



New records and description of four new species of spionids (Annelida: Polychaeta: Spionidae) from the Philippines: the genera *Dispio*, *Malacoceros*, *Polydora*, and *Scolelepis*, with notes on palp ciliation patterns of the genus *Scolelepis*

JASON D. WILLIAMS

Department of Biology, Hofstra University, Hempstead, NY 11549-1140, USA. E-mail: biojdw@hofstra.edu

Table of contents

Abstract	1
Introduction	
Materials and methods	
Systematics	
Family Spionidae Grube, 1850	
Subfamily Spioninae Söderström, 1920	
Genus Polydora Bosc, 1802	
Subfamily Nerininae Söderström, 1920	
Genus Dispio Hartman, 1951	
Dispio latilamella sp. n.	
Genus Malacoceros Quatrefages, 1843	
Malacoceros indicus (Fauvel, 1928)	
Genus Scolelepis Blainville, 1828	
Scolelepis alisonae sp. n.	
Scolelepis hutchingsae Dauer, 1985	
Scolelepis magnicornuta sp. n.	
Scolelepis villosivaina sp. n.	
Discussion	
Key to the Spionidae of the Philippines	
Acknowledgments	
References	

Abstract

Seven species of spionid worms of the Philippines are described based primarily on specimens collected from intertidal sandy beaches in 1999–2000. Four of these species are new to science and two are recorded for the first time from this region. *Dispio latilamella* **sp. n.**, is distinguished by large, spoon-shaped postsetal notopodial lamellae of setiger 1 and notopodial lamellae of setigers 1–13 with digitiform extensions along margin. *Malacoceros indicus* (Fauvel, 1928), a widely distributed species, is discovered for the first time in the Philippines. *Polydora cavitensis* Pillai, 1965 is reported from Manila Bay for the first time since its original description. Four species of *Scolelepis* were found: *S. hutchingsae* Dauer, 1985, *S. alisonae* **sp. n.**, *S. magnicornuta* **sp. n.**, and *S. villosivaina* **sp. n.** *Scolelepis hutchingsae* was previously only known from Australia; the Philippine specimens closely match the original description. *Scolelepis alisonae* **sp. n.** is distinguished by postsetal notopodial lamellae with conical lobes on anterior setigers, bidentate notopodial hooded hooks beginning on setiger 68–99, and bidentate neuropodial hooded hooks beginning on setiger 25–33. *Scolelepis magnicornuta* **sp. n.** has a large, conical occipital tentacle with cilia along the sides, unidentate or bidentate notopodial hooded

hooks beginning on setiger 38–55, and bidentate neuropodial hooded hooks beginning on setiger 25–30. *Scolelepis villo-sivaina* **sp. n.** has palp sheaths with patches of cilia near the insertion of palps, bidentate notopodial hooded hooks beginning on setiger 38, and unidentate or bidentate neuropodial hooded hooks beginning on setiger 25–29. The palp ciliation patterns of *Scolelepis* are reviewed and four distinct morphological types can be distinguished based on Scanning Electron Microscope investigations. A table reviewing the recently described species of *Scolelepis* is provided.

Key words: Polychaeta, Spionidae, taxonomy, non-native species, Indo-West Pacific

Introduction

The Spionidae is one of the most abundant polychaete families of the Indo-West Pacific (Knox 1957; Bailey-Brock 1995; Paxton & Chou 2000). While extensive surveys have been made in some areas of the Indo-West Pacific such as southeastern Australia (Blake & Kudenov 1978; Hutchings & Turvey 1984), knowledge of their diversity in many areas is still poor. Ecological research on the polychaete fauna of exposed beaches have shown that many undescribed spionids remain to be studied in the Indo-West Pacific, particularly within the genus *Scolelepis* (Eibye-Jacobsen 1997; Hutchings *et al.* 1998). The purpose of the present investigation is to report on collections of spionids made mainly on exposed beaches of the Philippines, part of the highly diverse East Indies Triangle. This region is home to the greatest concentration of species within many tropical marine groups (e.g., Briggs 1999; Carpenter *et al.* 2005).

Prior to this investigation only 13 species of the family Spionidae had been identified from the Philippines. Most of this previous research focused on members of the *Polydora* complex (nine genera that contain a modified fifth setiger, informally known as polydorids: *Amphipolydora*, *Boccardia*, *Boccardiella*, *Carazziella*, *Dipolydora*, *Polydora*, *Polydorella*, *Pseudopolydora* and *Tripolydora*), many of which are known to burrow into calcareous substrata (Grube 1878; Pillai 1965; Williams 2000, 2001). The polydorid genus *Polydorella* is associated with sponges, on the surface of which they form mud tubes; two species of this genus have been documented from the Philippines (Williams 2004). Aside from the polydorids, no other spionids have been described from the Philippines in spite of several surveys of polychaetes from these islands (Grube 1878; Hoagland 1920; Treadwell 1920, 1926, 1931, 1942, 1943; Holly 1934, 1935; Pillai 1965; Rosito 1980, 1983; Palpal-latoc 1981, 1990, 1994; Palpal-latoc & Gonzales 1981; Natividad & Palpal-latoc 1986).

Based on adult and larval morphology plus reproductive characters, Blake & Arnofsky (1999) and Blake (2006) found that the Spionidae is composed of three clades: one minor clade consisting of the genus *Pygospiopsis* and two large clades considered subfamilies. The subfamily Spioninae Söderström, 1920 consists of *Microspio, Pygospio, Spio* and the nine genera that form the *Polydora* complex. The subfamily Nerininae Söderström, 1920 consists of approximately 19 genera including *Aonides, Aonidella, Dispio, Laonice, Lindaspio, Malacoceros, Marenzellaria, Paraprionospio, Parascolelepis, Prionospio, Rhyncospio, Scolelepides, Scolelepis, Spiophanes and Streblospio plus four genera previously placed outside of the Spionidae (<i>Heterospio, Poecilochaetus, Trochochaeta* and *Uncispio*). Within the subfamily Nerininae, the subgenera of *Scolelepis* (*Scolelepis* and *Parascolelepis*) were considered sufficiently different to be raised to the rank of genera (Blake & Arnofsky 1999; Blake 2006). Although Blake (2006) indicated that the reclassification of the family Spionidae should not be considered definitive, the subfamily divisions and the generic rank of *Scolelepis* and *Parascolelepis* are followed in this manuscript. In total, the present work describes seven species of spionids from the Philippines, four of which are new to science.

Materials and methods

Polychaetes were collected from shallow subtidal sediments (<5 m) from exposed beaches in Bataan (Morong, 14°41′N, 120°16′E) and Aklan (Boracay: Diniwid Beach, 11°60′N, 121°54′E; Boracay: White

Beach, 11°59′N, 121°55′E) provinces of the Philippines (Fig. 1) from February to April 1999. All collections were made by the author. Specimens were separated from the sediment using a sieve (1–2 mm mesh size). In addition, a mass of green mussels *Perna viridis* (Linnaeus 1758) were collected by researchers at the Marine Science Institute of the University of the Philippines from Bacoor, Cavite in Manila Bay in 2000 and examined for associated polychaetes.

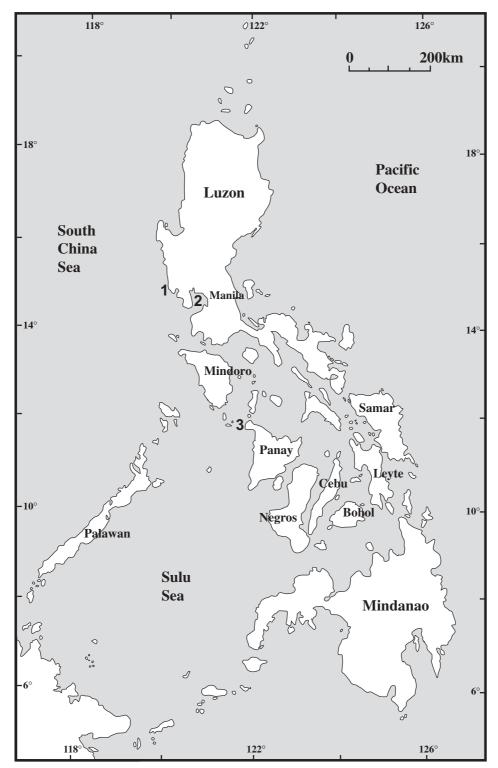


FIGURE 1. Map of the Philippines with three collecting sites indicated in the text: 1) Morong, Bataan, 2) Bacoor, Cavite (Manila Bay), 3) Boracay, Aklan.

Specimens were relaxed in 3% magnesium chloride in seawater, fixed in 4% formalin-seawater solution (one part 39% formalin to nine parts seawater), rinsed in fresh water, and preserved in 70% ethanol. Sketches of live and preserved specimens were completed using a compound microscope with a drawing tube attachment. Drawing tube sketches were scanned with a computer and final plates were prepared using the programs Adobe PhotoshopTM and Adobe IllustratorTM.

For SEM, fixed specimens were dehydrated in an ascending ethanol series followed by four changes of 100% ethanol. Drying was completed with a Samdri 795 Critical Point Drier. Dried specimens were mounted on an aluminum stub, coated with gold (EMS-550 Sputter coater), and viewed with a Hitachi S-2460N SEM. Type and voucher specimens are deposited in the Raffles Museum of Biodiversity Research, Singapore (ZRC) and the National Museum of Natural History, Smithsonian Institution, Washington, D. C., U.S.A. (USNM).

Systematics

Family Spionidae Grube, 1850

Subfamily Spioninae Söderström, 1920

Genus Polydora Bosc, 1802

Polydora cavitensis Pillai, 1965 (Figs. 2-3)

Polydora cavitensis Pillai, 1965: 152-154, Figs. 16E, F, 17A-G.

Material examined. Philippines, Bacoor, Cavite in Manila Bay, from mud tubes among live green mussels *Perna viridis*, 20 Jul 2000, coll. by researchers at the Marine Science Institute of the University of the Philippines (one complete specimen in alcohol, USNM 1096802; one anterior end on SEM stub, USNM 1096803).

Description. Complete specimen of 67 setigers 17.42-mm long, and 0.7mm wide at setiger 7. Prostomium weakly incised anteriorly (Fig. 2A–B); caruncle extending posteriorly to near end of setiger 3; four round, black eyes present in a trapezoidal pattern; cirriform occipital tentacle present behind eyes and between base of palps (Figs. 2A, C, 3A–B). Palps extending posteriorly for about 12 setigers. Color in alcohol opaque white to light tan, with very slight patch of pigmentation on dorsal side of setiger 3, palps with irregular patches of black pigmentation (Fig. 2A).

Setiger 1 with neurosetae, without notosetae, with weakly developed notopodial lobes (Figs. 2A, B, 3C). Winged capillary notosetae of setigers 2–4, 6 and subsequent setigers arranged in three successive rows; no specialized posterior notosetae (Figs. 2H, 3C). Winged capillary neurosetae of setigers 2–4, 6 and subsequent setigers arranged in two vertical rows (Figs. 2I, 3C); six bidentate hooded hooks begin on setiger 7, not accompanied by capillaries, up to nine in series at setiger 9; hooks with near right angle between main fang and shaft, wide angle between main fang and apical tooth, with constriction on shaft (Fig. 2G).

Setiger 5 almost twice as large as setigers 4 and 6, with slightly curved row of six exposed major spines and two embedded spines, major spines alternating with pennoned companion setae exhibiting broom-like tips; with posterior ventral fascicle of six winged capillary neurosetae; anterior dorsal fascicle of 4–6 geniculate notosetae present. Major spines simple, falcate, with very shallow lateral flange (Figs. 2E–F, 3B, D).

Branchiae from setiger 7, free from notopodial postsetal lamellae, continuing to postgerior setigers; branchiae nearly meeting at middle from setigers 8–19, diminishing in length posteriorly (Figs. 2A–B, D, 3A). Lateral organs (=interramal organs, interramal ciliary organs, or lateral ciliated organs; see Radashevsky 2005; Purschke & Hausen 2007) present between notopodial and neuropodial lamellae on setigers 1-3, 6 and subsequent setigers (Fig. 3C), lateral organs largest on setiger 1.

Pygidium broad, cup-shaped with dorsal gap, small patches of pigmentation present on sides (Fig. 2D).

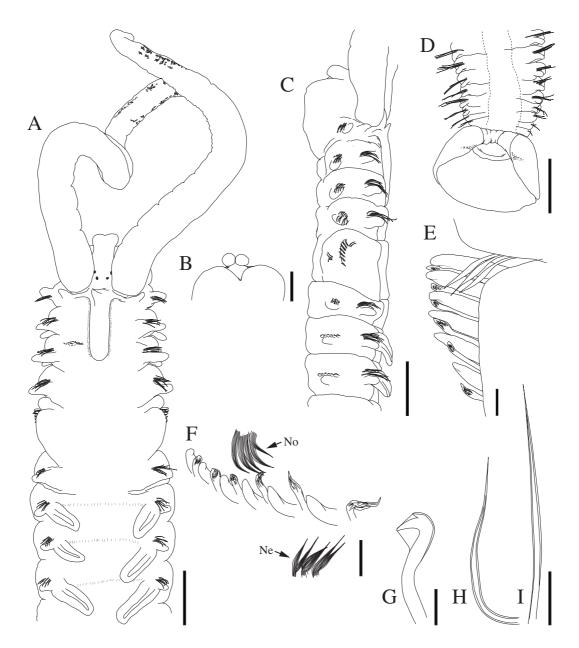


FIGURE 2. *Polydora cavitensis.* A–D, voucher specimen (USNM 1096802). A, anterior end, dorsal view; B, prostomium, ventral view; C, anterior end, lateral view; D, posterior setigers and pygidium, dorsal view; E, major spines of setiger 5, dorsal view; F, major spines of setiger 5, lateral view (No = notosetae, Ne = neurosetae); G, neuropodial hooded hook from setiger 27, lateral view; H, notoseta from posterior row, setiger 2; I, neuroseta from posterior row, setiger 2. Scale bars: A-C, $D=250 \mu m$; B, F, H, $I=25 \mu m$; E, $G=12.5 \mu m$.

No gizzard-like structure present in digestive tract. Glandular pouches not observed in preserved specimens.

Remarks. The present specimens are similar to the original description of *P. cavitensis* from among oysters in the Manila Bay, Philippines based on the bifid prostomium, presence of an occipital tentacle, and presence of superior and inferior bundles of spines on setiger 5 (Pillai 1965). *P. cavitensis* was noted by Pillai (1965) to have two transverse brown bands of pigmentation on the palps, patches of reddish-brown pigmentation on the dorsal side of each setiger, and pigment patches on each side of the pygidium. The present specimens lack distinct bands on the palps but do exhibit diffuse pigmentation along the sides of the palps and patches of pigmentation on the pygidium; no distinct patches of pigmentation were found on the dorsal side of each setiger. However, such pigmentation can be variable within polydorids. The only other potential distin-

guishing feature between Pillai's material and the present specimens is with the morphology of the major spines of setiger 5. Pillai (1965) described the spines as having a notched tip but the picture of the spines (Fig. 17D in Pillai (1965)) shows a flange-like structure, slightly more pronounced but similar to that found in the present specimens. For these reasons, the newly collected specimens are referred to *P. cavitensis*.

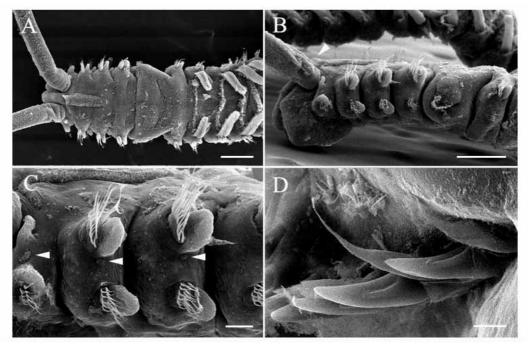


FIGURE 3. *Polydora cavitensis.* A–D, voucher specimen (USNM 1096803) SEM micrographs. A, anterior end, dorsal view; B, anterior end, lateral view (occipital tentacle indicated by arrowhead); C, setigers 1–4 (left to right), lateral view (lateral organs indicated by arrowheads); D, major spines of setiger 5, lateral view. Scale bars: $A-B=250~\mu m$; $C=50~\mu m$; $D=10~\mu m$.

Identification of this species is difficult because it is very similar to Polydora cornuta Bosc, 1802, a widely distributed species found to construct tubes in soft sediments of estuarine waters, often attaining large population sizes and acting as a pollution indicator species (Rice & Simon 1980). The species are similar in possession of a bifid prostomium, occipital tentacle, and length of caruncle. Radashevsky (2005) recently completed extensive morphological and larval studies of P. cornuta based on specimens collected worldwide (east and west coasts of North America, Mexico, Brazil, Argentina, Germany, Romania, Russia, Korea, Taiwan, and China). While the species are similar in many respects, *Polydora cavitensis* exhibits dorsal superior capillaries present on setiger 5, whereas according to Radashevsky (2005) these are invariably absent in P. cornuta. However, Radashevsky (2005) did not mention that dorsal superior capillaries were present on setiger 5 in populations of *P. cornuta* collected from Florida (see Figs. 9 and 15 in Rice & Simon 1980) although these specimens were listed among those in synonymy with P. cornuta. Additional characters that distinguish Polydora cavitensis and P. cornuta are the prostomial morphology and nature of the major spines of setiger 5. The prostomium of *Polydora cavitensis* is weakly bifid but could be confused as rounded unless specimens are viewed from the ventral side where the split nature of the prostomium is best observed (see Fig. 2B); in contrast, the prostomium of *P. cornuta* is widely bifurcated with flaring lateral sides. The spines of the two Polydora cavitensis specimens examined lacked a lateral tooth, even in the unworn spines, and exhibited only a slight lateral flange; in *P. cornuta* the spines exhibit both a large lateral tooth and subterminal flange.

In the Philippines *Polydora cavitensis* was found in Manila Bay inhabiting mud tubes constructed among masses of the green mussel *Perna viridis*. *Perna viridis* are commercially harvested mussels that have been transported to the Caribbean and Gulf of Mexico (Agard *et al.* 1992; Benson *et al.* 2001; Ingrao *et al.* 2001). While Benson *et al.* (2001) indicated *Perna viridis* was likely transported to the Caribbean and Florida in bal-

last water, it is possible that the mussels and associated fauna such as *Polydora cavitensis* have been transported to other islands in the Indo-West Pacific where they are cultured. Similarly, *Polydora cornuta* is believed to have been widely transported through transport of aquacultural products and uptake of larvae in ballast water (Carlton 1975; Gordon & Read 1991; Radashevsky & Hsieh 2000; Çinar et al. 2005). Such introductions are common among spionids (e.g., Bailey-Brock 1990, 2000; Carlton & Geller 1993; Röhner *et al.* 1996; Blake 1996; Williams 2001; Radashevsky & Olivares 2005) and can have both negative ecological and commercial impacts.

Distribution. From mud tubes between shells of the green mussel *Perna viridis* in Manila Bay, Philippines; subtidal.

Subfamily Nerininae Söderström, 1920

Genus Dispio Hartman, 1951

Dispio latilamella sp. n. (Figs. 4–5)

Material examined. Holotype. Philippines, Morong, Bataan, 14°41′N, 120°16′E, sandy beach, 1 Mar 1999, (USNM 1096794).—Paratypes. Same data as holotype (one anterior end, one posterior end, one middle section in alcohol, USNM 1096795; one anterior end on SEM stub, USNM 1096796).

Etymology. The species epithet *latilamella* (derived from the Latin adjective *latus* for broad, wide and the Latin noun *lamella* for a small plate) refers to the large, spoon-shaped postsetal notopodial lamellae on setiger

Diagnosis. Prostomium bluntly pointed anteriorly, with narrow, short caruncle extending to posterior margin of setiger 1; peristomium expanded laterally, partially enveloping prostomium and extending around base of palps. Two pairs of eyes present or eyes absent. Postsetal notopodial lamellae of setiger 1 large, spoonshaped, notopodial lamellae of setigers 1–13 with 2–8 digitiform extensions along margin, lamellae fused with base of branchiae. Notosetae of setiger 2 and succeeding setigers in three groups, including a group of capillary setae dorsal to an anterior row of stout capillaries, and a posterior row of thinner capillary setae. Neurosetae in three groups, two rows similar in morphology to notosetae, plus ventral fascicle of inferior sabre setae; unidentate neuropodial hooded hooks replacing anterior row of capillary neurosetae from setiger 19. Branchiae from setiger 1, smooth, partially fused with notopodial lamellae, distal end free. Accessory branchiae from setiger 19, initially with single digitate lobe, increasing to six digitate lobes in posterior setigers. Lateral organ between notopodial and neuropodial lamellae present from setiger 1. Pygidium reduced, with small papillae on ventral surface.

Description. All specimens incomplete; largest anterior fragment with 42 setigers, 18.3-mm long, 1.4-mm wide at setiger 10. Holotype with 37 setigers 14.5-mm long, 0.9-mm wide at setiger 10. Color in alcohol opaque off-white, no pigmentation present.

Prostomium elongate, bluntly pointed (Figs. 4A–C, 5A–C); anterior edge of peristomium with small papillae (Figs. 4B, 5A); peristomium expanded laterally, partially enveloping prostomium and extending around base of palps (Figs. 4B, 5A–C). Caruncle short, ending in middle of setiger one, rounded along posterior margin (Fig. 4D, 5C). Occipital tentacle absent. Two pairs of eyes present (may be obscured by palps and notopodial lobes of setiger 1), one pair of lateral small kidney-shaped eyes and one pair of rounded eyes medially, all eyes in nearly straight line between base of palps, or eyes absent. Palps short, extending to setiger 5; palps with single band of transverse rows of cilia on one side of ventral ciliated groove, rows of cilia approximately 44-µm long (Fig. 5A, E).

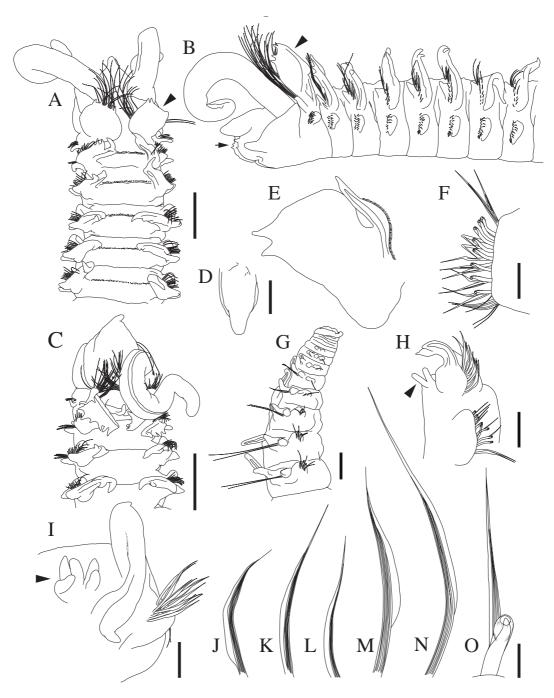


FIGURE 4. Dispio latilamella **sp. n.** A–B, D–F, H–O, holotype (USNM 1096794); C, paratype (USNM 1096796); G paratype (USNM 1096795). A, anterior end, dorsal view (arrowhead indicates large notopodial lobe of setiger 1 with digitiform extensions along margin); B, anterior end, lateral view (arrowhead indicates large notopodial lobe of setiger 1; horizontal arrow shows papillae on prostomium); C, anterior end, dorsal view; D, caruncle (rounded, posterior end toward bottom); E, setiger 1 notopodia and branchiae; F, setiger 19 neuropodium; G, posterior end and pygidium, lateral view; H, setiger 19, lateral view showing 2 lobed accessory branchiae (arrowhead); I, setiger 31, lateral view showing 5 lobed accessory branchiae (arrowhead); J, neuroseta from anterior row, setiger 2; K, neuroseta from posterior row, setiger 2; L, neuroseta from ventral row, setiger 2; M, notoseta from anterior row, setiger 2; N, notoseta from posterior row, setiger 2; O, hooded hook and neuroseta, setiger 19. Scale bars: $A-C = 500 \, \mu m$; $D-E = 125 \, \mu m$; F, $I = 100 \, \mu m$; $G = 250 \, \mu m$; $H = 200 \, \mu m$; $J-O = 25 \, \mu m$.

Setiger 1 with large, spoon-shaped postsetal notopodial lamellae, bearing 2–8 digitiform extensions along margin, fused with base of branchiae (Figs. 4A–C, E, 5B–D); setiger 1 with approximately 30–40 long, thin capillary notosetae extending beyond margins of notopodial lamellae, between palps (Figs. 4A–C, 5A–C),

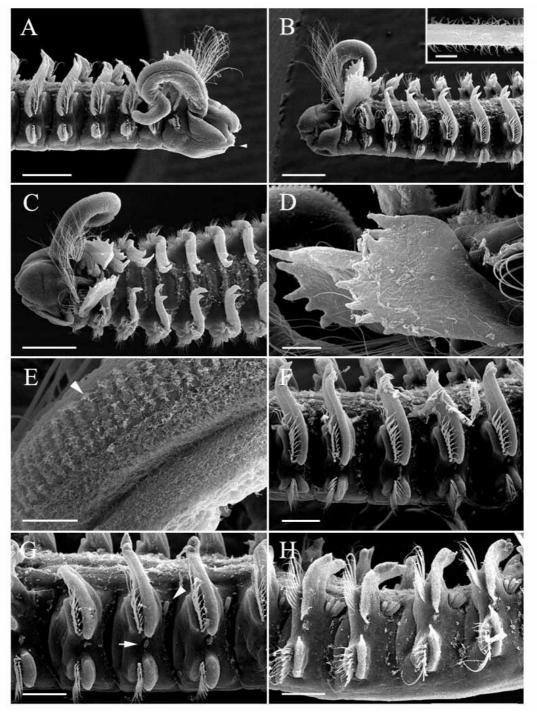


FIGURE 5. Dispio latilamella **sp. n.** A–H, paratype (USNM 1096796) SEM micrographs. A, anterior end, lateral view (arrowhead shows papillae on prostomium); B, anterior end, lateral view (opposite side of specimen in A, palp missing); inset shows spinelets on notoseta of setiger 1; C, anterior end, dorsal view; D, setiger 1 notopodia; E, proximal to middle region of palp, frontal view (arrowhead indicates a transverse row of cilia on one side of ventral ciliated groove); F, setigers 10–14 (left to right), lateral view; G, setigers 18–20 (left to right), lateral view (first accessory branchiae on setiger 19 shown by arrowhead; horizontal arrow indicates lateral organ); H, setiger 30–33 (right to left), lateral view. Scale bars: $A-C = 500 \mu m$; $D = 100 \mu m$; $E = 50 \mu m$; $E = 50 \mu m$; inset of $E = 2.5 \mu m$.

Capillaries with minute spinelets (Fig. 5B inset); small, rounded neuropodial lamellae, one row of 6–8 stout, capillary neurosetae, plus ventral fascicle of smaller sabre setae. Notopodial lamellae of setigers 2–13 may exhibit digitiform extensions along margin, lamellae of succeeding setigers smooth, fused with branchiae along most of length, basal end rounded, thinner toward distal end, with pointed tip, free from branchiae.

Notosetae of setiger 2 and succeeding setigers in three groups, a group of 2–3 thin, capillary setae dorsal to an anterior row of approximately eight stout heavily reticulated and granulated, unilimbate capillaries (Fig. 4M), and a posterior row of approximately eight shorter unilimbate capillary setae (Fig. 4N), all notosetae with minute spinelets along distal ends. Presetal notopodial lobes present from setiger 1 continuing through anterior and middle setigers, absent in posterior setigers, each presetal lobe with rounded basal portion extending into small triangular lobe. Neuropodial lamellae of setiger 2 and succeeding setigers rounded, becoming broader in posterior setigers; neurosetae in three groups, two rows similar in morphology to notosetae (Fig. 4J–K), plus ventral fascicle of 2–3 sabre setae (Fig. 4L), stouter in posterior setigers; unidentate neuropodial hooded hooks (Fig. 4O) replacing anterior row of capillary neurosetae from setiger 19 (7–9 in number), accompanied by row of capillary setae and ventral fascicle of 2–3 sabre setae (Fig. 4F). Presetal neuropodial lobes present from setiger 1 until posterior setigers, lobes rounded.

Branchiae from setiger 1, smooth, fused along length of notopodial lamellae, distal end free. Accessory branchiae from setiger 19, initially with single digitate lobe, increasing to six in posterior setigers (Figs. 4H–I, 5G–H). Lateral organs present between notopodial and neuropodial lamellae from setiger 1 (Fig. 5F–H).

Pygidium reduced, with small papillae on ventral surface (Fig. 4G).

Remarks. To date, six species of Dispio have been described [Dispio brachychaeta Blake, 1983 (from Argentina), Dispio glabrilamellata Blake & Kudenov, 1978 (from Australia), Dispio magna (Day, 1955) (from South Africa), Dispio maroroi Gibbs, 1971 (from the Solomon Islands), Dispio oculata Imajima, 1990 (from Japan), and Dispio uncinata Hartman, 1951 (from Gulf of Mexico, Massachusetts to Florida, Caribbean, California, Japan)]. Dispio latilamella sp. n., is most similar to D. maroroi from the Solomon Islands. However, D. maroroi has expanded notopodial lamellae on setigers 1 and 2, rather than only on setiger 1 as in D. latilamella. In addition, the lamellae of setigers 1 and 2 in D. maroroi are thinner with longer, digitiform extensions, and lamellae of subsequent setigers lack extensions whereas in D. latilamella the lamellae of setiger 1 are much broader (spoon-shaped) with shorter digitiform extensions along the margin and extensions are found on lamellae of up to setiger 13. There is variation in the degree of expansion of the lamellae in setiger 1 of the Philippine specimens, two specimens exhibit the broad spoon-shaped morphology with extensions while the third specimen exhibit more narrowly expanded lamellae with extensions. Similar variation in lamellar structure was documented by Foster (1971a) who showed that the number of lamellar extensions varied within Dispio uncinata; however, D. uncinata does not exhibit expanded notopodial lamellae as observed in D. latilamella and D. maroroi. Unfortunately the morphology of the pygidium in D. maroroi is not known and the presetal notopodial and neuropodial lobes and lateral organs were not noted by Gibbs (1971), although they are presumably present.

Distribution. Sandy beach in Morong of the Bataan province in the Philippines; shallow subtidal (< 5 m).

Genus Malacoceros Quatrefages, 1843

Malacoceros indicus (Fauvel, 1928) (Figs. 6–7)

Scolelepis indica Fauvel, 1928: 93, fig. 2g-m. Fauvel, 1930: 35, fig. 7g-m. Fauvel, 1953: 313–314, fig. 165g-m. Monro, 1931: 25. Berkeley and Berkeley, 1941: 21. Reish, 1961: 277.

Malacoceros indicus: Pettibone, 1963: 99. Day, 1967: 477, fig. 18.5.p-u. Blake and Kudenov, 1978: 185. Blake, 1983: 219, Blake, 1996: 105–107 [synonymy], fig. 4.4; Ben-Eliahu et al., 1984: 96. Dauer and Ewing, 1991: 395–400, fig. 1. Imajima, 1991: 6–9, figs. 2a–g, 3a–j.

Malacoceros (Malacoceros) indicus: Foster, 1971a: 50–53, figs. 93–99. Foster, 1971b: 1455–1457, figs, 1–6. *Spio punctata*: Hartman, 1961: 89–90, pl. 11, figs.1–3. Hartman, 1969: 175, figs. 1–3. Fide Blake, 1996.

Material examined. Philippines, Diniwid Beach, Boracay, 11°60′N, 121°54′E, sandy beach, 13 Apr 1999

(one posterior end in alcohol, USNM 1096797; one anterior end on SEM stub, USNM 1096798); **Boracay, White Beach**, 11°59′′N, 121°55′E, sandy beach, 14 Apr 1999 (three complete specimens in alcohol, USNM 1096799; one complete specimen on SEM stub, USNM 1096800; four anterior ends in alcohol, ZRC 2006.0221; one anterior end on SEM stub, USNM 1096801).

Description. Largest complete specimen with 184 setigers, 30.7-mm long and 1.0 mm-wide at setiger 16 (maximal width); an incomplete specimen of 140 setigers reached a length of 44.0-mm and 1.9-mm wide at setiger 16. Body broad, dorsally flattened anteriorly tapering in middle setigers, subcylindrical in cross section. Palp present on one individual, extending posteriorly for approximately 16 setigers; median groove on ventral side of palp lined by frontal cilia. Color in alcohol opaque off white, no pigmentation present.

Prostomium T-shaped with short frontal horns, rounded on distal margin (Figs. 6A, B, 7A, B); posteriorly short caruncle, extending to middle of setiger one (Figs. 6A, 7B); occipital tentacle absent; with 2–4 pairs of round eyes in two irregular clusters (Fig. 6A). Proboscis partially everted with two bulbous lobes below lateral horns (Fig. 7A).

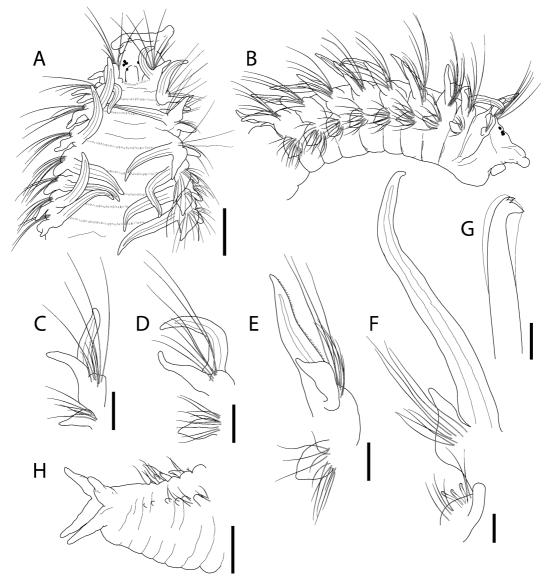


FIGURE 6. *Malacoceros indicus*. A–E, G–H, voucher specimens (USNM 1096799); F (ZRC 2006.0221). A, anterior end, dorsal view; B, anterior end, lateral view; C, setiger 1, anterior lateral view; D, setiger 2, anterior lateral view; E, setiger 19, lateral view (posterior end to left); F, setiger 79, anterior lateral view; G, hooded hook from posterior setiger; H, posterior setigers and pygidium, lateral view. Scale bars: A–B = 250 μm; C–F = 100 μm; G = 10 μm; H = 125 μm.

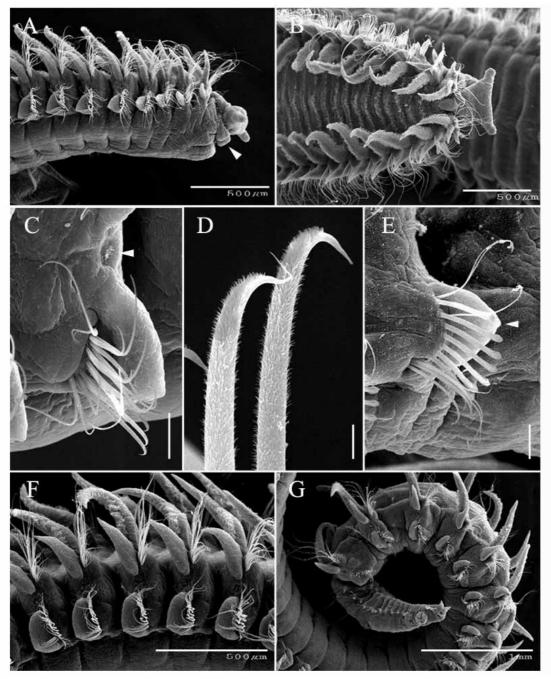


FIGURE 7. *Malacoceros indicus.* A–E, voucher specimens (USNM 1096801); F–G (USNM 1096800) SEM micrographs. A, anterior end, oblique lateral view (arrowhead indicates 2 bulbous lobes of proboscis); B, anterior end, dorsal view; C, neuropodium of setiger 10 (arrowhead indicates lateral organ); D, sabre setae of setiger 10; E, neuropodium of setiger 72 (arrowhead indicates nipple-like projection); F, setigers 20–24 (right to left), lateral view; G, posterior setigers and pygidium, lateral view. Scale bars: A–B = 500 μm; C = 5μm; D–E = 50 μm; F = 500 μm; G = 1 mm.

Branchiae from setiger 1 continuing to posteriormost setigers, branchiae elongate, slender, tapering to a blunt tip, fused basally with notopodial postsetal lamellae, branchiae slightly longer than notopodial lamellae of setiger 1 (Fig. 6C), increasing in length posteriorly (Figs. 6D–F, 7A, B, F), by setiger 10 twice as long as notopodial lamellae and slightly overlapping at midline, heavily ciliated on inner and outer margin, joined to corresponding branchiae on opposite side by band of cilia across dorsum, second band of cilia present on each setiger posterior to band joining branchiae (Fig. 7B).

Notopodial postsetal lamellae elongate, triangular, tapering to blunt tip on anterior setigers, gradually

becoming shorter in posterior setigers; notopodial presetal lamellae low, lobe surrounding base of notosetae (Fig. 7A, C, E–G). Neuropodial postsetal lamellae of anteriormost setigers small conical, base of lamellae broadening posteriorly, small, nipple-like projection at tip of lamellae (Fig. 7A, C, E). Lateral organs between notopodial and neuropodial postsetal lamellae present from setiger 1 to posteriormost setigers (Fig. 7C).

Notosetae thin, capillaries in two rows, anterior row slightly shorter than posterior row, anterior setigers with approximately 16–24 setae in each row, gradually decreasing in number in posterior setigers. Neurosetae on anterior setigers in two rows, similar in morphology to notosetae but shorter in length, plus ventral fascicle of 3–4 sabre setae (Fig. 7C–D); 1–2 neuropodial hooded hooks from setigers 28–62, with up to seven hooks in more posterior setigers, accompanied by dorsal fascicle of 3–4 fine capillary setae and ventral fascicle of sabre setae (Fig. 7E); hooded hooks with three small teeth above main fang (Fig. 6G). Notosetae and neurosetae (including sabre setae) with minute spinelets (see Fig. 7D).

Pygidium with two dorsal cirri and two slightly longer ventral cirri, cirri conical, tapering to blunt rounded tip; anus terminal (Figs. 6H, 7G).

Remarks. The genus *Malacoceros* is composed of 8 recognized species, including one recently described from hydrothermal vent chimney walls (Hourdez et al. 2006). Malacoceros indicus is a widely distributed species and the Philippine specimens closely match previous descriptions. However, the neuropodial hooded hooks of the Philippine specimens exhibited three secondary teeth while those examined by Blake (1996) from California had two secondary teeth and those examined by Imajima (1991) from Japan had four secondary teeth. As indicated by Foster (1971a, b) and Blake (1996), the morphology of the hooded hooks is variable within this species. The Philippine specimens do not exhibit large rounded lobes in an interparapodial position as found in specimens from California; however, these structures may represent interparapodial pouches that differ in size depending on maturity of the specimens (Blake 1996). This is the first time lateral organs have been found between notopodial and neuropodial postsetal lamellae of M. indicus, but this is not surprising since no previous taxonomic investigations utilized SEM for examination of this species. Recently, Purschke & Hausen (2007) investigated the ultrastructure of lateral organs in members of seven families of polychaetes including the Spionidae and Malacoceros fuliginosus (Claparède, 1886). Dauer & Ewing (1991) studied the palp ciliation patterns of M. indicus with SEM from specimens collected in Australia and found that they exhibited a single group of functional frontal cilia and based on behavioral observations they showed the worms were indiscriminate surface deposit-feeders. *Malacoceros indicus* apparently shed their palps readily when disturbed (i.e., they are deciduous) since all Philippine specimens except one were lacking these structures. Based on light microscopic examination, this specimen exhibited a single group of frontal cilia as found for specimens from Australia; in addition, one worm was also found to possess sand grains in the gut [mean size = $299.6 \pm 75.4 \,\mu m$ (n=12)] within the size range of those found in Australian specimens (Dauer & Ewing 1991).

Distribution. Sandy beaches in Boracay of the Aklan province in the Philippines; shallow subtidal (< 5 m); Caribbean; Chile; India; New Caledonia; southwest Africa; Australia (Queensland); Japan; USA (southern California, Massachusetts to Georgia).

Genus Scolelepis Blainville, 1828

Scolelepis alisonae sp. n. (Figs. 8–10)

Material examined. Holotype Philippines, Morong, Bataan, sandy beach, 28 Feb 1999 (USNM 1096804).—Paratypes, same data as holotype (16 anterior ends, two posterior ends, one middle piece in alcohol, USNM 1096805; one complete specimen on SEM stub, four anterior ends on SEM stubs, one set of palps

on SEM stub, USNM 1096806); same location as holotype, 1 Mar 1999 (one anterior end, USNM 1096807); same location as holotype, 25 April 1999 (one complete specimen, eight anterior ends, ZRC 2006.0222).

Etymology. The species is named in honor of my wife, Dr. Alison S. Carson, for her help in collection of these specimens (sometimes under quite adverse conditions). Her cultural psychology studies in the Philippines (supported by the National Science Foundation and a Fulbright Scholarship) allowed for travel to make these collections.

Diagnosis. A species of *Scolelepis* with notosetae on setiger 1, notopodial hooded hooks and lacking an occipital tentacle. Palps short, palp sheaths absent, palps with two weakly separated transverse rows of cilia. Prostomium conical, with two pairs of eyes. Caruncle extending to middle of setiger 1, nuchal cilia in U-shaped pattern on sides of caruncle. Postsetal notopodial lamellae fused with branchiae from setiger 2, lamellae composed of up to nine conical lobes by setiger 5, number of lobes gradually decreasing posteriorly. Bidentate notopodial hooded hooks from setiger 68–99, with up to three per fascicle. Postsetal neuropodial lamellae with up to three lobes in anterior setigers. Bidentate neuropodial hooded hooks from setiger 25–33, with up to 11 hooks in middle and posterior fascicles. Pygidium broadly rounded, with short conical papillae surrounding anus.

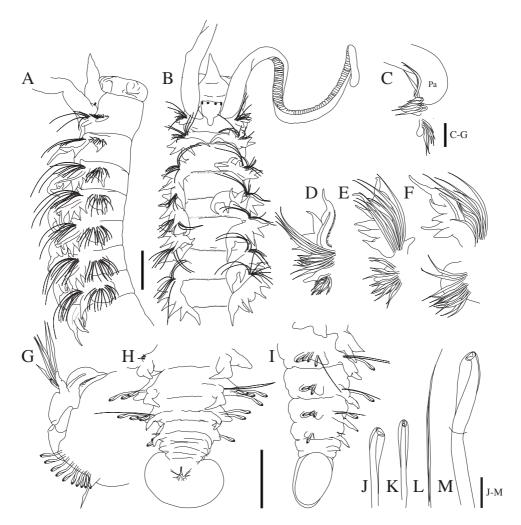


FIGURE 8. Scolelepis alisonae **sp. n.** A–B, H–I, holotype (USNM 1096804); C–G, J–M, paratypes (USNM 1096805). A, anterior end, lateral view; B, anterior end, dorsal view; C, setiger 1, lateral view (Pa indicates base of palp); D, setiger 2, anterior lateral view; E, setiger 4, anterior lateral view; F, setiger 10, anterior lateral view; G, setiger 89, anterior lateral view; H, posterior setigers and pygidium, dorsal view; I, posterior setigers and pygidium, lateral view; J, notopodial hooded hook from setiger 89, lateral view; K, notopodial hooded hook from setiger 89, frontal view; L, notoseta from setiger 89; M, neuropodial hooded hook from setiger 89, lateral view. Scale bars: A–B, H–I = 250 μ m; C–G = 100 μ m; J–M = 25 μ m.

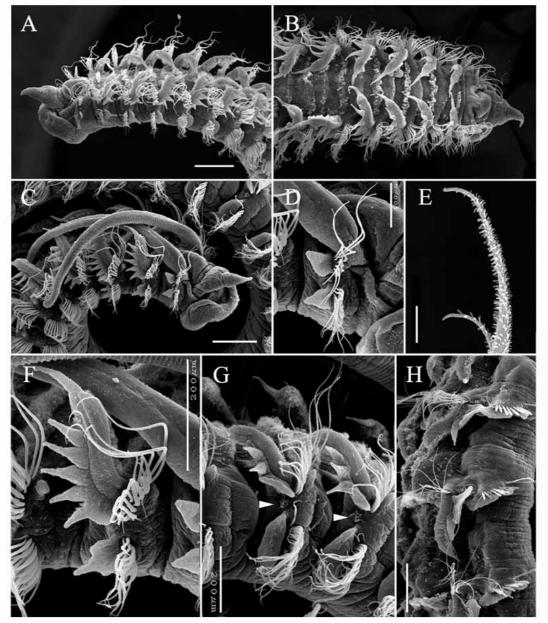


FIGURE 9. *Scolelepis alisonae* **sp. n.** A–H, paratypes (USNM 1096806) SEM micrographs. A, anterior end, oblique lateral view (palps missing); B, anterior end, dorsal view; C, anterior end, lateral view; D, setiger 1 and base of palp, lateral view; E, tips of neurosetae from setiger 3; F, setiger 2, lateral view; G, setiger 19 & 20 (left to right), lateral view (arrowheads indicate lateral organs); H, setigers 49–51 (top to bottom), lateral view. Scale bars: $A-C = 250 \mu m$; $D = 100 \mu m$; $E-H = 200 \mu m$.

Description. Largest specimen of 136 setigers, 47.6-mm long and 0.9-mm wide by setiger 8; holotype of 125 setigers, 37.5-mm long, 0.52-mm wide by setiger 8. Body widest anteriorly, gradually tapering to posterior end; body nearly rectangular in cross section. Color in alcohol opaque white, no pigmentation present.

Prostomium conical, extending anteriorly to long, tapering point, posteriorly extending to short caruncle with rounded posterior margin, ending in middle of setiger 1, caruncle not free on posterior margin (Figs. 8A–B, 9A–C). Two pairs of eyes, one pair of kidney-shaped eyes laterally, one pair of round eyes medially, all eyes in nearly straight row between base of palps (Fig. 8B); occipital tentacle absent. Palps short, extending to setigers 6–10 (Figs. 8B, 9C), with two weakly separated transverse rows of cilia along the ventral surface, long rows of cilia approximately 45 μ m long, short rows approximately 24 μ m long (short rows on medial side), long and short rows in approximately 1:1 ratio, rows of mucus secreting cells represented by tubular

necks present proximal to transverse ciliary rows; ciliary rows extending to distal ends of palps, median ciliated groove lacking (Figs. 10A–B, 18C). Palpal sheaths absent. Nuchal cilia in U-shaped pattern on both sides of caruncle, posterior to base of palps (Fig. 9B).

Setiger 1 well developed with bluntly pointed, triangular notopodial and neuropodial postsetal lamellae, notosetae and neurosetae present (Figs. 8C, 9D). Postsetal notopodial lamellae fused with branchiae from setiger 2 (Figs. 8D, 9F), lamella composed of 2–6 conical lobes, number of lobes increasing to 5–9 on lamellae by setiger 5 (Figs. 8E, 9A, C), then gradually decreasing to two conical lobes distally and rounded basal portion by setigers 20–30 (Figs. 8F, 9G), posteriormost setigers with one conical lobe distally, with rounded basal portion free from branchiae (Figs. 8G, 9H, 10C). Neuropodial postsetal lamellae of setiger 1 rounded or conical (Figs. 8C, 9D), lamellae of setiger 2 with rounded base extending into short, bluntly pointed lobe (Figs. 8D, 9F), lamellae of setigers 3–5 sometimes with 2–3 bluntly pointed lobes (Fig. 9C), lamellae from setigers 6-20 with broadly rounded lobe (Fig. 8F, 9G), developing notch dividing lamellae by setiger 30, on posterior setigers ventral lobe small, triangular, dorsal lobe elongate with dorsal end free and pointed, ventral end rounded (Figs. 8I, 9H), by setiger 65 ventral lobe reduced, dorsal lobe digitate (Fig. 10C). Lateral organs between notopodial and neuropodial postsetal lamellae present from setiger 1 to posterior setigers (Fig. 9G).

Notosetae of setiger 1 and subsequent setigers arranged in two vertical rows of bilimbate capillaries, the dorsal notosetae of these rows longer than ventral ones, often loosely coiled along their distal ends (Figs. 8L, 9A, C, F), one notopodial hooded hook beginning on setiger 68–99 (Figs. 8J, K, 10C), with up to three notopodial hooded hooks in posterior most setigers; notopodial hooded hooks with acute main fang and single accessory tooth. Neurosetae of setiger 1 and subsequent setigers arranged in two vertical rows of bilimbate capillaries (Fig. 9F–G), 1–3 neuropodial hooded hooks from setiger 25–33, up to 5–11 neuropodial hooded hooks in middle to posterior setigers (Fig. 8G); neuropodial hooded hooks with acute main fang and single accessory tooth (Fig. 8M). Notosetae and neurosetae with minute spinelets (Fig. 9E).

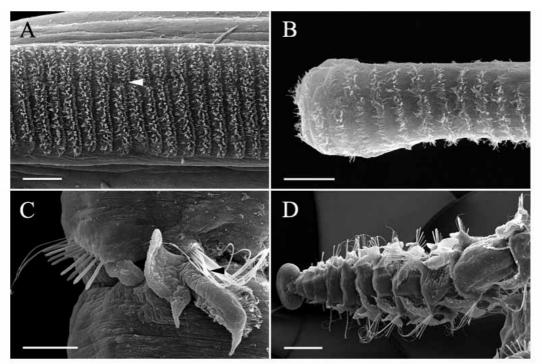


FIGURE 10. *Scolelepis alisonae* **sp. n.** A–D, paratypes (USNM 1096806) SEM micrographs. A, proximal region of palp, frontal view (arrowhead indicates faint division in transverse rows of cilia; short rows top, long rows bottom; note that at point of arrowhead there are two long rows below and only one short row above); B, distal tip of palp, frontal view; C, setiger 68, oblique dorsolateral view; D, posterior setigers and pygidium, dorsal view. Scale bars: $A-B = 25 \mu m$; $C = 100 \mu m$; $D = 250 \mu m$.

Branchiae present from setiger 2 to end of body, fused with postsetal notopodial lamellae but with tips free in anterior setigers (Fig. 9F), separated from notopodial lamellae in posterior setigers, with band of cilia along inner edge and joined to corresponding branchiae on opposite side by a single band of cilia across dorsum (Fig. 9B).

Pygidium broadly rounded, with short conical papillae surrounding dorsal anal opening (Figs. 8H–I, 10D).

Remarks. The genus *Scolelepis* was reviewed by Maciolek (1987) and more recently by Hutchings *et al.* (1998), both studies provided summary tables for the known members of the genus. Since then, nine species of *Scolelepis*, including those treated in this paper, have been described, and there are now 58–59 species within this genus (Table 1). Confusion exists in the total number of species because MacCord & Amaral (2005) resurrected *Scolelepis goodbodyi* (Jones, 1962), a species that was previously considered a synonym of *S. squamata* (Müller, 1806) (Pettibone 1963; Foster 1971a; Light 1978; Maciolek 1987). However, MacCord & Amaral (2005) provided no taxonomic evidence to support the conclusion that these species are distinct (their identification was based on the authority of Radashevsky; pg. 829).

Scolelepis alisonae sp. n. belongs to a group of six species including S. blakei Hartmann-Schröder, 1980; S. carunculata Blake & Kudenov, 1978; S. chilensis (Hartmann-Schröder, 1962); S. hutchingsae Dauer, 1985; and S. kudenovi Hartmann-Schröder, 1981, that possess notosetae on setiger 1, notopodial hooded hooks, bidentate neuropodial hooded hooks and that lack an occipital tentacle. Scolelepis alisonae sp. n. is distinguished from all these species in the possession of notopodial postsetal lamellae with up to nine lobes in anterior setigers and neuropodial postsetal lamellae with up to 3 lobes in anterior setigers. Scolelepis alisonae sp. n. and S. laciniata Eibye-Jacobsen, 1997 are similar in the possession of notopodial postsetal lamellae with conical lobes; however, Scolelepis alisonae sp. n. is easily distinguished by the presence of notosetae on setiger 1 and notopodial hooded hooks (both absent in S. laciniata).

The palp morphology of *S. alisonae* **sp. n.**, is uniquely different from previously described species in exhibiting weakly separated long and short transverse rows of cilia in a 1:1 ratio. See Discussion for a comparative analysis of the palp morphology in members of the genus *Scolelepis*.

Distribution. Sandy beach in Morong of the Bataan province in the Philippines; shallow subtidal (< 5 m).

Scolelepis hutchingsae **Dauer, 1985** (Figs. 11–13)

Scolelepis (Scolelepis) hutchingsae Dauer, 1985: 678-681, Fig. 1.

Material examined. Diniwid Beach, Boracay, 11°60′N, 121°54′E, sandy beach, 13 Apr 1999 (four complete specimens, four anterior ends (two with regenerating posterior ends), three posterior ends in alcohol, USNM 1096811).—**Philippines, Boracay, White Beach**, 11°59′N, 121°55′E, sandy beach, 14 Apr 1999 (three complete specimens, three anterior ends, four posterior ends in alcohol, ZRC 2006.0224; one complete specimen on two SEM stubs, one pair of palps on SEM stub, USNM 1096812).

Description. Largest specimen of 73 setigers, 16.3-mm long, 0.8-mm wide at setiger 16. Body widest anteriorly, gradually tapering to posterior end; body nearly rectangular in cross section. Color in alcohol opaque white, no pigmentation present.

Prostomium conical, extending anteriorly to sharp point, posteriorly continuing as short, pointed caruncle, to middle of setiger 1; peristomial wings surrounding base of palps (Figs. 11A–B, 12A–E). Eyes and occipital tentacle absent. Palps extending to about setiger 15, with two distinctly separated transverse rows of cilia along ventral surfaces, with long and short rows in approximately 2:1 ratio, longer rows of cilia approximately 35- μ m long, shorter rows approximately 10- μ m long and elevated on 5–10 μ m lobes (oriented medially)

TABLE 1. Taxonomic characters of species in the genus Scolelepis described since Hutchings et al. (1998).

Species	Author	Occipita	Occipital Neuropodial	Neuropodial	Notopodia	al Notoseta	Notopodial Notosetae Branchial fusion	Notes
		tentacle hooks,	hooks,	hooks, # of	hooks	setiger 1		
			begin on setiger	teeth				
S. alisonae sp. n.	present study	Absent	29-32	2	Present	Present	Present Partially fused (tips free)	notopodial postsetal lamellae
								with up to 9 lobes by setiger 5;
								neuropodial postsetal lamellae
								with up to 3 lobes by setiger 5
S. anakenae	Rozbaczylo & Castilla 1988	Absent	35-37	2	Absent	Present	Present Partially fused (tips free)	Not cited in Hutchings et al. 1998
S. dicha	Hutchings, Frouin & Hily, 1998 Absent	8 Absent	26-32	2	Absent	Absent	Fused basally	
S. laciniata	Eibye-Jacobsen, 1997	Absent	24-26	2-3	Absent	Absent	Partially fused (tips free)	Not cited in Hutchings et al.
								1998;
								notopodial postsetal lamellae with up to 5 lobes by setiger 18
S. magnicornuta sp. n. present study	1. present study	Present	25-30	2	Present	Present	Partially fused (tips free	
							anteriorly, at base posteriorly)	
S. magnus	Ozolin'sh, 1990	Present	34	2	Present	Present	Completely fused (anterior)	
S. marionis	Branch, 1998	Absent	42	2	Absent	Present	Partially fused (tips free)	
S. villosivaina sp. n.	present study	Absent	25-29	1-2	Present	Present	Partially fused (tips free)	
S. vazaha	Eibye-Jacobsen & Soares, 2000 Absent	0 Absent	25-31	3	Present	Present	Partially fused (at base)	large notopodial spines on
								setiger 4

(Figs. 12G–H, 18D); rows of mucus secreting cells (represented by tubular necks) present proximal to transverse ciliary rows, median ciliated groove absent; base of palps with ciliary patches (Fig. 12E–F). Nuchal cilia in U-shaped pattern on both sides of caruncle, posterior to the base of palps (Fig. 12E).

Setiger 1 well developed with rounded notopodial and neuropodial postsetal lamellae, notosetae and neurosetae present. Postsetal neuropodial lamellae of setigers 1–18 rounded, becoming broadest by setiger 10 (Figs. 12A–D; 13A–B), by setiger 20 lamellae forming low, broad lobe (Figs. 11C, 13B), lamellae of posterior setigers broadly triangular on dorsal end, rounded on ventral end with neurosetae (Fig. 13D–E). Lateral organs present from setiger 1 between notopodial and neuropodial postsetal lamellae continuing to posterior setigers (Fig. 13A, B).

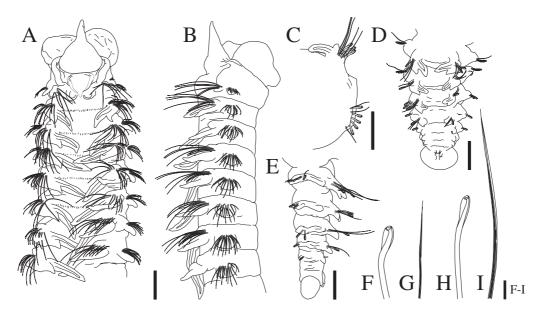


FIGURE 11. *Scolelepis hutchingsae* A–I, voucher specimens (USNM 1096811). A, anterior end, dorsal view (palps missing); B, anterior end, lateral view; C, setiger 48, anterior lateral view; D, posterior setigers and pygidium, dorsal view; E, posterior setigers and pygidium, lateral view; F, neuropodial hooded hook from setiger 48, lateral view; G, neuroseta from setiger 48; H, notopodial hooded hook from setiger 48, lateral view; I, notoseta from setiger 48. Scale bars: A-B, $D-E=200 \, \mu m$; $C=125 \, \mu m$; $F-I=25 \, \mu m$.

Notosetae of setiger 1 and subsequent setigers arranged in two vertical rows of limbate capillaries (Fig. 11I), dorsalmost notosetae of these rows longer than ventral ones; 1–3 notopodial hooded hooks from setiger 18–20, with up to four hooks per fascicle in posterior setigers; notopodial hooded hooks bidentate with acute main fang and single accessory tooth (Fig. 11H). Neurosetae of setiger 1 and subsequent setigers in two vertical rows of limbate capillaries (Fig. 11G), 1–3 neuropodial hooded hooks from setiger 17–20, typically with 5–8 hooks in middle to posterior setigers; neuropodial hooded hooks bidentate with acute main fang and single accessory tooth, neuropodial hooded hooks with longer shafts than notopodial hooded hooks (Figs. 11F, 13C).

Branchiae from setiger 2, fused to postsetal notopodial lamellae for about half of branchial length in anterior setigers, fusion reduced to about one-third of branchial length in posterior setigers; with band of cilia along inner edge of each branchia, joined to corresponding branchiae on opposite side by two dorsal ciliary bands, anterior band broader than posterior band (Fig. 12B).

Pygidium broadly rounded, with short conical papillae surrounding dorsal anal opening (Figs. 11D–E, 13D–E).

Remarks. The Philippine specimens agree with the original description of *Scolelepis hutchingsae* from Lizard Island, Australia by Dauer (1985) including the palp morphology (Dauer 1987, 1994). As indicated previously for *S. alisonae* **sp. n.**, *S. hutchingsae* belongs to a group of five species that possess notosetae on

setiger 1, notopodial hooded hooks, bidentate neuropodial hooded hooks, and lack an occipital tentacle. *Scolelepis hutchingsae* is unique in the genus in possessing notopodial hooded hooks that begin in the same setiger or one setiger posterior to the beginning of the neuropodial hooded hooks. In addition, *S. hutchingsae* has patches of cilia at the base of the palps on the dorsal side near the caruncle and nuchal organ, although these patches of cilia were not noted in specimens from Australia (Dauer 1985).

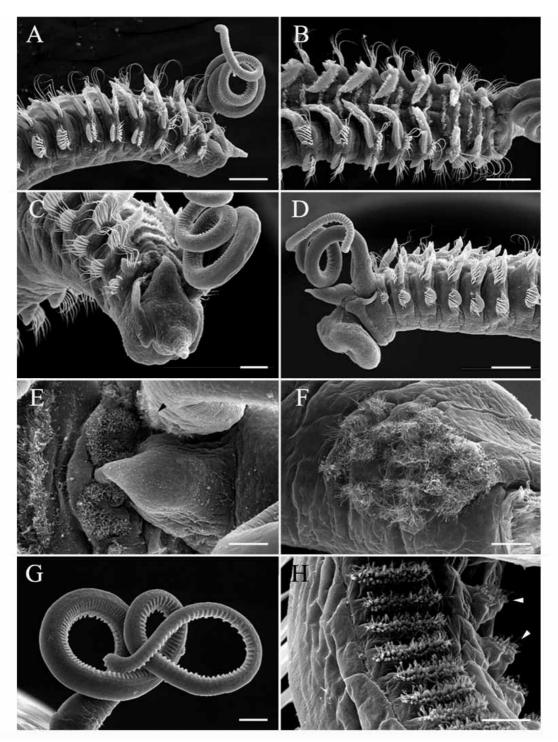


FIGURE 12. Scolelepis hutchingsae A–G, voucher specimens (USNM 1096812) SEM micrographs. A, anterior end, lateral view (palp missing on right side); B, anterior end, dorsal view; C, anterior end, oblique en-face view; D, anterior end, lateral view; E, caruncle and nuchal organ (base of palp at top, arrowhead indicates patches of cilia on palp base shown in F); F, base of palp with patches of cilia; G, lateral view of palp; H, middle region of palp, oblique frontal view (arrowheads show two short ciliary rows on elevated lobes). Scale bars: A–B, D = 250 μ m; C = 125 μ m; E = 50 μ m; F = 25 μ m; G = 100 μ m; H = 20 μ m.

Two of the specimens of *S. hutchingsae* exhibited posterior ends that were regenerating. Two incomplete specimens (posterior end fragments) collected in April had eggs within the body. One specimen had five bivalve larvae in the digestive tract, each approximately 480-µm long.

Distribution. Sandy beach in Boracay of the Aklan province in the Philippines; shallow subtidal (< 5 m); Australia (Lizard Island, GBR).

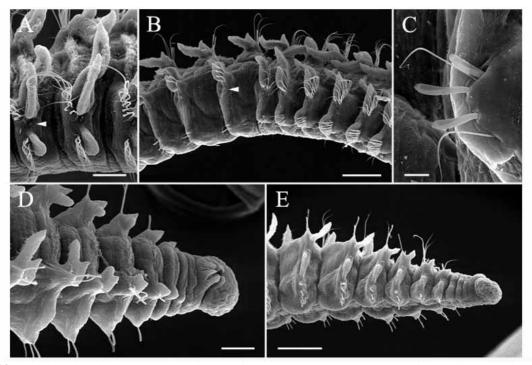


FIGURE 13. Scolelepis hutchingsae A–E, voucher specimens (USNM 1096812) SEM micrographs. A, setigers 2–4 (left to right), lateral view (arrowhead indicates lateral organ); B, setigers 13–21 (right to left), lateral view (arrowhead indicates lateral organ); C, setiger 20 neuropodial hooded hooks; D, posterior setigers and pygidium, dorsal view; E, posterior setigers and pygidium, lateral view. Scale bars: A, D = 100 μ m; B = 250 μ m; C = 25 μ m; E = 250 μ m.

Scolelepis magnicornuta sp. n. (Figs. 14–15)

Material examined. Holotype. Philippines, Diniwid Beach, Boracay, 11°60′N, 121°54′E, sandy beach, 13 Apr 1999 (USNM 1096808).—Paratypes, same data as holotype (three complete specimens, two anterior ends, two posterior ends in alcohol, USNM 1096809; two anterior ends on SEM stubs, one middle section on SEM stub, one pair of palps on SEM stub, USNM 1096810); same location as holotype, 14 Apr 1999 (one anterior end in alcohol, ZRC 2006.0223).

Etymology. The species epithet *magnicornuta* (derived from the Latin adjective *magni* for great, large and Latin adjective *cornutus* for horned) refers to the large, conical occipital tentacle found in this species.

Diagnosis. A species of *Scolelepis* exhibiting notosetae on setiger 1, notopodial hooded hooks and large occipital tentacle. Palps long, with small, smooth basal sheath, palps with two weakly separated transverse rows of cilia. Prostomium conical, with two pairs of eyes. Caruncle ending bluntly at middle of setiger 1, nuchal cilia in semi-circular pattern around base of palps, cilia extending onto sides of large, conical occipital tentacle. Postsetal notopodial lamellae nearly completely fused with branchiae from setiger 2 to middle setigers, lamellae elongate, rounded, distal end pointed and free from branchiae, lamellae and branchiae separated posteriorly. Bidentate notopodial hooded hooks from setiger 38–55, up to seven in posterior setigers. Bidentate neuropodial hooded hooks from setiger 25–30, up to 13 in middle to posterior setigers. Pygidium small, rounded, with dorsal anal open.

Description. Holotype of 82 setigers, largest complete specimen, 42.1-mm long, 1.9-mm wide by setiger 20; setigers 24–72 with eggs. Body widest anteriorly, gradually tapering to posterior end; body nearly rectangular in cross section. Color in alcohol opaque white, no pigmentation present.

Prostomium conical, extending anteriorly to sharp point, continuing posteriorly as short caruncle, ending bluntly at middle of setiger 1 along a low, indistinct margin; reduced peristomial wings surrounding base of palps (Figs. 14A, B, 15A–C). Two pairs of eyes obscured, deeply embedded, in nearly straight row between bases of palps; large, conical occipital tentacle present (Fig. 15B–D). Palps extending to setiger 15–20, with two weakly separated transverse rows of cilia along ventral surface, long rows of cilia approximately 41-µm long, short rows approximately 26-µm long (short rows on medial side), with long rows and short rows in approximately 1:1 ratio, rows of mucus secreting cells (represented by tubular necks) proximal to transverse ciliary rows, rows extending to distal ends of palps, median ciliated groove lacking (Figs. 15E, 18C). Palps with small, smooth basal sheath. Nuchal cilia in semi-circular pattern around base of palps, cilia extending onto lateral sides of base of occipital tentacle (Fig. 15C–D).

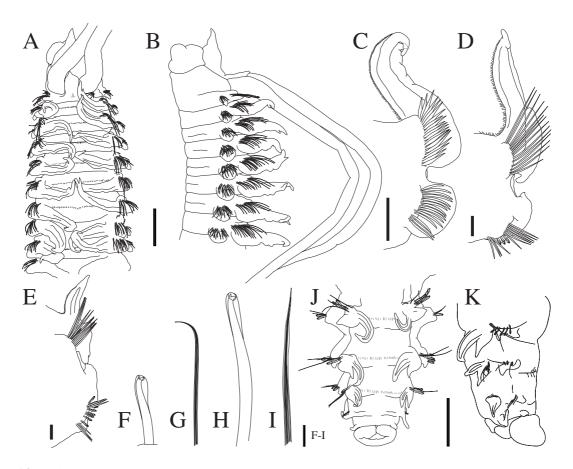


FIGURE 14. *Scolelepis magnicornuta* **sp. n.** A–B, J–K, holotype (USNM 1096808); C–I, paratypes (USNM 1096809). A, anterior end, dorsal view; B, anterior end, lateral view (palps partially drawn); C, setiger 10, anterior lateral view; D, setiger 30, anterior lateral view; E, setiger 54, anterior lateral view; F, neuropodial hooded hook from posterior setiger, lateral view; G, neuroseta from posterior setiger; H, notopodial hooded hook from posterior setiger, lateral view; I, notoseta from posterior setiger; J, posterior setigers and pygidium, dorsal view; K, posterior setigers and pygidium, lateral view. Scale bars: A–B, J, K = $500 \mu m$; C–D = $250 \mu m$; E = $200 \mu m$; F–I = $25 \mu m$.

Setiger 1 well developed with rounded notopodial and neuropodial postsetal lamellae, notosetae and neurosetae present; patch of cilia present dorsal to the notopodial lamellae. Postsetal notopodial lamellae nearly completely fused with branchiae from setiger 2 (Fig. 15A–B), lamellae elongate, rounded, distal end pointed and free from branchiae, fused with branchiae along about 90% of length in anterior setigers, degree of fusion

decreasing in posterior setigers (Figs. 14C–E, 15F–G). Postsetal neuropodial lamellae of setiger 1 with triangular lobe (Figs. 14B, 15A–B), lamellae of setigers 2–18 with rounded lobe (Figs. 14C, 15A–B, F), developing notch dividing lamellae by setigers 20-25, with broad dorsal lobe and small ventral lobe, dorsal lobe with pointed dorsal end and rounded ventral end (Figs. 14D, 15G), in posterior setigers dorsal lobe becomes broader and ventral lobe is reduced (Fig. 14E). Lateral organs between notopodial and neuropodial postsetal lamellae present from setiger 1 to posterior setigers (Fig. 15G).

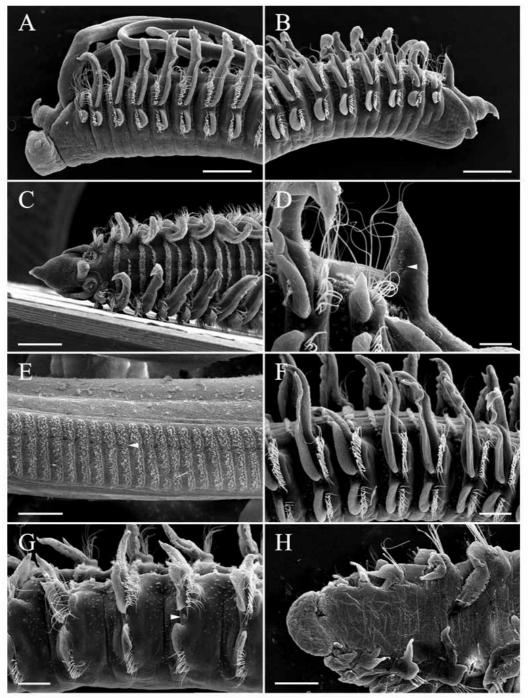


FIGURE 15. *Scolelepis magnicornuta* **sp. n.** A–H, paratypes (USNM 1096810) SEM micrographs. A, anterior end, lateral view; B, anterior end, lateral view (palps missing); C, anterior end, dorsal view; D, occipital tentacle (arrowhead shows cilia on side of tentacle); E, middle region of palp, frontal view (arrowhead indicates faint division in transverse rows of cilia; short rows top, long rows bottom); F, setigers 10–15 (right to left), lateral view; G, setigers 30–33 (right to left), lateral view (arrowhead indicates lateral organ); H, pygidium, dorsal view. Scale bars: $A-C = 500 \, \mu m$; $D = 100 \, \mu m$; $E = 50 \, \mu m$; E =

Notosetae of setiger 1 and subsequent setigers in two vertical rows of limbate capillaries (Fig. 14I); dorsal notosetae of these rows longer than those below, 1–2 notopodial hooded hooks from setiger 38–55, with up to seven notopodial hooded hooks in posterior setigers; notopodial hooded hooks bidentate with acute main fang and single accessory tooth (Fig. 14H). Neurosetae of setiger 1 and subsequent setigers in two vertical rows of limbate capillaries (Fig. 14G), 1–6 neuropodial hooded hooks from setiger 25–30, with up to 13 neuropodial hooded hooks in middle to posterior setigers; hooks bidentate with acute main fang and single accessory tooth (Fig. 14F).

Branchiae from setiger 2 to end of body, fused with postsetal notopodial lamellae but with tips free in anterior setigers (Fig. 15A–B, F–G), separated from notopodial lamellae in posterior setigers, with band of cilia along inner edge and joined to corresponding branchiae on opposite side by two bands of cilia across dorsum, anterior band broader than posterior band (Fig. 15C).

Pygidium small, rounded, with dorsal anal opening (Figs. 14J, K, 15H).

Remarks. Scolelepis magnicornuta sp. n., belongs to a group of nine species including S. antipoda (Augener, 1926); S. foliosa (Auduoin & Milne-Edwards, 1833); S. lingulata Imajima, 1992; S. magnus Ozolin'sh, 1990; S. occidentalis Hartman, 1961; S. oligobranchia Khlebovitsch, 1959; S. quadridentata Maciolek, 1987; and S. sagittaria Imajima, 1992 that possess an occipital tentacle, notosetae on setiger 1, and notopodial hooded hooks. Scolelepis magnicornuta sp. n. is unique among these species in having a large occipital tentacle with cilia extending along the sides. Among the species indicated above, S. magnicornuta sp. n. most closely resembles S. antipoda, S. lingulata, S. occidentalis, and S. sagittaria in having the tips of the notopodial lamellae free from the branchiae, whereas other species in this group exhibit complete fusion of the notopodial lamellae and branchiae in the anterior setigers. Scolelepis magnicornuta sp. n. is distinguished from S. antipoda based on the body size and initiation of neuropodial hooded hooks. S. antipoda is a large species with up to 194 setigers and with neuropodial hooded hooks from setiger 47–50 whereas S. magnicornuta sp. n. has up to 82 setigers and neuropodial hooded hooks from setiger 25–30. Scolelepis lingulata exhibits obliquely protruding neuropodial interramal lobes in posterior setigers for which it gets its name; such structures are absent in S. magnicornuta sp. n.. Scolelepis occidentalis has unidentate or bidentate notopodial hooded hooks, and a short occipital tentacle, whereas S. magnicornuta sp. n. has only bidentate notopodial hooded hooks and a large occipital tentacle. Finally, S. magnicornuta sp. n. is distinguished from S. sagittaria based on the form and the setiger on which the neuropodial hooded hooks first appear; the hooks are tridentate and begin on setiger 52–58 in S. sagittaria, whereas in S. magnicornuta sp. n. the neuropodial hooded hooks are bidentate and begin on setiger 25-30. As found in S. alisonae sp. n., the palps of S. magnicornuta sp. n. exhibit two weakly separated long and short transverse rows of cilia in approximately 1:1 ratio (see Discussion).

Two specimens of *S. magnicornuta* **sp. n.** collected in April had developing eggs within the body from setigers 24–72.

Distribution. Sandy beach in Boracay of the Aklan province in the Philippines; shallow subtidal (< 5 m).

Scolelepis villosivaina sp. n. (Figs. 16–17)

Material examined. Holotype. Diniwid Beach, Boracay, 11°60′N, 121°54′E, sandy beach, 13 Apr 1999 (USNM 1096813).—Paratypes, same data as for holotype (two anterior ends in alcohol, USNM 1096814; two anterior ends in alcohol, ZRC 2006.0225; two anterior ends and one pair of palps on SEM stubs, USNM 1096815).

Etymology. The species epithet *villosivaina* (derived from Latin adjective *villosus* for hairy and Spanish noun *vaina* for sheath or scabbard) refers to the presence of cilia at the base of the palp sheaths.

Diagnosis. A species of *Scolelepis* with notosetae on setiger 1, notopodial hooded hooks and lacking an occipital tentacle. Palps long, with basal palp sheath present, patches of cilia near insertion of palp, each palp with two distinctly separated transverse rows of cilia. Prostomium conical, with 2–4 eyes or eyes lacking. Caruncle extending to posterior end of setiger 1, with nuchal cilia in U-shaped pattern on both sides of caruncle, posterior to base of palps. Postsetal notopodial lamellae nearly completely fused with branchiae from setiger 2, lamellae elongate, rounded, distal end pointed, free from branchiae. Bidentate notopodial hooded hooks from setiger 38, up to two in posterior setigers. Uni- or bidentate neuropodial hooded hooks from setiger 25–29, up to six in middle to posterior setigers. Pygidium small, rounded, with dorsal anus.

Description. Holotype of 56 setigers, largest complete specimen, 20.0-mm long, 1.1-mm wide at setiger 10, setigers 1–38 full sized and posterior setigers 39–56 regenerating including pygidium. Body widest anteriorly; body approximately rectangular in cross section. Color in alcohol opaque white, no pigmentation present.

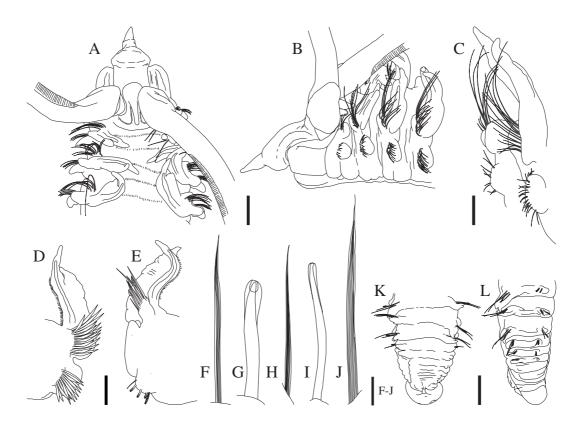


FIGURE 16. Scolelepis villosivaina **sp. n.** A–B, I–L, holotype (USNM 1096813); C, D–H, paratypes (ZRC 2006.0225). A, anterior end, dorsal view; B, anterior end, lateral view (palps partially drawn); C, setigers 1 and 2, lateral view (left to right); D, setiger 12, anterior lateral view; E, setiger 30, anterior lateral view; F, neuroseta from setiger 30; G, neuropodial hooded hook from setiger 30, oblique lateral view; H, notoseta from setiger 30; I, notopodial hooded hook from posterior setiger, lateral view; J, notoseta from posterior setiger; K, posterior setigers and pygidium, dorsal view; L, posterior setigers and pygidium, lateral view. Scale bars: A–C, K–L = 250 μ m; D–E = 500 μ m; F–J = 25 μ m.

Prostomium conical, widest in middle then tapering to sharp point anteriorly, posteriorly extending to thin, bluntly pointed caruncle, extending to posterior end of setiger 1; reduced peristomial wings surrounding base of palps (Figs. 16A, B, 17A–D). Four minute deeply embedded eyes or eyes absent; occipital tentacle absent. Palps extending to about setigers 12–15, each with two distinctly separated transverse rows of cilia along ventral surface, long rows of cilia approximately 65 µm long, short rows approximately 32-µm long with 16-µm gap between long and short rows (short rows on medial side), ratio of long to short rows approximately 1.2, rows of mucus secreting cells, represented by tubular necks, present proximal to transverse ciliary

rows, these rows extending to distal ends of palps, median ciliated groove lacking (Figs. 17F and inset, 18A, B). Palps with basal sheath, each sheath with small patches of cilia near insertion of palp (Fig. 17E). Nuchal cilia in a U-shaped pattern on both sides of caruncle, posterior to base of palps (Figs. 16A, 17D).

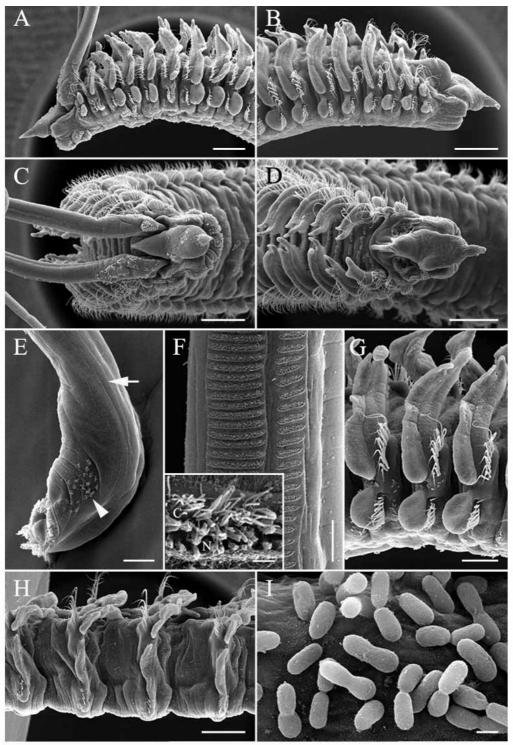


FIGURE 17. *Scolelepis villosivaina* **sp. n.** A–I, paratypes (USNM 1096815) SEM micrographs. A, anterior end, lateral view; B, anterior end, lateral view (palps missing); C, anterior end, oblique dorsal view; D, anterior end, dorsal view (palps missing); E, base of palp showing sheath (arrow indicates beginning of ciliary rows; arrowhead indicates groups of cilia on palp sheath); F, middle region of palp, frontal view; inset shows part of a single transverse ciliary row (N indicates neck of gland cells, C indicates cilia); G, setiger 8–10 (right to left), lateral view; H, setiger 33–36 (left to right), lateral view; I, bacterial cells attached to setiger 1 (same specimen as shown in A). Scale bars: A–D, H = 500 μ m; E = 100 μ m; F = 50 μ m; G = 250 μ m; I = 10 μ m.

Setiger 1 well developed with rounded notopodial and neuropodial postsetal lamellae, notosetae and neurosetae present. Postsetal notopodial lamellae nearly completely fused with branchiae from setiger 2 and subsequent anterior setigers (Figs. 16C, 17A–C), lamellae elongate, rounded, with distal end pointed, degree of fusion of lamellae and branchiae decreasing in middle setigers, with lamellae and branchiae almost completely separated in posterior setigers (Figs. 16D–E, 17G–H). Postsetal neuropodial lamellae of setigers 1–28 with elongate, rounded lobe (Figs. 16C–D, 17A–B, G), by setiger 30 with notch dividing broad dorsal lobe and small rounded ventral lobe with neurosetae (Figs. 16E, 17H). Lateral organs between notopodial and neuropodial postsetal lamellae present from setiger 1 to posterior setigers.

Notosetae of setiger 1 and subsequent setigers in two vertical rows of limbate capillaries (Fig. 16H, J), the dorsal notosetae of these rows longer than ventral ones, one notopodial hooded hook initially present on setiger 38, up to two notopodial hooded hooks from setiger 45 (in regenerating holotype); hooks bidentate with acute main fang and single accessory tooth (Fig. 16I). Neurosetae of setiger 1 and subsequent setigers arranged in two vertical rows of limbate capillaries (Fig. 16F), 2–4 neuropodial hooded hooks from setiger 25–29, up to six neuropodial hooded hooks in middle setigers; neuropodial hooded hooks unidentate (Fig. 16G) or bidentate with small lateral tooth (second tooth difficult to see in some specimens).

Branchiae from setiger 2 to end of body, fused with postsetal notopodial lamellae but with tips free in anterior setigers (Fig. 17A–C, G–H), branchiae and lamellae separated in posterior setigers; with two bands of cilia along inner edge of branchiae continuing across dorsum to join corresponding branchiae on opposite side of body.

Pygidium small, rounded, with dorsal anus (Fig. 16K-L).

Remarks. Scolelepis villosivaina sp. n., from the Philippines belongs to a group of 12 species including S. bonnieri Mesnil, 1896; S. lamellicincta Blake & Kudenov, 1978; S. squamata; S. blakei; S. carunculata; S. chilensis; S. hutchingsae; S. kudenovi; S. denmarkensis Hartmann-Schröder, 1983; S. mesnili Bellan & Lagardère, 1971; and S. vazaha Eibye-Jacobsen & Soares, 2000 that possess notosetae on setiger 1, notopodial hooded hooks, but that lack an occipital tentacle. Among these, S. villosivaina sp. n. most closely resembles S. blakei, S. carunculata, S. chilensis, S. hutchingsae, and S. kudenovi in possessing neuropodial hooded hooks with two teeth, S. bonnieri and S. squamata have a variable number of teeth, 1–2 and 1–3, respectively while the rest exhibit one or three teeth. The apical tooth of S. chilensis is notched while it is entire in S. villosivaina sp. n. Scolelepis villosivaina sp. n. is distinct from S. blakei and S. kudenovi based on branchial fusion. Branchiae are free in S. blakei and fused only at the base in S. kudenovi whereas in S. villosivaina sp. n. the branchiae of anterior setigers are fused along most of their length with only the tips free. The posterior margin of the caruncle in S. villosivaina sp. n. is attached whereas in S. carunculata it is free. The notopodial hooded hooks begin on similar setigers as the neuropodial hooded hooks in S. hutchingsae; in S. villosivaina sp. n. the notopodial hooks begin more posteriorly. Scolelepis villosivaina sp. n. was found to possess patches of cilia on the palp sheath, similar to those of S. hutchingsae described herein for the first time. These patches are easily overlooked, especially with light microscopy and this feature needs to be examined in other species of Scolelepis; the function of these cilia remains unknown.

Bacteria were found on the prostomium, peristomium, palps, and anterior setigers of two specimens of *S. villosivaina* **sp. n.** (Fig. 17A, C, I). The bacterial cells were approximately 20-μm long × 9-μm wide and found in patches over the epidermis. Douglas & Jones (1991) reported on bacteria associated with *Polydora nuchalis* Woodwick, 1953 where the bacteria caused a cuticular disease that was observable to the naked eye as "cauliflower-like". The appearance of the bacteria on the *S. villosivaina* **sp. n.** from the Philippines was similar. Douglas & Jones (1991) also found bacteria in the digestive tract of *Spio maculata* (Hartman, 1961) (cited as *Scolelepis maculata*).

Distribution. Sandy beach in Boracay of the Aklan province in the Philippines; shallow subtidal (< 5 m).

Discussion

The palp ciliary patterns of nine species of Scolelepis have been examined with SEM (Dauer 1983, 1987, 1994; Eibye-Jacobsen 1997; Eibye-Jacobsen & Soares 2000; present study). Among these species, four distinct morphological types can be distinguished (Fig. 18). Four species, S. lefebvrei (Gravier, 1905), S. squamata, S. vazaha, and S. villosivaina sp. n., exhibit two transverse rows of cilia with the long rows 30–64 μm in length while the short rows are 20-32 µm in length; a distance of 8-16 µm separate these rows (Fig. 18A) The ratio of long to short rows in these species is approximately 1.2–1.3. In contrast, two species, S. alisonae sp. n. and S. magnicornuta sp. n., exhibit long and short rows that are indistinctly separated with the long rows 41-45 µm in length and short rows 24-26 µm in length (Fig. 18C). The ratio of long to short rows is approximately 1.0 in these two species. Scolelepis hutchingsae has distinctly separated long and short rows measuring 35–45 μm and 10–21 μm, respectively, but the short rows are elevated on 5–15 μm lobes; in addition, the ratio of long to short rows is 2.0–2.2 (Fig. 18D). S. laciniata has long rows of cilia approximately 40– 45 μm in length and a band of small ciliated cushions (~5 μm) running parallel to the long rows (Eibye-Jacobsen 1997) (Fig. 18E). This band of ciliated protuberances was suggested to represent the reduced remnant of the short rows seen in other Scolelepis (Eibye-Jacobsen 1997; Eibye-Jacobsen & Soares 2000). Finally, S. williami (de Silva, 1961) has a mixture of the patterns found in S. laciniata and S. squamata and those members of the genus that exhibit distinctly separated long and short rows of cilia. Scolelepis williami has long rows of cilia (~30 μm) and small ciliated cushions (~7 μm) at the base of the palps; gradually these rows increase in size and by the middle of the palps the rows are 35 µm and 20 µm, respectively. The ratio of long rows to cushions is approximately 1.5-1.6 and the rows are separated by 18-20 µm (sizes estimated based on SEM micrographs in Eibye-Jacobsen & Soares, 2000).

These findings suggest that palp ciliation patterns are of taxonomic importance within this genus. All the Scolelepis species in the present study exhibited necks of mucus secreting cells that were present in rows proximal to the ciliary rows (Fig. 18B); not randomly mixed among the cilia. The functional significance of the pattern of the mucus secreting cells relative to ciliary rows and ciliary patterns in general remains unknown. All species were found on similar beaches; S. hutchingsae, S. magnicornuta sp. n. and S. villosivaina sp. n. were collected in the same samples from Boracay, Philppines, whereas S. alisonae sp. n. was found at a beach in Morong, Philippines. Living specimens of the Philippine Scolelepis were not examined; however, it is assumed that the cilia of the palps are non-motile and mucus is released by the tubular necks and aids in the capture of food particles. In some of the specimens examined, a band of amorphous material was found below the row of tubular necks and could be mucus deposited by these structures (Figs. 17F, 18B). Based on gut contents, the Scolelepis species examined from the Philippines ingest sand grains, as well as bivalve larvae; the size of the ingested sand grains and types of food items are similar to those found in S. squamata (Dauer 1983). Scolelepis species appear to be non-selective suspension feeders that utilize the mucus to capture food items suspended in swash zone of high-energy beaches (Dauer 1983; Frouin et al. 1998). In Scolelepis squamata the palps are held in a helically coiled pattern with the transverse rows of cilia held in the direction of flow; food items adhering to the mucus secreted along the palps are brought to the mouth by contraction of the entire tentacle (Dauer 1983). Further studies on the production of mucus along the palps and its role in particle capture could lead to more accurate models of feeding by these tentaculate feeders. In addition, although the differences in palp ciliation patterns may reflect habitat-specific adaptations (as indicated by Dauer 1987), comparative studies on members of the genus Parascolelepis and Scolelepis may be informative in distinguishing these two sister taxa. Such studies on palp morphology have provided further evidence for the separation of other spionids at the level of genera (e.g., Dipolydora and Polydora; Worsaae 2001).

The present study brings the total number of described spionid species from the Philippines to 19 (see following key for details), of which 10 species are potentially endemic to this region of the Indo-West Pacific.

This number is considerably (>3 times) lower than the total number of spionids reported in other regions of the Pacific such as Australia (Blake & Kudenov 1978; Hutchings & Turvey 1984). As discussed by Williams (2001) the lower diversity of spionid polychaetes from the Philippines most likely reflects differences in sampling efforts. More studies are needed to fully evaluate the diversity of Philippine polychaetes and such research is critical considering that polychaetes of ecological and economic importance (e.g., pests of commercially important molluscs) appear to have been introduced into the region on multiple occasions.

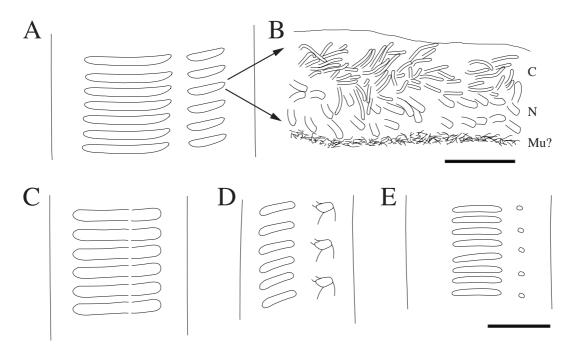


FIGURE 18. Semi-diagrammatic representations of the palp ciliation patterns among the genus *Scolelepis*; in each view (A–E) the distal end is toward the top. A, palp ciliary pattern of *Scolelepis lefebvrei*, *S. squamata*, *S. williami**, *S. vazaha*, and *S. villosivaina* **sp. n.**; B, close-up view of single ciliary row showing cilia (C), neck gland openings (N), and presumptive layer of mucus (Mu?); C, palp ciliary pattern of *S. alisonae* **sp. n.** and *S. magnicornuta* **sp. n.**; D, palp ciliary pattern of *S. hutchingsae*; E, palp ciliary pattern of *S. laciniata*. Scale bars: A, C–E = 50 μm, B = 5 μm. *Note: palp ciliation pattern of *S. williami* is similar to *S. laciniata* at the base (i.e., with reduced short rows as shown in E) but similar to the *S. lefebvrei* (as shown in A) along the remainder of the palp (Eibye-Jacobsen & Soares, 2000).

Key to the Spionidae of the Philippines*

1.	Specialized setae present on setiger 5	
-	Specialized setae absent on setiger 5	
2.	Prostomium pointed	
-	Prostomium with lateral horns	
3.	Branchiae from setiger 1; with accessory branchiae	
-	Branchiae from setiger 2; without accessory branchiae	
4.	Occipital tentacle present	
-	Occipital tentacle absent	
5.	Notopodial lamellae of anterior setigers with up to nine conical lobes	
-	Notopodial lamellae of anterior setigers without conical lobes	
6.	5. Notopodial hooded hooks begin on same setigers as neuropodial hooded hooks	

d hooks begin at least ten setigers posterior to beginning of neuropodial hooded hooks.	-
type of major spine	7.
types of major spines	-
etiger 2; tridentate hooded hooks present; setiger 4 with modified notosetae; setiger 5 fied	8.
osterior to setiger 5, or absent; bidentate hooded hooks; setiger 5 highly modified 9	-
on setiger 1; hooded hooks without constriction on shaft	9. -
tiger 5 bidentate with a large lateral tooth and cowling connecting teeth; posterior noto-	10.
e modified spines	
ia lacking modified spines	_
tiger 5 with small subterminal protuberance on convex side; pygidium with large ven-	11.
aller dorsal lobes	
tiger 5 with two lateral teeth; small cuff-shaped pygidium	_
like notosetae protruding through cuticle of posterior setigers; pygidium with anal cirri	12.
or notosetae absent; pygidium cup-shaped13	_
absent	13.
present	_
nentation	14.
of black pigment	_
tiger 5 simple, falcate	15.
tiger 5 with large lateral tooth	_
tiger 2Boccardia berkeleyorum Blake & Woodwick, 1971	16.
tiger 7, or absent	_
branchiae beginning on setiger 7; a borer in calcareous substrata	17.
d, one or two pairs beginning on setiger 7 or absent; associated with sponges	_
ary neurosetae in setigers 2–7; setiger 5 modified with two types of major spines	18.
ble row: dorsal row falcate with an apical shelf; ventral row with expanded distal end	
th along the apical edge and a capillary extension on the posterior end	
ne in setigers 2–7; setiger 5 modified with two types of major spines arranged in a dou- v simple, falcate; ventral row with slightly expanded distal end bearing small digitiform 	-

^{*}Polydora fulva (Grube, 1878) has not been found since it original description and is not included in this key. In addition, *Trochochaeta diverapoda* (Hoagland, 1920) was described from the Philippines and originally placed in the spionid genus *Aonides*. Although studies by Blake (2006) place *Trochochaeta* within the Spionidae, *T. diverapoda* is not included in this key.

^{**} Williams (2001) identified *Polydora* sp. A from a single specimen associated with hermit crab shells; the specimen belongs to the *Polydora ciliata/websteri* group but cannot be confidently identified to the species level.

^{***} Williams (2001) identified *C. reishi* from burrows in coralline algae on hermit crab shells from the Philippines. In the Marshall Island and Indonesia the species was found in coral rubble (Woodwick 1964; Blake 1979).

Acknowledgments

I thank three undergraduate students, Lauren Schuerlein, Diana Connolly, and Lara Luzak, who aided in the production of line-drawings and SEM figures as part of their training in a National Science Foundation – Partnerships for the Enhancement of Expertise in Taxonomy (PEET) Grant on Polychaetes. Drs. Gil Jacinto and Perry Aliño kindly provided space at the Marine Science Institute of the University of the Philippines during my stay in 2000. Drs. James Blake (ENSR, Woods Hole, MA), Danny Eibye-Jacobsen (Zoological Museum University of Copenhagen) and Pat Hutchings (Australian Museum) provided valuable comments during review of this work. *Maraming salamat po* to all that helped. This work was supported by the Lerner-Gray Fund for Marine Research (American Museum of Natural History) and is based upon work supported by the National Science Foundation under Grant No. 0118693 (PEET).

References

- Agard, J., Kishore, R. & Bayne, B. (1992) *Perna viridis* (Linnaeus, 1758): First Record Of The Indo-Pacific Green Mussel (Mollusca: Bivalvia) In The Caribbean. *Caribbean Marine Studies*, 3, 59–60.
- Audouin, J.V. & Milne-Edwards, H. (1833) Classification des annélides et description de celles qui habitent les côtes de la France. *Annales des Sciences Naturelles, Paris*, 30, 411–425.
- Augener, H. (1926) Polychaeta ven Neuseeland. II Sedentaria. Videnskabelige Meddelelser fra dansk naturhistorisk Forening (Københaven), 81, 157–294.
- Bailey-Brock, J.H. (1990) *Polydora nuchalis* (Polychaeta: Spionidae), a new Hawaiian record from aquaculture ponds. *Pacific Science*, 44, 81–87.
- Bailey-Brock, J.H. (1995) Polychaetes of Western Pacific Islands: A review of their systematics and ecology. *In*: J. E. Maragos, M.N.A.P., Eldredge, L. G., Bardach, J. E. & Takeuchi, H. F. (Eds.), *Marine and Coastal Biodiversity in the Tropical Island Pacific Region*. Vol. 1. East-West Center and Pacific Science Association, Honolulu, 121–134.
- Bailey-Brock, J.H. (2000) A new record of the polychaete *Boccardia proboscidea* (Family Spionidae), imported to Hawai'i with oysters. *Pacific Science*, 54, 27–30.
- Bellan, G.L. & LaGardère, F. (1971) *Nerine mesnili*, n. sp., Spionidien méconnu des plages sableuses de La Province Lusitanienne. *Bulletin de la Société Zoologique de France*, 96, 571–579.
- Ben-Eliahu, M.N., Hutchings, P.A. & Glasby, C.J. (1984) *Ceratonereis lizardensis*, n. sp. (Polychaeta: Nereididae) and *Malacoceros indicus* (Spionidae) from a mangrove habitat at Lizard Island, North Queensland. *In*: Hutchings, P. A. (Ed.), *Proceedings of the First International Polychaete Conference*, *Sydney*. Linnean Society of New South Wales, 91–97.
- Benson, A.J., Marelli, D.C., Frischer, M.E., Danforth, J.M. & Williams, J.D. (2001) Establishment of the green mussel, *Perna viridis* (Linnaeus 1758), (Mollusca: Mytilidae) on the west coast of Florida. *Journal of Shellfish Research* 20, 21–29.
- Berkeley, E. & Berkeley, C. (1941) On a collection of Polychaeta from Southern California. *Bulletin of the Southern California Academy of Sciences*, 40, 16–60.
- Blainville, H. de. (1828) Dictionnaire des Sciences Naturelles. 47, 368-501.
- Blake, J.A. (1979) Four new species of *Carazziella* (Polychaeta: Spionidae) from North and South America, with a redescription of two previously described forms. *Proceedings of the Biological Society of Washington* 92, 466–481.
- Blake, J.A. (1983) Polychaetes of the family Spionidae from South America, Antarctica and adjacent seas and islands. *In*: Kornicker, L. (Ed.), *Biology of Antarctic Seas 12. Antarctic Research Series*, American Geophysical Union, Washington, D.C., 39, 205–287.
- Blake, J.A. (1996) Family Spionidae Grube, 1850. Including a review of the genera and species from California and a revision of the genus *Polydora* Bosc, 1802. *In*: Blake, J.A., Hilbig, B. & Scott, P. H. (Eds.), *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel. Volume 6. The Annelida Part 3. Polychaeta: Orbiniidae to Cossuridae*. Santa Barbara Museum of Natural History, Santa Barbara, 81–223.
- Blake, J.A. (2006) Spionida. *In*: Rouse, G. & Pleijel, F. (Eds.), *Reproductive Biology and Phylogeny of Annelida*. Science Publishers, Enfield, NH, 4, 565–638.
- Blake, J.A. & Arnofsky, P.L. (1999) Reproduction and larval development of the spioniform Polychaeta with application to systematics and phylogeny. *Hydrobiologia*, 402, 57–106.
- Blake, J.A. & Kudenov, J.D. (1978) The Spionidae (Polychaeta) from southeastern Australia and adjacent areas with a revision of the genera. *Memoirs of the National Museum of Victoria*, 39, 171–280.

- Blake, J.A. & Woodwick, K.H. (1971) A review of the genus *Boccardia* Carazzi (Polychaeta: Spionidae) with descriptions of two new species. *Bulletin of the Southern California Academy of Sciences*, 70, 31–42.
- Bosc, L.A. G. (1802) Histoire naturelle des vers, contenant leur déscription et leurs moeurs, avec figures dessinées d'après nature. 1–3, 1–324.
- Briggs, J.C. (1999) Coincident biogeographic patterns: Indo-West Pacific Ocean. Evolution, 53, 326–335.
- Carlton, J.T. (1975) Introduced intertidal invertebrates. *In*: Smith, R.I. & Carlton, J. T. (Eds.), Light's Manual: Intertidal Invertebrates of the Central California Coast, 3rd Edition. University of California Press, Berkeley, pp. 17–25.
- Carlton, J.T. & Geller, J. B. (1993) Ecological roulette: the global transport of nonindigenous marine organisms. *Science*, 261, 78–82.
- Carpenter, K.E. & Springer, V.G. (2005) The center of the center of marine shore fish biodiversity: the Philippine Islands. *Environmental Biology of Fishes*, 72, 467–480.
- Çinar, M.E., Ergen, Z., Dagli, E., Petersen, M.E. (2005) Alien species of spionid polychaetes (*Streblospio gynobranchiata* and *Polydora cornuta*) in Izmir Bay, eastern Mediterranean. *Journal of the Marine Biological Association of the United Kingdom*, 85, 821–827.
- Claparède, E. (1869) Les Annélides Chétopodes du Golfe de Naples. Seconde partie. Annélides sédentaires. *Mémoires de la Société de physique et d'Histoire Naturelle de Genève*, 20, 1-225.
- Dauer, D.M. (1983) Functional morphology and feeding behavior of *Scolelepis squamata* (Polychaeta: Spionidae). *Marine Biology*, 77, 279–285.
- Dauer, D.M. (1985) A new species of *Scolelepis* (Polychaeta: Spionidae) from Lizard Island, Australia. *Proceedings of the Biological Society of Washington*, 98, 678–681.
- Dauer, D.M. (1987) Systematic significance of the morphology of spionid polychaete palps. *Bulletin of the Biological Society of Washington* No. 7, 41–45.
- Dauer, D.M. (1994) Functional ciliary groups of the feeding palps of Spionid polychaetes. *In*: Dauvin, J.-C., Laubier, L. & Reish, D. J. (Eds.) *Actes de la 4ème Conférence internationale des Polychètes. Mémoires du Muséum national d'Histoire naturelle*, 162, 81–84.
- Dauer, D.M. & Ewing, R.M. (1991) Functional morphology and feeding behavior of *Malacoceros indicus* (Polychaeta: Spionidae). *Bulletin of Marine Science*, 48, 395–400.
- Day, J.H. (1955) The Polychaeta of South Africa. Part 3. Sedentary species from Cape shores and estuaries. *Journal of the Linnean Society of London*, 42, 407–452.
- Day, J.H. (1967) A monograph on the Polychaeta of southern Africa. Part 2. Sedentaria. *British Museum of Natural History* Publication No. 656, 1–878.
- de Silva, P.H.D.H. (1961) Contributions to the knowledge of the polychaete fauna of Ceylon. Part 1, Five new species, two new varieties and several new records principally from the southern coast. *Spolia Zeylan*, 29, 164–194.
- Douglas, T.G. & Jones, I. (1991) Parasites of California spionid polychaetes. Bulletin of Marine Science, 48, 308–317.
- Eibye-Jacobsen, D. (1997) A new species of *Scolelepis* (Polychaeta: Spionidae), highly abundant on the sand beaches of western Phuket Island, Thailand. *Bulletin of Marine Science*, 60, 240–251.
- Eibye-Jacobsen, D. & Soares, A.G. (2000) New records of *Scolelepis* (Polychaeta: Spionidae) from the sandy beaches of Madagascar, with the description of a new species. *Bulletin of Marine Science*, 67, 571–586.
- Fauvel, P. (1928) Annélides polychètes nouvelles de l'Indie. Bulletin du Muséum d'Histoire Naturelle, Paris, 34, 90-96.
- Fauvel, P. (1930) Annelida Polychaeta of the Madras Government Museum. *Bulletin of the Madras Government Museum, new series, Natural History Section*, 1, 1–72.
- Fauvel, P. (1953). Annelida, Polychaeta. The Fauna of India, including Pakistan, Ceylon, Burma, and Malaya, Allahabad, 507 pp.
- Foster, N.M. (1971a) Spionidae (Polychaeta) of the Gulf of Mexico and the Caribbean Sea. *Studies on the Fauna of Curação and other Caribbean Islands*, 36, 1–183.
- Foster, N.M. (1971b) Redescription of the spionid polychaete *Malacoceros (Malacoceros) indicus* (Fauvel, 1928). *Journal of the Fisheries Research Board of Canada*, 28, 1455–1457.
- Frouin, P., Hily, C. & Hutchings, P. (1998) Ecology of spionid polychaetes in the swash zone of exposed beaches in Tahiti (French Polynesia). *Comptes Rendus de l'Academie des Sciences Paris, Sciences de la vie*, 321, 47–54.
- Gibbs, P.E. (1971) The polychaete fauna of the Solomon Islands. *Bulletin of the British Museum (Natural History) Zoology*, 21, 101–211.
- Gordon, D.P. & Read, G.B. (1991) Adventive occurrence of the fouling serpulid *Ficopomatus enigmaticus* (Polychaeta) in New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 25, 269–273.
- Gravier, C. (1905) Sur les annélides polychètes de la Mer Rouge (Cirratuliens, Spionidiens, Ariciens). *Bulletin du Muséum d'Histoire Naturelle, Paris.* 11, 42–46.
- Grube, A.-E. (1850) Die Familien der Anneliden. Archiv für Naturgeschichte, Berlin, 16, 249-364.
- Grube, A.-E. (1878) Annulata Semperiana. Beitrage zur Kenntnis der Annelidan-fauna der Philippinen nach den von Hern Prof. Semper mitgebrachten Sammlungen. *Mémoires De L'Académie Impériale Des Sciences De St.-Péters-bourg, VII Série*, 25, 1–300.

- Hartman, O. (1951) The littoral marine annelids of the Gulf of Mexico. *Publications of the Institute of Marine Science, University of Texas*, 2, 7-124.
- Hartman, O. (1961) Polychaetous annelids from California. Allan Hancock Pacific Expeditions, 25, 1–226.
- Hartman, O. (1969) *Atlas of the sedentariate polychaetous annelids from California*, Allan Hancock Foundation, University of Southern California, Los Angeles, 812 pp.
- Hartmann-Schröder, G. (1962) Die Polychaeten des Eulittorals. *In*: Hartmann-Schröder, G. & Hartman, G. (Eds.), Zur Kenntnis des Eulitorals der chilenischen Pazifikküste und argentinischen Küste Südpatagoniens unter besonderer Berücksichtigung der Polychaeten und Ostracoden. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, Supplement to 60, 57–167.
- Hartmann-Schröder, G. (1980) Teil 4. Die Polychaeten der tropischen Nordwestküste Australiens (zwischen Port Samson im Norden und Exmouth im Süden). *In*: Hartmann-Schröder, G. & Hartman, G. (Eds.), Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 77, 41–110.
- Hartmann-Schröder, G. (1981) Teil 6. Die Polychaeten der tropischen-subtropischen Westküste Australiens (zwischen Exmouth im Norden und Cervantes im Süden). *In*: Hartmann-Schröder, G. & Hartman, G. (Eds.), Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 78, 19–96.
- Hartmann-Schröder, G. (1983) Teil 9. Die Polychaeten der antiborealen Südwestküste Australiens (zwischen Dunsborough im Norden und Denmark im Süden). *In*: Hartmann-Schröder, G. & Hartman, G. (Eds.), Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 80, 123–167.
- Hoagland, R.A. (1920) Polychaetous annelids collected by the United States fisheries steamer "Albatross" during the Philippine expedition of 1907–1909. *Bulletin of the United States National Museum* 1, 603–643.
- Holly, M. (1934) Polychaeten von den Philippinen, I. Erste Mitteilung über Polychäten. *Zoologischer Anzeiger* 105, 147–150.
- Holly, M. (1935) Polychäten von den Philippinen, II. Zweite Mitteilung über Polychäten. *Zoologischer Anzeiger*, 111, 96–100.
- Hourdez, S., Desbruyères, D. & Laubier, L. (2006) *Malacoceros samurai*, a new species of Spionidae (Annelida: Polychaeta) from hydrothermal vent chimney walls on the south East Pacific Rise. *Proceedings of the Biological Society of Washington*, 119, 592–599.
- Hutchings, P.A. & Turvey, S.P. (1984) The Spionidae of South Australia (Annelida: Polychaeta). *Transactions of the Royal Society of South Australia*, 108, 1–20.
- Hutchings, P., Frouin, P. & Hily, C. (1998) Two new species of Spionidae from Tahiti, French Polynesia. *Proceedings of the Biological Society of Washington*, 111, 799–806.
- Imajima, M. (1990) Spionidae (Annelida, Polychaeta) from Japan V. The genera *Streblospio* and *Dispio*. *Bulletin of the National Science Museum Series A (Zoology)*, 16, 155–163.
- Imajima, M. (1991) Spionidae (Annelida Polychaeta) from Japan VI. The Genera *Malacoceros* and *Rhynchospio*. *Bulletin of the National Science Museum, Tokyo Series A (Zoology),* 17, 5–17.
- Imajima, M. (1992) Spionidae (Annelida, Polychaeta) from Japan VIII. The genus *Scolelepis*. *Bulletin of the National Science Museum Series A (Zoology)*, 18, 1–34.
- Ingrao, D., Mikkelsen, P.M. & Hicks, D. (2001) Another introduced marine mollusk in the Gulf of Mexico: the Indo-Pacific green mussel, *Perna viridis* (Linnaeus, 1758), in Tampa Bay, Florida. *Journal of Shellfish Research*, 20, 13–19.
- Jones, M.L. (1962) On some polychaetous annelids from Jamaica. *Bulletin of the America Museum of Natural History*, 124, 173-212.
- Khlebovitsch, V.V. (1959) [Some species of polychaete worms from the Kurile Islands, which are new or recorded for the first time in the U.S.S.R]. *Zoologiesheskii Zhurnal*, 28, 167–181. (In Russian)
- Knox, G.A. (1957) The distribution of polychaetes within the Indo-Pacific. *Proceedings of the 8th Pacific Science Congress*, 3, 403–411.
- Langerhans, P. (1880) Die Wurmfauna von Madeira. Zeitschrift für Wissenschaftliche Zoologie, 34, 87-143.
- Light, W.J. (1978) *Invertebrates of the San Francisco Bay Estuary System. Family Spionidae (Annelida: Polychaeta)*, The Boxwood Press, Pacific Grove, California, 211 pp.
- Linnaeus, C. (1758) Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Editio decima, reformata, Tom I. Laurentii Salvii, Holmiae.
- Maciolek, N.J. (1987) New species and records of *Scolelepis* (Polychaeta: Spionidae) from the east coast of North America, with a revision of the subgenera. *Bulletin of the Biological Society of Washington*, No. 7, 15–40.
- MacCord, F.S. & Amaral, A.C.Z. (2005) Morphometric analysis of two species of *Scolelepis* (Polychaeta: Spionidae). *Journal of the Marine Biological Association of the United Kingdom*, 84, 769–784.
- Mesnil, F. (1896) Études de morphologie externe chez les Annélides. I. Les Spionidiens des côtes de la Manche. Bulletin

- Scientifique de la France et de la Belgique, 29, 110-287.
- Monro, C.C.A. (1931) Polychaeta, Oligochaeta, Echiuroidea and Sipunculoidea. Great Barrier Reef (Queensland) Expedition, 1928–1929. *Scientific Reports of the British Museum (Natural History)*, 4, 1–37.
- Müller, O.F. (1806) Zoologica Danica seu Animalium Daniae et Norvegiae ruriorum ac minus notorum, Descriptiones et Historia, Havniaem, 160 pp.
- Natividad, F. & Palpal-latoc, V.S. (1986) Annelids. *In*: Umali, R. M., Zamora, P. M., Gotera, R. R. & Jara, R. S. (Eds.), *Guide to the Philippine Flora and Fauna. Volume VI. Gastropods, Pelecypods, Annelids.* Natural Resources Management Center and University of the Philippines, Manila, 267–342.
- Ozolin'Sh, A.V. (1990) Two New Species of Annelida Polychaeta from the Peter the Great Bay of the Japan Sea. *Zoologicheskii Zhurnal*, 69, 131–135.
- Palpal-latoc, V.S. (1981) Inventory of polychaetous annelids of Tayabas Bay. *Zoological Papers, National Museum, Manila*, no. 9, 1–55.
- Palpal-latoc, V.S. (1990) New records of polychaetous annelids from Ilocos Sur. National Museum Papers, 1, 45–69.
- Palpal-latoc, V.S. (1994) Some scale-bearing polychaetes of Ilocos Sur. National Museum Papers, 4, 67–77.
- Palpal-latoc, V.S. & Gonzales, P. C. (1981) New Records of polychaete worms (Polychaeta, Chaetopteridae) from Natunawan Cove, Tabaco, Albay. *Zoological Papers, National Museum, Manila*, no. 11, 1–7.
- Paxton, H.C., Chou, L.M. (2000) Polychaetous annelids from the South China Sea. *In*: Ng, P. K. L. & Tan, K. S. (Eds.), *The Biodiversity of the South China Sea, Raffles Bulletin of Zoology* Suppl, 8, 209–232.
- Pettibone, M.H. (1963) Revision of some genera of polychaete worms of the family Spionidae, including the description of a new species of *Scolelepis*. *Proceedings of the Biological Society of Washington*, 76, 89–104.
- Pillai, T.G. (1965) Annelida Polychaeta from the Philippines and Indonesia. *Ceylon Journal of Science (Biological Sciences)*, 5, 110–177.
- Purschke, G.H. & Hausen, H. (2007) Lateral organs in sedentary polychaetes (Annelida) Ultrastructure and phylogenetic significance of an insufficiently known sense organ. *Acta Zoologica*, 88, 23-39.
- Quatrefages, A. de. (1843) Déscription de quelques espèces nouvelles d'Annélides errantes recueillies sur côtes de la Manche. *Magasin de Zoologie de Paris* série, 2, 5, 1–16.
- Radashevsky, V.I. (1996) Morphology, ecology and asexual reproduction of a new *Polydorella* species (Polychaeta; Spionidae) from the South China Sea. *Bulletin of Marine Science*, 58, 684–693.
- Radashevsky, V.I. (2005) On adult and larval morphology of *Polydora cornuta* Bosc, 1802 (Annelida: Spionidae). *Zoot-axa* 1064, 1–24.
- Radashevsky, V.I. & Hsieh, H.-L. (2000) *Polydora* (Polychaeta: Spionidae) species from Taiwan. *Zoological Studies*, 39, 203–217.
- Radashevsky, V.I. & Olivares, C. (2005) *Polydora uncinata* (Polychaeta: Spionidae) in Chile: an accidental transportation across the Pacific. *Biological Invasions*, 7, 489 496.
- Reish, D.J. (1961) A new species of *Micronereis* (Annelida, Polychaeta) from the Marshall Islands. *Pacific Science*, 15, 273–277.
- Rice, S.A. & Simon, J.L. (1980) Intraspecific variation in the pollution indicator polychaete *Polydora ligni* (Spionidae). *Ophelia*, 19, 79–115.
- Röhner, M., Bastrop, R. & Jürss, K. (1996) Colonization of Europe by two American genetic types or species of the genus *Marenzelleria* (Polychaeta: Spionidae). An electrophoretic analysis of allozymes. *Marine Biology*, 127, 277–287.
- Rosito, R.M. (1980) Polychaeta from shallow waters off Mactan, Cebu, Part I. The Philippine Scientist, 17, 1–35.
- Rosito, R.M. (1983) Polychaeta from shallow waters off Mactan, Cebu, Part II. The Philippine Scientist, 20, 11–38.
- Schmarda, L. K. (1861) Neue wirbellose Thiere beobachtet und gesammelt auf einer Reise um die Erde 1853 bis 1857, Vol. 1. Turbellarien, Rotatorien und Anneliden. Wilhelm Engelmann, Leipzig.
- Söderström, A. (1920) *Studien über die Polychätenfamilie Spionidae*. Inaugural Dissertation, Uppsala, Almquist and Wicksells. 288 pp.
- Treadwell, A.L. (1920) Polychaetous annelids collected by the U.S. Fisheries steamer "Albatross" in the waters adjacent to the Philippine Islands in 1907–1910. *Bulletin of the United States National Museum*, 100, 589–602.
- Treadwell, A.L. (1926) Polychaetous annelids from Fiji, Samoa, China and Japan. *Proceedings of the United States National Museum*, 69, 1–26.
- Treadwell, A.L. (1931) Contributions to the biology of the Philippine Archipelago and adjacent regions. Four new species of polychaetous annelids collected by the United States fisheries steamer Albatross during the Philippine Expedition of 1907–1910. *Bulletin of the United States National Museum* 100, 313–321.
- Treadwell, A.L. (1942) Polychaetous annelids from Lower California and the Philippine Islands in the collections of the American Museum of Natural History. *American Museum Novitates*, No. 1172, 1–5.
- Treadwell, A.L. (1943) Polychaetous annelids from the Philippine Islands in the collections of the American Museum of Natural History. *American Museum Novitates*, No. 1220, 1–4.
- Williams, J.D. (2000) A new species of *Polydora* (Polychaeta: Spionidae) from the Indo-Pacific and first record of host

- hermit crab egg predation by a commensal polydorid worm. *Zoological Journal of the Linnean Society*, 129, 537–548.
- Williams, J.D. (2001) *Polydora* and related genera associated with hermit crabs from the Indo-West Pacific (Polychaeta: Spionidae), with descriptions of two new species and a second polydorid egg predator of hermit crabs. *Pacific Science*, 55, 429–465.
- Williams, J.D. (2004) Reproduction and morphology of *Polydorella* (Polychaeta: Spionidae), including the description of a new species from the Philippines. *Journal of Natural History*, 38, 1339–1358.
- Woodwick, K.H. (1953) *Polydora nuchalis*, a new species of polychaetous annelid from California. *Journal of the Washington Academy of Sciences* 43, 381–383.
- Woodwick, K.H. (1964) *Polydora* and related genera (Annelida, Polychaeta) from Eniwetok, Majuro, and Bikini Atolls, Marshall Islands. *Pacific Science*, 18, 146-159.
- Worsaae, K. (2001) The systematic significance of palp morphology in the *Polydora* complex (Polychaeta: Spionidae). *Zoologischer Anzeiger*, 240, 45–57.

