STUDIES ON THE FAUNA OF CURAÇAO AND OTHER CARIBBEAN ISLANDS: No. 129.

SPIONIDAE (POLYCHAETA) OF THE GULF OF MEXICO AND THE CARIBBEAN SEA

by

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INTRODUCTION

History

Although there have been several collections of polychaetous annelids from the Gulf of Mexico and Caribbean Sea, very few spionids have been included in the published species lists. This is not because they are poorly represented in this area but probably a result of their small size and the fact that they are easily overlooked both in collecting and in sorting of samples. It is also probable that their small size renders them an unpopular group with which to work. Very few spionids were reported from collections of the early large scale collecting cruises. This can be, at least in part, attributed to the fact that they are more common in littoral habitats than in deeper waters.

Schmarda (1861) reported three species as a result of his world cruise (1853–57) during which he visited several Caribbean Islands. Treadwell (1901, 1931a + b, 1939a, 1939b) reported only three species and this included his treatment of the annelids collected during the Scientific Survey of Puerto Rico and the Virgin Islands. Other contributions include works by Augener (1906, 1927, 1933), Horst (1922), Kavanagh (1940) and Behre (1950). Hartman (1951) reported on a collection of littoral polychaetes from the Gulf of Mexico. The latter included what is probably the largest number of spionids dealt with in a single study up to that time. Twelve species were reported, most of which represented new records. Later, small papers were contributed by Carpenter (1956) from the north-

ern Gulf, FRIEDRICH (1956) from Central and South America and WESENBERG-LUND (1958) from the Lesser Antilles. Finally in 1962, JONES reported on a collection of polychaetes from Jamaica which included two spionid species.

Although few spionids have been reported in faunal studies from the Gulf of Mexico and Caribbean, many authors have dealt with this family systematically. McINTOSH (1909, 1914, 1915b) dealt specifically with British spionids. His papers, however, are occasionally quite confusing and the species discussed are often indeterminable. CHAMBERLIN (1919) presented a workable key for the then known spionid genera. The most useful monographic works are those by MESNIL (1896, 1925) and SÖDERSTRÖM (1920).

FAUVEL (1927) treats the Spionidae in his monographic work on the polychaetes of France. He presents a good generic key, although it only includes eleven genera.

OKUDA (1937a) dealt with spioniform polychaetes (Spionidae, Magelonidae, Oweniidae) from Japan. A later paper by HARTMAN (1941) was concerned with California spionids and treated some fourteen species, with observations on reproductive biology in a few species. PETTIBONE (1963) revised the spionid genera characterized by branchiae and pointed prostomia and branchiae and frontal horns. In addition to the above, there have been innumerable papers dealing with selected genera in this family. The majority of these can be found in the synonymies included in the present paper.

HARTMAN (1966) summarized what was known about Antarctic spionids and reported twenty-three species. DAY (1967) included the spionids in a monograph of South African polychaetes and presented a generic as well as species key.

The present study is primarily a faunal study of spionids of the Gulf of Mexico and Caribbean Sea. It is obvious from the literature survey that this area is virtually unstudied with regard to its spionid fauna yet this family is usually one of the most abundant in benthic communities. With the increasing amount of ecological work being done in the study area, the lack of knowledge concerning this group will become more and more significant. The present work represents a starting point toward filling this gap. In spite of the fact that numerous papers have been written dealing with spionids, a great deal of confusion exists at the generic level. It has become increasingly apparent that a faunal study of a group is impractical unless the systematics of that group are well-defined. This study, therefore, has become somewhat more than a strict faunal survey and, of necessity, includes considerations of species outside the study area to insure more significance to later faunal studies. The present collections represent by no means the entire spionid

fauna in the Gulf and Caribbean. They are comprised of littoral samples collected by the author and those solicited from other workers. The latter often included samples of a single specimen. The species herein reported probably represent no more than one-third of those actually present in the study area. Twenty-six species, including sixteen genera, are described and figured. This includes four new species and the revision of the genus *Prionospio* to include three new genera.

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General Taxonomic Characters of the Spionidae

Spionids fall within that group of polycheates often designated collectively as the subclass Sedentaria; however, the classification of polychaetes in the subclasses Sedentaria and Errantia quickly breaks down when one considers individual species. There do not seem to be any definite characters by which the two "subclasses" can be consistently separated. The family Spionidae represents a group of poly-

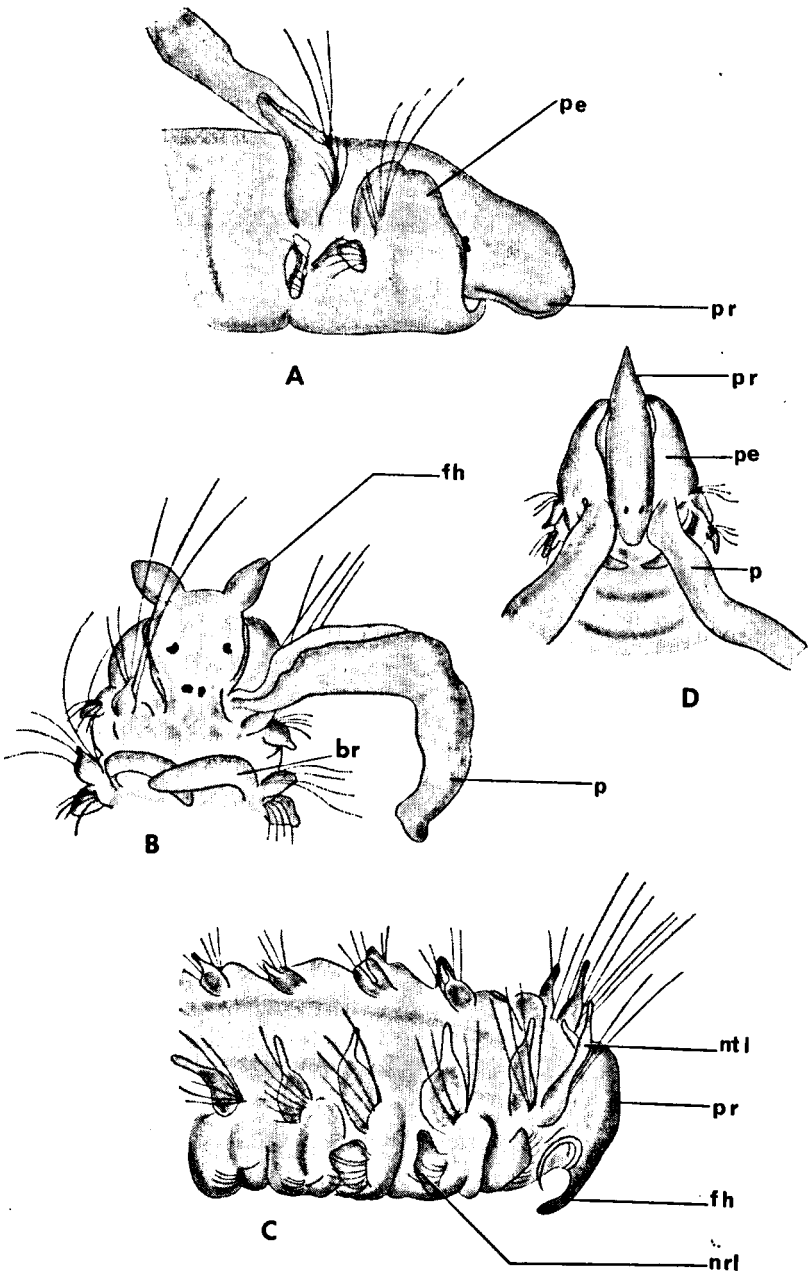

PLATE 1. – A. Anterior end of *Prionospio*, third and subsequent parapodia omitted. – B. Anterior end of *Malacoceros* (*Rhynchospio*), third and subsequent parapodia omitted. – C. Anterior end of *Spiophanes*. – D. Anterior end of *Scolelepis*, second and subsequent parapodia omitted. – pr = prostomium, pe = peristomium, ntl = notopodial lamella, nrl = neuropodial lamella, p = palp, fh = frontal horn, br = branchia.

chaetes which does not exhibit most of the typical characters of the Sedentaria. The following is a typical diagnosis of Sedentaria as a subclass. The spionid deviations will become obvious later in this discussion and, because of these inconsistencies, Sedentaria and Errantia are not recognized as formal taxa, but merely as generic terms in general language to indicate the two ends of a continuum representing progression from the more primitive errant forms to the more highly specialized sedentary forms.

Sedentaria (USHAKOV, 1965, p. 3)

"Body segments as a rule dissimilar. Body divided into distinct sections (thorax, abdomen and sometimes pygidium). Prostomium secondarily modified and often reduced. Pharynx lacking jaws. Parapodia usually with shortened parapodial lobes in the form of transverse tori bearing one or more rows of uncini (tori uncinigeri). Dorsal and abdominal cirri usually reduced. In most instances, nephridia developed in anterior segments only. The majority of species inhabiting sessile (adnate) or free tubes."

The following discussion describes the Spionidae with regard to those characters most commonly used in polychaete systematics.

Prostomium (Pl. 1A–D)

The spionid prostomium is a ridge which may be tapered posteriorly and/or anteriorly. Anteriorly it may be tapered, blunt, snoutlike, bifurcate or T-shaped, with the anterior edges extended laterally as frontal horns. The prostomium terminates at the level of the first setiger or extends for a variable number of setigers as an elongate, raised keel. Spionids do not possess true prostomial tentacles or antennae, but in certain genera there may be a short fingerlike occipital tentacle or nuchal papilla. Eyes may or may not be present; if present, there may be one to three pairs or, in some instances, a cluster on either side of the head. The presence, absence, and arrangement of eyes are not good systematic characters although they have often been considered as such. The eyes are often deeply embedded in the tissue and not easily seen. In some cases they are present in larvae and juveniles but absent in adults, causing confusion in identification.

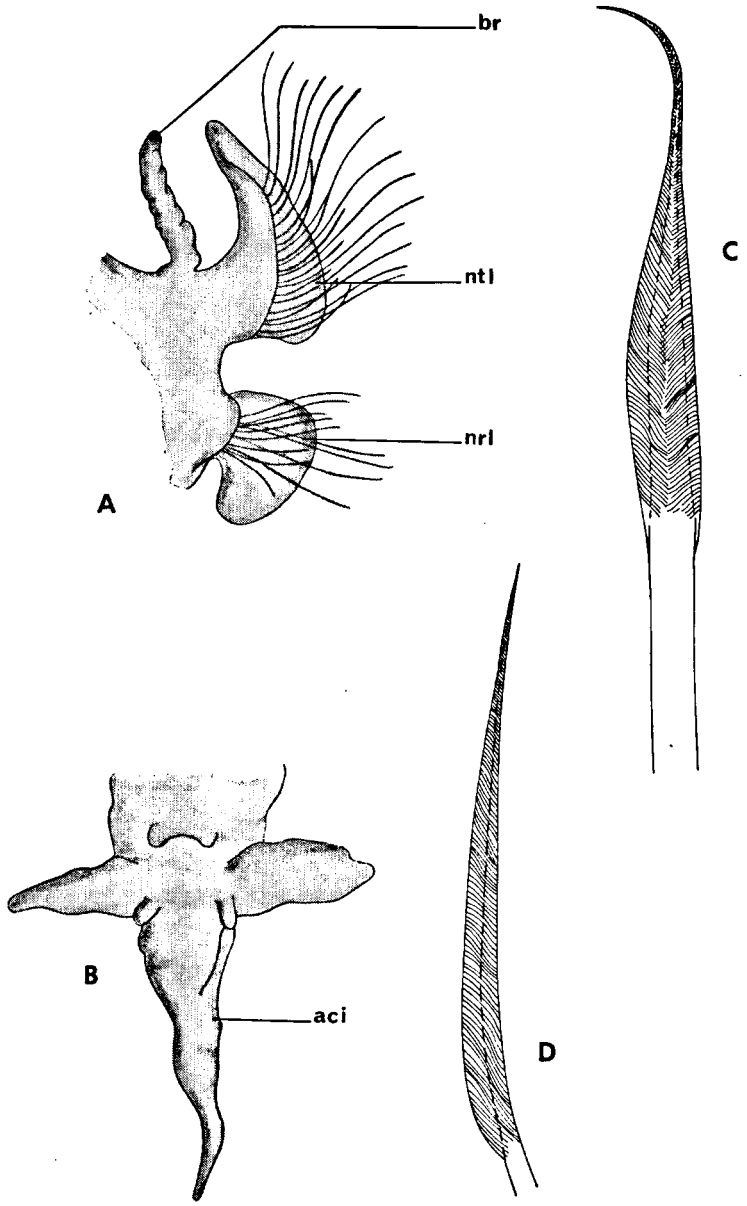

PLATE 2. – A. Parapodium of *Prionospio*. – B. Pygidium of *Prionospio*. – C. Capillary seta of *Sabella microphthalma*. – D. Capillary seta of *Lumbrineris gilisfra*. – br = branchia, ntl = notopodial lamella, nrl = neuropodial lamella, aci = anal cirri.

Peristomium

The peristomium generally projects forward ventrally beneath the prostomium as a "lower lip." It surrounds the prostomium laterally and the sides may be drawn up and out to form wings. This character is developed to a varying degree in the different genera. Spionids are characterized by the presence of a pair of long, coiling palpi inserted on the peristomium on either side of the prostomium. They are extensible, mobile and bear a median ciliated groove. The palpi are chemoreceptors for food detection and capture. They are quite deciduous and rarely present on preserved specimens.

Body Regions

The body cannot be clearly separated into thorax and abdomen, as in the typical Sedentaria. There are, however, changes in setal characters, in the shape of the parapodial lamellae and sometimes in branchial development. The body wall becomes thinner in the "posterior" region and preserved specimens are often fragmented at this point.

Pygidium (Pl. 2B)

The pygidium is the posterior-most structure on the body. The diameter of the body narrows considerably several segments in front of the pygidium, *i.e.*, the growth zone. The anus opens through the pygidium which is either drawn out into lobes or cirri and/or a flange or collar. The number and arrangement of these pygidial structures is of considerable taxonomic value.

Parapodia (Pl. 2A)

The first pair of parapodia is often quite small and displaced dorsally. The remaining anterior parapodia are usually larger and bear well-developed pre- and/or postsetal lamellae, their size and development decreasing posteriorly. This change in parapodial character may begin at the end of the branchial region or it may coincide with

setal changes. In the anterior parapodia the notopodial lamellae are larger and better developed than those of the neuropodia, and undergo drastic reductions in the posterior setigers. The neuropodial lamellae generally remain similar, except for decreasing in size, throughout the length of the body and are usually of little consequence in systematics. In posterior setigers the notopodial and neuropodial lamellae are quite often similar in size and appearance.

Setae (Pl. 2C–D)

Anterior notopodial and neuropodial setae are capillaries, with a fairly well-developed sheath or so-called limbation. The setal structure is discussed in detail in another publication (FOSTER, 1971) where it is shown that what have previously been referred to as wings or limbations are, in actual fact, sheaths enclosing the setal shaft. The term "limbation" is retained, however, throughout most of the taxonomic section in order to avoid confusion. Setae of the anterior parapodia are arranged in two rows, the notopodial setae being considerably longer than those of the neuropodium, though resembling them in appearance. In more posterior parapodia, hooded hooks appear in the neuropodia and, in some species, in the notopodia also. The place of appearance and kind of hooded hooks are generally consistent, and these important taxonomic characters are used at both the generic and specific level. In most species a few capillary setae remain throughout the body length. Many spionids possess a heavy recurved neuropodial seta in the ventral-most position of the setal bundle. It is curved downward and generally sheathed. There may be one to three of these "sabre-setae." They appear at or near the parapodia in which the hooded hooks are first present, and they remain throughout the length of the body. Certain genera bear specialized setae in addition to the above, and these are also of taxonomic value. They should not, however, be relied upon to a great extent in systematics since they are sometimes confined to the posterior body region which is very often missing in preserved material.

Branchiae

Number, kind and arrangement of branchiae or gills are of major taxonomic importance. The branchiae may be restricted to a few anterior setigers, extend along the length of the body, or disappear at some point beyond the mid-region of the body. The degree of fusion between the gills and notopodial lamellae is also of systematic value. The branchiae arise at the bases of the notopodia on the dorsal body surface. They may be cirriform or pinnate and may vary in length, number, and arrangement of pinnae within a single species. In certain genera the gills, like the palps, are deciduous and some may be missing in preserved material.

External Sense Organs

Spionids possess ciliated dorsal nuchal organs in the anterior body region. These chemoreceptors may be arranged in either longitudinal rows extending posteriorly from the prostomium for a varying number of segments or in intersegmental bands, running laterally. They may also be present as patches found on either side of the prostomium.

Development

Hannerz (1956) reported three major categories of spionid development. The first category includes those species with entirely pelagic development. Among the larvae of those species the majority can receive nourishment from the yolk only up to the 2–3 segment stage. It, then, feeds on plankton (predominantly planktotrophic). Other larvae, however, are lecithotrophic, and do not ingest any food, but rather are nourished by the yolk until metamorphosis. Development in the latter is apparently more rapid.

The second category of development includes those specimens which develop within structures produced by the female. These may be jellylike stalked structures in which eggs are embedded. The structures are attached to the substrata with no parental care. Another type of structure is the more common capsule which may be

brooded, attached to the wall of the female's tube. Duration of brood protection varies. Adelphophagia has been observed in a few species.

The third category includes spionids in which the young develop within the female body. This may involve either a limited portion of the body in which the soft parts disintegrate or specialized brood pouches not interferring with the normal tissue of the adult.

Poecilogony has been demonstrated in certain species with the obvious advantage of permitting the animal to both extend its range and build up large populations.

Asexual reproduction has been documented in at least one species (RASMUSSEN, 1953).

ECOLOGY AND DISTRIBUTION

Spionids are distributed on a world-wide basis with few endemic species and many cosmopolitan species. They are more common in shallow depths but are well represented even in the deeper submarine canyons. They are most commonly found on muddy and/or sandy beaches but have also been collected from rocky areas, debris, algae, etc.

The spionids have been grouped with various other families to form higher taxa aimed at illustrating something of the evolution within the class Polychaeta. This has differed according to the approach or evolutionary criteria used by the author.

BENHAM (1894) proposed what was perhaps the first grouping of polychaetes above the family level. He divided them into two "grades", the Eucephala and Cryptocephala. The first included four suborders including polychaetes with similar body segments and with the prostomium present as a lobe overlying the mouth, not overgrown by the peristomium. The second grade included two suborders composed of worms with body segments divided into two types and with the prostomium overgrown or concealed by the peristomium. The first suborder of the Cryptocephala is the Spioniformia which included the Spionidae, Magelonidae, Chaetopteridae and Ammocharidae (Oweniidae). BENHAM characterized these families

as all possessing a small prostomium without definite tentacles or palps, a large peristomium bearing tentacles (actually the spionid palps), feebly developed parapodia, no aciculae, simple setae and uncini, no jaws, and when present, dorsal cirri are branchial organs. It is evident from the preceding discussion of spionid characters that this grouping is not completely accurate. It was, however, used off and on by later authors who have continued to refine the diagnosis and to eventually remove the Oweniidae leaving the Spionidae, Magelonidae and Chaetopteridae.

More recently DALES (1963) proposed that evolutionary lines were based on development of feeding types and therefore on stomodaeal structures. On this basis the Magelonidae are removed from the spionid group. Differences between magelonids and spionids include the presence in the former of enucleate corpuscles containing haemerythrin and a balloonlike proboscis forming a sac situated below the esophagus when retracted. According to Dales the spionid line of evolution involves a transition from proboscis sand eating to tentacle feeding with loss of the proboscis. Tentacle innervation is similar in spionids and sabellariids. The sabellariids have adapted the tentacle feeding first found in spionids while the chaetopterids do not use tentacles but have perfected a method of filter feeding. In this family tentacles are used just for aiding in ingestion. Dales points out that the more primitive chaetopterids closely resemble spionids and he placed the Spionidae, Chaetopteridae and Sabellariidae in an order, Spionida. He depicts the spionid line giving rise first to sabellariids and then to chaetopterids.

ORRHAGE (1964a, b) considers the Spionidae, Disomidae and Poicilochaetidae to be closely related on the basis of similarities in the nervous systems. He points out (rightfully so) that SÖDERSTRÖM's (1920) idea of using the nuchal and dorsal organs as phylogenetic indicators is dubious because of the difficulty involved in locating them and in defining their shapes. SÖDERSTRÖM placed Disomidae as a subfamily of Spionidae based on similarities in the eggs. HANNERZ (1956), however, on the basis of larval characters agreed with MESNIL (1897) that the three families should be kept separate. ORRHAGE (1964b) came to the same conclusion after studying similarities and differences in nervous systems, lateral organs, foregut, anterior body

cavities and palpal structures. The latter information indicates almost without a doubt that the three families are very closely related, yet distinct at the family level.

The above conforms with DALES (1963) and I follow his use of the order Spionida as it is defined to include Spionidae, Disomidae, Poicilochaetidae, Longosomidae, Paraonidae, Chaetopteridae and Sabellariidae.

METHODS AND MATERIALS

This study, while based primarily on collections of the National Museum of Natural History, Smithsonian Institution, also includes specimens donated from various individuals. As might be expected, methods of collection, geographic areas represented, and numbers per collection were exceedingly variable and cannot be construed as rigorously characterizing the depth, zoogeography or population density of a given species.

Pencil sketches of the animals were made with the use of a camera lucida. These were subsequently copied onto tracing paper for the plates. Scales used for all figures are lettered A–E. The same lettering is used on all plates and each plate includes only those scales pertaining to figures found on that particular plate. The figure legends indicate to which figures the scales apply.

FAMILY DIAGNOSIS

Family SPIONIDAE Grube, 1850

The body is linear with a variable number of setigers. Body regions are delineated only by changes in parapodial shapes and setal types and arrangements. There are two long, contractile, deciduous, grooved peristomial palpi present on either side of the prostomium. The prostomium is elongate and anteriorly tapered, bifurcate, rounded or blunt and may or may not bear eyes and frontal horns. There are no true antennae but the prostomium may bear an occipital or nuchal papilla. The peristomium surrounds the prostomium and, in certain species, extends laterally in the form of wings. The

cirriform and pinnate branchiae are either present on a limited number of anterior setigers or extend along the length of the body. They are located dorsally at the bases of the notopodia and may be cirriform or pinnate. They are often partially fused to the notopodial lamellae. The parapodia are biramous and without aciculae. Notopodial setae are sheathed capillaries anteriorly and may or may not include posterior hooded hooks. Neuropodial setae are also sheathed capillaries anteriorly but hooded hooks are always present in posterior setigers. In certain genera hooded hooks possess a secondary internal hood. Specialized setae are sometimes present. The pygidium may be drawn out in the form of blunt lobes, digitate cirri and/or a collar or flange. The proboscis lacks teeth and jaws.

Key to Spionid Genera of the Gulf of Mexico and the Caribbean Sea

1a. Fifth setiger modified with enlarged hooks . . . . . *Polydora* Bosc (p. 18)

1b. Fifth setiger not modified. 2

2a. Prostomium pointed, more or less spindle-shaped. Cirriform branchiae present 3

2b. Prostomium not pointed. Branchiae present or lacking . . 6

3a. Branchiae beginning on setiger 1. 4

3b. Branchiae beginning on setiger 2. 5

4a. Branchiae not fused with dorsal lamellae, limited to anterior region of body. Pygidium with anal cirri. With notopodial and neuropodial hooks. . . . . *Aonides* Claparède (p. 65)

4b. Branchiae fused basally with dorsal lamellae, continuing to near posterior end of body. Pygidium with anal collar or cirri. Without notopodial hooks . . . . . *Dispio* Hartman (p. 72)

5a. Ventral lamellae of middle and posterior setigers cleft or bilobed, with smaller ventral lobe . . . . . *Scolelepis* (*Scolelepis*) Blainville (p. 58)

5b. Ventral lamellae entire, not cleft. . . . . *Scolelepis* (*Nerinides* Mesnil)* (p. 59)

6a. Branchiae lacking. With one to two specialized recurved setae on setiger 1 . . . . . *Spiophanes* Grube (p. 40)
6b. Branchiae present at some point along the body 7

7a. Prostomium with distinct frontal horns. 8
7b. Prostomium without frontal horns 10

8a. Cirriform branchiae beginning on setiger 1. With both noto- and neuropodial hooks on posterior setigers . . . . . *Scolecolepides* Ehlers † (p. 37)
8b. Cirriform branchiae beginning on setiger 1 or 2. With neuropodial hooks only 9

9a. Branchiae beginning on setiger 1. . . . . *Malacoceros* (*Malacoceros*) Quatrefages (p. 47)
9b. Branchiae beginning on setiger 2. . . . . *Malacoceros* (*Rhynchospio* Hartman) (p. 48)

10a. Branchiae beginning on setiger 1 and continuing successively for a varying number of segments 11
10b. Branchiae beginning on setiger 2 or later 13

11a. Anterior branchiae partially fused to dorsal lamellae; without notopodial hooks . . . . . *Spio* Fabricius (p. 33)
11b. Branchiae separate from dorsal lamellae, limited to anterior setigers. 12

12a. One pair of branchiae. Peristomium surrounding prostomium as a hood. With large dorsal collar or fold connecting notopodial lamellae of setiger 2 . . . *Streblospio* Webster (p. 112)
12b. Three pairs of branchiae. Peristomium enclosing prostomium, like a hood, with enlarged wings. Without collar on setiger 2 . . . . . *Paraprionospio* Caullery (p. 100)

13a. Branchiae beginning on setiger 2 and continuing for a variable number of setigers 14
13b. Branchiae beginning posterior to setiger 10 or with a small additional pair on the second setiger . . . . . *Pygospio* Claparède (p. 28)

14a. Branchiae both pinnate and cirriform 15
14b. Branchiae pinnate or cirriform only 16

15a. Fourth pair of branchiae pinnate and first three cirriform. . . . . *Apoprionospio* Foster (p. 93)
15b. Pinnate and cirriform branchiae, otherwise . . . . . *Prionospio* Malmgren (p. 80)

16a. Branchiae cirriform only, four to forty pairs. . . . . *Minuspio* Foster (p. 106)
16b. Branchiae pinnate only, two to four pairs. . . . . *Aquilaspio* Foster (p. 105)

*) Previously reported from the Gulf of Mexico but not found in present collections.
†) Collected in present study from Beaufort, North Carolina, but was not found in Gulf and Caribbean collections.

TAXONOMIC SECTION

Genus **Polydora** Bosc, 1802

Polydora Bosc, 1802, p. 151. Type-species: *Polydora cornuta* Bosc, 1802, p. 151. Gender: feminine.

Diplotis Montagu, 1813, p. 203. Type-species: *D. hyalina* Montagu, 1813, p. 203.

Leucodore Johnston, 1838, p. 66. Type-species: *L. ciliatus* Johnston, 1838, p. 67 [= *Polydora ciliata* (Johnston)].

Leipoceras Möbius, 1874, p. 254. Type-species: *Leipoceras uviferum* Möbius, 1874, p. 200 [= *Polydora caeca* (Oersted)].

Dipolydora Verrill, 1881, p. 320. Type-species: *Polydora concharum* Verrill, 1881, p. 320.

Protopolydora Czerniavsky, 1881, p. 360. Type-species: *Polydora hamata* Langerhans, 1880, p. 92 (Homonym of *Polydora hamata* Webster, 1879b, p. 251). [= *Polydora posthamata* Jones].

Pseudoleucodore Czerniavsky, 1881, p. 362. Type-species: *Leucodorum caecum* Oersted, 1844, p. 106 [= *Polydora caeca* (Oersted)].

Pseudopolydora Czerniavsky, 1881, p. 362. Type-species: *Polydora antennata* Claparède, 1870, p. 60.

Carazzia Mesnil, 1896, p. 227. Type-species: *Polydora antennata* Claparède, 1870, p. 60.

Diagnosis: Prostomium anteriorly bluntly rounded or bilobed, extending posteriorly as a more or less well-developed keel. With or without eyes and occipital antenna. Peristomium conspicuous, sometimes "swollen" on preserved specimens. Cirriform branchiae, separate from dorsal lamellae, first present posterior to setiger 5. Setiger 5 more or less enlarged, with stout hooks. Anterior setae all capillary. Neuropodial bidentate hooded hooks first present on setigers 7–14. With or without posterior specialized notosetae. Pygidium glandular and often collar-shaped.

Discussion: The genera of polydorid spionids have been in a state of disorder since Bosc first described the genus *Polydora* in 1802. There is a lack of consistency among polychaete systematists regarding acceptance of valid genera and choice of characters for generic diagnosis with the unfortunate result that there is no *one* arrangement generally accepted. Genera, such as *Boccardia, Carazzia* and *Pseudopolydora*, have on more than one occasion been brought out of synonymy and used as genera or subgenera. HARTMAN (1959) accepts as valid the genera *Polydora, Boccardia* and *Pseudopolydora*. WOODWICK (1964) follows this arrangement with the addition of a new genus *Tripolydora*. He is of the opinion that if one accepts the genus *Boccardia* as valid on the basis of branchial arrangement, then one must also accept *Pseudopolydora* because its fifth setiger is less modified than in *Polydora* and *Boccardia* and its hooks begin on setiger 8 rather than 7. He points out, however, that acceptance of these four genera, based on first appearance of hooks as a distinguishing character, leaves two species, *Polydora commensalis* Andrews, 1891a, and *Polydora citrona* Hartman, 1941, without a generic position. This is because in *P. commensalis* neuropodial hooks first appear on setigers 12–14 and in *P. citrona*, on setiger 10.

In this paper the following three genera are recognized: *Polydora, Boccardia* and *Tripolydora*. I must disagree with the above rationale for retaining *Pseudopolydora* if *Boccardia* is to be retained. It is my opinion that the distribution of branchiae is a more reliable character than first appearance of hooded hooks even though the latter is fairly consistent among polydorids. Another consideration, however, is the taxonomic position of the two above mentioned species. If one accepts WOODWICK's (1964) differentiation of genera, then new genera must be erected for these species. Rather than do that at this time, I prefer to extend this character for the genus *Polydora* so that *P. commensalis* and *P. citrona* are included. DAY (1967) characterizes this genus as possessing hooks from setigers 7–10. USHAKOV (1965) states that the hooks first appear on setiger 7 or 8, but then includes *P. commensalis* in his species key with hooks first present on setiger 12.

The three genera may be distinguished according to Table 1.

TABLE 1

COMPARISON OF GENERA OF POLYDORIDS

Genus	Branchiae	Dentition of neuropodial hooks
Polydora	posterior to setiger 5 absent on setiger 5	bidentate
Boccardia	anterior to setiger 5 absent on setiger 5	bidentate
Tripolydora	anterior to setiger 5 present on setiger 5	tridentate

It should be mentioned that a further problem, yet to be solved, exists with regard to the genus *Polydora*. The type-species *P. cornuta* Bosc (1802) was so insufficiently characterized that it is virtually impossible to distinguish it from several other species in the area of the type locality, Charleston, South Carolina.

Polydora commensalis Andrews, 1891

(Figures 1–12)

Polydora commensalis ANDREWS, 1891a, p. 25. – COWLES, 1930, p. 344. – BERKELEY & BERKELEY, 1936, p. 469; 1952, p. 18. – ANNENKOVA, 1938, p. 178. – HARTMAN, 1941, p. 308; 1945, p. 32. – RIOJA, 1943, p. 229. – HARTMAN & REISH, 1950, p. 28. – USHAKOV, 1955, p. 271; 1965, p. 250. – WELLS & GRAY, 1964, p. 63. – HATFIELD, 1965, p. 356. – SIMON, 1967, p. 420. – BLAKE, 1968, p. 797.

Polydora ?sp.? BERKELEY, 1927, p. 420.

Polydora ciliata brevipalpa ZACHS, 1933, p. 129.

Diagnosis: Palps large, short, conical. Prostomium small, anteriorly rounded or faintly bilobed. Eyes present. Branchiae begin on setiger 6. Bidentate neuropodial hooded hooks first present on setigers 12–14. Anterior notosetae long and thin. Modified hooks of setiger 5 with thin ovoid expansions near pointed tips. Pygidium dorsal, surrounded by erect papillae.

Description: The body length is up to 30 mm, with 70 setigers. The prostomium is concealed by the short, thick palps. In preserved

specimens, when the palps are removed, the prostomium is usually found retracted and partially concealed (Fig. 1). It is usually small and anteriorly rounded. Eyespots are usually present although they are often diffuse pigmented areas.

Cirriform branchiae begin on setiger 6. They are short on only the first one to two branchial setigers and then immediately increase in length so that by setiger 10 they meet or overlap dorsally. Branchiae are very broad, foliaceous, and, on some specimens, the two borders are very thin (Fig. 3). Posterior branchiae are longer and thinner (Fig. 4). Notopodial lamellae of setigers 1–4 are very well-developed, large, thick, erect and bluntly tapered (Fig. 2). They become much smaller on branchial setigers. By setigers 8–9, they are reduced to a hump at the base of the branchiae and by setigers 10–15, they have disappeared (Figs. 3, 4). Neuropodial lamellae are also well-developed on setigers 1–4 (Fig. 2). They become lower and wider until by setiger 13 they are not much more than a ridge with a dorsal subtriangular portion (Fig. 3). They are insignificant in posterior setigers (Fig. 4).

Setae of the first four setigers are all capillary. The long notosetae are thinly unilimbate with heavy striations or "hairlike" appearing sheath, similar to sabellid setae (see below). They may also appear nonlimbate with what may be distal remnants of a frayed sheath (Fig. 5). The shorter notosetae are thinly bi- or unilimbate, with granulations in the area of the heavily striated sheath. The neurosetae are similar (Fig. 6). Neuropodial bidentate hooded hooks first appear on setigers 12–14 and number six per row increasing in some specimens to thirteen to twenty in posterior setigers (Fig. 7).

The modified hooks of setiger 5 are arranged in an oblique row. Some have long, curved, tapered tips (Fig. 8), but this is extremely variable. The shorter hooks are more ventral. Each hook bears a thin lateral curved extension. From the convex side it appears thin and ovoid (Fig. 8) but from the concave side, because of the curvature, it appears almost as a tooth (Figs. 9, 10, 11). Ventral to the row of hooks is a small bundle of delicate capillary setae easily overlooked.

The anus is dorsal and surrounded by several small, erect, papillae. Ventrally there is a large bilobed cushion (Fig. 12).

Biology: *Polydora commensalis* is commonly found in gastropod shells occupied by hermit crabs. ANDREWS (1891a) describes it as boring into the columella and BERKELEY & BERKELEY (1936) reported it as hollowing a furrow on the shell surface which is covered by a thin calcareous layer. *P. commensalis* has been found in a variety of gastropod shells and its tubes are not visible externally. Fertilization is thought to take place by copulation as both sexes are often found in the same shell in close proximity. Also, worms in the size range of a female have been found to contain both eggs and sperm, indicating copulation had taken place; all egg masses found contained fertilized eggs (HATFIELD, 1965).

Material: *Polydora commensalis* Holotype: USNM 4909, Cotypes: USNM 4905, 4906, 4907. Beaufort, North Carolina; Curaçao.

Distribution: Connecticut to North Carolina; Curaçao.

Polydora ligni Webster, 1879

(Figures 13–21)

Polydora ligni WEBSTER, 1879a, p. 119; 1886, p. 148. – VERRILL, 1881, p. 322. – WEBSTER & BENEDICT, 1884, p. 729. – SÖDERSTRÖM, 1920, p. 265. – COWLES, 1930, p. 343. – BERKELEY & BERKELEY, 1936, p. 471; 1952, p. 19; 1954, p. 464. – FRIEDRICH, 1937, p. 345. – NELSON & STAUBER, 1940, p. 102. – HARTMAN, 1941, p. 309; 1944, p. 340; 1945, p. 32; 1951, p. 82; 1954, pp. 10, 18. – MORTENSEN & GALTSOFF, 1944, p. 164. – RIOJA, 1943, p. 232. – GALTSOFF, *et al.* 1947, p. 129. – HARTMAN & REISH, 1950, p. 28. – SMIDT, 1951, p. 63. – REISH & WINTER, 1954, pp. 113, 115, 118–121. – FILICE, 1954, p. 16; 1958, pp. 174, 177, 190. – STICKNEY, 1959, pp. 14, 17. – JONES, 1961, p. 266. – ELIASON, 1962a, p. 52. – REISH, 1963b, pp. 26, 30. – WELLS & GRAY, 1964, p. 73. – DEAN & HASKIN, 1964, pp. 555–559, 561. – CORY, 1967, p. 76. – MUUS, 1967, p. 91. – REISH & BARNARD, 1967, p. 9. – SIMON, 1967, p. 420.

Polydora amarincola HARTMAN, 1936, p. 49.

Diagnosis: Prostomium anteriorly bifid, with nuchal antenna. Branchiae beginning on setiger 7. Anterior setae all capillary. Hooks of setiger 5 falcate, with secondary tooth inside curved portion. Bidentate neuropodial hooded hooks first present on setiger 7. Pygidium disc-shaped, with dorsal notch.

Description: The body length is up to 5.66 mm, with 31 setigers. The prostomium is anteriorly bifid to the extent that it could almost be said to possess frontal horns (Fig. 13). It extends posteriorly to about the level of setiger 3, terminating in a long slender nuchal antenna. There are four small eyes on the posterior half of the prostomium. The peristomium is low and somewhat inflated.

Cirriform branchiae begin on setiger 7. The branchiae are at first short, increasing in length in mid-body setigers and usually continuing to near the end of the body, with the last few again short, almost papilliform (Fig. 15).

Notopodial lamellae of setiger 1 are erect, thin and tall, while those of setigers 2–4 are broader, more leaflike (Fig. 13). Neuropodial lamellae are thin and small. Setiger 6 bears a short, thick notopodial lamella and a smaller subtriangular neuropodial lamella (Fig. 14). On the posterior setigers, the notopodial postsetal lamellae are short, digitiform with triangular presetal lamellae (Fig. 15). Neuropodial lamellae are represented by a low ridge.

Anterior setae are all capillary and those of both rami are similar in appearance. The shorter setae are uni- or bilimbate and quite granular (Fig. 16). The longer setae are slender, thinly unilimbate, with a heavily striated sheath and a slightly granular shaft (Fig. 17). Bidentate neuropodial hooded hooks first appear on setiger 7, with about six to ten hooks per row (Figs. 15, 18).

There are about eight stout modified hooks on setiger 5. They are slightly tapered distally with a blunt to tapered more or less well-developed lateral secondary tooth (Figs. 19, 20). Each hook is accompanied by a closely applied, almost translucent seta with a brush tip (Fig. 20).

The pygidium is a large disc with a conspicuous dorsal notch. The dorsal edges of the disc are often turned up (Fig. 21).

Biology: *Polydora ligni* is a euryhaline shallow water species and is commonly found in thin mud tubes on tunicates, shells, wharfpilings and in crevices. It was demonstrated by MORTENSEN & GALTSOFF (1944) that tubes are necessary for its survival and that there is some physical and chemical selection with regard to tube-building materials.

Polydora ligni may be free living or commensal. It penetrates between the mantle and shell of oysters to form "mud blisters." It has also been known to destroy oyster beds by accumulating on the shells' surfaces a mass of mucus-trapped sediment, oyster feces and debris, which eventually decompose producing large quantities of hydrogen sulfide (NELSON & STAUBER, 1940).

Material: Eastport, Maine; Gloucester, Massachusetts; Newport, Rhode Island; Great Egg Harbor, New Jersey; Chesapeake Bay, Virginia; Tampa Bay, Florida; Port Aransas, Texas; Puerto Rico; Aberdeen, Washington; Salton Sea, California; Denmark.

Distribution: North Atlantic: New England to Florida; Gulf of Mexico; Caribbean Sea; North Pacific: Canada to Mexico; Denmark.

Discussion: *P. ligni* is easily recognized and not commonly confused with other species. The hooks of setiger 5 may be worn to the extent that the secondary tooth is not always obvious. It can usually be seen, however, on younger hooks located more ventrally in the bundle.

Polydora plena Berkeley & Berkeley, 1936

(Figures 22–29)

Polydora socialis plena Berkeley & Berkeley, 1936, p. 468; 1952, p. 22. – Pettibone, 1967, p. 11. – Reish, 1968a, pp. 69, 70, 82, 106.
Polydora socialis, Hartmann, 1948b, p. 37. *Not* Schmarda, 1861.
Polydora cf *socialis*, Hartmann-Schröder, 1962a, p. 137; 1965, p. 209. *Not* Schmarda, 1861.

Diagnosis: Prostomium anteriorly bifid. Cirriform branchiae beginning on setiger 8. Anterior setae all capillary. With bidentate neuropodial hooded hooks beginning on setiger 7. Modified hooks of setiger 5 falcate, tapered, with bluntly rounded tips. Pygidial collar notched dorsally, with two smaller dorso-lateral notches.

Description: The body length is up to 8.0 mm, with 76 setigers. Prostomium is anteriorly bilobed and extends posteriorly to about the level of setiger 1 (Fig. 22). There is no occipital antenna. There are four eyes, the anterior two larger and farther apart. The dorsal sense organ extends posteriorly for about five setigers. The peristomium is somewhat inflated and closely applied to the prostomium.

Cirriform branchiae begin on setiger 8 and extend to near the end of the body. When they first appear they are short, but immediately become longer (Fig. 24), decreasing again in length in posterior setigers (Fig. 25).

Lamellae of the first four setigers are well defined. The notopodial lamellae of setiger 1 are especially well-developed and are larger than those following (Fig. 22). Dorsal and ventral lamellae of setiger 6 are about equal in size and are smoothly rounded (Fig. 23). In the an-

terior branchial region the postsetal notopodial lamellae are short and subtriangular with well-developed presetal lamellae (Fig. 24). Neuropodial lamellae are little more than ridges. On posterior setigers, the lamellae are reduced still further in size (Fig. 25).

Anterior setae are all capillary, uni- or bilimbate, with heavily striated sheaths and granular shafts (Fig. 26). Bidentate neuropodial hooded hooks first appear on setiger 7 (Fig. 27). There is no evidence, in whole mounts, of secondary sheaths. Modified hooks of setiger 5 are falcate, tapered to varying degrees and bluntly rounded. Companion setae are limbate distally, with an extremely heavily striated sheath (Fig. 28).

The pygidium is disclike with a median dorsal notch and two smaller dorso-lateral notches (Fig. 29).

Darkly pigmented patches are scattered on the pygidium, posterior part of prostomium, and the anterior body (Figs. 22, 29).

Biology: *Polydora plena* has been collected from various substrata but is commonly found on sandy silts (REISH, 1968a). BERKELEY & BERKELEY (1952) report fragile, sandy tubes, which are sometimes branched and united basally.

Material: Holotype and paratypes (28) of *Polydora socialis plena*: Nanaimo, from British Columbia (Holotype: USNM 32705, Paratype: 32704); Port Aransas, Texas.

Distribution: North Pacific: Alaska, Gulf of California; Gulf of Mexico.

Discussion: *Polydora socialis plena* Berkeley & Berkeley (1936), was described as a subspecies because of the occurrence of notosetae on the first setiger. In the redescription of the species by MESNIL (1896), he points out very definitely the lack of notosetae on setiger 1. This character is often used at the specific level and in other instances has been reliable and stable. *P. socialis plena* is herein elevated to the level of species. HARTMAN (1948b) reports *P. socialis* as possessing both noto- and neuropodial setae on setiger 1. On this basis, it is included in the synonymy for *P. plena*. The same is true for reports of *Polydora* cf *socialis* by HARTMANN-SCHRÖDER (1962a, 1965). Other records of *Polydora socialis* need to be re-examined.

Polydora websteri Hartman, 1943

(Figures 30–36)

Polydora caeca WEBSTER, 1879b, p. 252. – ANDREWS, 1891b, p. 291. – *Not* Oersted, 1843.

Polydora ciliata, KAVANAGH, 1940, p. 31; 1941, p. 354. – *Not* Johnston, 1838.

Polydora websteri HARTMAN, 1943, *in* LOOSANOFF & ENGLE, p. 70; 1945, p. 33; 1951, p. 81; 1961, p. 99; 1966, p. 223. – STENZEL & TURNER, 1944, p. 307. – HOPKINS, 1947, p. 12; 1958, p. 268. – BEHRE, 1950, p. 13. – CARPENTER, 1956, p. 94. – OWEN, 1957, p. 35. – RIOJA, 1960, p. 304. – WELLS, 1961, p. 247. – WELLS & GRAY, 1964, p. 73. – SIMON, 1967, p. 420. – BLAKE, 1968, p. 797. – EVANS, 1968, p. 795. – HAIGLER, 1968, p. 797. – NAQVI, 1968, p. 319.

Diagnosis: Prostomium anteriorly bilobed, rounded posteriorly. With or without eyes. Cirriform branchiae beginning on setiger 7. Anterior setae all capillary. First setiger with neurosetae only. With bidentate neuropodial hooded hooks. Beginning on setiger 8. Modified hooks of setiger 5 falcate, with laterally projecting hardened sheaths. Pygidium a flaring disk with wide dorsal notch.

Description: The body length is up to 8.66 mm, with 47 setigers. The prostomium is anteriorly bilobed and terminates posteriorly at about the level of setigers 1–4 (Fig. 30). There are usually four small eyes but these may be missing. The peristomium is large and fairly closely applied to the prostomium.

Cirriform branchiae first appear on setiger 8 and immediately increase in length so that they overlap across the dorsum by setigers 10–12.

On the anterior four setigers parapodial lamellae are well-developed (Fig. 30). On setiger 1, neuropodial lamellae are ovoid and rounded, while those of the notopodia are small and erect, almost papilliform. In anterior branchial setigers, the lamellae are reduced (Fig. 31). Notopodial postsetal lamellae are subtriangular with presetal lamellae of similar size. Neuropodial lamellae are little more than a ridge.

Anterior setae are all capillary and are similar in appearance, uni- or bilimbate, with a striated sheath, and distally a granular shaft (Fig. 32). Neuropodial bidentate hooded hooks begin on setiger 8 (Fig. 33). There is no evidence, in whole mounts, of a secondary

hood. The modified hooks of setiger 5 are falcate, with a lateral flange or sheath (Figs. 34, 35). The acuteness varies. The companion setae are closely applied to the hooks and have a smooth to frayed distal sheath (Fig. 34). There is a small ventral bundle of capillary setae.

The pygidium is a flaring disc with a wide dorsal notch (Fig. 36).

Biology: *Polydora websteri* is known to penetrate commercial oysters, scallops, and other calcareous structures. It causes mud blisters and U-shaped etchings on the outside of the shell. EVANS (1968) reports it as one of the primary borers on young pecten shells. The mechanism by which it bores is thought to be a combination of chemical and mechanical action and is little understood (HAIGLER, 1968).

According to HOPKINS (1958), larval settling occurs at the seventeenth-segment stage. The larvae settle on the surface of oysters and on the shell margins, forming etched grooves which subsequently become pits containing the characteristic horseshoe-shaped burrows.

Material: Alligator Harbor, Florida.

Distribution: North Atlantic: Newfoundland to Florida; Gulf of Mexico; North Pacific: Oregon to Mexico; Hawaii.

Discussion: *Polydora caeca* Webster (1879b) was very inadequately described and the type material is missing. HARTMAN (1943) redescribed the species, based on material now deposited in the Allan Hancock Foundation, and changed the name to *P. websteri* since *P. caeca* was preoccupied by *Leucodorum caecum* Oersted (1843).

The following is a key to species of *Polydora* herein and previously reported from the Gulf of Mexico and Caribbean Sea.

KEY TO SELECTED SPECIES OF POLYDORA

1a. Posterior setigers with modified setae 2
1b. Posterior setigers without modified setae. 5

2a. Posterior modified hooks scythe-shaped, directed dorsally . . . . . *P. hamata* Webster, 1879
2b. Posterior modified hooks otherwise 3

3a. Branchiae relatively few in number, five to eight pairs . . . . . *P. armata* Langerhans, 1880
3b. Branchiae number more than ten pairs 4

4a. Posterior specialized setae needlelike. Modified hooks of setiger 5 unidentate, with fimbriated crest . *P. caulleryi* Mesnil, 1897
4b. Posterior specialized setae with recurved tips. Modified hooks of setiger 5 bifid, with subterminal collar . . . . . *P. ancistrata* Jones, 1962

5a. Prostomium with occipital antenna. . *P. ligni* Webster, 1879
5b. Prostomium without occipital antenna 6

6a. Prostomium small, rounded, concealed by short, thick conical palpi . . . . . *P. commensalis* Andrews, 1891
6b. Prostomium and palpi otherwise 7

7a. Setiger 1 without notosetae and with papilliform notopodial lamellae 8
7b. Setiger 1 with both noto- and neurosetae and with well-developed notopodial lamellae . . . . . *P. plena* Berkeley & Berkeley, 1936

8a. Modified hooks of setiger 5 with lateral sheath (not always visible on every hook). Pygidium with broad, dorsal notch . . . . . *P. websteri* Hartman, 1943
8b. Modified hooks of setiger 5 without lateral sheath. Pygidium with mid-dorsal notch and two smaller dorso-lateral notches . . . . . *P. socialis* (Schmarda, 1861)

Genus **Pygospio** Claparède, 1863

Type-species: *Pygospio elegans* CLAPARÈDE, 1863, p. 37. Gender: feminine.

Diagnosis: Prostomium without frontal horns, pointed posteriorly. Eyes present. Branchiae fused with notopodial lamellae. Fe-

male with branchiae beginning posterior to setiger 10. Male with branchiae on setiger 2, then absent until more posterior setigers. With capillary setae on anterior setigers. Notosetae only capillary, with neuropodial hooded hooks posteriorly. Pygidium with thick glandular cirri or lobes.

Pygospio elegans Claparède, 1863

(Figures 37–47)

Pygospio elegans Claparède, 1863, p. 37. – Mesnil, 1896, p. 175; 1897, p. 85. – Southern, 1910, p. 235. – McIntosh, 1874, p. 202; 1909, p. 166; 1915a, p. 189; 1922, p. 17; 1927, p. 85. – Elwes, 1910, p. 71. – Allen, 1915, p. 630. – Söderström, 1920, p. 267; 1923, p. 327. – Rioja, 1925, p. 46. – Fauvel, 1927, p. 46. – Augener, 1928, p. 102; 1932a, pp. 661, 671. – Rioja Lo Bianco, 1931, p. 62. – de Vos, 1936, p. 92; 1954, p. 186. – Annenkova, 1938, p. 173. – Bassindale, 1938, p. 93. – Thorson, 1946, p. 83. – Zatsepin, 1948, p. 132. – Holme, 1949, p. 220. – Ushakov, 1950, p. 200; 1955, p. 269; 1965, p. 245. – Wesenberg-Lund, 1950a, p. 76. – Smidt, 1951, p. 54. – Rasmussen, 1953, p. 1161. – Southward, 1953, p. 59. – Berkeley & Berkeley, 1954, p. 462. – Karling, 1954, p. 246. – Marinov, 1955, p. 111. – Hannerz, 1956, p. 91; 1961, p. 10. – Bassindale & Barrett, 1957, p. 259. – Chlebovitsch, 1961, p. 196. – Day, 1961, p. 485; 1967, p. 475. – Eliason, 1962a, p. 50. – Laubier & Paris, 1962, p. 43. – Sanders, *et al*, 1962, pp. 64–68. – Bellan, 1963a, p. 51; 1964, p. 111. – Dumitrescu, 1963, p. 186. – Kühlmorgen-Hille, 1963, p. 48; 1965, p. 174. – Rullier, 1963, p. 210. – Orrhage, 1964a, pp. 338, 350, 352, 358, 365, 383, 384. – Hamond, 1966, p. 409. – Laubier, 1966a, p. 216. – Muus, 1967, p. 88. – Simon, 1967, p. 421. – Cabioch, L'Hardy & Rullier, 1968, p. 51. – Hobson & Green, 1968, p. 410.

Spio seticornis, Oersted, 1843a, p. 40. – Dalyell, 1853, p. 159. – Cunningham & Ramage, 1888, p. 640. – Möbius, 1873, p. 108. – Quatrefages, 1865a, p. 307. – Malmgren, 1874, p. 90. – Tauber, 1879, p. 117. – Levinsen, 1893, p. 334. – Leschke, 1903, p. 122.

Spio rathbuni Webster & Benedict, 1884, p. 726; 1887, p. 736. – Treadwell, 1948, p. 43.

Pygospio minutus Giard, 1894, p. 246.

Pygospio elegans var. *minuta*, Mesnil, 1896, p. 175. – Soulier, 1904, p. 320.

Pygospio seticornis (Oersted), Oersted, 1844, p. 86. – Elwes, 1910, p. 71. – Eliason, 1920, p. 42. – *Not Nereis seticornis* Fabricius, 1780.

Diagnosis: Prostomium narrow, anteriorly rounded, slightly bilobed. Four to eight eyes. Peristomium inflated laterally. Branchiae first appearing on setigers 11–13, extending to within seven to fifteen setigers of end of body. Additional pair sometimes present on setiger

2 in males. Neuropodial bidentate hooded hooks first present on setigers 8–9. Notosetae all capillaries. Pygidium four-lobed.

Description: The body length is up to 12 mm, with 53 setigers. The narrow prostomium is anteriorly blunt or faintly bilobed (Fig. 37). It appears to end posteriorly at the level of the first setiger; however, higher magnification reveals a slender extension to about halfway between setigers 1 and 2. There are generally four to eight eyes arranged irregularly on the posterior half of the prostomium. The peristomium is inflated laterally and ventrally and forms a low hood surrounding the prostomium.

There are two crescent-shaped sensory organs behind the prostomium and a variable number of transverse bands. Branchiae first appear on setigers 11–13, though on males a pair may be present on the second setiger. The gills continue to seven to fifteen setigers from the posterior end.

The parapodia of setiger 1 are well-developed, with tall, thin neuropodial lamellae and larger, more angular notopodial lamellae (Fig. 38). In more posterior setigers the neuropodial lamellae become broader, lower, and asymmetrically rounded (Fig. 39). Notopodial lamellae are shorter and broader at the base. On the thirteenth setiger, where the branchiae usually begin, the dorsal lamellae are fused to the branchiae (Fig. 40) and are very thin, wider basally and tapering toward the tip. The branchial part is uniformly thick and does not taper. The branchiae are heavily ciliated; the cilia are extremely long. There appears to be a lateral organ or interramal patch of cilia. The neuropodial lamellae are asymmetrically small and rounded, with the hooks emerging below the level of the actual lamellae (Fig. 40). More posterior setigers are similar in appearance to setiger 13, (Fig. 41) with the notopodial lamellae slightly thinner and the neuropodial lamellae more symmetrical (Fig. 41). There is an abrupt decrease in branchial size coinciding with this change in lamellar form. On one setiger (Fig. 41) the parapodial shape is similar to the more anterior branchial setigers and in the following setigers the entire appearance changes (Fig. 42). Branchiae and lamellae are approximately half as tall as on the preceding setiger. The gills are rounded, knoblike and the lamellae no longer extend to the branchial

tip. Neuropodial lamellae have almost disappeared and the number of hooks is reduced to less than half their previous number.

Anterior setae are all capillaries and somewhat characteristic in appearance. In the neuropodia of the first setiger, the anterior setae are very wide and granular with a conspicuous unilimbation which sometimes continues into the tissue (Fig. 43). The posterior row of setae are longer, thinner, not particularly granular and with only a thin unilimbation. Some of the notosetae are slightly shorter and a little broader than the others and slightly bilimbate (Fig. 44). On more posterior setigers, the short, thick anterior neurosetae often appear either uni- or bilimbate. The longer posterior setae are very thin, not granular and with only a hint of a limbation. The limbations of the heavier setae are somewhat interesting in that they, at least superficially, resemble capillaries of certain sabellids. The shaft boundaries are difficult to detect because of striations or grooves in the sheath. Bidentate hooded hooks first appear in the neuropodia of setigers 8–9 (Figs. 45, 46). The upper tooth is very broad and both teeth are often worn away. There is apparently no internal hood and the opening in the primary hood is just above the setal teeth.

The pygidium is drawn out into four lobes, which may all be subequal in size or occasionally two may be longer (Fig. 47). One to two lobes are sometimes missing or in some stage of regeneration. The lobes vary in length and are glandular.

Biology: *Pygospio elegans* was collected from sandy clam flats, mud, gravely sand and muddy sand. It is generally found in shallow water and builds a characteristic quartz grain tube provided with a type of closing mechanism.

This species exhibits a kind of sexual dimorphism in that, in the case of females, branchiae do not appear before the eleventh setiger but on the male there is a pair on the second setiger. Before the discovery of this phenomenon by SÖDERSTRÖM (1920), the two were considered as separate species. Copulation occurs prior to fertilization and early development takes place in egg capsules fastened to the inner walls of the tubes occupied by the females (HANNERZ, 1956). The developing young apparently feed on eggs and embryos of the same egg-capsule so that only a few of the embryos reach maturity (SÖDERSTRÖM, 1920). The time spent in the capsule evidently varies in the spring and summer. There is a pelagic stage which is occasionally eliminated.

P. elegans is also capable of asexual reproduction. Within the tube, fission may occur at any point along the body resulting in fragments with varying numbers of setigers. Complete regeneration takes place within the tube at a rapid rate (8 days at 20°C) (RASMUSSEN, 1953; HOBSON & GREEN, 1968).

Material: *Spio rathbuni* Holotype: USNM 403; *Pygospio californica* Holotype: USNM 20219. Off Veracruz, Mexico; Massachusetts – Barnstable, Woods Hole; Maine – Sheepscot River, Glen Cove in Penobscot Bay, Samoset Point, Rockland, Fort Popham, Braye Boat Harbor north of Sea Point, Sagahoc Bay; New Hampshire – Hampton Harbor, Rye Harbor.

Distribution: Arctic; New England – Massachusetts, Maine, New Hampshire; North Atlantic: Norway to France; Baltic; Mediterranean; South Africa; North Pacific: California to Mexico; Okhotsk Sea.

Discussion: Three species are presently included in the genus *Pygospio*. These are *P. elegans* Claparède, 1863, *P. dubia* Monro, 1930 and *P. californica* Hartman, 1936. MONRO's species differs with respect to a number of generic characters, such as type of hooks (unidentate, not hooded) and pygidial features (with or without anal sucker; when present, with two vertical flaps); it is, therefore, doubtful that *P. dubia* is a member of this genus. The type material will need to be re-examined. The two remaining species of *Pygospio* are compared in Table 2.

TABLE 2

COMPARISON OF PYGOSPIO ELEGANS AND PYGOSPIO CALIFORNICA

Species	Prostomial shape	First appearance of branchiae	First appearance of neuropodial hooded hooks
P. elegans	anteriorly bilobed posterior extension faint	setigers 11–13	setigers 8–9
P. californica	anteriorly conical posterior caruncle	setiger 19	setiger 23

Genus **Spio** Fabricius, 1785, emended

Spio Fabricius, 1785. Type-species: *Nereis filicornis* Müller, 1776, designated by SÖDERSTRÖM, 1920, p. 245. Gender: feminine.

Paraspio Czerniavsky, 1881. Type-species: *Spio decoratus* Bobretzky, 1870, by monotypy. Gender: feminine.

Euspio McIntosh, 1915. Type-species: *Euspio mesnili* McIntosh, 1915a, herein designated. Gender: feminine. HOMONYM (preoccupied by *Spio mesnili* Augener, 1914). [= *Spio filicornis* (Müller, 1776)].

Subgenus **Microspio** Mesnil, 1896

Microspio Mesnil, 1896. Type-species: *Spio mecznikowianus* Claparède, 1869a, designated by SÖDERSTRÖM, 1920, p. 247. Gender: feminine.
Mesospio Gravier, 1911. Type-species: *Mesospio moorei* Gravier, 1911, by monotypy. Gender: feminine.

Diagnosis: Prostomium anteriorly rounded or faintly bilobed. Frontal horns lacking. With or without eyes. Branchiae present from setiger 1 (subgenus *Spio*) or from setiger 2 (subgenus *Microspio*) and continuing to near end of body. Anterior setae all capillary. With neuropodial hooded hooks (unidentate or quinquidentate) in posterior setigers. Without notopodial hooks. Pygidium with anal cirri.

Discussion: MESNIL (1896) erected the genus *Microspio* and diagnosed it as having branchiae beginning on setiger 2. SÖDERSTRÖM (1920) distinguished *Microspio* from *Spio* by the number of dorsal sensory organs. This, however, proved to be unsatisfactory. FAUVEL (1927) followed MESNIL by indicating that branchiae begin on setiger 2 but then he added: and sometimes on setiger 1. This parenthetical addition again makes it impossible to distinguish *Microspio* from *Spio*. In the literature, species have sometimes been assigned to *Microspio* on the basis of the presence of small rudimentary branchiae on setiger 1. Whether or not a species is placed under *Spio* or *Microspio* seems, then, to depend on the author's definition of what is small. This nebulous distinction, along with SÖDERSTRÖM's use of the dorsal sensory organs, has led to much confusion between these genera. For this reason, the genus *Microspio* is herein treated as a subgenus of *Spio*, though it may later be found more practical to synonomize them. HOLMQUIST (1967) indicates some of the difficulties and confusions in the species of *Spio* and related genera; she emphasizes the need for a complete revision of the genera involved on a comparative basis.

Species tentatively assigned to *Spio* (*Spio*):

S. (*S.*) *filicornis* (Müller), as *Nereis filicornis* MÜLLER, 1776, p. 218. Denmark.
S. (*S.*) *decorata* Bobretzky, as *Spio decoratus* BOBRETZKY, 1870, p. 256. Black Sea. [Referred to *Paraspio mecznikowianus* by HARTMAN (1959, p. 390); = distinct species, according to BELLAN (1967, p. 74); branchiae begin on setiger 1.]
S. (*S.*) *setosa* VERRILL, 1873, p. 602. Connecticut and Massachusetts.
S. (*S.*) *robusta* VERRILL, 1873, p. 603. Massachusetts. [Referred to *Spio setosa* Verrill by HARTMAN (1945, p. 31).]
S. (*S.*) *limicola* VERRILL, 1879, p. 176. Massachusetts. [Referred to *Spio setosa* Verrill by HARTMAN (1942, p. 63); referred to *Spio filicornis* by PETTIBONE (1954, p. 284); = distinct species, according to HOLMQUIST (1967, p. 303).]
S. (*S.*) *martinensis* MESNIL, 1896, p. 122. France. [Referred to *Spio filicornis* (Müller) by SÖDERSTRÖM (1920, p. 244); = distinct species, according to HANNERZ (1956, p. 84).]
S. (*S.*) *aequalis* EHLERS, 1905, p. 40. New Zealand.
S. (*S.*) *gattyi* MCINTOSH, 1909, p. 165. Scotland. [Referred to *Spio filicornis* (Müller) by MCINTOSH (1915a, p. 173).]
S. (*S.*) *obtusa* EHLERS, 1913, p. 508. Antarctic.
S. (*S.*) *mesnili* AUGENER, 1914, p. 10. Australia.
S. (*S.*) *mesnili* (McIntosh), as *Euspio mesnili* MCINTOSH, 1915a, p. 176. Bressay Sound, North Atlantic. HOMONYM. [Questionably referred to *Spio filicornis* (Müller) by SÖDERSTRÖM (1920, p. 245); referred to *Spio filicornis* (Müller) by THULIN (1957, p. 49).]
S. (*S.*) *multioculata* (Rioja), as *Euspio multioculata* RIOJA, 1918, p. 60. Spain. [Referred to *Spio* by FAUVEL (1927, p. 44).]
S. (*S.*) *arctica* (Söderström), as *Microspio arctica* SÖDERSTRÖM, 1920, p. 250. Greenland. [Referred to *Spio limicola* Verrill by HOLMQUIST (1967, p. 303).]
S. (*S.*) *theeli* (Söderström), as *Microspio theeli* SÖDERSTRÖM, 1920, p. 251. Siberian Arctic Ocean. [Referred to *Spio* by HOLMQUIST (1967, p. 307).]
S. (*S.*) *mimus* CHAMBERLIN, 1920, p. 16B. Alaska. [Doubtfully referred to *Spio filicornis* (Müller) by HARTMAN (1936, p. 13); referred to *Spio theeli* (Söderström) by HOLMQUIST (1967, p. 307).]
S. (*S.*) *theeli kolaensis* (Zachs), as *M. theeli kolaensis* ZACHS, 1925, p. 2. Murman, Kola Fjord.
S. (*S.*) *filicornis* var. *pacifica* (E. Berkeley), as *Spio martinensis* var. *pacifica* E. BERKELEY, 1927, p. 413. British Columbia. [Referred to *Spio filicornis* (Müller) by HARTMAN (1948b, p. 36).]
S. (*S.*) *filicornis picta* ZACHS, 1933, p. 129. North Japan Sea. [Referred to *Spio filicornis* (Müller) by CHLEBOVITSCH (1961, p. 194).]
S. (*S.*) *borealis* OKUDA, 1937a, p. 225. Japan.
S. (*S.*) *butleri* BERKELEY & BERKELEY, 1954, p. 461. Western Canada.
S. (*S.*) *armata* (Thulin), as *Microspio armata* THULIN, 1957, p. 57. Øresund.
S. (*S.*) *goniocephala* THULIN, 1957, p. 53. Øresund.
S. (*S.*) *unidentata* CHLEBOVITSCH, 1959, p. 172. Kurile Islands.
S. (*S.*) *africana* (Rullier), as *Microspio africana* RULLIER, 1964, p. 189. Cap Vert, West Africa.
S. (*S.*) *cirrifera* (Banse and Hobson), as *Paraspio cirrifera* BANSE & HOBSON, 1968, p. 27. Puget Sound, Washington.

Species tentatively assigned to *Spio* (*Microspio*):

S. (*M.*) *mecznikowiana* Claparède, as *Spio mecznikowiana* CLAPARÈDE, 1869a, p. 178. Mediterranean. [Referred to *Microspio* by MESNIL (1896, p. 119).]
S. (*M.*) *atlantica* Langerhans, as *Spio atlanticus* LANGERHANS, 1880, p. 89. Madeira. [Referred to *Microspio mecznikowiana* (Claparède) by SÖDERSTRÖM (1920); – distinct species according to HANNERZ (1956, p. 85).]
S. (*M.*) *moorei* (Gravier), as *Mesospio moorei* GRAVIER, 1911, p. 100. South Shetland Islands.
S. (*M.*) *rolasiana* (Augener), as *Microspio rolasiana* AUGENER, 1918, p. 408. West Africa.
S. (*M.*) *kussakini* (Chlebovitsch), as *Microspio kussakini* CHLEBOVITSCH, 1959, p. 173. Kurile Islands.
S. (*M.*) *pigmentata* (Reish), as *Spiophanes pigmentata* REISH, 1959b, p. 11. Southern California. [Referred to *Nerinides pigmentata* (Reish, 1959) by HARTMAN (1961, p. 92); referred questionably to *Microspio* by PETTIBONE (1962, p. 85).]
S. (*M.*) *maculata* (Hartman), as *Nerinides maculata* HARTMAN, 1961, p. 91. Lower California.
S. (*M.*) *minuta* (Hartmann-Schröder), as *Paraspio minuta* HARTMANN-SCHRÖDER, 1962a, p. 144. Chile.

Species assigned to *Spio* but should be referred elsewhere (?): *Spio bengalensis* WILLEY, 1908, p. 389. Bengal, Indian Ocean. *Spio punctata* HARTMAN, 1961, p. 89. Southern California. Perhaps to *Laonice*.

Spio (*M.*) *pigmentata* and *S.* (*M.*) *maculata* are reported as lacking branchiae on setiger 1. They are, however, very closely related to *S.* (*S.*) *cirrifera* Banse & Hobson (1968) and it is possible that small branchiae on the first setiger were overlooked.

Spio (Spio) pettiboneae sp. n.

(Fig. 48–56)

Etymology: This species is named for Dr. MARIAN PETTIBONE, Smithsonian Institution.

Diagnosis: Prostomium anteriorly rounded; branchiae beginning on setiger 1. Anterior setae capillary. With tridentate neuropodial hooded hooks beginning on setigers 12–16. Pygidium with four bluntly rounded anal cirri.

Description: The body length is up to 11 mm, with 35 setigers. The prostomium is anteriorly rounded. There are usually four small

eyes, the anterior pair crescent-shaped. The peristomium is closely applied to the prostomium.

Branchiae are well-developed on anterior setigers and extend to near the end of the body. Parapodial lamellae are well-developed. The dorsal lamellae of anterior setigers are partially fused with the branchiae and there is a conspicuous presetal lamella (Fig. 49). More posteriorly the notopodial lamellae become somewhat triangular and neuropodial lamellae lower (Fig. 50). The presetal lamellae are still evident but decrease in size in more posterior setigers. In far posterior setigers, the notopodial lamellae become well-separated distally from the branchiae and neuropodial lamellae have increased in size (Fig. 51).

Anterior setae are all capillary and are arranged in two rows. They are similar in appearance, being granular and broadly uni- or bilimbate (Fig. 52). Tridentate neuropodial hooded hooks first appear on setigers 12–16. They often vary in shape with regard to the angle of the setal head (Figs. 53, 54). They become quite long in posterior setigers (Fig. 51). There are two to four ventrally directed setae in the neuropodia of the middle and posterior setigers.

The pygidium bears four thick, bluntly rounded cirri (Figs. 55, 56). Occasionally one is bifucate (Fig. 55).

The prostomium and peristomium often bear pigmented patches (Fig. 48).

Biology: *Spio* (*S.*) *pettiboneae* was collected intertidally from the Gulf of Mexico.

Material: Tampa Bay, Florida; Grand Isle, Louisiana. *Paraspio cirrifera* Banse & Hobson Holotype: USNM 36270, Paratype: USNM 36271; *Paraspio minuta* Hartmann-Schröder (Hamburg Museum). Designated Holotype: USNM 42893, Paratype: USNM 42894.

Distribution: Gulf of Mexico.

Discussion: *Spio* (*S.*) *pettiboneae* differs from the majority of species of *Spio* (*Spio*) in that it possesses tridentate rather than bidentate hooks. *S.* (*S.*) *aequalis* Ehlers possesses tridentate hooks but differs in the nature of the anal appendages which are very short inconspicuous lobes. The prostomium of *S.* (*S.*) *aequalis* is not anteriorly rounded as in *S.* (*S.*) *pettiboneae*. *S.* (*S.*) *arctica* (= *S. limicola*

according to HOLMQUIST, 1967) also has tridentate hooks but differs in that its prostomium is anteriorly pointed. The closely related species, *S.* (*S.*) *cirrifera* possesses conspicuous notopodial presetal cirri on setigers of the midbody region and setiger 1 has rounded dorsal lamellae and very small branchiae.

Genus **Scolecolepides** Ehlers, 1907

Type-species: *Scolecolepides benhami* Ehlers, 1907, by monotypy.
Gender: masculine.

Diagnosis: Prostomium with frontal horns. Peristomium surrounding prostomium, not developed into conspicuous hood. Cirriform branchiae beginning on setiger 1, continuing to or just beyond the mid-body region. Anterior setae all capillary. With neuro- and notopodial bidentate hooded hooks in posterior setigers. Pygidium with anal cirri.

Scolecolepides viridis (Verrill, 1873)

(Figures 57–65)

Scolecolepis viridis VERRILL, 1873, p. 600; 1882, p. 301. – VERRILL & SMITH, 1874, pp. 306, 307. – WEBSTER, 1879a, p. 118. – RATHBUN, 1880, p. 123. – WEBSTER & BENEDICT, 1884, p. 726. – *Not* MEAD, 1897, p. 270. – SUMNER, OSBURN & COLE, 1913, p. 125. – COWLES, 1930, p. 343.

Scolecolepis tenuis VERRILL, 1873, p. 601; 1882, p. 301. – WEBSTER, 1879a, p. 118. – COWLES, 1930, p. 343. – HARTMAN, 1944, p. 340.

Scolecolepides arctius CHAMBERLIN, 1920, p. 17. – HARTMAN, 1938, p. 13.

Scolecolepides viridis, HARTMAN, 1944, p. 340. – SANDERS *et al*, 1962, p. 66. – BURBANCK, 1962, p. 721. – FRANKENBERG & BURBANCK, 1963, p. 88. – WELLS & GRAY, 1964, p. 73. – GEORGE, 1966a, p. 76; 1966b, p. 542. – SIMON, 1968, p. 505.

Laonice viridis, FERGUSON & JONES, 1949, p. 440.

Scolilepides [sic] *viridis*, STICKNEY, 1959, pp. 17, 18.

Diagnosis: Prostomium with frontal horns, somewhat bilobed anteriorly. With four eyes. Branchiae basally fused to lamellae, present from setiger 1 to the mid-body region. With capillary setae anteriorly. With small bundle of ventral acicular neurosetae. Bidentate neuropodial hooded hooks first present in setigers 24–51; biden-

tate notopodial hooded hooks appear in setigers 39–60. Pygidium with numerous anal cirri surrounding anus.

Description: The body length is up to 94 mm, with 281 setigers. The prostomium is short, blunt, appearing somewhat bilobed anteriorly, with frontal horns (Figs. 57, 58). There are two pairs of dark eyes, those of the anterior pair are lateral, somewhat hidden dorsally; the posterior pair are smaller, located closer together and on a slight elevation. They often appear as if in a straight line. The peristomium surrounds the prostomium, beginning just behind the frontal horns.

Cirriform branchiae begin on the first setiger and continue to about the mid-body region. They may be slightly longer than the notopodial lamellae to which they are basally fused (Fig. 57). The gills increase in length for the first few setigers and then about setigers 30–40 they rapidly decrease in size (Fig. 59). They decrease further and finally disappear around the thirty-fifth to fiftieth setiger. There seems to be a tendency, in specimens from areas north of Chesapeake Bay, for the gills to increase in length relative to the dorsal lamellae.

The anterior notopodial lamellae are elongate, foliaceous and somewhat tapering. They gradually become increasingly rounded until by setigers 30–40 they are low, rounded and very broad (Fig. 59). In posterior setigers they then become leaflike and pointed (Fig. 60). The neuropodial lamellae are anteriorly large and rounded. They gradually become less well-developed until in posterior setigers they are similar in appearance to those of the notopodia (Fig. 60).

The anterior setae are arranged in two rows. Those of the anterior row resemble setae found among species of the genus *Dispio*. They are stout, curved and only slightly sheathed, appearing bilimbate. They are heavily granulated along almost the entire length of the shaft. Setae of the posterior row are longer, thinner, and without granulations. In the lower part of most neuropodial fascicles, three to four setae are slightly separated from the others (Figs. 59, 60). They are longer, granular for about half the length of the shaft, slightly unilimbate, and curved ventrally. The notosetae are similar in appearance to the neurosetae. In more posterior setigers, the neu-

rosetae decrease in number in both rows and are almost the same length. The limbation is more apparent. There are two to three lower acicular setae, which occupy the same position and are similar in appearance to the typical *Prionospio* sabre-setae (see below).

Bidentate hooded hooks first appear in the neuropodia of setigers 24–51 (Fig. 61) and in the notopodia of setigers 39–60 (Figs. 62, 63). There are slender companion setae as long as or slightly longer than the hooded hooks (Figs. 59, 60, 64). They are faintly granulated near the distal end, with a very narrow sheath extending one-third to one-half the length of the shaft. In far posterior setigers (120–135), both granulations and limbations becomes more pronounced.

The hooks have no apparent secondary hood and the primary hood is long and slender (Figs. 61, 62, 63). The teeth on the hooks are often worn so that the upper tooth is missing. The main tooth varies in acuteness and in the angle it forms in relation to the shaft. The newer setae have very neatly pointed teeth, whereas the older ones become blunt with wear. A posterior setiger may possess what appears to be tridentate hooks but this is not a consistent character.

The pygidium bears numerous cirri, some of which may be bifurcated or bilobed (Fig. 65). In some specimens the cirri seem to be shorter on the ventral edge. The number of cirri is quite variable.

Biology: This species is typically estuarine.

Material: *Scolecolepides arctius* Paratype: Museum of Comparative Zoology; Gaspé, Quebec; Maine – Georgetown Island, Barter Island, Robbinston, St. Croix River, Sheepscot River, Phippsburg, Penobscot Estuary, Fort Popham; New Hampshire – Hilton Park, Sheafes Point in Little Harbor, Portsmouth, Beard's Creek near Durham, Emerson Beach, Oyster River, Rye Harbor, Wentworth, Portsmouth; Massachusetts – Woods Hole, West Falmouth, Hadley Harbor, Megansett Estuary, Martha's Vineyard, Sandwich, Naushon, Gloucester, Fresh Brook, Vineyard Sound, Pocasset River; Rhode Island – Greenwich Bay, Galilea; Connecticut River, Connecticut; New York – Dennings Point, Long Island Sound; Great Egg Harbor, New Jersey; Virginia – James Point, Bell Rock; Ediste River, South Carolina.

Distribution: Newfoundland to North Carolina; Alaska.

Discussion: The type specimen of *Scolecolepides arctius* Chamberlin, 1920 is no longer in the collections of the Victoria Memorial Museum, Ottawa, but the paratypes from the collections of Museum of Comparative Zoology, Harvard were examined. One was in fairly

good condition and as no valid difference could be detected the species is herein synonymized with *Scolecolepides viridis*. There seems to be a good possibility that *Scolecolepides benhami* Ehlers, 1907, from New Zealand is also a synonym of *S. viridis*. However, the type deposited in the Berlin Museum has been lost (Dr. G. HARTWICH, personal communication). ESTCOURT (1967) reports *S. benhami* from a New Zealand estuary and from the original description it would be difficult to distinguish his specimens from *S. viridis*.

Genus **Spiophanes** Grube, 1860

Type-species (by monotypy): *Spiophanes kroyeri* Grube, 1860. Gender: masculine.

Diagnosis: Spionid species lacking branchiae. Body with three more or less well-differentiated regions; first four setigers with well-developed dorsal and ventral lamellae (dorsal lamellae sometimes misidentified as gills); setigers 5 through 14 generally with interramal thread glands, forming bacillary setae (often broken off), with poorly developed padlike neuropodial lamellae; setiger 15 to posterior of body with neuropodial hooks and poorly developed neuropodial lamellae. With one to two large curved setae in neuropodia of setiger 1. With anterior capillary setae only. With capillary notosetae throughout the body, no notosetal hooks. With posterior neuropodial bidentate or tridentate hooded hooks and a sabre-seta present in most setigers. Pygidium with anal cirri. With bulbous proboscis. Pelagic development, predominantly planktotrophic (HANNERZ, 1956).

Spiophanes bombyx (Claparède, 1870)

(Figures 66–75)

Spiophanes bombyx, WEBSTER & BENEDICT, 1884, p. 735. – MESNIL, 1896, p. 249; 1897, pp. 91, 92. – SAINT-JOSEPH, 1898, p. 352. – MCINTOSH, 1909, p. 167; 1915a, p. 182; 1925, p. 85. – ELWES, 1910, p. 62. – SOUTHERN, 1914, p. 102. – ALLEN, 1915, p. 629. – CAULLERY, 1915, p. 108. – FAUVEL, 1916, pp. 420, 439; 1927, p. 41; 1936, pp. 5, 59. – ELIASON, 1920, p. 50; 1962a, p. 49; 1962b, p. 263. – SÖDERSTRÖM, 1920, p. 243. – BERKELEY, 1927, p. 12. – AUGENER, 1932a, pp. 661, 671. – OKUDA, 1937a, p. 222. – ANNENKOVA, 1938, p. 172. – HARTMAN, 1945, pp. 8, 31; 1951, p. 85; 1963b, p. 45; 1965a, pp. 389, 391; 1965b,

p. 152; 1966, p. 22. – THORSON, 1946, p. 91. – USHAKOV, 1950, p. 200; 1965, p. 244. – WESENBURG-LUND, 1951, p. 71. – BERKELEY & BERKELEY, 1952, p. 22; 1954, p. 463. – HANNERZ, 1956, pp. 33, 160, 167, 171, 180, 182–184, 188. – KIRKEGAARD, 1959, p. 19. – BELLAN, 1962, p. 15; 1964, p. 110. – RIOJA, 1962, p. 184. – SANDERS, *et al*, 1962, p. 66. – HAMOND, 1963, p. 570; 1966, p. 408. – RULLIER, 1963, p. 209. – IMAJIMA & HARTMAN, 1964, p. 289. – ORRHAGE, 1964a, pp. 338, 359. – WELLS & GRAY, 1964, p. 74. – GIBBS, 1965, p. 33. – REISH, 1965, p. 143; 1968a, p. 84. – GUILLE & LAUBIER, 1966, p. 272. – SIMON, 1967, p. 424. – CABIOCH, L'HARDY & RULLIER, 1968, p. 50.

Spio bombyx CLAPARÈDE, 1870, p. 485. – PANCERI, 1875, p. 28. – EISIG, 1887, p. 153. – MICHAELSEN, 1897, p. 154.

Spio crenaticornis, GIARD, 1881, p. 600. – *Not* Montagu, 1813.

Spiophanes verrilli WEBSTER & BENEDICT, 1884, p. 728. – PROCTER, 1933, p. 141.

Diagnosis: Prostomium with conspicuous frontal horns. First four parapodia dorsally situated, neuropodia reduced thereafter. Neuropodial bidentate and tridentate hooded hooks beginning on setigers 15–16. Notopodial setal capillaries throughout. Pygidium with two anal cirri.

Description: The body length is up to 25 mm, with 73 setigers. The prostomium is T-shaped, somewhat round to almost straight anteriorly (Fig. 66). The frontal horns are very prominent, variable in length, and usually elongate and thin. The prostomium tapers posteriorly and extends to about the level of setiger 1. There are up to four subequal eyes or these may be lacking.

The first four parapodia are situated slightly more dorsally than the following, with somewhat foliaceous parapodial lamellae. The notopodial lamellae of setiger 1 are long, thin and tapered, somewhat longer than those of the neuropodia (Fig. 68). The notopodial lamellae of the following few setigers are similar but wider and basally thicker (Fig. 69). The neuropodial lamellae become very reduced and cushion- or padlike (Fig. 67). The parapodia become glandular and bear an interramal opening through which the supernumerary setae emerge (Figs. 67, 69). Setigers 5 through 15 (variable) possess these parapodial thread glands (Figs. 67, 70). Notopodial lamellae remain similar throughout the entire body, becoming more attenuated. In posterior setigers the neuropodia are low and reduced (Fig. 71).

Setiger 1 bears one to two stout recurved neurosetae which appear

smooth basally and granular distally (Figs. 66, 68, 72). When observed with the phase contrast microscope, tiny "hairs" are visible along the distal portions of the setae, giving them a frayed appearance. The remaining neurosetae of setiger 1 are either short, slightly granular and bilimbate, or longer, appearing unilimbate. Notosetae are usually slightly unilimbate, though some show no limbations under high dry magnifications. In more posterior setigers, the limbations become very pronounced in both parapodial rami (Fig. 73). On those setigers with padlike neuropodia, the neurosetae are curved around the pad and the granulations are concentrated in this curved area. Neuropodial hooks appear about setigers 15–16, accompanied by a stouter, ventrally curved sabre-seta (Fig. 70). The hooks are predominantly bidentate, with a small, reduced hood extending from the main hook to the shaft (Figs. 74, 75). In lateral view the hood is visible only in this area but in frontal view it is seen to bulge laterally. Occasionally hooks are found with a tiny third tooth only visible laterally (Fig. 75).

The nuchal organs are present in the form of two longitudinal bands extending posteriorly from the prostomium to about the level of the third to fourth setiger.

The pygidium bears two anal cirri varying in length.

Biology: *Spiophanes bombyx* was collected from intertidal sand flats and at shallow depths. It has been dredged from deeper water and extends onto the continental shelf. It was found in tubes of a thin membranous or mucoid nature covered with fine quartz grains.

Mr. KENNETH EDDS, University of Rhode Island (personal communication), has found that the bacillary or supernumerary setae are retractile on specimens from the region of Woods Hole, Massachusetts. The pair of rounded structures or so-called thread glands in segments five to eight appear to rotate when the setae are extended and withdrawn.

Material: Maine – Booth Bay Harbor, Penobscot Bay, Cape Newagen, Pemaquid Beach, Rockland, Brave Boat Harbor north of Sea Point, Sea Point; New Hampshire – Rye Harbor, Hampton Beach, Portsmouth, Wentworth; Massachusetts – Barnstable Harbor, Wellfleet Harbor, West Falmouth Harbor, Marblehead Harbor, Orleans, Cape Cod, Woods Hole, Cape Cod Bay off Sagamore Beach, Provincetown; Virginia – Chesapeake Bay off Rappahannock River, Bell Rock, York River; Seahorse Key, Florida; Grand Isle, Louisiana; Port Aransas, Texas; San Juan Island, Washington; Netherlands; Bering Sea.

Distribution: Cosmopolitan.

Discussion: The neuropodial hooks of *Spiophanes bombyx* are characterized as being bidentate throughout; however, on most specimens a few hooks were found with a very small third tooth, visible only in lateral view. MESNIL (1897) mentioned this third tooth when comparing *S. bombyx* and *S. kroyeri*, calling it rudimentary. Though the hooks of *S. bombyx* can be distinguished from those of species with tridentate hooks, one should be aware of the fact that tridentate forms are occasionally present. With regard to the hooded hooks, DAY (1961) reported that, in the species he describes as *S. soderstromi*, adult hooks lacked hoods, while those of juveniles had reduced hoods. He further suggested that in *S. bombyx* the partial hood was a result of a growth difference and that hooks of adults may possibly lack hoods. In the present study, however, all of the adult specimens examined possessed hooded hooks.

DAY (1967) reported and figured specimens, identified as *S. bombyx*, with an occipital antenna; however, this species is characterized as lacking such an antenna. I suspect that his specimens either belong to another species or the report of the antenna was an observational error.

Spiophanes wigleyi Pettibone, 1962

(Figures 76–85)

Spiophanes wigleyi PETTIBONE, 1962, p. 83. – HARTMAN, 1965a, pp. 11, 38, 147, 153, 236, 242, 315.

Diagnosis: Prostomium without frontal horns and occipital antenna. With three to five eyes. Peristomium surrounding prostomium as a low hood. First three setigers located more dorsally. First four setigers with well-developed lamellae. Neuropodial lamellae poorly developed thereafter. With one stout curved neuroseta in neuropodia of setiger 1. With anterior capillary setae. With capillary notosetae only. With tridentate neuropodial hooded hooks beginning on setigers 15–16; bidentate in more posterior setigers; may be accompanied by capillary setae. With one to two lower curved neurosetae, beginning on setiger 9. Pygidium with four to six anal cirri.

Description: The body length is up to 10.5 mm, with 40 setigers. The prostomium is anteriorly rounded, without frontal horns (Fig. 76). It tapers slightly posteriorly, with a pigmented area at the posterior tip. There were three to five eyes on specimens examined (usually four). The anterior two are deep set and somewhat crescent-shaped, while the posterior ones are distinct and rounded. The dorsal sensory organs begin anteriorly at the posterior edge of the prostomium, extending back to the level of setiger 3, then turning back and extending anteriorly almost to setiger 1. The peristomium is wide and surrounds the prostomium ventrally and laterally forming a low hood.

On setigers 1–4 the parapodial lamellae are well-developed (Fig. 76). Notopodial lamellae are tall, thin and sharply tapered. Neuropodial lamellae are all leaflike, tapered, and somewhat angular. On setiger 1 the dorsal lamellae are shorter and thinner than those of the neuropodia (Fig. 76). Notopodial lamellae of setigers 2 and 3 are thick basally and taper sharply, becoming long and thin; the neuropodial lamellae are subulate (Fig. 77). On the fourth setiger, the notopodial lamellae are shorter, lacking the thin tip; the neuropodial lamellae are padlike (Fig. 78).

Parapodia of the mid-body region (setigers 5 through 14) have thread glands and occasionally heavy bacillary setae. The neuropodial lamellae are prominent, padlike, while those of the notopodia are similar to but longer than those of setiger 4 (Fig. 79). The notopodial lamellae of setigers 9 through 15 appear reddish-brown basally.

In the posterior body region, the notopodial lamellae are again long, tapered and broader basally; the ventral lamellae are considerably shorter and more flattened than those of the midbody region (Fig. 80). About setiger 14 or 15 and continuing for a variable number of setigers, on the one specimen collected in this study and on the type material, prominent "wings" or lateral expansions appear basally on the notopodial lamellae (Figs. 81, 82). Transverse dorsal ciliated ridges appear about setiger 15, becoming extremely prominent on setigers 18–30 and inconspicuous thereafter.

Anterior setae are all capillary with the exception of the stout, curved neurosetae in setiger 1 (Fig. 76). In setigers 1 to 3, the neuro-

setae are arranged in two rows; those of the anterior row are slightly shorter, unilimbate, and granular (Fig. 83); those of the posterior row are similar but longer. Notosetae are somewhat similar but longer and may be uni- or bilimbate (Fig. 84). In more posterior setigers, the neurosetae are curved around the padlike neuropodial lamellae. They are very granular in the curved area and appear to be either uni- or bilimbate; the notosetae are longer, with broad sheaths. By setiger 9, the neurosetae are reduced to a single row, with one seta ventrally located, somewhat apart from the others. The neuropodial hooded hooks begin on setigers 15–16 and, under low power observation, they appear bidentate, but with the oil objective those of the anterior setigers are seen to be clearly tridentate (Fig. 85). The hood is very reduced and is visible only between the main tooth and the shaft. There is no evidence of a secondary hood.

The pygidium was missing in the single specimen from the Gulf of Mexico but on the type material from Massachusetts, there are four to six anal cirri. There are no genital pouches.

Biology: The original material was dredged in 39–74 fathoms off Massachusetts and the single specimen from the Gulf of Mexico was collected from the intertidal zone. *Spiophanes wigleyi* was dredged from bottoms of fine to coarse sand and gravel. Tubes are thin and membranous, covered with sand and debris (PETTIBONE, 1962).

Material: *Spiophanes wigleyi* Holotype: USNM 30401, Paratype: USNM 30402; New Brunswick; Georges Bank area, Massachusetts; Panama City, Florida.

Distribution: Atlantic: Massachusetts to North Carolina; Gulf of Mexico.

Discussion: This species was originally described as possessing only bidentate hooded hooks. However, DAY (personal communication) observed specimens from Beaufort, North Carolina, with tridentate hooks anteriorly and bidentate hooks on more posterior setigers. This is the case for the specimen from Panama City and also on type specimens. The third tooth is easily overlooked due to its small size and its orientation. In posterior setigers it seems to be absent, perhaps due to wear. The transition from tridentate to bidentate hooks appears to be indefinite, varying from specimen to specimen.

Spiophanes wigleyi is similar to species of the *S. bombyx* group in

that it lacks an occipital antenna. The tridentate hooded hooks are apparently unique but it differs with respect to other characters (see key).

The species of the genus *Spiophanes* were reviewed by PETTIBONE (1962, p. 85). More recently, an additional subspecies (LAUBIER, 1964) and species (HARTMANN-SCHRÖDER, 1965) have been added.

S. kroyeri Grube, 1860. Greenland and cosmopolitan. [Includes *S. cirrata* Sars, 1871, Norway; *S. malayensis* Caullery, 1915, Malay Archipelago; *S. fimbriata* Moore, 1923, California]

S. bombyx (Claparède, 1870). France and cosmopolitan. [Includes *S. verrilli* Webster & Benedict, 1884, Massachusetts]

S. longicirrus Caullery, 1915. Malay Archipelago.

S. missionensis Hartman, 1941. California.

S. anoculata Hartman, 1960. California.

S. berkeleyorum Pettibone, 1962. British Columbia and Washington. [Includes *S. cirrata*, Berkeley & Berkeley, 1952; *not* Sars, 1871]

S. wigleyi Pettibone, 1962. Massachusetts.

S. kroyeri reyssi Laubier, 1964. Mediterranean.

S. chilensis Hartmann-Schröder, 1965. Chile.

The following species are indeterminable, since certain crucial characters are not mentioned in their description:

S. ushakovi Zachs, 1933. North Japan Sea.

S. tcherniai Fauvel, 1950. Antarctic.

S. soderstromi Hartman, 1953. Antarctic.

The three species listed below are referred to other genera, following PETTIBONE (1963, p. 85).

S. tenuis Verrill, 1879. Massachusetts. (= *Prionospio steenstrupi* Malmgren, 1867).

S. pigmentata Reish, 1959. California. (= *Microspio*)

S. pallidus Hartman, 1960. California. (= *Prionospio*)

KEY TO SPECIES OF SPIOPHANES

1a. Prostomial occipital antenna present. Neuropodial hooks without a hood 2

1b. Prostomial occipital antenna absent. Neuropodial hooks hooded 4

2a. First four notopodial lamellae or lobes long, greenish. Neuropodial lamellae pointed, subulate, not enlarged . . . . . *S. longicirrus* Caullery

2b. Enlarged noto- and neuropodial lamellae or lobes on setigers 1–4 3

3a. Notopodial lamellae of posterior setigers enlarged, white. Interramal genital pouches absent . . . *S. berkeleyorum* Pettibone
3b. Notopodial lamellae of posterior setigers digitiform. Interramal pouches present; first appearing on setigers 14–17. A. Bacillary setal shafts barbed. Pygidium with three pairs of anal cirri . . . . . *S. kroyeri kroyeri* Grube
B. Bacillary setal shafts smooth. Pygidium with two anal cirri (occasionally bifurcated) . . . . . *S. kroyeri reyssi* Laubier

4a. Prostomium with lateral horns 5
4b. Prostomium without lateral horns. Pygidium with four to six anal cirri . . . . . *S. wigleyi* Pettibone

5a. Lateral horns narrow, elongate 6
5b. Lateral horns short, blunt 7

6a. Parapodial lamellae of setigers 1 to 4 elongate, tapered. Notopodial lamellae of setiger 1 well-developed . . . . . *S. bombyx* (Claparède)
6b. Parapodial lamellae of setigers 1 to 5 foliaceous. Notopodial lamellae of setiger 1 reduced to papillar lobe . . . . . *S. anoculata* Hartman

7a. Pygidium short, with two anal cirri . . . . . *S. chilensis* Hartmann-Schröder
7b. Pygidium long, with two anal cirri and a thick mid-ventral papilla . . . . . *S. missionensis* Hartman

Genus **Malacoceros** Quatrefages, 1843. Emended Pettibone, 1963

Malacoceros QUATREFAGES, 1843, p. 8. Type-species, designated by PETTIBONE, 1963, p. 98. *Spio vulgaris* JOHNSTON, 1827, p. 335. Gender: masculine.
Colobranchus SCHMARDA, 1861, p. 66. Type-species, by monotypy: *C. tetracerus* SCHMARDA, 1861, p. 66. Gender: masculine.
Uncinia QUATREFAGES, 1865a, p. 439. Type-species, by monotypy: *Colobranchus ci-*

liatus KEFERSTEIN, 1862, p. 118 (= *Colobranchus tetracerus* Schmarda, 1861). Gender: feminine.

Scolecolepis MALMGREN, 1867, p. 90. Type-species, original designation: *Spio vulgaris* JOHNSTON, 1827, p. 335. Gender: feminine.

Subgenus **Rhynchospio** Hartman, 1936

Rhynchospio HARTMAN, 1936, p. 51. Type-species, by monotypy: *R. arenincola* HARTMAN, 1936, p. 51. Gender: feminine.

Diagnosis: Prostomium with frontal horns. Branchiae beginning on setiger 1 (subgenus *Malacoceros*), or on setiger 2 (subgenus *Rhynchospio*). Branchiae usually extending to near posterior end of the body, free from dorsal lamellae except basally. Notopodial setae capillaries only, with neuropodial hooks. Hooks bidentate or tridentate, occasionally quadridentate. Pygidium with anal cirri. Thick-shelled eggs with membrane vesicles; pelagic development, predominantly planktotrophic (HANNERZ, 1956).

Discussion: Determining hook dentations in this genus is further complicated by the fact that the hooks are often worn, resulting in a blunt top. It becomes increasingly evident that in certain spionid genera use of hook dentations as a primary species character has led to no end of confusion. The present study has emphasized the fact that, unless the hooks have been examined under oil immersion, the reports of dentation really cannot be trusted.

Malacoceros needs to be revised, based on type material, with a careful survey of the hooks and other characters as well.

Malacoceros (Malacoceros) vanderhorsti (Augener, 1927)

(Figures 86–92)

Scolecolepis vanderhorsti AUGENER, 1927, p. 64.
Malacoceros (*Malacoceros*) *vanderhorsti* PETTIBONE, 1963, p. 99.

Diagnosis: Prostomium with laterally projecting frontal horns. With four to eight eyes irregularly arranged. Tridentate neuropodial hooded hooks beginning on setigers 70–90. Many setigers also with

quadridentate hooks. With ventral acicular setae. Neuropodial lamellae rounded throughout, without nipplelike attenuation. Pygidium with two anal cirri.

Description: The body length is up to 55 mm, with 151 setigers. The prostomium is anteriorly curved (preserved), with prominent thick frontal horns, directly laterally (Fig. 86), narrowing posteriorly and becoming broadly triangular. The posterior one-third to one-fourth is an elevated area, somewhat like a caruncle or keel beginning about the level of setiger 1 and extending to near the end of setiger 2. There are numerous eyes irregularly arranged, three to five on each side. The peristomium is inconspicuous and bears two small globular papillae or bumps, laterally beneath the prostomial frontal horns.

The anterior half of the body is considerably flattened. The parapodia of the first setiger are small and dorsally located; those of setiger 2 are intermediate in position; from setiger 3 on, the parapodia are laterally situated (Fig. 86). The neuropodial lamellae of the first two setigers are somewhat triangular and long. Interramal glandular structures first appear on setigers 1–2; they appear to continue as notopodial presetal lamellae. They are somewhat inflated, becoming smaller toward the end of the body.

Branchiae begin on setiger 1 and continue to the posterior of the body, becoming longest on setigers of the mid-body. On about setigers 15–20, the notopodial lamellae are narrow and taper to fine tips (Fig. 87). Branchiae are basally fused to the notopodial lamellae and tapered distally. They are about two to two and one-half times the length of the dorsal lamellae. The interramal glandular structures are more closely associated with the notopodia. Neuropodial lamellae are low and rounded (Fig. 87). On more posterior setigers (55–65), the notopodial lamellae are somewhat longer but otherwise similar to the anterior ones (Fig. 88). The neuropodial lamellae are very broad and rounded with a slight tip (heart-shaped); branchiae are about three and one-half times the length of the notopodial lamellae. On far posterior setigers, the neuropodial lamellae decrease in size becoming asymmetrically rounded (Fig. 89). Notopodial lamellae decrease in height, becoming increasingly angular and broader ba-

sally; the branchiae are only about one and one-half to two times the length of the notopodial lamellae.

Anterior setae of both rami are very numerous. The notosetae bear no obvious limbations and, when they are broken, there is no evidence of a sheath. They are finely granular and arranged in a whorl. The neurosetae also seem to lack limbations and are finely granular; the anterior series are longer. Within the fascicle of neurosetae, there is a ventral group of seven to eight acicular setae with very fine hair-like tips (Fig. 90). They are curved ventrally just at the tip, are slightly granular near the end and slightly unilimbate. In more posterior setigers, the setae decrease in number but remain similar to the preceeding.

Tridentate hooded hooks first appear in the neuropodia of setigers 70–90 (Fig. 91); more posterior hooks may have a fourth tooth (Fig. 92). Clefts in the hoods allow the main fang to protrude and, occasionally, more of the setal head. There is no evidence of a secondary hood. Acicular setae remain and there are a few long, thin companion setae.

The pygidium was not observed on material examined, but the type was described as bearing two anal cirri.

Biology: Specimens were collected from intertidal sand from depths of 16.5 fathoms.

Material: Grand Isle, Louisiana; *Pelican* Station 19-2: Gulf of Mexico, 29° 26.5′ N, 88° 45′ W. 16½ fathoms.

Distribution: Caribbean Sea and Gulf of Mexico.

Discussion: See *Malacoceros* (*Malacoceros*) *indicus*, discussion below.

Malacoceros (Malacoceros) indicus (Fauvel, 1928)

(Figures 93–99)

Diagnosis: Prostomium T-shaped, with prominent frontal horns. Branchiae present from setiger 1 to near end of body. With nipple-like projection on neuropodial lamellae, becoming increasingly pro-

minent on posterior setigers. With only capillary setae anteriorly in neuropodia and capillary setae only in notopodia. With quadridentate and tridentate neuropodial hooded hooks first appearing on setigers 30–49. With additional small bundle of pale neuropodial acicular setae.

Description: Body length is up to 35 mm, with 98 setigers. The prostomium is T-shaped with thick, lateral frontal horns (Fig. 93). The anterior border is often inflated. There may be none or up to six eyes, with the anterior two larger and situated just behind the frontal horns. The proboscis is bulbous and was partially everted in all specimens examined. It bears two bulbous glandular structures, one on either side in the region just behind the frontal horns.

Branchiae begin on setiger 1 and extend to near the end of the body. Anteriorly they overlap across the dorsum (Fig. 93) and are quite broad. In the middle and posterior body regions they become thin, no longer overlap and are more or less erect.

Setiger 1 is very well-developed. Neuropodial lamellae are leaflike while those of the notopodia are long, tapered, and only slightly smaller than those of the following parapodia (Fig. 93). The interramal glandular structures (= notopodial presetal lamellae) are first present on anterior setigers (generally setigers 2–4). On more posterior setigers (10–15), the dorsal lamellae are broad basally and abruptly tapered, almost attenuate (Fig. 94). Those of the neuropodia are large, rounded and have a small nipplelike projection at some point along the free edge. This is developed to a greater or lesser extent in different specimens. Still more posteriorly (about setiger 50), the notopodial lamellae and branchiae are somewhat smaller (Fig. 95). The notopodial lamellae have the same general shape but are no longer as acutely tapered. The ventral lamellae are still broad and rounded with a conspicuous nipple. There are fairly well-developed presetal lamellae or setal ridges on both rami. On posterior setigers, the notopodial lamellae are reduced to very thin, short, almost digitiform processes, about one-third to one-fourth the length of the branchiae (Fig. 96). The neuropodia are broad, low structures with very inconspicuous lamellae, consisting primarily of the now accentuated nipple.

The anterior setae are all capillary. The neurosetae are arranged in two rows, those of the anterior row being shorter and curved dorsally. They are slightly, if at all granular and there are no apparent limbations even when examined with oil immersion optics (Fig. 97). Those of the posterior row are slightly unilimbate but otherwise similar. The notosetae are considerably longer and all are slightly unilimbate (Fig. 98). The limbations bear "striations" which under oil appear to be actual structures, such as ridges or spines. A small bundle of pale acicular neurosetae accompany the more typical capillaries and hooks, appearing behind the two rows of capillaries. The neuropodial hooded hooks first appear on setigers 30–49 (Fig. 99). They are quadridentate, the fourth tooth being often overlooked unless viewed under oil. The hood is open around the teeth and for a short distance laterally. The hooks bear a primary hood only. There is a small dorsal bundle of thin capillary setae.

The posterior ends were missing on all the specimens examined.

Biology: Specimens were collected in shallow water from sandy bottoms and *Thallasia* beds.

Material: Bimini – South Midmouth of Creek, North Tohas Bay; Puerto Rico – Ponce, Arecibo.

Distribution: Bimini; Caribbean.

Discussion: The fourth tooth of the hooded hooks is very tiny and easily overlooked. In fact, when looking at a single neuropodium from the posterior setigers, it is not unusual to find what appear to be both tri- and quadridentate hooks or to find some with apparently all tridentate or all quadridentate hooks. This would probably explain how some authors describe the hooks as tridentate and others as quadridentate. FAUVEL (1928) described *Scolelepis indica* as having bidentate hooks and nipples on the ventral lamellae. Later BERKELEY & BERKELEY (1941) report the same species and mention that some posterior setigers had tridentate hooks. DAY (1967) reports it as having bidentate hooks yet figures a tridentate hook. After examination of the type the species proved to be *Malacoceros* (*M*) *indicus*, as it possesses quadridentate hooks. Because of the variability which has been found concerning the nature of the hooks

in this genus, species should not be characterized solely on this character unless they have been carefully examined under high magnifications.

USHAKOV (1948) reported two new species of *Scolelepis* from the coast of Murman, *S. murmanica* Zachs and *S. derjugini*. The descriptions are very incomplete and deal mainly with the first appearance of hooded hooks and the number of teeth. The range of these characters in *M. (M.) derjugini* overlaps the new species from the Caribbean but because no mention is made of the neuropodial lamellae, it is considered indeterminable.

As no key can be presented until the revision is completed, for the present, the two species from the Gulf of Mexico and Caribbean can be distinguished according to Table 3.

Malacoceros (Rhynchospio) glutaeus (Ehlers, 1897)

(Figures 100–111)

Scolecolepis glutaea EHLERS, 1897, p. 83; 1901, p. 165.
Scolecolepis cornifera EHLERS, 1913, p. 509.
Microspio glutaea, SÖDERSTRÖM, 1920, p. 252. – AUGENER, 1932b, p. 108.
Rhynchospio arenincola HARTMAN, 1936, p. 51. – WIESER, 1959, pp. 105, 106. – BANSE, 1963, p. 203.
Scolelepis cornifera, MONRO, 1939, p. 125. – FAUVEL, 1953b, p. 9.
Scolelepis cornigera [sic], FAUVEL, 1952, p. 297.
Rhynchospio glutaea, HARTMAN, 1953, p. 42; 1955, p. 182; 1966, p. 21. – Day, 1961, p. 491; 1967, p. 478. – HARTMANN-SCHRÖDER, 1965, p. 213.
Rhynchospio cf. *arenincola* WIESER, 1959, p. 105.
Rhynchospio arenicola [sic] *asiatica* CHLEBOVITSCH, 1959, p. 175; 1961, p. 196.
Rhynchospio glutea [sic], HARTMANN-SCHRÖDER, 1962a, p. 138.
Malacoceros (Rhynchospio) arenincolus asiaticus, PETTIBONE, 1963, p. 90.
Malacoceros (Rhynchospio) glutaeus, PETTIBONE, 1963, p. 90.
Malacoceros (Rhynchospio) arenincolus, PETTIBONE, 1963, p. 90.

Diagnosis: Prostomium with frontal horns. Branchiae beginning on setiger 2, overlapping on dorsum and continuing to near end of body. Tridentate and quadridentate neuropodial hooded hooks first appearing on setigers 13–21. Pygidium with variable number of anal cirri.

TABLE 3

COMPARISON OF THE SPECIES OF MALACOCEROS (MALACOCEROS) from the Gulf of Mexico and the Caribbean

	M. (M.) vanderhorsti	*M. (M.) indicus*
First appearance of hooded hooks	setigers 70–90	setigers 30–49
Neuropodial hooded hooks	mostly tridentate	mostly quadridentate
Outer border of neuropodial lamellae	without nipple	with nipple

Description: The length of the body is up to 5.3 mm, with 29 setigers. The prostomium possesses frontal horns, directed somewhat anteriorly (Fig. 100). There are two pairs of eyes, with the anterior pair larger or the same size as the posterior. Some specimens possess additional anterior eyespots. Anterior eyes are often crescent-shaped The peristomium consists of lateral expansions or pouches which extend ventrally to form the lower lip.

Branchiae begin on setiger 2, curving dorsally and often overlapping (Fig. 100). Those of the mid-body region are about two to three times the length of the notopodial lamellae. Anterior branchiae are more erect. Branchiae are absent from about three to five setigers from the posterior end, with the last few appearing short and stubby.

Anterior neuropodial lamellae are fairly broad and subtriangular (Fig. 101). More posteriorly they become more rounded and eventually in the posterior setigers they are short and somewhat digitiform. Anterior notopodial lamellae are foliaceous, becoming increasingly digitiform in posterior setigers (Fig. 102).

Anterior setae are all capillaries. The neurosetae are arranged in two series, the anterior row containing short, wide, granular setae (Figs. 103, 104), and the posterior row with longer, curved, thin, non-granulated setae (Fig. 104). The notosetae are longer, but are similar in kind and arrangement. The granulations appear almost always on the edge within the sheath. About the level of the ninth setiger, two to three ventral neuropodial setae are somewhat separate from the others in the fascicle; in setigers 13–18, tridentate hooded hooks appear, replacing some of the more dorsal setae. The

hooks are accompanied by three to four companion setae (Fig. 105) and the ventral setae are now curved appearing like more typical sabre-setae. The hooks appear to have two small teeth above the large fang, though in hooks of anterior setigers, the second tooth is very easily missed because it is so small (Figs. 106, 107). In posterior setigers, there is a suggestion of a third tooth above the fang which becomes obvious in frontal-lateral view (Fig. 108). Some of the hoods may be covered with pale yellow granules or accretions (Fig. 108). The primary hood encloses the entire head of the hook and there does not appear to be a secondary hood.

The pygidium bears a variable number of anal cirri, usually four to eight (Figs. 109, 110). Two of them are generally thick, sometimes shorter, with two to six thinner ones arranged laterally and dorsally.

Two juvenile specimens of twenty-eight setigers each were collected from Key West, Florida. They are similar in most characters to the adults, the main difference being the first appearance of the tridentate neuropodial hooks on setiger 9. One of the specimens had red pigment in the mid-dorsal region of the seventh setiger, in front of and behind setiger 1, at the tips of the first seven notopodial lamellae, around the pygidium and on the anal cirri.

Biology: This species has been collected from shallow, sandy tide pools (HARTMAN, 1936), upper sublittoral and low littoral in *Laminaria*, muddy sand, sponge and under encrusting ice (CHLEBOVITSCH, 1959). Specimens were found on San Juan Island in habitats with tide levels of −2 ft. (BANSE, 1963) and at +2 to +3 ft. (WIESER, 1959). Thus the animals may be exposed for several hours. Specimens from the Gulf of Mexico were sieved from subtidal sand and collected from *Thalassia* holdfasts.

Material: *Rhynchospio arenicola* · Paratype: USNM 20221; Florida – Patio Beach, and near USN Hospital, Key West; Washington – False Bay, San Juan Island; Shilshole Bay, Ballard.

Distribution: Kurile Islands, north of Japan; Washington; California; Chile; Antarctic and Subantarctic; South Georgia; South Africa; Florida.

Discussion: Species of *Malacoceros* (*Rhynchospio*) have previously been separated primarily on the basis of the anal cirri. The present collections from Florida, however, seem to indicate that this

is not a reliable character. Specimens from one sample have the following kinds and arrangements of anal cirri: two ventral short, thick cirri and six thinner lateral ones; two thick ventrals, five lateral and dorsals; two thick ventrals, two somewhat thinner dorsals. BANSE (1963) reports specimens with: two long dorsal cirri, two shorter ventrals, an intermediate fifth and a sixth just budding; one conical cirrus and the remainder filiform; eight cirri. The holotype of *R. arenincola* possesses two pairs of bilobed cirri on each side, appearing as eight cirri. One of the paratypes possesses two thick ventrals and three thinner ones located only on one side; those of the other side were undoubtedly lost and might have regenerated, resulting in extreme variations (Fig. 111). CHLEBOVITSCH (1959) reported for specimens of *R. arenicola asiatica* from the Kurile Islands eight very slender anal cirri. Because of the obvious variation in this character, it is not used to distinguish species in this paper. Therefore, HARTMAN'S species and CHLEBOVITSCH'S subspecies are synonomized with *M. glutaeus*. Future collections and examination of material from the type locality of *M. glutaeus* may demonstrate that they are not synonomous but, at the present, based on available literature and collections, they cannot be distinguished. The type of *Rhynchospio glutaeus*, deposited in the Berlin Museum, is now missing from the collections (personal communication, Dr. G. HARTWICH).

R. arenincola asiatica Chlebovitsch was separated from *R. arenicola* Hartman on the basis of a difference in size of the anterior and posterior eyes. This would not seem to be a valid character, as even the number of eyes varies on specimens in a single collection.

The distribution pattern of *M. glutaeus* is very off-balanced with the material from Florida. I suspect it is not in reality a discontinuous distribution but rather a result of lack of collections from intermediate areas. The specimens are often very small and easily overlooked. Further collections will show whether this is the case or if the Florida material actually represents a new species.

Malacoceros (Rhynchospio) inflatus sp. n.

(Figures 112–117)

Diagnosis: Anterior body region inflated, beginning behind prostomial frontal horns. Prostomium ending bluntly at level of setiger 1. Two pairs of eyes. Peristomium very reduced. Branchiae beginning on setiger 2, not overlapping. Bidentate neuropodial hooded hooks, beginning on setiger 37.

Description: The length of the body is up to 5.3 mm, with 29 setigers. The prostomium is increasingly elevated from just behind the frontal horns, ending abruptly about the level of setiger 1 and not extending posteriorly as a keel or elevation (Fig. 112). There are two pairs of eyes; the anterior pair is larger and is obscured from dorsal view due to the elevation of the prostomium; the posterior pair is closer together and visible dorsally. The peristomium is very inconspicuous, being closely applied to the prostomium and not forming a ridge, hood, or collar. It extends ventrally around the mouth and does not protrude laterally.

Branchiae are generally about twice the length of the dorsal lamellae. They decrease in length posteriorly until they are about the same length as the lamellae and finally disappear on the thirty-ninth setiger.

The anterior notopodial lamellae are subtriangular in shape (Fig. 112); by setiger 4, they have become somewhat acuminate (Fig. 113). Anterior neuropodial lamellae are also triangular and eventually become broad and bluntly rounded (Fig. 113). Both lamellae narrow posteriorly until, at the level of setiger 39, the notopodial lamellae are fingerlike and those of the neuropodia are ovoid (Fig. 114). This tendency continues and, on posterior setigers, both are fingerlike, the notopodial lamellae being slightly shorter than those of the neuropodia (Fig. 115). Interparapodial pouches begin on setiger 5.

The anterior notosetae are thin and not particularly granular. There is a slight sheath giving either a unilimbate or bilimbate appearance. Some are slightly shorter than others, but they are generally the same length. The neurosetae are similar to the notosetae. A

single neuropodial tridentate hooded hook appears on setiger 37 and the number does not increase until setiger 44. The hooks are very long and are accompanied by a few long, thin companion setae (Figs. 115, 116). There is no secondary hood and the primary hood appears to insert on or to be closely applied to the main fang (Fig. 117). Posterior hooks are quadridentate, having a third medial tooth above the other three. There are small, thin, faintly sheathed sabre-setae.

The anterior body surface is speckled with red-brown pigment, concentrated on the anterior and posterior borders of the prostomium and along the mid-dorsal area of the body (Fig. 112). The posterior end is missing.

Biology: This species was collected from subtidal sand off the west coast of Bimini.

Material: One incomplete specimen from the west coast of Bimini collected intertidally by Dr. M. L. JONES. Designated Holotype: USNM 40178.

Distribution: Bimini.

Discussion: *M. inflatus* differs from *M. glutaeus* in the first appearance of the hooded hooks, inflation of the anterior body region, shape of posterior lamellae and in the fact that the branchiae do not continue to as near the posterior of the body. It is recognized that to describe a new species on the basis of a single specimen is perhaps unwise. This specimen, however, does not belong to a previously known species and, rather than call it *Malacoceros sp.* or ignore its presence, it has been decided to give it a name until more material can be collected and its taxonomic position more firmly established.

Genus **Scolelepis** Blainville, 1828, Emended Pettibone, 1963

Scolelepis BLAINVILLE, 1828, p. 492. Type-species, by monotypy: *Lumbricus squamatus* MÜLLER, 1806, p. 39. Gender: feminine.

Aonis AUDOUIN & MILNE-EDWARDS, 1833, p. 400. Type-species, by monotypy: *A. foliosa* AUDOUIN & MILNE-EDWARDS, 1833, p. 402. (= junior homonym of *Aonis* SAVIGNY, 1820, p. 45).

Nerine JOHNSTON, 1838, p. 68. Type-species, designated by Quatrefages (1843, p. 9): *N. coniocephala* JOHNSTON, 1838, p. 70. (= *Aonis foliosa* Audouin & Milne-Edwards).

Pseudomalacoceros CZERNIAVSKY, 1881, p. 361. Type-species, by monotypy: *Malacoceros longirostria* QUATREFAGES, 1843, p. 13. (= *Lumbricus squamatus* Müller, 1806).

Scolecolepis MICHAELSEN, 1897, p. 45. *Not* MALMGREN, 1867, p. 90.

Pseudonerine AUGENER, 1926, p. 159. Type-species, by monotypy: *P. antipoda* AUGENER, 1926, p. 159 (= junior homonym of *Pseudonerine* CZERNIAVSKY, 1881, p. 361).

Subgenus **Nerinides** Mesnil, 1896

Nerinides MESNIL, 1896, p. 152. Type-species, original designation: *Nerine longirostris* SAINT-JOSEPH, 1894, p. 74 (= *Nerinides cantabra* Rioja, 1918) (= junior homonym of *Malacoceros longirostris* QUATREFAGES, 1843, p. 13).

Diagnosis: Prostomium anteriorly tapered to a more or less narrow point, usually extended posteriorly as a narrow keel. Palps large in diameter and elongate, with large base for attachment. Peristomium enlarged, elongate, surrounding prostomium in hoodlike fashion, with lateral extensions developed to a varying extent. Branchiae beginning on setiger 2, continuing to or almost to posterior end; completely fused to dorsal lamellae or with only small portion of tip free. Fusion usually more complete on anterior setigers. Ventral lamellae notched in mid-body setigers and completely divided into two lobes in posterior setigers (subgenus *Scolelepis*) on ventral lamellae entire throughout the body (subgenus *Nerinides*). With neuropodial hooks. With or without notopodial hooks. Hooks hooded, unidentate to quadridentate. Pygidium with bulbous oval disc or multilobed appendage. Eggs with reticulated shells and membrane vesicles. Development pelagic and primarily planktotrophic (HANNERZ, 1956).

Scolelepis (Scolelepis) squamata (Müller, 1806)

(Figures 118–131)

Lumbricus squamatus MÜLLER, 1806, p. 39. – CUVIER, 1830, p. 204. – GRUBE, 1850, p. 317.

Lumbricus cirratulus DELLE CHIAJE, 1828, p. 177. – QUATREFAGES, 1865a, p. 586.

Malacoceros longirostris QUATREFAGES, 1843, p. 13; 1865a, p. 443.

Nerine cirratulus, CLAPARÈDE, 1868, p. 68; 1869a, p. 66. – CUNNINGHAM & RAMAGE, 1888, p. 637. – HORNELL, 1891, p. 254. – LO BIANCO, 1893, p. 32; 1899, p. 488;

1909, p. 382. – MESNIL, 1896, p. 152. – SAINT-JOSEPH, 1898, p. 349. – ALLEN & TODD, 1900, p. 194. – ALLEN, 1904, p. 227. – FAUVEL, 1909, p. 6; 1927, p. 36; 1936, p. 51; 1953a, p. 312. – MCINTOSH, 1909, p. 158; 1915a, p. 148; 1927, p. 84. – ELWES, 1910, p. 62. – SOUTHERN, 1910, p. 234; 1914, p. 99. – STORCH, 1912, p. 93. – RIOJA & LO BIANCO, 1916, p. 463. – RIOJA, 1917, p. 14; 1923, p. 341; 1925, p. 46. – JAKUBOVA, 1930, p. 874. – BERKELEY & BERKELEY, 1932, p. 313; 1952, p. 27. – AUGENER, 1933, p. 160. – BASSINDALE, 1938, p. 93. – HARTMAN, 1959, p. 380. – HARTMAN & REISH, 1950, p. 28. – WESENBERG-LUND, 1951, p. 66. – DEBOUTEVILLE, 1954, p. 426. – KNIGHT-JONES, 1954, p. 137. – PERES, 1954, p. 130. – DAY, 1955, p. 412; 1957, p. 96; 1962, p. 648. – MARINOV, 1955, p. 112. – HANNERZ, 1956, p. 16. – CHLEBOVITSCH, 1959, p. 168; 1961, p. 192. – KIRKEGAARD, 1959, p. 17. – FAUVEL & RULLIER, 1959, p. 953. – HASAN, 1960, p. 106. – BELLAN, 1961, p. 100; 1962, p. 78; 1964, p. 101. – JONES, 1961, pp. 288, 315. – JOYNER, 1962, p. 655. – LAUBIER & PARIS, 1962, p. 41. – DUMITRESCU, 1963, p. 186. – DE SILVA, 1965, p. 16. – AMOUREAUX, 1966, p. 75. – HAMOND, 1966, p. 408. – BHAUD, 1967, p. 549. – CABIOCH, L'HARDY & RULLIER, 1968, p. 50.

Nerine agilis VERRILL, 1873, p. 600. – VERRILL & SMITH, 1874, p. 306. – WEBSTER, 1879a, p. 118; 1886, p. 147. – ANDREWS, 1891b, p. 291. – HARTMAN, 1941, p. 340; 1942, p. 62; 1945, p. 31; 1951, p. 81. – CARPENTER, 1956, p. 94. – BELLAN, 1964, p. 310.

Nerine heteropoda WEBSTER, 1879b, p. 249.

Scolecolepis squamata, MICHAELSEN, 1897, p. 45. – SÖDERSTRÖM, 1920, p. 218.

Spio acuta TREADWELL, 1914, p. 199. – HARTMAN, 1956, p. 258.

Nerinides acuta, HARTMAN, 1941, p. 294; 1954, p. 10. – BERKELEY & BERKELEY, 1941, p. 42. – REISH & WINTER, 1954, pp. 5–9, 113, 120. – FILICE, 1958, p. 189. – REISH, 1959a, p. 86; 1961, p. 86; 1968a, p. 81. – JONES, 1961, pp. 288, 314, 317. – REISH & BARNARD, 1967, p. 9.

Nerine capensis MCINTOSH, 1925, p. 71.

Nerine minuta TREADWELL, 1939a, p. 5. – HARTMAN, 1956, p. 256.

Nerinides agilis, HARTMAN, 1956, pp. 256, 269, 291. – SANDERS *et al*, 1962, pp. 66, 68, 70. – DEAN & HATFIELD, 1963, p. 163.

Nerinides goodbodyi JONES, 1962, p. 187.

Nerine cirratulus chilensis HARTMANN-SCHRÖDER, 1962a, p. 142.

Scolelepis squamata, PETTIBONE, 1963, p. 92. – WELLS & GRAY, 1964, p. 73. – DAY, 1967, p. 483.

Diagnosis: Prostomium tapered and pointed both anteriorly and posteriorly. Peristomium often extremely inflated in preserved specimens (probably due to massive proboscis). Cirriform branchiae beginning on setiger 2, partially fused with dorsal lamellae. Notopodial lamellae of mid-body region with slight indentation. Anterior setae thick capillaries. Bidentate neuropodial hooded hooks beginning on setigers 26–40. Pygidium forming thick cushion-shaped pad.

Description: The body is up to 47 mm in length, with 118 seti-

gers. The prostomium is tapered at both ends and is slightly wider at the anterior edge (Fig. 118). The posterior third bears two pairs or a cluster of small eyes. The peristomium is closely applied to the prostomium and may be very inflated in preserved specimens.

The anterior portion of the body is somewhat flattened and the branchiae often give the body a ragged appearance, as in orbiniids. There are low dorsal transverse ridges between the branchiae on most of the setigers. The branchiae increase in size from the short, stubby ones on setiger 2 (Fig. 120) to long, thin, overlapping ones in the mid-body region (Figs. 121, 122, 123). They become smaller again in posterior setigers.

The lamellae of setiger 1 are well-developed (Fig. 119). The notopodial lamellae are longer and thinner than the more rounded neuropodial lamellae. On the first branchial setiger, the dorsal lamellae are small, rounded, with a slight free tip (Fig. 120). The free tip increases in length on more posterior setigers (Fig. 121). Eventually a slight indentation on the dorsal lamellae forms, which increases and then decreases in size in more posterior setigers (Figs. 122, 123, 124). The neuropodial lamellae develop a slight notch on setigers 18–25 (Fig. 122). This notch becomes deeper until the lamellae are completely divided (Figs. 123, 124). In the more anterior setigers the two halves are similar in size; then the ventral half becomes elongate and narrow (Fig. 123). In far posterior setigers, however, the dorsal half becomes broad and rounded and the ventral half almost papilliform (Fig. 124).

On some specimens the anterior capillary setae are broad and thick and do not taper to long fine tips (Fig. 125). Bidentate neuropodial hooded hooks begin on setigers 26–40 (Fig. 126). They are variable with regard to dentition and may sometimes appear unidentate (Figs. 129, 130, 131). There are also occasional tridentate hooks. There appears to be a secondary hood (Fig. 126). Notopodial hooks may be present in posterior setigers.

The pygidium forms a flat cushionlike pad, with a slight dorsal indentation (Figs. 127, 128).

Biology: *Scolelepis (Scolelepis) squamata* is commonly found in intertidal beach sand, where it constructs small vertical burrows.

Material: *Nerine minuta* Paratype: USNM 20419; Maine – Sheepscot Bay, Cape Small, York Beach; Hampton Beach, New Hampshire; Massachusetts – Truro, Woods Hole; Newport, Rhode Island; Wildwood Beach, New Jersey, Chesapeake Bay, Virginia; Florida – Alligator Harbor, Tampa Bay, Seahorse Key; Barbados – Crane Beach, St. James; Port Aransas, Texas; Cook Inlet, Alaska; Den Helder, Netherlands; Bay of Naples; Tunisia.

Distribution: North Atlantic – New England to Florida; Scotland, England to Senegal; Mediterranean; North Pacific – Western Canada to Southern California.

Discussion: The presence or absence of notopodial hooks in the species synonomized with *Scolelepis* (*S.*) *squamata* by PETTIBONE (1963) has caused considerable confusion to authors attempting to distinguish them. For example, HARTMAN (1951) reports *Nerine agilis* from the Gulf of Mexico as possessing both notopodial and neuropodial hooks. Then, in 1956 she transfers this same species to the genus *Nerinides* because "it lacks hooded hooks in the notopodia" and cites HARTMAN, 1951, p. 81 in her synonomy. This is the type of confusion prevailing in the literature with regard to this character. After examination of specimens from the Gulf of Mexico and Caribbean and up the Atlantic coast of North America, the reason for this becomes somewhat apparent. As reported in the literature, when present, dorsal hooks begin some twenty to forty setigers after those of the neuropodia and they very rarely number more than five per fascicle (usually two). In a sample of Gulf and Caribbean specimens, only two out of six were found to possess dorsal hooks and there was one in the fascicle. It is my opinion that this character is too undependable to be used in distinguishing species and I agree with the synonomy given by PETTIBONE (1963).

Hooded hooks of *S.* (*S.*) *squamata* are characterized as bidentate, and, while this is predominantly the case, there is much variation. In a single collection and on a single worm, one can distinguish unidentate, bidentate and tridentate hooks. The tridentate hooks are rare but those with entire tips are often quite numerous (Fig. 131). After examining a considerable number of specimens, however, it became increasingly clear that these apparent unidentate hooks must have been bidentate ones with the entire setal head worn away.

Gradations could be found between the two. The hood of the unidentate hooks, which appears so small in comparison to that of the bidentate hooks, is the proximal end of a bidentate hood. Further, the fact that the unidentate hooks have such a thick shaft so near the tip (they look like an aciculum at first glance) is due to the fact that they are the thick parts of former bidentate hooks (Figs. 129, 131). These observations would cause a bit of apprehension concerning species described as having unidentate hooks.

The type material of *S.* (*S.*) *squamata saipanensis* (Holotype USNM 26090; Paratype USNM 29091) was examined and found to definitely have cleft neuropodial lamellae (Fig. 142).

Scolelepis (Scolelepis) texana sp. n.

(Figures 132–142)

Etymology: The species name refers to the paratype locality.

Diagnosis: Prostomium pointed anteriorly, with posterior erect, occipital antenna. Peristomium small. Without notosetae on setiger 1. Branchiae and dorsal lamellae fused anteriorly. Notosetae capillary, with multidentate hooded hooks, beginning on setigers 13–27. Pygidium with ventral papillated lobe.

Description: The body length is up to 8.66 mm, with 27 setigers The anteriorly pointed prostomium extends posteriorly to the level of setiger 2 (Fig. 132). The occipital antenna is located posteriorly and is usually erect and prominent. The four eyes are small, the posterior two sometimes hard to detect.

The body is anteriorly broad and flat and the branchiae are completely fused with the dorsal lamellae for about twenty to thirty setigers (Figs. 132, 133). The anterior dorsal lamellae have a somewhat ruffled appearance (Fig. 133) and the neuropodial lamellae are low and rounded. There is a fairly well-developed presetal notopodial lamella. By setiger 28, the neuropodial lamellae are cleft, with a small papilliform ventral portion and a dorsally tapering dorsal portion (Fig. 134). The neuropodial hooks project from a ridge, which

is situated ventro-laterally. The dorsal lamellae are only basally fused with the branchiae; they are ventrally tapered and this portion may overlap the upper part of the neuropodial lamellae. In posterior setigers, the dorsal lamellae are somewhat smaller but similar in appearance to the preceeding; the neuropodial lamellae are more clearly separated and the hooks are very elongate (Figs. 134, 135). On a few of the setigers from near the posterior end, there are twenty-five to thirty hooks emerging from a well-defined ridge (Fig. 136).

The anterior setae are all capillary and thinly tapered. They are similar in both neuro- and notopodia, being arranged in two rows. The shorter anterior setae are granular without any obvious limbations (Fig. 137). The longer setae are not particularly granular and are very thinly limbate (Fig. 138). The setae often appear distally frayed. The neuropodial hooded hooks are multidentate from their first appearance on setigers 13–27, with small secondary and very long primary hoods (Figs. 139, 140).

The pygidium bears a small ventral papillated lobe (Fig. 141).

Biology: *Scolelepis* (*S.*) *texana* was collected from intertidal beach sand.

Material: Tampa Bay, Florida; Port Aransas, Texas. Designated Holotype: USNM 40175, 27° 51.3′ N., 82° 33.2′ W. Collected by Dr. M. L. Jones, 1959. Paratypes: USNM 40176, 40177.

Distribution: Gulf of Mexico.

Discussion: *Scolelepis* (*S.*) *texana* is closely related to *S.* (*S.*) *foliosa* but differs in that the neuropodial hooks of the latter are unidentate and begin on more posterior setigers. *S.* (*S.*) *texana* differs from the other species of this subgenus by the presence of an occipital antenna and by the anterior branchiae being fused with the dorsal lamellae.

Key to selected Species of Scolelepis (Scolelepis)

(Partially after Pettibone, 1963)

1a. Neuropodial hooded hooks bidentate 2
1b. Neuropodial hooded hooks otherwise 4

2a. Notosetae on setiger 1 . . . . . *S.* (*S.*) *squamata*
2b. Notosetae absent on setiger 1 3

3a. With posterior notopodial hooks. Branchiae cirriform, smooth . . . . . *S.* (*S.*) *perrieri* (Fauvel, 1902). West Africa
3b. Without posterior notopodial hooks. Some anterior branchiae with terminal papillae *S.* (*S.*) *williami* (De Silva, 1961). Ceylon

4a. Prostomium with occipital antenna. Branchiae completely fused with dorsal lamellae in anterior setigers 5
4b. Prostomium without occipital antenna. Branchiae only partially fused with dorsal lamellae in anterior setigers. 6

5a. With multidentate neuropodial hooded hooks beginning on setigers 13–27 . . . . . *S.* (*S.*) *texana* Foster. Gulf of Mexico
5b. With unidentate neuropodial hooded hooks beginning on setigers 58–60 . . . . . *S.* (*S.*) *foliosa* (Audouin & Milne-Edwards, 1833). France

6a. Neuropodial hooks beginning about setiger 31. Notopodial hooks beginning about setiger 55 . . . . . *S.* (*S.*) *bonnieri* (Mesnil, 1896). France
6b. Neuropodial hooks beginning after setiger 35. Notopodial hooks lacking or very few in number 7

7a. Neuropodial hooks first appearing about setiger 38 . . . . . *S.* (*S.*) *lefebvrei* (Gravier, 1905). Red Sea
7b. Neuropodial hooks first appearing about setiger 43 . . . . . *S.* (*S.*) *knightjonesi* (De Silva, 1961). Ceylon

Genus **Aonides** Claparède, 1864

Aonides Claparède, 1864, p. 505. Type-species, by monotypy: *A. auricularis* Claparède, 1864, p. 505 [= *A. oxycephala* (Sars, 1862)].
Paranerine Czerniavsky, 1881, p. 359. Type-species, by monotypy: *Nerine oxycephala* Sars, 1862, p. 64.

Etymology: Gender: feminine; *Aonides* – L. – the Boeotian Women, *i.e.*, the Muses.

Diagnosis: Prostomium conical, tapered both anteriorly and posteriorly. Peristomium poorly-developed. Branchiae cirriform, separate from dorsal lamellae, beginning on setiger 2 and present on variable number of anterior setigers. Hooded hooks present in both notopodia and neuropodia, bidentate or tridentate. Pygidium with anal cirri. Development pelagic and lecithotrophic. Eggs spherical, with thick membranes; sperm short-headed, with tapered acrosome (HANNERZ, 1956).

Aonides mayaguezensis Foster, 1969

(Figures 143–154)

Diagnosis: Branchiae fifteen to sixteen pairs. Bidentate hooded hooks beginning in neuropodia in setigers 19–23 and in notopodia in setigers 21–24. Pygidium with four anal cirri, a shorter ventral pair and a longer dorsal pair.

Description: The body length is up to 6.6 mm, with 37 setigers. The prostomium is elongate, narrow, slightly wider in the region of the eyes, and terminating at the level of the first setiger (Fig. 143). There is an elevation in the posterior half, at the end of which is a digitiform process or occipital antenna, which extends to or slightly beyond setiger 1 (Fig. 144). There are four eyes, the posterior pair located on the prostomial elevation being closer together than those of the anterior pair; the anterior pair is found near the base of the elevation and is difficult to detect dorsally (Figs. 143, 144). The peristomium surrounds the posterior one-third to one-half of the prostomium, giving a somewhat hoodlike appearance.

The anterior branchial region is slightly flattened dorsoventrally. There are fifteen to sixteen pairs of branchiae, beginning on setiger 2. The branchiae are almost as long as the body width, generally longer than the dorsal lamellae, and are held erect dorsally (Figs. 143, 144, 146, 147). The first pair is only slightly, if at all, shorter than those following. The last pair, however, is less than half as long as the preceding and somewhat thinner.

The parapodial lamellae of setiger 1 differ considerably from those

of the following parapodia (Fig. 145). The dorsal lamellae are broad, low and subtriangular. The neuropodial lamellae, however, are much narrower, almost digitiform. In the following parapodia, the notopodial lamellae become increasingly foliaceous and the neuropodia lamellae increase slightly in width (Fig. 146). At about the level of setiger 10, the notopodial lamellae begin decreasing in size (Fig. 147) until they are nearly the same height as those of the neuropodia, though they remain somewhat broader throughout the body length (Fig. 148). The decrease in size is quite abrupt in the postbranchial region.

The anterior setae are capillaries and are arranged in two rows. In the neuropodia the anterior series contains shorter, thicker setae with a slightly wider sheath than those of the posterior row (Figs. 149, 150). There is an obvious sheath but whether they appear uni- or bilimbate depends on the orientation of the seta (Fig. 151). Granulations are evident on the majority of capillaries. In a notopodial fascicle there are two to three dorsal, extremely thin, non-limbate capillaries, but the others are similar in appearance and arrangement to those of the neuropodia. Bidentate, hooded neuropodial hooks begin on setigers 19–23 (19, on the holotype) (Fig. 152). Notopodial hooks of the same type appear on setigers 21–24 (21, on the holotype) (Fig. 153). There is no obvious secondary hood. The two teeth are widely separated and there are faint striations on the primary hood.

The pygidium is drawn into four anal cirri, the ventral pair being short but about the same thickness as the longer dorsal pair (Fig. 154).

Material: Three specimens collected at a depth of ten feet off Mayagüez, Puerto Rico, August, 1963. Holotype: USNM 39485 and Paratype: USNM 39486.

Distribution: Caribbean.

Discussion: Two species of *Aonides*, *A. trifidus* Estcourt (1967) and *A. notoseta* Storch (1966), have been added since PETTIBONE (1963) revised the genus. Of the species possessing bidentate hooded hooks, *A. mayaguezensis* shows close affinity to *A. californiensis*

Rioja, having similar branchiae; they differ in the first appearance of neuro- and notopodial hooded hooks. In addition, in *A. californiensis*, the lamellae of setiger 1 are low and rounded whereas, in the new species, the ventral lamellae are tapered, almost digitiform. Type material for *A. californiensis* no longer exists (Dra. MARIA ELENA CASO MUÑOZ, personal communication), leaving the original description as the only source of comparative information. On this basis, *A. mayaguezensis* is considered a separate species.

Aonides notoseta Storch (1966) described from material from the Red Sea, does not conform to the generic diagnosis of *Aonides*. According to the description, the principle characters it shares with other species of *Aonides* are presence of anterior branchiae separate from the notopodial lamellae, hooks absent in anterior setigers and the presence of anal cirri; none of these are diagnostic generic characters. Other characters which suggest that it does not belong to this genus are the following: branchiae begin on setiger 3 (instead of setiger 2); the hooks have a node or swelling on the shaft (previously unknown among spionids); the parapodial lamellae are threadlike "fadig" (not foliaceous); the prostomium is oval (not pointed). No further designation beyond exclusion from *Aonides* will be attempted until type material has been examined. There is some doubt that it belongs to the Spionidae, since it fails to show a number of the spionid features.

KEY TO THE SPECIES OF AONIDES

1a. Hooded hooks bidentate 2
1b. Hooded hooks tridentate . . . . . *A. paucibranchiata* Southern, 1914. Ireland

2a. Second tooth of hooded hooks with longitudinal grooves, giving a tripartite appearance. Pygidium with six anal cirri. . . . . *A. trifida* Estcourt, 1967. New Zealand (Estuarine), as *A. trifidus*
2b. Second tooth of hooded hooks lacking longitudinal grooves. Pygidium with four anal cirri 3

3a. Branchiae twenty to thirty pairs . . . . . *A. oxycephala* (Sars, 1862), Norway (Includes *Aonides auricularis* Claparède, 1864. Mediterranean)

3b. Branchiae fewer than twenty pairs 4

4a. Neuropodial hooks beginning on setigers 19–23; notopodial hooks beginning on setigers 21–24. Branchiae fifteen to sixteen pairs . . . . . *A. mayaguezensis* Foster. Puerto Rico

4b. Neuropodial hooks beginning on setiger 40; notopodial hooks beginning on setiger 35. Branchiae thirteen to fourteen pairs . . . . . *A. californiensis* Rioja, 1947. Lower California

Genus **Laonice** Malmgren, 1867

Laonice MALMGREN, 1867, p. 200. Type-species, as designated by MALMGREN, 1867: *Nerine cirrata* M. SARS, 1851, p. 207. Gender: feminine.

Spionides WEBSTER & BENEDICT, 1887, p. 735. Type-species, by monotypy: *S. cirratus* WEBSTER & BENEDICT, 1887, p. 736 [HOMONYM, = *L. cirrata* (Sars)].

Aricideopsis JOHNSON, 1901, p. 413. Type-species, by monotypy: *A. megalops* JOHNSON, 1901, p. 413.

Diagnosis: Prostomium, bluntly rounded anteriorly, extending posteriorly as narrow longitudinal keel, with posterior conical occipital antenna. Cirriform branchiae beginning on setiger 2. Notosetae all capillary. With neuropodial hooded hooks in posterior setigers. With genital pouches. Pygidium with anal cirri.

Laonice cirrata (Sars, 1851)

(Figures 155–160)

Nerine cirrata SARS, 1851, p. 207; 1861, p. 64. – WIRÉN, 1883, p. 409.

Scolecolepis cirrata, MALMGREN, 1867, p. 199. – VERRILL, 1873, p. 411. – SMITH & HARGER, 1874, pp. 16, 21. – VERRILL & SMITH, 1874, p. 308. – EHLERS, 1875, p. 62. – MCINTOSH, 1876, p. 316; 1885, p. 380. – TAUBER, 1879, p. 116. – THÉEL, 1879, p. 53. – HASEN, 1882, p. 11. – HORST, 1882, p. 19. – WEBSTER & BENEDICT, 1884, p. 726; 1887, p. 735. – WHITEAVES, 1901, p. 76. – SÖDERSTRÖM, 1920, p. 227. – TREADWELL, 1948, p. 43.

Laonice cirrata, MALMGREN, 1867, p. 200. – VERRILL, 1881, pp. 298, 309, 312, 316. – MARENZELLER, 1889, p. 132. – MESNIL, 1896, p. 247. – SOUTHERN, 1914, p. 97.

– McIntosh, 1915a, p. 164. – Söderström, 1920, p. 220. – Fauvel, 1927, p. 38; 1932, p. 171; 1936, p. 58; 1953a, p. 315. – Rioja Lo Bianco, 1931, p. 56. – Annenkova, 1932, p. 176; 1937, p. 169; 1938, p. 172. – Augener, 1928, p. 738; 1933, p. 160; – Zachs, 1933, p. 129. – Wesenberg-Lund, 1934, p. 21; 1949, p. 323; 1950a, p. 30; 1950b, p. 75; 1951, p. 68, 1953; p. 56. – Berkeley & Berkeley, 1936, p. 474; 1941, p. 42; 1942, p. 196; 1952, p. 26. – Gustafson, 1936, p. 8. – Ditlevsen, 1937, p. 29. – Okuda, 1937a, p. 222. – Friedrich, 1939, p. 126. – Hartman, 1941, p. 293; 1948b, p. 36; 1956, p. 248; 1965a, p. 148; 1966, p. 15; 1967, p. 112. – Gorbunov, 1946, p. 38. – Zatsepin, 1948, p. 132. – Hartman & Reish, 1950, p. 28. – Ushakov, 1950, p. 199; 1955, p. 265; 1965, p. 243. – Hannerz, 1956, p. 23. – Pettibone, 1956, p. 561. – Southward, 1956, p. 267. – Kirkegaard, 1959, p. 18. – Reish, 1959a, p. 38; 1968a, p. 81. – Day, 1961, p. 484; 1967, p. 480. – Laubier & Paris, 1962, p. 41. – Rullier, 1963, p. 208. – Imajima & Hartman, 1964, p. 281. – Bellan, 1964, p. 110; 1965, p. 7. – Hartmann-Schröder, 1965, p. 204. – Levenstein, 1966, p. 37. – Banse & Hobson, 1968, p. 24. – Cabioch, L'Hardy & Rullier, 1968, p. 50.

Spionides cirratus Webster & Benedict, 1887, p. 736. – Söderström, 1920, p. 227. – Treadwell, 1948, p. 43.

Spio cirratus, Levinsen, 1893, p. 334. – Bidenkap, 1894, p. 95; 1907, p. 23.

Aricidea alata Treadwell, 1901, p. 202; 1939b, p. 265. – Cerruti, 1909, p. 465. – Augener, 1906, p. 172. – Horst, 1922, p. 196.

Spionides japonicus Moore, 1907, p. 204. – Berkeley, 1927, p. 421. – Weese, 1933, pp. 20, 21.

Aonides cirrata, Fauvel, 1909, p. 4; 1914, p. 220. – Rioja, 1917, p. 177. – Horst, 1922, p. 196. – Treadwell, 1939b, p. 270.

Laonice appelloefi Söderström, 1920, p. 225.

Laonice sarsi Söderström, 1920, p. 223. – Eliason, 1962b, p. 263.

Scolecolepis (*Laonice*) *cirrata*, McIntosh, 1915a, p. 164.

Spionides foliata Moore, 1923, p. 182. – Hartman, 1959, p. 391.

Spionides sacculata Moore, 1923, p. 184. – Hartman & Barnard, 1958, p. 63. – Hartman, 1959, p. 391.

Laonice cirrata antarcticae Hartman, 1953, p. 40.

Laonice foliata, Hartman, 1963b, p. 41.

Laonice cirrata var. *praecirrata* Hartmann-Schröder, 1965, p. 207.

Laonice cirrata var. *postcirrata* Hartmann-Schröder, 1965, p. 207.

Laonice antarcticae, Hartman, 1965b, p. 147. – Banse & Hobson, 1968, p. 24.

Laonice pugettensis Banse & Hobson, 1968, p. 25.

Laonice japonica, Banse & Hobson, 1968, p. 25.

Diagnosis: Prostomium bluntly rounded anteriorly, extending posteriorly as a longitudinal keel. With occipital antenna. With cirriform branchiae in anterior forty to sixty setigers. With neuropodial bi- and/or tridentate hooded hooks first present on setigers 29–60. Genital pouches first present on setigers 12–50. Pygidium with eight to thirteen anal cirri.

Description: The body length is up to 33 mm, with 55 setigers. The prostomium varies anteriorly from being bluntly rounded to bluntly squared (Fig. 155). It extends posteriorly as a median keel for a variable number of setigers (12–30). The occipital antenna varies in length and inserts at about the level of the first setiger. There are usually two pairs of eyes, the posterior pair being much the larger. On some specimens they are present as diffuse pigment spots or may be inconspicuous.

Cirriform branchiae begin on setiger 2 and are separate from the dorsal lamellae. The first pair is often shorter than the notopodial lamellae (Fig. 155). The branchiae increase in size thereafter and are longer than the lamellae (Fig. 157).

Parapodial lamellae are well-developed. Those of setiger 1 are subtriangular and smaller than the following; those of the neuropodia are often slightly larger. The following notopodial lamellae are foliaceous, broad, bluntly rounded and overlapping (Figs. 155, 156). In more posterior setigers, they become more angular (Fig. 157) and then in far posterior setigers, again become rounded.

Anterior setae are all capillary. Noto- and neurosetae are similar in appearance and arrangement. They are primarily unilimbate, with a heavily striated sheath and a distally granular shaft (Fig. 158). Neuropodial hooded hooks first appear on setigers 29–60. There are usually both bi- and tridentate hooks (Figs. 159, 160), with no evident pattern with regard to their distribution along the body. There is no visible internal hood.

Interramal or genital pouches begin on setigers 4–50. There are eight to thirteen anal cirri.

Biology: *Laonice cirrata* is found from shallow water to abyssal depths. It is primarily a cold water form and is rare in the Gulf of Mexico and Caribbean.

Material: *Aricidia alata* Holotype: USNM 16068; *Spionides cirratus* Holotype: USNM 29021; *Spionides foliata* Holotype: USNM 17100; *Spionides sacculata* Holotype: USNM 17101; *Laonice cirrata* var. *praecirrata*, Hamburg Museum; *Laonice cirrata* var. *postcirrata*, Hamburg Museum; *Laonice pugettensis* Holotype: USNM 36263, Paratype: USNM 36262. Newfoundland; Halifax, Nova Scotia; Bay of Fundy, Canada; Maine – Gulf of Maine, Casco Bay; Massachusetts – Cape Cod, Salem, Buzzards Bay; Longbranch, New Jersey; Dover, Delaware; Chesapeake Bay, Virginia; Seahorse Key, Florida; Mayagüez, Puerto Rico; Alaska; California.

Distribution: Cosmopolitan.

Discussion: SÖDERSTRÖM (1920) separated *L. cirrata* into four species, *L. bahusiensis, L. appeloefi, L. sarsi* and *L. cirrata*. BANSE & HOBSON (1968) follow SÖDERSTRÖM in his usage of distribution of genital pouches for distinguishing species of *Laonice*. This does not, however, seem acceptable. *L. cirrata* has been reported by several authors as possessing pouches beginning on setigers 25–50. BERKELEY & BERKELEY (1952) report this species with pouches first on setigers 7–30 and BANSE & HOBSON (1968) setigers 12–28. BANSE & HOBSON also describe a new species, *L. pugettensis* (USNM) with pouches beginning on setigers 2–7. It would appear that the variability in this character would make it suspect for diagnosing species. Along with the fact that within one collection the range may be twenty to thirty setigers, while, in another, only five to six setigers so that when they occur two to five setigers sooner, this does not seem particularly diagnostic. The same is true for the variability with regard to the first appearance of hooded hooks.

For these reasons until there is more evidence for the etasblishing of separate species, *L. cirrata*, only, is recognized in this paper. *Laonice annenkowae* Zachs, 1925, from the coast of Murman does not conform to the generic diagnosis. It lacks interramal pouches and has notopodial hooks in the posterior setigers.

Genus **Dispio** Hartman, 1951; Emended

Dispio HARTMAN, 1951, p. 86. Type-species, by monotypy and original designation: *Dispio uncinata* HARTMAN, 1951, p. 87. Gender: feminine.

Diagnosis: Prostomium fusiform, tapering at both ends and lacking frontal horns. Peristomium forming low hood surrounding the prostomium. Some anterior parapodial lamellae serrated. Branchiae beginning first setiger, more or less fused with dorsal lamellae. With only capillary notosetae. With neuropodial hooded hooks. Pygidium bearing anal cirri and mid-ventral flap or flange. With accessory branchiae in form of nodules or fingerlike palmate lobes behind notopodial bases on variable number of segments.

Dispio uncinata Hartman, 1951

(Figures 161–174)

Dispio uncinata HARTMAN, 1951, p. 87; 1961, p. 88. – CARPENTER, 1956, pp. 93, 96, 104. – MARSDEN, 1960, p. 1000.
Spio setosa, BEHRE, 1950, p. 13.

Diagnosis: Prostomium fusiform. Peristomium forming low hood surrounding prostomium. Branchiae beginning on setiger 1, continuing to near end of body, fused basally with dorsal lamellae. Accessory branchiae located basally on posterior faces of notopodia, in the form of fingerlike lobes, beginning on setigers 18–28. Anterior parapodial lamellae serrated for variable number of setigers. Neuropodial hooded hooks beginning on setigers 16–37 entire or entire and bidentate. Pygidium with collar and sometimes anal cirri.

Description: The body length is up to 62 mm, with 114 setigers. The prostomium is spindle-shaped, tapering at both ends. It extends posteriorly to about the level of setiger 2 and anteriorly there are lateral furrows setting off the anterior fourth (Fig. 161). There are up to four eyes or these may be lacking. When present, they are situated in the posterior one-fourth of the prostomium. The peristomium forms a low hood surrounding the protomium and is slightly elevated laterally.

Branchiae begin on the first setiger and continue, in some cases, along the length of the body. They are fused basally with the notopodial lamellae, leaving approximately the distal one-third of the gill free in the anterior setigers. The branchiae become longer and more digitiform in the posterior setigers, increasing in length relative to the lamellae so that much smaller proportions of the branchiae are fused with the lamellae. The branchiae and notopodial lamellae are held erect dorsally. Accessory branchiae are characteristic of this species, on setigers 18–28. Initially they are present as one to two small fingerlike lobes found basally on the posterior faces of the notopodia. Posteriorly they gradually increase in number of lobes, usually with the maximum number of eight. The branchiae are

easily overlooked, especially in anterior setigers where they are small and inconspicuous.

On a variable number of anterior setigers, the noto- and neuropodial lamellae are serrated or lobed. The notopodial marginal serrations vary from short and stubby, only involving the outer margins of the lamellae, to elongate and fingerlike, involving the lamellae almost to the edge of the branchia (Fig. 162). These serrations are generally, though not always, confined to the upper part of the notopodial lamellae. Such is not the case in the neuropodia where they are found all along the lamellar edge (Fig. 162). The number of serrations varies from one to seven in both the noto- and neuropodial lamellae. The number generally decreases in successive parapodia. There are generally more serrations in the notopodial lamellae and, in most cases, the neuropodial serrations do not continue as far back along the body as do those of the notopodia. The number of parapodia bearing these serrated lamellae varies from one to ten.

The posterior notopodial lamellae may become increasingly ruffled along the distal border (Fig. 163) and, in the majority of specimens, the ventral tips of the notopodial lamellae and the dorsal tips of the neuropodial lamellae become elongate, sometimes overlapping. The presetal lamellae become very pronounced, even extending beyond the edge of the postsetal lamellae. More posteriorly the lamellae become reduced and the lamellae of a single parapodium become separated from one another (Fig. 164).

The parapodia of the first setiger are located more dorsally than the following ones and are characterized by having exceptionally long notopodial capillary and setae (Fig. 161). They are very slender with an extremely narrow sheath, appearing slightly unilimbate. There are also a few shorter, thin capillary setae showing no evidence of a sheath but with very faint granulations. The neuropodial setae are arranged in two series; the anterior row is comprised of short, thick, quite granular setae which have a very wide sheath appearing uni- or bilimbate depending on their orientation (Figs. 165, 166); the posterior series consists of longer, thinner setae with less obvious sheaths and fewer granulations (Fig. 167). Setae of setiger 2 are similar to the foregoing except that the upper notosetae are not as long. In more posterior setigers, the notosetae become heavily

granular while the neurosetae are arranged in a row of about seven to twelve short, curved, broadly sheathed, heavily granular capillaries. Between each neuroseta is a narrow longer seta, less granular and very narrowly sheathed.

On setigers 16–37, the short, heavy neurosetae are replaced by hooded hooks which are accompanied by long, thin companion setae. In adult specimens, the hooks are obviously unidentate with a single primary hood (Figs. 168, 170). The hook is slightly curved distally and the hood extends somewhat beyond the tip, where it is open at the top and on one side. Distinctly bidentate hooks are also present in younger (?) and smaller specimens (Fig. 169). There are usually two to three in a fascicle with the unidentate hooks. The bidentate hooks are somewhat smaller than the unidentate hooks and are usually found in the ventral part of the setal fascicle. In adults, the unidentate hooks are sometimes worn down at the tip so that they appear somewhat truncated. Some of the specimens from Bimini and Woods Hole had ' orange-tipped" setae in several posterior setigers. These were found among both neuro- and notopodial setae. Upon closer examination, it was found that the color was due to brownish yellow granules or accretions embedded in the hoods of the hooks (Fig. 170) and in the sheaths of notopodial capillaries and neuropodial companion setae (Fig. 171). When this occurred in the notosetae, they were almost always broken, the accretions apparently rendering the setae more brittle and destroying the usual flexibility exhibited by these capillaries. This material seems to be laid down or accumulated as the setae become older, because in a single fascicle a gradual increase in accretion can be seen proceeding from the younger to the older hooks.

The pygidium bears a midventral flap or collar varying in width, and four lateral cirri, two on each side in very close proximity basally and in a somewhat ventro-lateral position (Figs. 172, 173). The collar may be more or less developed and sometimes very heavily pigmented; and often some or all of the cirri are missing (Fig. 174).

Biology: *Dispio uncinata* has been collected from the shallow intertidal to 3 fathoms, from sand with scattered shells.

Material: Stony Beach, Woods Hole, Massachusetts; Gloucester Point, Virginia; Beaufort, North Carolina; Bahamas – Bimini, Andros; Florida – Pensacola,

Seahorse Key; Magens Bay, St. Thomas; Ponce, Puerto Rico; Texas – Port Aransas, 3 fathoms, Port Aransas Channel, Mustang and Padre Islands; Viña del Mar, Chile; La Jolla, California.

Distribution: North Atlantic: Massachusetts to North Carolina; Caribbean; Gulf of Mexico; California; Central America.

Discussion: The following four species were assigned to the genus *Dispio* according to the revision by PETTIBONE (1963, p. 91). They are:

D. uncinata Hartman, 1951. Gulf of Mexico
D. magna (Day, 1955), as *Spio magnus*. South Africa
D. schusterae Friedrich, 1956. Central America
D. remanei Friedrich, 1956. Central America

Differentiation of the two latter species was based on the number of parapodia bearing lamellar serrations and on the fact that the neuropodial as well as notopodial lamellae were serrated or notched (FRIEDRICH, 1956). Little, if any, mention was made of any other distinguishing characters. Examination of present collections from the Gulf and Caribbean has illustrated the fact that the number of lamellar serrations is highly variable within a single collection, and the seame is true for the number of anterior parapodia bearing these serrated lamellae. The variation in this character among specimens from two collections from Bimini and Andros in the Bahamas is indicated in Table 4.

Thus it can be seen that in one sample the number of serrations, even on just the notopodial lamellae of the same setiger on six specimens, varies from two to ten. *Dispio remanei* Friedrich was separated from *D. uncinata* Hartman because the neuropodial lamellae possessed serrations. As indicated in Table 4, this is not a stable character to be used in species designations.

A second character of a similar nature is the number of parapodia possessing these serrated lamellae. *D. schusterae* Friedrich was designated as new, not only because of the neuropodial serrations but, also, because they were found only on the first three to four setigers as opposed to the first seven in *D. remanei*. In the present collections, the number of parapodia with serrations varied from one to four, with the exception of two specimens from two localities along the

Texas coast on which there were ten parapodia with notopodial serrations. In these specimens, however, the number of parapodia bearing neuropodial serrations varied from one to five. Since this character of parapodial serrations is so variable from so many other aspects, it leaves little doubt that the number of parapodia with serrations is of no more systematic value than the presence or absence of neuropodial serrations.

TABLE 4

NUMBER OF LAMELLAR SERRATIONS OF DISPIO UNCINATA

Locality	Specimen number	Setiger 1		Setiger 2		Setiger 3		Setiger 4	
		Notopodium	Neuropodium	Notopodium	Neuropodium	Notopodium	Neuropodium	Notopodium	Neuropodium
Bimini	1	8	5	4	6	3	4	0	2
	2	5	3	4	2	0	1	0	0
	3	5	2	3	2	0	0	0	0
	4	6	2	5	1	1	0	0	0
	5	7	4	5	3	2	1	0	0
	6	6	3	4	2	1	0	1	0
Andros	1	3	2	5	3	0	1	0	0
	2	5	5	5	1	0	1	0	0
	3	10	3	6	5	0	1	0	0
	4	8	4	4	1	0	0	0	0
	5	5	4	5	2	1	1	0	0
	6	2	0	0	0	0	0	0	0
	Range	2–10	0–5	0–6	0–6	0–3	0–4	0–1	0–2

Based on the abundant material available for this study, considerable doubt is cast on the value of using the parapodial serrations as distinguishing characters. This casts doubt on the validity of the two species of FRIEDRICH. Due to their incomplete descriptions and the fact that the types are unavailable, their systematic positions remain indeterminable. On the basis of the limited information available, it would seem that they should be referred to *D. uncinata.*

The remaining question, then, is whether *D. magna* is a valid

species or whether the genus *Dispio* is monotypic. A character commonly used in distinguishing spionid species is the first appearance of neuropodial hooks. In specimens of *D. magna* from South Africa, they are first present on setigers 30–44 (DAY, 1967), in specimens of *D. uncinata* from the Gulf of Mexico (HARTMAN, 1951), on setigers 25–27; yet in specimens collected from Andros Island, the range of first appearance of neuropodial hooks is from setigers 21–37. This wide range, found within a single collection, casts considerable doubt on the validity of this as a specific character in *Dispio*. There are two remaining characters which may distinguish *D. magna* from *D. uncinata*. The first of these is the lack of serrated parapodial lamellae in the former. This species is not represented in the present collections, and, until more material is available, the stability of the presence or absence of serrations cannot be established. *D. magna* also differs from *D. uncinata* in the character of the accessory branchiae. Instead of being fingerlike projections, as in *D. uncinata*, the branchiae are present as one or two bumps or knobs in the same position. For these reasons, at the present time, *D. magna* is considered a valid species. The characters of the two species are compared in Table 5.

While examining several small specimens from La Jolla, California, bidentate hooded hooks were found in the neuropodial fascicles in addition to the typical unidentate hooks. Further examination of small specimens from other collections revealed the presence of these hooks in almost every case. It would appear on the basis of the collections available for this study that the presence of bidentate hooks is perhaps a juvenile character. They may be lost as the animal becomes adult or, and much less likely, they are worn to such an extent that the secondary tooth is lost. The latter is not common in other spionid species, and it is unlikely that such is the case here. There is, however, some precedence for a slight difference between larval and adult setae. Larvae and newly-metamorphosed juveniles of *Spio martinensis* have triserrated (= tridentate) hooks and those of the adult are diserrated (= bidentate); such differences also characterize *Scolelepis foliosa* and *Polydora ciliata* (HANNERZ, 1956).

TABLE 5

COMPARISON OF DISPIO UNCINATA AND DISPIO MAGNA

	D. uncinata	*D. magna*
Parapodial serrations	present	absent
First appearance of neuropodial hooks	setigers 16 to 37	setigers 30 to 44
Type of accessory branchiae	digitiform	slightly raised nodules
Anal appendages	four cirri and small to large collar	?

REVISION OF **Prionospio** MALMGREN
and comparison with related genera

The genus *Prionospio* Malmgren (1867), was originally limited to species possessing branchiae beginning on setiger 2. CAULLERY (1914) erected *Paraprionospio* as a subgenus to accomodate the species *Prionospio pinnata*, which possesses branchiae beginning on the first setiger. *Paraprionospio* was used at the generic level by BERKELEY (1927) and WEESE (1933). This usage, however, was not continued by later systematists. Rather than accept *Paraprionospio* as a genus or subgenus, the limits of *Prionospio* were merely expanded to include it. This apparently has been the tendency with regard to *Prionospio*, with the result that at present *Prionospio* includes an extremely heterogenous group of species. Species with the following characters have been previously included in the genus *Prionospio*:

1. anterior branchiae begin on setigers 1, 2 or 3; separate from notopodial lamellae; pinnate and/or cirriform.
2. rounded prostomium, lacking frontal horns and occipital antenna.
3. neuropodial and notopodial hooded hooks, bidentate or multidentate.
4. well-developed anterior parapodial lamellae.

The species of this genus can be separated into distinct groups on the basis of a number of characters, including the type and arrangement of the branchiae. The type of branchiae, whether pinnate or

cirriform, has not been considered as a diagnostic generic character in *Prionospio*. In other valid genera of the Spionidae, the species form homogeneous groups with regard to the type of branchiae. Therefore, after consideration of the characters involved in the generic diagnoses within the family as a whole, I have decided to divide *Prionospio* into several genera. It is recognized that these divisions may be found to be artificial and that subgeneric designations would be more acceptable. These divisions have been anticipated in part in the recent review of the *Prionospio* species by LAUBIER (1962), in which he presents a dicotymous key to the species, and by WU & CHEN (1964), in which they divide the species of *Prionospio* into three groups.

Four groups of species have been removed from *Prionospio* and placed in *Paraprionospio* Caullery, *Apoprionospio* Foster, *Minuspio* gen. n. and *Aquilaspio* gen. n. (see Key p. 15).

The following genera and species are considered questionable:

1. Genus *Pteriptyches* GRUBE, 1872, p. 58. Type-species, by monotypy: *P. festiva* GRUBE, 1872, p. 58. Adriatic. Indeterminable. Referred to *Prionospio* by CAULLERY (1914, p. 359).
2. Genus *Kinbergella* MCINTOSH, 1909, p. 177. Type-species, by monotypy: *K. plumosa* MCINTOSH, 1909, p. 177. Portugal. Indeterminable. Referred to *Prionospio* by SÖDERSTRÖM (1920, p. 240) and given new name: *P. decipiens*, since *P. plumosa* is preoccupied by SARS (1867, 1872).
3. *Prionospio capensis* MCINTOSH, 1885, p. 381. South Africa. Type (British Museum) examined by DAY (1961, p. 490) and by present author and considered indeterminable.
4. *Spiophanes pallidus* HARTMAN, 1960, p. 118. Southern California. Doubtfully referred to *Prionospio* by PETTIBONE (1962, p. 85). No branchiae.
5. *Prionospio banyulensis* LAUBIER, 1966a, p. 258. France. *Nomen nudum*.

Genus **Prionospio** Malmgren, 1867, *sensu stricto*

Prionospio Malmgren, 1867. Type-species, by monotypy: *P. steenstrupi* Malmgren, 1867, p. 202. Iceland. Gender feminine.

Ctenospio M. Sars, 1867. Type-species, by monotypy: *C. plumosus* M. Sars, 1867, p. 291. Norway. *Nomen nudum* (= *Prionospio plumosus* Sars, 1872, p. 410.)

Diagnosis: Prostomium subtriangular, anteriorly rounded, lacking frontal horns, with posterior keel more or less developed, extending to about level of setiger 2; without occipital antenna. Peristomium (segment 1) more or less fused with setiger 1 (segment 2); often developed as low collar or yoke surrounding prostomium; without lateral wings. With deciduous tentacular palpi. Parapodia of setiger 1 reduced, smaller than those of following setigers. Branchial parapodia with large conspicuous notopodial lamellae; postbranchial lamellae increasingly low and inconspicuous. With a combination of pinnate and cirriform branchiae distinct from notopodial lamellae and beginning on setiger 2. Anterior setae all capillary. With posterior multidentate hooded hooks in neuro- and notopodia. Ventral sabre-setae present. Pygidium with three anal cirri, long middorsal one and two shorter laterals. Development completely pelagic and largely planktotrophic (Hannerz, 1956).

Discussion: According to this revision, the following species are retained in *Prionospio* Malmgren, *sensu stricto*:

1. *P. steenstrupi* Malmgren, 1867, p. 202. Iceland. Includes:
   Spiophanes tenuis Verrill, 1879, p. 176. Massachusetts. [= *Prionospio tenuis* (Verrill), Verrill, 1881, p. 320.]
   Prionospio steenstrupi malayensis Caullery, 1914, p. 355. Malay Archipelago.
   Prionospio bocki Söderström, 1920, p. 234. Japan.
   Prionospio malmgreni var. *dubia* Day, 1961, p. 489. South Africa.
2. *P. plumosa* Sars, 1872, p. 410 (as *plumosus*). Norway.
3. *P. heterobranchia* Moore, 1907, p. 195. Massachusetts. Includes:
   Prionospio heterobranchia texana Hartman, 1951, p. 85. Gulf of Mexico.
   Prionospio spongicola Wesenberg-Lund, 1958, p. 19. West-Indies.
   Prionospio heterobranchia newportensis Reish, 1959b, p. 13. Southern California.

4. *P. fallax* SÖDERSTRÖM, 1920, p. 235. Sweden.
5. *P. ehlersi* FAUVEL, 1928, p. 10. Morocco.
6. *P. sishaensis* WU & CHEN, 1964, p. 58. South China Sea.
7. *P. cristata* sp. n. North Carolina.

Prionospio malmgreni CLAPARÈDE, 1869a, p. 73, from the Gulf of Naples, is considered indeterminable until material has been collected from the type locality. It is impossible to determine the gill arrangement from the original description in which the pinnate gills are said to "... paraissent alterner plus ou moins regulierement avec des branchies simples ...". CLAPARÈDE goes on to say that he found specimens with a maximum of nine branchiae. This would indicate at least five branchial pairs yet *P. malmgreni* has become characterized as possessing four pairs, the first and fourth being pinnate. As a result, through the years, almost any specimen collected with that branchial arrangement has been called *P. malmgreni*. The original figure, however, shows branchial pairs one and two as pinnate (one of the second pair is smooth – regenerating?). In a later paper, MARION & BOBRETSKY (1875) figured *P. malmgreni* with cirriform branchiae on setigers 3, 4, and 5; the authors state that rarely were two individuals found to possess an identical number of gills.

Based on one of the original figures of CLAPARÈDE (1869a, pl. 22 fig. 3A) showing two body segments with low crests, and from present material, it appears that the majority of specimens previously identified as *P. malmgreni* could in actual fact be referred to *P. fallax* Söderström, 1920, and this is thought to be the case. The latter species possesses the high membranous crest on setiger 7, as well as all the other significant characters which have been attributed to *P. malmgreni*. It is impossible to determine the species involved in all previous reports of *P. malmgreni* because in many cases the nature of the dorsal crests was not mentioned. The species, therefore could have been *P. steenstrupi*, *P. fallax*, or *P. cristata*.

The terminology in this genus with regard to dorsal crests should be standardized in order to distinguish the two types of crests characteristic of *P. steenstrupi* and *P. fallax*. USHAKOV (1955) inadvertently attempted this by indicating that *P. malmgreni* had a ' dorsal fold of skin" on setiger 7. Hereafter, the type of crest on *P. fallax* will be referred to as a dorsal *fold* or a high *membranous* crest and those of *P. steenstrupi* will be called dorsal crests.

The type and arrangement of the branchiae for the seven species of *Prionospio* are indicated in Table 6. It will be noted that all of them have the first branchiae pinnate and the third branchiae cirriform. All but *P. plumosa* have the second branchiae cirriform. All but *P. ehlersi* have the fourth branchiae pinnate. Only *P. heterobranchia* has a fifth pair of branchiae, which is pinnate.

TABLE 6

TYPE AND ARRANGEMENT OF BRANCHIAE IN * PRIONOSPIO MALMGREN, SENSU STRICTO

Species	Branchiae				
	First	Second	Third	Fourth	Fifth
P. steenstrupi	pinnate	cirriform	cirriform	pinnate	—
P. plumosa	pinnate	pinnate	cirriform	pinnate	—
P. heterobranchia	pinnate	cirriform	cirriform	pinnate	pinnate
P. fallax	pinnate	cirriform	cirriform	pinnate	—
P. ehlersi	pinnate	cirriform	cirriform	cirriform	—
P. sishaensis	pinnate	cirriform	cirriform	pinnate	—
P. cristata	pinnate	cirriform	cirriform	pinnate	—

KEY TO SPECIES OF PRIONOSPIO, SENSU STRICTO

1a. With four pair of branchiae 2
1b. With five pair of branchiae. . . . . *P. heterobranchia* Moore

2a. First and fourth pair of branchiae pinnate, second and third cirriform. 3
2b. Pinnate and cirriform arrangement otherwise. 5

3a. Dorsal transverse membranous folds between anterior dorsal lamellae present 4
3b. Dorsal transverse membranous folds between anterior dorsal lamellae absent, but may or may not have consistently low transverse ridges between notopodial lamellae on postbranchial setigers 6

4a. Dorsal membranous fold on setiger 7, high . . . . . *P. fallax* Söderström
4b. Dorsal membranous folds on setigers 7 and 9, high, with a somewhat lower crest on setiger 8 . . . . . *P. cristata* sp. n.

5a. First branchial pair pinnate; only . . . . . *P. ehlersi* Fauvel
5b. First, second and fourth branchial pairs pinnate . . . . . *P. plumosa* Sars

6a. Peristomium forming hood surrounding prostomium, well-developed laterally . . . . . *P. steenstrupi* Malmgren
6b. Peristomium inconspicuous, not well-developed laterally (based on original figures by Wu & Chen, 1964). . . . . *P. sishaensis* Wu & Chen

Prionospio steenstrupi Malmgren, 1867

(Figures 175–185)

Prionospio steenstrupi MALMGREN, 1867, p. 202. – MCINTOSH, 1876, p. 307; 1914, p. 80; 1915a, p. 216. – CZERNIAVSKY, 1881, p. 363. – WEBSTER & BENEDICT, 1887, p. 737. – LEVINSEN, 1893, p. 335. – BIDENKAP, 1894, p. 93. – MESNIL, 1897, p. 90. – VANHÖFFEN, 1897, p. 223. – MICHAELSON, 1897, p. 154; 1898, p. 129. – WHITEAVES, 1901, p. 76. – AUGENER, 1906, p. 173. – SOUTHERN, 1910, p. 236; 1914, p. 101. – SUMNER, 1913, p. 624. – DITLEVSEN, 1914, p. 702. – SÖDERSTRÖM, 1920, p. 232. – HORST, 1922, p. 196. – FAUVEL, 1927, p. 60; 1935, p. 334. – PROCTER, 1933, p. 143. – ZACHS, 1933, p. 130. – ANNENKOVA, 1937, p. 171; 1938, p. 173. – CAULLERY, 1944, p. 14. – TREADWELL, 1948, p. 42. – ZATSEPIN, 1948, p. 132. – WESENBERG-LUND, 1950a, p. 31; 1950b, p. 79; 1951, p. 70; 1953, p. 57. – USHAKOV, 1955, p. 277. – ELIASON, 1962b, p. 264. – Day, 1963, p. 418; 1967, p. 489. – HARTMAN, 1965a, p. 152. – LAUBIER, 1965, p. 137. – SIMON, 1967, p. 421.

Spiophanes tenuis VERRILL, 1879, p. 176; 1881, p. 320. – FAUVEL, 1916, p. 103.

Prionospio tenuis, VERRILL, 1881, p. 370. – CAULLERY, 1914, p. 359. – SÖDERSTRÖM, 1920, p. 240.

Prionospio steenstrupi malayensis CAULLERY, 1914, p. 355; 1944, p. 14. – WU & CHEN, 1964, p. 59.

Prionospio bocki SÖDERSTRÖM, 1920, p. 234. – OKUDA, 1937a, p. 242. – WESENBERG-LUND, 1949, p. 326. – LAUBIER, 1962, p. 140. – WU & CHEN, 1964, p. 59. – HARTMAN, 1965a, p. 386. – DAY, 1967, p. 490.

Prionospio malmgreni, not Claparède, 1868. – PETTIBONE, 1954, p. 282.

Prionospio malmgreni var. *dubia* DAY, 1961, p. 489.

Diagnosis: Prostomium wedge-shaped. Peristomium fused dorsally with setiger 1. Branchiae four pairs on setigers two to five; first and fourth pinnate, second and third cirriform. Capillary setae anteriorly. Multidentate neuropodial hooded hooks first present on setigers 14–21. Notopodial hooks first present on setigers 31–73.

Pygidium with three anal cirri, two short laterals and a single longer middorsal.

Description: Body length is up to 16 mm, with 69 setigers. The prostomium is wedge-shaped and extends posteriorly as a raised keel to about the level of setiger 2 (Fig. 175). There may be up to four eyes, those of the anterior pair larger, crescent- or wedge-shaped, often with additional small pigment spots. The peristomium is fused with the first setiger dorsally and the notopodial lamellae appear as erect peristomial wings (Fig. 175).

There are four pairs of branchiae, the first and fourth are pinnate, the second and third, cirriform. The first pair is usually longer than the fourth, but occasionally they are equal in length. The length of the branchiae relative to the dorsal lamellae is extremely variable. The pinnae of the first and fourth pairs of branchiae are arranged in four rows on the posterior face of the branchial axis. In most specimens examined, they are very long and thin and do not extend to the tip of the shaft (Fig. 176). They are crowded close together but do not adhere to one another. The lanceolate cirriform branchiae may be slightly longer than the dorsal lamellae, broad and somewhat tapered (Fig. 177). Long cilia extend about one-half the length of the shaft, decreasing in size toward the tip.

The parapodial lamellae of the first parapodia are well-developed and smaller than those following (Fig. 178); those of the notopodia are large, rounded and turned antero-laterally; the neuropodial lamellae are smaller, rounded and longer than broad. The notopodial lamellae of setiger 2 are subtriangular, with a slight dorsal fold (Fig. 176); there are low presetal lamellae; the neuropodial lamellae are broader, somewhat truncate and angular, rather than rounded. The lamellae of setigers 3 (Fig. 177) and 4 are similar in that they are all somewhat larger than the preceeding, broader and more rounded. On the fifth setiger the dorsal lamellae are much smaller and more bluntly rounded; the ventral lamellae are similar to those of setiger 4 (Fig. 179). In the first postbranchial setigers, the notopodial lamellae change noticeably (Fig. 180); they are almost level with, and merging with the dorsum; they are somewhat angular. The notopodial lamellae become more rounded in posterior setigers (Fig. 181).

In some specimens the postbranchial notopodial lamellae meet across the dorsum to form low dorsal crests on a varying number of setigers; in others, this is not the case and crests are absent.

Anterior setae are still all capillaries, with one or more sabre-setae first appearing in the neuropodia of setigers 9–12. The noto- and neuropodial capillary setae are similar, granular and uni- or bilimbate (Figs. 182, 183). They are arranged in two rows, with those of the anterior row shorter and thicker. Multidentate hooded hooks (Fig. 184) first appear in the neuropodia of setigers 14–21 (usually 16) and in the notopodia of setigers 31–72 (usually 31–35). The hooks are accompanied by a few long, thin capillaries. There does not appear to be an obvious secondary hood. The primary hood is open at the top and for a short distance down the front.

The pygidium bears two short, lateral anal cirri or lobes and a longer mid-dorsal cirrus (Fig. 185).

Biology: *Prionospio steenstrupi* has been collected from soft, sticky mud, mud and gravel, gravel and larger pebbles, rocks and shell debris. It is eurybathyal and has been found in depths ranging from intertidal to 1500 fm.

Material: Alaska-Point Barrow, Cold Bay; Washington-Ballard, Puget Sound; Canada-Gaspe Bay, Bay of Chaleurs, Quebec, New Brunswick; Maine; Massachusetts; Beaufort, North Carolina; Tavernier Key, Florida.

Distribution: The following distribution record is based on only those references in which it is possible to tentatively determine that the species reported is *P. steenstrupi* and not *P. fallax*: Greenland and Iceland to Norway; New England; North Carolina; Florida; South Africa; Japan; Alaska; Washington and California.

Discussion: In the original description of *Prionospio steenstrupi* by MALMGREN (1867), figures suggest the presence of very low ridges between the notopodial lamellae. This species, however, has been indicated in the literature as lacking dorsal crests and, in some of these instances the accompanying figures clearly show low crests between the notopodial lamellae. This has been due in part to the fact that the crest on setiger 7 of what has previously been called *P. malmgreni* (= *P. fallax* Söderström, 1920, *not* Claparède, 1869a) is so distinct and gives that setiger a very different appearance from the others. Such is not the case with *P. steenstrupi* on which the crests

are present on fifteen to twenty-five setigers and are all uniformly low.

Further evidence for the presence of crests on *P. steenstrupi* was found in a collection examined in this study. Large individuals possess the obvious low crests beginning on setiger 6 but on some of the smaller individuals crests do not appear until more posterior setigers and some have no obvious crests. The dorsal lamellae on these specimens do not quite meet across the dorsum. This would account for reports of *P. steenstrupi* both with and without low crests.

It may later prove to be impossible to differentiate between *P. fallax* and *P. steenstrupi*, because one collection examined containing specimens identified as *P. malmgreni* by the Berkeleys, illustrated considerable variation in this character: some specimens possessed low dorsal crests but no membranous folds, while others possessed a high membranous fold on setiger 7 and obvious low crests on the next ten to twelve setigers. This was the only collection in which this occurred and, until more material is available from this area, both names will be retained.

P. tenuis and *P. bocki* are herein considered synonomous with *P. steenstrupi* as they are both characterized as possessing low crests across the dorsum from about setiger 6.

Prionospio cristata sp. n.

(Figures 186–199)

Etymology: L. – *cristata* – crested; referring to the membranous folds characteristic of this species.

Diagnosis: Prostomium subtriangular extending posteriorly as a narrow keel. With four eyes, anterior pair small and posterior pair larger, crescent-shaped. Peristomium and first setiger fused and peristomial wings developed as notopodial lamellae of setiger 1. Four pairs of branchiae; first and fourth pinnate, second and third cirriform. High membranous crests on setigers 7 and 9, with lower crest on setiger 8. Multidentate hooks first appearing in neuropodia of setigers 11–12; in notopodia, setigers 21–37. Pygidium with three

anal cirri, two short thick laterals and one longer thinner mid-dorsal one.

Description: The body length is up to 7.1 mm, with 33 setigers. The prostomium is subtriangular or wedge-shaped, extending posteriorly to about setiger 2 as a fairly well-developed keel (Fig. 186). The anterior border is blunt to slightly rounded. There are generally two pairs of eyes; those of the anterior pair are small and round while those of the posterior pair are large and crescent-shaped. The peristomium is fused with setiger 1, and the lateral wings are erect, appearing as the notopodial lamellae (Figs. 186, 189).

There are four pairs of branchiae; the first and fourth pinnate, second and third cirriform on setigers 2–5. The two cirriform pairs on setigers 3 and 4 are usually about the same length; the two pinnate pairs on setigers 2 and 5 are either the same length, or the first or fourth may be longer. They are similar in appearance. The pinnae of the first pair (Fig. 187) are generally a little longer than the width of the shaft. They extend about four-fifths of the way to the branchial tip. There appear to be four irregular rows of pinnae on the posterior face of the axis of each pinnate gill, the pinnae being not closely applied to one another. The second and third pair of gills are also similar to one another (Fig. 188). They are cirriform, about one-third to one-half longer than the notopodial lamellae and bear long cilia proximally which become shorter toward the tip.

The first parapodia are well-developed though smaller than the following (Figs. 186, 189). The notopodial lamellae are large, rounded, slightly cupped and facing somewhat antero-laterally; the neuropodia are symmetrical, smaller, and ovoid. The notopodial lamellae of setiger 2 are small, with rounded edges, not cupped or folded; those of the neuropodia are somewhat broad and rounded (Fig. 187). The lamellae of the remaining branchial setigers are truncate laterally, those of the neuropodia being quite angular and those of the notopodia attenuated to varying degrees (Fig. 188). On the first postbranchial setiger, the notopodial lamellae are still somewhat pointed though not as high; they are already extended somewhat upon to the dorsum. On setigers 7, 8, and 9, the notopodial lamellae are united across the dorsum to form membranous crests (Figs. 190,

191). The crest of setiger 7 is either higher than or the same height as that of setiger 9. The crest on setiger 8 is always lower than the other two. Low dorsal crests may or may not be present on a variable number of setigers posterior to the ninth. Neuropodial lamellae become rounded about the fourth or fifth setiger. Usually by setigers 10–12, the notopodial lamellae are again separate and no longer meet dorsally though they still extend onto the dorsum (Fig. 192). More posteriorly both dorsal and ventral lamellae become increasingly low and rounded, with those of the neuropodia becoming smaller (Fig. 193). The anterior setae are all capillaries and are arranged in two series. The anterior ones are granular and appear bilimbate for most of their length and are shorter than the posterior ones (Fig.194) which are thin and slightly unilimbate. Ventral sabre-setae appear about setiger 10; they are broadly sheathed and heavily granular (Fig. 195). Multidentate hooded hooks first appear in the neuropodia of setigers 11–12 and in the notopodia of setigers 21–37 (Figs. 196, 197). There are indications of a secondary hood, which seems to be attached to the opening of the primary hood.

The pygidium bears two short lateral lobes or cirri and one longer, thinner mid-dorsal cirrus of variable length (Fig. 198).

Biology: *Prionospio cristata* was collected from shallow depths up to 0.5 to 32 meters. Substrata of the shallower depths included rocky pools, sand and sandy mud.

Material: Beaufort, North Carolina; Florida – off shore, Panama City, North Bay; Port Aransas, Texas; Puerto Rico, Curaçao; Designated Holotype: USNM 43001, collected by FRED GRASSLY, 1966, Beaufort, North Carolina; Paratypes: USNM 43002.

Distribution: North Atlantic: North Carolina, Florida; Gulf of Mexico; Caribbean Sea.

Discussion: *Prionospio cristata* is easily distinguished from *P. steenstrupi* by the presence of the two very high, distinct, membranous folds on setigers 7 and 9. It is probably more closely related to *P. fallax* but the two differ in that *P. fallax* possesses only a single high fold on setiger 7.

Prionospio heterobranchia Moore, 1907

(Figures 199–212)

Prionospio heterobranchia MOORE, 1907, p. 195. – SUMNER *et al*, 1913, p. 62. – CAULLERY, 1914, p. 359. – SÖDERSTRÖM, 1920, p. 240. – LAUBIER, 1962, p. 149. – SANDERS, *et al*, 1962, p. 66. – WELLS & GRAY, 1964, p. 73. – WU & CHEN, 1964, p. 59.

Prionospio tenuis, HARTMAN, 1944, p. 340, *not* Verrill, 1879.

Prionospio heterobranchia texana HARTMAN, 1951, p. 85. – LAUBIER, 1962, p. 199. – WU & CHEN, 1964, p. 59.

Prionospio spongicola WESENBERG-LUND, 1958, p. 19. – LAUBIER, 1962, p. 148. – WU & CHEN, 1964, p. 59.

Prionospio heterobranchia newportensis REISH, 1959b, p. 13; 1960, p. 94; 1961, pp. 86, 90; 1963a, p. 407. – LAUBIER, 1962, p. 149. – WU & CHEN, 1964, p. 59.

Diagnosis: *Prinospio* with five pairs of branchiae, first, fourth and fifth pinnate, second and third cirriform. With neuropodial hooded hooks beginning on setigers 11–15; notopodial hooks beginning on setigers 25–50. Pygidium with two ventrolateral lobes or cirri and one longer mid-dorsal cirrus.

Description: The body length is up to 16.3 mm, with 70 setigers. The prostomium is raised in the middle region, rather blunt anteriorly, narrowing at the level of the second larger pair of eyes and extending backward as a narrow keel to the area between setigers 2 and 3 (Fig. 199). There are two pairs of black or reddish pale yellow eyes. The anterior pair of eyes are small, round and located just in front of the narrow part of the prostomium. The posterior pair of eyes are much larger, elongate, tapezoidal or bar-shaped. In a few instances the large pair of eyes is present as amorphous pigmented areas. The peristomium surrounds the prostomium extending ventrally to near its anterior edge and being raised dorsally at the level of the large pair of eyes.

Branchiae are first present on setiger 2. There are five pairs, the first, fourth and fifth pairs being pinnate (Figs. 200, 201), the second and third, lanceolate (Fig. 202). In general, the pinnae are present near the base of the branchia but absent from the tip. The length of the free tip is quite variable, though it often increases in the last two

branchial pairs. In most cases the pinnae on the fourth and fifth pair of branchiae are longer and thinner than on the first pair and often reduced in number (Figs. 200, 201). In most instances the two pairs of lanceolate branchiae are shorter than the pinnate ones; occasionally within the same collection, however, they are the same length or longer. The branchiae are usually short, less than the body width; in some specimens, however, they may be very elongate, with the pinnae widely separated along the shaft. The two pairs of lanceolate branchiae are erect and bordered with extremely long cilia (Fig. 202).

The first setiger is smaller than those following (Figs. 199, 203). The notopodial lamellae are low, rounded, and about twice the size of the neuropodial lamellae. The notopodial lamellae of setiger 2 are anteriorly curved or folded, tapering dorsally with a gently curving dorso-lateral border (Fig. 200). The fold or cup-shaped appearance becomes more pronounced on more posterior setigers when the lamellae increase in size, with the dorso-lateral edge becoming more curved. The cups may result from the fusion of the medial edges of the pre- and postsetal lamellae rather than folds in the postsetal lamellae. The neuropodial lamellae on the setigers posterior to setiger 1 remain approximately the same, i.e., rounded and slightly decreasing in height. The lamellae rapidly decrease in size in the postbranchial region, becoming low and rounded, the presetal ridges or lamellae increasing in height to about one-third that of the postsetal lamellae (Fig. 204). On the first or second postbranchial setiger, a dorsal ridge or flap is present as a continuation of the notopodial lamellae. These ridges extend transversely across the dorsum and are present on about seven to ten setigers. The height of the flap varies, i.e., it may be even with the lamellae or there may be a dip with the flap being somewhat lower at the fourteenth setiger (Figs. 204, 205). Both neuro- and notopodial lamellae are low, rounded and about equal in height. This becomes more pronounced in posterior setigers (Fig. 206).

In anterior setigers there are two rows of capillary setae in both the noto- and neuropodia. The notopodial setae emerge from the cup formed by the dorsal lamellae (Figs. 200, 201, 202). The setae in the anterior rows are shorter and wider than those of the posterior rows. In the notopodium there are six to thirteen short anterior setae and

these appear granular for almost their entire length; there is a sheath of variable width on the proximal half of the shaft (Fig. 207). The setae of the posterior row (about 16 in number) are about one-third longer and very thin; the shaft is almost completely granulated with the sheath extending about two-thirds its length (Fig. 208). Setae of the neuropodia are similar in appearance and arrangement. Hooded hooks begin in the neuropodia on setigers 11–15 and in the notopodia on setigers 25–50 (Figs. 209, 210, 211). Sabre-setae appear one to two setigers before the first appearance of the hooks or sometimes in the same setiger. There may be one or two sabre-setae in each neuropodium. In the anterior hook-bearing neuropodia, there are often two to three longer dorsal capillary setae as well as finely granulated and thinly sheathed companion setae. More posteriorly the capillaries disappear. The hooks have obvious secondary hoods, which are very short and low (Fig. 210). The opening of the hood encircles the teeth; the edges of this opening appear to be in close contact with the opening in the primary hood and often with the seta. The two hoods sometimes slip away from one another and from the hook (Fig. 211). The neuropodial hooks have three to four pairs of teeth above the main fang and the notopodial hooks have four to five.

The pygidium bears two heavy ventral lobes and a single thinner mid-dorsal cirrus (Fig. 212).

Biology: The specimens collected for this study were taken intertidally from *Halimeda* algae, coral debris, sand in *Thalassia* beds, mud, and from rocks in subtidal ponds. HARTMAN (1951) described specimens collected from fine sand and decaying vegetation. It has also been collected from sponges in somewhat brackish water. *Prionospio heterobranchia* does not seem to thrive in polluted waters. In a study concerning the use of marine invertebrates as pollution indicators, it was found in dominate numbers only in the largely unpolluted bays (REISH, 1960).

Material: *Prionospio heterobranchia texana* Hartman, Holotype (Allan Hancock Foundation); *P. spongicola* Wesenberg-Lund, Holotype (British Museum); Massachusetts – Vineyard Sound, Woods Hole, Barnstable; Rhode Island; York River, Gloucester, Virginia; Florida – St. Andrews Bay, Tampa Bay, Boca Ciega Bay, Alligator Harbor, Stock Island, Key West, Tavernier Key; Bahamas – Bimini, Andros.

Distribution: North Atlantic: Massachusetts, Rhode Island, Virginia, West Coast of Florida; Bimini; Bahamas; Trinidad; Gulf of Mexico.

Discussion: The subspecies *Prionospio heterobranchia texana* Hartman, 1951, and *P. heterobranchia newportensis* Reish, 1959b, were separated from the stem species *P. heterobranchia* Moore, 1907, on the basis of the first appearance of neuro- and notopodial hooded hooks in the following manner:

P. heterobranchia Moore, 1907
Hooks begin: Neuropodia setiger 15
Notopodia setiger 40
P. heterobranchia texana Hartman, 1951
Hooks begin: Neuropodia setiger 12
Notopodia setiger 35
P. heterobranchia newportensis Reish, 1959
Hooks begin: Neuropodia setiger 14
Notopodia setigers 42–55

In the present study within a single collection, a range of variation was found on different specimens which includes that of the stem species and both subspecies. For this reason and because no other taxonomic differences could be found upon examination of the type material, both subspecies have been synonomized with the stem species.

Examination of the holotype of *P. spongicola* Wesenberg-Lund showed that the third pair of branchiae are cirriform rather than pinnate as indicated in the original description. They have fairly long cilia and are similar to those of the second pair. The branchial pattern, therefore, conforms with that of *P. heterobranchia* and is herein synonomized with that species.

Genus **Apoprionospio** Foster, 1969

Type-species: *A. dayi* Foster, 1969, p. 383. Gender: feminine.

Diagnosis: Prostomium subtriangular, flared anteriorly, lacking frontal horns. Peristomium fused with setiger 1, surrounding prostomium posteriorly as a yoke or collar; with no lateral wings or elevations. Four pairs of branchiae beginning on setiger 2; first three pairs cirriform, fourth pinnate. Neuropodial lamellae of setiger 2

somewhat enlarged, triangular, directed ventrally. Pygidium with anal cirri. Hooded hooks in posterior neuropodia and notopodia; bidentate or multidentate. Dorsal membranous ridges connecting notopodial lamellae at some point along body.

Discussion: According to this revision, the following species of *Prionospio* are referred to *Apoprionospio* Foster:

1. *A. saldanha* (DAY, 1961, p. 485). South Africa.
2. *A. pygmaea* (HARTMAN, 1961, p. 93, as *pygmaeus*). Southern California.
3. *A. caspersi* (LAUBIER, 1962, p. 135). Adriatic.
4. *A. dayi* (FOSTER, 1969, p. 383). North Carolina, Gulf of Mexico.

Prionospio nova ANNENKOVA, 1938, p. 175, based on an incomplete specimen from the Japan Sea, is considered indeterminable at the species level; however, the arrangement and shape of the second neuropodial lamellae indicate that it agrees with *Apoprionospio*.

KEY TO THE SPECIES OF APOPRIONOSPIO

1a. Neuropodial hooded hooks multidentate. Pinnae of fourth branchial pair regularly situated in two opposing rows, not extending to the end of the shaft 2
1b. Neuropodial hooded hooks bidentate. Pinnae of fourth branchial pair irregularly arranged along the shaft, extending to near the tip of the shaft 3

2a. Dorsal membranous ridge on setiger 7 present . . . *A. dayi*
2b. Dorsal membranous ridge on setiger 7 absent . . *A. pygmaea*

3a. Dorsal membranous ridge on setiger 7 present . . *A. caspersi*
3b. Dorsal membranous ridge on setiger 7 absent . . *A. saldanha*

Apoprionospio pygmaea (Hartman, 1961)

(Figures 213–225)

Prionospio pygmaeus HARTMAN, 1961, p. 93; 1963b, p. 44. – LAUBIER, 1962, pp. 147, 150. – REISH, 1963a, p. 427; 1968b, p. 84. – WU & CHEN, 1964, p. 59. – REISH & BARNARD, 1967, p. 9.

Diagnosis: Prostomium subtriangular, flared anteriorly. Peristomium inconspicuous. Branchiae four pairs; first three pairs cirriform; fourth pair pinnate with pinnae extending almost the length of the shaft. Neuropodial lamellae of setiger 2 enlarged. No dorsal crest on setiger 7. Multidentate hooded hooks first appearing in neuropodia on setigers 14–15 and in notopodia on setigers 18–37. Pygidium with one long mid-dorsal cirrus and two shorter lateral cirri.

Description: Body length is up to 14.1 mm, with 55 setigers. The prostomium is subtriangular or wedge-shaped, often anteriorly flared and extending posteriorly to the level of setiger 2 (Fig. 213). There are none to four eyes; when present, the slightly larger anterior pair is situated just behind the anterior enlarged part. There may be slight indications of transverse ridges extending between the branchial bases. The peristomium extends ventrally beneath the prostomium but does not project laterally to any degree and does not form a hood. It slopes upward at the level of setiger 1 and here a V-shaped ridge or collar extends across the dorsum around the posterior tip of the prostomium (Fig. 213).

There are four pairs of branchiae beginning on setiger 2; the first three pair smooth and ciliated and the fourth pinnate. Branchiae of the first pair are slender, only slightly tapered, noticeably ciliated, and approximately the same length as the notopodial lamellae (Fig. 214). Branchiae of setigers 3 and 4 are similar to the first pair, but are broader, with longer cilia extending the length of the shaft (Figs. 215, 216). The pinnate branchiae of the fifth setiger are almost twice the length of the dorsal lamellae (Fig. 217). The pinnae are closely applied to one another and appear to be approximately the same length, though distally they may be slightly shorter. They are longer than the width of the shaft and extend along almost the entire branchia, leaving only the distal one-fifth free and tapering.

The anterior body region is somewhat flattened and the parapodia do not change drastically in shape until setigers 10–14. The notopodial lamellae of setiger 1 are rounded and slightly cupped; those of the neuropodia are about the same height but are narrow and bluntly rounded (Fig. 218). On the second setiger the neuropodial

lamellae are asymmetrical, and enlarged with a ventral extension; the notopodial lamellae are extremely long caused by the erection of the notopodia; the lamellae are cupped, with the setae emerging from within the fold (Fig. 214). Neuropodial lamellae of setiger 3 are smaller than the preceeding. The posterior face of the notopodial cup is broader than the preceeding and remains this way along its entire length, while the anterior face is indented; the cup does not extend to the distal tip of the lamella (Fig. 215). By setiger 4, the neuropodial lamellae are no longer asymmetrical but are similar to those of setiger 1 being bluntly rounded and small (Fig. 216). In the first postbranchial setigers, the notopodia are still elongate but the lamellae are shorter and no longer attenuated at the tip (Fig. 219). Between setigers 10 and 14, the notopodial lamellae become low and rounded, extending onto the body dorso-laterally; the presetal lamellae well-developed, rounded and almost as long as the postsetal lamellae; the neuropodial lamellae are wider than in the preceeding setigers and the presetal lamellae are low and rounded (Fig. 220). In the posterior body region, the notopodial lamellae have shifted more ventro-laterally; they are more angular and the presetal lamellae are no longer well-developed (Fig. 221).

The anterior setae are all capillary. In setiger 1 they are arranged in two series, those of the anterior series being about two-thirds the length of those in the posterior row; the neuropodial setae are broadly sheathed, appearing uni- or bilimbate depending on their orientation and are heavily granulated; notopodial capillaries are similar in appearance (Figs. 222, 223). In succeeding parapodia, the notopodial setae increase greatly in number, emerging from the lamellar cup as a whorl; they vary in length and are thicker and longer than those of the neuropodia. In posterior setigers the setae all become thinner; the granulations remain but the sheaths become negligible. With the appearance of the hooded hooks, companion setae are found which show few if any granulations and no apparent sheaths. The neuropodial hooded hooks first appear in setigers 14–15. This is apparently a very stable character since, out of twenty-six specimens from nine stations, all but one individual had hooks beginning on setiger 15; in all cases the characteristic sabre-seta was first present on setiger 11. The hooks have four to six small teeth above the

main fang (Fig. 224). There is a small inconspicuous secondary hood within the much larger primary hood. Notopodial hooded hooks, beginning on setigers 18–37, are similar in appearance but are considerably longer than the neuropodial hooks and the setal head is smaller in proportion to the shaft.

The pygidium bears one long mid-dorsal cirrus and two shorter laterals (Fig. 225). The tips of all three cirri are usually pigmented. At the base of the two lateral cirri, in a somewhat ventral position, are two small lobes or knobs which are also pigmented.

Biology: This species was collected in the Gulf of Mexico intertidally to 5 fathoms from *Thalassia* flats, sand and mud bottoms. It has been reported off California from depths of 5 to 12 fathoms from hard-packed sandy mud and black sandy mud.

Material: *Prionospio pygmaeus* Holotype (Allan Hancock Foundation) and Paratype: USNM; Florida – Tampa Bay, Panama City, Seahorse Key; Port Aransas, Texas.

Distribution: California; Gulf of Mexico.

Discussion: Examination of type material of *Prionospio pygmaeus*, deposited in the Allan Hancock Foundation, revealed the presence of multidentate hooded hooks rather than bidentate hooks, as indicated in the original description.

It seems likely that *A. pygmaea* may prove to be a synonym of *A. nova* (Annenkova) from the Japan Sea. The latter, however, is incompletely described and no information exists regarding the presence or absence of a dorsal crest or the first appearance and nature of the neuropodial hooded hooks. Until such time as additional material from this area is available for comparisons, it seems best to refer the present specimens to *A. pygmaea.*

Apoprionospio dayi Foster, 1969

(Figures 226–236)

Apoprionospio dayi Foster, 1969, p. 383.

Diagnosis: Prostomium subtriangular with two pairs of eyes and occasionally additional eyespots. Peristomium forming a yoke or collar around the prostomium. Branchiae, four pairs, first three pairs

cirriform, fourth pair pinnate, with pinnae extending only one-half to two-thirds length of shaft. Neuropodial lamellae of setiger 2 larger than those of remaining setigers. Dorsal crest between notopodial lamellae, on setiger 7. Multidentate hooded hooks first appearing in setigers 16–18 of neuropodia and in setigers 27–40 of notopodia. Pygidium with three anal cirri, one long mid-dorsal and two shorter laterals.

Description: The body length is up to 10 mm, with 46 setigers. The prostomium (Fig. 226) is subtriangular in shape, widest anteriorly. It narrows posteriorly, extending to about the level of setiger 2. There are two pairs of eyes, the anterior pair being farther apart and often larger. There is a transverse dorsal ridge behind the prostomium and first parapodia (Fig. 226). The peristomium is low and surrounds the prostomium like a collar rather than the more typical hood. There are no lateral wings. In some specimens the transverse ridge appears to be the posterior continuation of this peristomial collar.

There are four pairs of branchiae, the first three cirriform and the fourth pinnate. The first pair is slender and neither obviously ciliated nor tapered (Figs. 226, 227). The second and third pairs are thicker and tapered, with long cilia on the proximal one-half to two-thirds of the branchial shafts, with shorter cilia continuing to the branchial tips (Figs. 226, 228). The pinnate branchiae of setiger 5 are the longest of the four pairs, the pinnae extending one-half to two-thirds the length of the shafts. The pinnae are as long as the branchial width, closely adhering to one another and forming one row on either side of the branchia (Fig. 229).

The anterior notopodia are long and erect. The notopodial lamellae of setiger 1 are low, rounded and slightly cupped, while those of the neuropodia are longer and thinner (Figs. 226, 230). The parapodial lamellae of setiger 2 are conspicuously different from those of the preceeding in that the neuropodial lamellae are especially large and triangular, with the long axis extending ventrally (Figs. 226, 227). The notopodial lamellae are elongate, erect, and triangular, with a slight anterior fold or cup opening laterally, from which the notosetae emerge. The fold becomes more pronounced in the follow-

ing setigers and, by setigers 4–5, it is almost symmetrical, forming a V-shaped cup or groove with both sides equal. At this point the notopodial lamellae are very elongate and the neuropodial lamellae are thinner and tapered (Fig. 228).

On setiger 7 a transverse dorsal ridge or crest extends between the notopodial lamellae. The anterior face of the notopodial cup is more like a presetal lamellae and is rounded (Fig. 231). The ridge extends from the point where the pre- and postsetal lamellae join. The neuropodial lamella is bluntly rounded, similar to that of setiger 1. The neuropodial presetal lamella is fairly well-developed, low and rounded.

On the next few setigers the notopodial lamellae are flattened, low, and may extend upon the dorsal surface but do not connect to form ridges; both noto- and neuropodial presetal lamellae are well-developed (Fig. 232). In posterior setigers the notopodial lamellae are much more lateral, forming low ridges approximately level with the dorsum; the presetal lamellae have decreased in prominence and are present as low ridges; the setal bundle has shifted to a more ventral position (Fig. 233). The neuropodial lamellae are similar in shape to those of the notopodia but remain smaller. Posteriorly the notopodial lamellae become longer and thinner and those of the neuropodia become lower and more rounded.

Anterior capillary setae are all similar, appearing unilimbate (Fig. 234). There are only a few setae in setiger 1. In the second setiger the notosetae increase significantly in number; they are arranged in a whorl and vary considerably in length. By setigers 4–5, the neuropodial setae are thinner and not as broadly sheathed as those of the notopodia. A large sabre-seta appears in setiger 11 on all specimens examined. It differs from the typical spionid sabre-seta in that it is very broadly sheathed (Figs. 232, 235). Furthermore, the sabre-setae do not always occupy the ventral-most position in the neuropodial fascicle but may emerge on the same level as some of the hooded hooks (Fig. 233).

In several setigers anterior to the first appearance of hooded hooks, the neuropodial setae are very long and no longer granulated or broadly sheathed. The neuropodial hooded hooks first appear in setigers 16–18. The hooks have long primary hoods and very small,

closely-applied secondary or internal hoods. The hooded hooks have two to three small teeth above the main fang (Fig. 236). The distribution of two and three denticled hooks varies but there does not seem to be a pattern. The neuropodial fascicle also includes long, thin, companion setae (Fig. 233). Notopodial hooded hooks, similar to those of the neuropodia, first appear in setigers 27–40.

The pygidium bears a single, long, slender, mid-dorsal and two shorter, lateral anal cirri.

Material: Beaufort, North Carolina; Grand Isle, Louisiana; Port Aransas, Texas. Holotype: USNM 39487; Paratype: USNM 39488.

Distribution: North Carolina; Gulf of Mexico.

Discussion: *Apoprionospio dayi* differs from the closely related *A. pygmaea* by the presence of the dorsal membranous ridge on setiger 7. The pinnate branchiae of *A. dayi* differ from those of *A. caspersi* and *A. saldanha* by having the pinnae regularly arranged in two opposing rows along the shaft, closely applied to one another and extending only about one-half the length of the branchia. Examination of paratypes of *Prionospio caspersi* (personal collection of L. LAUBIER) and *P. saldanha* (British Museum) confirmed the irregular arrangement of the pinnae and their extension along almost the entire length of the shaft. *A. pygmaea* and *A. dayi* possess multidentate hooks, whereas they are bidentate in *A. caspersi* and *A. saldanha.*

Genus **Paraprionospio** Caullery, 1914

Type-species: *Prionospio pinnata* Ehlers, 1901. Designated by CAULLERY, 1914, p. 358. Gender: feminine.

Diagnosis: Spindle-shaped prostomium surrounded by well-developed peristomial hood forming lateral wings. Hood formed by fusion of peristomium and achaetous second segment. Branchiae pinnate, numbering three pairs beginning on setiger 1. Parapodia of first setiger well-developed. With conspicuous ridge connecting branchial bases on setiger 1. Noto- and neuropodial hooded hooks multidentate. Pygidium with anal cirri.

Discussion: The genus *Paraprionospio* Caullery contains a single species:

P. pinnata (Ehlers). Included are:

Prionospio (Paraprionospio) pinnata inaequibranchia CAULLERY, 1914, p. 356. Amboina.

Prionospio africana AUGENER, 1918, p. 402. West Africa.

Prionospio alata MOORE, 1923, p. 185. Southern California.

Paraprionospio tribranchiata BERKELEY, 1927, p. 415. British Columbia.

Prionospio plumosa TREADWELL, 1931a, p. 4. Chesapeake Bay.

Prionospio treadwelli HARTMAN, 1951, p. 84. New name for *P. plumosa* Treadwell, preoccupied.

Prionospio ornata BERKELEY & BERKELEY, 1961, p. 660. Off Peru (larvae).

Paraprionospio was originally erected for the widely distributed and well-known *Prionospio pinnata.* In *Prionospio sensu stricto* (including the three genera separated from *Prionospio* by FOSTER, *Apoprionospio, Aquilaspio* and *Minuspio*), the first setiger (not segment) is reduced and does not bear the gills; segments 1 and 2 are more or less fused with reduction in the parapodia. In *P. pinnata,* however, setiger 1 (segment 3) is only slightly smaller and bears the first pair of gills. CAULLERY (1914) established the subgenus *Paraprionospio* for *P. pinnata* on this basis. He pointed out that possibly either the first setiger was simply not reduced, as it was in *Prionospio,* or that the first parapodia had disappeared, with the lateral wings of the peristomium remaining as vestiges of the first setiger. Later SÖDERSTRÖM (1920) synonomized the subgenus saying that, as in *Prionospio,* segments 1 and 2 have fused resulting in parapodial loss so that the gills actually begin on segment 3. The fact remains, however, that if one considers a suite of characters, *Paraprionospio* can be distinguished as a separate genus. Table 7 illustrates some of these differences.

Paraprionospio also shows a very close relationship to the genus *Streblospio.* Characteristics in common include prostomium enclosed in a hood, branchiae beginning on setiger 1 and similar setae.

TABLE 7

COMPARISON OF PARAPRIONOSPIO AND PRIONOSPIO

Genus	First appearance of branchiae	Branchial sheath	Peristomial wings	Size of first parapodia
Paraprionospio Caullery	setiger 1	present	very pronounced	not significantly reduced
Prionospio Malmgren	setiger 2	absent	absent	much reduced

Paraprionospio pinnata (Ehlers, 1901)

(Figures 237–246)

Prionospio pinnata EHLERS, 1901, p. 163; 1908, p. 110. – AUGENER, 1927, p. 351. – MONRO, 1933, p. 1047; 1937, p. 299. – FAUVEL, 1936, p. 60; 1953a, p. 323; 1953c, p. 36. – OKUDA, 1937a, p. 247; 1937b, p. 49. – BERKELEY & BERKELEY, 1941, p. 42; 1952, p. 30; 1963, p. 149; 1964, p. 132. – WESENBERG-LUND, 1949, p. 324. – TEBBLE, 1955, p. 124. – HARTMAN, 1955, p. 182; 1960, p. 114; 1963a, p. 43; 1963b, pp. 74, 123, 131, 148, 167, 179, 194, 211, 231, 247, 258, 277, 296, 328, 344, 358, 375, 398; 1966, p. 19; 1967, pp. 11, 113. – KIRKEGAARD, 1959, p. 22. – REISH, 1959a, pp. 38, 61, 64, 67, 71, 75, 78; 1961, p. 86; 1968a, p. 84. – BARNARD & REISH, 1959, pp. 9, 71, 73, 88. – DAY, 1961, p. 485; 1967, p. 488. – WU & CHEN, 1964, p. 59. – BELLAN, 1964, p. 112. – SHEPHERD, 1964, p. 71. – IMAJIMA & HARTMAN, 1964, p. 286. – HARTMANN-SCHRÖDER, 1965, p. 211. – GUILLE & LAUBIER, 1966, p. 272. – ESTCOURT, 1967, p. 76. – BANSE & HOBSON, 1968, p. 29.

Prionospio (*Paraprionospio*) *pinnata inaequibranchia* CAULLERY, 1914, p. 356; 1944, p. 13.

Prionospio africana AUGENER, 1918, p. 402. – MONRO, 1930, p. 149.

Prionospio alata MOORE, 1923, p. 185. – HARTMAN, 1941, p. 298.

Paraprionospio tribranchiata BERKELEY, 1927, p. 415. – WEESE, 1933, pp. 20, 21. – PETTIBONE, 1967, p. 12.

Prionospio plumosa TREADWELL, 1931a, p. 4. – *Not* Sars, 1872.

Prionospio tenuis, HARTMAN, 1945, p. 32. – *Not* Verrill, 1879.

Prionospio tribranchiata, HARTMAN & REISH, 1950, p. 29.

Prionospio treadwelli HARTMAN, 1951, p. 84.

Prionospio ornata BERKELEY & BERKELEY, 1961, p. 660; 1964, p. 132. – PETTIBONE, 1967, p. 12.

Diagnosis: Prostomium spindle-shaped, enclosed by lateral wings formed by fusion of peristomium (segment 1) and achaetous first

segment. Three pairs of pinnate branchiae beginning on setiger 1. Prominent dorsal ridge connecting branchial bases on setiger 1. Hooded hooks multidentate, beginning in neuropodia on setiger 9 and in notopodia posterior to setiger 19. Pygidium with three anal cirri; two shorter laterals and a longer, unpaired dorsal cirrus.

Description: The body length is up to 48 mm, with 122 setigers. The prostomium varies slightly in shape, from a very narrow tapered cylinder to a spindle-shaped structure, widest in the area of the eyes. In the adult, there may be none to four well-defined prostomial eyes; occasionally there are two larger areas of diffuse pigment. The peristomium is fused dorsally and laterally with the first achaetous segment, forming an envelope enclosing the prostomium. There are two large winglike dorsal peristomial expansions which may be closely applied to the prostomium or extended laterally (Fig. 237).

The palps are rarely present, being extremely deciduous; they are ventrally grooved and often possess a conspicuous basal sheath. The three pair of branchiae are pinnate and very often missing. In the majority of cases where branchiae are present, one or more are in some stage of regeneration resulting in extreme variation in both number of pinnae and proportion of the shaft which is pinnate. In some instances the regenerating branchia is completely smooth. The branchiae are variable in length and may extend from setiger 2 to setiger 15. The branchiae begin on the first setiger, which is homologous to setiger 2 in species of *Prionospio*. In some instances, a threadlike filament may arise at the base of the third pair of gills. There is a conspicuous dorsal ridge connecting the two branchial bases on setiger 1 (Fig. 237).

The anterior parapodial lamellae are well-developed; the notopodial lamellae of setigers 1–5 are lanceolate; the corresponding neuropodial lamellae are somewhat smaller and less foliaceous (Fig. 238). Posterior to setiger 5, noto- and neuropodial lamellae become increasingly rounded until they are somewhat similar in shape, though the neuropodial lamellae are shorter (Fig. 239). Progressively the notopodial lamellae become thin and long until posteriorly they are increasingly acuminate (Fig. 240).

Anterior setae are all capillary and similar in appearance. The

notopodial setae appear to be in three rows, the posterior row containing the longest ones. The sheath often gives the setae a bilimbate appearance, with granulations apparent; the latter, however, often appear on the sheath rather than the shaft which is where they are usually found (Fig. 241). At setiger 9, the neuropodia change abruptly with the appearance of multidentate hooded hooks, accompanied by long, thin companion setae (Figs. 240, 242). There are one to three sabre-setae at the ventral edge of the setal fascicle. Notopodial hooks appear posterior to setiger 19. Both neuro- and notopodial hooks have large, clear, primary hoods and smaller, internal, secondary hoods. The latter are closely applied to the setal shafts and are heavily striated (Figs. 242, 243, 244).

On the dorsal surface between the parapodia of a number of specimens, beginning about setiger 20, there are large, clear hyalinelike circles with small dots in the center, accompanied by pouches or thin membranes. The function of these structures is still unknown.

The proboscis is bilobed and cylindrical (Fig. 245). The pygidium bears three anal cirri, a short lateral pair and a single, mid-dorsal, long, thin one (Fig. 246).

Biology: *Paraprionospio pinnata* has been dredged from substrata composed of mud, mud and clay, and mud and sand. It has been found in thin-walled tubes of mud (BERKELEY & BERKELEY, 1952) and tubes of fine mud and clay (WESENBERG-LUND, 1949). The only tubes observed on Caribbean specimens are transparent, fibrous and covered by relatively large quartz grains. *P. pinnata* is eurybathyal and found at depths ranging from less than three to 1300 meters.

Material: *Prionospio alata* Holotype: USNM 17369; *Prionospio plumosa* Holotype: USNM 19596; *Prionospio ornata* Holotype: USNM 32697; Paratype: USNM 32698. Other material includes collections from the following: Peru coast; Mayagüez, Puerto Rico; Florida – Cedar Key, Clearwater Beach, Alligator Harbor, off shore Panama City, North Bay near Lynn Haven, Gasparilla Island, Horseshoe Point; Grand Isle, Louisiana; Port Aransas, Texas; Beaufort, North Carolina; Yorktown, Virginia; Maldives; Gold Coast off West Africa; Capetown, South Africa; Concepcion Bay, Chile; Portuguese Guinea.

Distribution: Atlantic: Chesapeake Bay to Florida, Morocco, West Africa to South Africa; Gulf of Mexico; Caribbean; Indian Ocean; Pacific: Western Canada to Chile, Japan; New Zealand.

Paraprionospio pinnata larvae

(Figures 247–261)

Prionospio ornata BERKELEY & BERKELEY, 1961, p. 660; 1963, p. 149; 1964, p. 132. – PETTIBONE, 1967, p. 12.

Prionospio pinnata, BERKELEY & BERKELEY, 1963, p. 150. – *Not* BERKELEY & BERKELEY, 1964, p. 132.

Discussion: BERKELEY & BERKELEY (1961) described some larvae from off Peru as a new species, *Prionospio ornata* based on the form of the branchiae. They mention *Prionospio pinnata* as the nearest ally, differing in the absence of the lateral peristomial wings, and its dorsal fusion with setiger 1. Later, in 1963 and 1964, the same authors reported neotenous *P. ornata* and *P. pinnata* larvae. The two were distinguished by the presence in *P. pinnata* larvae of large, heavy, straight acicular spines in the neuropodia.

Examination of the material described above provided evidence for the synonomy of *P. ornata* with *P. pinnata*. Specimens of *P. ornata* possess large peristomial wings (Figs. 247, 248), even more obvious in the type specimen (not figured here). It was also noted that there is a conspicuous sheath on the base of the palps on some of the specimens, much like that of the adult *Paraprionospio pinnata*. Other characteristics in common with the latter are presence of a ridge between the notopodia of setiger 1 (Fig. 247), identical hooded hooks beginning on setiger 9 (Figs. 250, 251), similarly shaped parapodial lamellae and similar capillary setae. *P. ornata* also possesses the sabre-seta, characteristic of *P. pinnata* (Fig. 252).

The unusual branchiae particularly diagnostic of *P. ornata* (Berkeley & Berkeley, 1961) are generally circular in outline giving the animal a "bushy appearance". It was noted, however, that the branchial pinnation, and correspondingly the branchial shape, is extremely variable. In the larvae, the branchiae vary from small and almost smooth to large and bushy (Figs. 253–257). In the adults, the branchiae vary in the same manner but are generally longer (Figs. 258, 259). Pinnation varies in adults, resulting in variation of "bushiness" in the branchiae. The spacing of the platelike pinnae affect the width of the branchiae (Figs. 260, 261). The branchial structure is similar in specimens of adult *P. pinnata* and in larval *P. ornata*.

The single acicular spine found on setiger 10 and subsequent setigers of specimens identified as *P. pinnata* by the BERKELEYS (1964) differs from any previously observed setae on spionids in this study. The larvae, however, are spionids though they are not herein considered as *P. pinnata*. The acicular setae do not resemble spionid sabre-setae but are more reminiscent of true aciculae. They could possibly be larval setae but they are not of the typical spionid larval type. The identity of these larvae remains questionable.

Genus **Aquilaspio** Foster gen. n.

Type-species: *Prionospio sexoculata* AUGENER, 1918, p. 405. Gender: feminine.
Etymology: L. – *aquila* = eagle. This genus is named in honor of the Apollo Eagle moon landing.

Diagnosis: Prostomium subtriangular. Anterior border rounded or sometimes extended slightly laterally; continues posteriorly as a more or less well-developed keel. Peristomium surrounding prostomium as a hood, developed to varying degrees. Branchiae all pinnate, two to four pairs, beginning on setiger 2. Anterior setae all capillary. Tridentate or multidentate hooded hooks present in posterior setigers of neuro- and notopodia. Pygidium with anal cirri.

Discussion: According to this revision, the following species of *Prionospio* are referred to *Aquilaspio*:

1. *A. sexoculata* (AUGENER, 1918, p. 405). West Africa.
2. *A. aucklandica* (AUGENER, 1924, p. 69). New Zealand. Includes: *P. krusadensis* FAUVEL, 1929, p. 182. India.
3. *A. peruana* (HARTMANN-SCHRÖDER, 1962b, p. 138). Peru.

KEY TO SPECIES OF AQUILASPIO

1a. Notosetae present on setiger 1 2
1b. Notosetae absent on setiger 1. No dorsal crests. Neuropodial hooded hooks beginning on setigers 14–16; notopodial hooks from about setiger 30 . . . . . *A. sexoculata*

2a. With four pairs of branchiae. With well-developed dorsal crests from setigers 6–7. Neuropodial hooded hooks first appearing on setigers 16–17; notopodial hooks from about setiger 27 . . . . . *A. peruana*
2b. With three pairs of branchiae. With low dorsal crests. Neuropodial hooded hooks first appearing on setigers 18–20; notopodial hooks from setigers 30–31 . . . . . *A. aucklandica*

Genus **Minuspio** Foster gen. n.

Type-species: *Prionospio cirrifera* Wirén, 1883. Gender: feminine.
Etymology: L. – *minus* = bare, smooth. Referring to the smooth non-pinnate branchiae.

Diagnosis: Prostomium subtriangular, anteriorly rounded, blunt or inflated, extending posteriorly as a more or less well-developed

keel. Peristomium forming a hood surrounding prostomium developed to varying extents. Branchiae all cirriform, beginning on setiger 2, varying from four to forty pairs. Anterior setae all capillary. Hooded hooks in posterior neuro- and notopodia, bidentate to multidentate. Pygidium with anal cirri.

Discussion: According to this revision, the following species are referred to *Minuspio*:

1. *M. cirrifera* (WIRÉN, 1883, p. 409). Bering Sea. Includes:
   Prionospio patagonica AUGENER, 1923, p. 3. West Patagonia.
   Prionospio multibranchiata BERKELEY, 1927, p. 414. British Columbia.
   Prionospio delta HARTMAN, 1965a, p. 151. Northeastern South America.
2. *M. polybranchiata* (FAUVEL, 1929, p. 184). New name for *P. multibranchiata* FAUVEL, 1928, p. 94, preoccupied. Indian Ocean.
3. *M. japonica* (OKUDA, 1935, p. 241). Japan. As *P. japonicus*.
4. *M. cirrobranchiata* (DAY, 1961, p. 488). South Africa.
5. *M. chilensis* (HARTMANN-SCHRÖDER, 1962a, p. 138). Chile.
6. *M. gracilis* (HARTMANN-SCHRÖDER, 1962a, p. 141). Chile.
7. *M. longibranchiata* (REISH, 1968a, p. 82). Baja California, Mexico.

KEY TO SPECIES OF MINUSPIO

1a. Branchiae long, thin, filamentous; five pairs . . . . . *M. longibranchiata*
1b. Branchiae not filamentous 2

2a. First setiger extremely reduced; notosetae absent . . . . . *M. chilensis*
2b. First setiger smaller than following but well-developed; notosetae present 3

3a. Branchiae fewer than twenty pairs 4
3b. Branchiae more than twenty pairs . . . . *M. polybranchiata*

4a. Neuropodial hooded hooks multidentate 5

4b. Neuropodial hooded hooks bidentate . . . *M. cirrobranchiata*

5a. Pygidium with eight anal cirri or lobes. . . . . *M. gracilis*
5b. Pygidium with three anal cirri; one long and two short . . 6

6a. Branchiae four pairs . . . . . *M. japonica*
6b. Branchiae six to twelve pairs . . . . . *M. cirrifera*

Minuspio cirrifera (Wirén 1883) new combination

(Figures 262–275)

Prionospio (?) *cirrifera* WIRÉN, 1883, p. 409.
Prionospio cirrifera, BIRULA, 1897, p. 102. – AUGENER, 1912, p. 178; 1928a, p. 740. – CAULLERY, 1914, p. 359. – FAUVEL, 1916, p. 103; 1927, p. 62; 1932, p. 174; 1953a, p. 324. – SÖDERSTRÖM, 1920, p. 237. – FAGE & LEGENDRE, 1927, p. 123. – JAKUBOVA, 1930, p. 874. – RIOJA LO BIANCO, 1931, p. 75. – BERKELEY & BERKELEY, 1942, p. 196; 1952, p. 28. – GORBUNOV, 1946, p. 39. – ZATSEPIN, 1948, p. 132. – USHAKOV, 1950, p. 202; 1955, p. 278; 1965, p. 255. – WESENBERG-LUND, 1950a, p. 78; 1950b, p. 31; 1951, p. 70; 1953, p. 58. – HARTMAN, 1955, p. 182; 1959, p. 378; 1963b, p. 44; 1965a, p. 150. – MARINOV, 1955, p. 113. – HANNERZ, 1956, p. 49. – REISH, 1956, p. 58; 1959a, p. 38; 1959b, p. 87; 1961, pp. 86, 88, 89, 90; 1963b, pp. 26, 28, 31; 1964, p. 89; 1968b, p. 221. – BARNARD & HARTMAN, 1959, p. 11. – BARNARD & REISH, 1959, pp. 9, 87. – TEBBLE, 1959, p. 23. – DUMITRESCU, 1960, p. 76; 1963, p. 187. – CHLEBOVITSCH, 1961, p. 201. – JONES, 1961, pp. 266, 288, 316. – MCINTYRE, 1961, p. 359. – TENERILLI, 1961, p. 252; 1962, p. 78. – ELIASON, 1962b, p. 263. – LAUBIER, 1962, p. 133. – ORRHAGE, 1964a, pp. 338, 359, 364, 380–383. – WU & CHEN, 1964, p. 59. – DE SILVA, 1965, p. 17. – GUILLE, 1965, p. 287. – GUILLE & LAUBIER, 1966, p. 271. – DAY, 1961, p. 487; 1967, p. 486. – REISH & BARNARD, 1967, p. 9. – SIMON, 1967, p. 420.
Prionospio patagonica AUGENER, 1923, p. 3. – HARTMAN, 1966, p. 19.
Prionospio (?) *patagonica*, HARTMAN, 1953, p. 42.
Prionospio nr. *cirrifera*, HARTMAN, 1960, p. 115.
Prionospio (?) *cirrifera*, HARTMAN, 1951, p. 84.
Prionospio multibranchiata BERKELEY, 1927, p. 414. – PETTIBONE, 1967, p. 12.
Prionospio delta HARTMAN, 1965a, pp. 11, 46, 47, 147, 151, 249.

Diagnosis: Prostomium anteriorly rounded, extending posteriorly as more or less well-developed keel. Peristomium surrounding prostomium as low hood. Branchiae all cirriform, six to twelve pairs, beginning on setiger 2. With low dorsal crests on variable number of postbranchial setigers. Anterior setae capillary. Multidentate hooks first appearing in neuropodia on setigers 12–19, in notopodia on

setigers 15–44. Pygidium with long median ventral cirrus and pair of lateral cirri.

Description: The body length is up to 10 mm, with 30 setigers. The prostomium is anteriorly rounded and may be slightly inflated (Fig. 262). It narrows posteriorly and is narrowest at about the level of the eyes. The posterior half is elevated and extends back to the second setiger as a narrow keel. The keel is evident to a greater or lesser extent on specimens from different collections, ranging from almost flat to longer than the notopodial lamellae (Fig. 263). There are none to four eyes on adult specimens. When present, the anterior pair may be round to crescent-shaped and the larger, posterior pair may be rounded, triangular or bar-shaped (Fig. 262). The peristomium is more or less developed as a hood surrounding the prostomium.

The branchiae, beginning on setiger 2, are all cirriform and range in number from six to twelve pairs. They are quite variable in length and, in a single specimen collection, they may be all short and compact (Fig. 264), long and thin (Figs. 265, 266), or a combination of the two. Occasionally regenerating branchiae were found.

The first parapodial lamellae are somewhat rounded with that of the notopodium being slightly cup-shaped; the neuropodial lamella is blunt to round and smaller than the dorsal lamella (Fig. 267). On succeeding parapodia, the lamellae become increasingly larger, leaf-like, and long (Figs. 265, 266). In the midbranchial region the lamellae begin gradually decreasing in prominence; the notopodial lamellae are no longer cup-shaped but are triangular, becoming increasingly rounded, wider and more flattened (Fig. 264). Low dorsal ridges become evident in the postbranchial setigers as a result of the extension of the notopodial lamellae across the dorsum (Fig. 268). These ridges have been found up to the thirty-fifth setiger, beyond which for a few setigers the notopodial lamellae still extend onto the dorsum but no longer connect. In the posterior setigers the notopodial lamellae decrease in width and once again become triangular (Fig. 270). In this region the noto- and neuropodial lamellae are similar in size and shape. Presetal lamellae are very well-developed and anteriorly appear long and tonguelike; more posteriorly they become triangular and are present as low crests in posterior setigers.

Some specimens were found to possess inter-parapodial pouches, similar to those characteristic of the genus *Laonice* (Fig. 269). When present, they begin between setigers 5–6 and extend to setigers 27–28. They are not easily overlooked and are lined with long cilia.

Anterior noto- and neuropodial capillary setae are arranged in two rows. The setae of the posterior row are longer and thinner than those of the anterior row and are often extremely granulated for their entire length (Fig. 271). Setae of the anterior series are very short, thick and heavily granulated and possess a conspicuous sheath which is widest near the base. Anterior notosetae are encircled by the cup-shaped notopodial lamellae. The sheaths of the anterior setae are often extremely full and wide (as in *Dispio*) but become less so in more posterior setigers where they become closely applied to the setal shaft.

Multidentate hooded hooks first appear in neuropodia of setigers 12–18. There may be a secondary hood but, if so, it is extremely closely applied to the hook and is barely distinguishable (Fig. 273). Notopodial hooded hooks are similar and appear first in setigers 15–44 (Fig. 274).

The pygidium bears one long mid-dorsal cirrus and a pair of shorter lateral lobes or cirri (Fig. 275). The length of the median cirrus is quite variable.

Biology: *P. cirrifera* has been reported to construct mud tubes (REISH, 1961) but this was not observed in the present collections. It was found to be a principal species in terms of occurrence and abundance in a newly constructed boat harbor (REISH, 1961). According to HANNERZ (1956), it is found more commonly on mud bottoms. In the present study, it was collected from off jettys, intertidal rock pools, sand among *Rhizophora, Bantia, Halimeda* and *Thalassia*. It was found in depths ranging from the intertidal to 29 meters. Planktonic larvae have been found from July to September (HANNERZ, 1956). FAGE & LEGENDRE (1927) collected sexually mature specimens in the plankton indicative of epitokous spawning.

Material: *Prionospio cirrifera chilensis* (Hamburg Museum); *Prionospio delta* Paratype: Allan Hancock Foundation; North Carolina – Beaufort, Cape Lookout; Florida – Tavernier Key, Key West, Tampa Bay; Grand Isle, Louisiana; Mayagüez Harbor, Puerto Rico; Piscadera Baai, Curaçao; Puget Sound, Washington.

Distribution: Cosmopolitan: Arctic; Greenland to South America, Sweden, English Channel, Portugal; Bering Sea to Southern California.

Discussion: Examination of type material of *P. cirrifera chilensis* (HARTMANN-SCHRÖDER, 1962a, deposited in the Hamburg Museum) revealed differences of a specific magnitude. In *M. cirrifera*, the notopodial lamellae of a number of postbranchial setigers extend onto the dorsum and unite to form low ridges. Such is not the case with *P. cirrifera chilensis* where there is a slight suggestion of crests but they are not a result of fusion of dorsal lamellae since the lamellae do not extend onto the dorsum. Also the postbranchial notopodial lamellae are never rounded as in *P. cirrifera* but retain a consistent subtriangular shape; for about five postbranchial setigers notopodial and neuropodial lamellae are the same size and shape. These lamellar differences would perhaps be sufficient to warrant specific rank but an even more striking difference is the nature of the first setiger. In *P. cirrifera* it is well-developed though small, with definite dorsal and ventral lamellae (Fig. 267). In *P. cirrifera chilensis*, however, there is only one neuropodial setal fascicle and no distinct lamellae. For these reasons, it is herein considered as a distinct species.

M. cirrifera has been assigned a variable number of branchial pairs, ranging from five to six and up to thirteen. Samples from the present collections indicate a range of at least six to twelve. In one sample from Beaufort, North Carolina, the number ranged from six to eight pairs and in a second sample from Grand Isle, Louisiana, seven to twelve. Because of these two samples the range for the species has been placed at five to twelve pairs.

Specimens from two samples, one from Beaufort, North Carolina, and one from Grand Isle, Louisiana, possessed very long, thin branchiae as described for *Prionospio delta* Hartman, 1965a. In others, however, the branchial length and thickness were often extremely variable. For example, on a single specimen the first pair was very long and thin, the next five barely longer than the lamellae and the last two again long and thin. Other specimens in the same sample had quite different branchial types. Because of the variation observed in this character, all specimens examined were assigned to *M. cirrifera*. Examination of the paratype of *Prionospio delta* Hartman (Allan Hancock Foundation) revealed multidentate neuropodial hooks beginning on setiger 19, thus falling within the range observed

for *P. cirrifera*. It is possible that *P. delta* either represents a subspecies or that the long, thin branchiae are a result of variation in some ecological factor, such as oxygen availability. For the present, the two species are synonomized. *P. longibranchiata* Reish, 1968a, from Baja California, has also been characterized as having long, thin branchiae. Examination of the types (Holotype: USNM 28396; Paratype: USNM 38397) revealed branchiae of a somewhat different nature than those characteristic of *Prionospio* species. They are extremely long and thin, similar to long filiamentous branchiae found on certain cirratulids.

Genus **Streblospio** Webster, 1879

Type-species, by monotypy: *S. benedicti* WEBSTER, 1879a, p. 120. *Hekaterobranchus* BUCHANAN, 1890, p. 175. Type-species, by monotypy: *H. shrubsolii* Buchanan, 1890, = *S. benedicti*. Gender: feminine.

Diagnosis: Prostomium narrow, elongate. With poorly developed notopodia, and a single pair of branchiae on first setiger (segment 3). Setiger 2 with dorsal collar or membrane extending transversely between notopodia. Capillary notosetae throughout body. With capillary anterior neurosetae and multidentate hooded hooks on posterior setigers. Pygidium simple, without cirri, with inconspicuous lobes.

Discussion: The genus *Streblospio* Webster contains a single species:

S. benedicti Webster, 1879. New Jersey and Connecticut. Includes:
Hekaterobranchus shrubsolii BUCHANAN, 1890, p. 175. England.
Streblospio dekhuyzeni HORST, 1909, p. 149. Holland.
Streblospio lutinicola HARTMAN, 1936, p. 45. Central California.

Streblospio benedicti Webster, 1879a

(Figures 276–283)

Streblospio benedicti WEBSTER, 1879a, p. 120; 1886, p. 149. – WEBSTER & BENEDICT, 1884, p. 728; 1887, p. 736. – MESNIL & CAULLERY, 1898, p. 132. – TREADWELL

in COWLES, 1930, p. 343. – HARTMAN, 1944, p. 260; 1945, p. 34; 1954, p. 10. – BERKELEY & BERKELEY, 1954, p. 464. – FILICE, 1954, p. 16. – REISH, 1954, p. 113; 1959a, p. 88; 1961, p. 3. – REISH & WINTER, 1954, p. 113. – CAMPBELL, 1957, p. 336. – REISH & BARNARD, 1959, p. 88; 1967, p. 10. – STICKNEY, 1959, p. 14. – JONES, 1961, p. 243. – SANDERS *et al*, 1962, p. 65. – BELLAN, 1964, p. 113. – WELLS & GRAY, 1964, p. 73. – DEAN & HASKIN, 1964, pp. 555, 557. – DEAN, 1965, p. 67. – KEITH & HULINGS, 1965, p. 37. – STONE & REISH, 1965, p. 113. – COLLIER & JONES, 1967, p. 462.

Hekaterobranchus shrubsolii BUCHANAN, 1890, p. 175.

Streblospio shrubsolii MCINTOSH, 1915a, p. 230. – FAUVEL, 1927, p. 106. – AUGENER, 1932a, p. 667; 1939, p. 146. – THORSON, 1946, p. 95. – WESENBERG-LUND, 1941, p. 39; 1942, p. 39. – MARINOV, 1955, p. 113. – ELIASON, 1962a, p. 57. – LAUBIER, 1962, p. 151. – LAUBIER & PARIS, 1962, p. 43. – BELLAN, 1964, p. 113. – HAMOND, 1966, p. 411. – MUUS, 1967, p. 92. – CABIOCH, L'HARDY & RULLIER, 1968, p. 55.

Streblospio dekhuyzeni HORST, 1909, p. 149; 1922, p. 271. – FAUVEL, 1927, p. 107. – HOFKER, 1930, pp. 194, 195. – DE VOS, 1936, p. 94. – KORRINGA, 1951, p. 102. – DEBOUTTEVILLE, 1954, p. 427. – CABIOCH, L'HARDY & RULLIER, 1968, p. 55.

Streblospio lutincola HARTMAN, 1936, p. 45.

Diagnosis: Prostomium elongate, narrow. With four to eight eyes. Setiger 1 reduced; no dorsal lamellae. With single pair of branchiae on setiger 1. With transverse collar on setiger 2. Anterior setae all capillary; multidentate neuropodial hooded hooks first present on setigers 7–9. Pygidium simple.

Description: Body length is up to 6.1 mm, with 44 setigers. The narrow prostomium is somewhat bluntly rounded anteriorly and extends posteriorly almost to the level of setiger 1 (Fig. 276). There are usually four eyes (4–8) located on the posterior one-half to one-third of the prostomium, the two anterior eyes being slightly larger than the posterior two, farther apart and often difficult to detect dorsally. The first three segments (achaetous segments 1, 2 and setiger 1) are fused to form a conspicuous hood surrounding the prostomium ventrally and laterally (Fig. 276). A transverse dorsal ridge connects the bases of the single pair of ciliated branchiae inserted just behind the prostomium on the first setiger.

The first setiger (segment 3) bears small and rounded neuropodial lamellae (Fig. 276). There are no notopodial lamellae but one to two long notosetae are present. The second setiger is characterized by a low dorsal transverse collar formed by the fusion of the two notopodial lamellae; neuropodial lamellae are low and rounded. On the

following setigers, the neuro- and notopodial lamellae are similar, low and rounded (Fig. 277). On the posterior setigers, the notopodial lamellae become small, short and conical and the neuropodial lamellae become low and inconspicuous, appearing as a ridge or bump (Figs. 278, 279).

Anterior neuro- and notosetae are all capillaries and similar in appearance (Fig. 280). They appear uni- or bilimbate and are lightly granular. The length of the limbation depends upon the angle at which the setae are viewed. Multidentate neuropodial hooded hooks are first present on setigers 7–9 (almost always 7) (Fig. 281). There appears to be a secondary hood, similar to that of *Paraprionospio pinnata*. There are long slender companion setae in each parapodium bearing hooks and the typical sabre-setae appear on setigers 6–7 (Fig. 279).

Mature females carry developing young in dorsal brood pouches on about the middle one-third of the body. The pygidium is somewhat simple with two small ventral lobes inconspicuous, often overlooked (Fig. 282).

Biology: *Streblospio benedicti* constructs temporary silty tubes. The animal leaves the tube if disturbed and moves with jerky body motions. As soon as it resettles, it constructs a new tube from any available loose dirt or debris (WEBSTER, 1879a). The tube is situated vertically on the bottom and is several times longer than the animal. It is commonly found intertidally and in the shallow sublittoral. It is common on *Mytilus* beds and in tidal ditches and often found under estuarine conditions. COWLES (1930), reports it from salinities of 10.08–17.27 per mille.

S. benedicti is larviparous and this phenomonon was mentioned briefly by WEBSTER (1879a), CAMPBELL (1957) and JONES (1961). The development was later described by DEAN (1965). It was found that the young are brooded until the nine-setiger stage, at which time they may metamorphose or, if conditions are not right, they may postpone it until the thirteen-setiger stage. None of the above studies, however, mentioned the method or rate by which the eggs reached the dorsal pouches. It was later found by COLLIER & JONES (1967) that these pouches were extensions of the coelom and not just epidermal flaps. In this study larvae were found in the pouches at the twelve-setiger stage. Seminal receptacles were found between neuropiles of the ventral nerve cord.

Material: *Streblospio benedicti* Syntype: USNM 29025; *S. lutincola* Holotype: USNM 20220; Maine – Georgetown Island, Sawyer Island, Southport, Sheepscot River, Falmouth Foreside, Casco Bay; New Hampshire – Newcastle, Newington, Wentworth; Massachusetts – Sandwich, Greenwich Bay, Rhode Island; York River, Virginia; Panama City, Florida; Tamiahua; Texas – Bolivar Peninsula, Mustang and Padre Island, Port Aransas; Maracaibo estuary, South America.

Distribution: Gulf of Maine, Gulf of St. Lawrence; Denmark; France; Virginia; Florida; Texas; South America; Washington to California.

Discussion: A population of *Streblospio* found in the present study from the Maracaibo estuary seem to differ uniquely in brooding methods from the reported *S. benedicti*. In this sample several females were found on which the brood pouches are laterally situated. They appear as long fingerlike extensions between the noto- and neuropodia (Fig. 283). The pouches become evident about the twenty-eighth setiger from the posterior and extend for ten setigers. The eggs are situated in a lateral row in the body cavity anterior to these pouches and seem to move out into them as they become more developed. The pouches contain a vascular loop and about three to four eggs. It would appear that this population represents a separate species or at least subspecies. No morphological distinctions, however, were found between these specimens and specimens of *S. benedicti* from other areas. Therefore it is not being designated as new at the present time until a more detailed investigation is made.

ZOOGEOGRAPHY

The Gulf of Mexico and the Caribbean Sea are included in the Carolinian of the Transatlantic province, Cape Hatteras to Cape Kennedy and Tampa Bay to south Texas, and in the Caribbean province, from Cape Kennedy and Tampa Bay into the tropics, outer shelf to beyond Cape Hatteras, and Bermuda (CERAME-VIVAS & GRAY, 1966).

HARTMAN (1951) divided the polychaete fauna of the Gulf of Mexico into four major categories: a dominant, perhaps endemic fauna of the environs of the Mississippi delta, a West Indian fauna, a western Atlantic fauna, and a cirrummundane fauna. These were not necessarily the major groupings of spionid species in the present study.

The only species, other than those which are newly described, is *Malacoceros* (*M.*) *vanderhorsti*, which is endemic to this area. *Dispio uncinata* was originally described from the Gulf but has since been found from the western Atlantic through the Virginian province (Cape Cod to Cape Hatteras) of the Transatlantic to the southern boundary of the Boreal province (Arctic to Cape Cod). There is no evidence in the present collections for the Delta fauna of HARTMAN (1951) and, according to HEDGPETH (1953), this idea is not supported by the distribution of other groups either.

With regard to a western Atlantic fauna, there are three representatives in the Gulf and Caribbean. These are *Polydora websteri*, *Polydora commensalis* and *Spiophanes wigleyi*. Several species were

found which were common to Beaufort, North Carolina and Panama City, Florida. This is possibly the result of a faunal continuity prior to the formation of the Florida peninsula (HEDGPETH, 1953).

Polydora ligni and *Prionospio heterobranchia* are known from both coasts of North America and were in the Gulf and Caribbean samples. One species, *Apoprionospio pygmaea*, was known previously only from the west coast of North America but is widely distributed throughout the Gulf of Mexico. HEDGPETH (1953) pointed out the close affinity between Pacific and Gulf of Mexico faunas. The former probably crossed the Isthmus of Panama in the late Eocene or early Oligocene.

The largest number of Gulf and Caribbean spionids appear to be circummundane or cosmopolitan in distribution. *Pygospio elegans* and *Prionospio steenstrupi*, with the exception of DAY's (1967) South African record, are only found north of the equator. *Spiophanes bombyx* is primarily a European form but might be considered near cosmopolitan as are *Minuspio cirrifera* and *Laonice cirrata*. *Paraprionospio pinnata* has a wide distribution and is cosmopolitan in warm seas.

WU & CHEN (1964) grouped the species of the genus *Prionospio* according to branchial pattern. They point out that species with all simple branchiae (*Minuspio*) are primarily cold water forms; those with all pinnate branchiae (*Aquilaspio* and *Paraprionospio*) are warm water forms and those with a combination of simple and pinnate branchiae are tropical, sub-tropical and temperate forms (*Prionospio* and *Apoprionospio*). Figure 284 shows the distribution for the above groups. *Minuspio* is seen to be distributed not only in cold water but representatives are found commonly in the Gulf of Mexico and Caribbean Sea and near the equator off India. *Aquilaspio* was not restricted to warm waters. *Paraprionospio pinnata* was the only species with only pinnate branchiae found in the Gulf and Caribbean and is reported also from cold waters. *Prionospio* is distributed in tropical as well as colder waters, and *Apoprionospio* is found in a fairly narrow zone, including the Gulf, off southern California and the Japan Sea.

Figure 285 illustrates the distribution of *Dispio*, *Aonides*, and *Scolelepis* in the Gulf of Mexico, Caribbean Sea and southern Atlantic

Coast of the United States. *Dispio* and *Scolelepis* (*Scolelepis*) are the most common in present samples, and *Aonides* was collected only once.

Species of the genus *Malacoceros* have not often been reported. Of the four species found in the Gulf and Caribbean, *Malacoceros* (*Rhynchospio*) *glutaeus* and *M.* (*M.*) *indicus* seem to be more widely distributed while *Malacoceros* (*R.*) *inflatus* and *Malacoceros* (*M.*) *vanderhorsti* have been collected only from the Gulf of Mexico and Caribbean Sea.

DISCUSSION OF TAXONOMIC CHARACTERS

For several years the concept of the morphological species has been changing and giving way to the idea of a biological species. We still retain the old idea, however, that if any two populations differ morphologically to a certain degree, they must in fact represent separate species. This leads to considerable confusion when dealing with small collections or isolated specimens. In these cases it is amazingly easy to lose sight of the inevitable "character range" and "ecological variation." In fact, many times in these instances one has no way of judging the value of character differences between populations. Although the ideal answer is to examine widely distributed large collections of specimens, one cannot ignore the isolated individuals and samples for these make up by far the majority of the material with which we work. The next logical solution is to attempt to distinguish and utilize those characters which are least subject to individual and ecological variation. This is, of course, a difficult task to accomplish and requires a familiarity with the animal group in question which can only result from examination of large collections.

In other words in order to know a group well enough to designate good species characters one must have looked at many specimens.

The present study has not by any means afforded all the answers to this problem with regard to spionids but it has at least provided bases for questioning certain currently used taxonomic characters.

The first character considered is the nature of the hooded hooks.

The number of teeth and the distribution of different type hooks along the body have long been considered constant characters within a species. The question of the adaptive significance of, for example, the possession of bi- or tridentate hooks has been of considerable concern to systematists because it was thought that if a character was retained it was being selected for. Now, however, we know that not all factors of the phenotype need necessarily to be adaptively pertinent. In other words, neutral characters can be carried along, not selected for but also not selected against and these too can be sound taxonomic characters. This idea is discussed further by MAYR (1966) and KING & JUKES (1969) and is perhaps applicable to the dentition of hooked setae.

Indications from the present study are that, for example, for species described as possessing bidentate hooded hooks one has only to look at enough parapodia and a tri- or quadridentate hook will show up. *Dispio uncinata* was originally characterized as having unidentate hooded hooks yet several specimens examined had, in addition, bidentate hooks. Certain species of *Malacoceros*, *Scolelepis*, *Laonice* and *Spiophanes* were found to possess more than one type of hook, the distribution of which followed no particular pattern. In cases like this, species can often be characterized as having *predominantly* bi- or tridentate hooks and the character still incorporated into the specific diagnosis. It seems, however, that one should no longer lean so heavily on this as a character. Another problem with this is the fact that more often than not, the information in the literature regarding this character is not dependable. It has become obvious that the results given by a particular author depend largely on whether he looked at anterior or posterior parapodia, the number of parapodia examined and, just as important, the magnification at which the observations were made. The latter information is necessary because hooks often look bi- or tridentate under lower power while with oil immersion they are seen to be quadridentate.

Another specific character often used is the first appearance of neuropodial hooded hooks. In some genera, such as *Paraprionospio Streblospio*, *Spiophanes* and *Polydora*, the hooks almost invariably appear on the same setiger. Then there is a group of species of *Prionospio*, *Apoprionospio*, *Minuspio*, *Malacoceros*, *Scolelepis* and

Aonides in which hooks appear within a small enough range of setigers so that, in most instances, this can be used as a specific character. In the third group, which includes *Scolecolepides* and *Dispio*, this is not a good specific character because within some collections the range is as great as thirty to forty setigers. In order to use this character effectively one must be familiar with the genera involved.

Another character often used is the length of branchiae. New species have even been described on this basis. In the present collections of *Paraprionospio pinnata*, specimens were found with branchiae fifteen setigers in length and others with branchiae two to three setigers in length. *Minuspio cirrifera* was found with very short stubby branchiae and with extremely long, thin ones. *Prionospio steenstrupi* has been described as having one of the first and fourth branchiae longer than the others yet specimens in my samples had either the first longer, the fourth longer or both the same length. Branchial length could well be a result of physiological adaptation as it is an established fact in certain other animal groups.

Still another invalid character is the presence or absence of eyes.

One cannot disregard the above as taxonomic characters since we have nothing with which to replace them. We should, however, be aware of their weak points and attempt to combine them with such things as the nature of the branchiae, parapodial lamellae,prostomial shape, and anal cirri. These characters seem to be fairly constant and no extreme variations have been detected in the present study.

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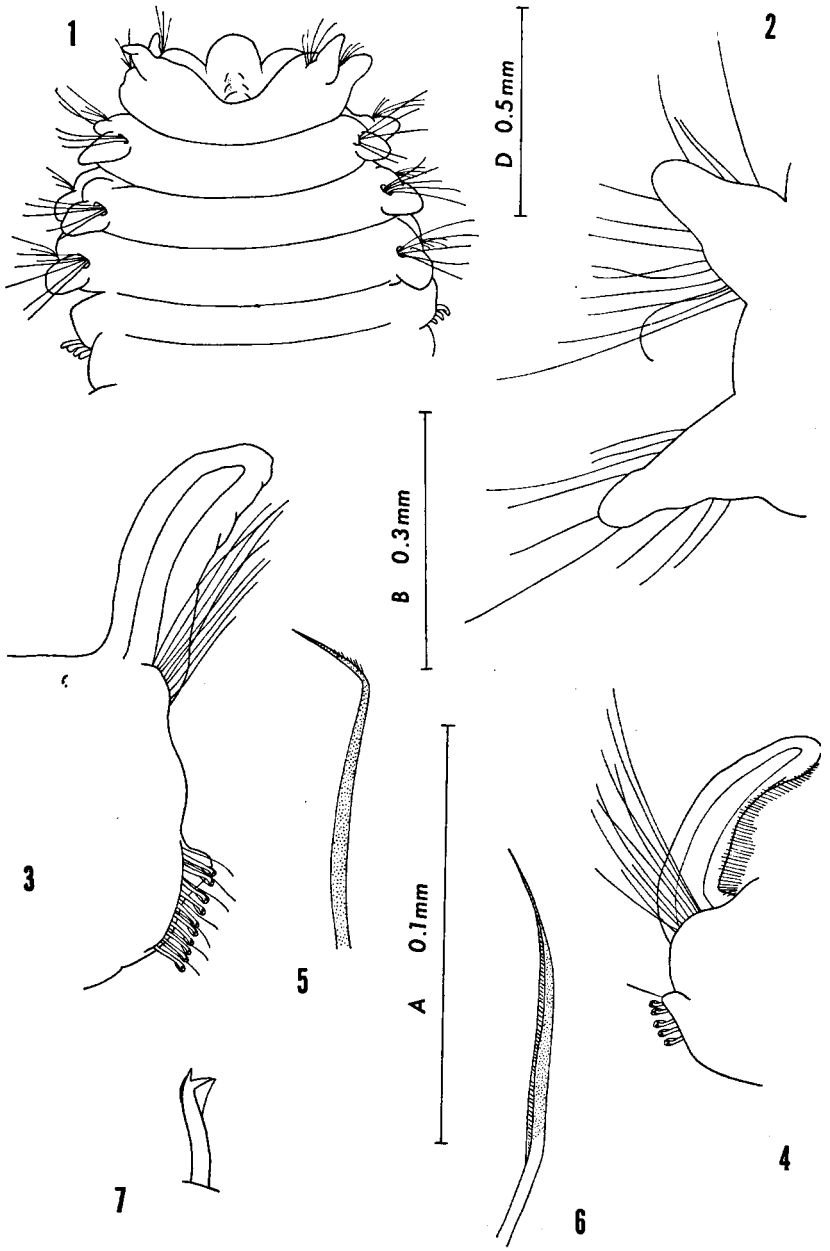
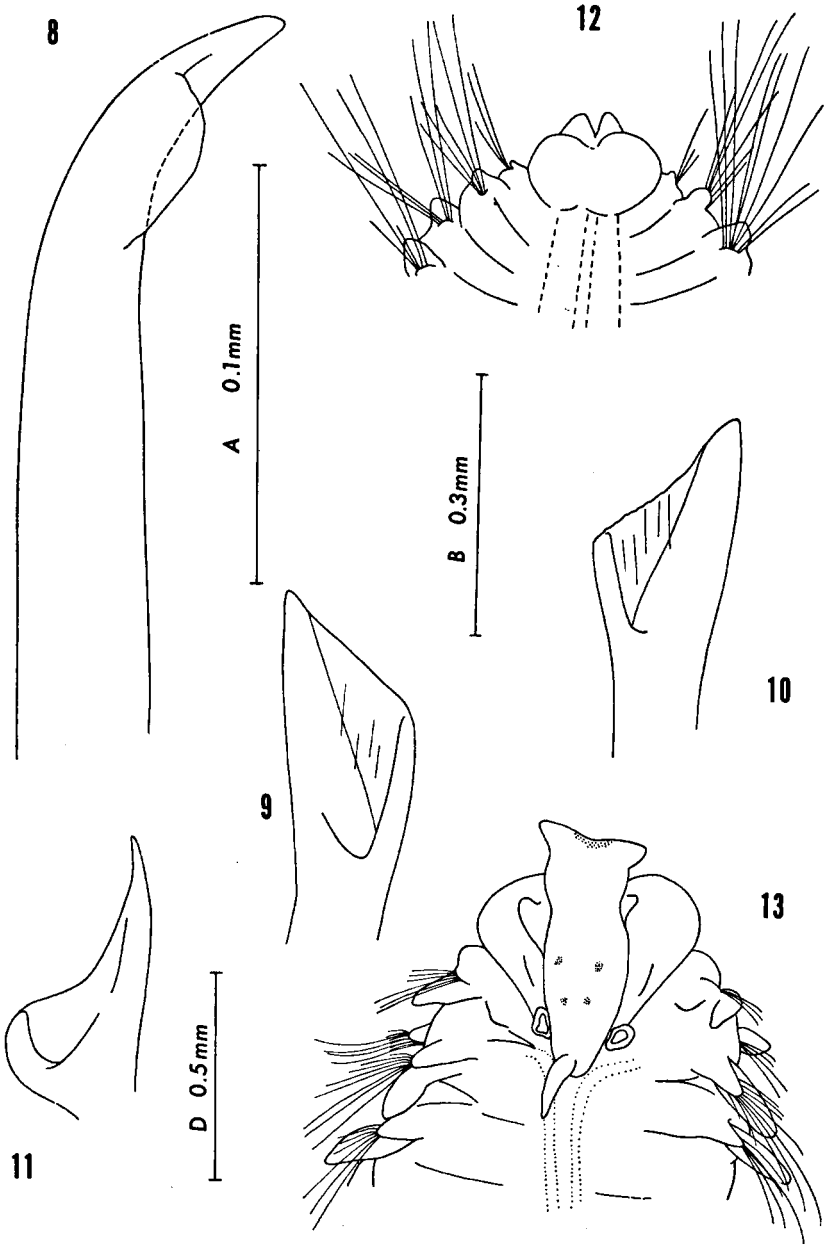
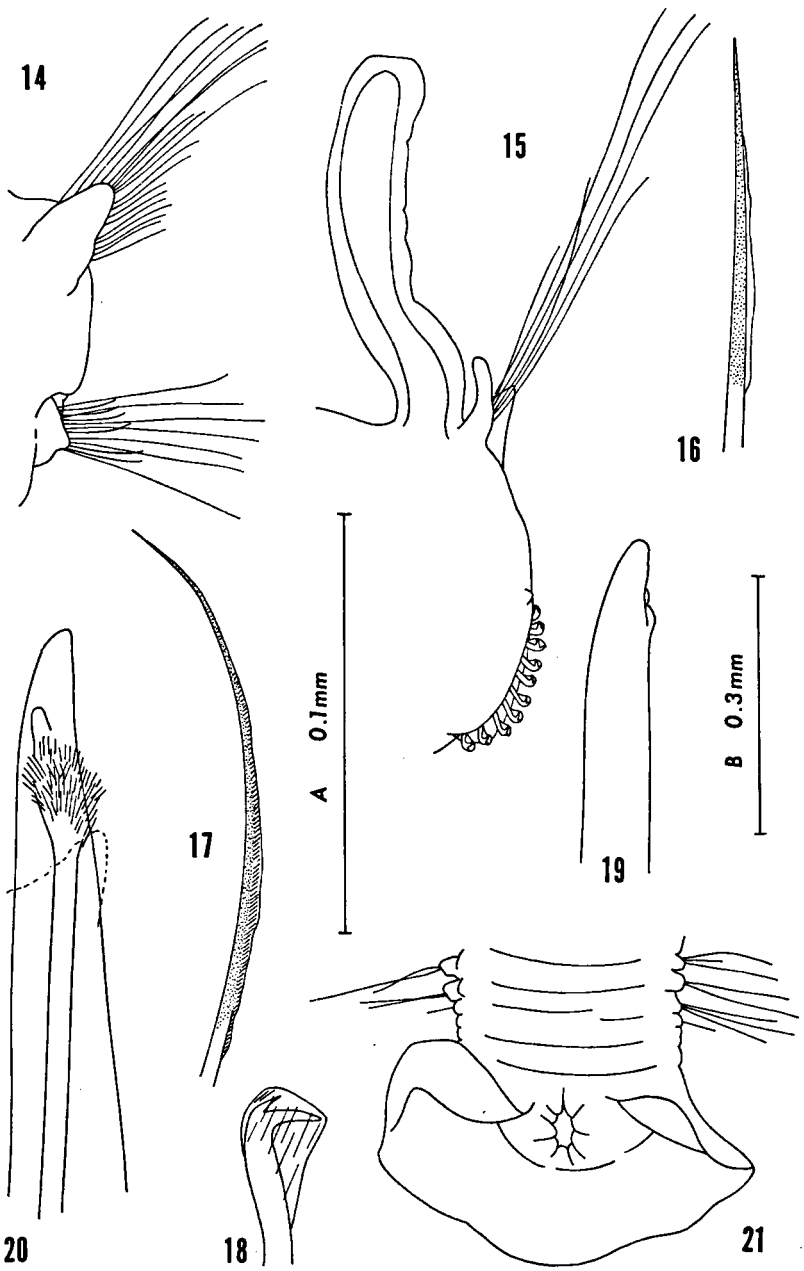


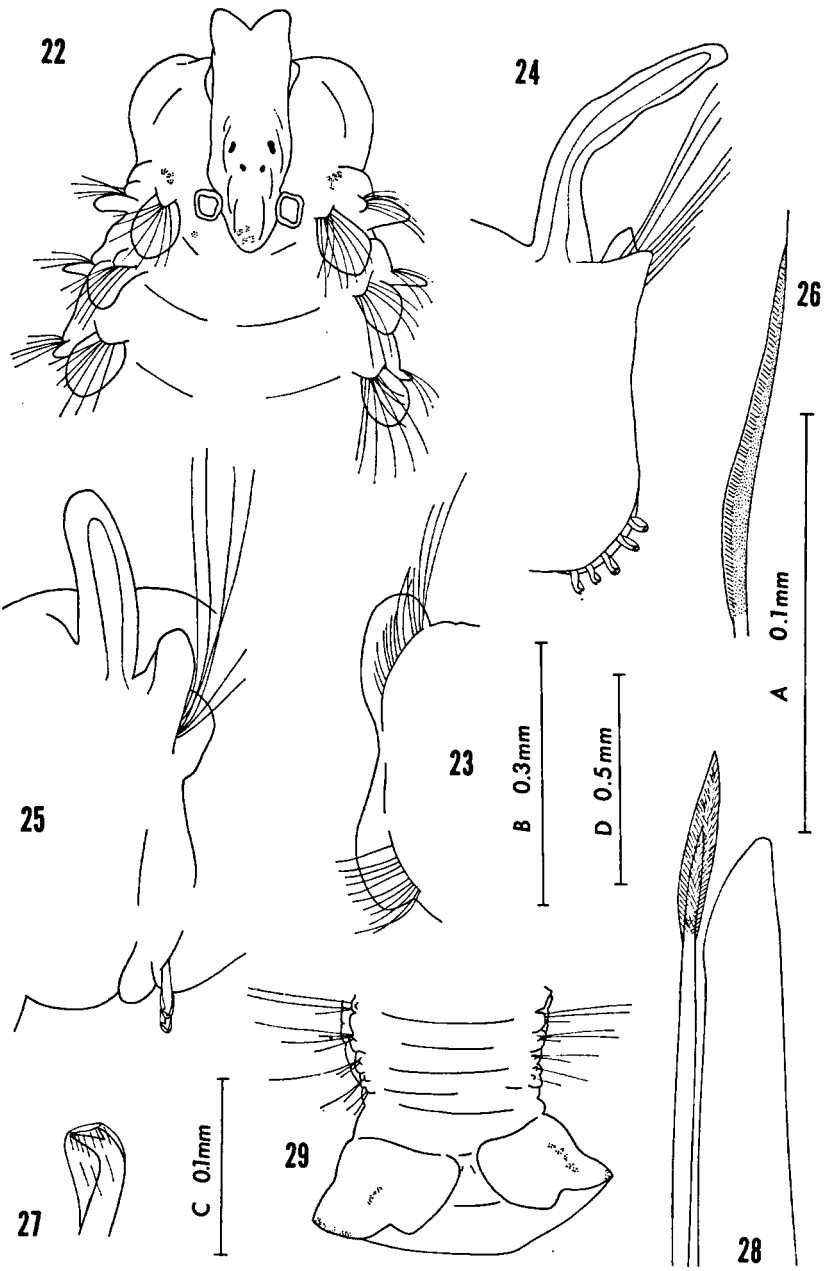
FIGURES 1–7. *Polydora commensalis*. 1: Anterior end, dorsal view, palpi removed. 2: Left parapodium setiger 1. 3: Left parapodium setiger 12. 4: Right parapodium posterior setiger. 5: Anterior notoseta. 6: Anterior neuroseta. 7: Neuropodial hooded hook. – Figures 5–7, scale A; Figures 2–3, scale B; Figure 1, scale D.



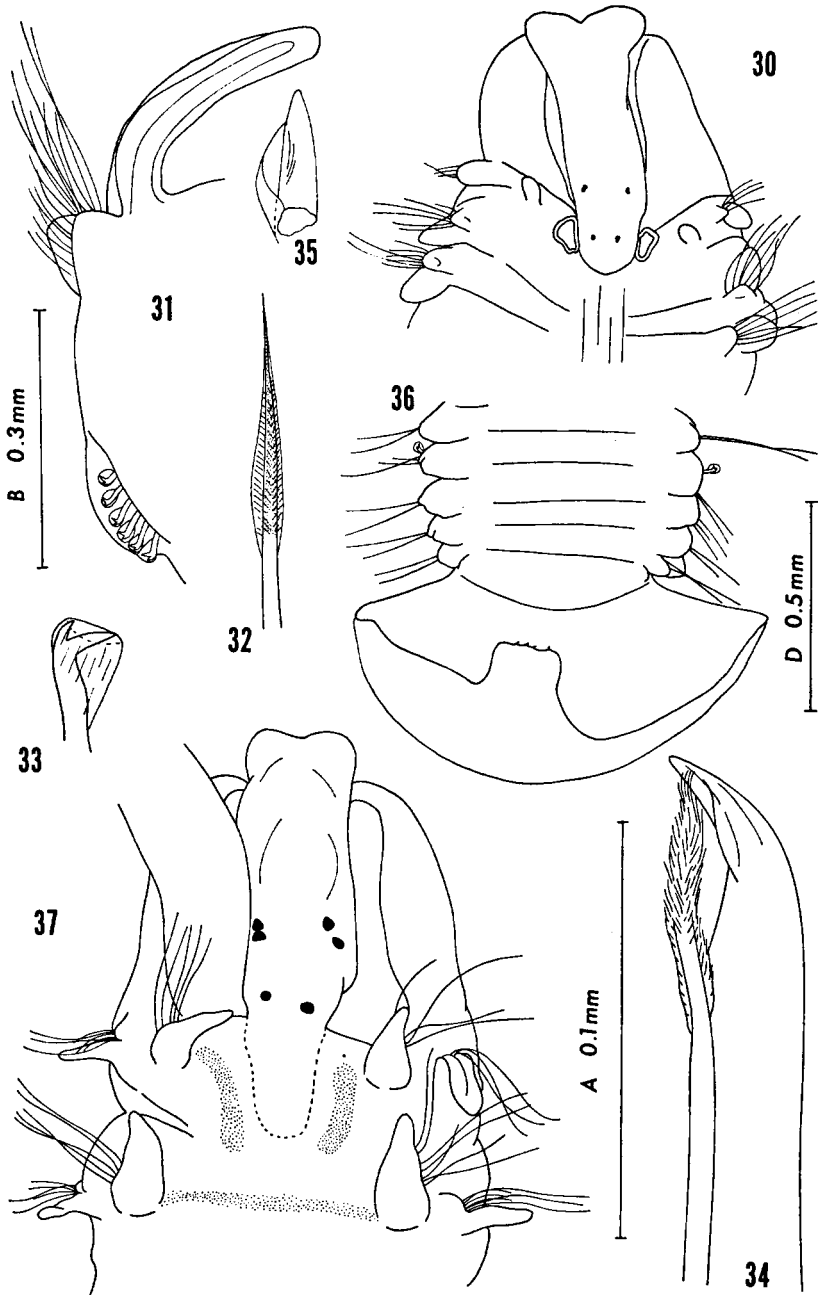
FIGURES 8–12. *Polydora commensalis*. 8: Enlarged hook from modified fifth setiger. 9–11: Distal tips of hooks from setiger 5. 12: Pygidium, ventral view. – FIGURE 13. *Polydora ligni*. Anterior end, dorsal view, palpi removed. – Figures 8–11, scale A; Figure 12, scale B; Figure 13, scale D.



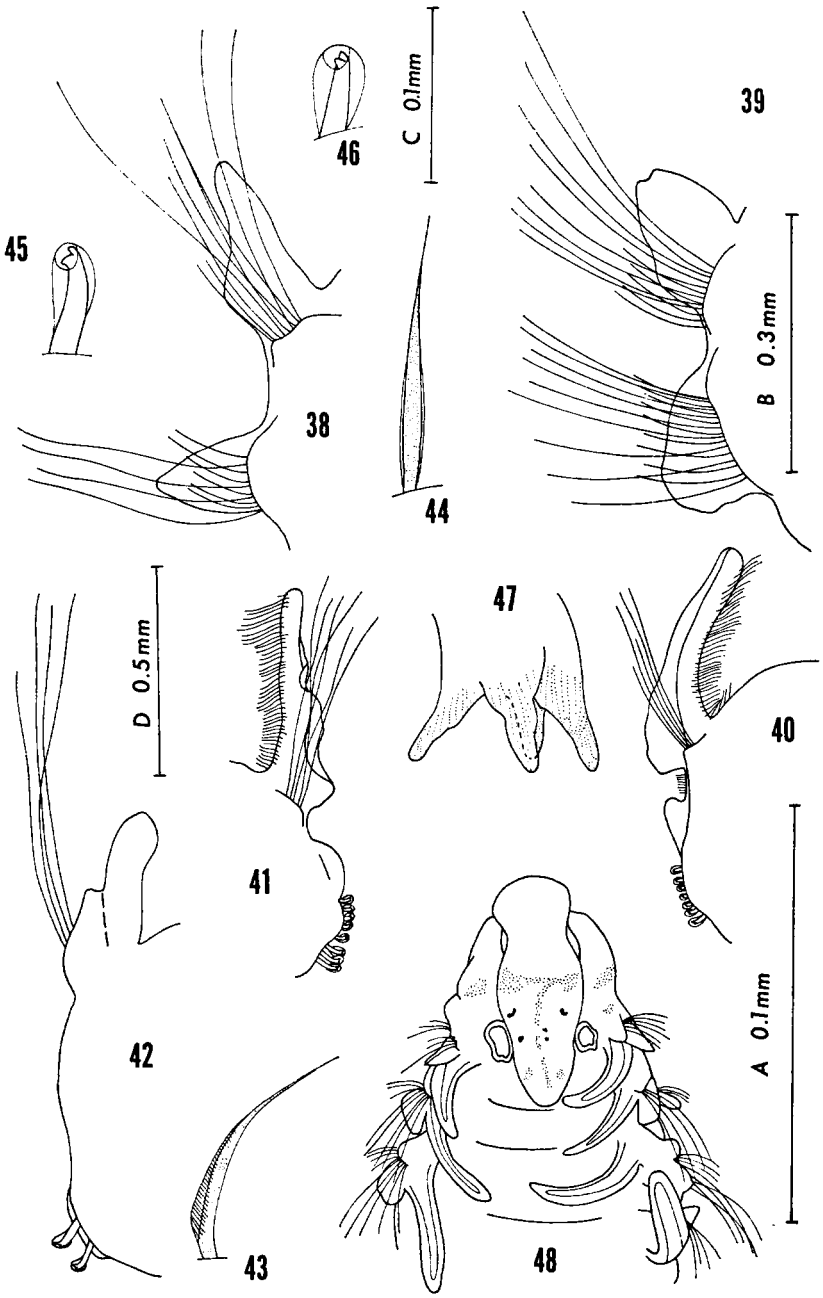
FIGURES 14–21. *Polydora ligni*. 14: Right parapodium setiger 6. 15: Right parapodium posterior setiger. 16: Short anterior notopodial seta. 17: Long anterior notopodial seta. 18: Neuropodial hooded hook. 19: Hook from setiger 5. 20: Hook and companion seta from setiger 5. 21: Pygidium, dorsal view. – Figures 16–20 scale A; Figures 14–15, 21, scale B.



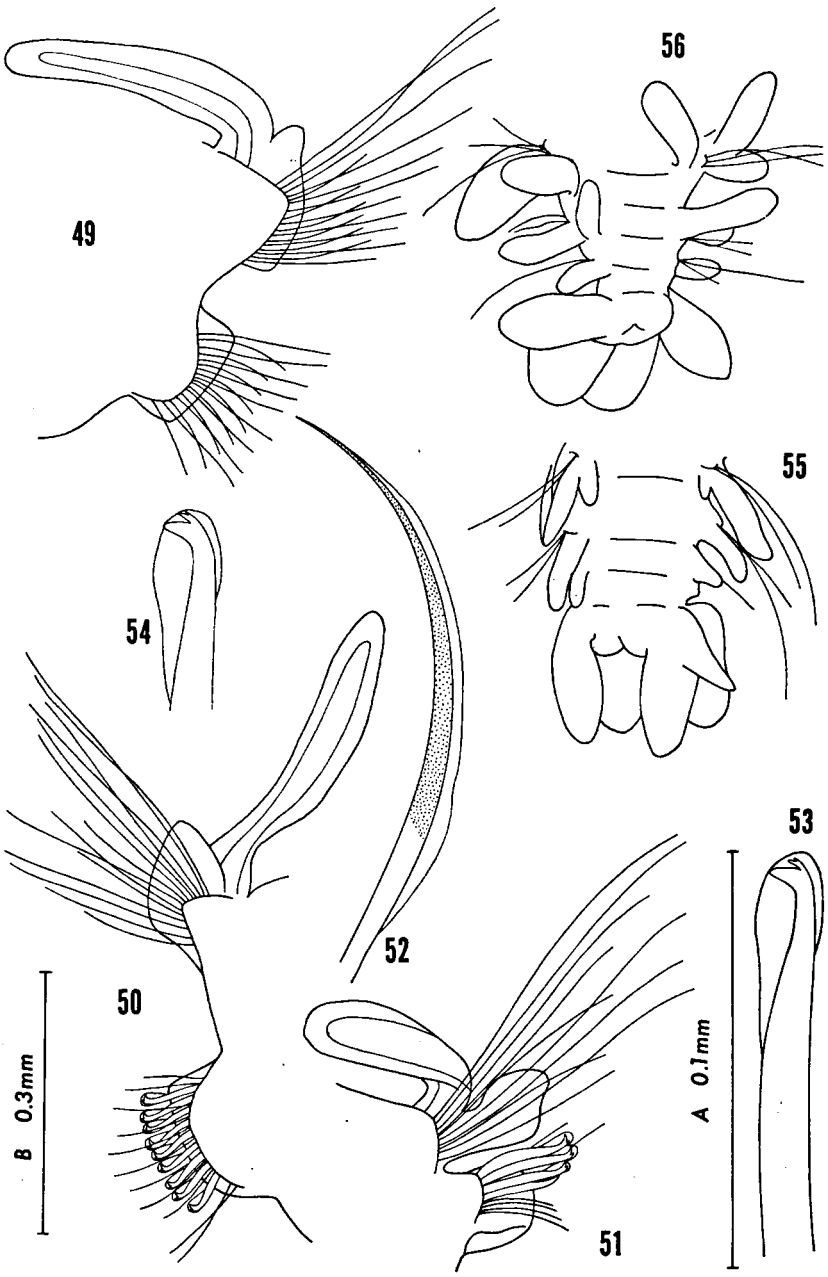
FIGURES 22–29. *Polydora plena*. 22: Anterior end, dorsal view, palpi removed. 23: Right parapodium setiger 6. 24: Right parapodium setiger 12. 25: Posterior setiger, oblique view. 26: Capillary seta from setiger 5. 27: Neuropodial hooded hook. 28: Hook and companion seta from setiger 5. 29: Pygidium, dorsal view. – Figures 26–28, scale A; Figures 23, 24, scale B; Figure 25, scale C; Figures 22, 29, scale D.



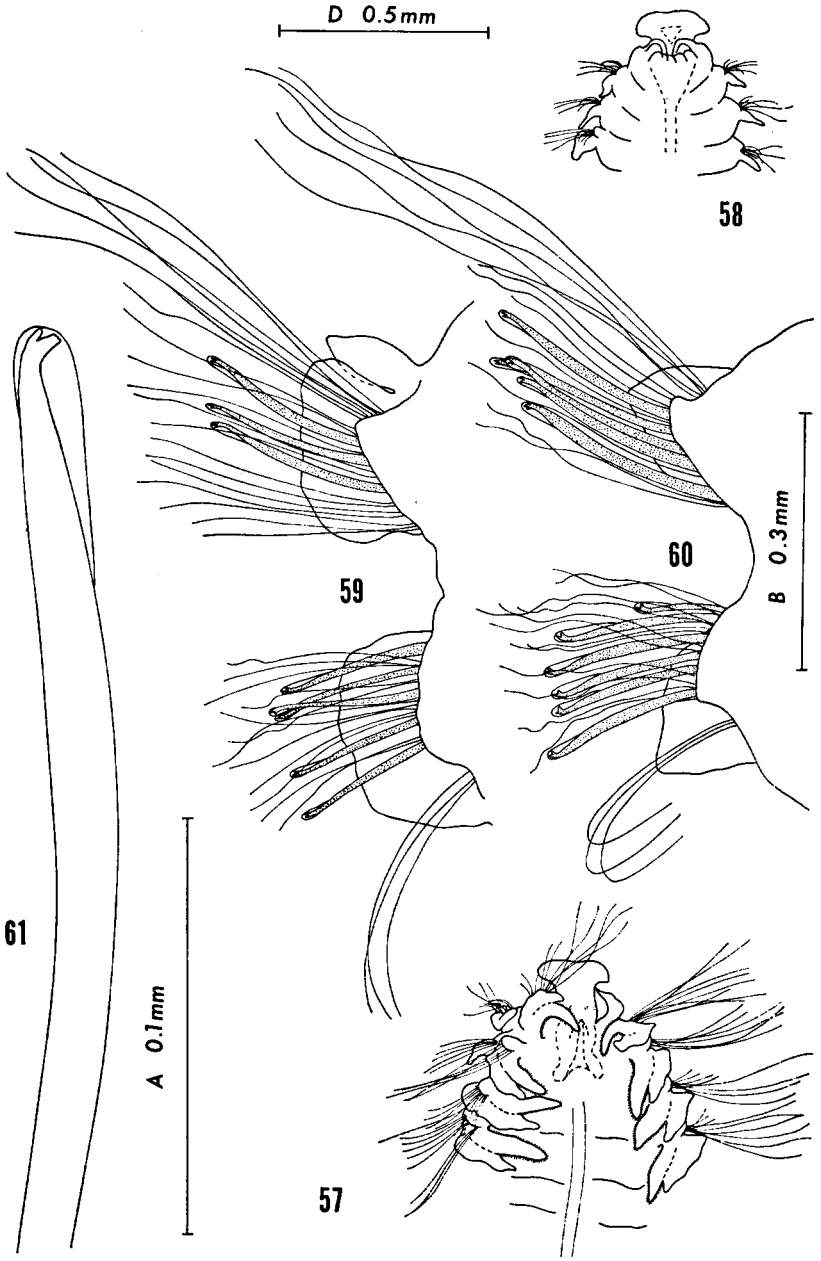
FIGURES 30–36. *Polydora websteri*. 30: Anterior end, dorsal view, palpi removed. 31: Right branchial setiger from anterior region. 32: Short anterior notosetae. 33: Neuropodial hooded hook. 34: Hook and companion seta from setiger 5. 35: Distal tip of hook from setiger 5. 36: Pygidium, dorsal view. – FIGURE 37. *Pygospio elegans*. Dorsal view, anterior end with one palp intact. – Figures 32–35, scale A; Figures 30, 36–37, scale B; Figure 31, scale D.



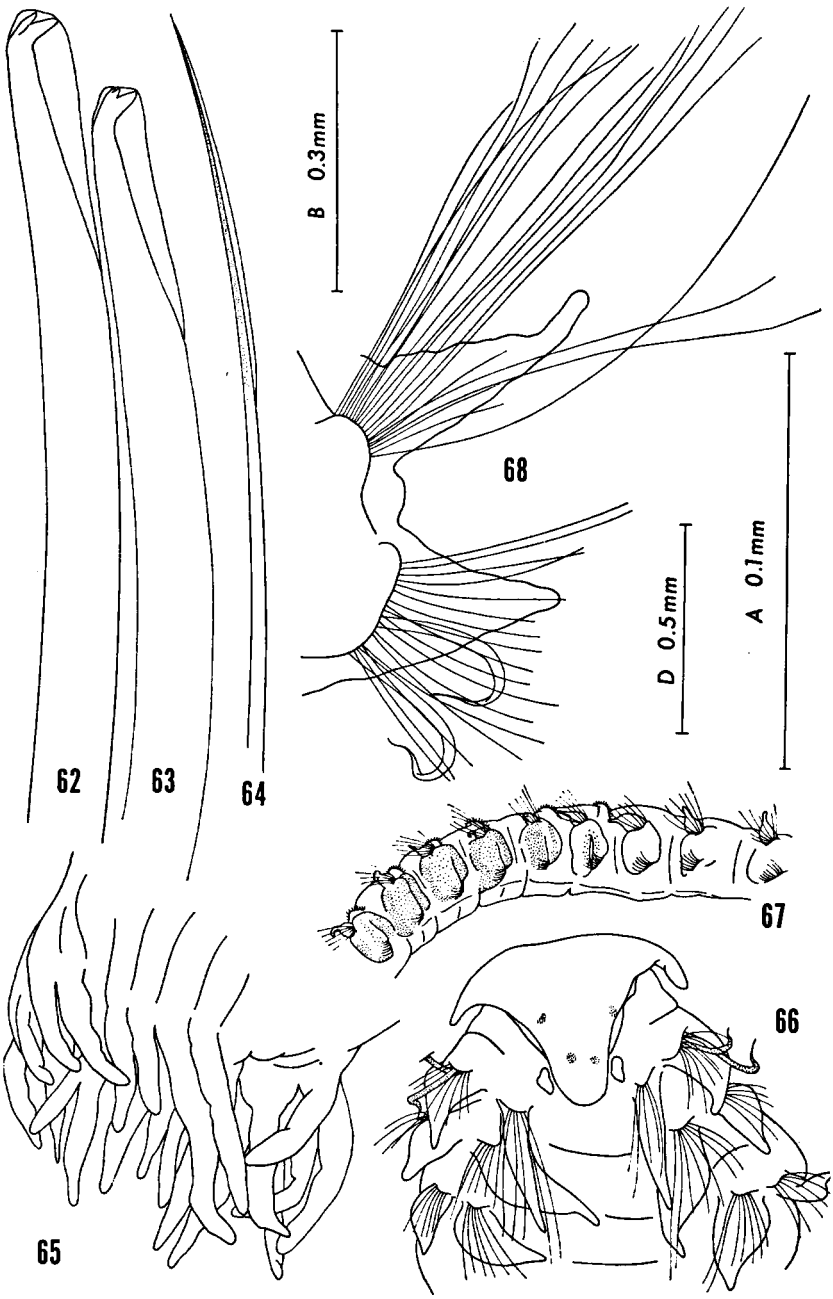
FIGURES 38–47. *Pygospio elegans*. 38: Right parapodium setiger 1. 39: Right parapodium setiger 4. 40: Right parapodium setiger 13. 41: Left parapodium setiger 21. 42: Left parapodium setiger 22. 43: Lower neuroseta from setiger 4. 44: Short notoseta from setiger 4. 45: Neuropodial hooded hook. 46: Neuropodial hooded hooks, frontal view. 47: Pygidium. – FIGURE 48. *Spio* (*Spio*) *pettiboneae*. Anterior end, dorsal view, palpi removed. – Figures 43–46, scale A; Figures 40–41, 47, scale B; Figures 38–39, 42, scale C; Figure 48, scale D.



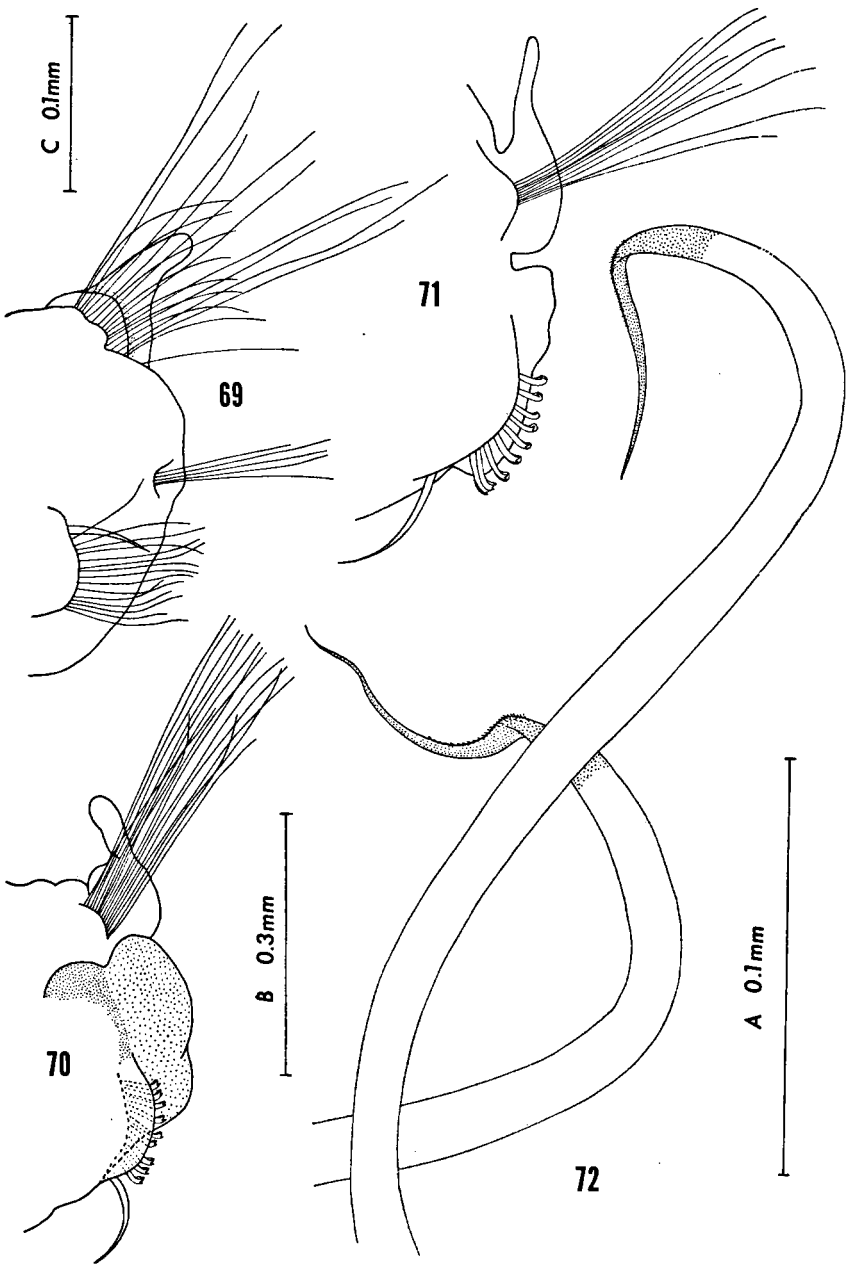
FIGURES 49–56. *Spio* (*Spio*) *pettiboneae*. 49: Left parapodium setiger 8. 50: Right parapodium posterior setiger. 51: Left parapodium sixth last setiger. 52: Short notoseta from setiger 8. 53: Neuropodial hooded hook. 54: Neuropodial hooded hook. 55: Pygidium, dorsal view. 56: Pygidium, oblique view. – Figures 52–56, scale A; Figures 49–51, scale B.



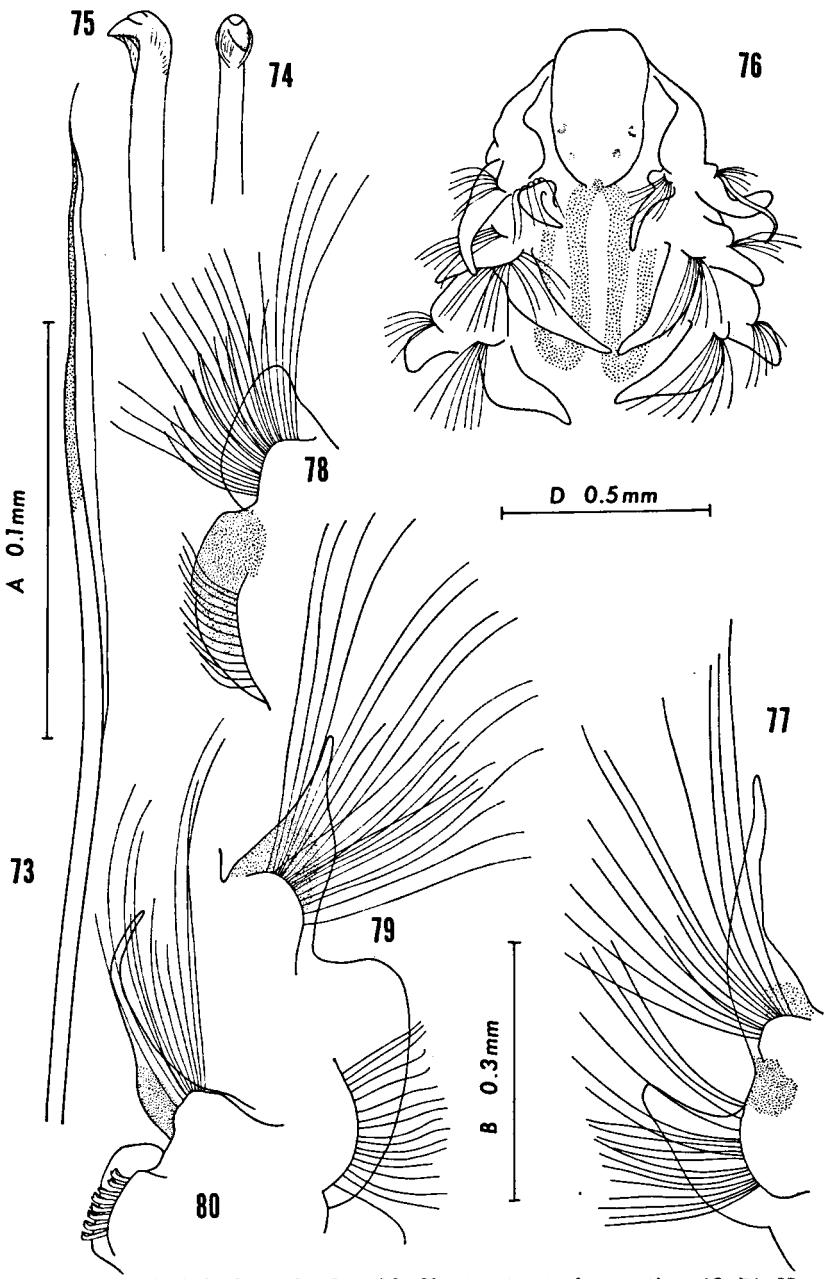
FIGURES 57–61. *Scolecolepides viridis*. 57: Anterior end, dorsal view, palpi removed 58: Anterior end, ventral view. 59: Right parapodium setiger 46. 60: Right parapodium setiger 79. 61: Neuropodial hooded hook. – Figure 61, scale A; Figures 59–60, scale B; Figures 57–58, scale D.



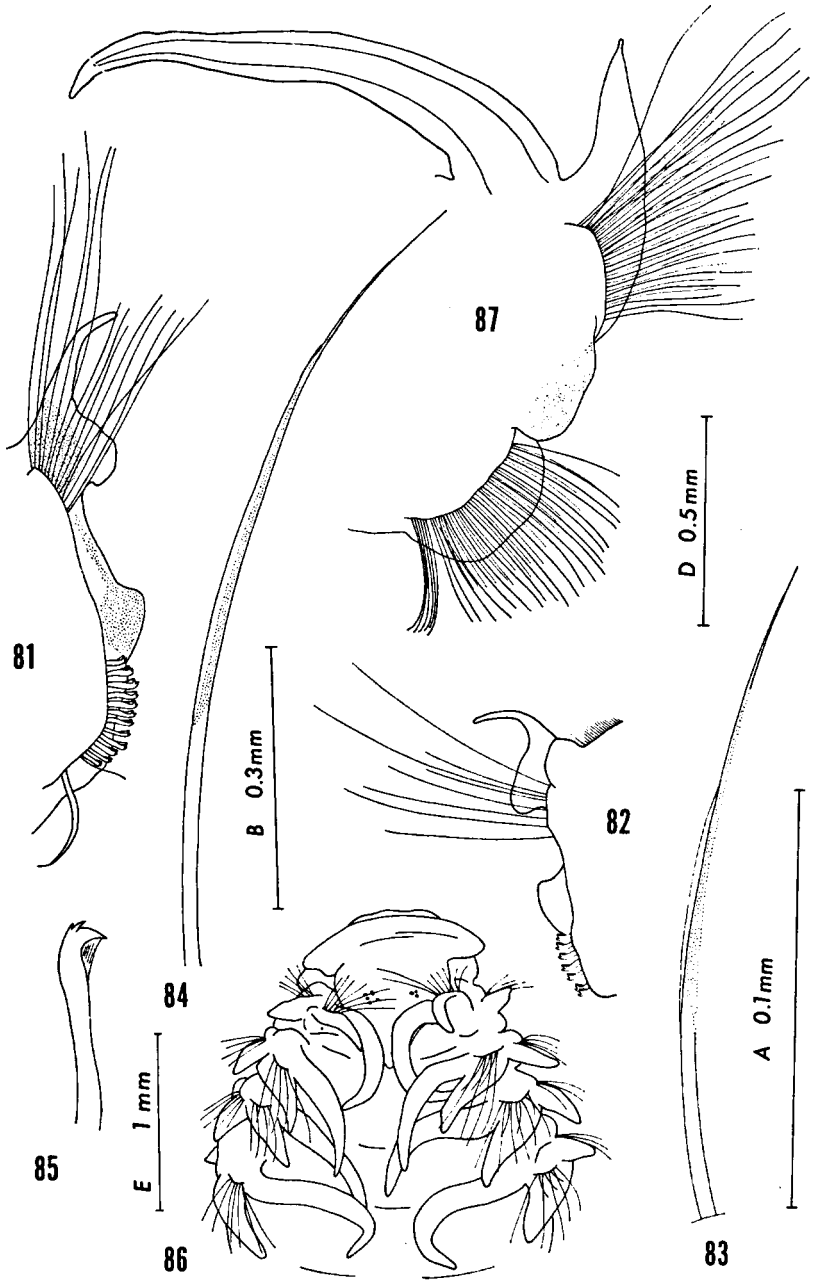
FIGURES 62–65. *Scolecolepides viridis*. 62: Bidentate notopodial hooded hook. 63: Tridentate notopodial hooded hook. 64: Neuropodial companion seta. 65: Pygidium, lateral view. – FIGURES 66–68. *Spiophanes bombyx*. 66: Anterior end, dorsal view, palpi removed. 67: Setigers 6 to 14, right lateral view, stippled area represents glandular area. 68: Left parapodium setiger 1. – Figures 62–64, scale A; Figures 65, 67–68, scale B; Figure 66, scale D.



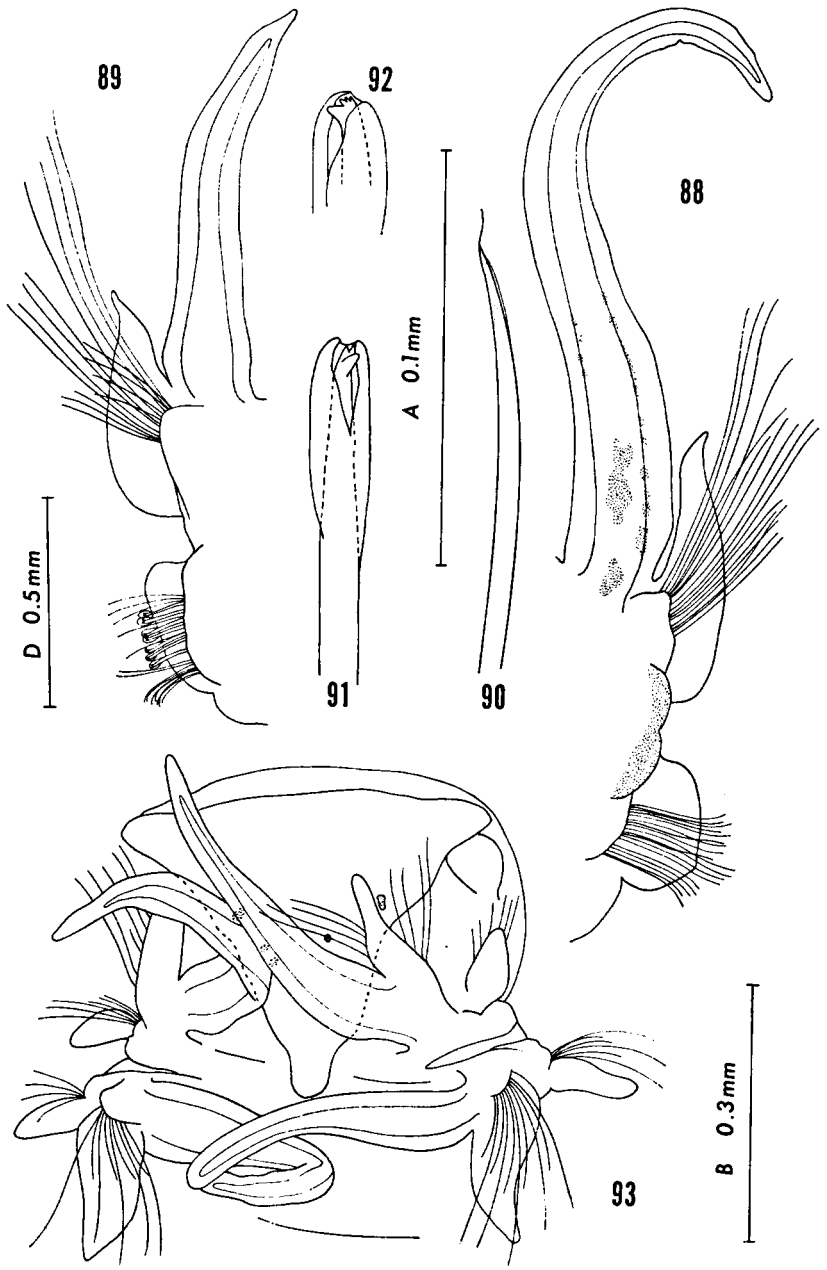
FIGURES 69–72. *Spiophanes bombyx*. 69: Left parapodium setiger 6. 70: Left parapodium setiger 15, glandular area stippled. 71: Left parapodium posterior setiger. 72: Recurved setae from setiger 1. – Figure 72, scale A; Figures 70–71, scale B; Figure 69, scale C.



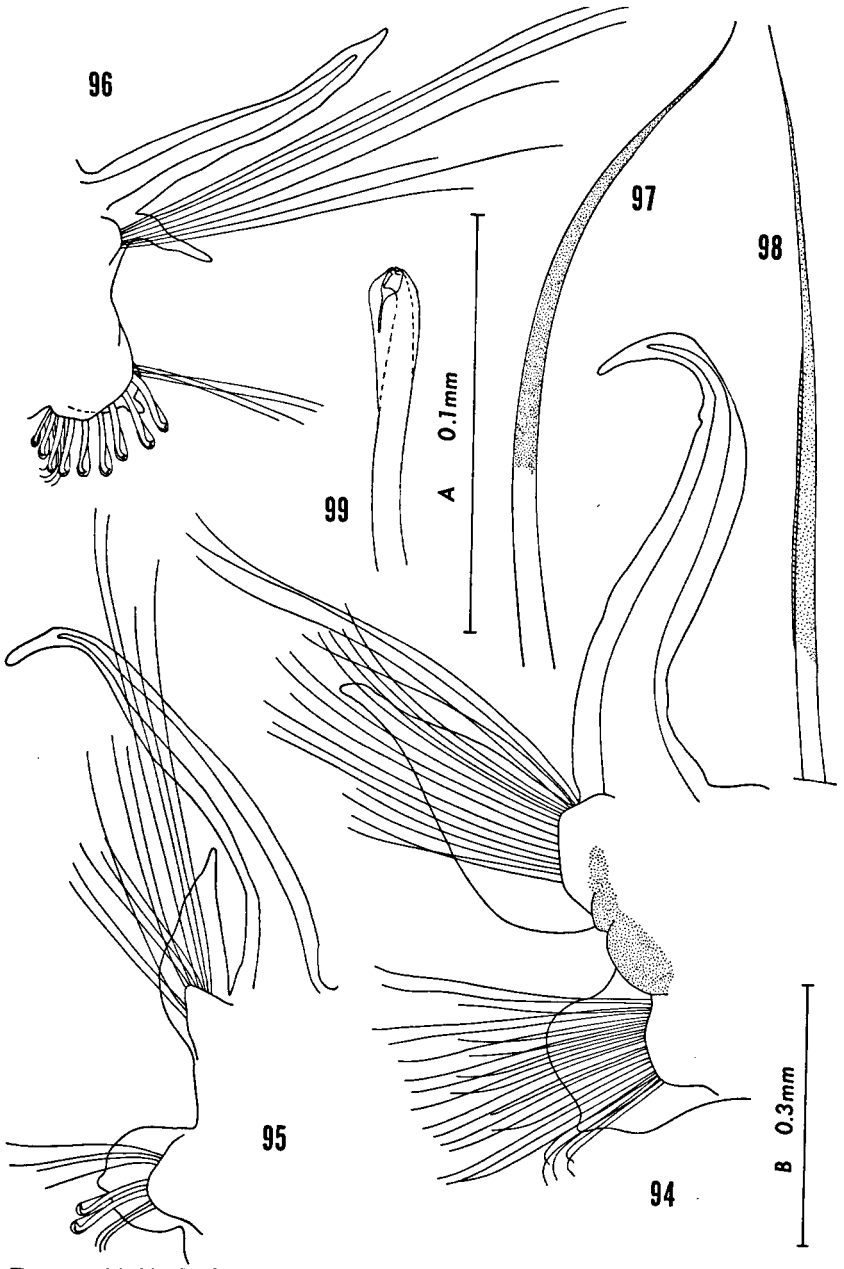
FIGURES 73–75. *Spiophanes bombyx*. 73: Short notoseta from setiger 12. 74: Neuropodial hooded hook, frontal view. 75: Neuropodial hooded hook showing third tooth. – FIGURES 76–80. *Spiophanes wigleyi*. 76: Anterior end, dorsal view, palpi removed. 77: Right parapodium setiger 2. 78: Right parapodium setiger 4. 79: Right parapodium setiger 9. 80: Right parapodium posterior setiger. – Figures 73–75, scale A; Figures 77–80, scale B; Figure 76, scale D.



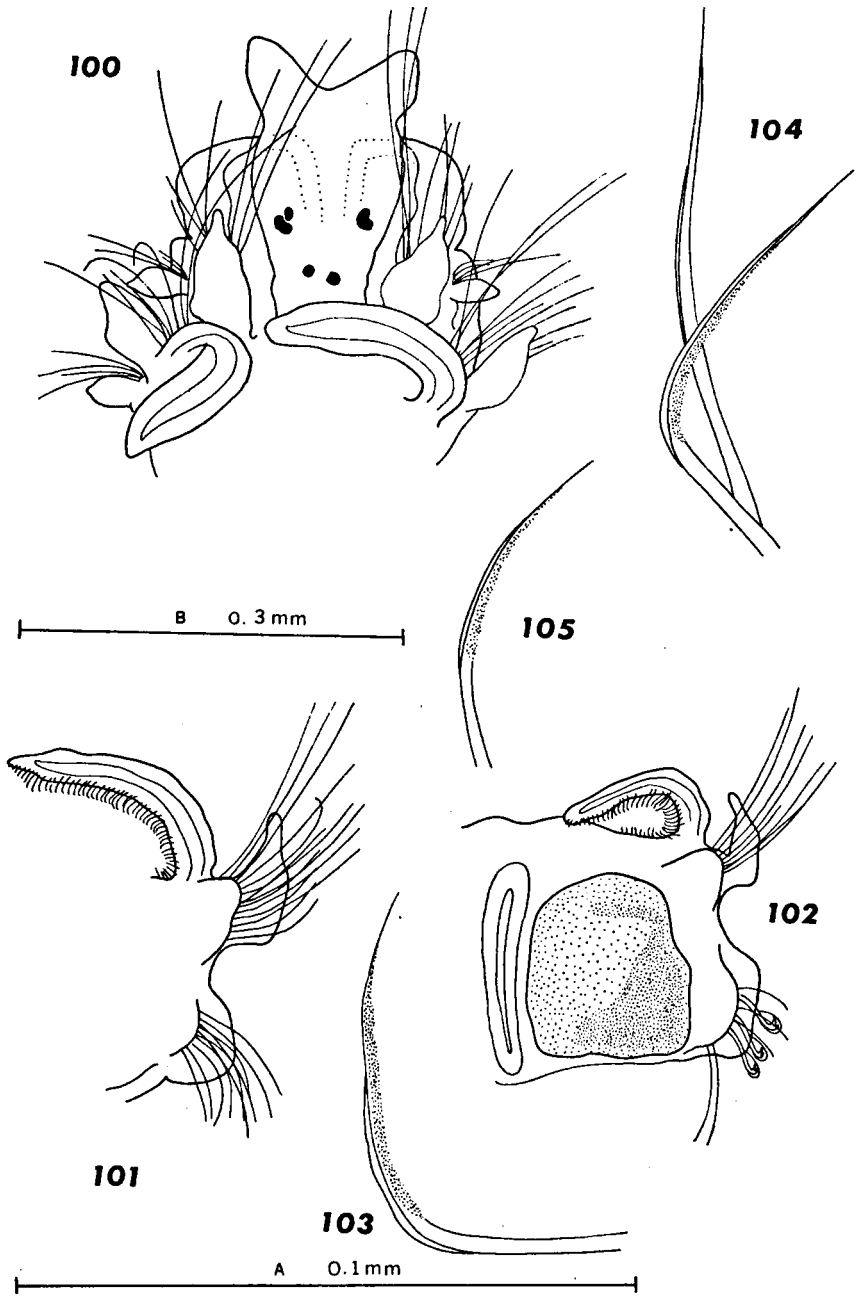
FIGURES 81–85. *Spiophanes wigleyi*. 81: Left parapodium setiger 18. 82: Right parapodium middle setiger of paratype. 83: Short anterior neuroseta. 84: Long anterior notoseta. 85: Neuropodial tridentate hooded hook. – FIGURES 86–87. *Malacoceros* (*Malacoceros*) *vanderhorsti*. 86: Anterior end, dorsal view, palpi removed. 87: Left parapodium setiger 18. – Figures 83–85, scale A; Figures 81–82, scale B; Figure 87, scale D; Figure 86, scale E.



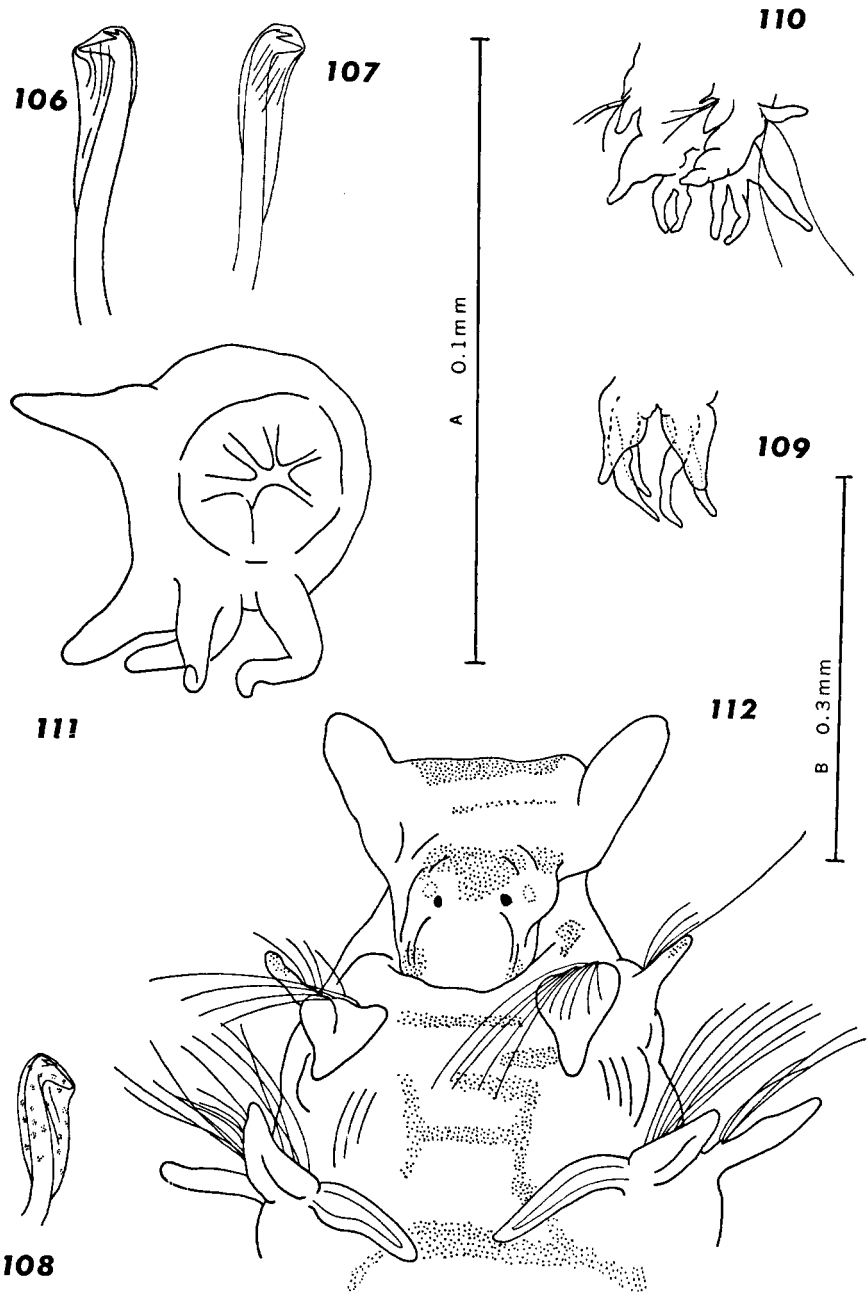
FIGURES 88–92. *Malacoceros* (*Malacoceros*) *vanderhorsti*. 88: Left parapodium setiger 60. 89: Right parapodium setiger 97. 90: Posterior acicular seta. 91: Bidentate neuropodial hooded hook. 92: Quadridentate neuropodial hooded hook. – FIGURE 93. *Malacoceros* (*Malacoceros*) *indicus*. Anterior end, dorsal view, palpi removed. – Figures 90–92, scale A; Figure 93, scale B; Figures 88–89, scale D.



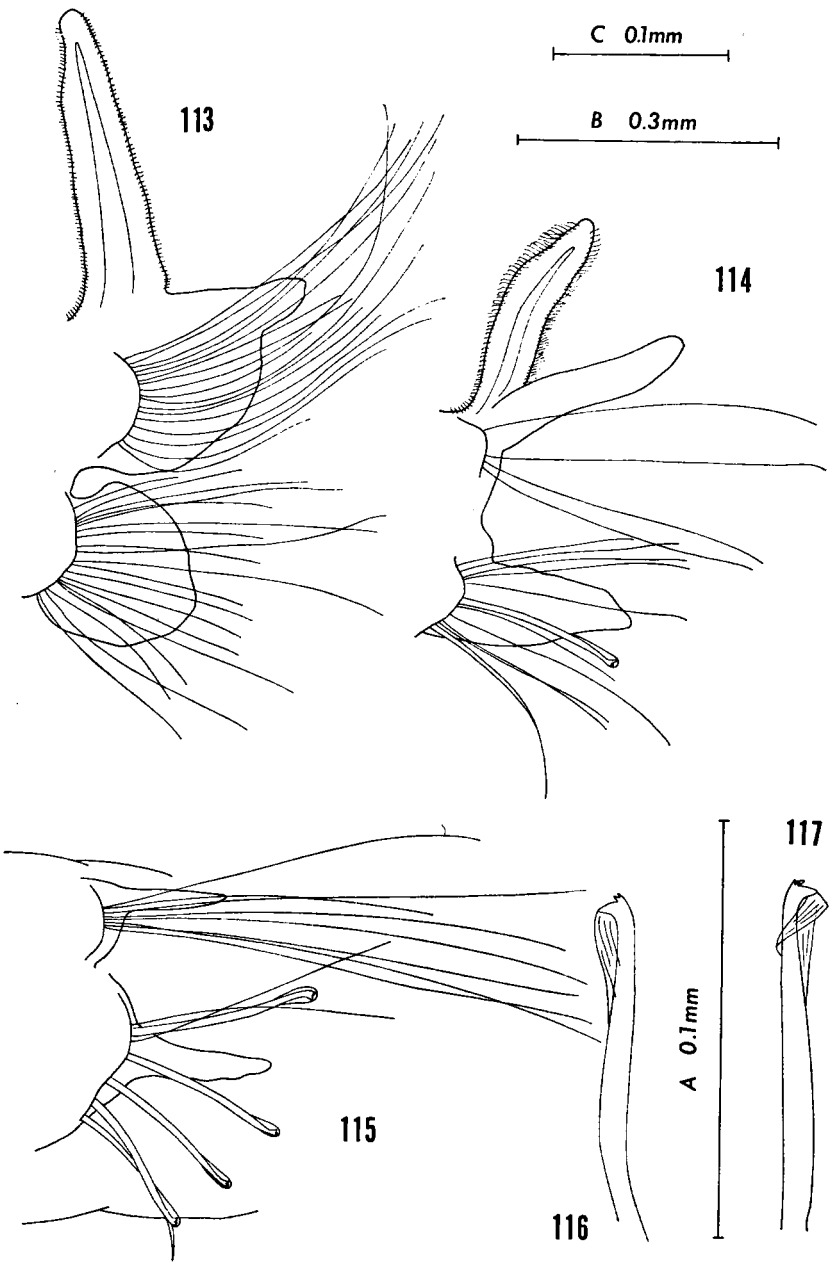
FIGURES 94–99. *Malacoceros (Malacoceros) indicus*. 94 :Right parapodium setiger 15. 95: Right parapodium setiger 51. 96: Left parapodium posterior setiger. 97: Short anterior neuroseta. 98: Long anterior notoseta. 99: Quadridentate neuropodial hooded hook. – Figures 97–99, scale A; Figures 94–96, scale B.



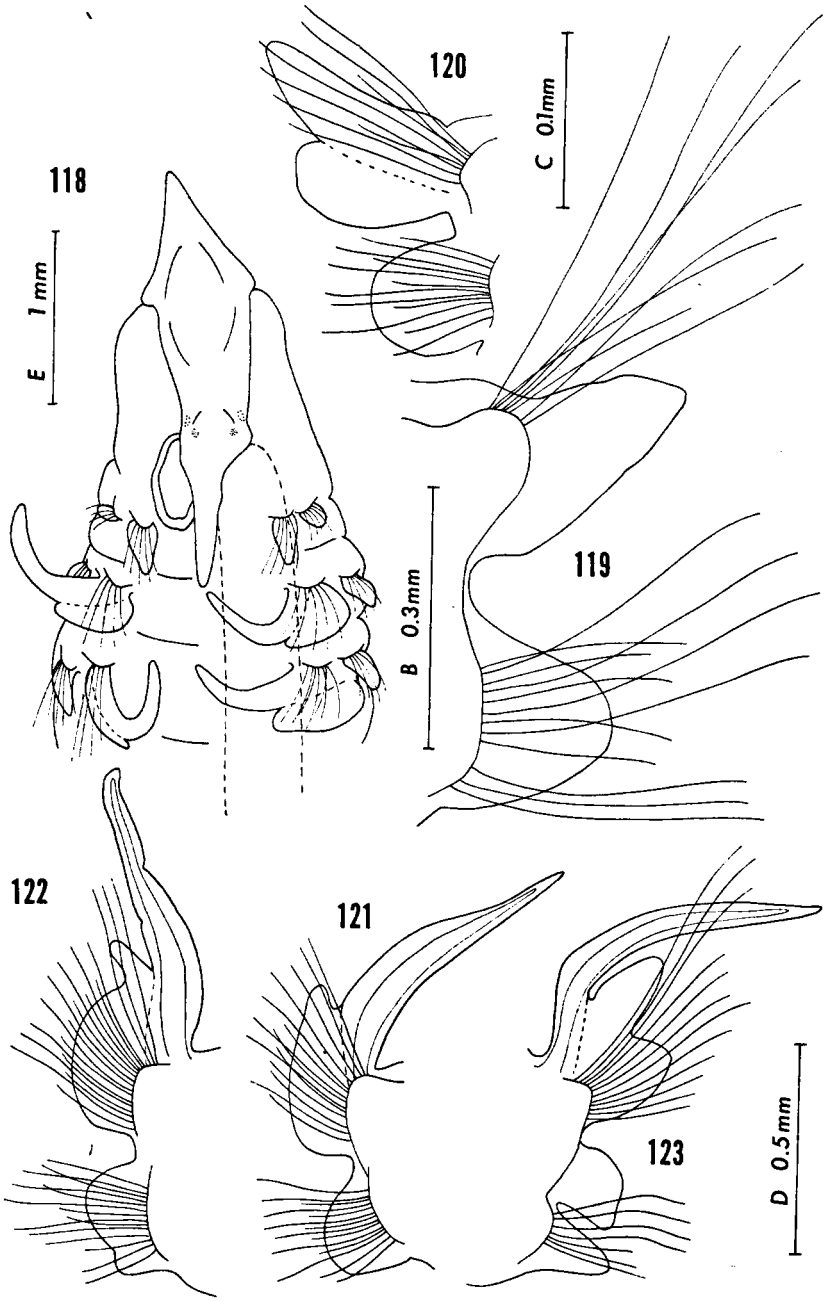
FIGURES 100–105. *Malacoceros* (*Rhynchospio*) *glutaeus*. 100: Anterior end, dorsal view, palpi removed. 101: Left parapodium setiger 9. 102: Left parapodium setiger 20, showing internal egg and intestine. 103: Short anterior neuroseta. 104: Short and long anterior neurosetae. 105: Neuropodial companion seta. – Figures 103–105, scale A; Figures 100–102, scale B.



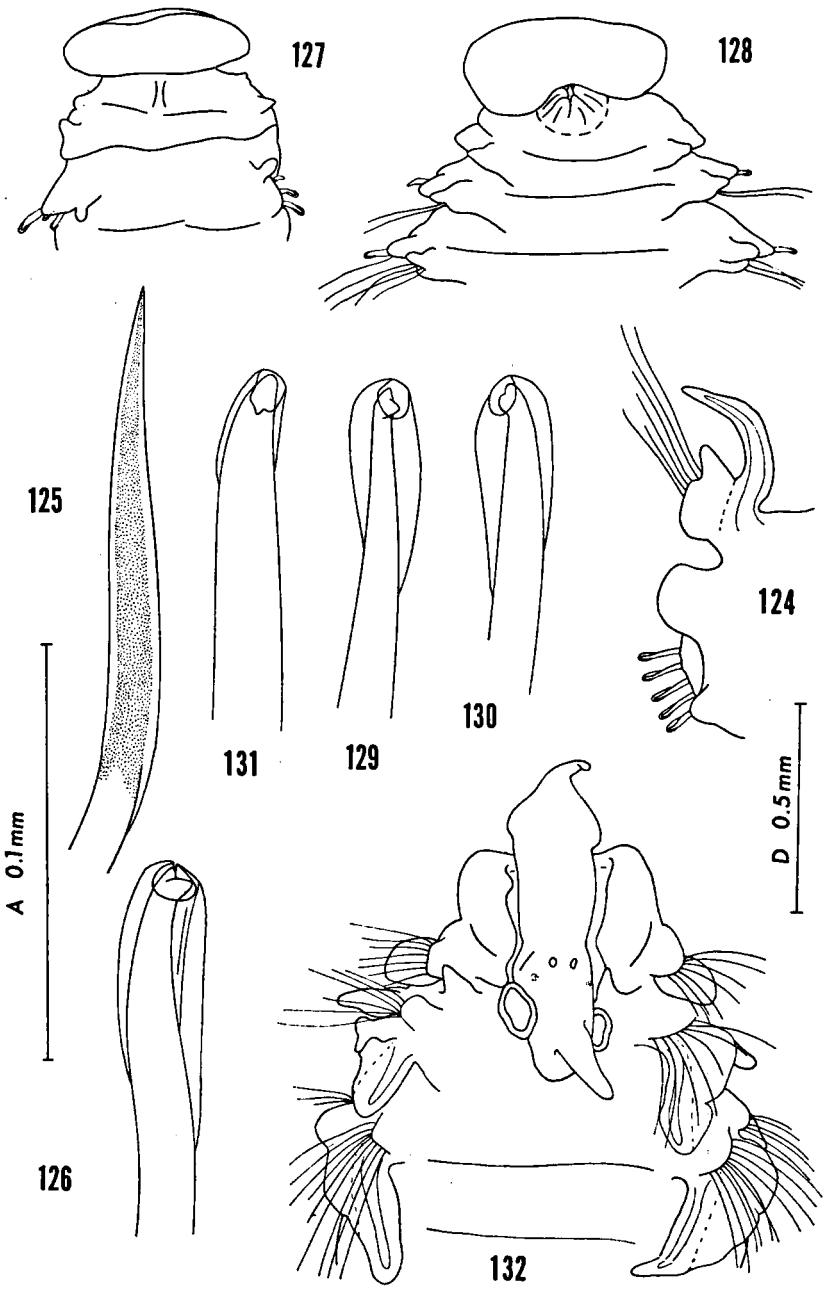
FIGURES 106–111. *Malacoceros* (*Rhynchospio*) *glutaeus*. 106: Tridentate neuropodial hooded hook. 107: Tridentate neuropodial hooded hook. 108: Quadridentate neuropodial hooded hook. 109: Pygidium, ventral view. 110: Pygidium, second specimen, oblique view. 111: Pygidium, paratype of *Rhynchospio arenincola*, terminal view. – FIGURE 112. *Malacoceros* (*Rhynchospio*) *inflatus*. Anterior end, dorsal view, palpi removed. Stippling indicates pigmentation. – Figures 106–108, scale A; Figures 109–112, scale B.



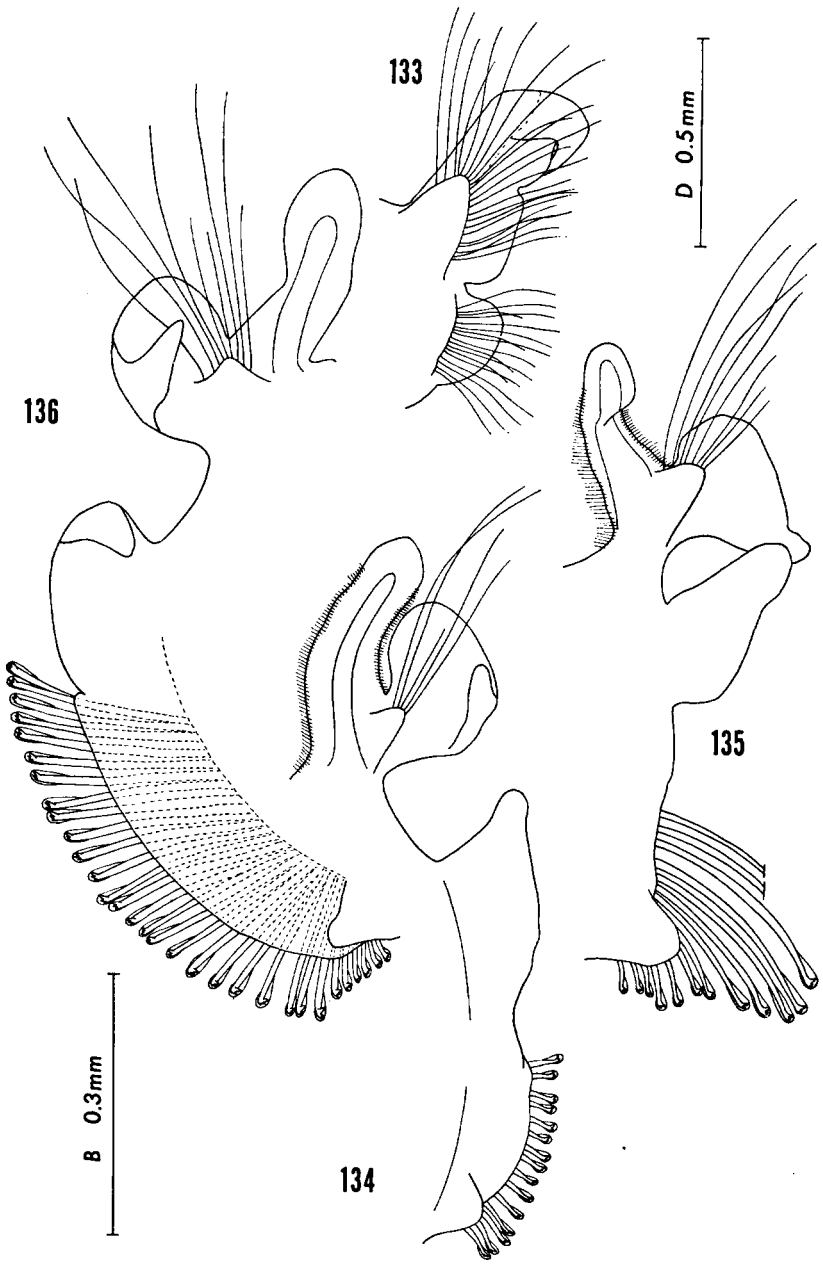
FIGURES 113–117. *Malacoceros* (*Rhynchospio*) *inflatus*. 113: Left parapodium setiger 8. 114: Left parapodium setiger 39. 115: Left parapodium far posterior setiger, oblique view. 116: Tridentate neuropodial hooded hook. 117: Quadridentate neuropodial hooded hook with hood displaced. – Figures 116–117, scale A; Figures 113–115, scale C.



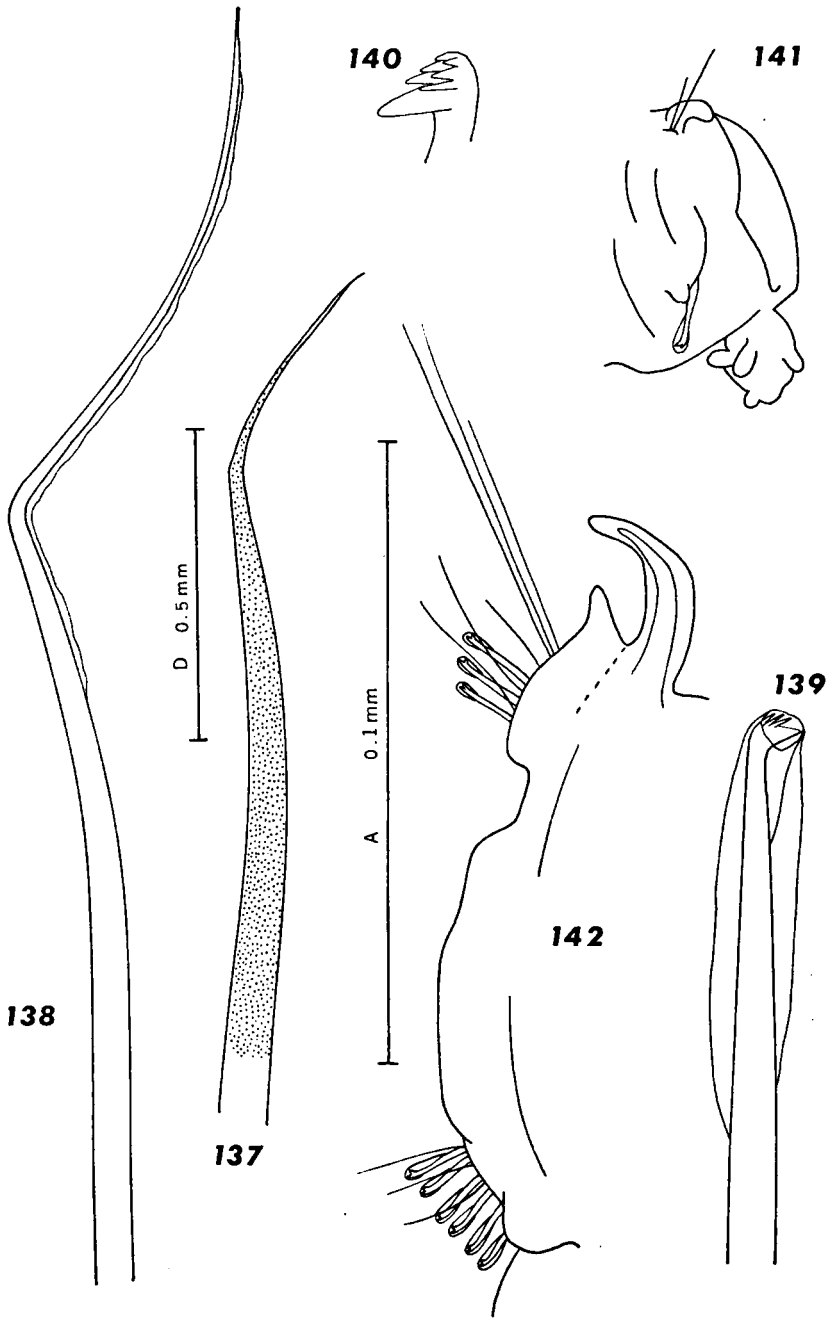
FIGURES 118–123. *Scolelepis* (*Scolelepis*) *squamata*. 118: Anterior end, dorsal view, palpi removed. 119: Left parapodium setiger 1. 120: Right parapodium setiger 2. 121: Right parapodium setiger 9. 122: Right parapodium setiger 20. 123: Left parapodium setiger 29. – Figure 120, scale B; Figure 119, scale C; Figures 121–123, scale D; Figure 118, scale E.



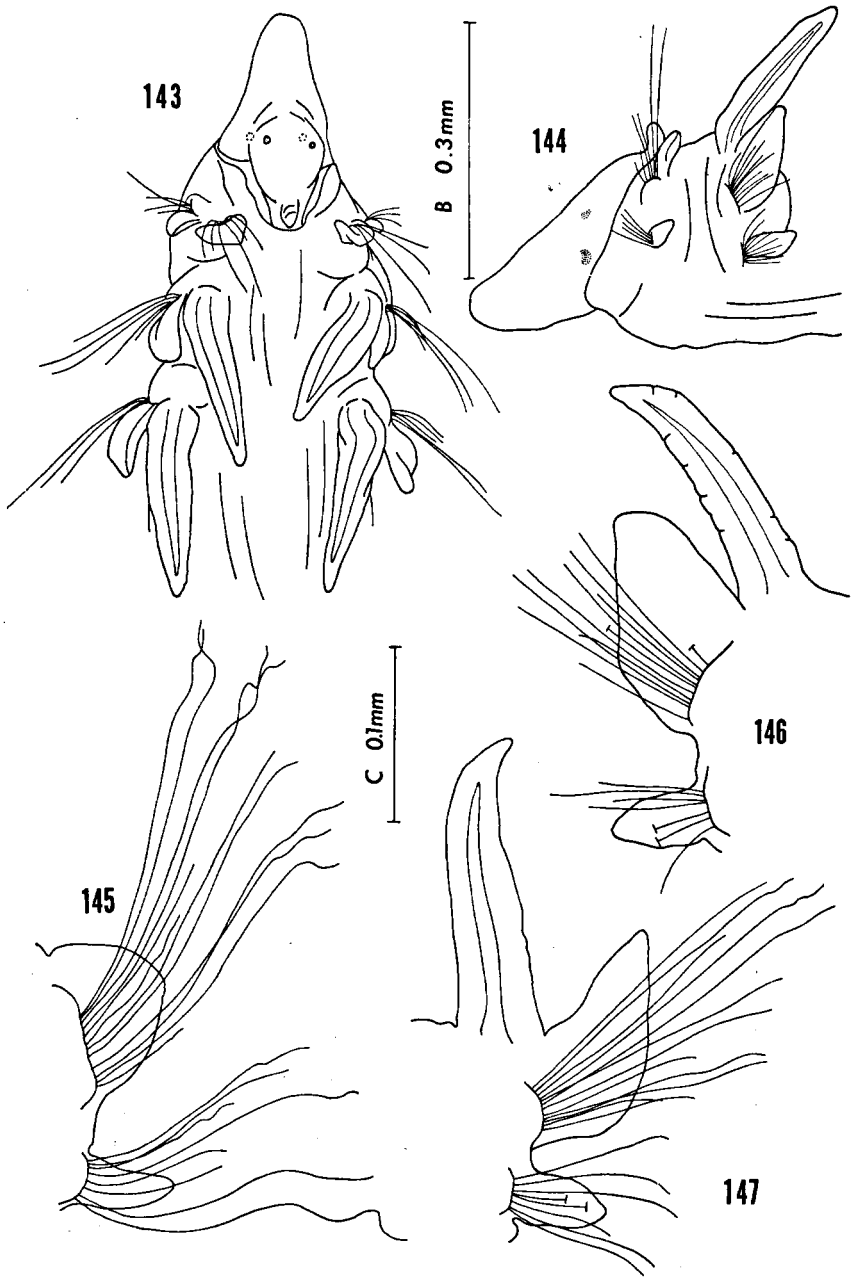
FIGURES 124–131. *Scolelepis* (*Scolelepis*) *squamata*. 124: Left parapodium posterior setiger. 125: Short anterior neuroseta. 126: Neuropodial hooded hook. 127: Pygidium, ventral view. 128: Pygidium, dorsal view. 129: Bidentate neuropodial hooded hook. 130: Worn neuropodial hooded hook. 131: Unidentate neuropodial hooded hook. – FIGURE 132. *Scolelepis* (*Scolelepis*) new species. Anterior end, dorsal view, palpi removed. – Figures 125, 129–131, scale A; Figures 124, 127–128, 132, scale D.



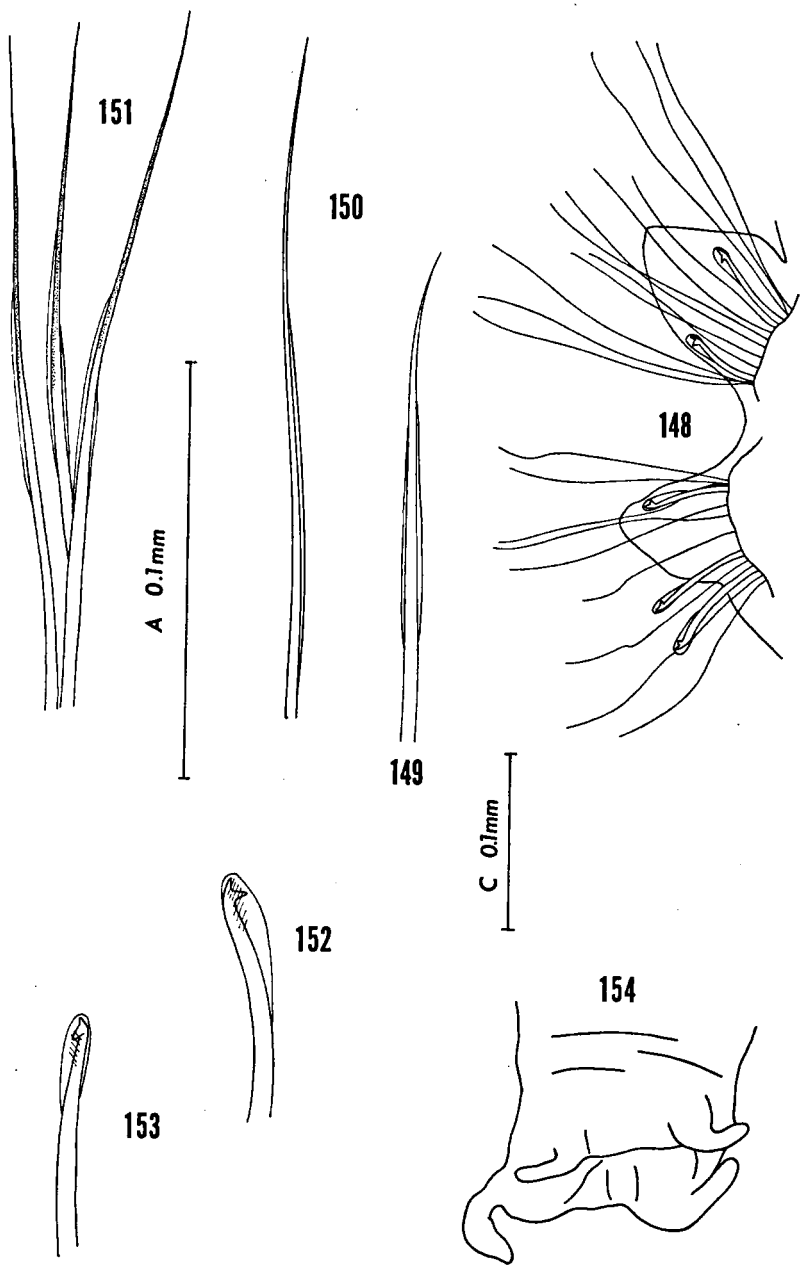
FIGURES 133–136. *Scolelepis* (*Scolelepis*) *texana*. 133: Left parapodium setiger 8. 134: Left parapodium setiger 28. 135: Left parapodium posterior setiger. 136: Right parapodium posterior setiger near end of body. – Figures 134–136, scale B; Figure 133, scale D.



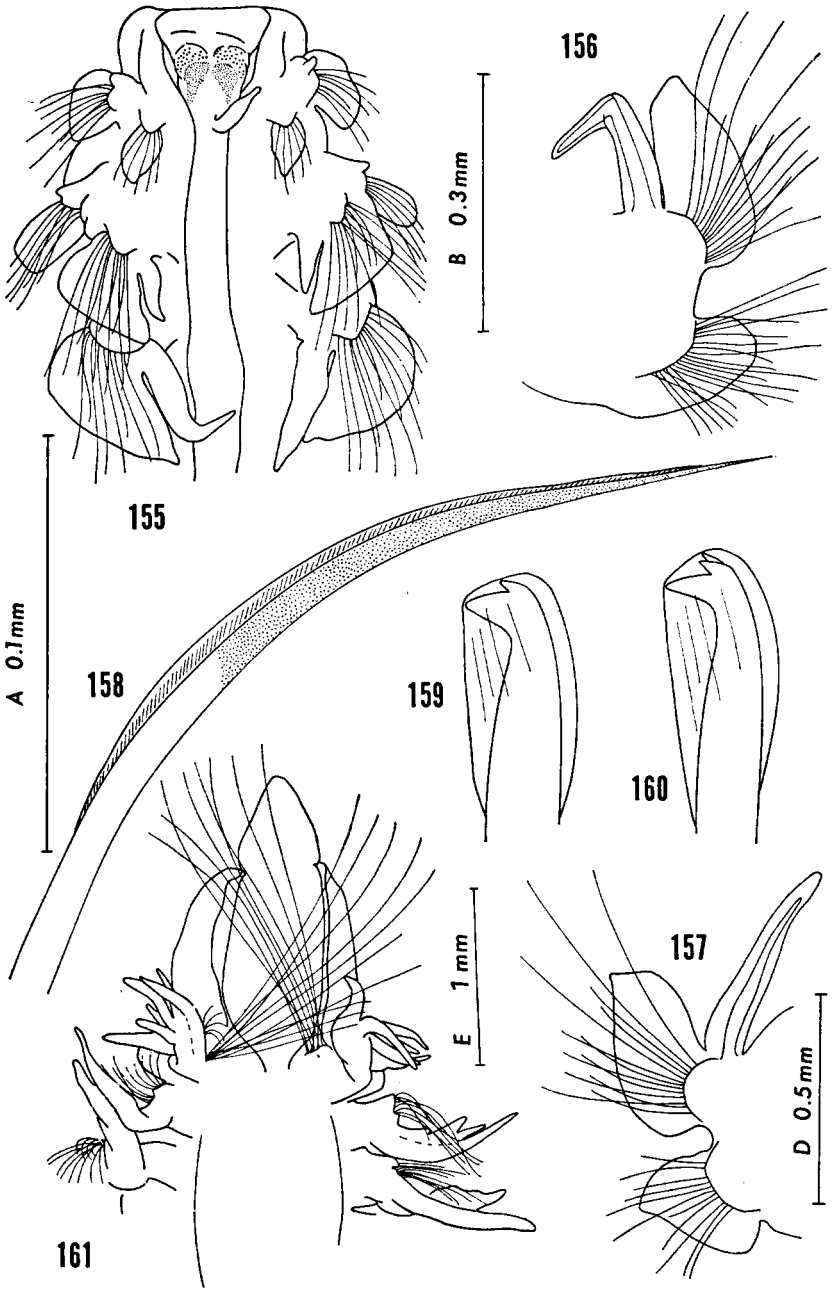
FIGURES 137–141. *Scolelepis* (*Scolelepis*) *texana*. 137: Short, anterior neuroseta. 138: Long anterior neuroseta. 139: Lateral view, neuropodial hooded hook. 140: Anterior view neuropodial hooded hook, hood omitted. 141: Pygidium, lateral view. –FIGURE 142. *Scolelepis squamata saipanensis*. Left posterior parapodium of paratype. – Figures 137–140, scale A; Figures 141–142, scale D.



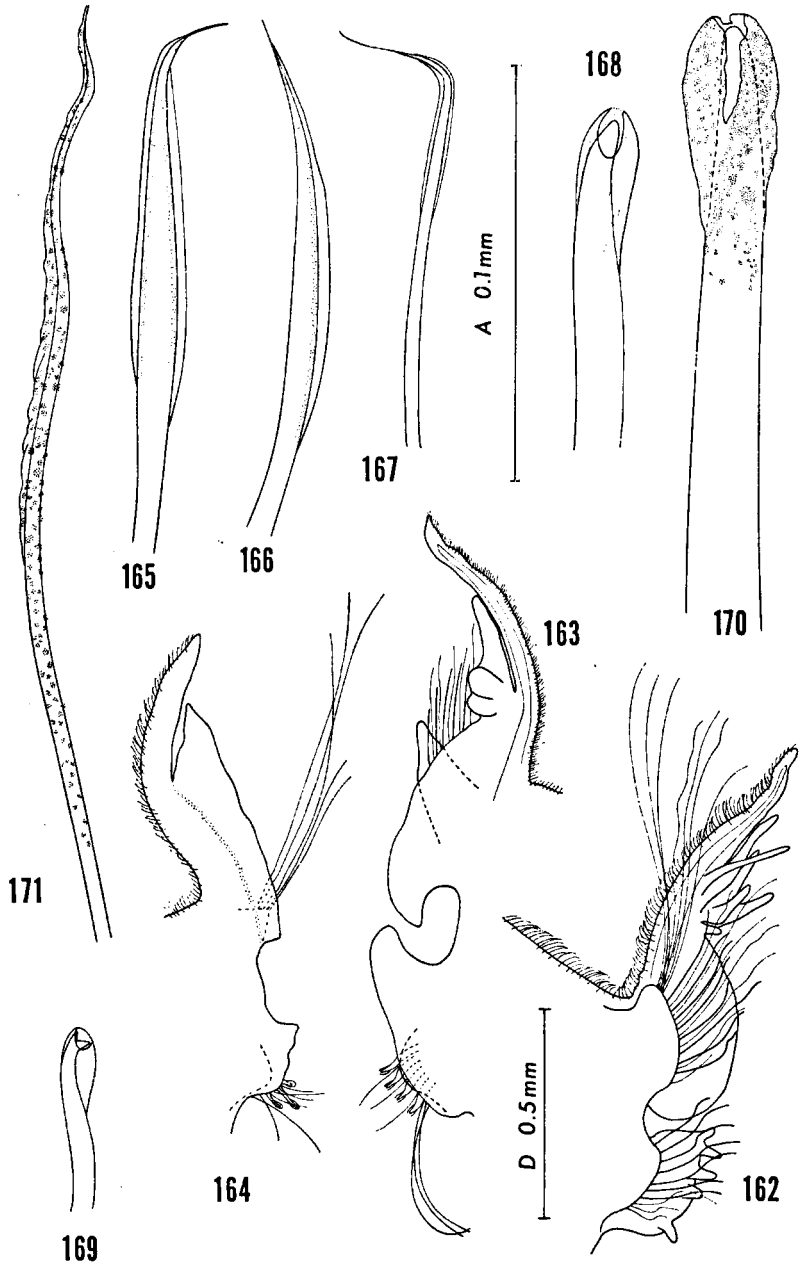
FIGURES 143–147. *Aonides mayaguezensis*. 143: Anterior end, dorsal view, palpi removed. 144: Anterior end, lateral view. 145: Left parapodium setiger 1. 146: Right parapodium setiger 6. 147: Left parapodium setiger 10. – Figures 143–144, 146–147, scale B; Figure 145, scale C.



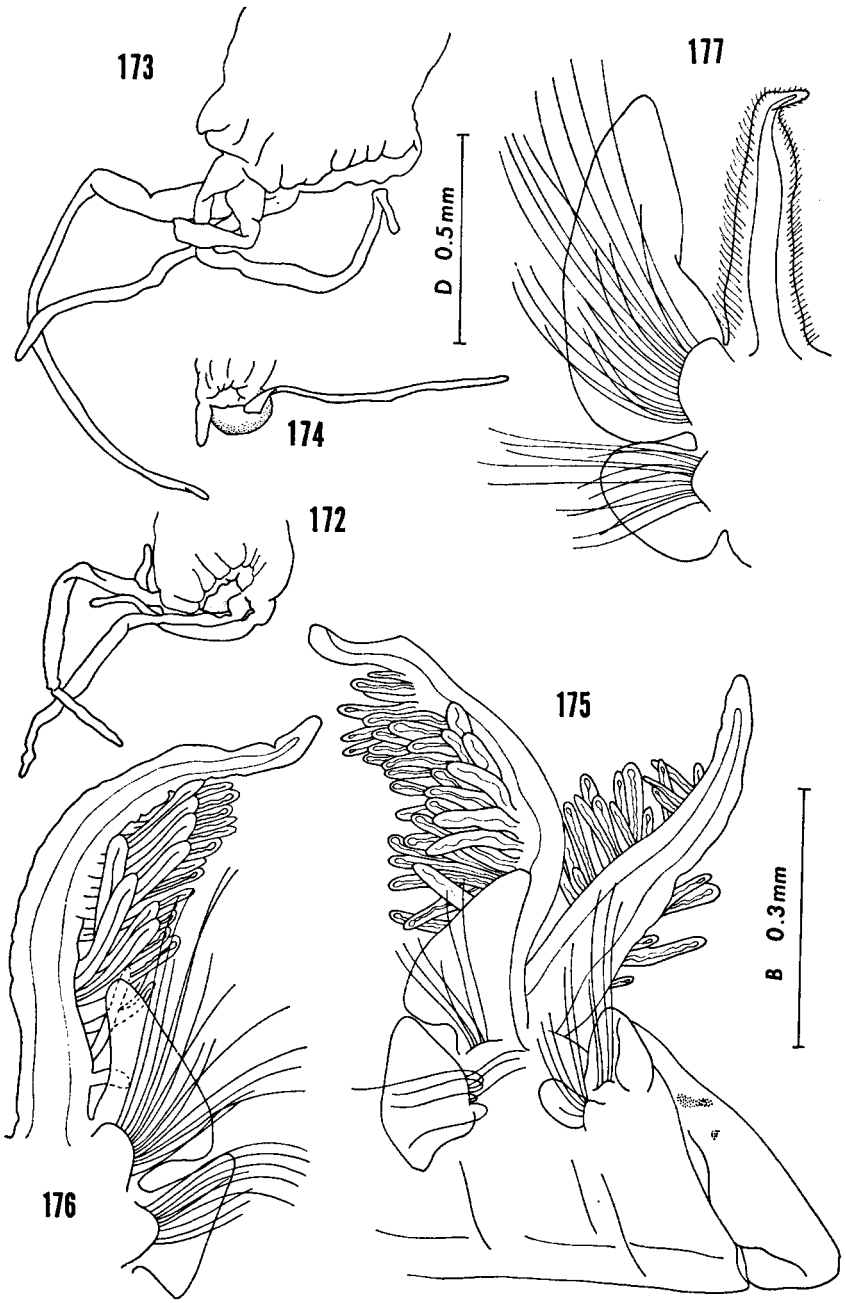
FIGURES 148–154. *Aonides mayaguezensis*. 148: Right parapodium setiger 26. 149: Short neuroseta from setiger 2. 150: Long neuroseta from setiger 2. 151: Three neurosetae from setiger 3. 152: Neuropodial hooded hook from setiger 26. 153: Notopodial hooded hook from setiger 26. 154: Pygidium. – Figures 149–153, scale A; Figures 148, 154, scale C.



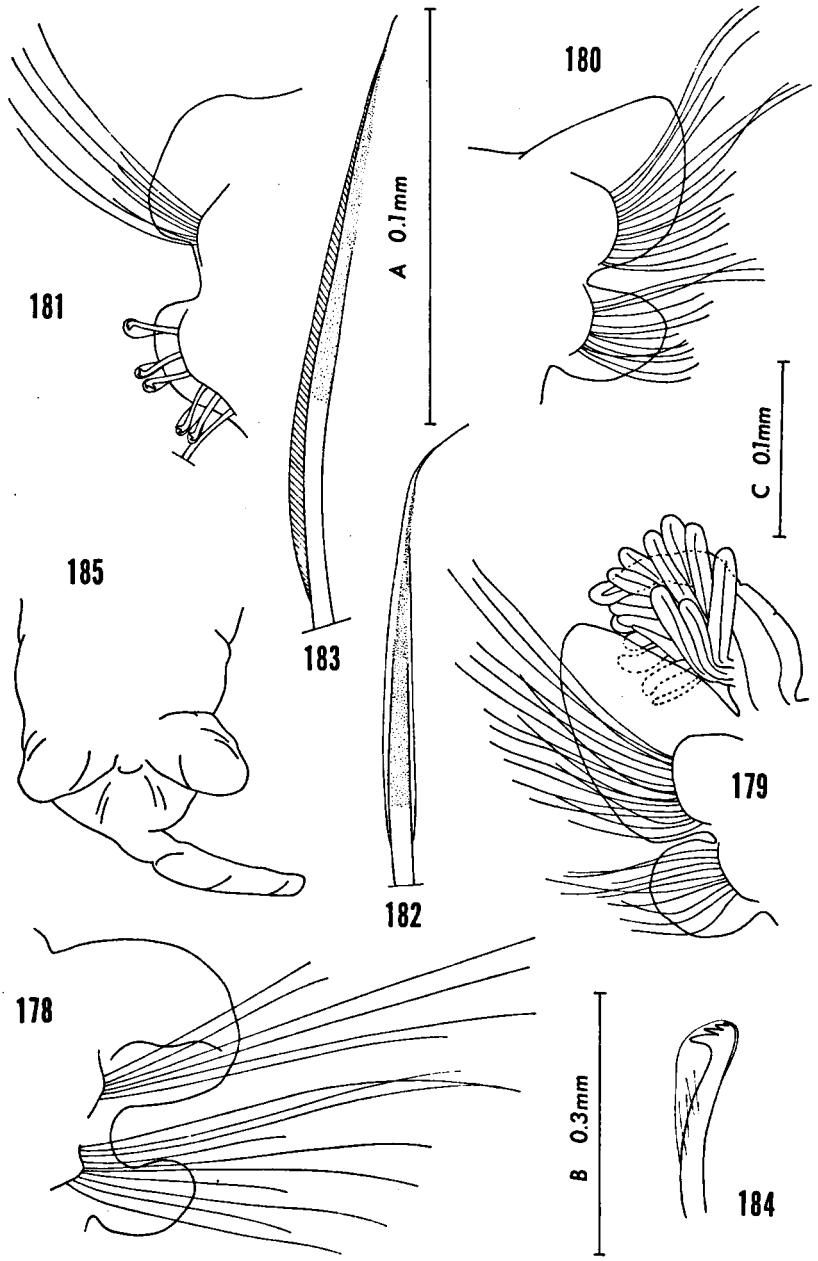
FIGURES 155–160. *Laonice cirrata*. 155: Anterior end, dorsal view, palpi removed. 156: Left parapodium setiger 7. 157: Right parapodium setiger 22. 158: Short anterior notoseta. 159: Bidentate neuropodial hooded hook. 160: Tridentate neuropodial hooded hook. – FIGURE 161. *Dispio uncinata*. Anterior end, dorsal view, palpi removed. – Figures 158–160, scale A; Figures 156–157, scale B; Figure 155, scale D; Figure 161, scale E.



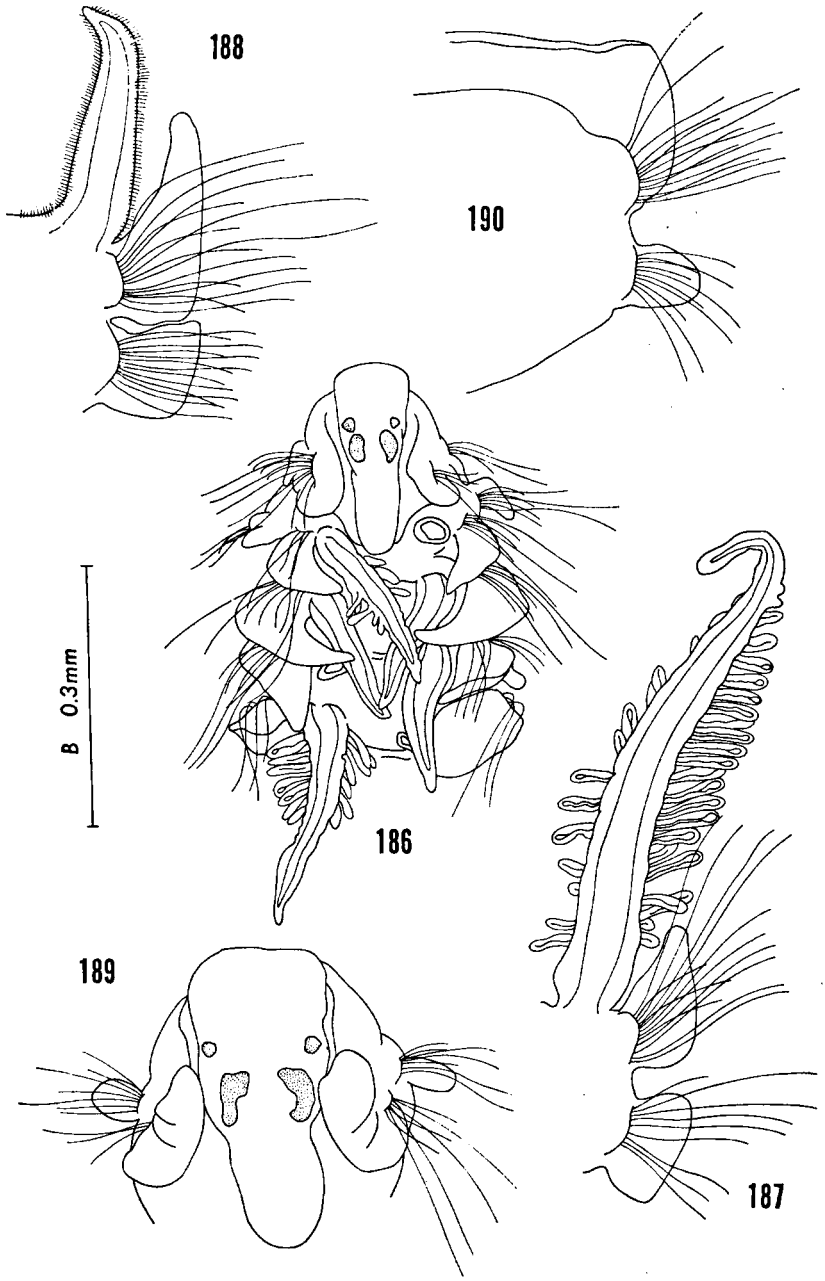
FIGURES 162–171. *Dispio uncinata*. 162: Left parapodium setiger 2. 163: Left parapodium setiger 74. 164: Right parapodium far posterior setiger. 165: Bilimbate anterior neuroseta. 166: Unilimbate anterior neuroseta from same parapodium as Fig. 165. 167: Anterior nongranular neuroseta. 168: Unidentate neuropodial hooded hook. 169: Bidentate neuropodial hooded hook. 170: Orange-tipped neuropodial hooded hook. 171: Neuropodial companion seta. – Figures 165–171, scale A; Figures 162–164, scale D.



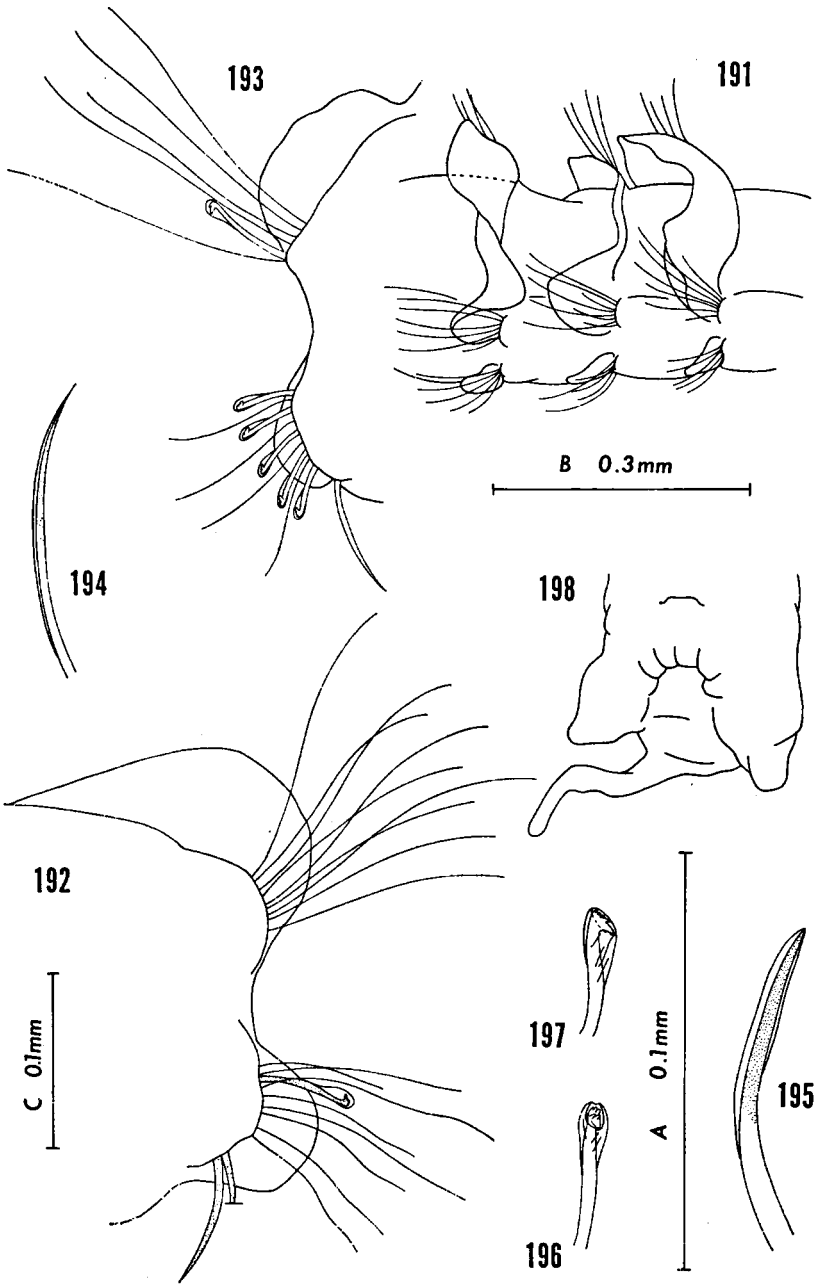
FIGURES 172–174. *Dispio uncinata*. Pygidia, showing collar and/or cirri; stippling on collar represents pigmentation. FIGURES 175–177: *Prionospio steenstrupi*. 175: Lateral view, anterior end, palpi removed. 176: Left parapodium setiger 2. 177: Right parapodium setiger 4. – Figures 175–177, scale B; Figures 172–174, scale D.



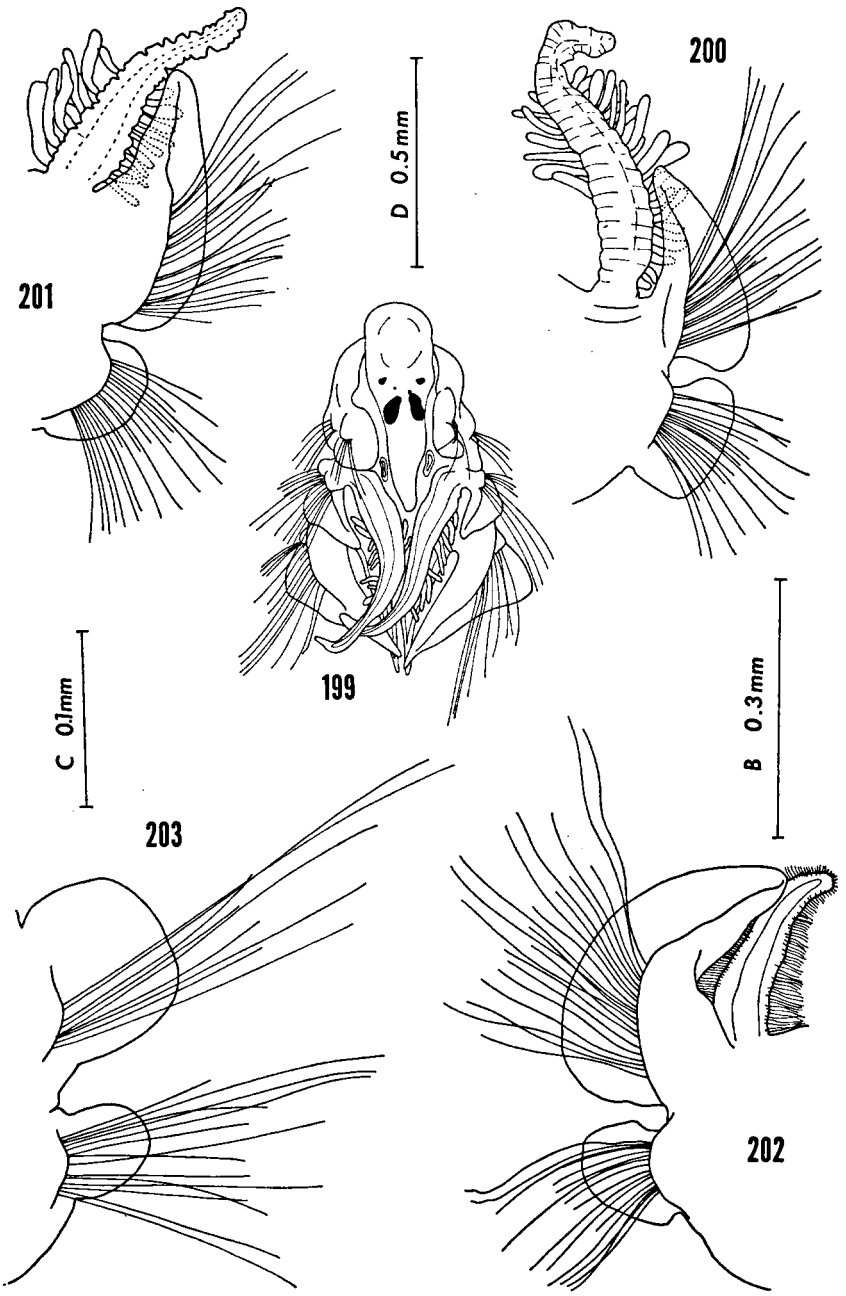
FIGURES 178–185. *Prionospio steenstrupi*. 178: Left parapodium setiger 1. 179: Right parapodium setiger 5. 180: Left parapodium setiger 9. 181: Right parapodium far posterior setiger. 182: Short anterior neuroseta. 183: Short anterior notoseta. 184: Notopodial hooded hook. 185: Pygidium, ventral view. – Figures 182–184, scale A; Figures 179–180, scale B; Figures 178, 181, 185, scale C.



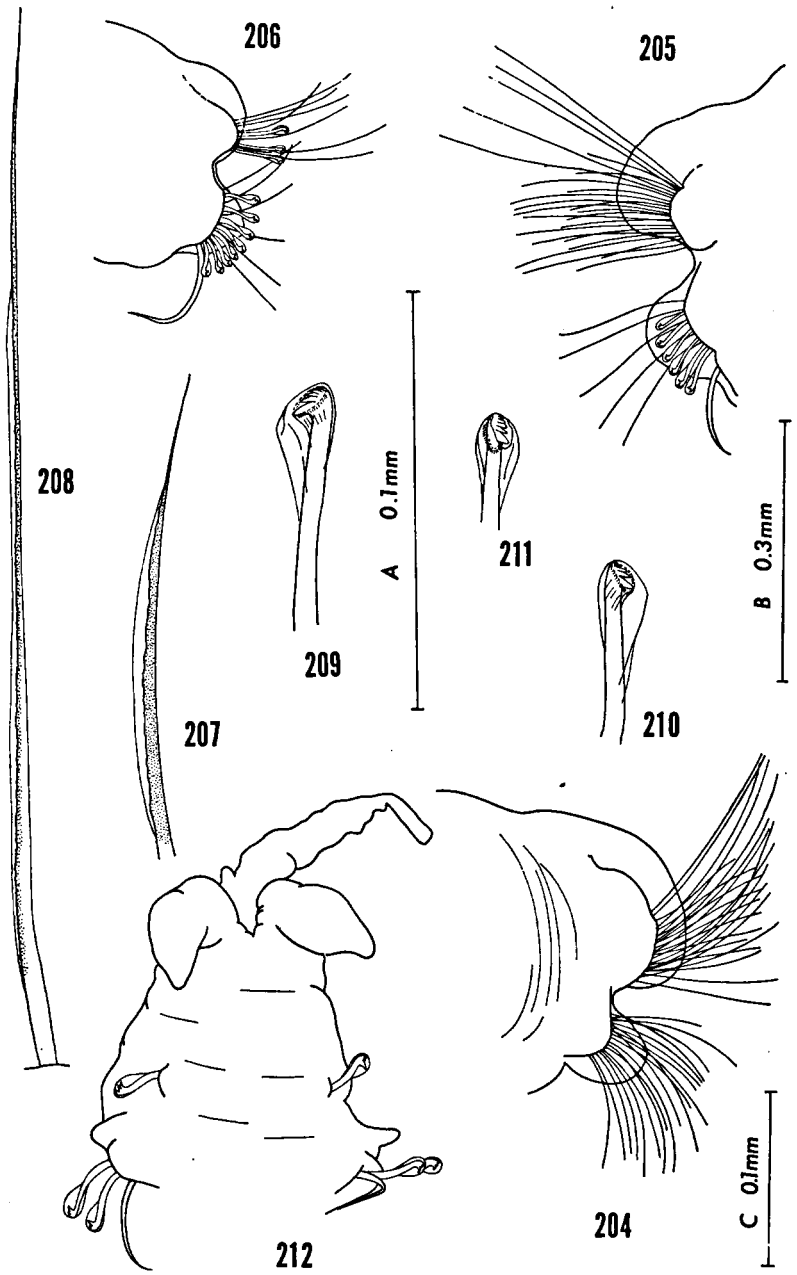
FIGURES 186–190. *Prionospio cristata*. 186: Anterior end, dorsal view, palpi removed. 187: Left parapodium setiger 2. 188: Left parapodium setiger 3. 189: Prostomium and setiger 1, dorsal view. 190: Left parapodium setiger 7. – Figures 186–190, scale B.



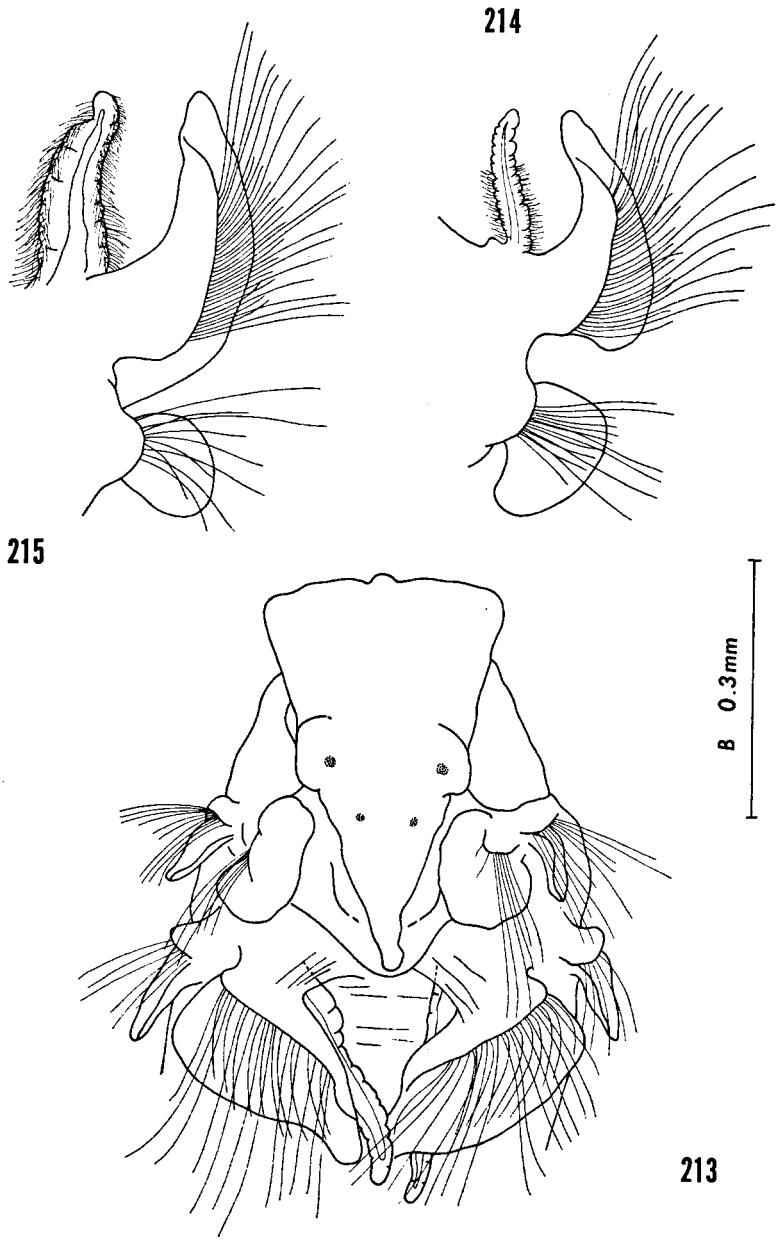
FIGURES 191–198. *Prionospio cristata*. 191: Setigers 7–9, right dorso-lateral view. 192: Left parapodium setiger 12. 193: Right parapodium setiger 40. 194: Short anterior neuroseta. 195: Anterior sabre-seta. 196: Neuropodial hooded hook. 197: Neuropodial hooded hook. 198: Pygidium, ventral view. – Figures 194–197, scale A; Figure 191, scale B; Figures 192–193, 198, scale C.



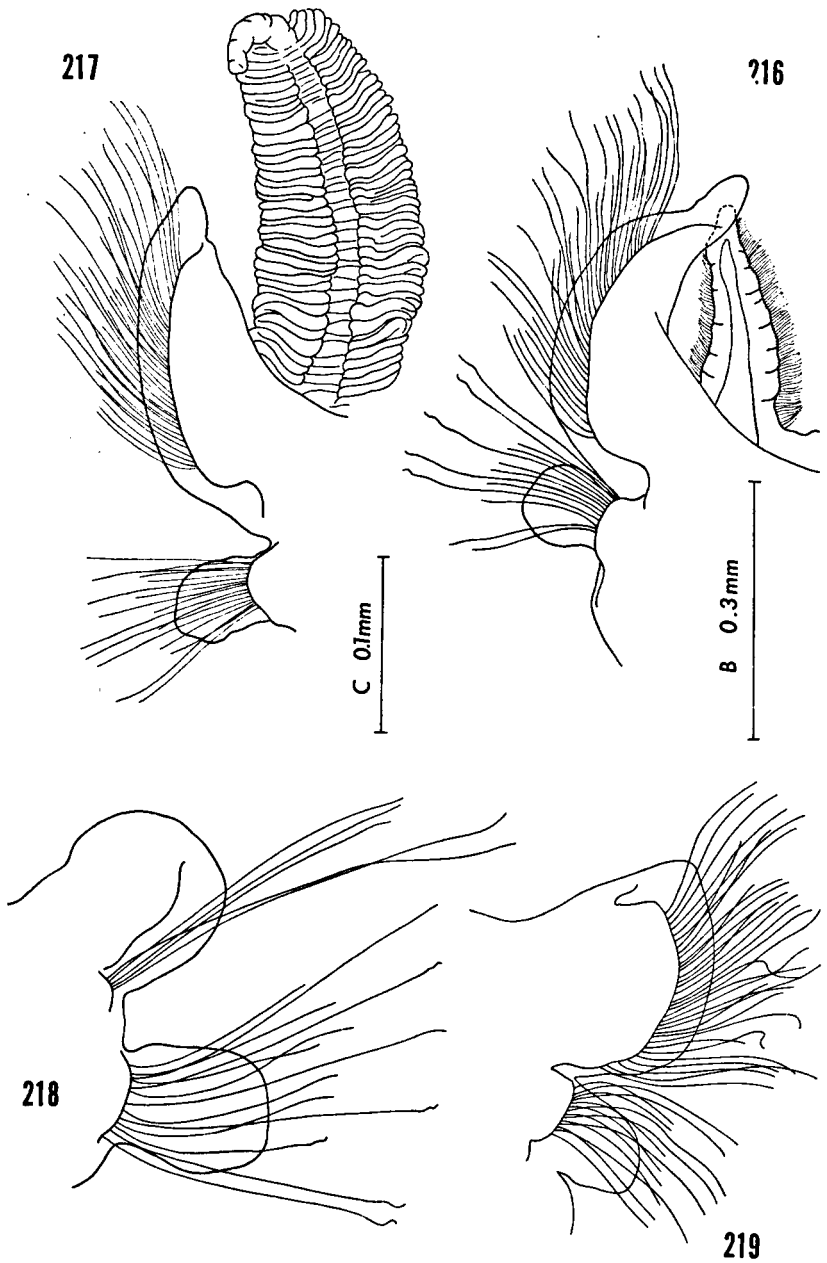
FIGURES 199–203. *Prionospio heterobranchia*. 199: Anterior end, dorsal view, palpi removed. 200: Left parapodium setiger 2. 201: Left parapodium setiger 6. 202: Right parapodium setiger 3. 203: Left parapodium setiger 1. – Figures 200–202, scale B; Figure 203, scale C; Figure 199, scale D.



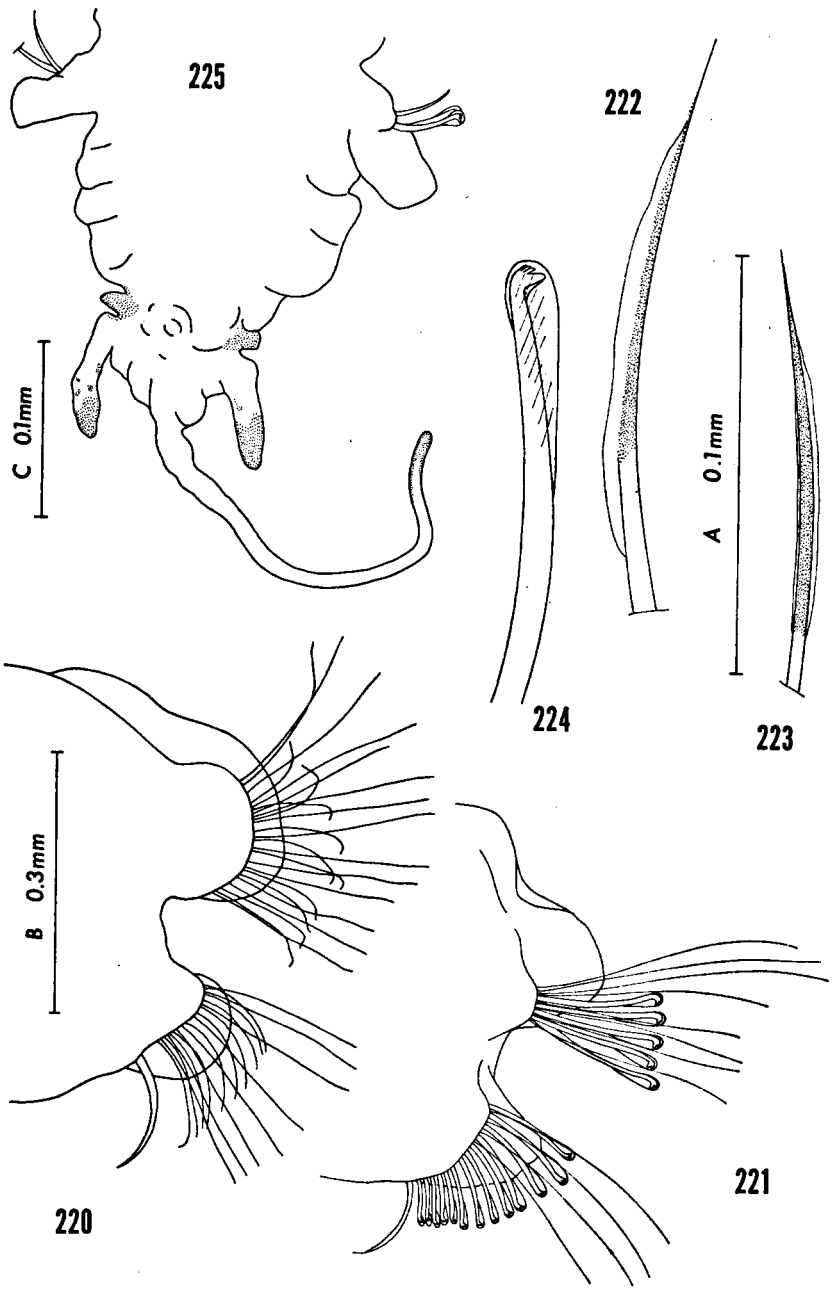
FIGURES 204–212. *Prionospio heterobranchia*. 204: Left parapodium setiger 9. 205: Right parapodium setiger 15. 206: Left parapodium setiger 53. 207: Short neuroseta. 208: Long neuroseta. 209: Notopodial hooded hook. 210: Neuropodial hooded hook. 211: Notopodial hooded hook, frontal view. 212: Pygidium, ventral view. – Figures 207–211, scale A; Figures 204–206, scale B; Figure 212, scale C.



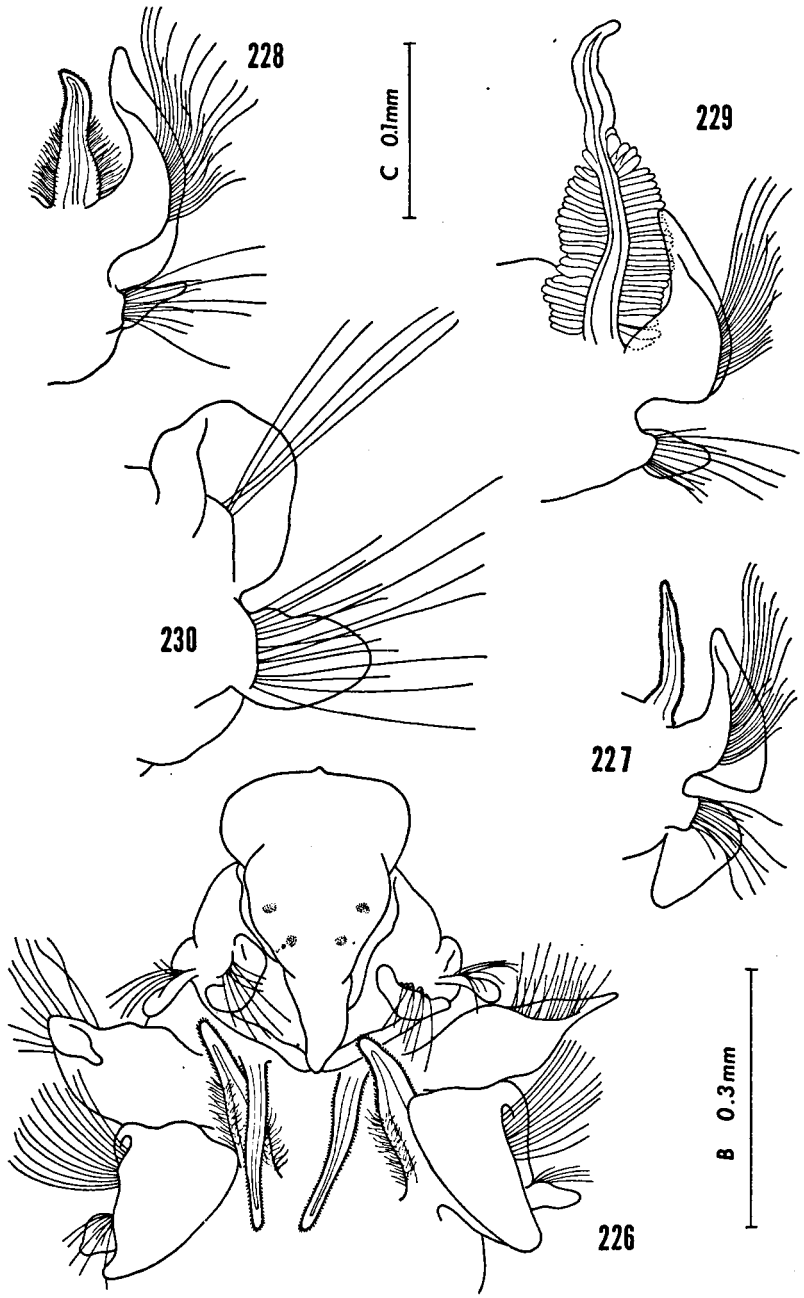
FIGURES 213–215. *Apoprionospio pygmaea*. 213: Anterior end, dorsal view, palpi removed. 214: Left parapodium setiger 2. 215: Left parapodium setiger 3. – Figures 213–215, scale B.



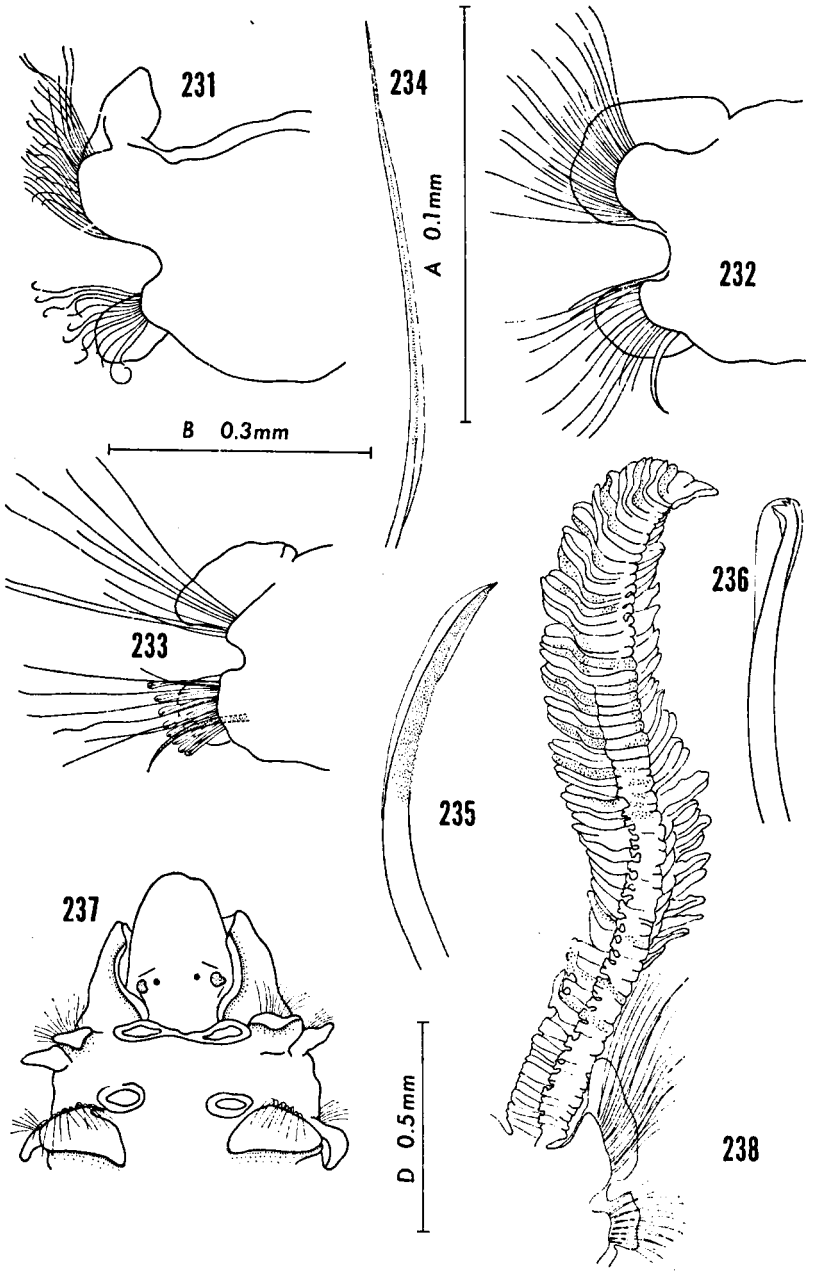
FIGURES 216–219. *Apoprionospio pygmaea*. 216: Right parapodium setiger 4. 217: Right parapodium setiger 5. 218: Left parapodium setiger 1. 219: Left parapodium setiger 10. – Figures 216–217, 219, scale B; Figure 218, scale C.



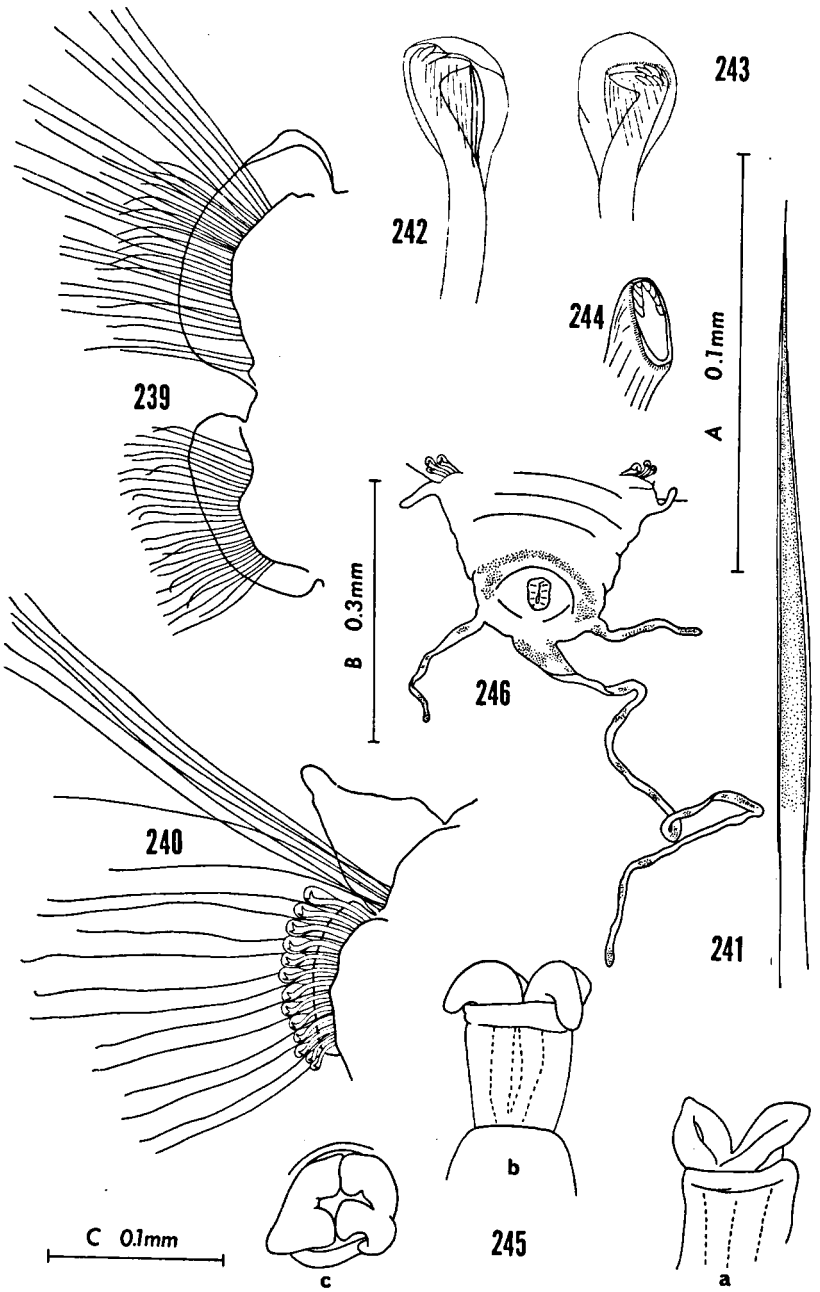
FIGURES 220–225. *Apoprionospio pygmaea*. 220: Left parapodium anterior postbranchial setiger. 221: Left parapodium posterior setiger. 222: Short anterior notoseta. 223: Short anterior neuroseta. 224: Neuropodial hooded hook. 225: Pygidium, ventral view. – Figures 222–224, scale A; Figures 220–221, scale B; Figure 225, scale C.



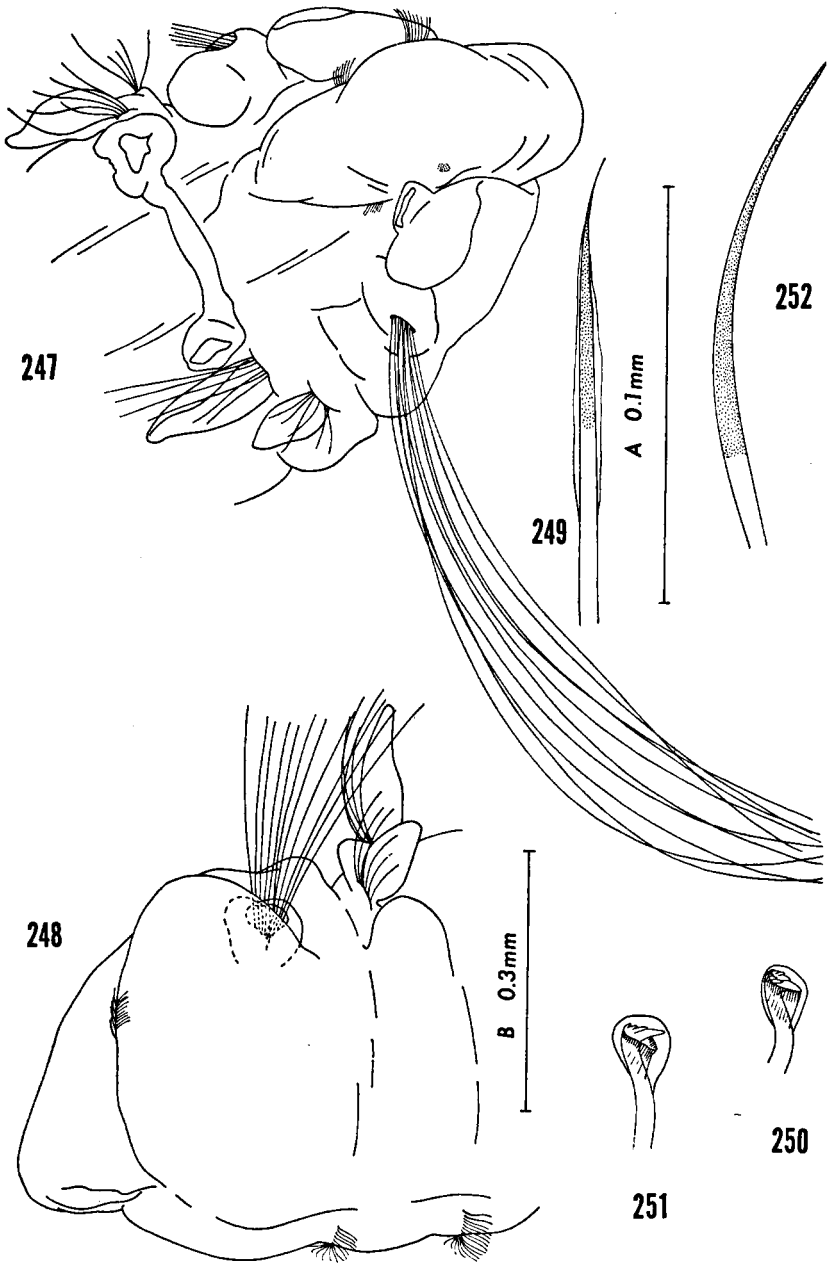
FIGURES 226–230. *Apoprionospio dayi*. 226: Anterior end, dorsal view, palpi removed. 227: Left parapodium setiger 2. 228: Left parapodium setiger 3. 229: Left parapodium setiger 5. 230: Left parapodium setiger 1. – Figures 226–229, scale B; Figure 230, scale C.



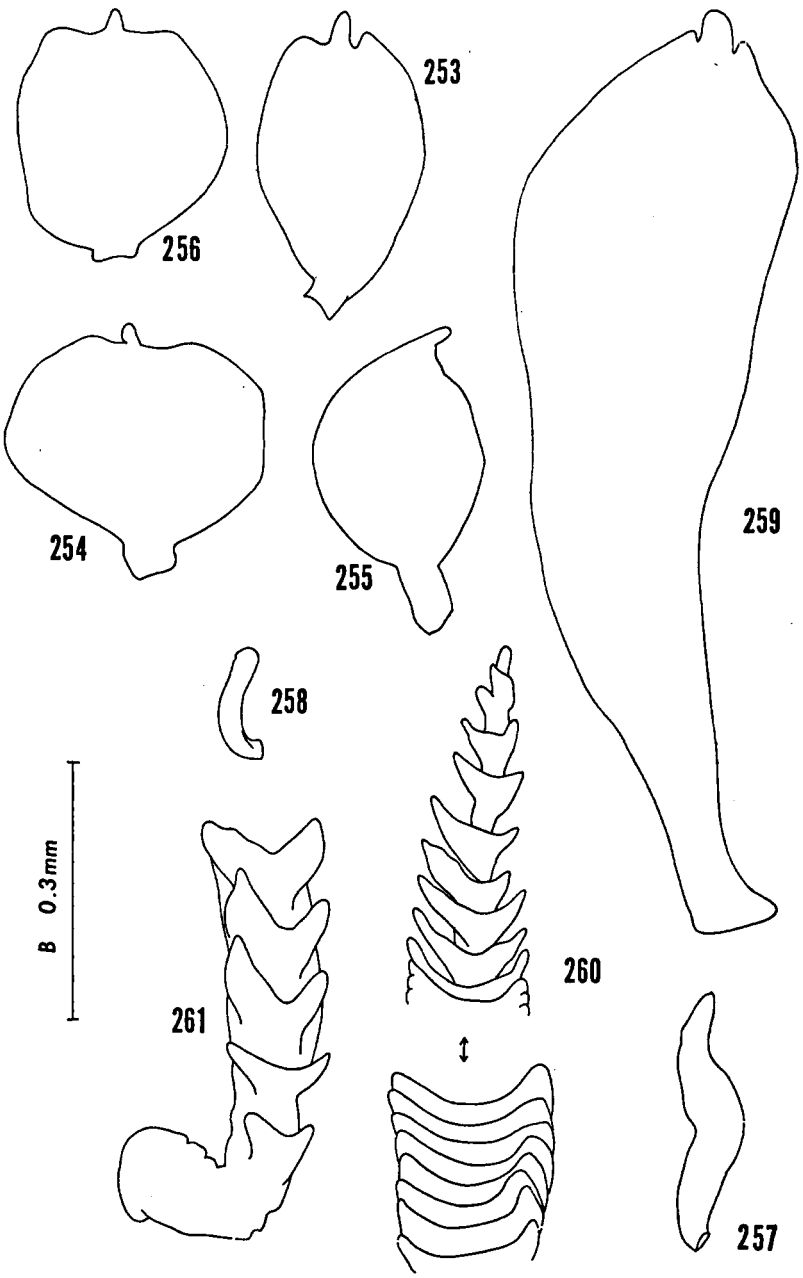
FIGURES 231–236. *Apoprionospio dayi*. 231: Right parapodium setiger 7. 232: Right parapodium setiger 11. 233: Right parapodium setiger 22. 234: Neuropodial seta from setiger 1. 235: Sabre-seta from setiger 12. 236: Neuropodial hooded hook from posterior setiger. – FIGURES 237–238. *Paraprionospio pinnata*. 237: Anterior end, dorsal view, bases only of branchiae shown, palpi removed. 238: Left parapodium setiger 1, pigmentation of branchia shown by stippling. – Figures 234–236, scale A; Figures 231–233, 238, scale B; Figure 237, scale D.



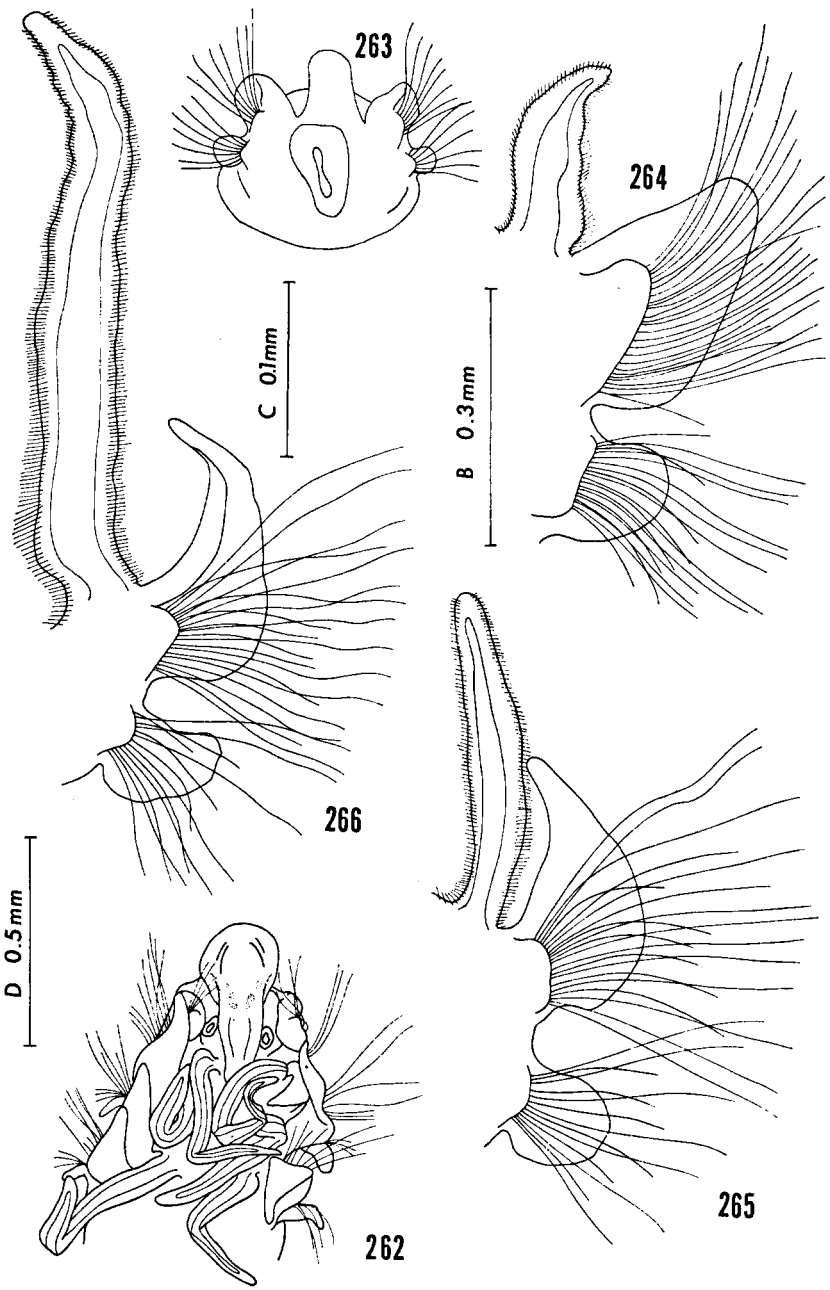
FIGURES 239–246. *Paraprionospio pinnata*. 239: Right parapodium setiger 8. 240: Right parapodium setiger 34. 241: Notoseta from setiger 1. 242: Neuropodial hook from posterior setiger. 243: Neuropodial hook showing boundaries of internal hood. 244: Tip of hook with primary hood removed, dorsal view, 245: Everted proboscis; a. dorsal view b. ventral view c. anterior view (not drawn to scale). 246. Pygidium, ventral view, pigmentation shown by stippling. – Figures 241–244, scale A; Figures 239, 246, scale B; Figure 240, scale C.



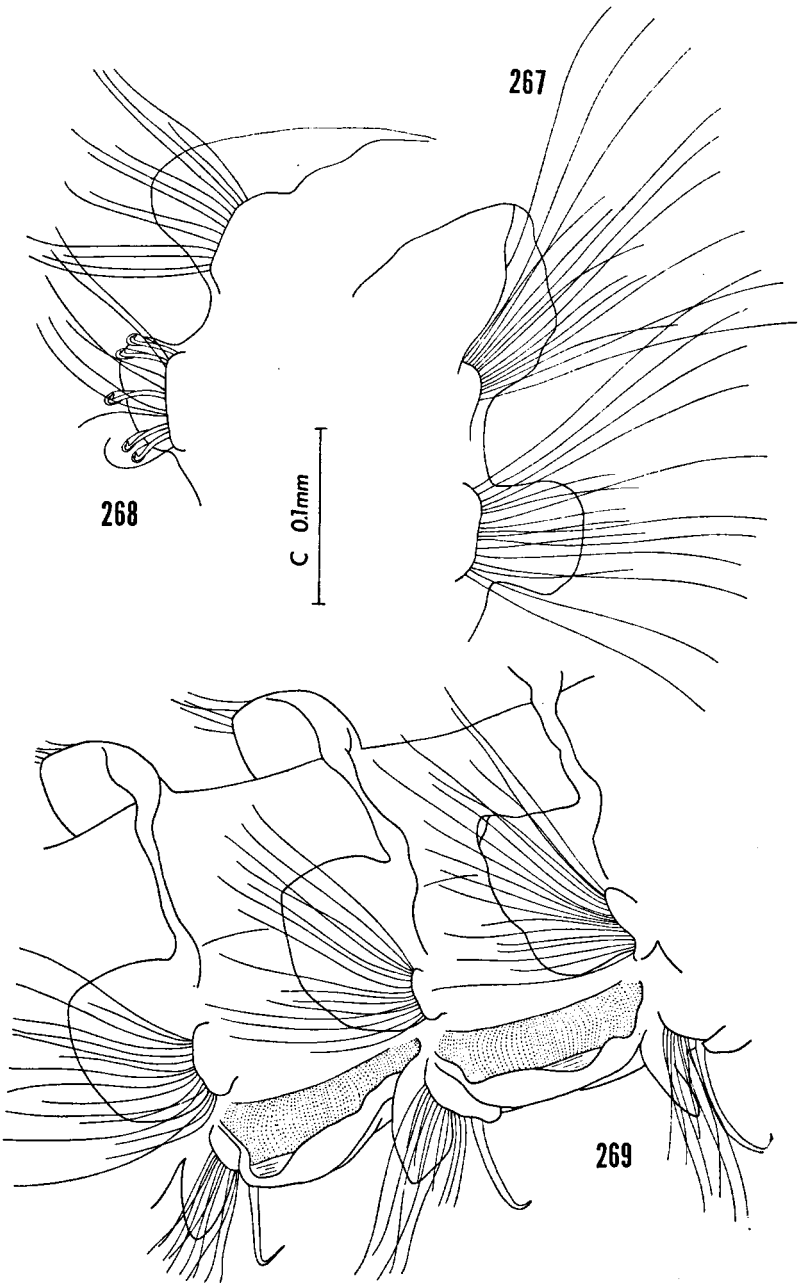
FIGURES 247–252. *Paraprionospio pinnata* larvae. 247: Anterior end, right dorsolateral view, left natatory setal bases only shown. 248: Anterior end, left lateral view. 249: Short anterior capillary notoseta. 250–251: Neuropodial hooded hooks. 252: Sabre-seta. – Figures 249–252, scale A; Figures 247–248, scale B.



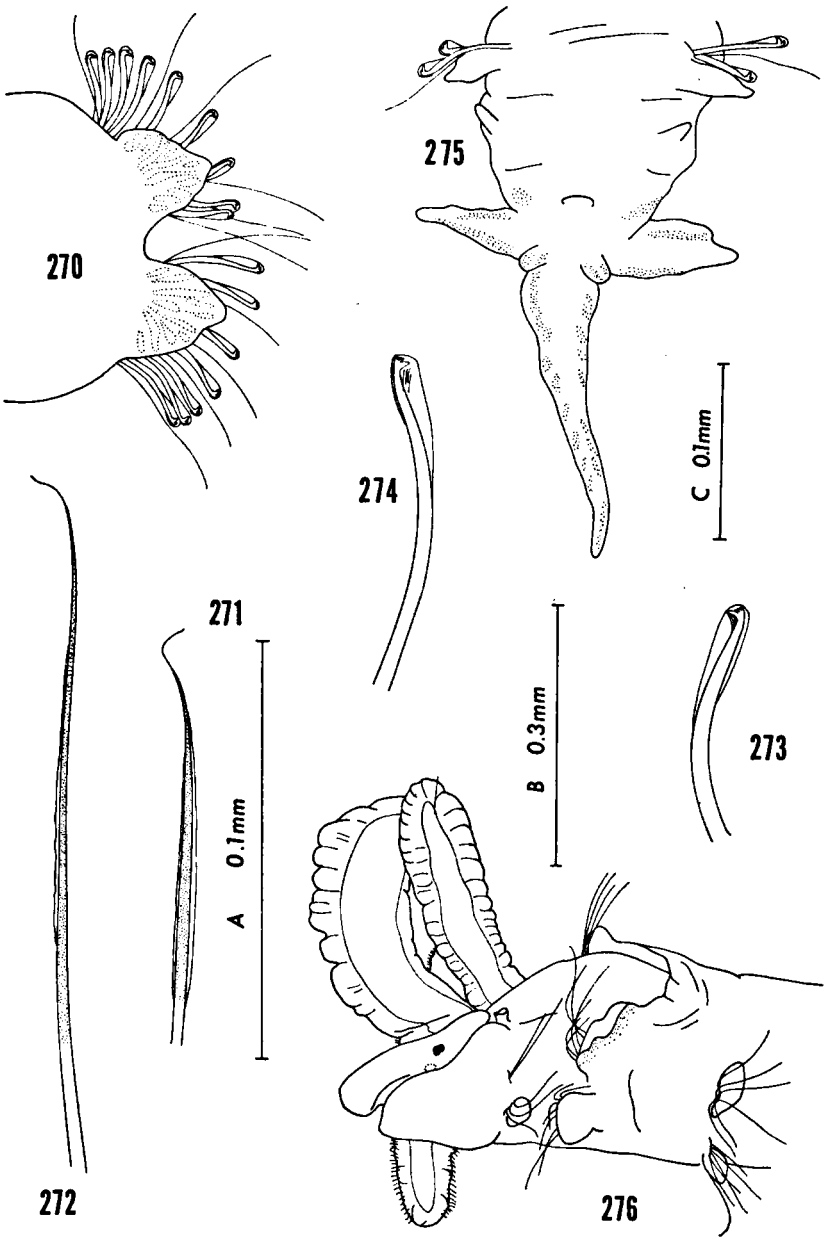
FIGURES 253–261. *Paraprionospio pinnata* larvae. 253–257: Generalized outlines of larval branchiae. 258–259: Generalized outline of adult branchiae. 260–261: More detailed outline of adult branchiae. – Figures 253-261, scale B.



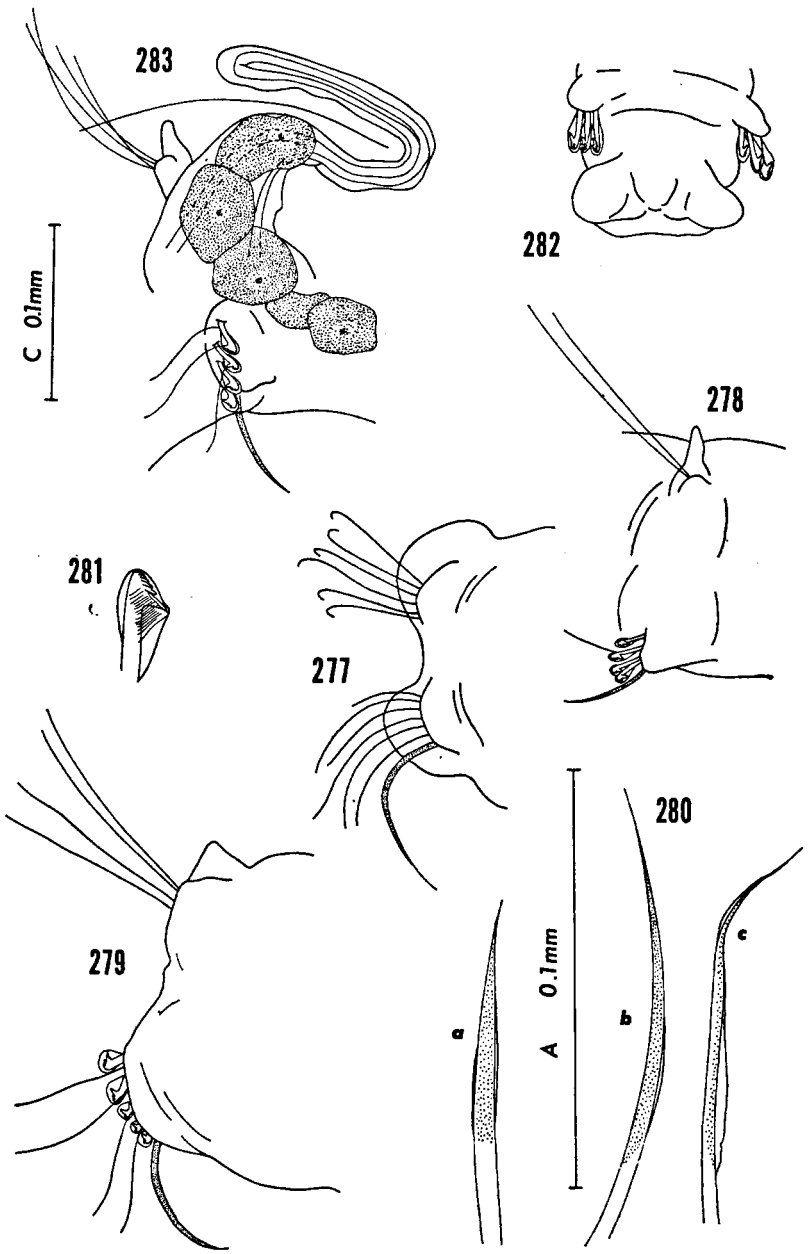
FIGURES 262–266. *Minuspio cirrifera*. 262. Anterior end, dorsal view, palpi removed. 263: Setiger 1, showing height of prostomial keel. 264: Left parapodium setiger 7. 265: Left parapodium setiger 7. 266: Left parapodium setiger 3. – Figure 264, scale B; Figures 265–266, scale C; Figures 262–263, scale D.



FIGURES 267–269. *Minuspio cirrifera*. 267: Left parapodium setiger 1. 268: Right parapodium setiger 16. 269: Setigers 11–13, right dorso-lateral view, showing genital pouches stippled. – Figures 267–269, scale C.



FIGURES 270–275. *Minuspio cirrifera*. 270: Right parapodium far posterior setiger. 271: Short anterior notoseta. 272: Long anterior notoseta. 273: Neuropodial hooded hook. 274. Notopodial hooded hook. 275: Pygidium, ventral view. – FIGURE 276. *Streblospio benedicti*. Anterior end, left lateral view, left palp and branchia omitted. – Figures 271–274, scale A; Figure 270, scale B; Figure 275, scale C.



FIGURES 277–283. *Streblospio benedicti*. 277: Right parapodium setiger 7. 278–279: Far posterior setigers. 280: Notopodial capillary setae. 281: Neuropodial hooded hook. 282: Pygidium, ventral view, 283: Posterior setiger of specimen from Maracaibo estuary, lateral view, eggs in brood pouch stippled. – Figures 280–281, scale A; Figures 277–279, 282–283, scale C.

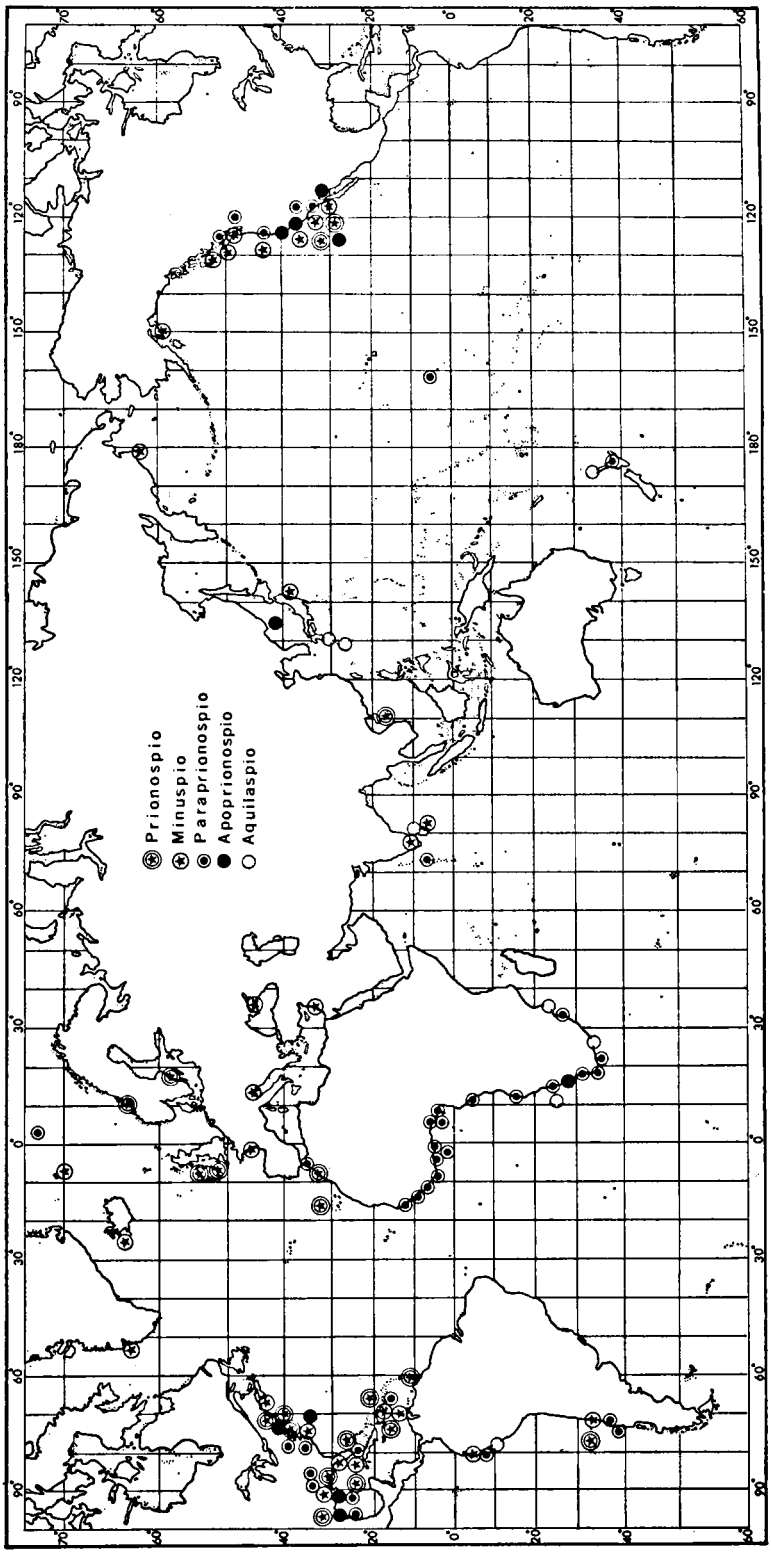


FIGURE 284. Distribution of the genera *Prionospio, Minuspio, Paraprionospio, Apoprionospio* and *Aquilaspio.*

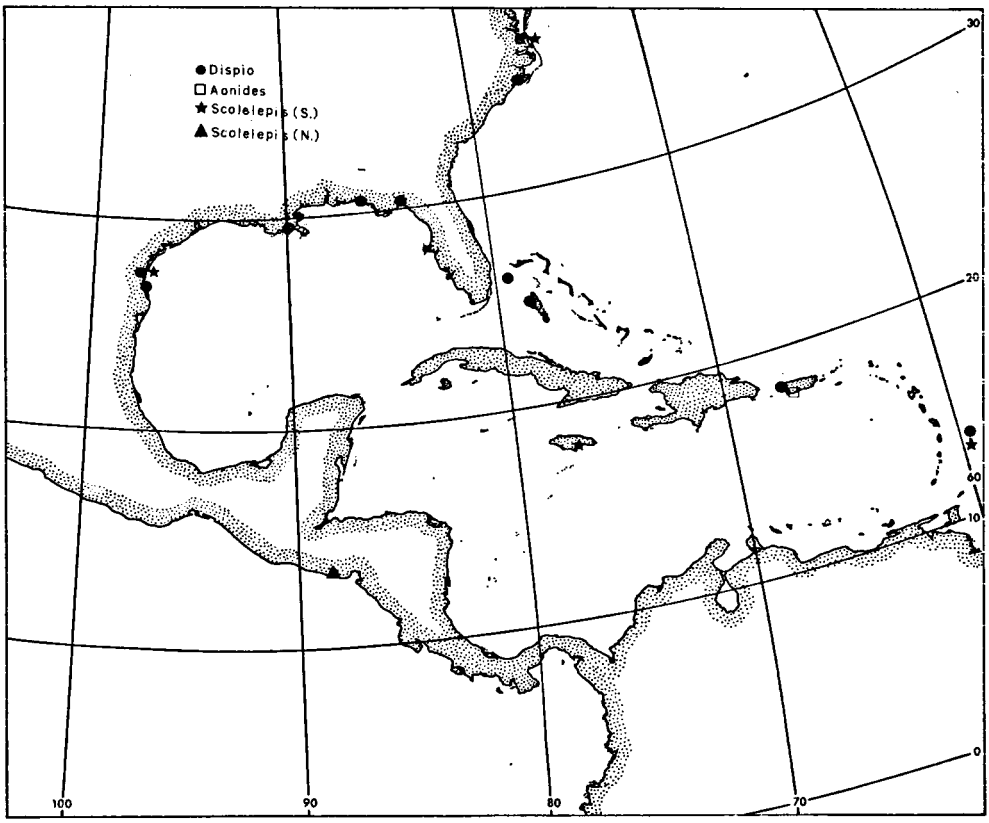


FIGURE 285. Distribution of the genera *Dispio*, *Aonides* and *Scolelepis* in Central American waters.