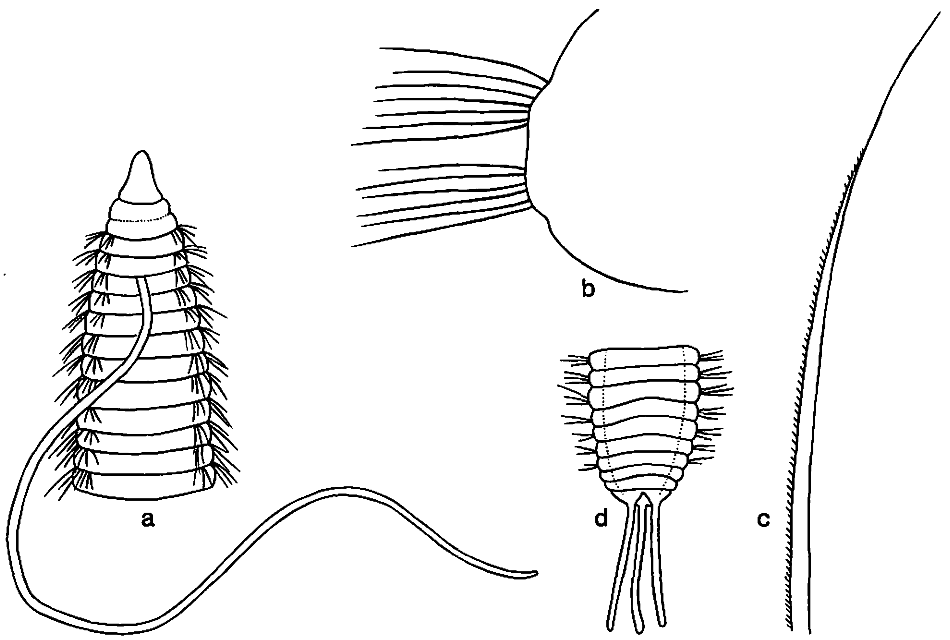


Figure 3.II.161.—*Cossura coasta*: a, anterior region and dorsal tentacle; b, parapodium; c, capillary seta; d, pygidium. (After Day 1967.)

distribution including southern Africa, Japan, and the Solomon Islands (Gibbs 1971).

Family **Scalibregmidae**

Scalibregmids are uncommon worms with an inflated anterior region bearing a small prostomium and a narrower posterior region. Segmental branchiae, acicular setae, and furcate setae may be present on some segments. These worms are thought to be detritivores, living on the surface of muddy sediment (Day 1967).

Hyboscolex longiseta Schmarda, 1861

This is a small species, up to 15 mm long, with a broad anterior region and a narrow posterior region. The prostomium is small, T-shaped, and bears a pair of red eyes (Fig. 3.II.162a). The peristomium is achaetous and the proboscis is a soft, eversible bulb. There are approximately 35 anterior segments, which appear swollen and triannulate, and all are biramous (Fig. 3.II.162b). The parapodial lobes are reduced and all setae are fine capillaries (Fig. 3.II.162d). The posterior region is missing from the Hawaiian specimen, but posterior segments have been described as biramous, without annulations, and having a few forked setae (Fig. 3.II.162c) and 5 small anal cirri (Day 1967). This new Hawaiian record is based on specimens collected on Oahu from Fort Kamehameha reef flat and among fine sand and coral rubble on the reef near Sampan Channel in Kaneohe Bay. *Hyboscolex longiseta* has a broad distribution including the Indian Ocean, southern Africa, New Zealand (Day 1967), and the Solomon Islands (Gibbs 1971).

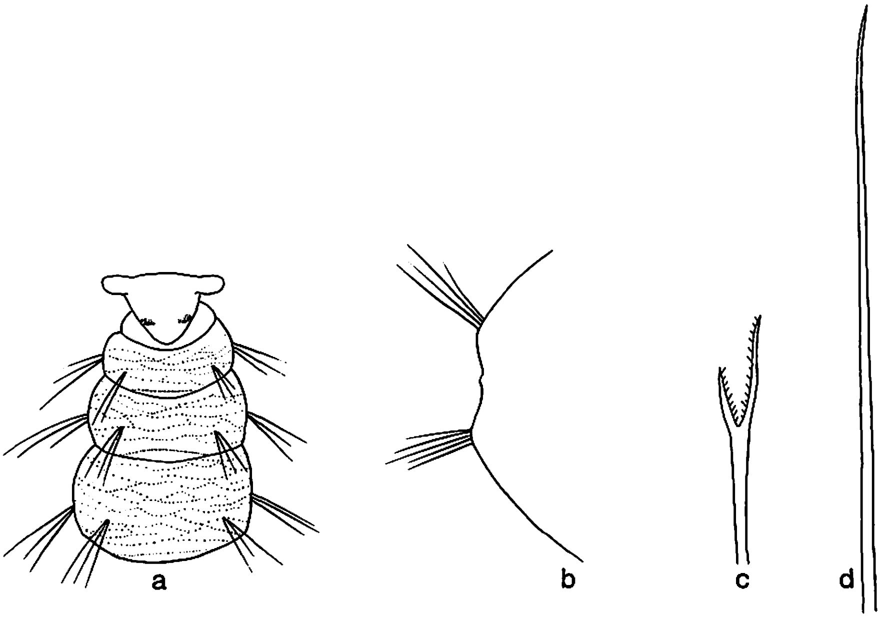


Figure 3.II.162.—*Hyboscolex longiseta*: a, anterior region showing T-shaped head; b, parapodium; c, forked seta; d, capillary seta.

Family **Capitellidae**

Members of this family are burrowing worms that live in sand and mud; they ingest particulate food together with a large volume of inorganic matter in typical earthworm fashion. Conspicuous features include an eversible proboscis for burrowing and feeding and, in some species, parapodial gills, which may be small and retractile. The body is divided into a short thorax with a fixed number of segments, and a long slender abdomen of more numerous segments. The small, hooded hooks characteristic of the family may occur in both body regions or may be restricted to the abdomen.

KEY TO HAWAIIAN CAPITELLID SPECIES

1 Thorax composed of 9 setigers........................ *Capitella capitata*
Thorax composed of more than 9 setigers 2
2(1) Abdomen ends with a flat, anal plate bearing spines
.... *Scyphoproctus ?djiboutiensis*
Abdomen ends with normal, rounded segments bearing setae 3
3(2) Thorax composed of 11 setigers... *Notomastus* (*Clistomastus*) *anoculatus*
Thorax composed of 13 setigers............ *Dasybranchus ?lumbricoides*

Capitella capitata (Fabricius, 1780)

These worms are threadlike and have a cylindrical body 15 to 30 mm long. The conical prostomium bears a pair of ventrolateral eyes and an eversible proboscis. Thoracic segments are biannulate, rounded in profile, and bear

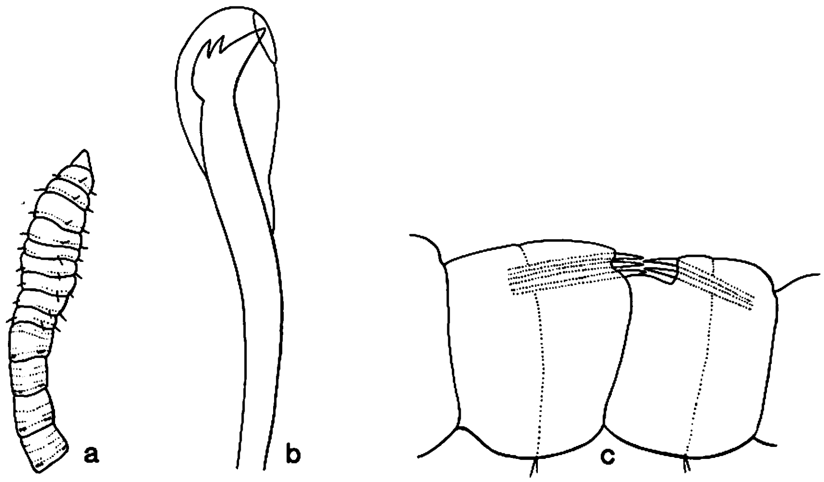


Figure 3.II.163.—*Capitella capitata*: a, anterior region composed of 9 biannulate thoracic and 4 abdominal segments; b, hooded hook seta; c, genital hooks of a male on setigers 8 and 9. (b,c after Day 1967.)

capillary setae beginning on the peristomial segment. Abdominal segments are smooth and narrower than those of the rather swollen thoracic region (Fig. 3.II.163a). Hooded hook setae (Fig. 3.II.163b) begin on the fifth thoracic segment, although the seventh segment may have capillaries only, hooks only, or both. This species is sexually dimorphic, the setae of the eighth and ninth segments differing in males and females; females have both notopodial and neuropodial hooks on the eighth and ninth segments, while males have enlarged genital spines (copulatory setae) dorsally (Fig. 3.II.163c) and normal hooks on the neuropodia. The genital spines of segment 8 point posteriorly, those of segment 9 anteriorly; all point towards the genital opening. The abdomen has hooded hooks, each with 3 to 4 teeth above the main fangs, in both notopodia and neuropodia. Branchiae are absent. The number of thoracic setigers may vary between populations of *C. capitata*; some have only 7 setigers with capillary setae, the hooded hooks beginning on setiger 8 (K. Fauchald, pers. comm.).

Capitella capitata has a cosmopolitan distribution. It is regarded as an indicator of pollution (Day 1967). Recent genetic research distinguishes at least 6 sibling species, each with differing life histories and generation times (Grassle and Grassle 1976). *Capitella capitata* is euryhaline and very tolerant of low oxygen tensions, hence its distribution in polluted, near-shore habitats. This species was first identified from larvae collected from Ala Wai Canal that metamorphosed in the laboratory (Ward 1978). Adult *C. capitata* specimens have since been found in large numbers in sediments on fringing reefs near stream outlets in Kaneohe Bay, at Niu near Aina Haina (Bailey-Brock 1984a), in oyster culture ponds, and from other areas around Oahu.

Dasybranchus ?lumbricoides Grube, 1878

Live specimens usually coil tightly, fragment easily, and may be more than 100 mm long. The color in life is usually dark blue to purplish red, fading in alcohol. The thorax has an areolated epithelium and is 5 to 9 mm wide, while the

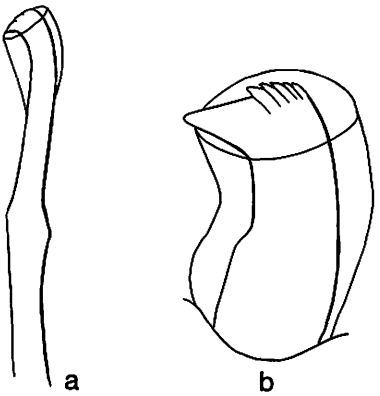


Figure 3.II.164.—*Notomastus* (*C.*) *anoculatus*: a, abdominal hook; b, abdominal hook, distal end. (After Hartmann-Schröder 1965.)

abdomen is much more slender and tenuous. The prostomium is a small, short lobe with an anterior palpode that projects above a frilly protrusible proboscis. The first segment is biannulate and achaetous. The next 13 segments have only capillary setae and the abdomen has long-handled hooked setae in the notopodia and neuropodia. Branchiae may be withdrawn or visible as bushy, parapodial tufts in the most posterior segments. *Dasybranchus lumbricoides* is widely recorded from Indo-West Pacific waters. A number of specimens were collected from muddy sediments in Kaneohe Bay and Niu Valley, Oahu. Fragments from Waikiki, Oahu, and Halape, Hawaii, were questionably referred to this species by Hartman (1966).

Notomastus (*Clistomastus*) *anoculatus* Hartmann-Schröder, 1965

The body of this worm is slender and attenuate. An incomplete specimen composed of the thorax and 15 abdominal segments is 14 mm long and 1.1 mm wide. The prostomium is bluntly triangular and terminates in a biannulated palpode. The peristomium is a smooth ring. The first setiger has notosetae and neurosetae like those of the additional 10 thoracic parapodia. The surface of the first 6 thoracic segments is areolated; thereafter it is wrinkled or smooth. Abdominal parapodia have only long-handled hooks (Fig. 3.II.164a), in which the distal end has a large fang surmounted by several small teeth (Fig. 3.II.164b). Branchiae are absent. This species was collected from coral sand in Kaneohe Bay, Oahu (Hartmann-Schröder 1965).

Scyphoproctus ?djiboutiensis Gravier, 1906

Small worm 8–10 mm in length and less than 0.5 mm in width. There are 2 clusters of 4–5 eyespots on the head. Typically there are 12 thoracic setigers in this species, but only 11 setigers could be counted. Capillaries are present in both rami of the thoracic setigers. There are 32 setigers, the last 6 form a flat anal plate with a pair of cirri. Anal plate setae are spinous hooks, with 1 hook in the most posterior parapodia and 3, 4, 5, or 6 in the remaining parapodia of the anal plate. The specimen differs from the description (Day 1967) in the number of thoracic setigers, the presence of eyes, and in the overall size and total number of setigers.

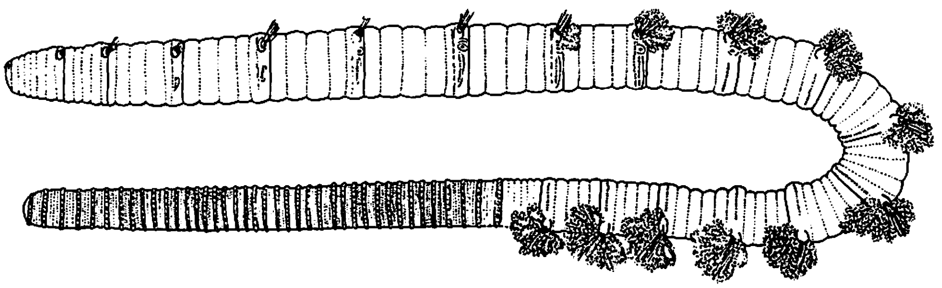


Figure 3.II.165.—*Arenicola brasiliensis*: entire specimen showing branchiferous setigerous region and apodous tail. (After Ashworth 1912.)

This specimen may be a juvenile that has not developed the full set of setigers. Collected with coral sand from a 70 m depth off the south shore of Oahu. *Scyphoproctus djiboutiensis* is known from the Indian Ocean and South Africa (Day 1967).

Family **Arenicolidae**

Arenicolids are large, soft-bodied worms that typically form U-shaped burrows in soft sediments by excavating with an extensible proboscis and swallowing some of the loosened materials. They are considered surface deposit-feeders, utilizing the organic component of sediments that accumulate in the vicinity of the head shaft (Fauchald and Jumars 1979). A funnel-shaped depression in the substrate is at the head end of the burrow; the tail region of the animal backs up to the other opening, which is ringed by fecal sand castings. In some temperate regions arenicolid worms may be quite numerous on sand beaches and are used by local fishermen for bait. The anterior region is setigerous and has paired, bushy branchiae on some segments; it lacks septa between some of the segments and can act as a piston or an anchor while burrowing. The asetigerous posterior region lacks septa, is narrower than the anterior region, and bears a terminal anus. Notopodia have capillary setae; neuropodia have dentate hooks that are never hooded (in constrast to the Capitellidae with hooded hooks).

Arenicola brasiliensis (Nonato, 1958)
[syn. *Arenicola* sp.: Edmondson 1946]

The body attains 200 mm in length, with the anterior region 10 to 15 mm in width and the posterior only 4 to 5 mm in width. Living worms are light red to dark gray, with a yellow posterior end. Preserved worms are darker and the posterior end is brown to black. There are 17 setigers anteriorly and a long, apodous posterior region (Fig. 3.II.165). Eleven pairs of large, bushy branchiae occur on setigers 7 to 17, and 6 pairs of nephridiopores on setigers 5 to 10. Notosetae are capillaries and neurosetae are simple hooks. Bands of neurosetae from right and left parapodia meet or almost meet along the midventral line and form a nearly continuous ridge of hooks on the ventrolateral surface. This species is widely distributed in warm seas and occurs in intertidal waters in sand or rubble. It has been found on Oahu at Hanauma and Kaneohe Bays (Edmondson 1946; Hartman 1966), Maunalua Bay, and among the algal-detrital mat in fish tanks at the

National Marine Fisheries Service Facility at Kewalo. *Arenicola brasiliensis* spawns gelatinous cocoons from the head shaft of the burrow and larvae are liberated from the cocoons at the 3 setiger stage (Bailey-Brock 1984b).

Family **Maldanidae**

Maldanids are burrowing worms that form tubes covered with attached sand grains or mud and feed on detritus and organic materials within the sediments (Fauchald and Jumars 1979). They lack conspicuous external appendages except for an elaborate pygidium. The segments may be somewhat swollen so that the entire worm resembles jointed bamboo, hence their common name of bamboo-worms. Species are distinguished from each other by the shape of the pygidium, grooves on the head, and specialized hooked setae. Only 1 genus, *Praxillella*, is known from shallow depths in the Northwestern Hawaiian Islands, and Hartman (1966) regards this as a tentative identification. Additional species have been tentatively identified from depths of 300 to 600 m (164 to 328 fm) around the high Hawaiian Islands. These include *Clymenura* sp., *Axiothella quadrimaculata*, *Lumbriclymene* sp., and *Nicomache mossambiqua*.

?*Praxillella* sp.
[syn. *Praxilla* sp.: Treadwell 1906]

The Hawaiian record is based on a description of the anterior regions of 2 worms. The hooked setae resemble those of *Praxilla kerguelensis* (McIntosh, 1885) but lack the anterior collar fold on somites 2 and 3. Material was dredged from 70 m on a white sand, shell, and coral substrate off Laysan Island, and the tubes were composed of radiolarians.

Family **Sternaspidae**

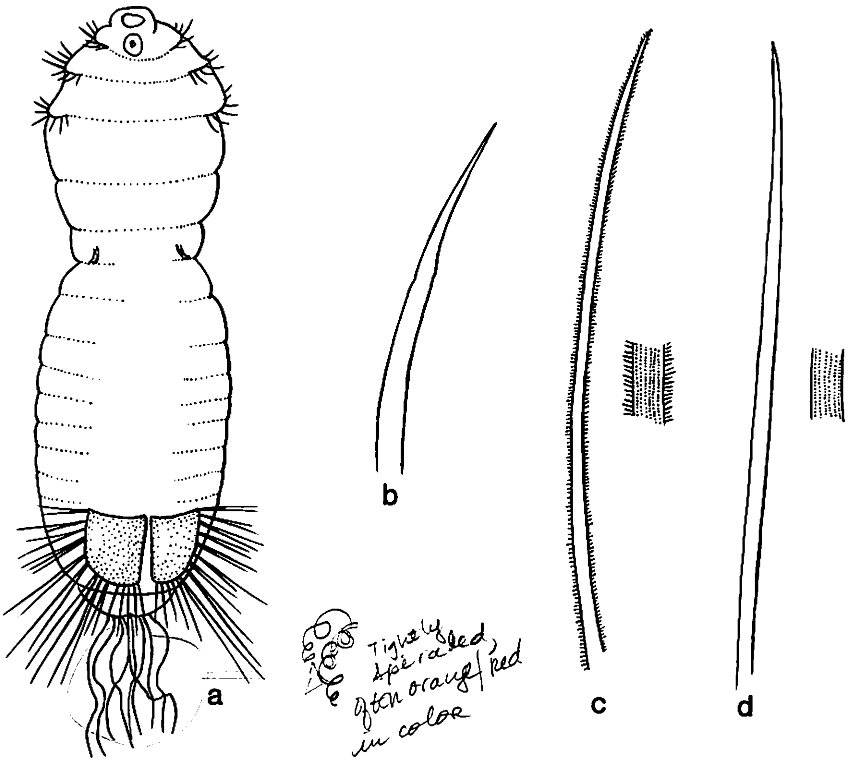
Sternaspids are small, peanut-shaped worms with an anterior end capable of being invaginated and bearing the mouth, and a broader posterior region with a pair of anal plates. Three anterior segments bear rings of acicular setae, segment 7 has a pair of genital papillae, and the posterior end bears filamentous branchiae. The worms bury themselves head down in the sediments, with the anal plates and branchiae uppermost. This family has not previously been recorded from the Hawaiian Islands.

Sternaspis sp.

The body is about 4 to 5 mm long, peanut-shaped, and composed of only a few segments (Fig. 3.II.166a). Anterior segments bear conspicuous rows of acicular setae (Fig. 3 II.166b). Genital papillae are not evident on segment 7 but 2 shield-shaped anal plates cover the ventrum of the posterior segments. Bundles of 15 to 17 capillary setae, some pilose (Fig. 3.II.166c) and others smooth (Fig. 3.II.166d), surround the outer edges of the plates. Branchial filaments are spirally coiled and numerous. Specimens have been collected from sediments at shallow depths in Kaneohe Bay and Honolulu Harbor, Oahu.

Family **Oweniidae**

Oweniids are long, cylindrical worms with sand grain tubes that project above the surface of the sand. The body is composed of a head that may have a



Tightly spiraled, often orange/red in color

Figure 3.II.166.—*Sternaspis* sp.: a, entire specimen showing anal plates and branchial filaments, ventral view; b, acicular seta from an anterior segment; c, pilose capillary seta with magnified inset; d, smooth capillary seta with magnified inset. (b,c,d after Day 1967.)

food-gathering membrane but without antennae and a few segments with poorly developed parapodia. Notosetae are capillaries and neurosetae are long-shafted hooks.

Myriochele hiruensis Gibbs, 1971

Small worms measuring 7 mm in length and less than 0.5 mm in width. The head lacks a feeding membrane or palps. There is a transverse, curved groove on the dorsum of the head extending between, and just posterior to, the pair of ventrolateral eyes. The 1st 3 setigers have notosetae only, setiger 1 has 1 pair and setigers 2 and 3 each have 2 pairs. Setiger 4 has 3 pairs of setae and a broad band of hooked uncini arranged in 5 rows. Setigers 1–3 are short; setiger 4 and mid-body setigers are long. The posterior region has shorter setigers with 1 or 2 setae and a group of uncini. The uncini are all 2-barbed hooks typical of this genus. The tubes are composed of sand and shell fragments and are approximately 1 mm in diameter. Specimens were collected in fine calcareous sand at a depth of 70 m off the south shore of Oahu. This species is known from the type locality in Marova Lagoon, New Georgia, Solomon Islands (Gibbs 1971), where it was dredged with sand from a 16 m depth.

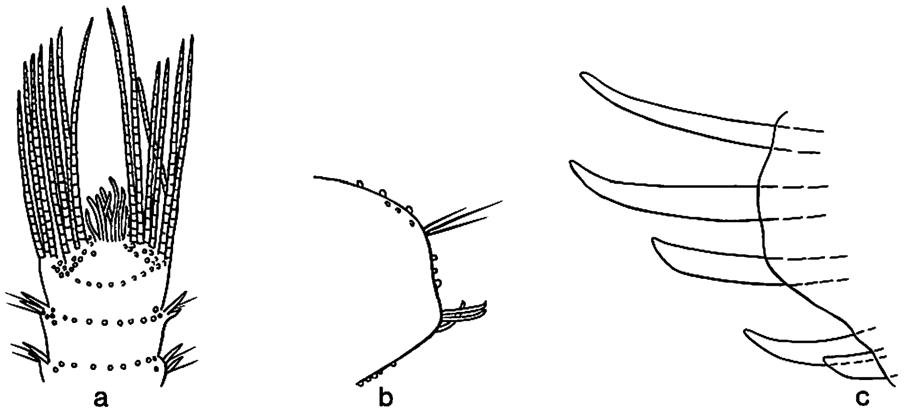


Figure 3.II.167.—*Pherusa havaica*: a, anterior region, ventral view; b, parapodium; c, neuropodial acicular spines. (a,b after Kinberg 1910; c after Hartman 1948.)

Family **Flabelligeridae**

Members of this family are tapered worms of relatively few segments; the head region bears palps and branchiae and is usually surrounded by a cephalic cage formed by elongate capillary setae of the first few segments (Fig. 3.II.167a). Parapodia are biramous; notosetae are annulated capillaries, while neurosetae may be annulated capillaries (but stouter than the notosetae) or simple hooks. Some species have the surface of the body papillose and covered with adherent sand grains, making it very difficult to see the worm, count setigers, or examine setae. Worms may be placed in dilute nitric acid following formalin fixation to remove calcareous sand and shell fragments without damaging diagnostic features (Brock and Brock 1977). The blood is green. These worms are surface-deposit feeders, using the palps to collect food particles (Fauchald and Jumars 1979). Some forms are sedentary, and some species burrow in surface sediments with the palps projecting for food gathering.

Pherusa havaica (Kinberg, 1867)
[syn. *Chloraema havaica* Kinberg, 1867]

In this species, the surface of the body lacks adhering sand grains and appears smooth except for the circlets of surface papillae, which are most abundant on the ventral side of the anterior end of the body and on the segmental boundaries (Fig. 3.II.167a). Annulated setae of the first 3 segments form a cephalic cage, and the oral tentacles, when everted, are long and slender. Parapodia are broadly biramous (Fig. 3.II.167b); notopodia have slender fascicles of long, annulated setae; neuropodia from the fifth segment have transverse rows of acicular, curved spines numbering about 5 in a series (Fig. 3.II.167c). This species is known in Hawaii only from the original collection on coral reefs near Honolulu.

Family **Sabellariidae**

Sabellariids are tubicolous worms that build strong sand-grain tubes attached to rocks, shells, and other firm substrates. Many species are gregarious (Eckelbarger 1978), and aggregations of tubes may form extensive reefs in shallow seas. The head bears a crown of golden paleae (modified setae) that forms an operculum (borne on an opercular peduncle) that closes the mouth of the tube, thus reducing desiccation at low tide and excluding predators. Sabellariids are suspension feeders, collecting food materials with extensible ciliated tentacles. Anterior prehensile palps aid in tube building, a process necessary to keep pace with the growth of the worm and erosion by wave action. The body is composed of 4 regions. The first region has 2 uniramous segments with capillary setae, and the second region (parathoracic) has biramous parapodia bearing gills, oar-shaped notosetae, and capillary neurosetae. The third region (abdomen) has dorsal gills

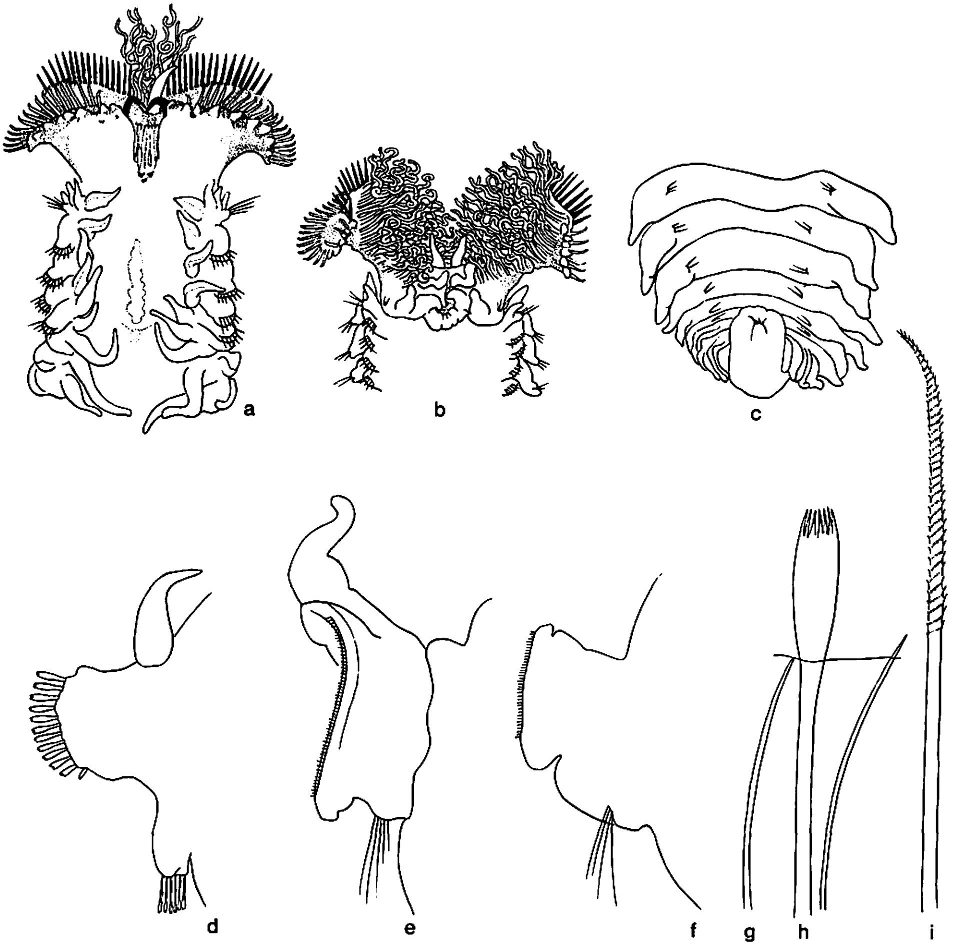


Figure 3.II.168.—*Lygdamis nesiotes*: a, anterior region showing opercular peduncles and pair of hooks, dorsal view; b, anterior region showing opercular palea and buccal cirri, ventral view; c, caudal region; d, parathoracic parapodium; e, anterior parapodium; f, posterior parapodium; g, chitinous rod; h, oar seta; i, ringed capillary seta.

and biramous parapodia with notopodial uncini and neuropodial capillaries. The fourth region is a long, slender, apodous cauda, which is capable of voiding fecal pellets through the mouth of the tube.

KEY TO HAWAIIAN SABELLARIID SPECIES

1 One row of opercular paleae 2
Two or 3 rows of opercular paleae (Figs. 3.II.168a,b) 3
2(1) Four parathoracic setigers; opercular peduncles long and separate (Fig. 3.II.168b) .... *Phalacrostemma setosa*
Three parathoracic setigers; opercular peduncles short and fused .... *Monorchos varians*
3(1) Two rows of opercular paleae; 4 parathoracic setigers .... *Lygdamis nesiotes*
Three rows of opercular paleae; 3 parathoracic setigers .... *Phragmatopoma moerchi*

Lygdamis nesiotes (Chamberlin, 1919)
[syn. *Lygdamis indicus* Kinberg, 1867]

Worms reach about 30 mm in length, 4 to 5 mm in width, and form well-cemented sand-grain tubes that may be aggregated in masses. The body consists of an anterior operculum followed by 2 rudimentary segments, 4 parathoracic setigers, an abdominal region, and a caudal region (Figs. 3.II.168a,b,c). Opercular paleae (Figs. 3.II.168a,b) are yellow and are arranged in 2 rows, the outer row with 28 pairs of paleae, the inner with 14 pairs. There is a pair of thick dorsal hooks visible at the mid-dorsum of the operculum (Fig. 3.II.168a) and numerous filiform tentacles emerge between the opercular peduncles (Fig. 3.II.168b). Parathoracic parapodia (Fig. 3.II.168d) bear dorsal cirriform branchiae, oar setae (Fig. 3.II.168h), and chitinous supporting rods (Fig. 3.II.168g). Abdominal parapodia (Figs. 3.II.168e,f) have branchiae on anterior setigers, as well as notopodial uncini and neuropodial ringed capillaries (Fig. 3.II.168i). Widely dispersed in the Indo-West Pacific region, this species was found in sand and mud near Halape, Hawaii (Hartman 1966).

Monorchos varians Hartman and Fauchald, 1971
[syn. ?*Hermella varians* Treadwell, 1906. *Lygdamis indicus* Kinberg, 1867: Hartman 1966 (Kirtley, pers. comm.)]

This species attains a length of 30 mm and a width of 4 to 5 mm. Opercular peduncles are fused dorsally and incompletely fused ventrally as a midventral cleft (Figs. 3.II.169a,c). Nuchal hooks are large and have stout bases (Figs. 3.II.169b,c,d). There is a single row of opercular paleae, which are slightly expanded through the middle portion then taper abruptly to a smooth tip (Fig. 3.II.169e). Between the paleae are 2 rows of accessory setae, which are cylindrical, tapered, dark-brown spines (Fig. 3.II.169f). The first setiger bears a tuft of capillary setae; this is followed by 4 parathoracic segments with oar setae (Fig.

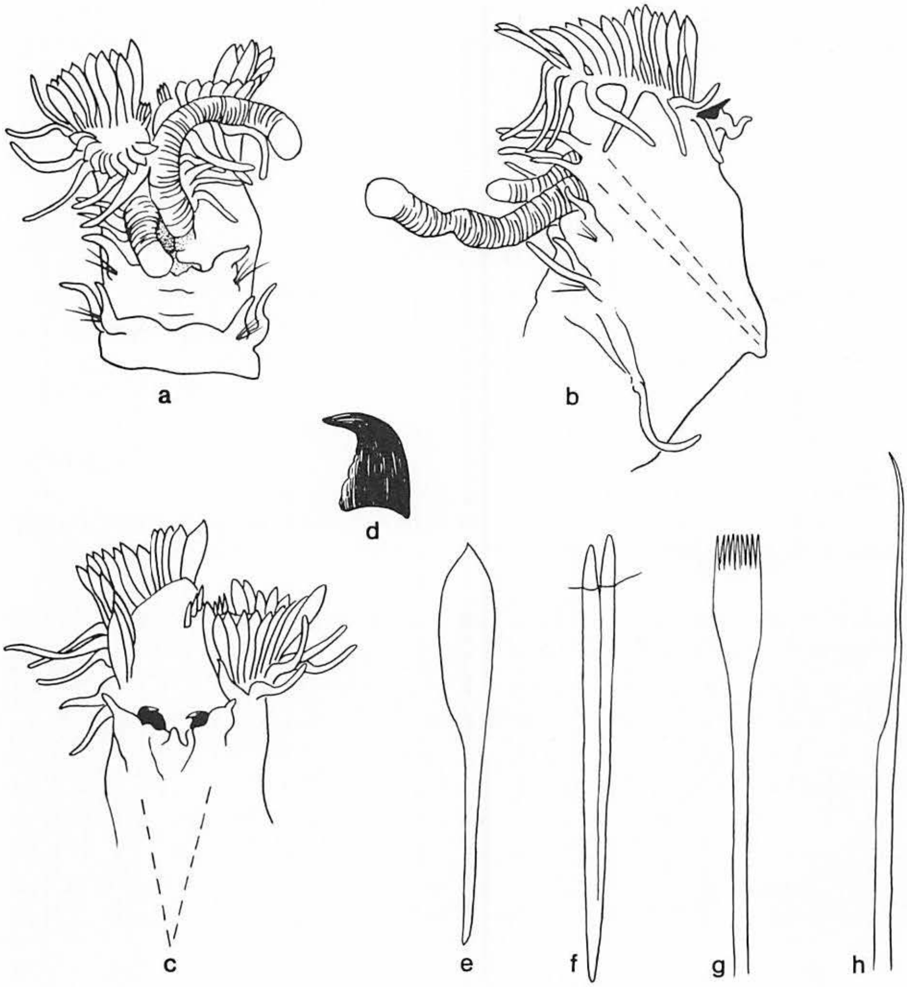


Figure 3.II.169.—*Monorchos varians*: a, anterior region, dorsal view; b, anterior region, lateral view (position of nuchal hooks indicated with dashed line); c, anterior region, ventral view showing nuchal hooks; d, nuchal hook; e, palea; f, accessory setae; g, oar seta; h, simple capillary seta.

3.II.169g) and narrow capillaries (Fig. 3.II.169h). A long abdomen and an apodous cauda make up the rest of the body. This is a relatively deep-water species, and the first specimen was taken off the south coast of Hawaii from depths between 563 and 589 m (308 and 322 fm). This species was also collected from South Point, Hawaii, at a depth of 600 m (328 fm), and from the North Atlantic (Hartman and Fauchald 1971).

Phalacrostemma setosa (Treadwell, 1906)
[syn. *Sabellaria setosa* Treadwell, 1906]

The length of the head and anterior 12 segments of 1 specimen is 16 mm; the width is 5 mm. Small oral tentacles are present along both sides of the ventrum of the prostomium as a continuation of the ring of palps that surrounds the crown.

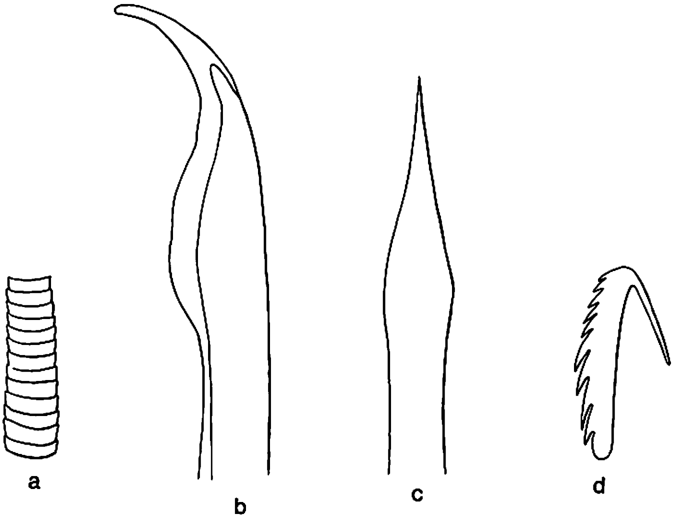


Figure 3.II.170.—*Phalacrostemma setosa*: a, portion of an opercular palea showing spiral rings; b, nuchal hook; c, parathoracic notoseta; d, abdominal uncinus. (After Treadwell 1906.)

The paired palps are large, prehensile tentacles, which arise just anterior to the oral aperture and are used for tube building. There is a single row of pale yellow opercular paleae; they are all of the same type and taper uniformly to the apex. The tips of the paleae are spirally serrated or ringed in appearance (Fig. 3.II.170a). There are 4 or 5 [up to 6 according to Treadwell (1906)] pairs of nuchal hooks, each with a thin wing on the curved side (Fig. 3.II.170b). There are 4 parathoracic segments bearing broad-bladed notosetae with tapered tips (Fig. 3.II.170c) and capillary neurosetae. Abdominal segments bear notopodial uncini (Fig. 3.II.170d) and neuropodial capillaries. This is another deep-water species; it was collected originally from depths of 500 to 750 m (274 to 410 fm) off the west coast of Hawaii

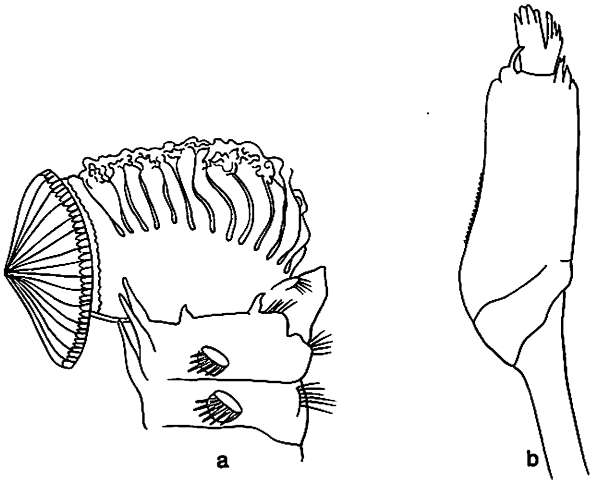


Figure 3.II.171.—*Phragmatopoma moerchi*: a, anterior end with operculum, lateral view; b, outer opercular palea. (After Hartman 1944.)

and from 200 to 600 m (109 to 328 fm) off Molokai, where the worms encrust the lower surface of the carrier shell, *Xenophora tenuis* (Bailey-Brock 1976). Specimens collected off Hawaii are described as having thick-walled tubes composed of foraminiferan tests, while those from Molokai have tubes of solidly cemented sand grains.

Phragmatopoma moerchi Kinberg, 1867

These worms reach about 23 mm in length, of which the slender cauda contributes about 2.5 mm. The operculum, a flattened cone, is nearly circular in outline and bears 3 rows of paleae (Fig. 3.II.171a) and is black. Outer paleae are flat and terminate in a broad plate (Fig. 3.II.171b) forming a fringe. The third (inner) row of opercular spines is visible only when the middle row is pulled away. Worms form aggregations of sand tubes that may be quite extensive. Occurring at depths of 0 to 15 mm off Oahu, *P. moerchi* is also known from both sides of Central America, Peru, and Chile. This species was originally reported from Honolulu and was figured by Hartman (1944).

Family **Trichobranchidae**

Members of this family are tubicolous worms having a body separated into 2 regions: a broad thorax with biramous setigers, and a narrow abdomen with neuropodia. Day (1967) considered this group a subfamily of the Terebellidae, but Fauchald (1977a) commented on differences between the 2 groups and reinstated familial status. Trichobranchids are distinguished by having body regions that are better defined and more muscular than those of the Terebellidae and thoracic neurosetae that are long-shafted hooks.

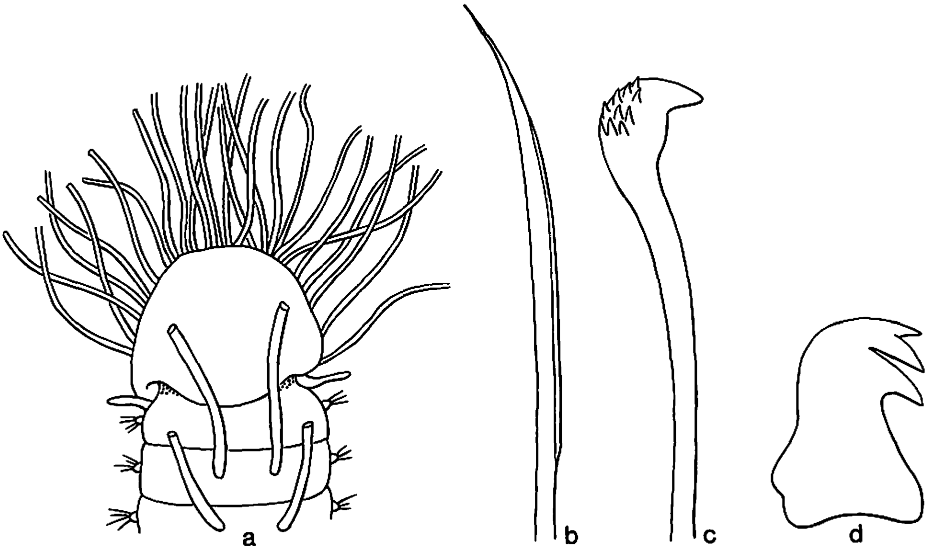


Figure 3.II.172.—*Trichobranchus* sp.: a, anterior region with filamentous tentacles and eyespots, dorsal view; b, capillary notoseta; c, long-shafted neuropodial hook; d, abdominal uncinus.

Trichobranchus sp.

A small, damaged specimen 9 mm long has been collected in Hawaii. The prostomium forms a lobe over the mouth and is surrounded by numerous filamentous palps used for feeding (Fig. 3.II.172a). There is a collar of 2 lateral lobes, and discrete bands of eyespots are present on both sides of the dorsum. Only 1 pair of lanceolate branchiae are attached to the second setigerous thoracic segment, but the bases of 1 subsequent pair can be distinguished (Fig. 3.II.172a). There are 12 thoracic setigers with capillary notosetae (Fig. 3.II.172b) and long-shafted hooks (Fig. 3.II.172c) on the neuropodia. Abdominal segments bear crested uncini (Fig. 3.II.172d) on fan-shaped neuropodia. The specimen may be a juvenile that has not yet developed all diagnostic features. It was found in an experimental microcosm tank at Ulupau near Kaneohe Bay, Oahu. This specimen has tentatively been placed in the genus *Trichobranchus*, members of which have 15 thoracic segments and 3 pairs of slender branchiae (Fauchald 1977a).

Family **Terebellidae**

Terebellids are tubicolous, deposit-feeding worms with pink, purple, or white buccal tentacles that are extended over the substrate to gather particulate materials. The tentacles give the family its common name of spaghetti worms. Suitably sized food particles are either conveyed to the mouth along grooves in the buccal tentacles by ciliary activity or are lassoed by tentacular contraction and removed by the palps bordering the mouth (Dales 1955). Tubes are elaborately ornamented with coarse sand and shell fragments and may be buried in sediments attached to the undersides of rocks or within crevices.

Anterior thoracic segments often bear 2 or 3 pairs of dendritically branched or filamentous gills; the first gill is on the second segment. There are 17 biramous thoracic parapodia bearing capillary notosetae and toothed uncini, which may be pectinate or have 1 or more rows of teeth above the main fang. Glandular cells are concentrated on the ventral surface of the thoracic segments as glandular pads (sometimes termed shields or cushions). These pads become ridges when the worm contracts, but the number of pads is constant and diagnostic. Other thoracic features of diagnostic importance are the nephridial papillae on the parapodia of the first 3 to 6 setigers of *Polycirrus*. These papillae are more conspicuous when the worm is producing gametes and appear as small bumps near the uncini. Dissection of the thorax is recommended to ascertain the number of nephridia if there is any doubt. The soft abdomen has uniramous setigers composed of neuropodial uncini; it may lack parapodia entirely, or have some biramous setigers with both setae and uncini (as in *Thelepus* and *Terebella*). Some species may be 30 cm long, with buccal tentacles reaching over an area of 1 m^2 or more. Nine genera with 11 species are known from Hawaii. Six of the species are quite widely distributed elsewhere, 1 is known only from deeper (200+ m) Hawaiian waters, and 2 are as yet undetermined.

KEY TO HAWAIIAN TEREBELLID GENERA

1	Anterior segments without branchiae	2
	With branchiae on 1 or more anterior segments	3
2(1)	Abdominal neurosetae present	*Polycirrus*
	Abdominal neurosetae absent	*Lysilla*
3(1)	Thorax with 20 or more setigerous segments	4
	Thorax with up to 17 setigerous segments	5
4(3)	Stalked branchiae dendritically branched	*Terebella*
	Branchiae as tufts of filaments	*Thelepus*
5(3)	Anterior segments without lateral lobes	*Nicolea*
	Anterior segments bearing lateral lobes	6
6(5)	One or 2 pairs of dendritically branched, stalked branchiae	*Pista*
	Three pairs of dendritically branched, stalked branchiae	7
7(6)	Thoracic capillary notosetae with serrated tips	*Neoamphitrite*
	Thoracic capillary notosetae with smooth tips	8
8(7)	Uncini bear rows of small teeth above a main fang (crested)	*Lanice*
	Uncini with 4 to 5 curved teeth in a single pectinate row	*Loimia*

KEY TO HAWAIIAN *LANICE* SPECIES

Body of worm as long as 300 mm; ventral pads gradually taper posteriorly	*L. conchilega*
Body of worm less than 300 mm; ventral pads become abruptly larger on segment 14	*L. expansa*

Lanice conchilega (Pallas, 1766)
[undetermined terebellid: Edmondson 1946]

The body of these large worms is as long as 300 mm. The color in life is yellow to tan, and tentacles are bluish white. The thoracic region is thick and the body tapers posteriorly. Anterior tentacles (Fig. 3.II.173a) are very numerous and extensile in life and are as long as 600 mm. The thorax consists of 17 setigerous segments; the abdomen comprises more numerous setigerous segments. There are 3 pairs of branchiae, each large and dendritically branched, and broad, lateral lobes occur on segment 3 (second branchiferous) (Fig. 3.II.173b). Crested uncini with rows of small teeth above the main fang are arranged in single rows in the most anterior setigers, but in double rows, back to back, in posterior thoracic setigers. Thoracic notosetae are capillaries with smooth tips. The tube is membranous and is anteriorly flared and latticed (Fig. 3.II.173c); it is cylindrical throughout its length and is covered with sand and shell fragments. The tube is known to harbor the commensal pinnotherid crab *Aphanodactylus edmondsoni*. Cosmopolitan in warm seas, this worm species has been found among rubble in shallow waters around the Hawaiian Islands (Hartman 1966).

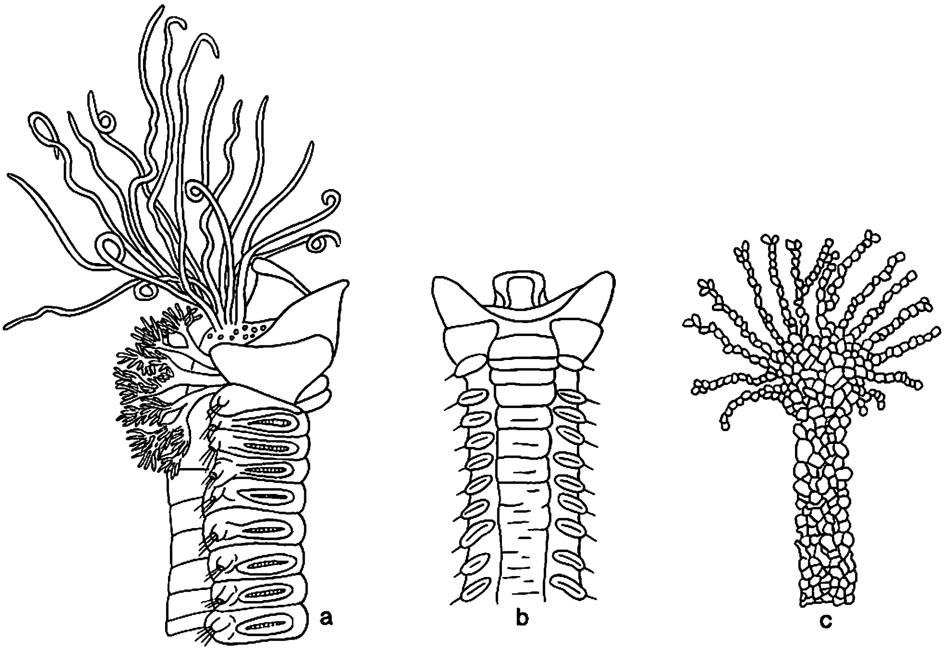


Figure 3.II.173.—*Lanice conchilega*: a, anterior region showing tentacles and branched branchiae, lateral view; b, anterior region (branchiae and tentacles removed), ventral view; c, anterior portion of tube. (After Fauvel 1927.)

Lanice expansa Treadwell, 1906
[syn. *Pista expansa* (Treadwell): Hartman 1966]

This species has more than 30 segments but the body length is unrecorded. The anterior region has a conspicuous dorsal collar extending laterally to form prominent lobes that are fused midventrally. Behind the collar is a smaller, less prominent lobe. Ventral pads are broadest in the first few segments, narrow to segment 6, and are then of uniform size to segment 14 where they are abruptly larger and more prominent. Of the 3 pairs of branchiae, the first is largest, the second about half as large, and the third about half as large as the second pair. All branchiae are dendritically branched and have broad bases. Notosetae are capillaries with smooth tips; thoracic uncini of anterior setigers have broad, expanded bases. The membranous tube is about 3 mm wide for most of the length but expands distally as 2 kidney-shaped expansions to 10 mm. The tube is covered with shell and coral fragments. *Lanice expansa* was collected at depths of 250 to 280 m (137 to 153 fm) from a coral sand and shell bottom in the Pailolo Channel between Molokai and Maui (Treadwell 1906). Hartman (1966) placed this form in the genus *Pista* because of the thoracic uncini with "prolonged" bases. It is returned to *Lanice* because there are 3 pairs of dendritically branched branchiae (*Pista* has 1 or 2 pairs) and because the description of the tube is similar to that for *Lanice conchilega*.

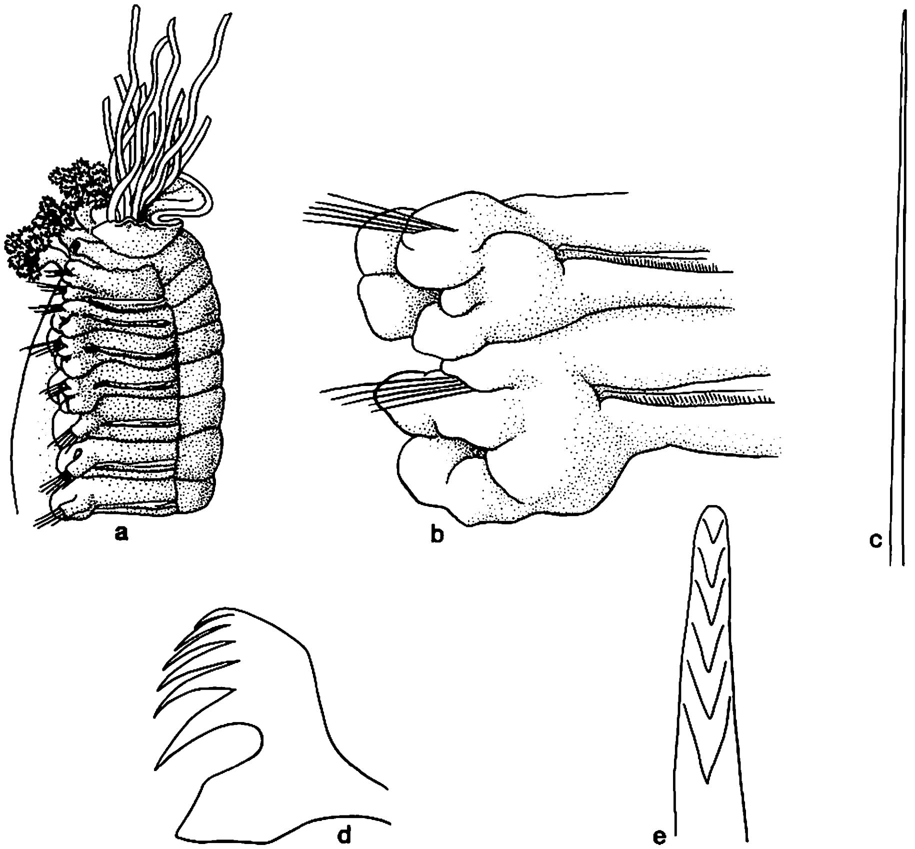


Figure 3.II.174.—*Loimia medusa*: a, anterior region (cephalic tentacles have been cut); b, nephridiopores of segments 5 and 6; c, capillary seta; d, thoracic uncinus, side view; e, thoracic uncinus, face view.

Loimia medusa (Savigny, 1818)
[syn. *Loimia crassifilis* (Grube, 1878): Treadwell 1906, Hartman 1966]

The cephalic tentacles are numerous, long (Fig. 3.II.174a), and bluish white or banded with purple when alive (Plate 3.II.4a), largely concealing the 3 pairs of unequally long, dendritically branched branchiae (Fig. 3.II.174a). In life the ventral gland shields may be bright red, the rest of the body orange to yellow. Lateral lobes of the first segment are conspicuously developed. There are 17 thoracic segments with simple, smooth-tipped capillary setae (Figs. 3.II.174b,c) and pectinate uncini with 5 to 6 teeth (Figs. 3.II.174d,e) in a single row. There is 1 row of uncini in anterior thoracic setigers but there are double rows, back to back, in posterior thoracic setigers. There are 9 to 10 ventral shields, becoming narrower posteriorly, and 3 pairs of nephridial papillae on segments 5 to 7 (Figs. 3.II.174a,b). The abdomen is considerably narrower than the anterior region and possesses uncini on flaplike pinnules but no notosetae. The tube has a tough, membranous lining covered with attached shell fragments and coral rubble, and has an unadorned opening. Widespread in the Indo-West Pacific, this species has

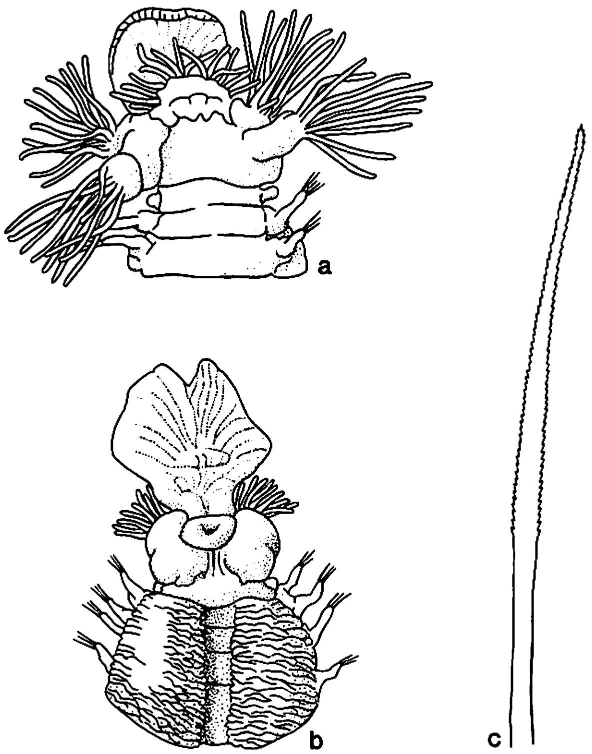


Figure 3.II.175.—*Lysilla ubianensis*: a, anterior end showing tentacles on the lower margin of the tentacular lobe, dorsal view; b, anterior end showing tentacular lobe, ventral view; c, barbed seta.

been collected from sand and rubble areas on reefs or in deeper waters (to 90 m) around the Hawaiian Islands. It is quite possible that *Loimia medusa* and *Lanice conchilega* have been confused in Hawaii. The former is probably the most conspicuous terebellid in Hawaiian waters; the latter is much less common in shallow waters than previously thought, and it can readily be distinguished from *Loimia medusa* because the uncini have 2 or more rows of teeth.

Lysilla ubianensis Caullery, 1944

These soft-bodied worms are from 30 to 35 mm long and have a swollen thorax and a tapered, achaetous abdomen. The head is covered by a broad tentacular lobe bearing numerous grooved tentacles (Figs. 3.II.175a,b). There are no eyespots, branchiae, or lateral lobes. There are 10 thoracic setigers, with notopodia from segment 3 but no neuropodia. Notopodia are slightly swollen basally; each bears setae with serrated tips (Fig. 3.II.175c) and a nephridiopore on the ventrolateral aspect. The ventral surface is swollen except for a median groove (Fig. 3.II.175b) containing small ventral pads. This groove continues into the abdomen, which also has a pair of lateral grooves. The abdomen lacks parapodia and setae and is very soft; abdominal segments are virtually indistinguishable. Two specimens were collected from experimental microcosm tanks at Ulupau near Kaneohe Bay, Oahu. This species is also

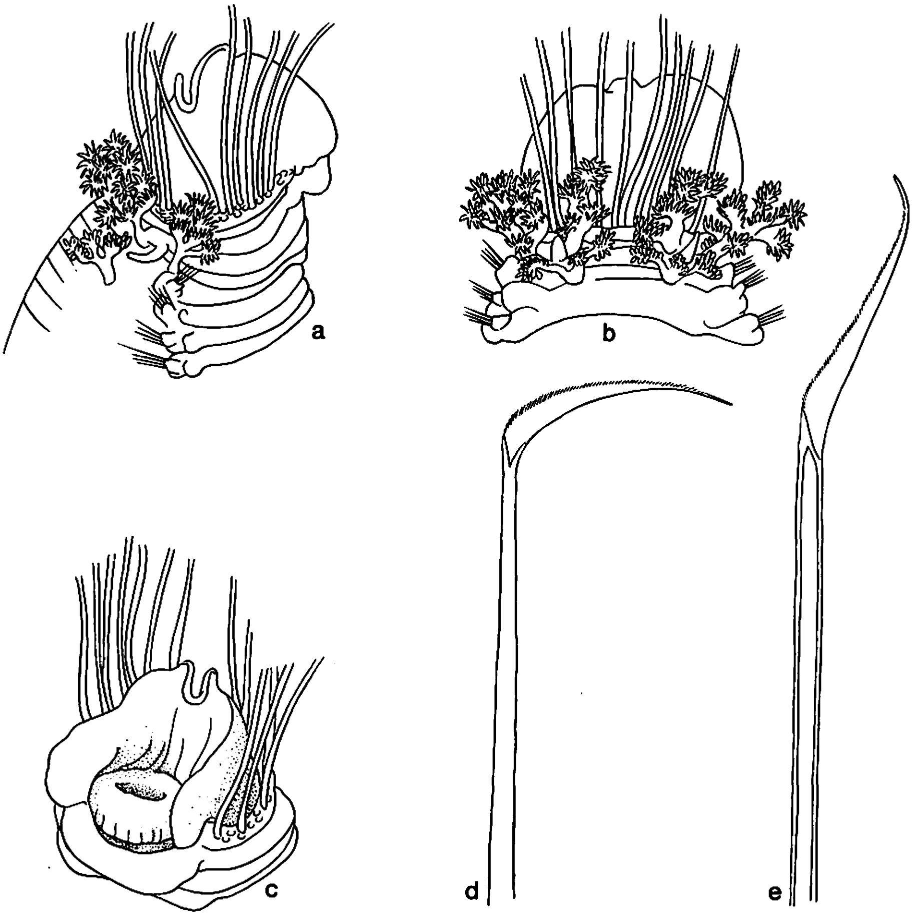


Figure 3.II.176.—*Neoamphitrite* sp.: a, anterior region with branchiae and tentacular lobe, lateral view; b, anterior region, dorsal view; c, prostomium and collar; d,e, serrated thoracic notosetae.

reported from the East Indies, South Africa, and the Solomon Islands (Day 1967; Gibbs 1971).

Neoamphitrite sp.

This genus is represented by soft-bodied worms 35 to 40 mm long and 3 mm wide. Thoracic segments 2, 3, and 4 each have a pair of dendritically branched branchiae (Figs. 3.II.176a,b). There is a pair of slender lateral lobes at the base of the second pair of branchiae that are separate from the basal stalks of the branchiae (Fig. 3.II.176a). There are no eyespots, but numerous tentacles arise from the base of the tentacular lobe (Fig. 3.II.176c), and a pair of nephridial papillae occur on setigers 2, 3, and 4. The thorax is composed of 17 segments, and the ventral pads are well developed. Notosetae are capillaries with finely serrated tips (Figs. 3.II.176d,e); neurosetae are crested uncini, which begin on the second

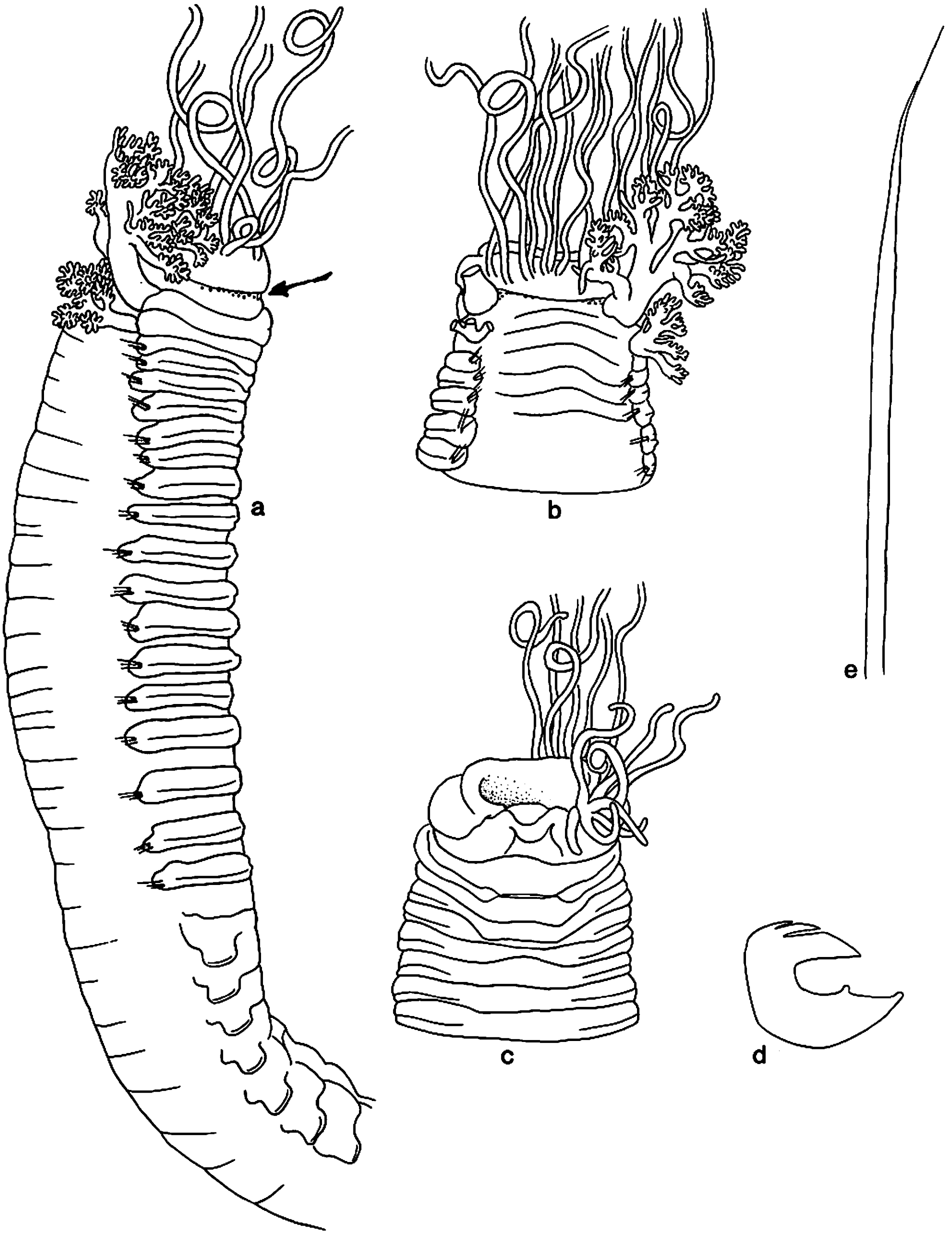


Figure 3.II.177.—*Nicolea gracilibranchis*: a, anterior region and part of abdomen, ventrolateral view; b, anterior region, dorsal view; c, anterior region, ventral view; d, thoracic uncinus; e, thoracic notoseta.

thoracic setiger and occur in double rows in some segments. A narrow, cylindrical abdomen bears capillary notosetae and uncinigerous neurosetae. Three specimens were collected from experimental microcosm tanks at Ulupau near Kaneohe Bay, Oahu.

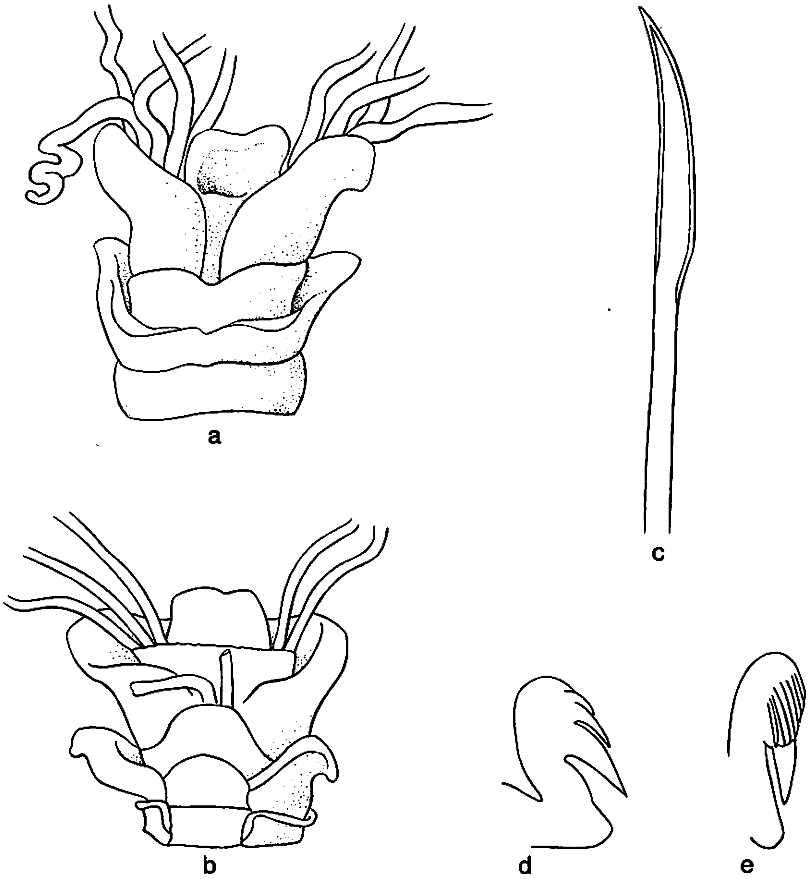


Figure 3.II.178.—*Pista dibranchis*: a, anterior region with tentacular lobes, and lateral lobes on first thoracic segment, ventral view; b, anterior region, dorsal view, with bases of paired gills at junction of collar lobes; c, thoracic seta; d, thoracic uncinus, lateral view; e, thoracic uncinus, almost face view.

Nicolea gracilibranchis (Grube, 1878)
[syn. *Terebella gracilibranchis* Grube: Treadwell 1906]

The body is up to 25 mm long and 2.5 mm wide in the anterior region. The short, collarlike tentacular lobe has numerous tiny eyespots (Fig. 3.II.177a). There are 2 pairs of dendritically branched, stalked branchiae (Figs. 3.II.177a,b). Ventral pads are very small, becoming more slender posteriorly (Figs. 3.II.177a,c). Notosetae are present on 17 segments from the fourth segment, uncini from the fifth segment. Notosetae are smooth capillaries (Fig. 3.II.177e), and neurosetae are avicular uncini (Fig. 3.II.177d). Paired nephridia open on segments 3, 6, and 7. This species has been reported attached to rock and among coral rubble in shallow water in Hawaii (Treadwell 1906; Kohn 1959; Hartman 1966; Bailey-Brock 1976). *Nicolea gracilibranchis* has an Indo-West Pacific distribution.

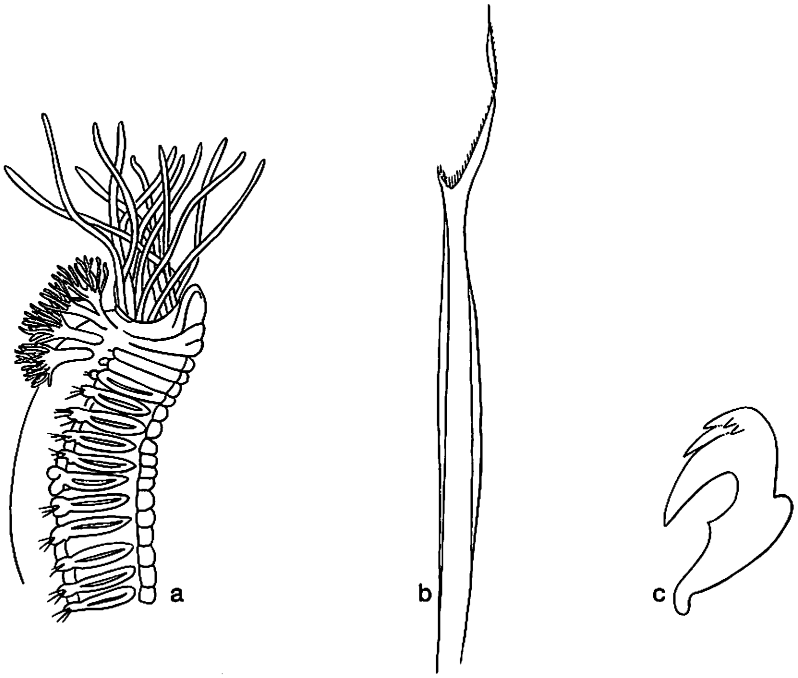


Figure 3.II.179.—*Terebella lapidaria*: a, anterior region with branchiae, lateral view; b, distally furcate seta; c, thoracic uncinus. (After Fauvel 1927.)

Pista dibranchis Gibbs, 1971

These are small, delicate worms reaching 20 to 25 mm in length. Tentacular lobes lack eyespots. The first thoracic segment has a pair of large lateral lobes directed anteriorly, forming a sheath around the tentacles (Figs. 3.II.178a,b). The second segment has a pair of small, ventrolateral lobes and the third segment an expanded pair of lateral lobes (Figs. 3.II.178a,b). The fourth segment lacks lobes. One pair of tufted, filamentous branchiae with long stalks is borne on the second segment (Fig. 3.II.178b, branchiae missing). Smooth-tipped capillary notosetae (Fig. 3.II.178c) begin on segment 4 and uncini on segment 5. Uncini are composed of 1 large fang surmounted by a keel of small teeth (Figs. 3.II.178d,e). About 12 ventral pads are present on the thorax. The abdomen bears uncini on square neuropodial flaps. This species was first reported from the Solomon Islands (Gibbs 1971). Two specimens have since been found at depths of 5 m in Kaneohe Bay in silt and coral rubble.

Polycirrus sp.

The size of this worm is not recorded. The body is bright red, luminescent, and fragile when alive. The prostomium has a broad tentacular lobe with many long tentacles. There are no branchiae, and ventral pads are conspicuous. The thorax consists of approximately 12 setigers; notosetae are serrated and smooth capillaries; neurosetae are avicular uncini with broad bases. Abdominal segments have similar avicular uncini. This unidentified species is known from subtidal reefs (Kohn 1959) and more recently from mud-filled crevices in dead coral in intertidal waters on Oahu.

Terebella lapidaria Linnaeus, 1767

The length of the body reaches about 21 mm and segments number up to 53. Notosetae are present throughout most of the body continuing nearly to the posterior end. There are 3 pairs of branchiae and each is dendritic (Fig. 3.II.179a). The thorax has setae of 2 kinds: larger ones are smooth and shorter ones are distally furcate (Fig. 3.II.179b). Each thoracic uncinus has a large fang surmounted by teeth in several rows (Fig. 3.II.179c). Uncini occur in double rows from the seventh uncinigerous segment as far as the end of the thorax. The abdomen has inconspicuous tori bearing uncini that are ventral in position. This is a cosmopolitan species in warm seas and is usually found under stones, among

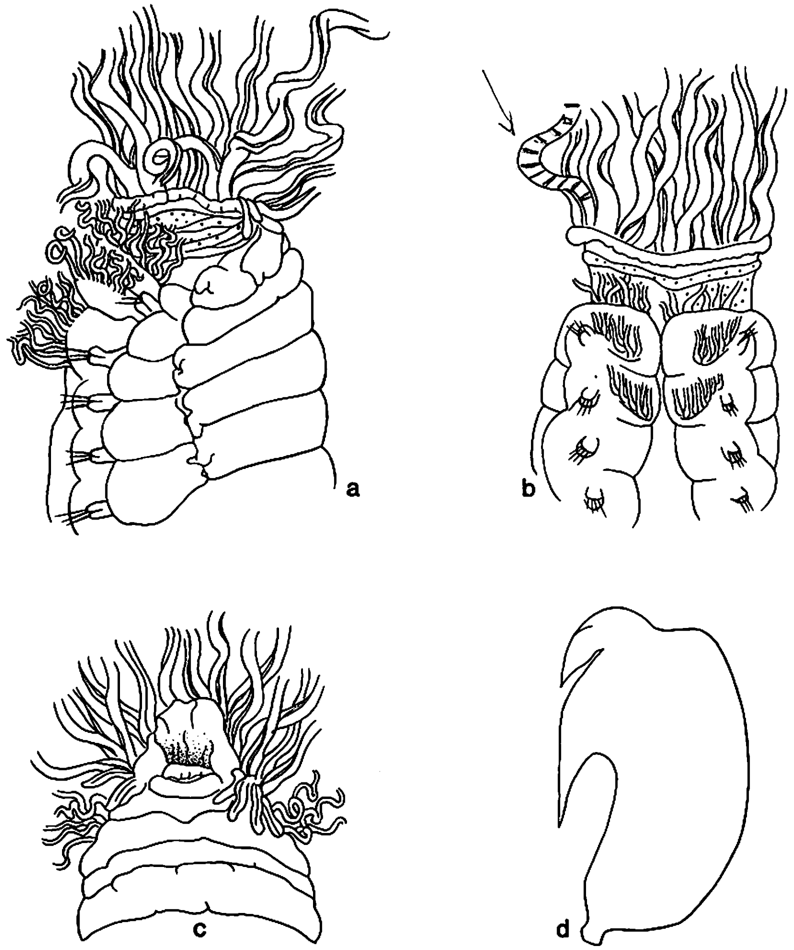


Figure 3.II.180.—*Thelepus setosus*: a, anterior region showing numerous eyespots and filamentous branchiae, lateral view; b, anterior region, ventral view; c, anterior region, dorsal view; d, thoracic uncinus, lateral view showing only 1 row of small teeth above the fang. (d after Day 1967.)

corals and algae, and in sponges. *Terebella lapidaria* has been recorded from Maui and Hilo, Hawaii (Hartmann-Schröder 1965).

KEY TO HAWAIIAN *THELEPUS* SPECIES

Each uncinus a large fang with smaller teeth above it; deep water (200 m) .... *T. branchiatus*

Each uncinus a large fang surmounted by 3 to 5 teeth in 2 rows; shallow water (intertidal to a few meters) .... *T. setosus*

Thelepus branchiatus Treadwell, 1906

The length of the thorax is about 15 mm, the width 6 mm. The prostomium lacks eyes. There are 3 pairs of branchiae. Each pair consists of many cirriform processes: the first pair has about 8 processes on a side, the second pair has fewer, and the third pair has only 1. (Treadwell suggested that the reduced number of cirri on the second and third pairs of branchiae was probably the result of loss or damage.) Notosetae begin on segment 3 and continue posteriorly through at least 30 segments. Uncini begin on setiger 3, occurring in single rows; each uncinus has a large fang surmounted by 2 smaller teeth. This species is known from the Pailolo Channel (between Maui and Molokai), where it was collected in coarse sand at moderate depths (250 m, 137 fm).

Thelepus setosus (Quatrefages, 1865)

stripes

The body measures 60 mm or longer. The color in life is pale yellow to tan; branchiae are bright red, and oral tentacles are orange to brown. Numerous small eyespots are present on the yokelike tentacular lobe (Figs. 3.II.180a,b). Lateral lobes are lacking. There are 3 pairs of branchiae, each consisting of a tuft of many filaments (Figs. 3.II.180a,b,c). Smooth-tipped capillary notosetae are present from segment 3 (2nd branchiferous) and continue through 20 or more segments. Uncini begin on segment 5 (setiger 3) and each has a large fang surmounted by 3 to 5 teeth in 2 rows (Fig. 3.II.180d, lateral view of uncinus shows only 1 row of teeth above the fang). The tube has a tough inner lining and is covered with shell fragments and pieces of gravel. This species is widely distributed in cool temperate and tropical regions and has been found in Hawaiian intertidal and shallow subtidal habitats attached to rocks or among coral rubble (Kohn 1959; Bailey-Brock 1976).

Family **Sabellidae**

Sabellids are tube-dwelling worms with a conspicuous branchial crown for respiration and suspension feeding. The tube, a mucoprotein lining covered with a layer of fine mud or sand, is tough. Worms retract rapidly and completely within the tubes when disturbed, providing effective protection from predators. The branchial crown is formed by bipinnate tentacles (radioles) borne on 2 lobes. These tentacles have ciliated gutters for directing food particles to the mouth and each may bear a terminal eye and a series of paired eyespots and stylodes (small external flaps) (Fig. 3.II.182b). The radioles of some genera are joined by a membranous web so that the crown is funnellike. The degree of completeness of the webbing along the length of the tentacles varies among species.

Sabellids have a midventral groove on the abdomen (most posterior segments), becoming dorsal along the thorax, which directs fecal pellets to the mouth of the tube for elimination. The setae and structure of the collar around the base of the branchial crown are of taxonomic importance. The collar is in 2 halves (which may be joined ventrally) and each may be subdivided to form 4 lobes, 2 dorsal and 2 ventral, of variable shape. Thoracic notosetae are limbate or spatulate capillaries; thoracic neurosetae are avicular (z-shaped) uncini, which may be accompanied by a row of companion setae. Abdominal notosetae are uncini; neurosetae are winged capillaries. Thoracic and abdominal setigers can be distinguished from each other by the location of the setae. Thoracic uncini are ventral in position (neuropodial) and abdominal uncini are dorsally situated (notopodial).

Sabellids are found on harbor structures, floating docks and buoys, and on reef flats, where the lower portions of the tubes are firmly anchored in the interstices of rocks. They appear to flourish in waters of high sediment content, which contain both food and tube-building materials.

KEY TO HAWAIIAN SABELLID GENERA

1 Three pairs of radioles; abdomen composed of 2 or 3 (possibly 4) setigers .... *Augeneriella*
More than 3 pairs of radioles; abdomen composed of 4 or more setigers 2

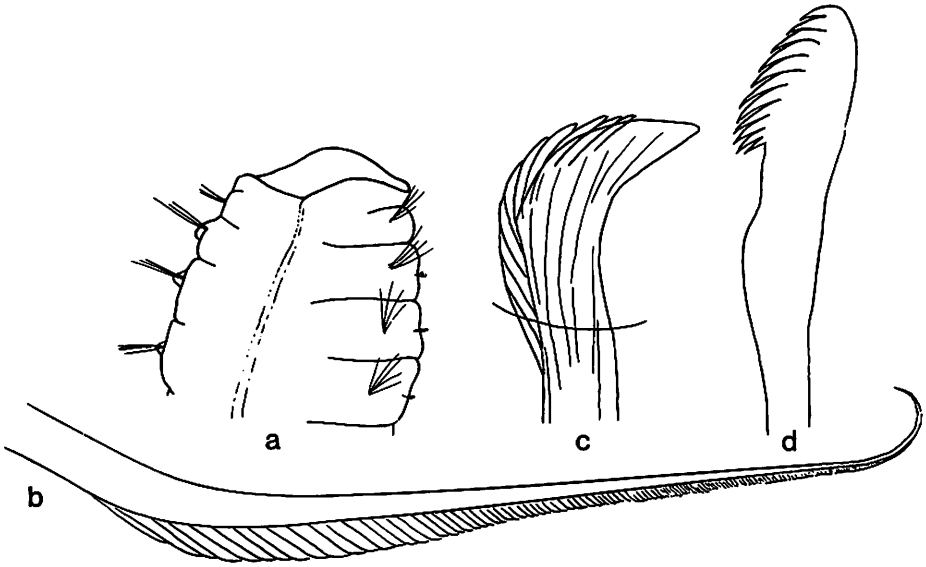


Figure 3.II.181.—*Augeneriella dubia*: a, anterior end without tentacular crown, dorsal view; b, thoracic notopodial seta; c, thoracic neuropodial uncinus; d, abdominal uncinus. (After Hartmann-Schröder 1965.)

2(1) Radioles without eyespots and stylodes 3
Radioles with eyespots and with or without stylodes 5
3(2) Collar well developed, widely separated dorsally; spatulate and companion setae absent .... *Sabellastarte*[1]
Collar a low rim, forming 2 triangular lobes ventrally; spatulate and companion setae present 4
4(3) Worms reach 7 mm in length; radioles nearly as long as the body .... *Potamilla*
Worms reach 40 mm in length; radioles are about half the total length of the body .... *Potamethus*
5(2) Each radiole with a linear row of straplike stylodes; eyespots in a linear series .... *Branchiomma*
Stylodes absent; eyes in a linear series or singly at the tips of the radioles 6
6(5) A single large eye at the tip of a few of the radioles .... *Megalomma*
A number of small eyespots in a linear series along the radioles 7
7(6) Radioles arranged spirally; notosetae of collar segment in a tuft *Demonax*

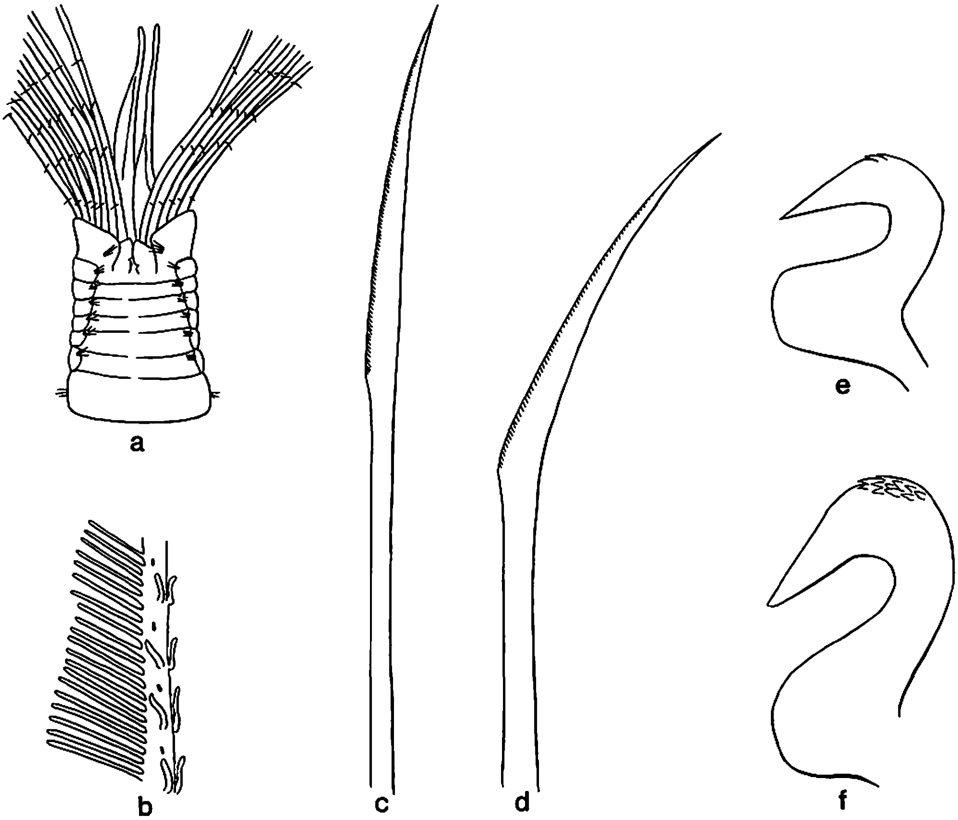


Figure 3.II.182.—*Branchiomma nigromaculata*: a, anterior region with thorax, branchial crown and palps, dorsal view; b, portion of a radiole with eyespots and paired stylodes; c, narrow capillary seta; d, broad capillary seta; e,f, thoracic uncini. (b,e after Day 1967.)

Radioles arranged in 2 semicircles; notosetae of collar segment in a long, slanting row (not as a tuft) .... *Hypsicomus*

Augeneriella dubia Hartmann-Schröder, 1965

The body of this worm reaches 2.9 mm, the width 0.4 mm; segments include 8 thoracic and 3 abdominal setigers. The color in life is brown, especially on the tentacular crown and anterior end. The crown consists of 3 pairs of radioles and a pair of simple, ventral filaments. A webbed membrane is lacking. Each radiole has about 5 pinnules, all extending distally to the ends of the radioles. The collar (Fig. 3.II.181a) is entire, highest ventrally, and weakly developed; eyes are absent. Thoracic notosetae are limbate capillaries (Fig. 3.II.181b) and neurosetae are long-handled uncini with falcate tips (Fig. 3.II.181c). Abdominal uncini have avicular tips (Fig. 3.II.181d) with long stems. This species was described from material collected from the algal turf at Paia, Maui (Hartmann-Schröder 1965). The correct diagnosis of this species must still be ascertained, since Banse (1957) described the genus *Augeneriella* as having 3 abdominal setigers (Banse 1957; Fauchald 1977a), while Hartmann-Schröder (1965 and pers. comm.) says there are 4 abdominal setigers.

Branchiomma nigromaculata (Baird, 1865)

[syn. *Sabella havaica* Kinberg, 1867. ?*Branchiomma cingulata* (Grube, 1870): Hartman 1966]

The body of this species is up to 70 mm long and is nearly colorless, with rust-colored radioles and dark spots at the upper bases of the notopodia. The thorax consists of 5 to 8 setigers (Fig. 3.II.182a) and the abdomen of 30 to 36 setigers. The tentacular crown constitutes about half the length of the body; it has about 9 pairs of radioles, each with a long, tapered tip, paired lateral eyespots, and 2 rows of slender stylodes (Fig. 3.II.182b). The collar is 2-lobed, without lateral incisions, nearly uniformly high all around, and ends in a pair of long, ventral flaps. Collar setae are of 2 kinds: narrow (Fig. 3.II.182c) and broadly limbate winged capillaries (Fig. 3.II.182d). Other thoracic notosetae are all broadly limbate winged capillaries, and neuropodia have avicular uncini with 2 arcs of a few to many small teeth above the main fang (Figs. 3.II.182e,f). Known from the Indo-West Pacific, including Japan and the Red Sea, as well as the tropical Atlantic, and the West Indies, this species has been collected from Halape, Hawaii, and from Pearl Harbor, Kaneohe Bay, and from buoys and docks of small boat harbors on Oahu.

Demonax leucaspis Kinberg, 1867

[?syn. *D. krusensterni* Kinberg, 1867. *D. cooki* Kinberg, 1867]

The length of the body of this sabellid is about 25 mm, and there are up to 59 segments. The thorax consists of 8 segments and the abdomen of 51. Radioles are characteristically flattened (edge perspective), have eyespots, and terminate in long, free tips. There are more than 18 radioles on each side, which are spirally arranged. The thoracic collar is described by Hartman (1966) as 4-lobed with 2 small dorsal lappets and dorsolateral incisions; it terminates in a pair of longer ventral lobes. Thoracic notopodia have slender and limbate setae; neuropodia have avicular

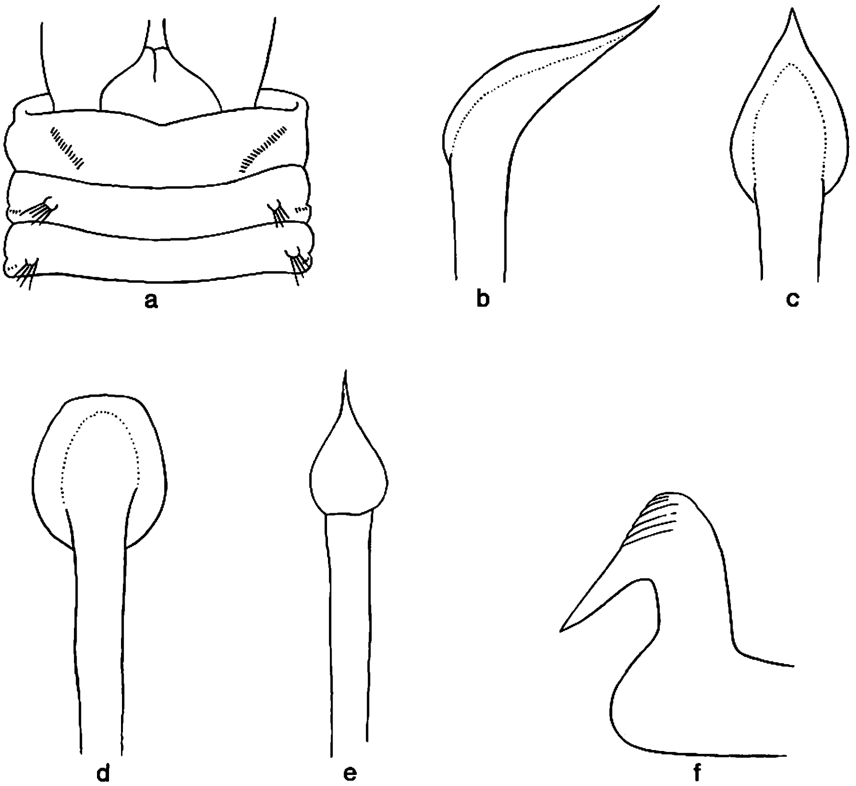


Figure 3.II.183.—*Hypsicomus phaeotaenia*: a, dorsal view of anterior setigers and short collar setae in slanting rows; b, side and c, face view of collar seta; d, thoracic palea; e, pick-axe seta; f, thoracic uncinus. (After Day 1967.)

uncini and companion setae. This species originally reported from Chile is recorded from dead coral in intertidal waters at Honolulu, Oahu (Hartman 1966).

Kinberg (1867) described 2 species of *Demonax*, *D. krusensterni* and *D. cooki*, from the Hawaiian Islands. Hartman (1966) considered the former a synonym and the latter a questionable synonym of *D. leucaspis*. However, P. Knight-Jones (pers. comm.) after examining Kinberg's type specimens of these 3 species, indicates that: 1) *D. leucaspis* and *D. krusensterni* are different species and *D. cooki* is based on a small specimen with regenerating radioles of the latter species; 2) *D. krusensterni* differs from *D. leucaspis* in the form of the radioles, in the proportion of the thoracic segments that are short, and in the nature of the collar, which is vestigial; and 3) the type specimen of *D. leucaspis* has only the faintest lateral notch on the large collar indicating that it is bilobed rather than 4-lobed and that the 4-lobed collar is characteristic of the genus *Pseudopotamilla*.

Hypsicomus phaeotaenia (Schmarda, 1861)

This species is represented by slender worms that are up to 50 mm long. Radioles are arranged in 2 semicircles; they lack stylodes but bear small, lateral eyespots. The 1st thoracic setiger has slanting rows (Fig. 3.II.183a) of palea-like notosetae (Figs. 3.II.183b,c). All other notosetae are paleae (Fig. 3.II.183d) arranged in tufts. Thoracic neuropodia bear a row of pick-axe-shaped companion

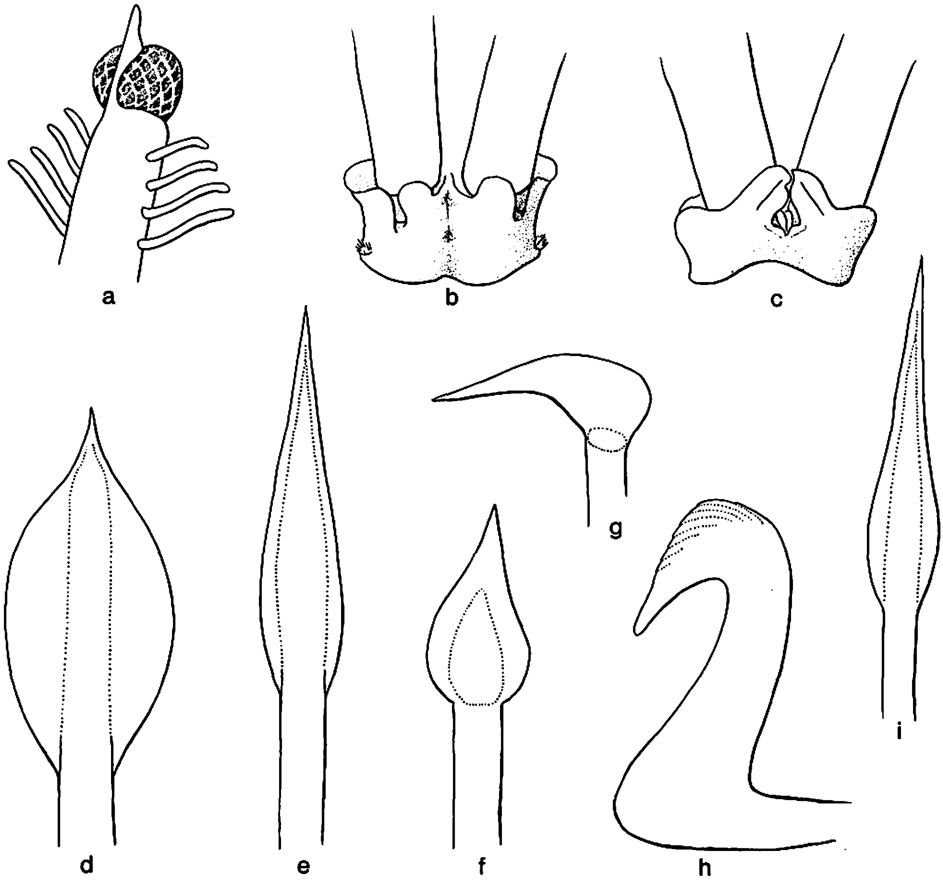


Figure 3.II.184.—*Megalomma intermedium*: a, tip of radiole with subterminal eye; b, collar, dorsal view; c, collar, ventral view; d, thoracic notoseta, palea; e, thoracic notoseta, winged capillary; f,g, thoracic neurosetae, pick-axe setae; h, thoracic uncinus; i, abdominal neuroseta.

setae (Fig. 3.II.183e) adjacent to the row of avicular uncini (Fig. 3.II.183f) in segments 2 to 8. Abdominal uncini are similar to thoracic uncini; abdominal neurosetae may be slender capillaries or stout paleae with oval blades and a slender, sharp tip. The species is recognized as a bioeroder of coralline materials in the tropics (Day 1967; Fauchald 1977a) and it is a very abundant burrower in coral rock and rubble in Kaneohe Bay, Oahu.

Megalomma intermedium (Beddard, 1888)
[syn. *Potamilla torelli* Treadwell, 1906. ?*Megalomma* sp.: Hartman 1966]

These worms build tough tubes of cemented sand grains and shell fragments. Removed from the tube, 1 specimen was 50 mm long and 4 mm wide. Body color in life is an overall light gray to buff, and green eggs could be seen through the wall of the abdomen of 1 specimen. These worms are light brown to cream when stored in ethanol. There are 19 radioles on each side, each with 2 rows of pinnules; the 2 dorsal, innermost radioles are slightly longer than the rest and bear large, subterminal eyes (Fig. 3.II.184a). A few other dorsally situated radioles also bear subterminal eyes, but these are smaller and less conspicuous. Radioles are brown

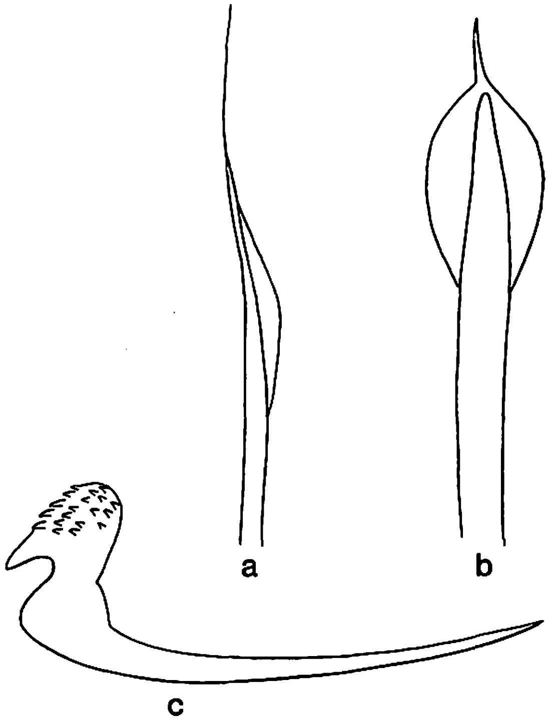


Figure 3.II.185.—*Potamethus elongatus*: a, capillary seta; b, spatulate seta; c, long-handled uncinus. (After Treadwell 1906.)

and cream and are free at their bases. The collar is 4-lobed, including 2 small, rounded dorsal lobes (Fig. 3.II.184b) and 2 larger ventrolateral lobes (Fig. 3.II.184c). Ventrally there is a pair of long, tapered palps usually hidden by the bases of the radioles. There are 8 thoracic segments. Thoracic notosetae are paleae (Fig. 3.II.184d) and winged capillaries (Fig. 3.II.184e); thoracic companion setae are pick-axe-shaped setae (Figs. 3.II.184f,g) and long-shafted avicular uncini (Fig. 3.II.184h). Abdominal neurosetae are winged capillaries (Fig. 3.II.184i); the notosetae are avicular uncini. This species has been found on reef flats on the south shore of Oahu, partially buried in silty sand. It is an Indo-West Pacific species (Fauvel 1953; Pillai 1965; Gibbs 1971).

Potamethus elongatus (Treadwell, 1906)
[syn. *Potamilla elongata* Treadwell, 1906]

This slender worm reaches about 40 mm in length and less than 2 mm in width; its radioles contribute about half the total length. The radioles are colorless, lack eyespots, and are weakly attached to the peristomium. The collar forms a low rim all around the bases of the radioles, and there are 2 triangular lobes ventrally. Thoracic notosetae include both broad-based capillaries (Fig. 3.II.185a) and spatulate setae (Fig. 3.II.185b); neurosetae are long-handled avicular uncini with a large tooth covered by a number of smaller teeth (Fig. 3.II.185c) and pennoned companion setae. The tube is 2 mm in diameter, fragile,

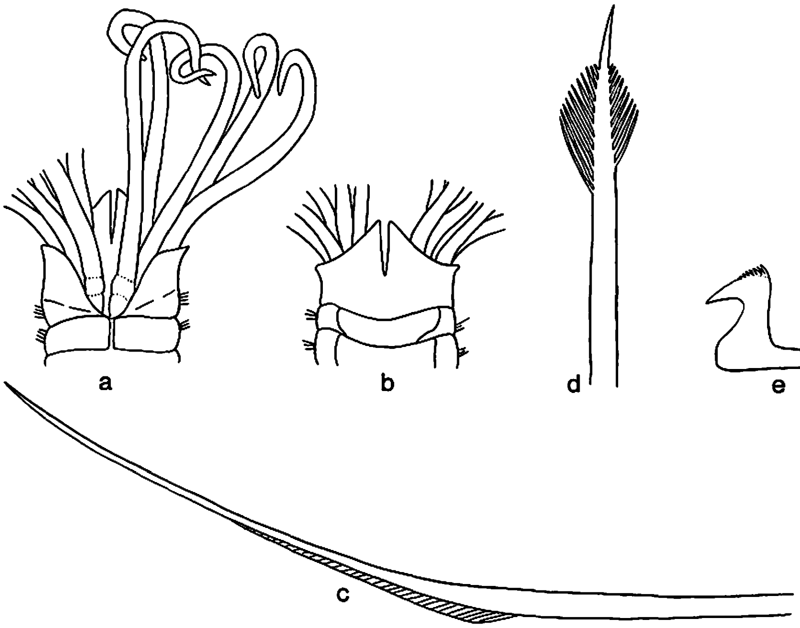


Figure 3.II.186.—*Potamilla* sp.: a, anterior end, dorsal view; b, anterior end, ventral view; c, thoracic winged capillary seta; d, thoracic palea; e, thoracic uncinus. (After Abbott 1946.)

and covered with silt. *Potamethus elongata* is a deep-water species that was originally collected in fine sand from depths greater than 500 m (274 fm) in the Pailolo Channel and from even deeper waters in the northeast Pacific Ocean (Berkeley and Berkeley 1951).

Potamilla sp.
[syn. *Potamilla elongata* Treadwell, 1906, in Abbott 1946: Hartman 1966]

The length of the body of this worm is about 10 mm and the width less than 1.5 mm. The body consists of 24 setigerous segments, 9 thoracic and 15 abdominal. The radioles, lacking eyespots, are nearly as long as the body, number 5 pairs, and are arranged in 2 semicircles (Fig. 3.II.186a). Each radiole has many pinnules (not shown in Fig. 3.II.186a). The collar is 2-lobed, incomplete dorsally, and prolonged ventrally as a pair of triangular lobes (Fig. 3.II.186b). Collar setae are slender, winged capillaries; other thoracic notosetae are of 2 kinds: the dorsalmost are long, slender, winged capillaries (Fig. 3.II.186c) and ventral ones are paleae, each with a long, slender tip (Fig. 3.II.186d). Thoracic neuropodia have avicular uncini (Fig. 3.II.186e) and companion setae. This worm was collected from Kaneohe Bay and at Wailupe Pond, Oahu, which has since been filled in for a housing development (now called Wailupe Peninsula).

Sabellastarte sanctijosephi (Gravier, 1906b)

This species attains 80 mm or more in length (including branchial crown) and 10 to 12 mm in width. The entire body of the worm is buff colored with flecks of purple pigment. These worms inhabit tough, leathery tubes covered with fine

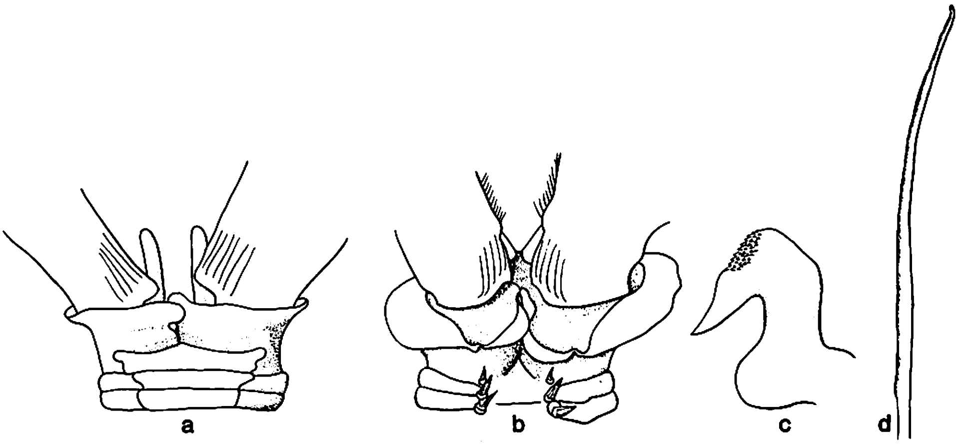


Figure 3.II.187.—*Sabellastarte sanctijosephi*: a, collar region, ventral view; b, collar region, dorsal view; c, thoracic uncinus; d, thoracic capillary seta.

mud. Branchial lobes are not spiralled; radioles lack stylodes and eyespots and are patterned with dark brown and buff bands, which persist in preserved specimens. There is a pair of long, slender palps and a 4-lobed collar. The ventral lobes of the collar are large and well defined (Fig. 3.II.187a), and the dorsal lobes are small and rounded (Fig. 3.II.187b). There are 7 thoracic setigers, with only avicular uncini (Fig. 3.II.187c) present on the neuropodia and long- and short-shafted capillaries on the notopodia (Fig. 3.II.187d). The abdomen is composed of numerous biramous segments with notopodial avicular uncini and capillary setae on the neuropodia. The abdomen is rather broad and flattened when contracted. These worms are very conspicuous on reef flats and harbor structures because of the large size and banded pattern of the branchial crowns (Plate 3.II.4b). They are abundant on Oahu's south shore reefs, and in Pearl Harbor and Kaneohe Bay at shallow depths, especially in dredged areas that receive silt-laden waters. They have also been found at depths of 25 to 30 m (14 to 16 fm) off Molokini Island near Maui. Worms held in a water table at the Hawaii Institute of Marine Biology, Kaneohe, Oahu, spawned on 12 October 1979. The eggs were in a jelly envelope and the water turned milky white with sperm. Eggs were fertilized and cleaving after 3 hours. The trochophore larvae are gray, with maroon-red eyes and a conspicuous prototroch. Larvae developed to the metatrochophore stage within 4 days. *Sabellastarte sanctijosephi* is known from the Indo-West Pacific, including the Red Sea, as well as western Africa (Day 1967; Bailey-Brock 1976).

Family **Serpulidae**

Serpulids are suspension-feeding worms that secrete white calcareous tubes. The tubes may be sinuous, partially erect, clumped in encrusting masses, and attached to rocks or other benthic structures. Until recently this family included the Spirorbidae, members of which also have calcareous tubes, but such characteristics as spiral coiling, fewer thoracic segments, hermaphroditism, and brooding of developing larvae in spirorbids justify separating these 2 large groups into separate families (Pillai 1970).

Morphological features important in the taxonomy of serpulids include the operculum and opercular stalk (when present), number of thoracic segments, length of the thoracic membrane, types of thoracic setae and uncini, and to a lesser extent, the abdominal setae. The operculum may have a calcareous plate, a crown of spines, a chitinous domed cap, a bulblike ampulla, a cup-shaped funnel, or a cap ornamented with spines. The stalk may be cylindrical or flattened in section and represents a modified radiole. Primitive genera have pinnulate opercular stalks and a larger number of thoracic segments.

Hawaiian serpulids show some habitat specificity. The coral *Porites lobata* is the preferred habitat of *Spirobranchus giganteus corniculatus* often called the Christmas-tree worm because of its brightly colored, spiralled branchiae (resembling coniferous trees). Some *Hydroides* species are typically fouling organisms, while *Pomatoleios kraussii* and *Pseudovermilia occidentalis* are virtually intertidal in their distribution on reef flats. *Ficopomatus enigmaticus* is known to live in brackish waters (Bailey-Brock 1976). The slender, threadlike tubes of *Salmacina dysteri* almost always form aggregations on harbor structures, coral rubble, and rocks at shallow depths. Many serpulids occur in relatively calm and protected locations where there is a plentiful food supply, and most are oviparous, releasing eggs and sperm for external fertilization with free development as planktonic trochophore larvae. Serpulid larval requirements and settlement behavior are not as well known as they are for some of the spirorbids, but life histories of a few species have been investigated: *Ficopomatus enigmaticus* (= *Mercierella enigmatica*) in Australia (Straughan 1972) and Nigeria (Hill 1967); *Hydroides elegans* (= *H. norvegica*) in Australia (Wisely 1958); *Pomatoleios kraussii* in the Arabian Gulf (Crisp 1977); and *Spirobranchus giganteus corniculatus* in Hawaii (White 1976) and Australia (Smith 1984).

There is still controversy over the taxonomy of some genera having many closely related species. Generic revisions are being prepared by various authorities and some have been published: *Spirobranchus* and *Pseudovermilia* by ten Hove (1970 and 1975, respectively); *Vermiliopsis* and *Hydroides* by Zibrowius (1971 and 1973, respectively) and Imajima (1976a).

Fourteen species in 9 genera of Serpulidae are known from Hawaiian waters. Only one species, *Vermiliopsis torquata*, is considered to be endemic to the Hawaiian Islands; most have a broad Indo-West Pacific or an eastern Pacific distribution. Indo-West Pacific serpulids are becoming better known. Information from Fiji (Bailey-Brock 1985), Tonga (Bailey-Brock, in press), the Palau and Yap Islands (Imajima 1982), Truk, Ponape, and Majuro (Imajima and ten Hove 1984), and from southern Japan (Imajima 1976b, 1977) is useful for zoogeographical affinities. Serpulids are transported great distances by ships (Allen 1953) and readily establish populations in protected harbors and on coastal structures (Edmondson and Ingram 1939; Long 1974).

KEY TO HAWAIIAN SERPULID GENERA

1 A stalked operculum present 2
Usually without an operculum 8
2(1) Opercular stalk with flattened lateral wings (Figs. 3.II.193b, 198b) 3
Opercular stalk without flattened lateral wings (Fig. 3.II.196b).......... 4

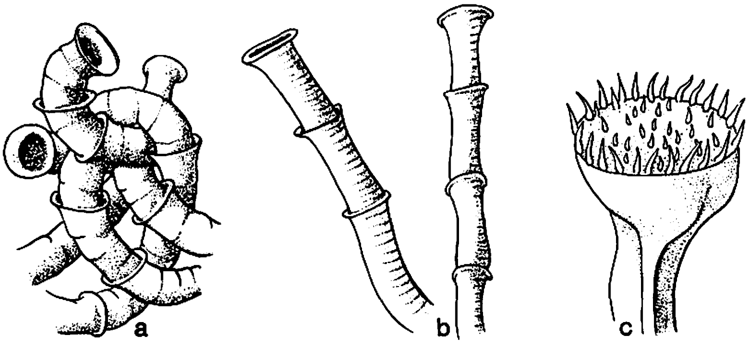


Figure 3.II.188.—*Ficopomatus enigmaticus*: a, tubes of gregarious worms; b, tubes of solitary worms; c, operculum with chitinous spines.

3(2) Opercular plate flat to concave, without spines or protuberances .... *Pomatoleios*
Opercular plate otherwise .... *Spirobranchus*
4(2) Operculum a delicate, fluted funnel formed of tissue (Fig. 3.II.196b) .... *Serpula*
Operculum otherwise 5
5(4) Operculum with a crown of spines 6
Operculum an ampulla topped with a chitinous cap 7
6(5) Operculum vesicular with short, dark spines covering the surface (Fig. 3.II.188c) .... *Ficopomatus*
Operculum a fluted funnel topped by a crown of spines at the center .... *Hydroides*
7(5) Opercular cap brown, may have faint transverse lines around circumference, and without a sharply pointed spine (Figs. 3.II.199b, 200) .... *Vermiliopsis*
Opercular cap black and usually with a sharply pointed spine (Fig. 3.II.194) .... *Pseudovermilia*
8(1) Small, narrow white tubes (less than 3 mm wide); forming colonies .... *Salmacina*
Large white tubes (greater than 3 mm wide); solitary .... *Protula*

Ficopomatus enigmaticus (Fauvel, 1923)
[syn. *Mercierella enigmatica* Fauvel: Hartman 1966, Bailey-Brock 1976]

Flaring mouths and a series of collars along their length give a drainpipe effect to tubes of *F. enigmaticus* (Figs. 3.II.188a,b). Populations of these worms may be so dense that masses of tubes twist together and often ascend from the substrate. Tubes are 30 to 40 mm long and 4 to 8 mm wide. The operculum bears approximately 25 dark, chitinous spines (Fig. 3.II.188c), which are usually obscured by a plug of sediment. *Ficopomatus enigmaticus* is a brackish water species from temperate and subtropical estuarine areas (ten Hove 1974; Straughan 1972) and was fully described by ten Hove and Weerdenburg (1978). This serpulid is found in the Ala Wai Canal,

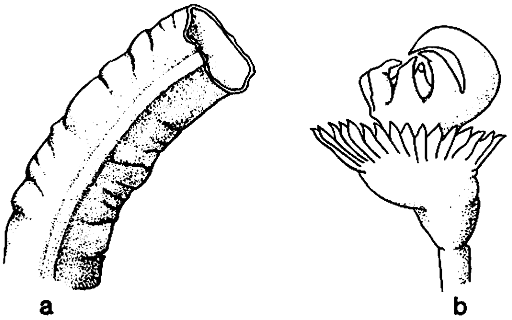


Figure 3.II.189.—*Hydroides brachyacantha*: a, portion of tube; b, operculum showing asymmetrical funnel, lateral view.

Pearl Harbor, Hawaii Kai, and in the drainage canal at Kahala, Oahu; it also occurs at Kealia Pond, Maui (Bailey-Brock 1976).

KEY TO HAWAIIAN *HYDROIDES* SPECIES

1 Spines of opercular crown all the same size 2
Spines of opercular crown of unequal size .... *H. brachyacantha*
2(1) Spines of opercular crown with finely pointed tips 3
Spines of opercular crown with bifid flattened tips .... *H. dirampha*
3(2) Spines of opercular crown, each with a pair of lateral projections, curve inward so that tips touch at the apex .... *H. crucigera*
Spines of opercular crown with numerous paired, lateral projections that radiate from the point of attachment .... *H. elegans*

Hydroides brachyacantha Rioja, 1941

The tube of this species is white and sinuous, with a medial longitudinal ridge (Fig 3.II.189a); it is 25 to 35 mm long and up to 0.6 mm wide. The operculum is composed of 2 parts: a basal funnel of fused radii and an upper crown of spines (typical of the operculum of *Hydroides* species). The basal funnel has 17 to 30 pointed radii supporting a crown of 7 stout spines with recurved, pointed tips. One

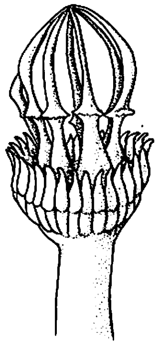


Figure 3.II.190.—*Hydroides crucigera*: operculum, lateral view. (After Straughan 1969a.)

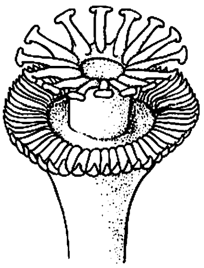


Figure 3.II.191.—*Hydroides dirampha*: operculum showing radii with bifid tips. (After Day 1967.)

of the spines is larger than the others and projects above the crown (Fig. 3.II.189b). The smaller spines bear an inwardly directed projection near their bases. There are 7 thoracic setigers; the first has bayonet-shaped collar setae with blunt bosses at the base of the blade; other thoracic setae are capillaries. Abdominal setigers have flat-topped, trumpet-shaped setae. This serpulid has been recorded from western Mexico, eastern Australia, Hawaii, and Brazil. It is problematical whether or not these records really refer to 1 species or to a complex of closely related species (Straughan 1969a).

Hydroides crucigera (Mörch, 1863)

The tube of this worm is sinuous and white without any conspicuous distinguishing features; it is 20 to 25 mm long and 0.5 mm wide. An opercular funnel (Fig. 3.II.190) composed of 40 pointed radii supports a crown of 8 thin spines that are bent towards the center. Each spine has 1 pair of transverse processes, all at the same level, less than halfway along the spine. This species has been recorded from the eastern Pacific coasts of southern California, Mexico, and Panama, and from Hawaii (Monro 1933; Straughan 1969a).

Hydroides dirampha Mörch, 1863

[syn. *Hydroides lunifera* (Claparède, 1868): Edmondson and Ingram 1939, Edmondson 1944. *H. lunulifera* (Claparède, 1868): Edmondson 1946, Straughan 1969a. *Eupomatus lunifer* Claparède, 1870: Hartman 1966]

The white tube of this serpulid is sinuous, with 3 to 5 faint longitudinal ridges, and is 20 to 35 mm long and 0.3 to 0.6 mm wide. The opercular funnel is composed of about 35 to 40 pointed radii supporting a crown of 10 to 14 flattened spines, each with a laterally oriented, anchor-shaped tip giving a bifid appearance (Fig. 3.II.191). *Hydroides dirampha* has a cosmopolitan distribution in tropical and temperate waters (Zibrowius 1973).

Hydroides elegans (Haswell, 1883)

[syn. *H. norvegicus* Gunnerus, 1768: Edmondson 1946, Hartman 1966, Straughan 1969a]

In this species, the white tubes with blunt longitudinal ridges may be delicate and occur in masses; they are 15 to 30 mm long and 0.3 to 0.5 mm wide. The opercular funnel is composed of approximately 25 to 35 blunt radii, which

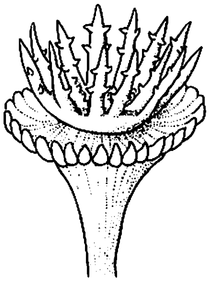


Figure 3.II.192.—*Hydroides elegans*: operculum showing radii with paired lateral spines. (After Day 1967.)

support a crown of 10 to 16 equal-sized, diverging spines with pairs of lateral processes (Fig. 3.II.192) and an inner row of short spines. There is a central spine in the middle of the crown on the upwardly directed face. Collar setae are capillaries and fin and blade setae with finely toothed blades. There is a conspicuous gap between the blades and the fins. The latter has 2 large teeth and a number of smaller teeth (Zibrowius 1971). Large numbers of these worms foul boats and harbor structures throughout the world (ten Hove 1974), and Hawaii is no exception.

Pomatoleios kraussii (Baird, 1865)

This species has a strong white tube, bluish inside and bearing a median projection over the mouth (Fig. 3.II.193a) that may be modified as a spine or flattened as a flap. The tube is 25 to 40 mm long and 0.5 to 0.8 mm wide. The body of live worms is blue or purplish black; it is blue when preserved in formalin. The operculum is borne on a winged stalk (Fig. 3.II.193b); the plate is flattened on the upper surface and bears a short, blunt ventrolateral talon (talon not visible in Fig. 3.II.193b). Collar setae are only occasionally present in juveniles and eyespots are entirely absent. Thoracic notosetae are simple blades; thoracic uncini have a deep indentation and 8 to 10 teeth in a row. This tropical Indo-West Pacific species (Crisp 1977) is common on intertidal reef flats and in shallow subtidal Hawaiian waters (Straughan 1969a,b).

Protula atypha Bush, 1904

This species is characterized by a thick white tube that is circular in cross section and firmly attached to the substrate near the base, and whose later whorls are free-growing and frequently coiled upon earlier whorls. Tubes are 25 to 45 mm long and 0.5 mm wide. The branchial crown is bright red in live specimens, and there is no operculum. The thorax has 7 setigers; thoracic membranes extend to the end of the thorax and are not fused. Thoracic setae are capillaries, and uncini have numerous small teeth and a single anterior tooth, which is stout and elongate. Found on basalt rocks in shallow coral reef habitats, this serpulid has an eastern Pacific distribution restricted to California and the Hawaiian Islands (Straughan 1969a).

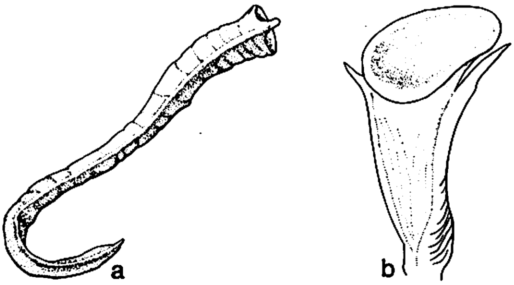


Figure 3.II.193.—*Pomatoleios kraussii*: a, tube with median keel forming a spine over the mouth; b, operculum and winged opercular stalk. (b after Day 1967.)

Pseudovermilia occidentalis (McIntosh, 1885)
[syn. *Vermiliopsis hawaiiensis* Treadwell, 1943. *V. multiannulata* (Moore, 1923), in part: Hartman 1966]

Worms are 3.5 to 4.5 mm long. A white tube, triangular in cross section, with a median ridge forming a small tooth over the mouth and having 2 lateral longitudinal ridges, characterizes this species. Tubes are 20 to 30 mm long and 0.3 to 0.5 mm wide. Thoracic membranes extend to the second thoracic segment. The operculum is vesicular, with a black, cone-shaped top that may have a terminal projection (Fig. 3.II.194). This species is found commonly on coral rubble in shallow Hawaiian waters (Straughan 1969a). Complete synonymies and the distribution of this species in tropical locations throughout the world were given by ten Hove (1975).

Salmacina dysteri (Huxley, 1855)

This species is characterized by having very slender, white tubes, 15 mm long and 0.5 mm wide, which form thick encrustations on harbor structures throughout the world (Fig. 3.II.195). The branchial crown is composed of 8 radioles, 4 on each side, each with a terminal filament that is thicker than the radiolar pinnules. Species in this genus lack an operculum and are hermaphroditic (Fauvel 1927). There are 7 to 9 thoracic segments; fin and blade setae occur on the first setiger and simple wingless setae and sickle setae are present on the remaining setigers. Abdominal setae resemble wingless thoracic setae. These worms are gregarious and may reproduce asexually by transverse division (Fauvel

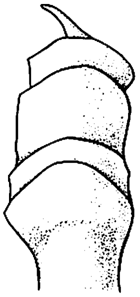


Figure 3.II.194.—*Pseudovermilia occidentalis*: operculum. (After Straughan 1969a.)

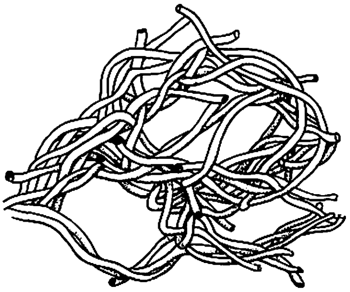


Figure 3.II.195.—*Salmacina dysteri*: massed tubes encrusting the substrate.

1927; Straughan 1969a). This species, common on fouling panels and hard substrates in sheltered waters, e.g., Pearl Harbor (Plate 3.II.4c) and Kaneohe Bay, Oahu, has a cosmopolitan distribution in warm seas (Straughan 1969b).

Serpula vermicularis Linnaeus, 1767

This species has a white, sinuous tube with an indistinct, rounded median ridge (Fig. 3.II.196a). Tubes are 20 to 25 mm long and 0.2 to 0.3 mm wide. The operculum is a deeply and symmetrically fluted funnel, formed of approximately 40 fused fleshy radii and lacks hard parts (Fig. 3.II.196b). The collar appears trilobed, with 2 small dorsal lobes and 1 ventrolateral lobe. Collar setae are of 2 types: capillaries and bayonets with 2 bosses at the base of the blade. Thoracic uncini have 6 teeth, and abdominal uncini have 4 to 8 teeth. Abdominal setae have toothed blades set horizontally on the shaft, appearing T-shaped. This is a widely distributed species (or complex of species) occurring in shallow waters in Hawaii (Straughan 1969a).

KEY TO HAWAIIAN *SPIROBRANCHUS* SPECIES

Operculum bearing branched, antlerlike spines; tube usually surrounded by living coral	*S. giganteus corniculatus*
Operculum bearing a stack of calcareous disks of diminishing size, tube salmon colored; attached to shells	*S. latiscapus*

Spirobranchus giganteus corniculatus (Grube, 1862)
[syn. *S. giganteus* (Pallas, 1766): Hartman 1966]

Most of the tube is usually surrounded by the living coral *Porites lobata* (Plate 3.II.4d). The free end has a median ridge that forms a tooth over the mouth (Fig. 3.II.197a). The body is large for a serpulid (worms are 45 -120 mm long and 0.5 cm ~~mm~~ wide), and the abdomen can have 200 or more segments. The calcareous opercular plate bears antlerlike spines and the stalk has flattened lateral wings (Fig. 3.II.197b). Thoracic setae have a fin, with thoracic uncini having a deep gouge and 8 to 10 teeth in a row. This serpulid is found in *Porites lobata* coral in Hawaiian waters, and it is found on other coral genera elsewhere in the Pacific.

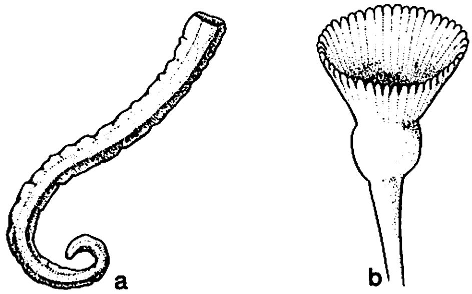


Figure 3.II.196.—*Serpula vermicularis*: a, tube; b, funnel-shaped operculum. (After Day 1967.)

This tropical Indo-West Pacific serpulid occurs subtidally in the Hawaiian Islands (Hartman 1966; ten Hove 1970).

Spirobranchus latiscapus Marenzeller, 1885

Tubes of this species are 22 to 33 mm long, and 0.5 mm wide, pink to salmon colored, and have 1 to 5 longitudinal ridges of spiny teeth (Fig. 3.II.198a). The operculum is composed of 1 to 7 calcareous tiers stacked on top of each other, and the stalk has broad lateral wings (Fig 3.II.198b). There are 7 thoracic and approximately 48 abdominal segments. Collar setae are winged and abdominal setae are simple. Abdominal uncini have 10 to 12 lateral teeth and 1 enlarged anterior tooth. This species has been found attached to shells, precious pink corals, and other hard substrates in Hawaiian waters from depths of 200 to 600 m (109 to 328 fm). Hawaii is the most easterly location known for this tropical Indo-West Pacific species (Bailey-Brock 1972).

KEY TO HAWAIIAN *VERMILIOPSIS* AND *SEMIVERMILIA* SPECIES

1 Operculum a ringed chitinous dome, tube with 5 or more longitudinal ridges or a series of fluted sections 2

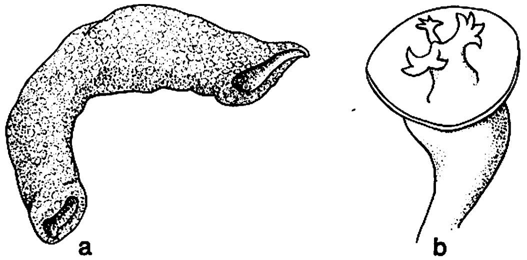


Figure 3.II.197.—*Spirobranchus giganteus corniculatus*: a, tube overgrown with coral; b, operculum with branched spines. (b after Day 1967.)

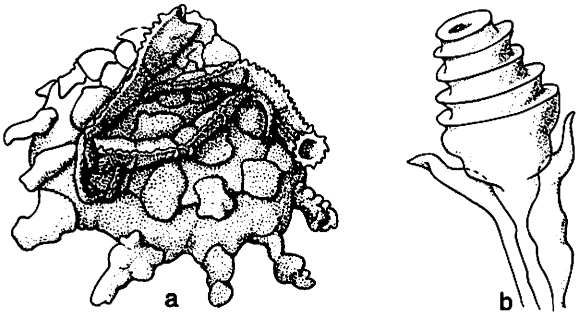


Figure 3.II.198.—*Spirobranchus latiscapus*: a, 3 tubes attached to a carrier-shell (Gastropoda: Xenophoridae); b, tiered operculum borne on a winged stalk. (After Bailey-Brock 1976.)

Operculum a series of stacked chitinous plates separated from each other by cylindrical pieces, tube with 3 rounded longitudinal ridges and broad lateral flanges .... *Semivermilia pomatostegoides*

2(1) Tube a series of interlocking fluted sections, with an expanded flute at the mouth .... *Vermiliopsis infundibulum*

Tube massive with 5 or more narrow longitudinal ridges .... *Vermiliopsis torquata*

Semivermilia pomatostegoides (Zibrowius, 1969)
[syn. *Vermiliopsis pomatostegoides* Zibrowius, 1969]

Sinuous white tubes flattened against the substrate with 3 longitudinal ridges that are rounded and smooth. There are broad lateral flanges attaching the tube to the substrate. The operculum is an ampulla with a thin chitinous plate bearing a series of 1–8 chitinous plates that decrease in size distally. The plates are separated from each other by a cylindrical piece with the same or slightly smaller diameter than the adjacent plates (see Fig. 34 in Bianchi 1981). The stalk is the 1st structure in the left cluster of radioles and lacks wings. The collar is entire, and thoracic membranes extend to setiger 2. Collar setae are simple blades and number 3 or 4 in each fascicle. Thoracic setae are simple blades, and sickle setae in setigers 3–7. Abdominal setae are geniculate and triangular in outline. Thoracic uncini have a large anterior tooth. This species was collected on coral rubble from a 20 m depth off Keahole Point, Hawaii, and from a 15 m depth in Lahaina Harbor, Maui. It is known from the type locality, the Gulf of Gabès in Tripoli (Zibrowius 1969) and the Mediterranean (Bianchi 1981).

Vermiliopsis infundibulum (Philippi, 1844)

The fluted white tubes of this species are composed of a number of interlocking sections and have an expanded flange forming the mouth (Fig. 3.II.199a). Tubes are 20 to 30 mm long and 0.3 to 0.6 mm wide. The operculum is a ringed, golden brown, chitinous cone capping a vesicular chamber (Fig. 3.II.199b). The opercular peduncle lacks lateral wings. This species has a world-wide distribution and has been recorded below 200 m (109 fm) in Hawaii (Bailey-Brock 1972).

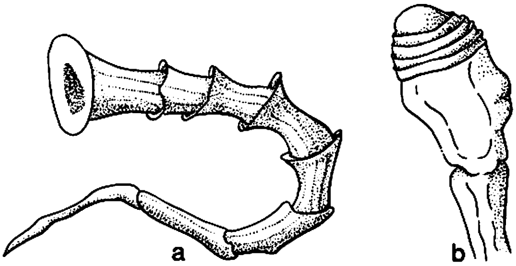


Figure 3.II.199.—*Vermiliopsis infundibulum*: a, fluted tube; b, operculum with ringed chitinous cap. (After Bailey-Brock 1976.)

Vermiliopsis torquata Treadwell, 1943
[syn. *V. multiannulata* (Moore, 1923), in part: Hartman 1966]

This is a large species, the body from 5.0 to 12.0 mm long. It has a massive white tube, 35 to 45 mm long and 0.4 to 0.6 mm wide, with surface sculpturing. Thoracic membranes extend down to the 5th thoracic segment. The thick, wingless opercular peduncle bears a vesicular operculum with a ringed, brown, chitinous cap (Fig. 3.II.200). The species is found in shallow waters that are relatively free of suspended materials and is thought to be endemic to the Hawaiian Islands (Straughan 1969b).

Family **Spirorbidae**

The Spirorbidae were until recently regarded as a subfamily within the Serpulidae because both groups are characterized by white, calcareous tubes and a similar morphology. Pillai (1970) proposed that the 2 groups should be separated, and Bailey (1969b), Vine (1972b), Knight-Jones (1973), Knight-Jones et al. (1979), Knight-Jones and Fordy (1979), and Knight-Jones (1984) gave detailed descriptions of the family, genera, and subgenera. The Spirorbidae is a large family including more than 160 species belonging to 26 genera distributed throughout tropical, temperate, and polar seas from the intertidal to great depths (Bailey-Brock and Knight-Jones 1977). A recent review of the characteristics of 7 genera known from the Pacific was given by Knight-Jones et al. (1979).

Spirorbids secrete a calcareous tube that is either chalky white or translucent and is typically spirally coiled, rarely exceeds 5 mm in total diameter, and is

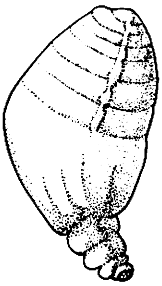


Figure 3.II.200.—*Vermiliopsis torquata*: operculum with lightly ringed chitinous cap. (After Straughan 1969a.)

attached to the substrate; the tube occasionally uncoils if it grows away from the surface of attachment. Direction of coiling is either sinistral (mouth faces clockwise) or dextral (mouth faces counterclockwise) and is generally considered to be species-specific, although in a few instances both sinistrally and dextrally coiled individuals have been found in the same population (Bock 1953; Potswald 1965; Vine 1972b). All the species known from Hawaiian waters are presently thought to have species-specific coiling.

The organization of the worms into thoracic and abdominal regions can readily be seen when they are removed from their tubes by carefully chipping away the walls with forceps. The thorax has 3 to 5 segments each with notopodial setae and neuropodial uncini (Knight-Jones and Fordy 1979). Setae of the first setiger are termed collar setae and exhibit species-specific characteristics (Figs. 3.II.215a–j). They usually comprise a basal fin and a proximal blade. The fin is divided into a number of teeth (Figs. 3.II.215a–e) and the blade may be coarse or finely serrated, or cross-striated (Figs. 3.II.215b,d). Some have a rudimentary fin (Fig. 3.II.215c) or lack a fin altogether (Figs. 3.II.215e–j). Part or all of one parapodium of the last thoracic setiger may be missing or represented by a rudiment so that the thorax is asymmetrical, with 3 1/4, 3 1/2, 3 3/4, or 4 or more segments. The number of thoracic setigers, including rudiments, is species-specific and diagnostic of certain genera. A branchial crown of bipinnate radioles surrounds the mouth and serves to sieve out food particles during suspension feeding. One radiole lacks pinnules and bears the operculum, which blocks the mouth of the tube when the worm is retracted. Opercular features are also diagnostic. There are 2 kinds of opercular plates: thick solid plates with knobs or thickenings (e.g., *Spirorbis marioni* and *Protolaeospira capensis*), and thin plates that may be domed and elaborately ornamented with spines (e.g., *Pileolaria militaris*), which form brood chambers to accommodate developing embryos. The opercular plate may be cast off when the larvae emerge, as in *Leodora knightjonesi*, and the basal plate forms the chamber roof for the subsequent brood, or the same chamber may be reused for subsequent broods, as in *Pileolaria militaris* (Knight-Jones and Thorp 1984). Juveniles of opercular brooders have opercular plates quite unlike those of adults; in the past, this has lead to misidentification of juveniles and adults as different species (Bailey 1969a).

A thoracic membrane surrounds the thorax, and a collar folds over the lip of the tube when the worm is extended. Behind the thorax is the abdomen, which comprises a long asetigerous region preceding a varying number of segments, each with setae and uncini. The abdominal segments have been rotated so that neuropodial uncini lie above the notopodial setae in each setiger, and the nerve cord is now dorsal in relation to the thorax. Parapodia on the inner side of the coiled body frequently contain more uncini per fascicle than those on the outer side of the coil. This asymmetry of thoracic and abdominal segments, as well as the presence of an asetigerous region, is related to the tube-dwelling existence of these worms and to the spiral shape of the tubes.

Spirorbid worms are hermaphroditic; the first 2 abdominal segments produce oocytes, and the remainder all contain male gametes. Ripe gametes are spawned every 2 weeks (in European species) during the breeding season and cross-fertilization is typical (King et al. 1969). Incubation of embryos takes place within an opercular chamber or within the tube (Knight-Jones et al. 1972). In *Spirorbis*

spirorbis, an example of the latter case, eggs are fertilized inside the tube by sperm drawn in with the water current that flushes the tube and are stored in a spermatheca near the mouth (Daly and Golding 1977). The fertilized eggs are then arranged in an egg string lying between the worm's abdomen and the tube wall (King et al. 1969). After a 2-week incubation, metatrochophore larvae are released from the mouth of the parent's tube. Pelagic larval life is only a few hours long, and larvae settle after actively searching for an appropriate settlement site (Knight-Jones 1951; de Silva 1958; Gee 1963; Knight-Jones et al. 1971). Spirorbids are among the primary colonizers of settlement plates and newly exposed substrates in most marine habitats. On coral reefs they are found on the undersides of living corals, on coral rubble, algae, and sea grasses, and survival is affected by sedimentation, overgrowth by encrusting forms, and grazers (Vine and Bailey-Brock 1984).

Microscopic examination of thoracic and abdominal setae and uncini is necessary for species identification. Whole mounts should be prepared by carefully removing worms from their tubes, breaking off the operculum, and covering specimens with polyvinyl-lactophenol and a cover slip, then drying on a warming table or in a low-temperature oven (Knight-Jones 1972). This technique renders tissue transparent and the fine structure of setae and uncini clearly visible. Further details are given in the section on polychaete study techniques (p. 220).

KEY TO HAWAIIAN SPIRORBID GENERA

1	Embryos incubated in tube; 3 or 4 thoracic setigers	2
	Embryos incubated in opercular brood chamber; 3 thoracic setigers	4
2(1)	Tube coiled dextrally (opening faces counterclockwise) (Fig. 3.II.213a)	*Spirorbis*
	Tube coiled sinistrally (opening faces clockwise) (Fig. 3.II.211a)	3
3(2)	Tube hard and translucent; 4 thoracic setigers	*Protolaeospira*
	Tube friable, opaque, and chalky white; 3 thoracic setigers	*Eulaeospira*
4(1)	Tube coiled sinistrally	5
	Tube coiled dextrally	9
5(4)	Operculum a closed brood chamber with distal plate	6
	Operculum an open, cup-shaped brood chamber	*Nidificaria*
6(5)	Operculum of 1, 2, or 3 brood chambers in series	*Leodora*
	Operculum a single brood chamber	7
7(6)	Operculum helmet-shaped with spines, collar setae fins, and cross-striated blades	8
	Operculum 2 interlocking plates forming a brood chamber, collar setae fins, and blades without cross-striations	*Vinearia*
8(7)	Setae of 3rd thoracic setiger include sickles (Fig. 3.II.215k)	*Pileolaria*
	Setae of 3rd thoracic setiger without sickles	*Simplicaria*
9(4)	Brood chamber walls not calcified, sickle setae present in setiger 3	*Janua*
	Brood chamber walls calcified, setae are simple blades in setiger 3	*Neodexiospira*

sin

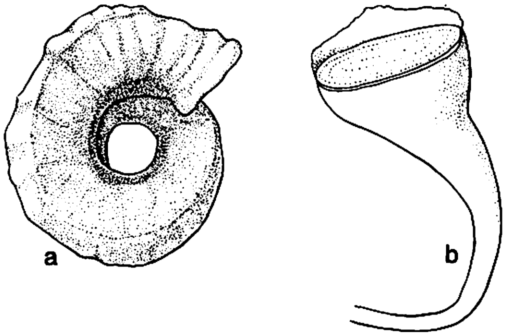


Figure 3.II.201.—*Eulaeospira orientalis*: a, tube; b, operculum with delicate calcareous rim. (After Vine 1972b.)

Eulaeospira orientalis (Pillai, 1960)
[syn. *Spirorbis* (*Laeospira*) *orientalis* Pillai, 1960]

The tube is 1.0 mm in diameter. It coils sinistrally and is white with transverse thickenings and steep sides (Fig. 3.II.201a). The operculum is a flat plate with a delicate rim (Fig. 3.II.201b). Collar setae have fins with serrated blades but no cross-striations. Embryo chains are incubated in the tube. This species was found on the green alga *Dictyosphaeria cavernosa* in Kaneohe Bay, Oahu, and on rocks in Honokohau Harbor, Hawaii (Bailey-Bröck 1976). The extra-Hawaiian distribution of this species includes Sri Lanka (Ceylon) and the Red Sea (Vine 1972b; Vine and Bailey-Brock 1984).

Janua pagenstecheri (Quatrefages, 1865)
[syn. *Spirorbis pagenstecheri* Quatrefages, 1865]

The tube of this spirorbid is 1.3 mm in diameter. It is white and has 3 longitudinal ridges and dextral coiling (Fig. 3.II.202a). The opercular plate varies from flat to slightly concave and has an excentric pinlike talon projecting into the underlying cup-shaped brood chamber without calcified walls (Figs. 3.II.202b,c); the basal plate of the chamber becomes the lid of the chamber for the subsequent brood, and it may lack the talon. Collar setae have blades with a rudimentary fin that is not separate from the blade (Fig. 3.II.215c). The third thoracic segment bears sickle-shaped setae (Fig. 3.II.215k). This species is

dex

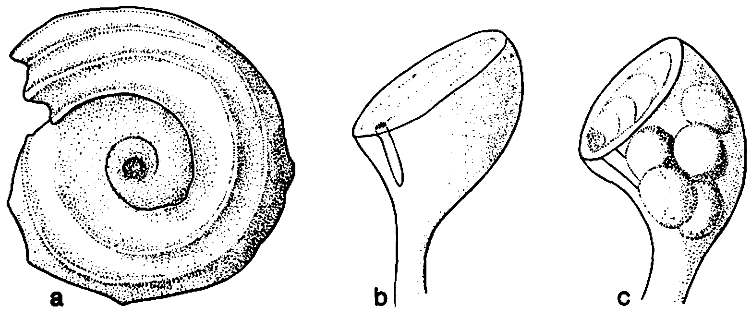


Figure 3.II.202.—*Janua pagenstecheri*: a, tube; b, operculum; c, brood chamber with embryos. (After Bailey and Harris 1968.)

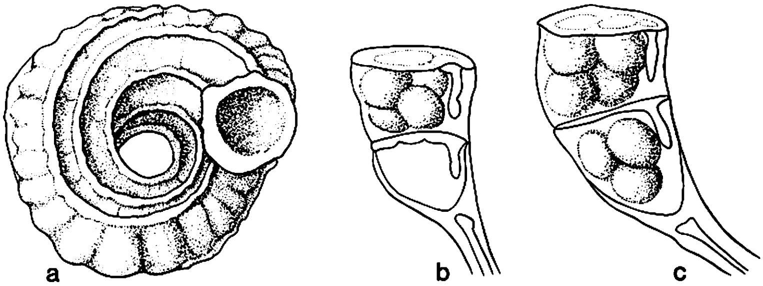


Figure 3.II.203.—*Leodora knightjonesi*: a, tube; b, tiered opercula with a brood of embyros; c, opercular brood chambers with consecutive broods. (a after Vine et al. 1972; b,c after Bailey 1970.)

cosmopolitan in temperate and tropical waters (Vine et al. 1972; Knight-Jones et al. 1975).

Leodora knightjonesi (de Silva, 1965)
[syn. *Spirorbis (Laeodora) knightjonesi* de Silva, 1965]

The tube of this worm is 1.5 mm in diameter. It is sinistral, with 3 distinct longitudinal ridges (Fig. 3.II.203a). The operculum has 1, 2, or occasionally 3 brood chambers in series, each with a flat, calcareous plate bearing a peglike talon on 1 side (Fig. 3.II.203b). The embryos in the uppermost chamber are the furthest along in development (Fig. 3.II.203c). Collar setae are broad blades without fins (Figs. 3.II.215g,h). In Hawaii this species is very common on basalt rocks of the intertidal region of the Kona, Hawaii, coast (Brock and Brock 1974). It has been recorded from Sri Lanka (Ceylon), Australia, and the West Indies (Vine et al. 1972).

KEY TO HAWAIIAN *NEODEXIOSPIRA* SPECIES

1 Opercular talon, when present, bifid or wedge-shaped (Figs. 3.II.204b,c, 205b,c, 207b,c), not reaching floor of operculum 2
Opercular talon, when present, an arrow-shaped peg reaching and often extending through floor of operculum (Fig. 3.II.206b)...... *N. preacuta*
2(1) Collar setae on convex side of body with cross-striations 3
Collar setae on convex side of body without cross-striations .... *N. nipponica*
3(2) Tube with deep indentations between longitudinal ridges, giving a fenestrated appearance (Fig. 3.II.204a); bifid opercular talon with calcified wings .... *N. foraminosa*
Tube with ridges formed of small, calcified knobs (Fig. 3.II.207a); bifid opercular talon without calcified wings .... *N. pseudocorrugata*

Neodexiospira foraminosa (Moore and Bush, 1904)
[syn. *Janua steueri* Sterzinger, 1909: Vine et al. 1972]

In this species the tube is 1.5 to 2.0 mm in diameter. It is dextral, with longitudinal ridges forming blunt projections, and with indentations between the ridges giving the appearance of deep holes or perforations (Fig. 3.II.204a). The opercular plate is slightly concave, with a peripheral, bifid talon bearing lateral wings (Fig. 3.II.204b). The walls of the brood chamber are lightly calcified (Fig. 3.II.204c). The collar setae (Figs. 3.II.215e,f) lack fins and only the setae of the convex side are cross-striated. *Neodexiospira foraminosa* occurs in bays and

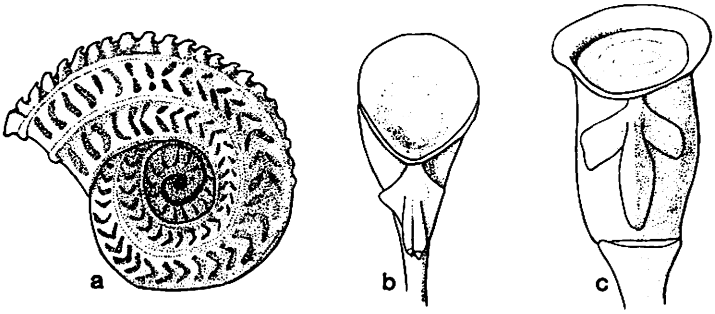


Figure 3.II.204.—*Neodexiospira foraminosa*: a, tube; b, opercular plate and talon; c, brood chamber with talon forming part of the wall. (After Vine et al. 1972.)

harbors, often on algae attached to floating docks. This species has a Pacific distribution and has been collected at Johnston Atoll (Bailey-Brock 1976), Fiji (Bailey-Brock 1985), and Tonga (Bailey-Brock, in press).

Neodexiospira nipponica (Okuda, 1934)
[syn. *Janua (Dexiospira) nipponica* Okuda. *Spirorbis alveolatus sensu* Imajima and Hartman 1964]

The tube is 1.5 to 2.0 mm in diameter. It is dextral, with 3 longitudinal ridges and transverse bars between them, giving the impression of deep, oblong indentations in the surface of the tube (Fig. 3.II.205a). A flat to concave opercular plate has a peripheral talon that is less bifid and more wedge-shaped than in *Neodexiospira pseudocorrugata* (cf. Figs. 3.II.205b,c and Fig. 3.II.207b). Collar setae of both tori are simple, finely serrated blades (Figs. 3.II.215i,j). There is a thin-walled, calcified brood chamber. This species has been recorded from Japan and South Africa, as well as from Hawaii (Vine et al. 1972).

Neodexiospira preacuta (Vine, 1972b)
[syn. *Janua (Dexiospira) turrita* Vine, 1972a]

The tube of this species is 2.0 to 2.5 mm in diameter. It has 3 longitudinal ridges, transverse growth lines, and dextral coiling (Fig. 3.II.206a). The opercular plate is slightly concave, with a long, spear-shaped talon with an asymmetrically pointed end. The talon persists in the first brood chamber that develops and can easily be distinguished through the delicate, calcified walls (Figs. 3.II.206b,c). Subsequent brood chambers lack the talon (Fig. 3.II.206d). Collar setae from the

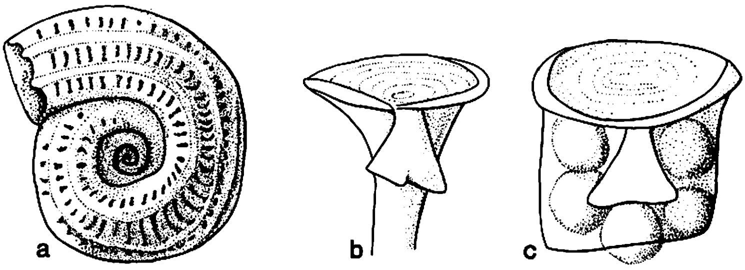


Figure 3.II.205.—*Neodexiospira nipponica*: a, tube; b, operculum; c, brood chamber. (After Vine et al. 1972.)

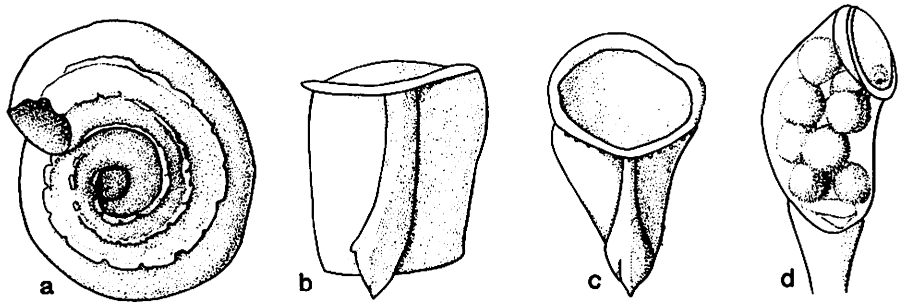


Figure 3.II.206.—*Neodexiospira preacuta*: a, tube; b,c, primary opercular brood chambers; d, subsequent brood chamber without a talon. (After Vine 1972a.)

convex side of the thorax have cross-striated blades but lack fins (Fig. 3.II.215d), while the blades of collar setae from the concave side have fine serrations and lack cross-striations. This species has been found at shallow depths in sheltered waters and subtidally on coral reefs from Hawaii and the Red Sea (Bailey-Brock 1976), Fiji (Bailey-Brock 1985), and Tonga (Bailey-Brock, in press).

Neodexiospira pseudocorrugata (Bush, 1904)
[syn. *Spirorbis pseudocorrugatus* Bush, 1904]

The tube of this worm is 1.5 to 2.0 mm in diameter. It is dextral, with 3 longitudinal ridges formed of small knobs (Fig. 3.II.207a). The operculum has a bifid calcified talon, which is almost peripheral (Fig. 3.II.207b). The brood chamber (Fig. 3.II.207c) has virtually transparent walls, and subsequently formed chambers have opercular plates that lack the talon. Collar setae lack fins, have coarse teeth and faint cross-striations on their convex side, and are finely striated on the concave side (similar to Figs. 3.II.215e,f). This species is cosmopolitan in temperate and warm seas and is very common in shallow waters of Hawaii and at Johnston Atoll (Bailey-Brock 1976).

Nidificaria dalestraughanae (Vine, 1972a)
[syn. *Pileolaria* (*Duplicaria*) *dalestraughani* Vine, 1972a]

In this species the tube is 1.5 to 2.0 mm in diameter. It is white, with 3 longitudinal ridges, and coils sinistrally (Fig. 3.II.208a). The operculum is a thin, calcified plate in juveniles (Fig. 3.II.208b) and a cup-shaped brood chamber in

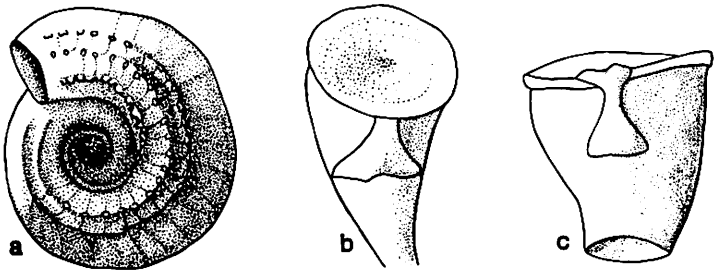


Figure 3.II.207.—*Neodexiospira pseudocorrugata*: a, tube; b, operculum and talon; c, brood chamber. (After Vine et al. 1972.)

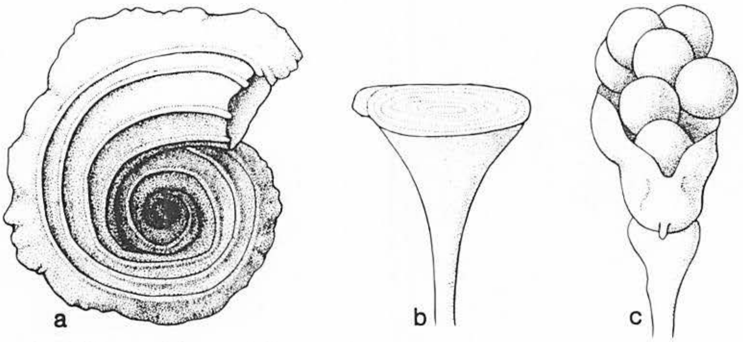


Figure 3.II.208.—*Nidificaria dalestraughanae*: a, tube; b, opercular plate; c, brood chamber with embryos. (After Vine 1972a.)

adults (Fig. 3.II.208c). There is only room for a few embryos within the cup; the rest of the brood appears to overflow the rim, but the embryos adhere to each other and form a cluster. Collar setae have fins formed of 3 large and 4 smaller teeth and a serrated blade with cross-striations (similar to Fig. 3.II.215b). The open brood chamber sugests a calm-water habitat. This species has been found at depths between 8 and 600 m (2 to 328 fm). It has been recorded from Cape Verde in the Atlantic, southern Africa, and the Hawaiian Islands.

KEY TO HAWAIIAN *PILEOLARIA* SPECIES

Operculum helmet-shaped, with a nearly complete rim of spines around the dome that is densely calcified and forms part of an opercular brood chamber .... *P. militaris*

Operculum not helmet-shaped but slightly convex, with a rim of blunt spines; the structure is lightly calcified .... *P. pseudoclavus*

Pileolaria militaris Claparède, 1868

In this species the tube is 3.0 mm in diameter. It is sinistral, with transverse growth thickenings; whorls tend to be more tightly coiled than for *Simplicaria pseudomilitaris* (cf. Fig. 3.II.209a and Fig. 3.II.212a). The juvenile operculum is a slightly concave plate having an excentric talon with lateral flanges (Fig. 3.II.209b), whereas the adult operculum is a large, helmet-shaped brood chamber,

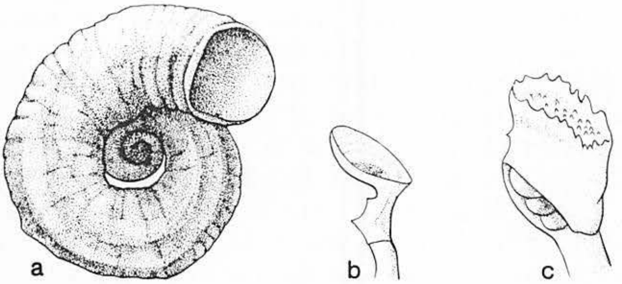


Figure 3.II.209.—*Pileolaria militaris*: a, tube; b, juvenile operculum; c, helmet-shaped brood chamber with spines.

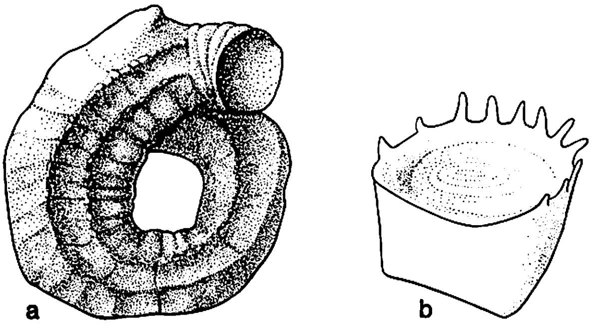


Figure 3.II.210.—*Pileolaria pseudoclavus*: a, tube; b, opercular plate with rim of spines. (After Vine 1972a.)

well calcified, with a rim and numerous spines over the surface (Fig. 3.II.209c). Collar setae have a cross-striated blade and fin (similar to Fig. 3.II.215b). Third thoracic setigers have sickle setae. *Pileolaria militaris* is found commonly in harbors and protected bays in Hawaii, and less frequently on exposed shores. It has a world-wide distribution in tropical and warm seas (Vine et al. 1972).

Pileolaria pseudoclavus Vine, 1972b
[syn. *P.* (*P.*) *semimilitaris* Vine, 1972a]

The tube of this species is 2.0 to 3.0 mm in diameter. It is sinistral, with 3 longitudinal ridges formed of knobs and transverse ridges between them (Fig. 3.II.210a). Brooding takes place in the operculum, which resembles a flat-topped helmet with a peripheral rim of spines (Fig. 3.II.210b). Collar setae have cross-striated blades and fins (Fig. 3.II.215b). Third thoracic setigers have sickle setae. Specimens were found on settling plates at shallow depths on Oahu, Hawaii (Vine 1972a). This species was first recorded from fringing reefs in the Red Sea (Vine 1972b).

Protolaeospira capensis (Day, 1961)
[syn. *Protolaeospira* sp. A: Vine et al. 1972. *P. translucens* Bailey and Harris, 1968: Bailey-Brock 1976]

The tube of *P. capensis* is about 3.5 mm in diameter. It is sinistral, translucent, vitreous, and has bulging transverse ridges (Fig 3.II.211a). The operculum is a concave plate with a median calcified rod and a talon with asymmetrical lobes (Fig. 3 II.211b). The thorax has a trace of a fourth segment instead of the usual 3. The extra segment is represented by setae and uncini on the concave side and a few uncini on the convex side. Each collar seta has a proximal fin of 3 or 4 large teeth and a distal serrated blade with cross-striations (similar to Fig. 3.II.215b). Embryos are incubated within the tube in a brood pouch, which is attached by a stalk originating near the 1st thoracic torus. This appears to be a rare species; it occurs on black lava rock, shells, and even on the carapace as of slipper lobsters. This species was first described from South Africa and it is known from New Zealand, the Galapagos Archipelago, and from shallow depths to 38 m around the Hawaiian Islands (Bailey-Brock 1976; Knight-Jones et al. 1979).

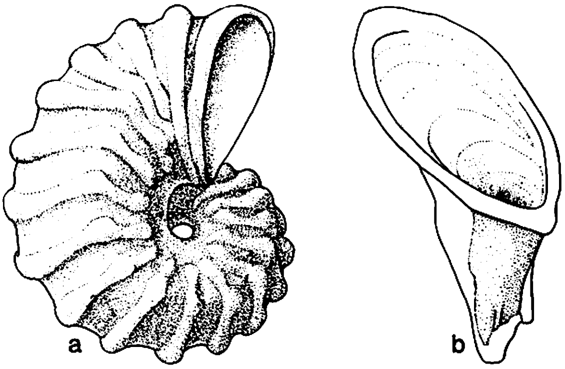


Figure 3.II.211.—*Protolaeospira capensis*: a, tube; b, opercular plate and talon. (a after Bailey and Harris 1968; b after Vine et al. 1972.)

Simplicaria pseudomilitaris (Thiriot-Quiévreux, 1965)
[syn. *Spirorbis pseudomilitaris* Thiriot-Quiévreux, 1965]

The tube of this spirorbid is 2.0 mm in diameter. It is sinistral, white, and has transverse growth thickenings (Fig. 3.II.212a), features that are characteristic of this species. The mouth of the tube may ascend from the substrate. Opercula of juveniles have a concave plate with an excentric peglike talon; adults have a helmet-shaped brood chamber with a peripheral rim of short spines and a few spines over the surface (Fig. 3.II.212b). Fin and blade collar setae have slight cross-striations (similar to Fig. 3.II.215b). Third thoracic setigers have simple blade setae. Very common in harbors and shallow reef waters of the Hawaiian Islands and at Johnston Atoll (Bailey-Brock 1976), this species is also known from the Mediterranean, Aegean, West Indies, Galapagos, Australia, and New Zealand (Vine et al. 1972).

Spirorbis marioni (Caullery and Mesnil, 1897)
[syn. *Spirorbella marioni* (Caullery and Mesnil, 1897): Pillai 1970]

In this species the tube is 1.5 to 2.0 mm in diameter. It is dextral and white with a heavy median ridge; the terminal part of the tube and mouth overlap previous whorls to give a compact, rounded arrangement (Fig. 3.II.213a). The

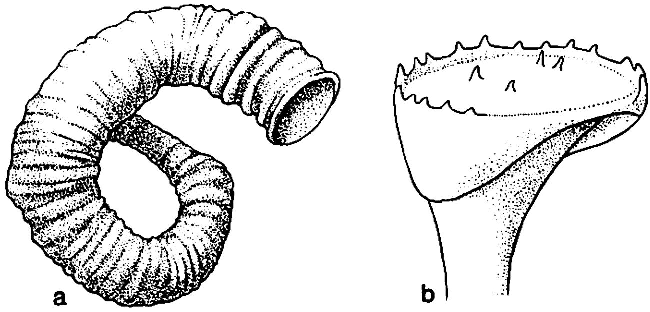


Figure 3.II.212.—*Simplicaria pseudomilitaris*: a, tube; b, operculum with a few spines. (After Vine et al. 1972.)

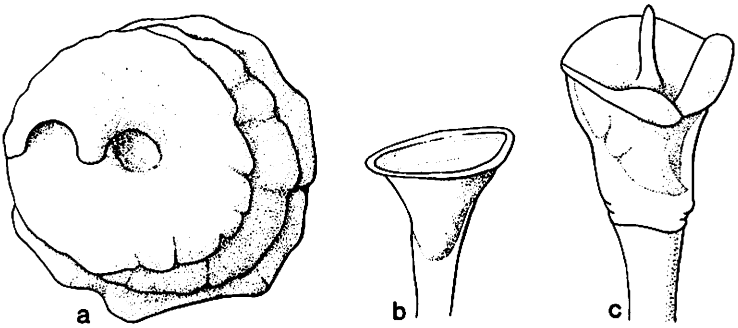


Figure 3.II.213.—*Spirorbis marioni*: a, tube; b, juvenile operculum; c, mature operculum with distal spine. (After Vine et al. 1972.)

operculum varies from a flat-topped structure with a conspicuous conical talon (Fig. 3.II.213b) to a concave plate with lateral wings, bearing an upwardly projecting peg and the same talon (Fig. 3.II.213c). Each collar seta has a fin and a cross-striated blade (similar to Fig. 3.II.215b). Incubation takes place in the tube. This species has been found intertidally on black basaltic rocks at Mokolii Islet, Oahu (Bailey-Brock 1976). It is known from Panama, Mexico, Easter Island (Kohn and Lloyd 1973), the Galapagos, and southern California, as well as from Hawaii (Vine et al. 1972).

Vinearia koehleri (Caullery and Mesnil, 1897)
[syn. *Pileolaria (Duplicaria) koehleri* (Caullery and Mesnil, 1897): Vine et al. 1972]

The tube of this worm is 1.5 mm in diameter. It is sinistral and has well-defined longitudinal ridges (Fig. 3.II.214a). The operculum is composed of 2 or 3 concave plates interlocking by a peg-and-socket arrangement (Fig. 3.II.214b). A brood chamber with lightly calcified walls forms below these plates and the developing embryos are thus held between the plates and the underlying brood chamber (Fig. 3.II.214c). Collar setae (Fig. 3.II.215a) have fins, finely serrated blades, and no cross-striations. This is a relatively common species in shallow waters around the Hawaiian Islands and at Johnston Atoll (Bailey-Brock 1976). This species is also

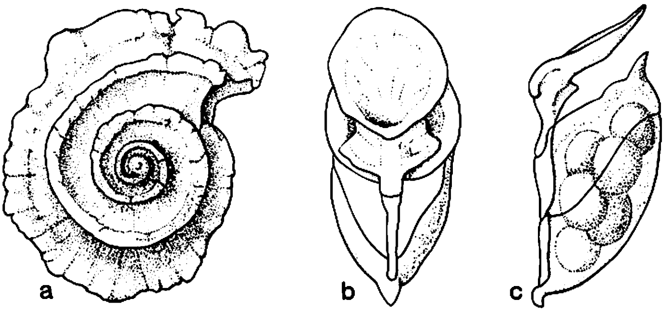


Figure 3.II.214.—*Vinearia koehleri*: a, tube; b, operculum of interlocking plates; c, brood chamber, lateral view. (After Bailey 1970.)

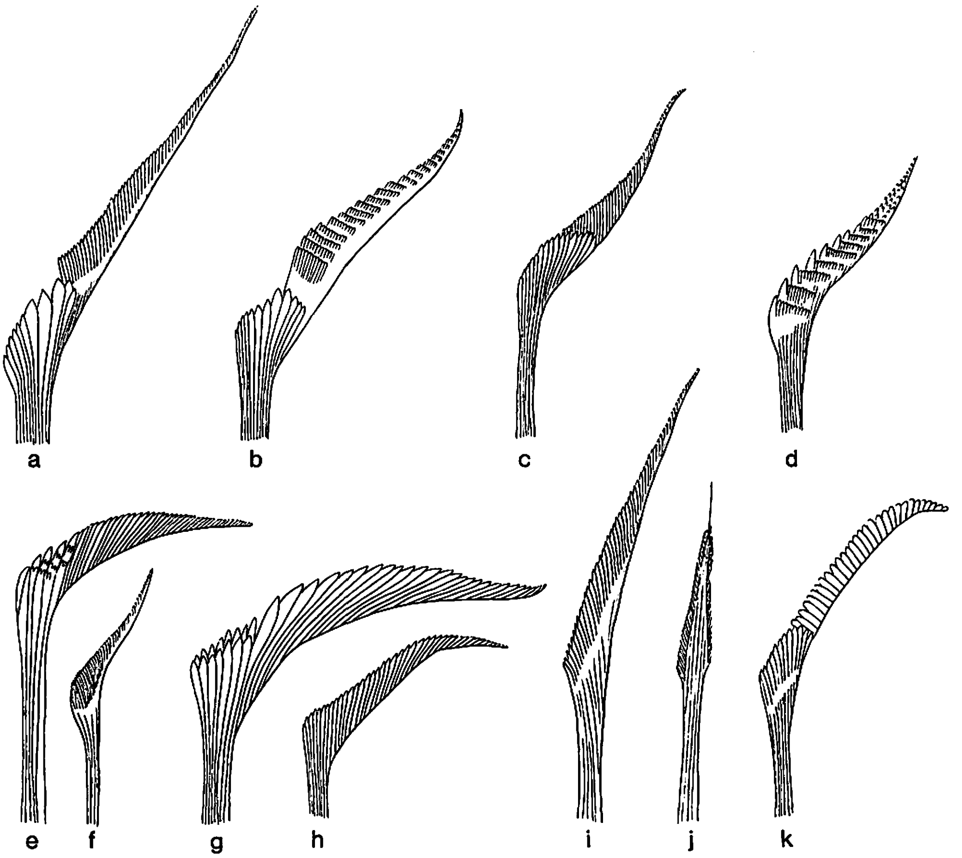


Figure 3.II.215.—Types of spirorbid collar setae (1st thoracic setae): a, fin and blade (*Vinearia koehleri*); b, fin and serrated blade with cross-striations (*Pileolaria pseudoclavus*); c, seta with rudimentary fin (*Janua pagenstecheri*); d, simple seta with serrations and cross-striations (*Neodexiospira preacuta*); e,f, simple setae from convex and concave side, respectively (*Neodexiospira foraminosa*); g,h, simple setae from convex and concave side, respectively (*Leodora knightjonesi*); i,j, simple setae from concave and convex side, respectively (*Neodexiospira nipponica*); k, 3rd thoracic sickle seta (*Janua pagenstecheri*). (a,c,e–k after Vine et al. 1972; b,d after Vine 1972a.)

known from the Mediterranean, West Indies, Red Sea, Australia, New Zealand (Vine et al. 1972), Fiji, and Tonga (Bailey-Brock 1985, in press).

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This polychaete revision is based on the manuscript originally submitted for publication by Dr. Hartman in 1969. The present updated version is still far from complete, and a thorough understanding of Hawaiian polychaetes is some years away. Without the encouragement of the late Dr. Dennis Devaney, senior editor of the revised edition of C. H. Edmondson's *Reef and Shore Fauna of Hawaii*, I would not have undertaken the revision of Dr. Hartman's manuscript. When Dennis discussed updating the polychaete section, my knowledge of polychaete taxonomy was limited to the calcareous tubeworms. While working on this revision I have learned a tremendous amount about Hawaiian polychaetes and have become much better informed about many aspects of polychaete taxonomy

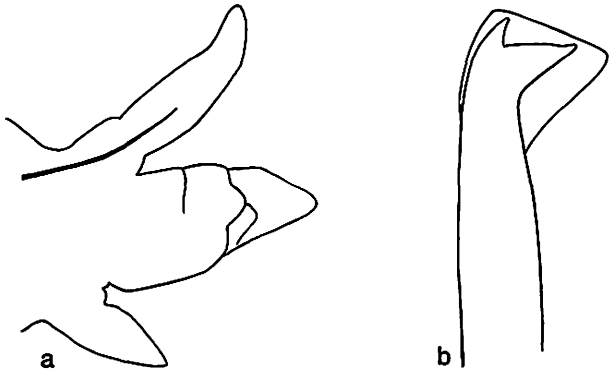

Figure 3.II.216.—*Diopatra leuckarti*: a, second parapodium (setae omitted), anterior view; b, hooded acicular seta from 25th parapodium. (After Hartman 1948.)

and ecology. I am grateful to Dennis for his continued advice, constructive discussions, and collegiality. I have thoroughly enjoyed contributing to this section of the revision and would have missed so much if I had not taken on the annelid chapter. I know that Dennis also enjoyed the polychaetes and that he would be pleased with his contributions.

It is with great pleasure that I dedicate my efforts on the taxonomy of Hawaiian polychaetes to Dr. Marian H. Pettibone (U.S. National Museum of Natural History) and to Professor E. W. Knight-Jones (University College of Swansea, Wales) in appreciation of their inspiration and guidance over the past few years. I also thank my students, Linda A. Ward and Janet K. Friend, for revising the families Spionidae and Syllidae, respectively. These are mainly their contributions and a number of newly recorded species could not have been included were it not for their expertise. The revision benefitted from the help of many colleagues who advised on their specialty groups by identifying specimens, reviewing keys, and checking drafts of the manuscript. Colleagues who reviewed and contributed to other families are M. H. Pettibone, Polynoidae; J. D. Kudenov, Amphinomidae; W. Westheide, Syllidae; M. Dutch, Nereididae; K. Fauchald and M. C. Lloyd, Eunicidae; A. Myers and H. Paxton, Onuphidae; J. A. Blake, Spionidae; M. Bhaud, Chaetopteridae; D. Davis, Oweniidae; M. L. Jones, Magelonidae; D. Kirtley, Sabellariidae; K. Banse, J. H. Day, and P. Knight-Jones, Sabellidae; H. ten Hove and H. Zibrowius, Serpulidae; and P. J. Vine, E. W. and P. Knight-Jones, Spirorbidae. Linda A. Ward, M. H. Pettibone, and K. Fauchald read various stages of this revision, which has been improved as a result of their assistance. Field collecting over the last 15 years by R. E. Brock has added many new records and extended the distribution and habitat information of many species. Thanks are also extended to Dr. E. C. Evans, J. G. Grovhoug, and P. Hiller of the Naval Ocean Systems Center, Kaneohe, and to the Hawaiian Electric Company for providing many unrecorded polychaetes to me for identification and inclusion in the revision. The following agencies have supported parts of this work: the National Science Foundation, No. GB-4033 (awarded to Dr. O. Hartman); the Environmental Protection Agency, No. R803983010 (awarded to Dr. S.V. Smith, University of Hawaii); and the University of Hawaii Sea Grant Program, No. 04-8-M01-178. Specimens have been loaned or donated by B.

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NOTE

1. *Sabellastarte sanctijosephi* has no radiolar eyespots; other species in this genus may or may not have these (Day 1967).

GLOSSARY (ANNELIDA)

abdomen: Posterior segments of the body that differ morphologically from the anterior ones (thorax); most clearly seen in tube-dwellers.

achaetous: Without setae.

acicular seta: Stout, chitinous seta that resembles the aciculum of the parapodial ramus but may have a toothed or curved tip.

aciculum: Chitinous rod that supports the parapodial lobe; biramous parapodia have dorsal notoacicula and ventral neuroacicula.

aileron: Winglike, elaborate jaw structure of the glycerids.

alimbate: Simple seta without a flattened wing.

ampulla: Swollen, globular structure that appears hollow.

annulated: Ringed, as the segments of *Arenicola brasiliensis* that bear a number of rings that are not segmental boundaries.

antenna: Epithelial projection of the prostomium, bearing sensory receptors.

aristate seta: Thick seta with a tuft of fine hairs or a single spine at the tip.

asetigerous: Without setae.

atokes: Sexually immature worms, which in the eunicids bud off gamete-producing segments posteriorly (an epitoke). In nereidids the atoke becomes epitokous prior to spawning.

avicular: Z-shaped or swan-shaped; describes the shape of thoracic uncini of the sabellids.

biramous: Two parapodial lobes are present.

branchia: Extension of the body wall containing blood vessels that may be elaborately branched or a simple filament; respiratory function.

branchial crown: Extensions of the peristomium in tubicolous worms, which form pinnate tentacular radioles for suspension feeding and respiration.

branchial tentacle (see **radiole**).

buccal: Pertaining to the mouth.

capillary seta: Slender, tapering seta.

caruncle: Dorsal lobe just behind the head of amphinomids (fire worms) and spionids, which may be smooth or pleated; thought to be chemosensory.

cauda: Distinct tail region at the most posterior end of the worm.

cephalic cage: Structure surrounding the head that is made up of anteriorly directed, elongate setae.

ceratophore: Basal region of an antenna, often swollen or ringed, as in onuphids.

chevrons: V-shaped chitinous elements at the base of the proboscis of goniadids.

cirrophore: Basal projection that bears a cirrus.

cirrostyle: Distal end of a cirrus.

cirrus: Sensory projection of the parapodia that is attached to a cirrophore or directly to the body wall; variably modified in different families.

clitellum: Typically a girdle of swollen, glandular epidermis found on a variable number of anterior segments in the oligochaetes and leeches; secretes fluids for reproduction and cocoon formation.

collar: Flap of tissue at the anterior end of the thorax that folds over the tube and assists in tube building.

collar setae: Specialized setae on the 1st thoracic setiger of serpulids and spirorbids.

companion setae: Setae composed of a blade and a shaft, accompanying the uncini of thoracic setigers, as in some sabellids.

compound seta: Jointed seta.

crenulated seta: Seta with a blade edge having a series of small cusps.

ctenidium: Gill.

cupule: Cup-shaped structure.

dorsum: Dorsal surface of the body.

elytra: Dorsal scales that are borne by the parapodia of polynoids; may partially or entirely cover the dorsum.

elytrophore: Protuberance on the notopodium that bears an elytron, as in polynoids.

epitokes: Sexually mature individuals budded off from a nonreproductive anterior end, usually equipped with sense organs and special setae for swimming.

falcate: Hooked.

falciger: Simple or compound seta with a hooked tip.

fascicle: Bundle or tuft of setae.

flail seta: Capillary with its tip bent at an angle.

foliaceous: Leaflike.

furcate: Branched.

geniculate seta: Seta that is bent like a knee.

heterogomph: Compound seta with an oblique joint between the 2 components.

heteronereids: Spawning stage of some nereidids, which develop specialized head structures and swimming setae; often erroneously described as new genera.

homogomph: Compound seta with a symmetrical joint between the blade and the shaft.

interramal pouches: Pockets between the 2 branches of the parapodium.

lamella: Flattened flap of tissue.

lanceolate: Evenly pointed like a lance.

"langerhansia" seta: Seta with a tapering blade at least 3 times the length of other setal blades, as in syllids.

lenticulate eye: Eye with a lens.

ligule: Tonguelike projection on the parapodium.

limbate or winged seta: Seta with a flattened blade.

metatrochophore: Trochophore larva that has developed 3 or more segments, as seen in the spirorbids.

moniliform: Like a strand of beads.

multiarticulate: Composed of a number of joints, as antennae of some eunicids and dorsal cirri of syllids.

natatory: For swimming, describes specialized structures that aid swimming, e.g., natatory seta of the heteronereids.

nephridiopores: Openings of the excretory organs (nephridia).

neuropodium: Ventral lobe of the parapodium.

notopodium: Dorsal lobe of the parapodium.

nuchal organs: Epidermal chemosensory structures of the prostomium and peristomium, which may be ciliated grooves or lobate or tentacular processes.

nuchal flaps: Sensory organs projecting posterolaterally as a ridge or fold from the prostomium.

occipital tentacles: Epithelial structures attached to the posterior part of the prostomium.

operculum: Pluglike structure for closing the tube, present in some tubicolous families, such as serpulids and spirorbids.

palea: Broad, flattened seta characteristic of the sabellariids and palmyrids.

palpode: Tapering projection on the anterior region of the prostomium.

palps (palpi): Paired projections from the side of the head. Palps of errant worms are short and limbate; sedentary forms have extensile, grooved tentacles used for feeding.

papillose: Covered with papillae.

paragnaths: Small chitinous teeth borne on the proboscis of the nereidids that aid in obtaining or swallowing food.

parapodium: Segmental appendage, directed laterally and usually having a dorsal and ventral component.

pectinate: Comblike; a term often used to describe serrated paragnaths, branchiae, or setae.

peduncle: Stalk, e.g., eye stalks and the opercular stalks of serpulids.

pennoned: Broad blade seta terminating in a pointed tip, resembling a triangular flag.

peristomial tentacles (or cirri): Epithelial projections of the peristomium; peristomial cirri are short tentacles.

peristomium: First true segment; bears the mouth and eyes when present.

penicillate seta: Broad, brushlike seta.

pharynx: Cavity connecting the mouth with the digestive tract.

pinnate: Featherlike branching arrangement composed of a central midrib and smaller lateral branches.

pinnules: Side branches of pinnate structure, such as a branchial tentacle (radioles) of sabellids.

proboscis: Protrusible anterior part of the buccal region; may be armed with teeth or be bulbous and unarmed.

prostomium: Most anterior part of the worm; not a true segment.

proventriculus: Forepart of the pharynx; often eversible.

pseudocompound seta: Simple seta with a constriction on the shaft that makes it appear compound.

pygidium: Postsegmental region that bears the anus.

radiole: One of the branchial tentacles forming the tentacular crown of sabellids, serpulids, and spirorbids.

ramus: Branch of the parapodium; refers to the notopodium and neuropodium; collectively termed rami.

reniform: Kidney-shaped.

septum: Thin wall of tissue dividing 1 segment from another internally.

setae: Chitinous (more rarely calcareous) bristles secreted by follicle cells (chaetoblasts) and borne in clumps on the parapodial lobes.

setiger: Segment with setae.

sickle seta: Seta with curved blade distally bearing distinct teeth on the inner side of curve; found in thoracic setigers of serpulids and spirorbids (may be called *Apomatus* seta).

spatulate: Flattened blade with a blunt tip.

spiniger: Compound seta with a tapered tip.

spinning gland: Modified parapodial gland between the notopodium of worms in the Polyodontidae; it secretes the threads that form a protective tube.

subacicular hook: Acicular seta with a bifid tip.

sub-biramous: Parapodium that is neither biramous or uniramous owing to partial loss of 1 of the lobes.

stylodes: Small, finger- or straplike projections on the pinnulate tentacles of some sabellids.

talon: Structure attached to the opercular plate of spirorbids that has a variable shape of taxonomic importance.

tentacle (see occipital tentacles, palps, peristomial tentacles).

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