Pacific Science (1976), Vol. 30, No. 1, p. 69–81
Printed in Great Britain

Habitats of Tubicolous Polychaetes from the Hawaiian Islands and Johnston Atoll[1]

JULIE H. BAILEY-BROCK[2]

ABSTRACT: Forty-seven species of tube-building polychaetes, belonging to the families Spionidae, Chaetopteridae, Sabellariidae, Terebellidae, Sabellidae, and Serpulidae, were collected from the Hawaiian Islands and Johnston Atoll. Eight different habitat types or zones were distinguished, each having a characteristic polychaete fauna.

The tidepools of rocky shores support up to 20 species, including the only tube-incubating spirorbine found in Hawaii, *Spirorbis marioni*. Two of the three known Hawaiian chaetopterids, the large fan worm *Sabellastarte sanctijosephi*, and 13 serpulid species occur on reef platforms that lack lush coral growth. Four species of algae were found with associated polychaetes. The greatest number of species was associated with *Dictyosphaeria cavernosa*, which provides suitable habitats for cryptic and sessile organisms. Live coral heads and the subtidal, fringing reefs apparently have an impoverished tube-worm fauna. *Spirobranchus giganteus* is the only living serpuline associated with live corals. The hard parts of mobile crustaceans and gastropods reveal a diverse invertebrate fauna, and the species composition of the associated polychaetes reflects that of the surrounding environment. Boat harbors and lagoons have a typically rich fauna due to the introduction of benthic invertebrates on the bottoms of boats. Such habitats remain reservoirs of introduced species, which are important in the geographical distribution of tube worms within the islands. *Mercierella enigmatica* and other euryhaline polychaetes are found in brackish waters. The unique anchialine pond systems of lava flows on Maui and Hawaii have discrete polychaete faunas and physical characteristics influenced by a freshwater lens. Six serpulids and a sabellariid were dredged from depths of 200 to 600 meters off Oahu and Molokai.

BENTHIC POLYCHAETES are important components of the invertebrate fauna of coastal areas surrounding the Hawaiian Islands. They contribute to the physical and biological climate of the fringing reefs as effectors of sand stability on the reef flats (Fager 1964) and as burrowers and cementors (Scoffin 1972); further, they contribute to the calcium carbonate budget of the reef (Marsden 1962, Ebbs 1966). Polychaetes are components in the diet of many reef fishes and invertebrates, some of which are exclusively vermivorous. The contributions made by polychaetes to shallow-water ecosystems cannot be overlooked when any aspect of reef ecology is being considered. Kohn and Lloyd (1973*a*) presented data on the numbers of individuals, species diversity, and geographic distribution of polychaetes from coral reefs in the eastern Indian Ocean. This was the first quantitative study of reef polychaete species, and it emphasized the high population density of polychaetes in reef ecosystems.

The present paper deals with tubicolous polychaetes of the Hawaiian Islands: their habitats, zoogeography, possible dispersal mechanisms, and the significance of tube-dwelling polychaetes in reef ecosystems. In addition, the spirorbine fauna of Johnston Atoll, comprising two low-lying coral islets, 700 nautical miles southwest of Oahu, is described. Johnston is regarded as an outlier of the Hawaiian faunal region. Ninety percent of the shoal-water

[1] Manuscript received 30 April 1975.

[2] University of Hawaii, Department of Zoology, Honolulu, Hawaii 96822.

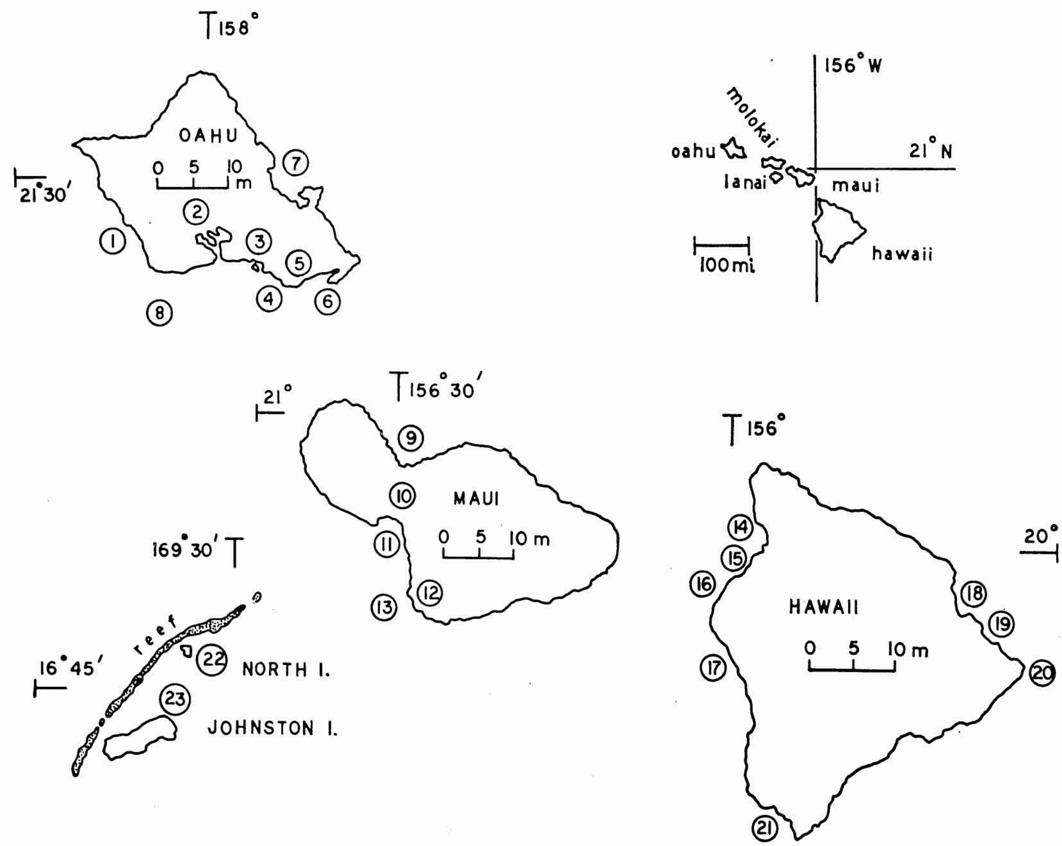

FIGURE 1. Map showing collection areas in the Hawaiian Islands and Johnston Atoll. See Appendix 1 for places where collections were made and types of areas collected, referred to by numerals here.

crustaceans are of Hawaiian, rather than of South Pacific, origin (Edmondson et al. 1925); however, only half of the inshore fish fauna is of Hawaiian origin (Gosline 1955).

Records of all the polychaetes then known from Hawaiian waters were presented by Hartman (1966). Her paper included data from the 1902 U.S.S. *Albatross* expedition originally described by A. L. Treadwell (1906); from the 1946 collections from Halape, Hawaii, and Oahu; and from miscellaneous collections. Straughan (1969*a*) expanded Hartman's record of 7 serpulines to 12. Vine (1972*a*) described three new species in the Spirorbinae; while Vine, Bailey-Brock, and Straughan (1972) discussed the distribution of 13 Spirorbinae species from Oahu and Hilo, Hawaii. Distributional records for some deeper water serpulids, attached to precious coral and the carrier-shells *Xenophora tenuis* and dredged from 200 to 600 meters deep, were discussed by Bailey-Brock (1972).

DISTRIBUTION OF TUBICOLOUS POLYCHAETES

Rocky Intertidal Areas

The rocky intertidal includes those parts of the coastline composed of lava rocks or limestone benches and associated tide pools (Appendix 1, Figure 1). The benches may support dense algal turfs and a distinctive tide-pool and bench fauna that vary according to the amount of exposure the coastline receives. Kohn (1959) described these habitats and divided the benches into zones on the basis of more detailed faunistic analysis. Tidal range in the Hawaiian Islands is rarely more than 1 meter, but surge and conditions of high surf can greatly increase the area of shoreline affected by wave action. In temperate latitudes extensive tidal movements result in the development of horizontal zones of frondose algae and associated fauna.

Serpulids are the dominant polychaetes in this habitat where a large number of species are represented. The 13 species recorded are listed in Appendix 2. An abundance of the spirorbine *Janua knightjonesi* forms white encrustations on the lava rocks at Waiulua Bay, Anaehoomalu, Hawaii. Other tubicolous polychaetes recorded from this habitat include the sabellariid *Lygdamis indicus* and two species of chaetopterids, terebellids, and sabellids.

Reef Flats

Reef flats studied are listed in Appendix 1 and shown in Figure 1. In Hawaii, reef flats are all subtidal, between 0.5 to 3 meters below mean sea level, and form the tops of narrow fringing reefs. They are composed primarily of sand patches, limestone rubble, calcareous algae, macrothalloid algal turf and, toward the seaward edge, of corals. Polychaetes associated with hard substrata such as coral rubble, small boulders, molluscan shells, and other debris are presented in Appendix 2.

Sand patches are habitats of the chaetopterids *Mesochaetopterus sagittarius* and *Phyllochaetopterus verrilli*, which may be abundant in these areas. These species form sand-grain tubes that project approximately 2.5 cm above the level of the flat. Their tubes may stabilize sand on the reef. Extensive masses of tubes, approximately 1 square meter or more, appear as slightly raised areas on the reef flat. The south shore reefs of Oahu at Fort Kamehameha and Sand Island receive much surf and wave action, especially during the winter months, and are fine examples of flats which are literally a patchwork of these low hillocks.

The dominant intertidal serpulid *Pomatoleios kraussii* forms a distinct zone on the shoreward side of some leeward reefs and sea walls of Mokuoloe (Coconut) Island, Kaneohe Bay (Straughan 1969*b*) and occurs in the rocky intertidal and shallow subtidal on all the islands.

The large fan worm *Sabellastarte sanctijosephi* is found in pockets and crevices in the reef flat. It is especially abundant along the edges of reefs that have been dredged to make small-boat harbors and swimming areas, as at Ala Moana and Fort Kamehameha, Oahu; it may be an indicator of waters with high sediment content.

On Living Substrata

This habitat includes macrothalloid algae and live corals. Algae that have been found with polychaetes include the chlorophytes *Dictyosphaeria cavernosa*, *Caulerpa serrulata*, and *Valonia aegagropila*, the phaeophyte *Acanthophora* sp., and encrusting red coralline algae.

The greatest number of species was observed on the bubbly thallus of *Dictyosphaeria cavernosa* from Kaneohe Bay (Appendix 2). The chaetopterid *Chaetopterus* sp. is abundant on the alga in the southern and middle sections of the bay, which receive secondarily treated sewage and most of the bay's freshwater inflow and which have the poorest water circulation of the total bay area (Banner and Bailey 1970).

The reason for the large number of species forming the epifauna of *Dictyosphaeria cavernosa* may be due to its greater vertical range (0–10 m) as compared with other algal species, as well as to its cavernulous shape which provides protection for cryptic organisms.

Only one serpulid appears to be associated with living corals in Hawaii. *Spirobranchus giganteus* is found only in massive heads of *Porites lobata*. The tubes are usually surrounded by an overgrowth of the coral and the branchial crown and operculum of the worm protrude during feeding. *S. giganteus* occurs subtidally and is found from a depth of 1 m to more than 15 m; its distribution follows that of the coral.

Epifauna of Benthic Mobile Crustacea and Gastropoda

Mobile substrata refers to those benthic animals that have hard external coverings and that move freely on the reef. Both mollusks and crustaceans are included in this category of habitat; their polychaetous epifauna is composed almost entirely of serpulids.

Two species of slipper lobster, *Paribaccus antarcticus* and *Scyllarides squammosus*, from caves at a 3-meter depth off Sand Island near Honolulu Harbor and subtidally off Waikiki, revealed an epifauna of encrusting sponges, bryozoa, folliculinid protozoans, and serpulids (Appendix 2). The serpuline tubes were attached to the ventral surface of the carapace, the apertures being directed toward the lobster's mouth. The orientation of the worm suggests that direction of growth may be influenced by feeding currents generated by the lobster's mouthparts, as occurs in the barnacle *Balanus triginus*, which is associated with the mouthparts of a spiny lobster (Bowers 1965). Polychaete species found as epifauna are the same species that encrust benthic substrata. The intertidal spirorbine *Janua knightjonesi* has been found covering the shells of *Nerita picea* and *N. polita* occupied by hermit crabs in the rock-bench tidepools on the Kona Coast, Hawaii. A specimen of the large gastropod *Charonia tritonis* from a 6-meter depth off Waikiki, Oahu, had an epibiota of encrusting coralline algae, bryozoa, foraminifera, and six serpulids—*Hydroides crucigera*, *Protolaeospira translucens*, *Pileolaria militaris*, *P. koehleri*, *Janua preacuta*, and *J. nipponica*. A specimen of the gastropod *Conus quercinus* collected from a depth of 2 m at Sand Island reef, Kaneohe, was found with a sabellid, *Sabellastarte sanctijosephi*, attached to the shell (A. J. Kohn, personal communication).

Protolaeospira translucens was recorded from Hawaii as *Protolaeospira* sp. *A* (Vine et al. 1972), from a single specimen found in Kaneohe Bay, Oahu. Additional worms have been collected and are considered conspecific with *P. translucens* Bailey, from the Galápagos Islands (Bailey and Harris 1968; British Museum [Nat. Hist.] numbers 1967-8-18-21).

Six species of serpulids and one sabellariid have been found on the carrier shell *Xenophora tenuis* dredged from 200 to 600 m. One point of interest lies in the distribution of the serpulids and the arenaceous sabellariid on the conical shells. In cross section the shell has the form of an equilateral triangle. The serpulids were found more commonly on the conical dorsal portion of the shells; the sabellariids were found always on the flat, lower face, often on the inner whorls of the shell, so that the worm's tube projected from the mouth of the shell. The orientation can be explained partly by the tube-building and feeding methods of the two groups. The serpulines on the upper surface are ideally situated for suspension feeding. The sabellariids, which have been described as suspension feeders (Day 1967), have a system of paleae, buccal cirri, and grooved palps that separate food materials from the heavier particles used for tube building. Thus, the sabellariids occur on the lower surface nearest the substratum, where tube-building materials are more readily available; and the serpulid tubes are usually facing up into the water column and, therefore, are less subject to becoming plugged with large particles.

Boat Harbors and Lagoons

Boat harbors on leeward coasts, as well as on two with a northern exposure, were sampled. Worms were found on pilings, wharfs, the undersides of boats and buoys, etc. (Appendix 1, 2, and Figure 1). The greatest number of species occurs in these areas, perhaps as a result of the calm conditions and of the frequent boat traffic which is an important mechanism for dispersing serpulids (Allen 1953, Knight-Jones et al. 1975). The cosmopolitan fouler *Hydroides norvegica* has been dispersed by boats, and it is quite possible that *H. lunulifera*, *Pileolaria militaris*, and others have been spread to and between the islands in the same manner.

Lava Ponds

Anchialine ponds in the lava along the coastline of Cape Kinau on Maui and the Kona Coast, Hawaii, are unique in having variable salinities ranging from near freshwater to true marine conditions. The mixohaline ponds have varying degrees of horizontal salinity stratification and a distinct biota (Maciolek and Brock 1974).

Two of the pools examined were open to the sea; the others were isolated, often by a few hundred meters, and were connected to the ocean only by seepage through the lava. The water in the pools rises and falls with the tides. The tube worms characteristic of the pools connected with the ocean are shown in Appendix 2 and are distinguished from those of isolated ponds.

In the isolated ponds, tube-dwelling polychaetes include *Spiophanes bombyx*, *Cirriformia semicincta*, and *Janua nipponica* which was on the alga *Caulerpa serrulata*. The distribution of polychaete species within these pond systems appears to be associated both with salinity and distance from the ocean. More species were found in the more saline ponds nearest the ocean than in the more freshwater landward ponds. Two mechanisms may account for the colonization of these pond systems by polychaetes: the movement of larvae and, perhaps, more mobile adults from the sea through subterranean channels into the ponds, and the heavy surf created by storms that could transport these organisms to the more isolated ponds.

Brackish Waters

Brackish waters in the Hawaiian Islands are found where rivers and streams reach the sea, or where there are freshwater incursions along the coast. The Ala Wai Canal and Pearl Harbor on Oahu are typical of this habitat.

The brackish-water serpulid *Mercierella enigmatica* is present along the length of the Ala Wai Canal; the most extensive population is seen in the section between the Manoa-Palolo channel and Kapahulu. Other areas on Oahu where this species may be found include the beach park at Paiko where the freshwater influence is reflected in the change across the reef flat from brackish to marine organisms, and in the canals of neighboring Hawaii Kai. Empty tubes were found in a drainage canal at Kahala. On Maui, extensive masses of *Mercierella* were seen at a commercial fish farm located at Kealia Pond. It is believed that *Mercierella* was introduced to Maui with oysters sent from Pearl Harbor to stock the pond. These serpulids may pose a problem to aquaculturists because they are so easily introduced and are able to withstand considerable exposure to freshwater. They frequently clog the pipes used for circulation between holding ponds and cover settlement sites. Other tubicolous worms associated with *Mercierella* in the Ala Wai Canal are the cosmopolitan foulers *Hydroides norvegica* and *Salmacina dysteri*.

Reef Slope to 600 Meters Depth

This habitat includes polychaetes from the upper edge of the reef slope and from deeper waters between 200 and 600 m. Tubeworms associated with living and mobile substrate could have been included here, but instead have been put in separate categories. Twelve species were collected from coral rubble at 10 to 20 m off the leeward and south shores of Oahu. Of these, 10 were serpulids, 1 a sabellariid, and the other a sabellid (Appendix 2).

Nine polychaete species were dredged from 200 to 600 m. Three of the serpulids—*Spirobranchus latiscapus*, *Vermiliopsis infundibulum*, and *Pileolaria dalestraughanae*—were recorded earlier (Bailey-Brock 1972). *Serpula vermicularis*, *Salmacina dysteri*, and *Pileolaria dalestraughanae* were collected at the 10 to 20 m stations and taken in the dredged material. The exclusively deepwater species are distinguished from the more eurybathic ones in Appendix 2.

Spirorbinae from Johnston Atoll

Spirorbinae were collected by J. A. Brock in 1971 from coral rubble in dredged areas on the leeward side of North Island and near Johnston Island pier from depths of 5 and 2 meters, respectively. Four opercular-incubating species were identified: *Pileolaria pseudomilitaris*, *P. koehleri*, *Janua pseudocorrugata*, and *J. foraminosa*.

DISCUSSION

Despite the narrow intertidal region and absence of the broad algal zones characteristic of more temperate regions, there are a variety of diverse habitats for tube worms in Hawaii. The only places with a depauperate tube-worm fauna are exposed locations that receive excessive surf and areas of lush coral. In the latter situation, larvae may be prevented from settling by the lack of available space or by the copious mucus produced by corals, or they may be eaten by the polyps. *Spirobranchus giganteus* is the only polychaete recorded that colonizes living corals.

The list of Hawaiian polychaetes associated with macrothalloid algae is meager when compared with other areas of the world. On British coasts red coralline algae and brown fucoids are often heavily encrusted with spirorbines (Gee and Knight-Jones 1962, Gee 1964). The Mediterranean spirorbines are found on eelgrass, *Padina*, and pavementlike growths of coralline algae (Harris and Knight-Jones 1964). Mangroves, eelgrasses, the green calcareous alga *Halimeda*, and *Sargassum* sp. in the West Indies all have associated serpulids (Bailey 1970). Two spirorbine species found on mangrove prop roots and on algae in the Caribbean, *Pileolaria koehleri* and *Janua knightjonesi*, are also found in Hawaii on algae and hard substrata. No serpulids have been found on mangrove roots in Hawaii. On the other hand, floating mangrove fruits, coconuts, driftwood, and other debris are often encrusted with spirorbines in Hawaiian waters, such debris providing an efficient dispersal mechanism for these gregarious worms.

It is not known whether any of the spirorbines are substrate-specific to the algal species listed in Appendix 2, as has been found in more temperate waters. In Britain, larvae from two populations of *Spirorbis spirorbis* are able to distinguish between pieces of the alga *Fucus vesiculosus* taken from corresponding geographic locations (Knight-Jones, Bailey, and Isaac 1971). Although the intertidal species *Janua knightjonesi* has been found on only one species of alga in Hawaii, it has been found also on a variety of substrata in this zone, an indication that there is little preference for a specific type of substratum.

The ecology of *Protolaeospira translucens* appears to be analogous to a similar transparent-tubed species, *Paradexiospira vitrea*, of Arctic waters. Crisp, Bailey, and Knight-Jones (1967) have concluded that survival of *P. vitrea* is influenced by the strength of the tube and its resistance to abrasion during the animal's life cycle. Adult *Paradexiospira vitrea* and *Protolaeospira translucens* have thick, glassy tubes that are resistant to mechanical damage. In the Galápagos, *P. translucens* is distributed spottily on four of the islands, occurring in clear water on lava rock and on the exoskeleton of the spiny lobster *Panulirus penicillatus* (Bailey and Harris 1968). The absence of *P. translucens* and serpulids in general from this species and from the endemic Hawaiian panulirid *P. marginatus* cannot easily be explained.

The euryhaline serpulid *Mercierella enigmatica* is found in brackish waters in Hawaii although it is able to tolerate extremes of salinity. It has been reported from a river in Tunisia (Seurat 1927), from mixohaline conditions in northwest France (Fischer-Piette 1937), from coastal localities in Britain (Harris 1970), and from the hypersaline lake at Tunis (Vuillemin 1965). The tubes form encrustations on rocks, harbor structures, and along the banks of estuaries and canals. Hawaii is the most tropical record of this species which otherwise has a more temperate distribution (Hartmann-Schröder 1971). A closely related form that has until recently been confused with *Mercierella enigmatica* is *Neopomatus uschakovi* Pillai, which occurs in the same type of environment in the tropics. Hartmann-Schröder (1971) mapped the known world distribution of these two euryhaline serpulids. The geographic distribution and characteristic habitats of these species in shallow, coastal waters appear to be determined by their tolerance to salinity variations. Hill (1967) and Straughan (1972) showed that the life cycle of *Mercierella enigmatica* is synchronized with seasonal salinity and temperature changes.

Straughan (1972) determined that reproduction does not occur below a minimum temperature (18° C), or outside a broad range of salinity (7–35 ‰). The larvae are released at neap tides, spend 3 weeks in the plankton, and settle gregariously. Other factors influencing larval settlement include the concentration of calcium ions, competition, predation, and pollution.

Many of these coastal areas receive silt-laden waters from streams and rivers, most of the silt being deposited along the banks before reaching the sea under normal rates of flow. *Mercierella enigmatica* withstands considerable amounts of silt; its tubes are often covered in a thick layer of sediment, the openings project slightly above it, and the chitinous spines on the operculum are usually clogged with a core of silt which otherwise would plug the tube.

Tube worms listed as *Mercierella enigmatica* but probably including *Neopomatus uschakovi* are among the many invertebrates that are transported widely by shipping, which accounts for the abundance of both genera in harbors and canals throughout the world (Allen 1953).

Polychaetes are an important food source for a number of reef organisms. Some genera of mollusks have been found to be entirely or partially vermivorous in their diets. Many of the prey species are free-living and are associated with algal mats and sand pockets on rock benches or with the subtidal sandy areas of reefs. Tubicolous polychaetes also are eaten: *Mesochaetopterus* is preyed on by *Vasum* and *Engina* and *Morula anaxeres* feed on Spirorbinae (Miller 1974). Polychaetes in the diet of the common species of *Conus* in Hawaii have been well documented (Kohn 1959).

Representatives of many families of reef fishes also utilize polychaetes as a food source. Stomach contents of reef fishes from the Marshall Islands contained remains of serpulids and other polychaetes (Hiatt and Strasburg 1960). Stomachs of sharp-backed puffers, *Canthigaster jactator*, taken from Kaneohe Bay, Oahu, during July 1971, contained spirorbines (Bailey-Brock, unpublished).

Wide geographical distribution is typical of polychaetes (Day 1967), and most polychaetes have pelagic larvae that are transported by water currents. Of the tube worms discussed here, the Spirorbinae have an unusual life history that includes brooding of the developing larvae (Bailey 1969). They are hermaphroditic and cross-fertilization is the norm, although viable larvae have been produced by self-fertilization in isolated individuals of two European species (Gee and Brinley-Williams 1965). Self-fertilization produces low numbers of viable larvae as compared with the number of progeny produced by cross-fertilization (Gee and Brinley-Williams 1965). The readiness to self-fertilize and the degree of viability of larvae produced appears to vary from species to species (Gee and Brinley-Williams 1965). The Spirorbinae are gregarious and specific as to types of substrata where they settle; their larvae hatch in the vicinity of a suitable settlement site and promptly metamorphose, reducing the pelagic dispersal phase to a minimum. Viability is almost totally lost if metamorphosis does not occur within 24 hours of hatching (Gee 1963).

The reproductive features cited above would appear to discourage the dispersal of species to different geographic areas. Although the larval pelagic phase is short, adults or groups of adults may be rafted from one land mass to another. The rich serpulid fauna attached to the undersides of boats, coconuts, driftwood, and other floating debris supports the hypothesis of Allen (1953) that drifting is an important means of dispersal in this family of tube worms.

Although the Spirorbinae may have a short pelagic life, other serpulids have a pelagic development more typical of polychaetes. Gametes of the serpuline *Hydroides norvegica* are shed into the water, and larvae develop over an 8 to 10 day period, during which they are actively feeding (Wisely 1958).

Hawaiian polychaetes mostly are either cosmopolitan or Indo-Pacific in origin, with only four species known to be endemic to the islands (Hartman 1966). The number of endemics (Appendix 3) among Hawaiian polychaetes is uncertain in view of the numerous Pacific islands from which polychaetes have not been collected and the vastness of the Pacific Ocean. The Hawaiian faunal area includes the Hawaiian Islands and Johnston Atoll and is regarded as the eastern boundary of the tropical Indo-West-Pacific; but the polychaete fauna does show some similarities with the eastern Pacific (Appendix 3). Four serpulids known from Hawaii have also been recorded from the eastern Pacific: *Protula atypha* and *Hydroides crucigera* from California; *Protolaeospira translucens* and *Spirorbis marioni* from the Galápagos; and *S. marioni* from Easter Island (Kohn and Lloyd 1973*b*). Of the remaining species, 16 are cosmopolitan, 12 are known from the Indo-West-Pacific region, and 8 from the Atlantic and other areas.

The report of the ecology and distribution of Hawaiian tubiculous polychaetes presented here is far from complete. Further habitat-intensive studies and investigations of the biology of individual species will greatly add to our knowledge of these tubicolous families in the Hawaiian Islands.

ACKNOWLEDGMENTS

My thanks to everyone who assisted with collecting polychaetes, including R. E. Brock on Oahu, Maui, Molokini, and Hawaii; J. A. Brock on Johnston Island; J. Lenic on Maui; K. Thomas on Oahu; and Dr. D. Bonar for larvae from plankton tows. For advice on polychaete systematic problems, I am grateful to Dr. J. H. Day, Capetown University; the late Dr. Olga Hartman, and Dr. K. Fauchald, Allan Hancock Foundation; Dr. H. A. ten Hove, Utrecht; Dr. and Mrs. E. W. Knight-Jones, University College of Swansea, South Wales; and Dr. H. Zibrowius, Endoume, Marseille. The algae were identified by Dr. K. Mshigeni and B. Allender. British Museum type specimens were kindly loaned by Dr. J. D. George. I am grateful to the University of Hawaii for two biomedical support grants, 1969–1971, which facilitated sampling on the outer islands and the purchase of equipment. Richard E. Brock and Drs. E. Alison Kay, Alan J. Kohn, and Michael G. Hadfield made helpful comments on the preparation of the manuscript.

APPENDIX 1

COMPLETE LIST OF STATIONS IN THE HAWAIIAN ISLANDS FROM WHICH POLYCHAETES WERE COLLECTED

OAHU

1. Leeward (northwest to southwest): Pokai Bay, Maile Point, Nanakuli—living coral and rubble; Barber's Point —limestone bench.
2. Pearl Harbor: harbor, Fort Kamehameha—reef flat.
3. Sand Island: Honolulu Harbor entrance—harbor; Keehi Lagoon—marina, reef flat.
4. Waikiki: Ala Moana reef—reef flat; Kewalo Basin—harbor; Kewalo reef—reef flat; Ala Wai Yacht Harbor—marina; Fort DeRussy reef—reef flat; Waikiki Aquarium—dredged reef flat; Waikiki (15–20 m)—living coral and rubble; Black Point—basalt beach.
5. Ala Wai Canal—shallow, brackish.
6. Paiko Lagoon: lagoon—sandy-mud (now a housing development); Beach Park—reef flat.
7. Kaneohe Bay: Mokolii Island—basalt beach; North Bay sector—reef flat, algae and coral; Rubble Island—reef flat; Checker reef—reef flat, algae and coral; Mokuoloe Reef (Coconut Island)—reef flat, algae and coral; Mokuoloe Lagoon—small boat harbor, algae; Southern Bay reefs—reef flat and algae.
8. Dredged serpulids: Dredged from 200–600 m at 21°9.6′; 157°25.1′ W and 20°51.6′ N; 157°19.3′ W. Off Ewa, at 200 m.

MAUI

9. Kahului: harbor—basalt.
10. Kealia: pond—brackish, inland pond.
11. Maalaea Bay: shallow—subtidal bench; deep (17–20 m)—living coral and rubble; Maalaea Harbor—marina; McGregor Point—bench.
12. Cape Kinau: Ahihi Bay—living coral and rubble; Ahihi intertidal rock beach; anchialine lava ponds—brackish.
13. Molokini Island: shallow (7 m)—living corals; deep (17–23 m, leeward)—living coral.

HAWAII

14. Kawaihae: Mahukona—lava, intertidal; Kawaihae—living coral; Puako—lava, intertidal; Lahuipuaa—lava rock and living coral.
15. Anaehoomalu: Anaehoomalu Bay—limestone bench and living coral; Waiulua Bay—lava beach.
16. Makalawena: tidepools—lava; shallow rock bench and living coral; deep (17–30 m)—living coral and rubble; Kiholo—rock bench, coral and brackish ponds.
17. South Kona: Kaloko—brackish pond and living coral; Honokohau Harbor—marina; Kailua—living coral; Keahole Point—lava bench; Keahou—rock beach; Honaunau—lava bench; Hookena—lava bench.
18. Hilo: Hilo Bay (Vine 1972*a*)—boat harbor and bay.
19. Onekahakaha: tidepool—bench, shoal inlet, lava.
20. Kapoho: bench and living coral.
21. South Point: Kapua—lava bench; Waialua—lava bench.

JOHNSTON ATOLL

22. North Island: coral rubble, subtidal.
23. Johnston Island: coral rubble, subtidal.

APPENDIX 2

DISTRIBUTION OF TUBICOLOUS POLYCHAETES IN THE HAWAIIAN ISLANDS ACCORDING TO HABITAT

TAXA	ROCKY INTER-TIDAL	REEF FLATS	LIVE SUB-STRATA	EPIFAUNA OF MOBILE SUB-STRATA	BOAT HARBORS AND LAGOONS	ANCHIA-LINE LAVA PONDS	BRACK-ISH WATERS	REEF SLOPE TO 600 m	JOHNSTON
Spionidae									
Spiophanes bombyx						C□			
Chaetopteridae									
Mesochaetopterus sagittarius	C	A							
Phyllochaetopterus socialis		C							
P. verrilli	C	A							
Chaetopterus sp.		A	A(D)						
Cirratulidae									
Cirriformia punctata			P						
C. hawaiensis		C							
C. semicincta		C				C□			
Sabellariidae									
Lygdamis indicus	C	C							
Phalacrostemma setosa								C	
Terebellidae									
Lanice conchilega					A			C	
Thelepus setosus	A	C							
Nicolea gracilibranchis	P								
Terebella lapidaria					P				
Sabellidae									
Branchiomma nigromaculata					A				
Branchiomma sp.	P								
Sabellastarte sanctijosephi		C		P	A				
S. punctata	P							P	
Serpulidae									
Pomatoleios kraussii	A	A		C	A				
Spirobranchus giganteus			C					C	
S. latiscapus								E	
Hydroides norvegica		A	C(D)	C	A		A	C	
H. lunulifera		A		C	A			C	
H. crucigera		P		P	P			C	
H. brachyacantha								P	
Mercierella enigmatica							A		
Serpula vermicularis				P	C			C	
Pseudovermilia occidentalis	C	A	C(D)			C○			
Vermiliopsis torquata	P	P			C	C○		C	
V. infundibulum								E	
V. multicristata								E	
Protula atypha	A	C		P	C	C○		C	
Salmacina dysteri	C	C	C(D)		A	C□		C	
Spirorbinae									
Protolaeospira translucens	P			C				C	
Spirorbis marioni	A	C	P(D)						
Pileolaria militaris		C		C	A	A○		C	
P. semimilitaris					C				
P. pseudomilitaris	A	A	C(D)	C	A	A○		A	C
P. koehleri		C	C(D)	P		C○			C
P. dalestraughanae								C	
Janua pegenstecheri	C				C			C	
J. pseudocorrugata	C	A		C	C			C	C

APPENDIX 2 (*cont.*)

TAXA	ROCKY INTER-TIDAL	REEF FLATS	LIVE SUB-STRATA	EPIFAUNA OF MOBILE SUB-STRATA	BOAT HARBORS AND LAGOONS	ANCHIA-LINE LAVA PONDS	BRACK-ISH WATERS	REEF SLOPE TO 600 m	JOHNSTON
Janua foraminosa		A	C(D,Ac) A(Ca)	C	A	A□		C	C
J. preacuta			P(D)	C	C	C○		C	
J. nipponica	C		C(D)	C		P○ C□			
J. knightjonesi	A	C	A(V)	P		A○			
Eulaeospira orientalis	C		C(D)		C				

NOTE: A, abundant (50+ per initial search); C, common (10–50 per initial search); P, present (less than 10 per initial search); E, exclusively deep water (200–600 m); (D), *Dictyosphaeria cavernosa*; (V), *Valonia aegagropila*; (Ac), *Acanthophora* sp.; (Ca), *Caulerpa*; □, pools without surface connections; ○, pools connected to the ocean.

APPENDIX 3

AUTECOLOGICAL DESCRIPTIONS OF SPECIES AND THEIR GEOGRAPHICAL DISTRIBUTION

SPIONIDAE: *Spiophanes bombyx* (Claparède)—burrowing in mud of coastal brackish fish ponds; Kona, Hawaii; cosmopolitan (15).

CHAETOPTERIDAE: *Mesochaetopterus sagittarius* (Claparède)—reef flats and subtidal sandy areas; Indo-West-Pacific (northern Australia, Japan, southern Africa, Mozambique) (2–4, 7, 19, 21). *Phyllochaetopterus socialis* Claparède—near shore in muddy estuarine or lagoon conditions; pan-tropical (6). *P. verrilli* Treadwell—attached to hard substrata, including rocks, coral rubble, and algae in shallow water; Pacific (4, 7, 18, 21). *Chaetopterus* sp.—on the alga *Dictyosphaeria cavernosa* and coral rubble (4, 7).

CIRRATULIDAE: *Cirriformia punctata* (Grube)—associated with empty tubes of *Chaetopterus* sp. in Kaneohe Bay; body light gray, conspicuously speckled with black, tentacles and branchiae with blue bands; one specimen was associated with five, blue-banded brittle stars, *Ophiactis savigni*, which are often present within the tube; tropical to subtropical (7). *C. hawaiensis* Hartman—in shallow lagoon areas of mud or fine sand deposits; Hawaiian Islands (6). *C. semicincta* (Ehlers)—in shallow water and in marine fish ponds. Indo-Pacific (7, 11).

SABELLARIIDAE: *Lygdamis indicus* Kinberg—hard, sand-grain tubes on the undersides of rocks and coral rubble in the intertidal and shallow waters; tropical Indo-West-Pacific (1, 5, 15). *Phalacrostemma setosa* (Treadwell)—from depths between 200–600 m; endemic (8).

TEREBELLIDAE: *Lanice conchilega* (Pallas)—subtidal to 30 m in coral rubble or under rocks, numerous in localized areas; Atlantic, Mediterranean, eastern Pacific (1, 3, 7, 11, 15–17). *Thelepus setosus* (Quatrefages)—intertidal and subtidal, on the undersides of rocks and in crevices; cosmopolitan (7, 11). *Nicolea gracilibranchis* (Grube)—on the undersides of rocks and in the crevices of beach rock in shallow water; Indo-Pacific (15). *Terebella lapidaria* Linnaeus—in tide pools and under rocks in the intertidal; cosmopolitan (14, 17).

SABELLIDAE: *Branchiomma nigromaculata* (Baird)—abundant on hard substrates, piers, buoys, and floating docks in relatively calm waters; tropical Indo-West-Pacific (3–5, 7, 20). *Sabellastarte sanctijosephi* (Gravier)—in calm waters of harbors and marinas, along the edges of reef pockets, in dredged areas; tubes may protrude from crevices in the rock or from between large boulders; Indo-West-Pacific, Red Sea, western Africa (2–4, 7). *S. punctata* Treadwell—in calm waters, deep tide pools, and down to 10 m; less abundant than *S. sanctijosephi*; endemic (1, 11, 13).

SERPULIDAE: *Pomatoleios kraussii* (Baird)—dominant intertidal species not found below low tide; widely distributed through the tropical Indo-West-Pacific (2–4, 6, 7, 9, 17, 18). *Spirorbranchus giganteus* (Pallas)—subtidal, associated with living coral heads; circumtropical (1, 7, 11, 14, 20). *S. latiscapus* Marenzeller—dredged from 200–600 m; tube and animal salmon pink; Indo-West-Pacific (8). *Hydroides norvegica* (Gunnerus)—a dominant fouling organism in shallow subtidal areas, especially near docks and harbors; cosmopolitan (2–5, 7, 18). *H. lunulifera* Clàparede—often with *H. norvegica* in nearshore areas; cosmopolitan, restricted to warm seas (2–7, 18). *H. crucigera* Mörch—less common than *H. norvegica* and *H. lunulifera*; on rubble, subtidally; southern California, Mexico (1–4, 7). *H. brachyacantha* Rioja—this species has not been found by the author and is probably rare in the islands; the single specimen deposited in the Bernice P. Bishop Museum was collected by R. W. Hiatt from Halape, Hawaii, in 1946; western Mexico, eastern Australia (4, 7). *Serpula vermicularis* Linnaeus—subtidal, relatively uncommon; cosmopolitan (1–4, 7, 18). *Mercierella enigmatica* Fauvel—brackish waters; temperate to tropical distribution (2, 4–6, 21). *Pseudovermilia occidentalis* (McIntosh)—intertidal under coral rubble and in shallow waters; warm seas (1, 4, 7, 12–14, 16). *Vermiliopsis torquata* Treadwell—reef flats and shallow waters free of silt; endemic (1–4, 6, 7, 12, 14). *V. infundibulum* Philippi—at depths of 200–600 m; cosmopolitan (8). *V. multicristata* (Philippi)—at depths below 200 m; identification based on tubes only (8). *Salmacina dysteri* (Huxley)—from shallow depths to 200–600 m; cosmopolitan in warm seas (2, 4, 5, 7, 8, 12, 13, 15–17, 19). *Protula atypha* Bush—intertidal and shallow seas, especially common where there is a freshwater influence; recorded from California (1–4, 7, 12–19, 21). *Protolaeospira translucens* Bailey & Harris—shallow subtidal, on shells or crustacean carapace; uncommon; Galápagos and Hawaiian islands (3, 4, 7, 12, 15). *Spirorbis marioni* (Caullery & Mesnil)—shallow water, often on lava rock; California, Galápagos, Easter Island, Caribbean (1, 7, 14–19, 21). *Pileolaria militaris* Claparède—in shallow waters, often in harbors; cosmopolitan in warm seas (2–4, 7, 11, 12, 17). *P. semimilitaris* Vine—in nearshore waters; endemic (7). *P. pseudomilitaris* (Thiriot-Quiévreux)—intertidal and subtidal, abundant on any available hard surfaces; Mediterranean, Caribbean (2–4, 6, 7, 9, 12–19, 21, 23). *P. koehleri* (Caullery & Mesnil)—subtidal from shallows to depths of 20 m; cosmopolitan in warm seas (1, 4, 7, 12–17, 20–22). *P. dalestraughanae* Vine—at depths of 20–200 m; Cape Verde, southern Africa (1, 4, 8). *Janua pagenstecheri* Quatrefages—subtidal, not as common in the Hawaiian Islands as compared with other regions; cosmopolitan (4, 7, 14–17). *J. pseudocorrugata* (Bush)—shallow, calm waters; Atlantic, Mediterranean, southern Australia (1, 3, 4, 7, 15–18, 21, 22). *J. foraminosa* Bush—on algae and hard substrata on the reef and in protected harbors and lagoons; Indo-West-Pacific (1, 3, 4, 6, 7, 11, 12, 14, 16, 17, 23). *J. preacuta* Vine, 1972*b*—subtidal to depths of 25 m on hard substrata; Red Sea and Hawaii; previously described as *J. turrita* (Vine, 1972*a*) (4, 7, 11–13, 17, 18). *J. nipponica* Okuda—subtidal marine areas; Japan and southern Africa (1, 4, 7, 12, 14–16, 19). *J. knightjonesi* (de Silva)—intertidal, most abundantly on lava shoreline, Kona, Hawaii; pantropical (7, 12, 14–17, 19, 21). *Eulaeospira orientalis* (Pillai)—shallow water on rock, algae, and harbor structures; Red Sea, Ceylon, Pacific (7, 15, 17).

NOTE: Numerals in parentheses refer to places where collections were made and types of areas collected as described in Appendix 1.

LITERATURE CITED

ALLEN, F. E. 1953. Distribution of marine invertebrates by ships. Aust. J. Mar. Freshwater Res. 4: 307–316.

BAILEY, J. H. 1969. Methods of brood protection as a basis for the reclassification of the Spirorbinae (Serpulidae). J. Linn. Soc. London, Zool. 48: 387–407.

———. 1970. Spirorbinae (Polychaeta) from the West Indies. Stud. Fauna Curaçao 32: 58–81.

BAILEY-BROCK, J. H. 1972. Deepwater tube worms (Polychaeta, Serpulidae) from the Hawaiian Islands. Pac. Sci. 26(4): 405–408.

BAILEY, J. H., and M. P. HARRIS. 1968. Spirorbinae (Polychaeta: Serpulidae) of the Galapagos Islands. J. Zool. 155: 161–184.

BANNER, A. H., and J. H. BAILEY. 1970. The effects of urban population upon a coral reef system. A preliminary report. HIMB Tech. Rep. 25. University of Hawaii, Hawaii Institute of Marine Biology, Kaneohe, Hawaii. 66 pp.

BOWERS, R. L. 1965. Observations on the orientation and feeding behavior of barnacles associated with lobsters. M.S. Thesis. University of Hawaii, Honolulu.

CRISP, D. J., J. H. BAILEY, and E. W. KNIGHT-JONES. 1967. The tube worm *Spirorbis vitreus* and its distribution in Britain. J. Mar. Biol. Assoc. U.K. 47: 511–521.

DAY, J. H. 1967. A monograph of the Polychaeta of southern Africa. Part 1. Errantia. Part 2. Sedentaria. British Museum (Natural History), London. 2 vols., 878 pp.

EBBS, N. R. 1966. The coral-inhabiting polychaetes of the northern Florida reef tract. 1. Aphroditidae, Polynoidae, Amphinomidae, Eunicidae, and Lysaretidae. Bull. Mar. Sci. Gulf Caribb. 16(3): 485–555.

EDMONDSON, C. H., W. K. FISHER, H. L. CLARK, A. L. TREADWELL, and J. A. CUSHMAN. 1925. Marine zoology of the tropical central Pacific. Bull. Bernice P. Bishop Mus. 27. 148 pp.

FAGER, E. W. 1964. Marine sediments: effects of a tube-building polychaete. Science 143: 356–359.

FISCHER-PIETTE, E. 1937. Sur la biologie du serpulien d'eau saumâtre *Mercierella enigmatica* Fauvel. Bull. Soc. Zool. Fr. 62: 197–208.

GEE, J. M. 1963. Pelagic life of *Spirorbis* larvae. Nature (London) 198 (4885): 1109–1110.

———. 1964. The British Spirorbinae (Polychaeta: Serpulidae) with a description of *Spirorbis cuneatus* sp. n. and a review of the genus *Spirorbis*. Proc. Zool. Soc. London 143(3): 405–441.

GEE, J. M., and G. BRINLEY-WILLIAMS. 1965. Self- and cross-fertilization in *Spirorbis borealis* and *S. pagenstrecheri*. J. Mar. Biol. Assoc. U.K. 45: 275–285.

GEE, J. M., and E. W. KNIGHT-JONES. 1962. The morphology and larval behaviour of a new species of *Spirorbis* (Serpulidae). J. Mar. Biol. Assoc. U.K. 42: 641–654.

GOSLINE, W. A. 1955. The inshore fish fauna of Johnston Island, a central Pacific atoll. Pac. Sci. 9(4): 442–480.

HARRIS, T. 1970. The occurrence of *Manayunkia aestuarina* (Bourne) and *Mercierella enigmatica* Fauvel (Polychaeta) in non-brackish localities in Britain. J. Exp. Mar. Biol. Ecol. 5: 105–112.

HARRIS, T., and E. W. KNIGHT-JONES. 1964. *Spirorbis infundibulum* sp. nov. (Polychaeta: Serpulidae) from *Tenarea* shelves on the Costa Brava. Ann. Mag. Nat. Hist. 7(13): 347–351.

HARTMAN, O. 1966. Polychaetous annelids of the Hawaiian Islands. Occas. Pap. Bernice P. Bishop Mus. 23(11): 163–252.

HARTMANN-SCHRÖDER, G. 1971. Zur Unterscheidung von *Neopomatus* Pillai und *Mercierella* Fauvel (Serpulidae, Polychaeta). (Mit neuen Beiträgen zur Kenntnis der Ökologie und der Röhrenform von *Mercierella enigmatica* Fauvel). Mitt. Hamb. Zool. Mus. Inst. 67: 7–27.

HIATT, R. W., and D. W. STRASBURG. 1960. Ecological relationships of the fish fauna on coral reefs on the Marshall Islands. Ecol. Monogr. 30: 65–127.

HILL, M. B. 1967. The life cycles and salinity tolerances of the serpulids *Mercierella enigmatica* Fauvel and *Hydroides uncinata* (Philippi) at Lagos, Nigeria. J. Anim. Ecol. 36: 303–322.

KNIGHT-JONES, E. W., J. H. BAILEY, and M. J. ISAAC. 1971. Choice of algae by larvae of *Spirorbis*, particularly of *Spirorbis spirorbis*. Pages 89–104 *in* D. J. Crisp, ed. Fourth European marine biology symposium. At the University Press, Cambridge.

KNIGHT-JONES, P., E. W. KNIGHT-JONES, C. H. THORP, and P. W. G. GRAY. 1975. Immigrant spirorbids (Polychaeta Sedentaria) on the Japanese *Sargassum* at Portsmouth, England. Zool. Scr. 4: 145–149.

KOHN, A. 1959. The ecology of *Conus* in Hawaii. Ecol. Monogr. 29: 47–90.

KOHN, A., and M. C. LLOYD. 1973*a*. Polychaetes of truncated reef limestone substrates on eastern Indian Ocean coral reefs: diversity, abundance and taxonomy. Int. Revue Gesamten Hydrobiol. 58(3): 369–399.

———. 1973*b*. Marine polychaete annelids of Easter Island. Int. Revue Gesamten Hydrobiol. 58(5): 691–712.

MACIOLEK, J. A., and R. E. BROCK. 1974. Aquatic survey of the Kona Coast ponds, Hawaii Island. UNIHI-SEAGRANT-AR-74-04. Sea Grant College Program, University of Hawaii, Honolulu. 73 pp.

MARSDEN, J. R. 1962. A coral-eating poly chaete. Nature (London) 193: 598.

MILLER, A. 1974. A comparison of gastropod species diversity and trophic structure in the rocky intertidal zone of the temperate and tropical west Americas. Ph.D. Dissertation. University of Oregon, Eugene. 143 pp.

SCOFFIN, T. P. 1972. Fossilization of Bermuda patch reefs. Science 178: 1280–1282.

SEURAT, L.-G. 1927. Sur la présence d'une serpule *Mercierella enigmatica* Fauvel, dans une rivière de la Tunisie. C. R. Acad. Sci. 185(10): 549–550.

STRAUGHAN, D. 1969*a*. Serpulidae (Annelida: Polychaeta) from Oahu, Hawaii. Bull. South. Calif. Acad. Sci. 68(4): 229–240.

———. 1969*b*. Intertidal zone—formation in *Pomatoleios kraussii* (Annelida: Polychaeta). Biol. Bull. (Woods Hole, Mass.) 136(3): 469–482.

———. 1972. Ecological Studies of *Mercierella enigmatica* Fauvel (Annelida: Polychaeta) in the Brisbane River. J. Anim. Ecol. 41: 93–136.

TREADWELL, A. L. 1906. Polychaetous annelids of the Hawaiian Islands, collected by the steamer "Albatross" in 1902. Bull. U.S. Fish Comm. 23: 1145–1181.

VINE, P. J. 1972*a*. Spirorbinae (Polychaeta, Serpulidae) of the Hawaiian Chain. Part 1. New species. Pac. Sci. 26(2): 140–149.

VINE, P. J. 1972*b*. Spirorbinae (Polychaeta: Serpulidae) from the Red Sea, including descriptions of a new genus and four new species. J. Linn. Soc. London, Zool. 51: 177–201.

VINE, P. J., J. H. BAILEY-BROCK, and D. STRAUGHAN. 1972. Spirorbinae (Polychaeta, Serpulidae) of the Hawaiian chain. Part 2. Hawaiian Spirorbinae. Pac. Sci. 26(2): 150–182.

VUILLEMIN, S. 1965. Contribution à l'étude écologie du lac de Tunis. Biologie de *Mercierella enigmatica* Fauvel. Première thèses pour Docteur-des-Sciences Naturelles, Université de Paris, sér. A, no. 4622, no. d'ordre 5469.

WISELY, B. 1958. The development and settling of a serpulid worm, *Hydroides norvegica* Gunnerus (Polychaeta). Aust. J. Mar. Freshwater Res. 9(3): 351–361.