

A REVISION OF THE SUBGENUS *PHASCOLOSOMA* (SIPUNCULA: *PHASCOLOSOMA*)

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Abstract.—The 54 putative species of the nominate sipunculan subgenus *Phascolosoma* (*Phascolosoma*) and the morphological characters used to differentiate them are critically reviewed. The monograph of Stephen & Edmonds (1972) is used as a starting place and all changes made in the intervening years are reiterated here. Available type material was studied and new collections of Hawaiian and Caribbean worms are used to analyze within-deme variation. Twenty chromosomes of gradually differing sizes are present. Four characters are broadly useful at the species level (number of hook rings, secondary tooth of hook, pigment on introvert, and pre-anal papillae). Eight characters can be used in a more restricted manner for subsets or special cases (hook size, angle of hook-tip, internal clear areas, basal elaborations, nephridial length, trunk papillae shape, papillae platelets, and retractor origins). Six appear to be of no value to the taxonomist (hook presence, introvert length, number of longitudinal muscle bands, nephridiopore/anus relationship, rectal caecum, and contractile vessel). A key to, and a discussion of, the 16 remaining species (plus two reduced to subspecies) with newly designated synonyms are presented. A brief statement of the distribution of each species is given. An overall summary of the zoogeography and habitat shows the border area between the Indian and Pacific Oceans to be the most diverse with respect to *Phascolosoma* (81% of known species). Nineteen percent (three species) live in the Caribbean. With a few exceptions this genus lives in warm, shallow waters and hard substrates.

This work concludes our reexamination of the sipunculan genera (Cutler & Jurczak 1975; Cutler & Murina 1977; Cutler 1979, 1986; Cutler & Cutler 1982, 1983, 1985a, 1985b, 1986, 1987a, 1988, 1989; Cutler et al. 1983; Gibbs et al. 1983). The monograph of Stephen & Edmonds (1972) is the starting place for this work (40 species names). The five species erected and the nine species transferred into this genus since that time are also included (Table 1).

The genus *Phascolosoma* was erected by Leuckart in 1828, placed in the family, Phascolosomatidae by Stephen & Edmonds (1972), and in the order Phascolosomatiformes by Cutler & Gibbs (1985). The general name *Phascolosoma* went through an unfortunate period when it was incorrectly

used to replace *Golfingia* for seventy years (1880 to 1950). During this time the names *Phymosoma* and *Physcosoma* replaced *Phascolosoma*. In 1950 Fisher reestablished the correct usage of these names, but the non-specialist literature and biological supply houses continued using the incorrect names for another 30 years.

Four subgenera of *Phascolosoma* were proposed by Stephen & Edmonds (1972: 270). Three of these (*Antillesoma*, *Ruepellisoma*, and *Satonus*) were reviewed by Cutler & Cutler (1983) resulting in the elimination of all but one *Antillesoma* (elevated to generic status) and one *P. (Satonus)* species. This action was reviewed in Gibbs & Cutler (1987) where the subgenus *Satonus* was redefined and replaced by the name *Ed-*

Table 1.—Species considered and proposed taxonomic changes.

Present name	Proposed name
<i>Phascolosoma abyssorum</i> (Southern, 1913)	<i>Apionsoma capitatum</i>
<i>Phascolosoma agassizii</i> Keferstein, 1867	no change
<i>Phascolosoma albolineatum</i> Baird, 1868	no change
<i>Phascolosoma ambonense</i> (Fischer, 1896)	<i>Phascolosoma arcuatum</i>
<i>Phascolosoma andamanensis</i> Johnson, 1971	<i>Phascolosoma albolineatum</i>
<i>Phascolosoma annulatum</i> Hutton, 1879	no change
<i>Phascolosoma arcuatum</i> Gray, 1828	no change
<i>Phascolosoma coralicolum</i> (ten Broeke, 1925)	incertae sedis
<i>Phascolosoma deani</i> (Ikeda, 1905a)	<i>Phascolosoma arcuatum</i>
<i>Phascolosoma diaphanes</i> (Sluiter, 1886)	<i>Phascolosoma nigrescens</i>
<i>Phascolosoma dunwichi</i> Edmonds, 1956	<i>Phascolosoma scolops</i>
<i>Phascolosoma duplicigranulatum</i> (Sluiter, 1886)	<i>Phascolosoma nigrescens</i>
<i>Phascolosoma esculentum</i> (Chen & Yeh, 1958)	<i>Phascolosoma arcuatum</i>
<i>Phascolosoma evisceratum</i> (Lanchester, 1905a)	<i>Phascolosoma nigrescens</i>
<i>Phascolosoma extortum</i> (Sluiter, 1902)	<i>Phascolosoma nigrescens</i>
<i>Phascolosoma formosense</i> (Satô, 1939)	<i>Phascolosoma agassizii</i>
<i>Phascolosoma funafutiense</i> (Fischer, 1914)	<i>Phascolosoma glabrum</i>
<i>Phascolosoma glabrum</i> (Sluiter, 1902)	no change
<i>Phascolosoma glaucum</i> (Satô, 1930)	<i>Phascolosoma agassizii</i>
<i>Phascolosoma granulatum</i> Leuckart, 1828	no change
<i>Phascolosoma heronis</i> Edmonds, 1956	<i>Phascolosoma stephensoni</i>
<i>Phascolosoma horsti</i> (ten Broeke, 1925)	<i>Phascolosoma nigrescens</i>
<i>Phascolosoma japonicum</i> Grûbe, 1877	<i>Phascolosoma agassizii</i>
<i>Phascolosoma kapalum</i> Edmonds, 1985	<i>Phascolosoma turnerae</i>
<i>Phascolosoma kurilense</i> (Satô, 1937a)	<i>Phascolosoma agassizii kurilense</i>
<i>Phascolosoma lacteum</i> (Sluiter, 1886)	<i>Phascolosoma nigrescens</i>
<i>Phascolosoma maculatum</i> (Sluiter, 1886)	no change
<i>Phascolosoma meteori</i> (Hérubel, 1904a)	no change
<i>Phascolosoma microdentigerum</i> (ten Broeke, 1925)	<i>Phascolosoma perlucens</i>
<i>Phascolosoma microdontoton</i> (Sluiter, 1886)	<i>Phascolosoma albolineatum</i>
<i>Phascolosoma minutum</i> (ten Broeke, 1925)	<i>Phascolosoma nigrescens</i>
<i>Phascolosoma multiannulatum</i> Wesenberg-Lund, 1954b	<i>Phascolosoma glabrum multiannulatum</i>
<i>Phascolosoma nahaense</i> (Ikeda, 1904)	<i>Phascolosoma scolops</i>
<i>Phascolosoma nigrescens</i> Keferstein, 1865a	no change
<i>Phascolosoma nigritorquatum</i> (Sluiter, 1881)	incertae sedis
<i>Phascolosoma noduliferum</i> Stimpson, 1855	no change
<i>Phascolosoma pacificum</i> Keferstein, 1866	no change
<i>Phascolosoma perlucens</i> Baird, 1868	no change
<i>Phascolosoma psaron</i> (Sluiter, 1886)	<i>Phascolosoma scolops</i>
<i>Phascolosoma puntarenae</i> Grûbe, 1858	<i>Phascolosoma nigrescens</i>
<i>Phascolosoma riukiensis</i> Murina, 1975	<i>Phascolosoma scolops</i>
<i>Phascolosoma rotnesti</i> Edmonds, 1956	<i>Phascolosoma scolops</i>
<i>Phascolosoma saprophagicum</i> Gibbs, 1987	no change
<i>Phascolosoma scolops</i> (Selenka, de Man & Bülow 1883)	no change
<i>Phascolosoma socium</i> (Lanchester, 1905b)	<i>Phascolosoma scolops</i>
<i>Phascolosoma spengeli</i> (Sluiter, 1886)	<i>Phascolosoma nigrescens</i>
<i>Phascolosoma spinosum</i> Johnson, 1971	<i>Phascolosoma perlucens</i>
<i>Phascolosoma spongicolum</i> (Sluiter, 1902)	<i>Phascolosoma scolops</i>
<i>Phascolosoma stephensoni</i> (Stephen, 1942)	no change
<i>Phascolosoma thomense</i> (Augener, 1903)	<i>Phascolosoma perlucens</i>
<i>Phascolosoma turnerae</i> Rice, 1985	no change
<i>Phascolosoma varians</i> Keferstein, 1865	<i>Phascolosoma nigrescens</i>
<i>Phascolosoma vermiculus</i> (de Quatrefages, 1865)	<i>Phascolosoma perlucens</i>
<i>Phascolosoma yezoense</i> (Ikeda, 1924)	<i>Phascolosoma agassizii</i>
<i>Aspidosiphon insularis</i> Lanchester, 1905	<i>Phascolosoma perlucens</i>

mondsius with its single species *P. pectinatum* Keferstein. This uncommon, circum-tropical species has bilobed nephridia, a spindle muscle not attached to the posterior end of the trunk, and introvert hooks with basal spinelets.

Whenever possible, type material has been obtained to verify the original descriptions. In several cases we have made detailed observations on series of recently collected individuals to better evaluate the traditionally used morphological characters. Recent collecting trips to Hawaii, Curaçao and Venezuela (Cumaná and Islas de Los Roques) have greatly facilitated this effort. The opportunity to observe living material is invaluable.

The order of this paper is: an analysis of the morphological characters that have been used by previous authors in their species descriptions in light of our recent analyses; a discussion of those taxa clearly not belonging to the genus; a key to the newly validated species; a discussion of each species including a synonymy, comments on newly added junior synonyms, and known distribution; and a short zoogeographical summary of the genus.

The following abbreviations are used in the text for the museums from which we borrowed material: Australian Museum, South Sydney (AMSS), British Museum (Natural History), London (BMNH); Museum of Comparative Zoology, Harvard, Cambridge, MA (MCZH), Muséum National d'Histoire Naturelle, Paris (MNHN); Museum für Naturkunde der Humboldt-Universität zu Berlin (MNHU); Naturhistoriska Riksmuseet, Stockholm (NHRM); Royal Scottish Museum, Edinburgh (RSME); National Museum of Natural History, Washington (USNM); Wrocław University Museum, Poland (UWMP); University Museum of Zoology, Cambridge, England (UZMC), Zoologisk Museum, Copenhagen (UZMK); Zoölogisch Museum Universiteit van Amsterdam (ZMUA); Zoologisches Museum Universität Ham-

burg (ZMUH); Zoology Museum, University of Tokyo (ZMUT).

Morphological Characters

While Stephen & Edmonds (1972) were able to construct a key to all other genera, they could only construct a table with comparative morphological data for *Phascolosoma* (p. 291). We include those characters and add additional ones.

1. *Introvert hooks*. — A. Presence: All *Phascolosoma* bear laterally compressed, posteriorly directed hooks arranged in rings around the distal portion of the introvert. Historically, one exception has been *P. meteoris*, but small pale hooks are present in type material we examined (see below). Other accounts of hookless *Phascolosoma* species are also erroneous.

B. Number of rings: Although many authors describe the number of rings of hooks present, only a few have attempted to analyze the information. Our work shows that new hooks are produced at the distal tip of the introvert (see also Cutler 1979). What we do not know is whether this production of hooks continues throughout the life of a worm or if there is some species specific upper limit to the number. Proximal rings often are partially (especially on the ventral surface) or completely missing in some specimens. We presume this is caused by abrasion against the surrounding substrate. While new ones are produced at the distal end, old hooks may be lost elsewhere. Nevertheless, a pattern does emerge wherein about half the species have fewer than 50 hook rings (commonly 15–25) while the remainder have over 50 (often over 100). In a few species (e.g., *P. nigrescens*) areas of scattered hooks are present proximal to the rings.

C. Size: When hooks are measured they should be flat; otherwise distortions occur both in size and shape. Measured from the posterior base straight to the tip *Phascolosoma* hooks commonly measure 30–70 μm

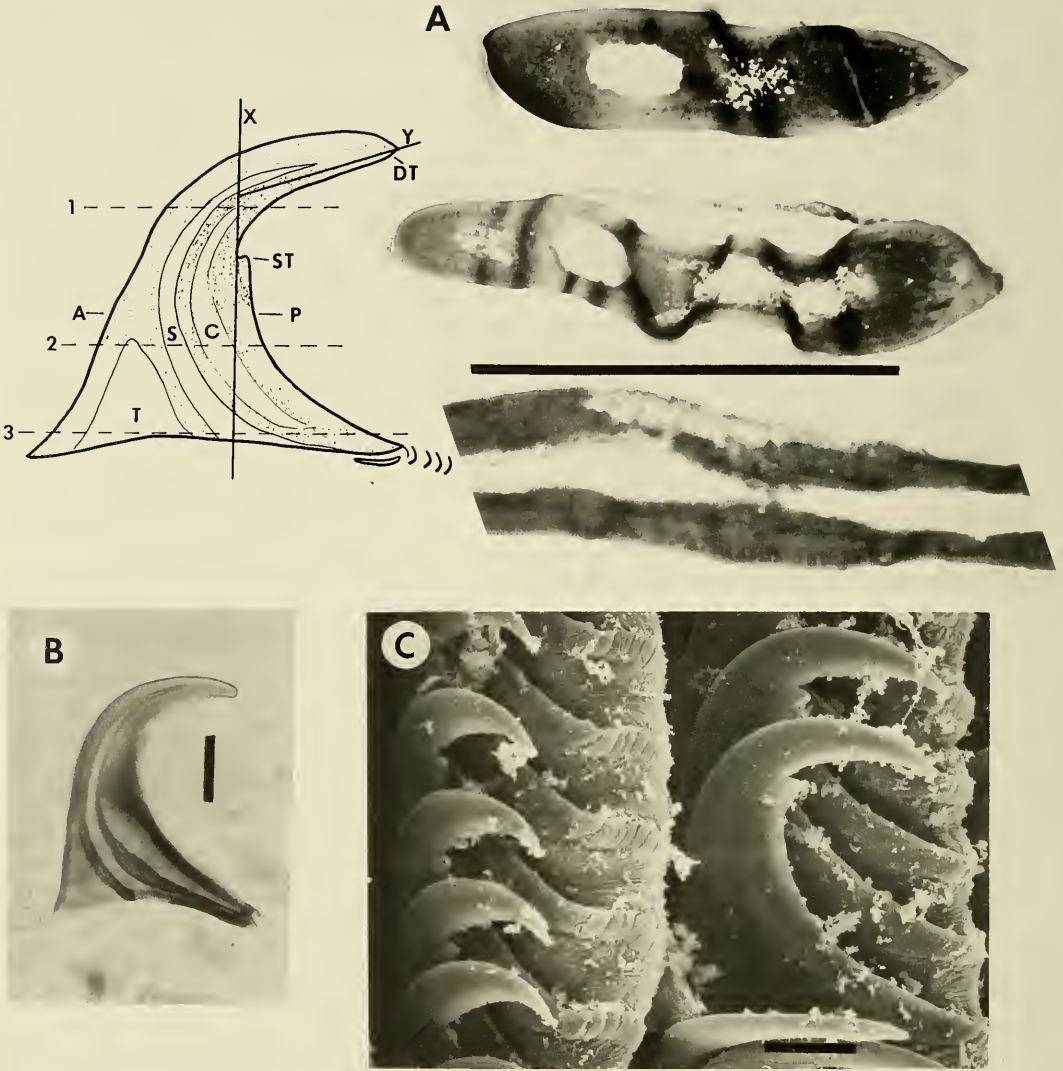


Fig. 1. Introvert hook of *P. stephensoni*. A. Generalized hook showing: anterior (A), posterior (P), distal tip (DT), and secondary tooth (ST), plus the interior clear streak (S), crescent (C), and triangle (T). The lines numbered 1, 2, 3, indicate where the three adjacent Transmission Electron photomicrographs were taken. The upper angle formed between X and Y is used when referring to tip angle. B. Light microscope view. C. Scanning electron photomicrograph of two rings of hooks. Scale lines = 20 μm . Tissue for TEM embedded in Spurr's medium, sectioned 2000 \AA thick, and photographed on a Zeiss 902.

(Fig. 1A). Exceptions to this include *P. pacificum* (90–125 μm), *P. meteori* and *P. saprophagicum* (15–30 μm). Three species (*P. arcuatum*, *P. nigrescens*, and *P. stephensoni*) are reported to have hooks in the 50–80 μm range, but we have measured hooks up to 120 μm in the latter. Small worms

tend to have smaller hooks than larger members of the same population (see Appendix). Therefore, while this character state is not diagnostic for most species it can be helpful for a few at the two ends of this continuum.

D. Shape (secondary tooth and tip): In-

trovert hooks differ in shape but how to describe the differences has often proved difficult. Consequently the same hook is not always consistently described. A "secondary" or "accessory" tooth or "keel" is commonly present on the posterior edge (concave side) of most species of *Phascolosoma* (Figs. 1, 2). It ranges from being small, fragile, and sharp to being large, hump-like and blunt. The tooth is constant within a species (except for *P. nigrescens*) and has taxonomic importance.

The distal tip may also vary from an acute point to a rounded, blunt apex. While there is a generally consistent pattern within a species, one does find worn and rounded hooks on an individual with normally pointed hooks, consequently more than a few hooks per worm must be examined. The tip of the hook bends at an angle to the perpendicular and this angle varies within (and among) populations. We have measured this angle as shown in Fig. 1A. Line X is drawn perpendicular to the base through the most anterior part of the concave side and Y is drawn from the tip to intersect X in the middle of the point. Some species have angles less than 90°, and others in the 90–115° range. This second group includes those species commonly described as having hooks bent at a right angle (e.g., *P. albolineatum* and *P. glabrum*). The variation in angle within a deme shows no correlation to hook size or whether the hook came from a proximal or distal ring.

E. Internal clear streak (apical canal) and triangle: When viewed by transmitted light one sees zones of differing opacity. Transmission electron micrographs show the paler, lighter regions are where there is little or no organic material (Fig. 1A). The hooks are open basally so that a hollow space (clear streak) extends along the basal edge. This may not always be apparent when the hooks are removed from the tissue. The clear streak (hollow space) extends upward from the base to near the apex. There may also be a triangular clear area in the antero-basal cor-

ner that may or may not be separated from the slender clear streak. Additionally, *P. stephensoni* has a pale "crescent" posterior to the clear streak (Fig. 1A, B).

The width of the streak, whether it has a sharp or gradual bend near the midpoint, and the presence of swellings along its length have been used in species diagnoses. Using TEM, SEM, and light microscopy together with a comparison of the internal architecture of newly formed hooks (from very small worms or from the first two rings) to older, more mature hooks (Fig. 7G, H), it becomes clear that *Phascolosoma* hooks begin with an open internal space into which partitions of reinforcing material are secreted eventually. The resulting subdivisions into triangles, streaks, or crescents must be at least partially genetically determined. Our examination of the literature and many hooks from within demes suggests that there are some species with distinctive morphs (e.g., *P. nigrescens* and *P. stephensoni*), but the degree of variation in many populations is great. One must accept the fact that within some species-complexes (e.g., *P. scolops/agassizii*) there is overlap and a degree of variation that can be confusing. Therefore, one must use caution when looking at internal hook-structure despite its potential usefulness.

F. Posterior basal elaborations: Separate, small units of diverse shape are associated with the posterior basal edge of most hooks in *Phascolosoma* (only *P. arcuatum* has no basal ornamentation). The units are separated from the main body of the hook and each other, but they really form a single structure which is considered part of the hook. Scanning electron micrographs illustrate three variations: like *P. stephensoni* most species are warty (Fig. 3A). In *P. saprophagicum* and *P. turnerae* these basal processes (rootlets) are taller and thinner (Rice 1985, fig. 1e; Gibbs 1987, fig. 1) while in *P. glabrum* an elaborate series of toes to the side of the hook and differing in the two subspecies (Fig. 3B, C) is present. Therefore,

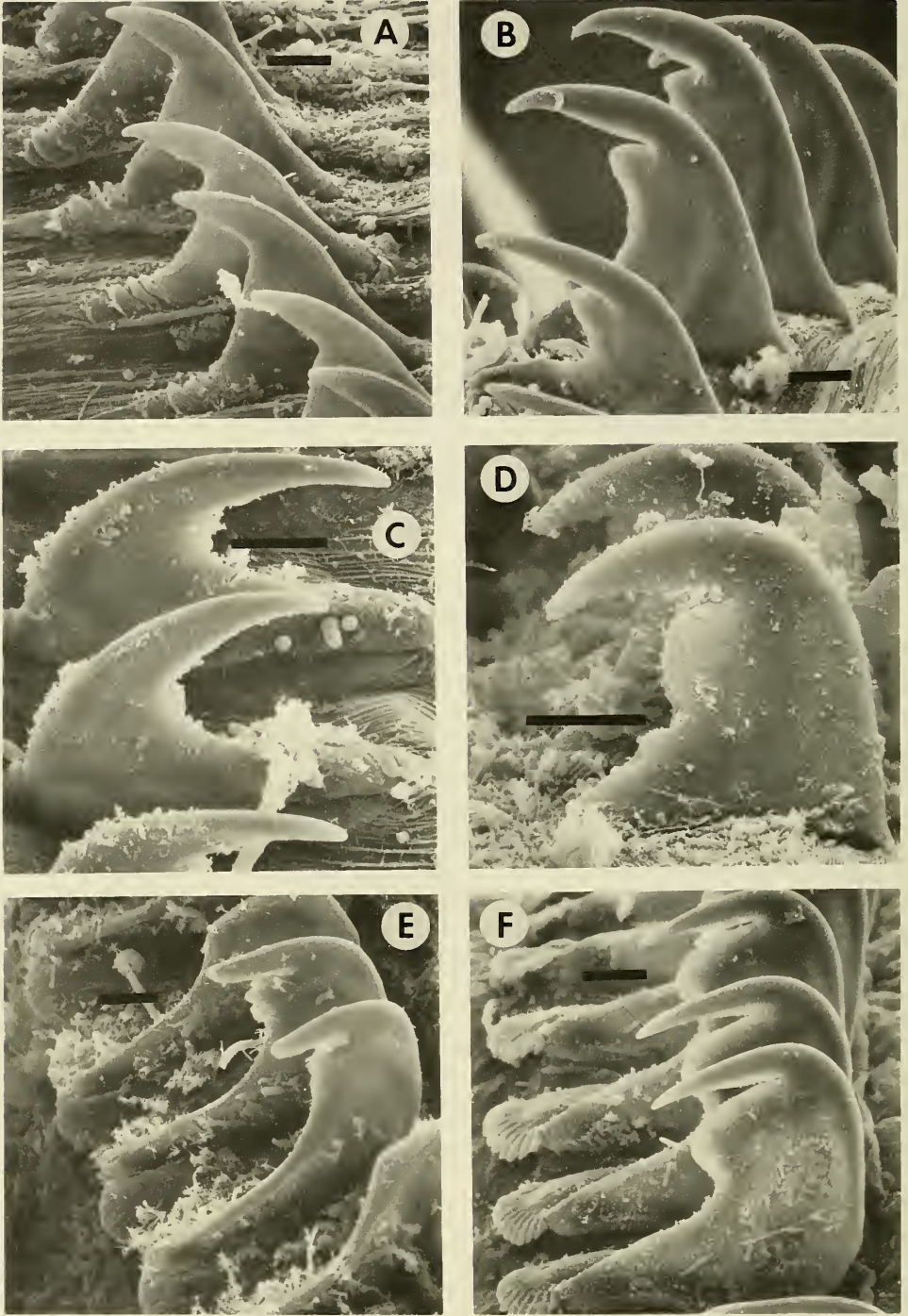


Fig. 2. SEM photographs of hooks from several *Phascolosoma*: A. *P. granulatum*; B. *P. perlucens*; C. *P. scolops*; D. *P. albolineatum*; E. *P. glabrum glabrum*; F. *P. glabrum multiannulatum*. Scale lines equal 10 μm .

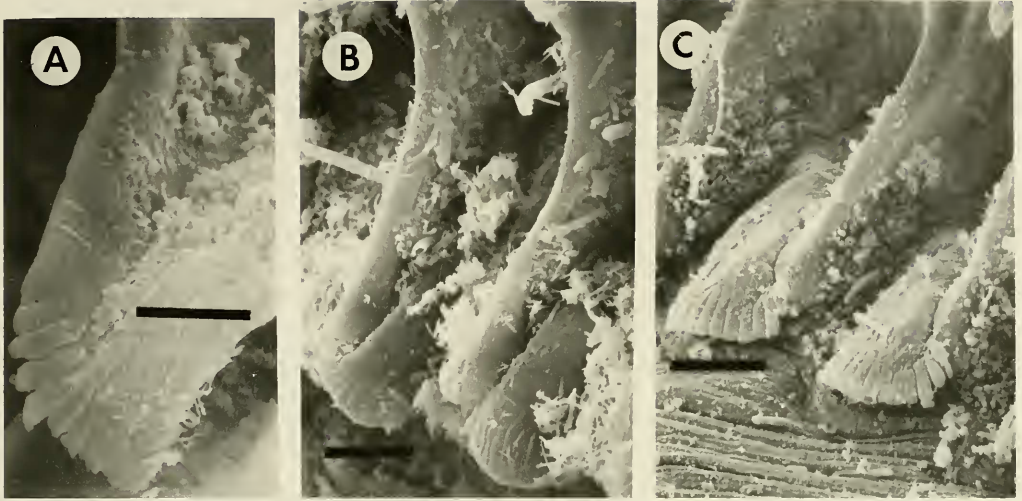


Fig. 3. SEM photographs of basal elaborations: A. Warts of *P. stephensoni*; B. Toes of *P. glabrum glabrum*; C. Toes of *P. glabrum multiannulatum*. Scale lines equal 10 μm .

for these latter species basal elaborations are taxonomically useful.

2. *Pigmented introvert bands/stripes*.—The dorsal side of the introvert is darker than the ventral side in many species. When present, this reddish-brown color is distributed in patches of varying size, from large and almost continuous in *P. perlucens*, to the more common pattern of irregular, narrow bands as in *P. scolops* and *P. agassizii*. With the exception of *P. nigrescens* the presence or absence of pigmented bands is consistent within a species and, therefore, of systematic value.

3. *Introvert length*.—The difficulty in using the relative length of the introvert lies in the elastic nature of this body region, easily observed in living worms. Additionally, as demonstrated in other genera, the trunk grows faster than the introvert so that the introvert becomes a smaller part of the whole in larger worms (allometric growth). The slope of the linear regression is always negative (Fig. 4). Depending on whether or not the introvert was extended and, if so, how well narcotized the worm was when preserved, the same introvert may appear to be from 75% to 125% of the trunk length.

Within one population such a range is common in preserved material (see Appendix). Despite the fact that some populations have introverts averaging less than 90% of the trunk and others average over 125%, the overlapping ranges around these means preclude use of these data to identify an individual worm (Fig. 4 insert).

4. *Number of longitudinal muscle bands*.—The longitudinal muscle layer on the inside of the body wall is divided into a variable number of bundles or bands. In almost every species there are 18–24, occasionally as few as 15 in smaller or as many as 30 in larger worms (*P. pacificum* has 30–40). The bands anastomose occasionally and generally are more numerous towards the posterior end (see Appendix). This anterior/posterior difference can range from 0 to 10, and the order of magnitude of this difference is larger for some species than others. The number of bands is not as absolute or constant as stated in Stephen & Edmonds (1972:291), and appears to have no systematic value in the genus.

5. *Nephridiopore/anus relationship*.—These openings almost always occur at the same anterior/posterior level. If there is a

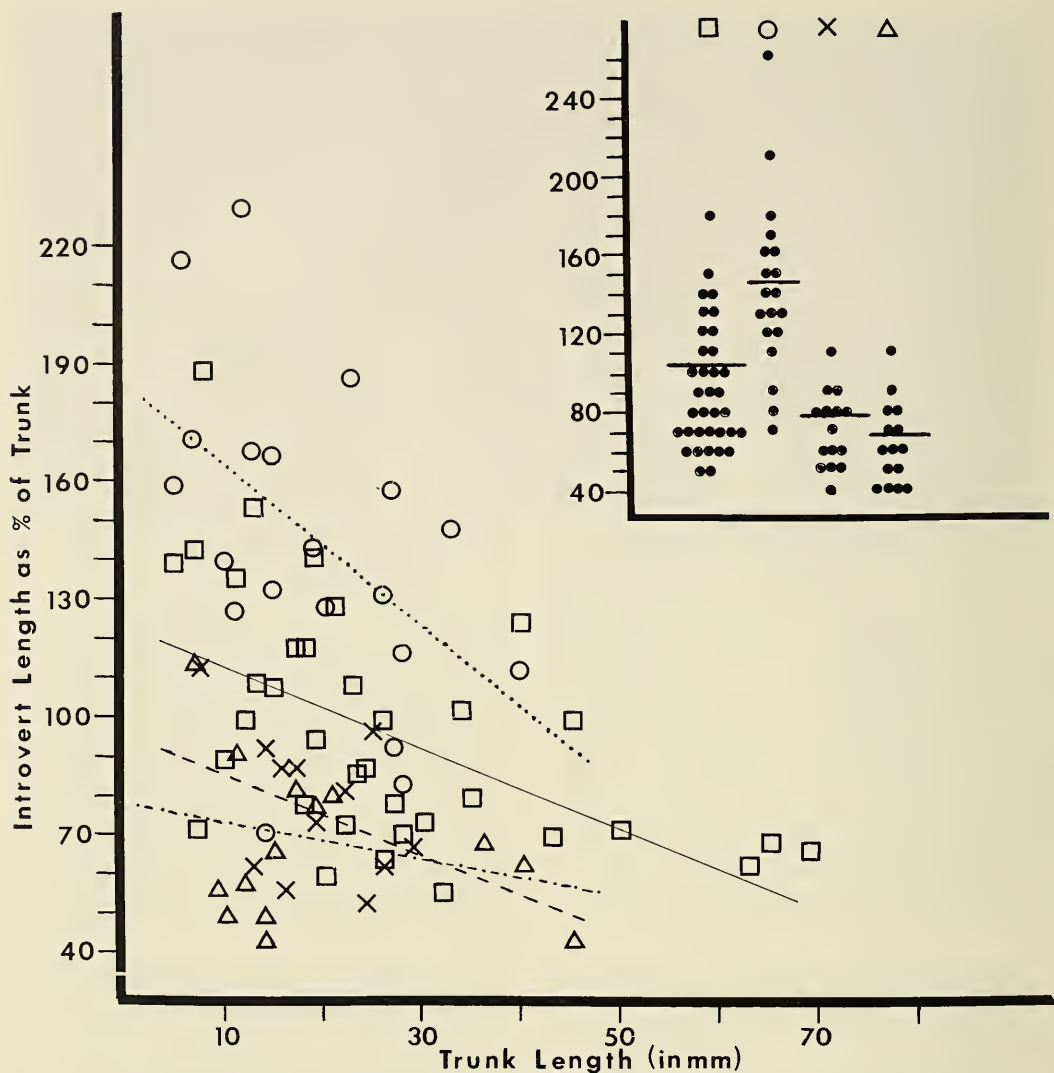


Fig. 4. Relationship between trunk length and introvert length of four *Phascolosoma* species; lines are linear regressions ($y = a + bx$): Squares = *P. agassizii*, $b = -1.01$; Circles = *P. nigrescens*, $b = -2.06$; X's = *P. perlucens*, $b = -1.04$; Triangles = *P. albolineatum*, $b = -0.47$. Insert shows introvert length of same four species to illustrate overlapping ranges despite significantly different means. Each dot represents one extended worm; the horizontal lines are the mean length for each species.

difference, the nephridiopores shift anterior (occasionally) or posterior (rarely) to the anus. When a shift occurs, the distance is on the order of 0.5 mm. To use this character in a taxonomic context for this genus would be a mistake.

6. *Nephridia length and attachment.*—The nephridia are a pair of tubular organs extending towards the posterior end of the

trunk. In a few species (e.g., *P. pacificum* and *P. glabrum*) they are quite long, 95–100% of the trunk, and in a few species (e.g., *P. perlucens*) they are short (25–45%). In most species they are 40–65% of the trunk length (see Appendix).

Between the body wall and the nephridia there are thin connective tissue strands and most authors have noted the extent of their

attachment. While in most species the value averages around 50%, the range within any population can be 30–70% of the nephridia length with no clear correlation to size of nephridia or trunk. Because of the delicate nature of this attachment it can be easily torn during dissection. In a few species this organ is attached along almost its entire length (e.g., *P. pacificum*). These nephridial features are taxonomically helpful for only a few special cases. Most species are similar, i.e., in the broad mid-range and variable.

7. *Rectal caecum*.—Located near the beginning of the rectum there may be a small digitiform or bulbous caecum. The presence or absence of this structure has been assumed to be consistent within a species. In Stephen & Edmonds' table (1972:291) they list 10 species with a caecum, 12 without, and 14 unknown. In our analysis (see Appendix) we find from 11–57% of the individuals in a population have a caecum. Sometimes it is clearly visible on the straight part of the gut, but at other times it is covered by the coiled portion and more difficult to find. It is hard to understand how this degree of polymorphism can exist if this structure might have some physiological function. Nevertheless, based on these data, we conclude that this character cannot be used for taxonomic purposes.

8. *Papillae (shape/platelets/size)*.—Descriptions of the glandular epidermal structures known as papillae are varied, but not always precise or helpful. The careful drawings and measurements provided by many early workers are an expression of a typological species concept that overlooks the variations present within demes. These structures do differ but in less precise ways.

Three general shapes occur: domelike, mammillate, and conical. Many worms exhibit at least two types in various regions of the same animal. The papillae around the base of the introvert (pre-anal) are of particular interest because they help to differentiate species (Fig. 5).

When observed by transmitted light the papillae appear to have granular platelets of

different sizes arranged in diverse patterns around a central pore. The pattern, however, seems to be consistent and unique only in *P. noduliferum*. When viewed with the SEM the papillae surface appears smooth. This observation suggests that the platelets are sub-cuticular. Additionally, the cuticle over the pre-anal papillae of a few species (e.g., *P. stephensoni* and *P. perlucens*) has a smooth hardened appearance (not granular in transmitted light).

Size measurements (height, basal diameter) have been presented, but the possible range of the measurements over the surface of a single worm is great, usually being smaller in the mid-trunk and larger towards the ends. In a general manner one can speak of large or small papillae, but this is a subjective, overall impression and larger worms tend to have larger papillae.

9. *Contractile vessel villi*.—Along the dorsal side of the esophagus runs a tubular contractile vessel. In some genera the vessel possesses digitiform extensions or villi, but *Phascolosoma* species do not. Stephen & Edmonds (1972:315) repeat ten Broeke's (1925) assertion that *P. nigrescens* has villi, but our examination of her material shows only a bulbous vessel with vesicular pouches, not villi.

10. *Retractor muscle origins*.—In most species the pair of dorsal retractor muscles has its origins from the body wall about 45% of the distance towards the posterior end of the trunk (the range may be as wide as 30–60% in a given population). The ventral pair originates at about 65% but may range from 50–75% within a population (see Appendix). Only *P. saprophagicum* has the ventral retractors in the posterior quarter of the trunk. In this species and *P. arcuatum*, both pairs of muscles originate at about the same distance from the ventral nerve cord so that the terms dorsal and ventral lose their meaning. Except for these two species, retractor origins cannot be used as an aid in identifying specimens.

11. *Karyotypes*.—While karyology may eventually be useful to systematists, our

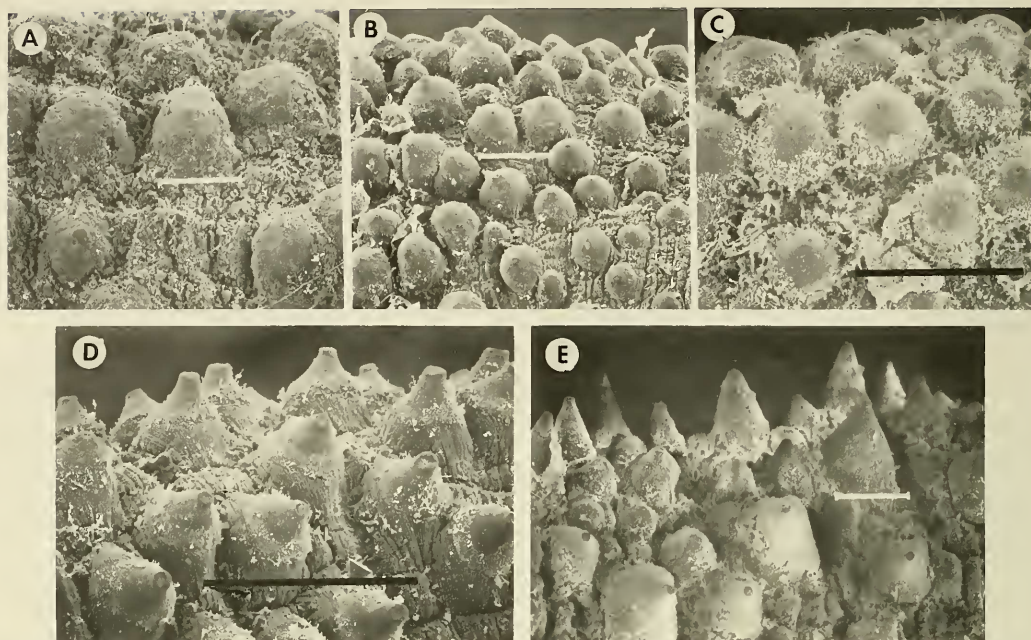


Fig. 5. SEM photographs of different shaped pre-anal papillae from several *Phascolosoma*: A. *P. granulatum* (dome); B. *P. scolops* (mamillate); C. *P. albolineatum* (dome); D. *P. perlucens* (cone); E. *P. stephensoni* (cone). Scale lines = 0.2 mm.

present data base is too small to be of value at the species level. Through the efforts of J. Silverstein (pers. comm.) we have information on the chromosomal morphology of *Phascolosoma scolops*, *P. pacificum*, *P. perlucens*, and *P. agassizii*. All have $2N = 20$ with a common tendency toward asymmetry of chromosome arm length, e.g., 70–100% of the chromosomes are subtelocentric or telocentric. They all show a gradual reduction in chromosome length from pair one to pair 10 rather than a bimodal pattern of distinctly large and small chromosomes as is seen in other sipunculan genera.

Summary.—Four character states are determined to be consistent and broadly useful to the taxonomist at the species level. These are the number of hook rings, nature of the secondary tooth of the hook, pigment bands on introvert, and shape/size/texture of the pre-anal papillae. Eight characters can be used in a more restricted manner for smaller subsets or special cases. These in-

clude hook size, tip angle, internal clear streak/triangle/crescent, basal elaborations (warts/toes), nephridial length, trunk papillae shape, arrangement of papillae platelets, and the position of the retractor muscle origins. Six previously used attributes are of no value to the taxonomist, because of the within-deme variability. These are the presence/absence of hooks, introvert length, the number of longitudinal muscle bands, nephridiopore/anus relationship, the presence of a rectal caecum, and the nature of the contractile vessel.

Systematic Section

Genus *Phascolosoma* Leuckart, 1828

Phascolosoma Leuckart, 1828:22, fig. 5.—Keferstein, 1863:39 (part); 1865a:422 (part).—Baird, 1868:91.—Fisher, 1950:551; 1952:422.—Stephen & Edmonds, 1972:270–271.—Gibbs & Cutler, 1987:54.

Phascolosomum Diesing, 1851:63 (part); 1859:758 (part).

Phymosomum de Quatrefages, 1865:621.

Phymosoma Selenka et al., 1883:54 (emendation of *Phymosomum*).

Phyrcosoma Selenka, 1897:460.—Spengel, 1898:50.

Diagnosis.—Introvert of variable length often equal to trunk with numerous rings of recurved hooks. Body wall with longitudinal muscle layer gathered into bands. Tentacles (less than 30) in crescent around nuchal organ (peripheral tentacles lacking). Contractile vessel without true villi. Four introvert retractor muscles, lateral pairs sometimes partially, rarely completely, fused. Spindle muscle may or may not be attached posteriorly. Two nephridia.

Type species.—*Phascolosoma granulatatum* Leuckart, 1828.

Subgenus *Phascolosoma* Leuckart, 1828

Phascolosoma (Phascolosoma) Stephen & Edmonds, 1972:289–291.—Gibbs & Cutler, 1987:54.

Diagnosis.—Spindle muscle attached posteriorly. Introvert hooks without accessory spinelets.

The following three taxa are not considered valid members of this genus and are discussed first. After the key, the remaining species are alphabetically arranged.

Phascolosoma corallicola
(ten Broeke, 1925)

Phyrcosoma corallicola ten Broeke, 1925: 90, text fig. 12 (not *Sipunculus corallicolus* Pourtalès, 1851:41).

Phascolosoma (Phascolosoma) corallicolum.—Stephen & Edmonds, 1972:298–299.

Discussion.—In the bottle at ZMUA labeled as type (V.Si. 96) is one piece of coral and three anthozoans but no sipunculans. There are unresolvable peculiarities in ten

Broeke's description of a damaged, hookless worm of unspecified size. She did say it had 12 tentacles despite Stephen & Edmonds (1972) statement that they were absent. Extensive collections in the type locality in recent decades by ourselves and others have failed to yield any worms like this. For these reasons it seems most prudent to place this name on the list of incertae sedis.

Phascolosoma longicolle
Rüppell & Leuckart, 1828

Phascolosoma longicolle Rüppell & Leuckart, 1828:6, fig. 1. Grube, 1840:47; 1868: 644.—Diesing, 1851:64; 1859:762.—Baird, 1868:95.—Stephen & Edmonds, 1972:339.—Saiz Salinas, 1989:208.

Material examined.—MNHU, Grube's Red Sea specimen (3171).

Discussion.—The recent analysis by Saiz Salinas shows this name (considered incertae sedis by Stephen & Edmonds, 1972) to be associated with worms that belong to the species *Golfingia vulgaris*. Grube's specimen in Berlin is a *P. scolops*.

Phascolosoma nigritorquatum
(Sluiter, 1881)

Phymosoma nigritorquatum Sluiter, 1881: 151–152, pl. 1, figs. 3, 8, 11; 1891:117.—Selenka et al., 1883:68–69.

Phyrcosoma nigritorquatum.—Sluiter, 1902: 13.—Fischer, 1919:280; 1921:4–5; 1927: 416.

Phascolosoma (Satonus) nigritorquatum.—Stephen & Edmonds, 1972:286–287.—Edmonds, 1980:61–62.—Cutler & Cutler, 1983:186.

Material examined.—ZMUA, type (V.Si. 80); ZMUH, Fischer's 1921 material (V8916).

Discussion.—We reaffirm our position taken in Cutler & Cutler (1983) that these worms belong in this subgenus, but the quality of the material precludes a meaningful definition of this species and the sta-

tus of incertae sedis is appropriate including Fischer's material.

Phascolosoma abyssorum
(Southern, 1913)

Physcosoma abyssorum Southern, 1913:12-14, pl. 1, fig. 1, pl. 2, fig. 1.—Fischer, 1916:6; 1922b:6; (not *Phascolosoma abyssorum* Koren & Danielssen, 1877 = *Golfingia abyssora*).

Phascolosoma (Phascolosoma) abyssorum.—Stephen & Edmonds, 1972:292.

Discussion.—We concur with Gibbs (1986), who showed Southern's species to be conspecific with, and a junior synonym to, *Apionsoma capitatum*.

Key to *Phascolosoma* Species

This is based on the characters of mature hooks taken from complete rings (not distal 2 or 3 or posterior worn and scattered ones).

1. More than 50 rings (complete and/or incomplete) of hooks 2
 - Less than 50 rings (complete and/or incomplete) of hooks 9
2. Most hooks over 100 μm tall, nephridia as long as trunk (Fig. 6A) *P. pacificum*
 - Hooks less than 100 μm tall 3
3. Concave side of hook with large rounded hump, toes present but not warts (2 subspecies, Fig. 6B) *P. glabrum*
 - Concave side of hook is smoothly tapered or with small secondary tooth 4
4. Hooks with long, thin basal processes (Fig. 3C) *P. turnerae*
 - Basal processes, if present, as normal warts 5
5. Hooks without basal warts (Fig. 6D) *P. arcuatum*
 - Hooks with basal warts 6
6. Clear streak of hook with swelling
 - in middle of vertical and horizontal portion (Fig. 6E) *P. nigrescens*
 - Clear streak without abrupt swellings 7
7. Hooks with posterior crescent, many over 75 μm tall, pre-anal papillae smooth cones, pigment bands on introvert (Fig. 1) *P. stephensoni*
 - Hooks without crescents, most less than 75 μm tall, no pigment bands on introvert 8
8. Hooks with granular triangle (Fig. 6F), close-set, randomly distributed papillae platelets *P. granulatum*
 - Hooks without triangle, posterior hooks more triangular shape and narrower clear streak (Fig. 7D, E), papillae platelets around pore small and close-set then abruptly more wide-spread *P. noduliferum*
9. Hooks less than 25 μm tall 10
 - Hooks over 25 μm tall 11
10. Fewer than 10 rings of inconspicuous hooks. (Fig. 6G) *P. meteori*
 - More than 15 hook rings (Fig. 6H) *P. saprophagicum*
11. Angle of hook tip greater than 90° (Fig. 6I) *P. albolineatum*
 - Angle of hook tip 90° or less 12
12. Large rounded hump on concave side of hook, pre-anal papillae smooth, posteriorly directed, cone-shaped (Fig. 7A) *P. perlucens*
 - Concave side smooth or with small tooth 13
13. Hooks with separate anterior basal triangle 14
 - Hooks without triangles (Fig. 7B) *P. maculatum*
14. Trunk papillae platelets extending onto inter-papillae surfaces (Fig. 7C) *P. annulatum*
 - Papillae platelets restricted to papillae surfaces 15
15. Hook with distinct triangle, narrow band of red cone-shaped pre-

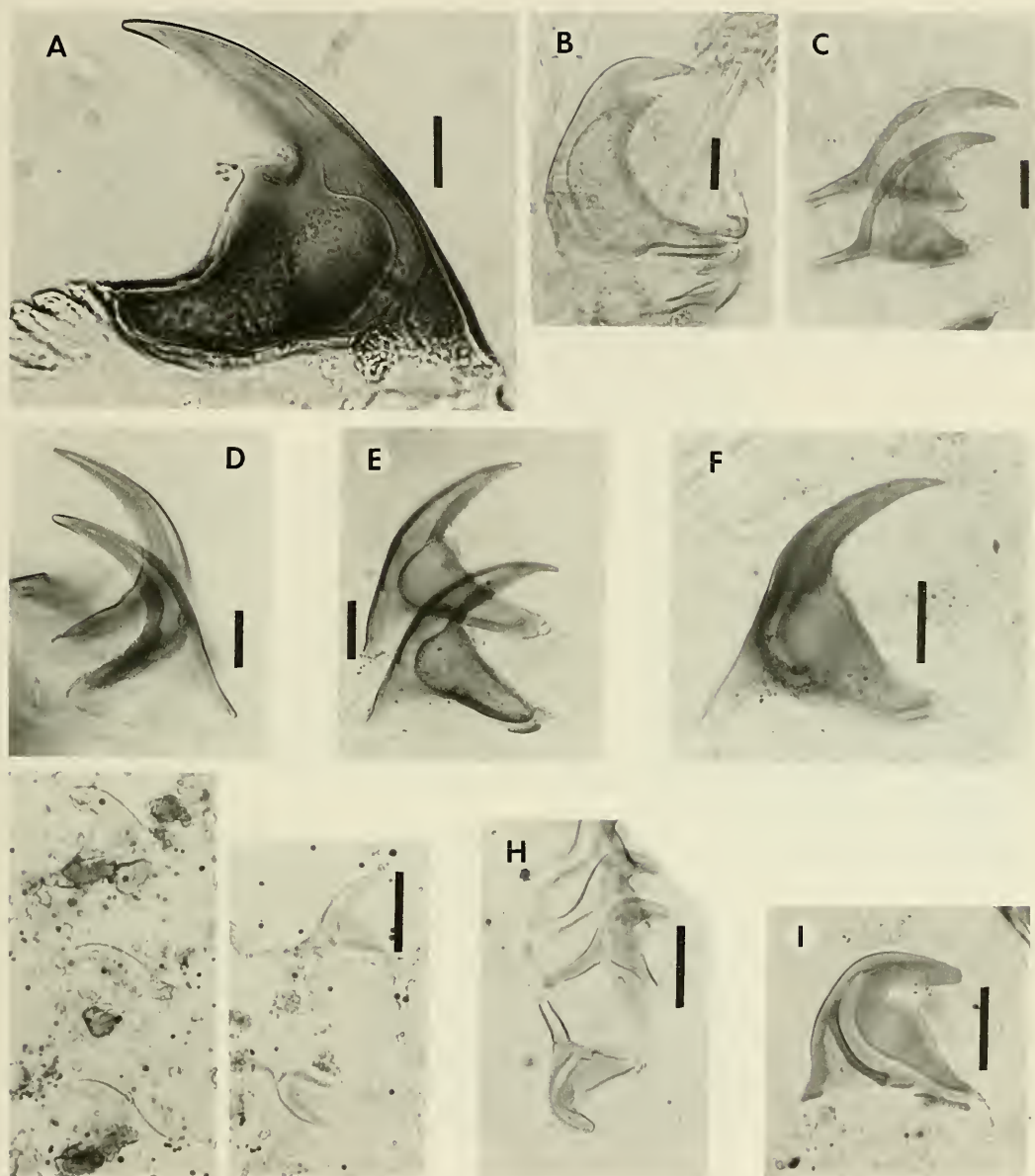


Fig. 6. Light microscope photographs of *Phascolosoma* introvert hooks arranged as in the Key. Scale lines = 20 μ m; A. *P. pacificum*; B. *P. glabrum*; C. *P. turnerae*; D. *P. arcuatum*; E. *P. nigrescens*; F. *P. granulatum*; G. *P. meteori*; H. *P. saprophagicum*; I. *P. albolineatum*.

- anal papillae (Fig. 7F) . . . *P. scolops*
- Hook triangle indistinct or absent, pre-anal papillae not distinct from dome-shaped trunk papillae (Fig. 7G, H) . . . *P. agassizii*

Phascolosoma agassizii
Keferstein, 1866

Phascolosoma agassizii Keferstein, 1866:
218-219; 1867:46.—Baird, 1868:92;

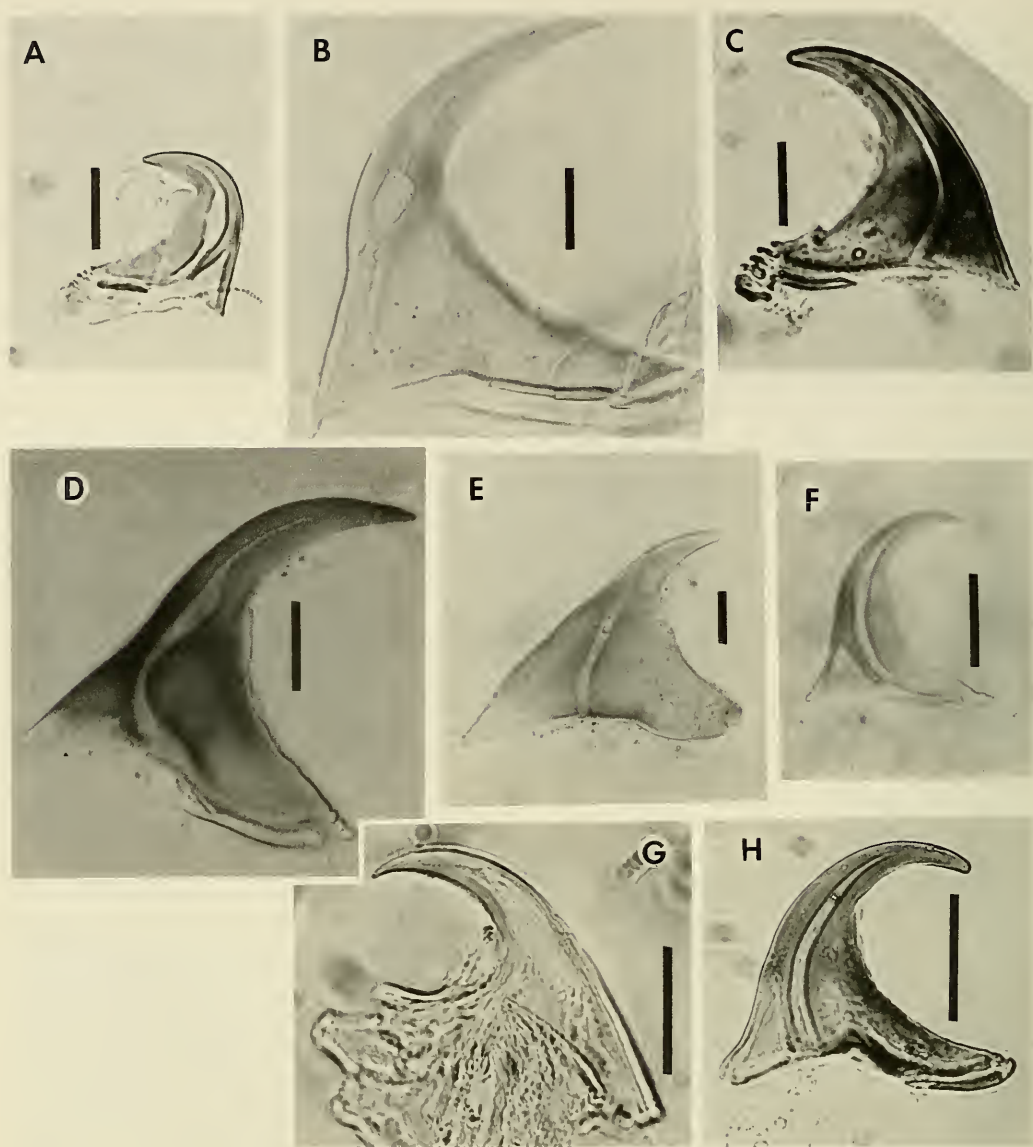


Fig. 7. As for Fig. 6: A. *P. perlucens*; B. *P. maculatum*; C. *P. annulatum*; D & E. *P. noduliferum* (anterior & posterior); F. *P. scolops*; G & H. *P. agassizii* from most distal ring, not completely erupted (G) & middle ring (H).

- Fisher, 1952:424-430.—Wesenberg-Lund, 1954a:8-9; 1957a:3; 1959b:210; 1963:126.—Stephen, 1960:516-517; 1966:147-148.—Rice, 1967:143-171; 1973:1-51.—Stephen & Cutler, 1969:115; Johnson, 1971:599-600.
- Phymosoma agassizii*.—Selenka et al., 1883: 78-79. *Physcosoma agassizii*.—Fischer, 1895:10; 1914a:6; 1914b:67-68; 1923:23; 1927:200.—Shipley, 1891:123; 1899a: 155; 1902:133; 1903:174.—Chamberlin, 1920a:30; 1920b:5D.—Leroy, 1936:424 (not Fischer, 1919:280; 1922a:7-9).
- Phascalosoma (Phascalosoma) agassizii*.— Stephen & Edmonds, 1972:292-293.— Dybas, 1976:67-75.—Cutler & Cutler,

1979a:982–983.—Rice, 1980:492.—Frank, 1983:23–24.—Saiz Salinas, 1986:52–55.

Phymosoma lordi Baird, 1868:92.—Rice & Stephen, 1970:62.

Phascolosoma japonicum Grube, 1877:73.—Fisher, 1952:429.—Wesenberg-Lund, 1963:116–119.—Stephen & Cutler, 1969:115.—Cutler 1977b:154–155.—Cutler et al., 1984:293–296.

Phymosoma japonicum.—Selenka et al., 1883:76–78.—Ikeda, 1904:22–23.

Physoosoma japonicum.—Selenka, 1888:220.—Shiple, 1891:122.—Fischer, 1895:12; 1914a:5–6; 1916:15; 1922a:13–14; 1923:3.—Chamberlin, 1920b:5D.—Ostroumov, 1909:321–322.—Satô, 1930:9–11; 1937b:149–150; 1939:383–386.—Stephen, 1942:247–248; 1948:220 (vide *P. noduliferum*).—Leroy, 1936:424 (not Selenka, 1885:21.—Fischer, 1922b:7–8).

Phascolosoma (Phascolosoma) japonicum.—Stephen & Edmonds, 1972:309–310.

Physoosoma yezoense Ikeda, 1924:32–34, pl. 1, figs. 3–6.

Phascolosoma (Phascolosoma) yezoense.—Stephen & Edmonds, 1972:328–329.—Cutler & Cutler, 1981:91–92.

Physoosoma glaucum Satô, 1930:15–17, pl. 1, fig. 6, fl. 2, figs. 7–8, text fig. 4 (not *Phascolosoma glaucum* Lanchester, 1905a:32 = *Golfingia glauca*).

Phascolosoma (Phascolosoma) glaucum.—Stephen & Edmonds, 1972:306.—Cutler & Cutler, 1981:89–90.

Physoosoma formosense Satô, 1939:398–401, pl. 20, fig. 15, text figs. 36–41.

Phascolosoma (Phascolosoma) formosense.—Stephen & Edmonds, 1972:304.—Cutler & Cutler, 1981:89.

Phascolosoma (Rueppellisoma) golikovi Murina, 1975:54–55, fig. 1.—Cutler & Cutler, 1983:180.

Material examined.—MCZH, type material (186, 439); our recent California collections; *P. japonicum*, MNHU, type (1024) plus 979 & 1025, and Fischer's 1922 Port

Elizabeth specimens (6087); NHRS, Fischer's 1922 Eugenie material (162, 164); recent Japanese collections (Cutler et al. 1984).

Discussion.—Considerable lack of clarity about this taxon has existed. Our decision to combine these names comes after protracted analysis of numerous specimens. As presently defined *P. agassizii* has fewer than 30 rings of hooks that are 30–70 μm tall, each having a variable clear streak, a triangle that is usually indistinct, and if a secondary tooth is present, it is small (Fig. 7G, H, and Fisher 1952, plates 37–38 for variety). When others have reported this species as having more than 30 rings of hooks they were probably looking at a different species. The introvert has irregular pigment bands and is about as long as the trunk. The trunk is covered with papillae that exhibit much variety in color (generally darker than the skin). Papillae platelets are variable in size (3–9 μm) and with a random distribution. Published illustrations overlook the variation present, even on a single worm.

Previous decisions to reduce some taxa to junior synonyms of *P. japonicum* are reaffirmed here with the subsequent move into synonymy with *P. agassizii*. These are *P. glaucum* and *P. yezoense* (Cutler & Cutler 1981), plus *P. golikovi* (Cutler & Cutler 1983).

In the description of *P. formosense*, Satô (1939) seems inconsistent. He stated that the hooks are scattered but later wrote about the number of rings. His figure shows three hooks in a line as if part of a ring. As suggested in Cutler & Cutler (1981) Satô probably had two worms with few hook rings that were partially covered by a fold of skin. The hook and papillae shape fit within our concept of *P. agassizii*.

Distribution.—Common on both sides of the north Pacific Ocean (Mexico to Alaska on the eastern side and Japanese waters in the west), plus scattered records from cooler Indian Ocean waters. Several records from south and west Africa exist, and while these may include some misidentified *P. granu-*

latum, others are correct. Australian and other warm water Indian and Pacific Ocean records (including Keferstein's Panama material) are considered to be other *Phascolosoma* species.

Phascolosoma agassizii kurilense
(Satô, 1937)

Physcosoma kurilense Satô, 1937a:117–120, text fig. 14.

Phascolosoma (Phascolosoma) kurilense.—Stephen & Edmonds, 1972:310–311.—Cutler & Cutler, 1981:91.

Material examined.—None.

Discussion.—The earlier decision (Cutler & Cutler 1981) to reduce the northern *P. kurilense* to a subspecies of *P. japonicum* is reaffirmed here. However, *P. japonicum* is now a junior synonym of *P. agassizii*. The one morphological difference is the presence of a small secondary lobe on the nephridia of mature worms.

Distribution.—Kurile Islands.

Phascolosoma albolineatum (Baird, 1868)

Phascolosoma albolineatum Baird, 1868:91–92.—Wesenberg-Lund, 1963:128.—Stephen, 1967:45.—Rice & Stephen, 1970:59.—Edmonds, 1980:56–57.—Murina, 1981:13.—Cutler et al., 1984:292–293.

Phymosoma albolineatum.—Selenka et al., 1883:71–72.—Augener, 1903:301–302.

Physcosoma albolineatum.—Fischer, 1913:99; 1914a:6; 1922a:9.—Ikeda, 1924:32.—Leroy, 1942:6–9.—Satô, 1935:312; 1939:395–396.—Tokioka, 1953:140.

Phascolosoma (Phascolosoma) albolineatum.—Stephen & Edmonds, 1972:293–295.—Cutler & Cutler, 1979a:983.

Phymosoma microdontoton Sluiter, 1886:506, pl. 4, fig. 9; 1891:118; 1902:13.

Phascolosoma (Phascolosoma) microdontoton.—Stephen & Edmonds, 1972:312–313.

Phascolosoma multiannulata Wesenberg-Lund, 1954b:378–383, text figs. 2–6 (part).

Phascolosoma andamanensis Johnson,

1971:603–604, pl. 1, figs. 1–7.—Haldar, 1976:3–4.

Material examined.—BMNH, type; Indian Ocean and Japanese material (Cutler & Cutler 1979a, Cutler et al. 1984); *P. multiannulatum*, UZMK, type material, (cataloged as *Golfingia multiannulata*); *P. microdontoton*, ZMUA, type (V.Si. 77).

Discussion.—This taxon is characterized by the tip of the hooks being bent at an angle of more than 90°. Superficially it strongly resembles pale specimens of *P. scolops*, and unless hooks are examined the two species could be misidentified. On the concave side the hooks have a large bulge but no secondary tooth, giving the base a less triangular form. The clear streak often does not extend beyond the mid-point (Fig. 6I). The hooks are from 25–65 μm tall and arranged in less than 40 rings. The introvert is shorter than the trunk, and the nephridia are usually less than one-half the trunk length. In some specimens only two or three retractor muscles are present owing to some degree of fusion (Cutler & Cutler 1979a:983, Cutler et al. 1984:292).

Phascolosoma microdontoton (Sluiter, 1886) is considered a junior synonym. The original illustration of a hook is misleading. The internal structure and the external shape match *P. albolineatum* except that the tips of some hooks are worn down. The band of pre-anal papillae are also comparable.

When Wesenberg-Lund (1954b) described *P. multiannulatum* she reported 500 specimens, of which only 20 can now be located. Of these, 16 are clearly *P. albolineatum*, with pale trunks 8–25 mm long. Her description was a combination of characters and we have redefined her taxon below.

The name *P. andamanensis* was introduced by Johnson (1971) and used by Haldar in 1976 for a population that was like *P. albolineatum* except that the hooks had basal bar and warts (see discussion in Morphological Section). Haldar (1988), after collecting many specimens in the Andaman

Islands, placed the name in synonymy with *P. albolineatum* and we concur.

Distribution.—Wide spread but not common in Indo-West Pacific tropical shallow waters.

Phascolosoma annulatum (Hutton, 1879)

Phascolosoma annulatum Hutton, 1879: 278.—Benham, 1903:174.—Edmonds, 1960:160–162.

Phascolosoma (Phascolosoma) annulatum.—Stephen & Edmonds, 1972:296–297.—Cutler, 1977a:151–152.—Edmonds, 1980:57–58.

Physcosoma scolops var. *mossambiense.*—Augener, 1903:339.

Physcosoma scolops tasmaniense Fischer, 1914a:3–4.

Physcosoma scolops.—Wheeler, 1938:346.

Phascolosoma tasmaniense Edmonds, 1956: 285–286.

Material examined.—BMNH, type; two worms identified by Edmonds from New Zealand and Australia.

Discussion.—This species has been recorded up to 50 mm long with introverts 1–2 times the trunk bearing up to 30 tentacles. The hooks in this species are very similar to *P. scolops*, 45–60 μm tall, in up to 25 complete rings. The separate triangle is less distinct (Fig. 7C). Proximal, incomplete, dorsal rings of smaller (30–35 μm), more triangular hooks are partially obscured by the papillae and pigment. The bases of the trunk papillae appear polygonal (not oval) and are covered by dark polygonal platelets. These platelets spread out over the skin in the interpapillae spaces in a distinctive manner.

Distribution.—Southern Australia, New Zealand, and Campbell Island in cooler water.

Phascolosoma arcuatum (Gray, 1828)

Siphunculus arcuatus Gray, 1828:8.—Baird, 1868:88.—Rice & Stephen, 1970:50–51.

Phascolosoma (Phascolosoma) arcuatum

arcuatum.—Stephen & Edmonds, 1972: 297–298.—Edmonds, 1980:58–59.

Phymosoma lurco Selenka et al., 1883:61–63.

Physcosoma lurco.—Fischer, 1895:12; 1914a:4–5; 1922a:15.—Sluiter, 1902: 12.—Lanchester, 1905b:37.—Leroy, 1936:424.

Phascolosoma lurco.—Edmonds, 1956:290–291.

Phymosoma lurco malaccensis Selenka et al., 1883:63.

Physcosoma lurco malaccensis.—Sluiter, 1902:12.

Phascolosoma arcuatum malaccense.—Stephen & Edmonds, 1972:298.

Phascolosoma rhizophora Sluiter, 1891:119–121; 1902:13.

Physcosoma ambonense Fischer, 1896:337–338, text figs. 1–3.

Phascolosoma (Phascolosoma) ambonense.—Stephen & Edmonds, 1972:295–296.

Phymosoma deani Ikeda, 1905:171–172, pl. 8, figs. 5–8.

Phascolosoma (Phascolosoma) deani.—Stephen & Edmonds, 1972:299.—Cutler & Cutler, 1981:88–89.

Physcosoma esculenta Chen & Yeh, 1958: 273–274, text figs. 1–2.

Phascolosoma esculenta.—Murina, 1964: 263.

Phascolosoma (Phascolosoma) esculentum.—Stephen & Edmonds, 1972:301.

Material examined.—*P. deani*, ZMUT, type; *P. esculenta*, material identified by Murina; *P. lurco*, MNHU, type (488, 971); UZMC, Lanchester's material; *P. rhizophora*, ZMUA, type (V.Si. 84).

Discussion.—This species has very dark, large papillae with sharp borders against a light yellow-brown skin. The introvert may be twice the trunk length and bears over 100 complete and incomplete rings of hooks. The hooks are 40–70 μm tall, without secondary teeth, warts, or toes. Internally the hooks are simple, with the clear streak greatly expanded basally. The retractor muscles

are unique in that the origins of the broad posterior pair have shifted dorsally (to longitudinal muscle bands 2–3) and the origins of the thinner anterior pair have shifted ventrally (to muscle band 1). Also, the entire retractor complex may appear as a single fused unit with four roots when contracted. The circular muscle layer is divided into anastomosing bands thereby creating “coelomic sacs” where gas exchange between the environment and the coelomic fluid can occur more readily as in many Sipunculidae.

In 1970 Rice & Stephen concluded that *P. arcuatum* and *P. lurco* were conspecific and in 1972 Stephen & Edmonds added *P. rhizophora*. In 1981 Cutler & Cutler continued this process by adding *P. deani* and *P. esculenta* to the list of junior synonyms.

The justification for retaining *P. arcuatum malaccense* as a valid subspecies is weak. “The papillae on the middle of the trunk are formed of many concentric plates instead of being arranged irregularly” (Stephen & Edmonds 1972:298). Later they state “. . . figure of . . . nominate form shows only a partial concentric arrangement of the plates.” Selenka et al. (1883) did not provide any illustrations of their subspecies, and we conclude that this taxon does not merit separate status.

The type material of *P. ambonense* Fischer, 1896, is not located in those museums where Fischer deposited other specimens, and there are no other records of this taxon. The similarities of this to *P. arcuatum*, a species common in Indonesia, have been noted by earlier writers and include: the retractor muscles (ventral pair anterior to dorsal), the weakly developed and few longitudinal muscle bands (only 16 in a 140 mm worm (total length and not 14 mm as in Stephen & Edmonds 1972:285)), and hook shape. Our inability to verify this information is not helpful. Rather than add this name on the list of species inquirendum, pending future clarification, we place it in the present synonymy.

Distribution.—Northeast India, Andaman Islands, southern China, Vietnam, Philippines, Malaysia, Indonesia, and northern Australia. Tolerates extended periods out of the water and in brackish water, e.g., in mangrove estuaries.

Phascolosoma glabrum glabrum
(Sluiter, 1902)

Physcosoma glabrum Sluiter, 1902:14–15, pl. 1, figs. 7–8.

Phascolosoma (Phascolosoma) glabrum.—Stephen & Edmonds, 1972:305.

Phymosoma microdontoton.—Shipley, 1898:471; 1899b:56.

Physcosoma funafutiense Fischer, 1914a:6–8, pl. 1, fig. 8; 1922a:11–13.

Phascolosoma (Phascolosoma) funafutiense.—Stephen & Edmonds, 1972:304–305; Cutler & Cutler, 1979a:983–984.

Material examined.—ZMUA, type (V.Si. 128/5); *P. funafutiense*, ZMUH, 4 worms collected in West Java by Beneden and determined by Augener but never published (V10983); NHRS, Fischer’s 1922 material; Pacific and Indian Ocean specimens (Cutler & Cutler 1979a). *P. microdontoton*, UZMC, Shipley’s 1898 worms.

Discussion.—In several ways (nephridia 75–100% of trunk, trunk papillae evenly distributed and of uniform size all over, a large number of hook rings) *P. glabrum* is similar to *P. pacificum*, but is distinguished by having somewhat smaller hooks (60–85 μm) with a different shape and internal structure (Fig. 6B). The hooks have a large hump on the posterior edge, the clear streak has an apical expansion, and they are the only hooks that have basal toes (Fig. 3B). In addition, the skin has a smoother texture because of smaller dome-shaped papillae (vs. tall cones). The differences between the two subspecies are described in the following section.

When Fischer (1914a) described *P. funafutiense* he made no reference to *P. glabrum*.

Sluiter's illustration does not show any basal toes while Fischer's material has them. Sluiter overlooked them, although they are present on the type. Cutler & Cutler (1979a) focused on the hook structure and used Fischer's name. It is now clear that these two species are conspecific.

Fischer (1914a) maintained that Shipley's (1898, 1899b) *P. microdontoton* actually was synonymous with his new species. Our analysis confirms that conclusion, and, thus, Shipley's reports are included here.

Distribution.—Scattered records from Indo-West Pacific (Diego Garcia, Indonesia, Niwetok, Funafuti, Rotuma, and Christmas Island).

Phascolosoma glabrum multiannulatum
(Wesenberg-Lund, 1954)

Phascolosoma multiannulata Wesenberg-Lund, 1954b:378–383, text figs. 2–6 (part).

Phascolosoma (Phascolosoma) multiannulatum.—Stephen & Edmonds, 1972:313–314.

Material examined.—UZMK, type material, (cataloged as *Golfingia multiannulata*).

Discussion.—In the museum collections there are 20 specimens from Wesenberg-Lund's type material; only four of which have hooks that fit her description. The other 16 worms are *P. albolineatum*. We do not know what happened to the other 480 worms in the original collection and suspect that Wesenberg-Lund's description is an amalgamation of features of both populations. Her description and drawings of the hooks (her figs. 3–5) are of *P. g. multiannulatum*. Her comments about the papillae and her drawings of these and the internal anatomy (her figs. 2 and 6) fit the *P. albolineatum* morph.

The differences between these four specimens and the nominate form are subtle. Our present action allows for future workers, having access to a larger sample size, to

treat this population as conspecific or re-establish it as a species. The hooks are smaller (up to 60 μm), the clear streak is without an apical expansion, and there are 12 toes on the left instead of 10 toes on the right side (Fig. 3C). The hook rings are farther apart, the trunk papillae are larger domes, and sometimes lie in rectangles formed by folds of skin.

Distribution.—Type locality at Hikueru, Tahiti. This is at the eastern edge of the species' range.

Phascolosoma granulatum
Leuckart, 1828

Phascolosoma granulatum Leuckart, 1828: 22, text fig. 5. (For references between 1828 and 1969 see Stephen & Edmonds, 1972:306–307 and Saiz Salinas, 1984b: 203–205.)

Phascolosoma (Phascolosoma) granulatum.—Stephen & Edmonds, 1972:306–309.—Walter, 1973:487.—Haldar, 1975: 59.—Zavodnik, 1975:99.—Zavodnik & Murina, 1975:127; 1976:83.—Gibbs, 1977:28–29.—Saiz et al., 1979:209–210.—Saiz Salinas & Rallo Gruss, 1980: 114.—Saiz Salinas, 1984a:185–186; 1984b:203–205; 1986:55–62; 1988b: 11.—Ocharan, 1980:115–116.—Murina, 1977:160–162; 1981:13–14 (not Cutler & Cutler, 1979b:109; 1987b:71).

Physcosoma lanzarotae Harms, 1921:307 (part).

Physcosoma japonicum.—Fischer, 1922b: 7–8.

Material examined.—UZMK, Wesenberg-Lund's 1959a material from Cape Verde and Canary Islands; Saiz Salinas' 1986 material from Spain; Brazil and Cape Verde material (Cutler & Cutler 1979b); *P. japonicum*, MNHU, Fischer's 1922b Port Elizabeth material (6087); *P. laeve*, MNHU, Keferstein's 1865a worms (6990); *P. loveni*, UZMK, Wesenberg-Lund's 1930 material.

Discussion.—There has been a lack of

clarity about the distinction between this species and *P. stephensoni*. Some of the earlier reports of *P. granulatum* are really *P. stephensoni*. Their ranges overlap. It is also probable that some descriptions have been based on a mixture of the two species. The papillae of *P. granulatum* are granular and dome-shaped, occasionally darker than the body wall, without the taller, smoother, cone-shaped pre-anal papillae that characterize *P. stephensoni*. The introvert is without any dark pigmented bands. The hooks are arranged in over 50 rings, some incomplete. The hooks are 35–70 μm tall, have a narrow clear streak with an indistinct granular triangle, and ill-defined or no secondary tooth (Fig. 6F). The number of longitudinal muscle bands varies considerably between the anterior and posterior in a given worm, averaging 18 and 26 respectively. In general, there is a lack of diagnostic apomorphic characters suggesting that this may represent an evolutionarily significant morphology—closest to the ancestral stock.

The material described by Wesenberg-Lund (1930) as *P. loveni* is clearly *Apionosoma capitatum*. Satô's two reports (1935, 1939) cannot be verified, but based on his comments, and upon zoogeographical considerations, we propose that his worms were probably *P. scolops*.

Collin (1892), Wesenberg-Lund (1959c), and Murina (1981) have reported *P. granulatum* from the Indian Ocean. We have not been able to examine these collections, the descriptions are brief with no figures, and we suggest that the worms belong to one of the tropical *Phascolosoma* species. Reexamination of the material from Brazil and Cape Verde (Cutler & Cutler 1979b), as well as Wesenberg-Lund's (1959a) from the Canary Islands, show them to be what we now consider *P. stephensoni*.

Distribution.—Common in the north-eastern Atlantic Ocean from southern Norway along the coasts of Europe and the British Isles to northern Africa out to the Azores

and Cape Verde Islands. It extends into the Mediterranean and Adriatic Seas. The Brazilian record was an error and we suspect that the Indian Ocean records are not this species either.

Phascolosoma maculatum (Sluiter, 1886)

Phymosoma maculatum Sluiter, 1886:511–512, pl. 4, fig. 4; 1891:118–119.—Augener, 1903:308–310.

Physcosoma maculatum.—Sluiter, 1902:11.

Phascolosoma (Satonus) maculatum.—Stephen & Edmonds, 1972:285.—Cutler & Cutler, 1983:185.

Material examined.—ZMUA, type (V.Si. 76).

Discussion.—Although based on only three individuals whose differences from other species are not clear, *P. maculatum* is retained as a species. The hooks are distinctive: 90–95 μm tall, slender, with the clear streak reaching one-half to two-thirds the distance towards the tip and usually expanding into a broad basal triangle (Fig. 7B). Only some of the hooks have a secondary tooth and up to 12 basal warts are present. The posterior trunk papillae are tall cone-shaped while the anterior papillae are mammiform.

The decision by Cutler & Cutler (1983) to move this from the subgenus *Satonus* was based on our observation that a posteriorly attached spindle muscle was present.

Distribution.—Indonesia.

Phascolosoma meteori (Hérubel, 1904)

Phymosoma meteori Hérubel, 1904a:477–478, figs. 2–3; 1904b:563; 1907:123–128.

Physcosoma meteori.—Stephen, 1941:405.

Phascolosoma meteori.—Wesenberg-Lund, 1957b:12.

Phascolosoma (Phascolosoma) meteori.—Stephen & Edmonds, 1972:312.

Material examined.—MNHN, type material (V-22).

Discussion.—These are grayish worms with introvert shorter than the trunk. The trunk papillae are small domes and the pre-anal papillae are not randomly arranged but in clusters of 2–5. We found up to ten incomplete rings of pale hooks (15–30 μ m) with a bent clear streak and anterior triangle only on the ventral surface. These were overlooked by Hérubel.

This species is well founded on well preserved specimens and, except for an assumed lack of hooks, is very similar to the other members of this genus. Hérubel's three papers are all based on the same material, the second 1904 paper is simply a listing of the stations while in 1907 he gave a more detailed morphological description. However, not all of the museum material is this species (the six Djibouti worms are a mixture of *P. nigrescens* and *P. scolops*).

Some of the animals were surrounded by a mud coating that must have been formed by mucus secretions much like that of *Phascolion lutense*. One had a commensal polychaete sharing the shelter as do some *Phascolion* species. The contractile vessel is large and folded with vesicular swellings, and not villi (even in those specimens with the introvert completely extended.) The many tentacles and enlarged contractile vessel are probably adaptations to increase the surface area for gas exchange, a feature seen in other sipunculans from this region (*Sipunculus*, *Phascolion*).

Distribution.—Red Sea and Gulf of Aden, 18–38 m.

Phascolosoma nigrescens
(Keferstein, 1865)

Phascolosoma nigrescens Keferstein, 1865a: 424, pl. 31, fig. 2, pl. 32, figs. 14–15; 1865b:198–199. (For references between 1865 and 1965 see Stephen & Edmonds, 1972:315.)—Murina, 1964:263–265; 1967:43–44; 1968:422; 1970:68; 1971: 83.—Stephen, 1965:82; 1967:46.—Cut-

ler & Kirsteuer, 1968:353.—Edmonds, 1971:148–149.—Amor, 1975:22–23.—Haldar, 1975:59–60; 1976:4–5.—Saiz Salinas, 1988a:165; 1988b:12.

Phascolosoma (Phascolosoma) nigrescens.—Stephen & Edmonds, 1972:315–316.—Cutler, 1977a:152.—Cutler & Cutler, 1979a:984–985; 1979b:108.—Edmonds, 1980:59–61.—Murina, 1981:14; Cutler et al., 1984:296.—Saiz Salinas, 1984b:208–210.

Phascolosoma puntarenae Grube & Örsted, 1858:13.—Diesing, 1859:761.—Keferstein, 1863:40.—Fisher, 1952:430–432 (not Wesenberg-Lund, 1959a:191–193).

Sipunculus (Phymosomum) puntarenae.—de Quatrefages, 1865:624.

Phascolosoma (Phascolosoma) puntarenae.—Stephen & Edmonds, 1972:319–320.

Phascolosoma varians Keferstein, 1865a: 424–426, pl. 32, fig. 22; 1865b:199–200; 1867:48–49.—de Quatrefages, 1865: 623.—Wesenberg-Lund, 1954a:7–8.—Rice, 1975:35–49.

Phymosoma varians.—Selenka et al., 1883: 69–70.—Shiple, 1890:1–24.—Augener, 1903:340.

Physcosoma varians.—Shiple, 1898:468–473.—Gerould, 1913:419–420.—Fischer, 1922a:16.—ten Broeke, 1925:5.—Satô, 1939:391–394.—Leroy, 1936:424.

Phascolosoma (Phascolosoma) varians.—Stephen & Edmonds, 1972:327–328.—Cutler, 1977a:153.—Rice & MacIntyre, 1979:314.

Phascolosoma agassizii Keferstein, 1867:46 (part).

Physcosoma agassizii var. *puntarenae.*—Selenka et al., 1883:79.

Phascolosoma planispinosum Baird, 1868: 93.—Rice & Stephen, 1970:65.

Phymosoma spengeli Sluiter, 1886:498–499, pl. 3, fig. 3, pl. 4, fig. 7; 1891:117.

Physcosoma spengeli.—Shiple, 1899a:156.

Phascolosoma (Phascolosoma) spengeli.—Stephen & Edmonds, 1972:325.

Phymosoma duplicigranulatum Sluiter,

- 1886:501–502; 1891:118.—Augener, 1903:307–308.
- Phyosoma duplicigranulatum*.—Shiple, 1899a:155.—Sluiter, 1902:13.
- Phascolosoma (Satonus) duplicigranulatum*.—Stephen & Edmonds, 1972:283–284.—Cutler & Cutler, 1983:185.
- Phyosoma lacteum* Sluiter, 1886:507–508, pl. 4, figs. 1, 10, 12; 1891:118.
- Phyosoma lacteum*.—Sluiter, 1902:13.—Shiple, 1899a:155; 1902:134.
- Phascolosoma (Phascolosoma) lacteum*.—Stephen & Edmonds, 1972:311–312.
- Phyosoma diaphanes* Sluiter, 1886:509–510, pl. 4, figs. 2, 11; 1891:118.
- Phascolosoma (Phascolosoma) diaphanes*.—Stephen & Edmonds, 1972:299–300.
- Phyosoma extortum* Sluiter, 1902:15–16, pl. 1, figs. 9–10.
- Phascolosoma (Phascolosoma) extortum*.—Stephen & Edmonds, 1972:303–304.
- Phyosoma evisceratum* Lanchester, 1905a:31, pl. 1, fig. 1.—Stephen & Robertson, 1952:437.
- Phascolosoma (Phascolosoma) evisceratum*.—Stephen & Edmonds, 1972:301–303.
- Phyosoma minutum* ten Broeke, 1925:87–88, text figs. 6–7 (not *Phascolosoma minutum* Keferstein, 1863:40 = *Golfingia minuta* (Kef.)).
- Phascolosoma (Antillesoma) minutum*.—Stephen & Edmonds, 1972:281.—Cutler & Cutler, 1983:179.
- Phyosoma horsti* ten Broeke, 1925:89, text fig. 11.
- Phascolosoma (Antillesoma) horsti*.—Stephen & Edmonds, 1972:280.—Cutler & Cutler, 1983:178.
- Material examined*.—MNHU, type (6976) plus Keferstein's from Nordwachter (6998); UWMP, listed as type; RSME, Stephen's from Senegal (1960.48.10); Indian Ocean material (Cutler & Cutler 1979a); Japanese material (Cutler et al. 1984); our 1988 Caribbean material; *P. diaphanes*, ZMUA, type (V.Si. 101); *P. duplicigranulatum*, BMNH, ZMUA (V.Si. 102), co-types; UZMC, Shipley's 1899a material; *P. evisceratum*, BMNH, type (1924.3.1.163); RSME, Stephen & Robertson's 1952 material (1958.23.66 & 67); *P. extortum*, ZMUA, type (V.Si. 128/6); *P. horsti*, ZMUA, type (V.Si. 108); *P. lacteum*, ZMUA, type (V.Si. 75); *P. minutum*, ZMUA, type (V.Si. 117); *P. puntarenae*, MNHU, type (1023); UZMK, from Grube's original collections; USNM, identified by W. K. Fisher from Bay of Panama (21463) and from Mexico (24732); *P. spengeli*, ZMUA, type (V.Si. 128); UZMC, Shipley's material; *P. varians*, MCZH, type material (423, 428, 1604).
- Discussion*.—The character that most easily distinguishes this species is the clear streak in the hook that has an expansion near the mid-point of both the vertical and the horizontal portion (Fig. 6E). The angle of the point is usually less (as low as 65°) but may be slightly more than 90°, and within one deme the secondary tooth may be large or absent, but is usually small. Hooks are arranged in over 100 mostly incomplete rings and measure 35–90 μm tall. The trunk and the uniform dome-shaped papillae are commonly brown. The introvert is longer than the trunk and may have pigmented bands. The contractile vessel may be enlarged with vesicular swellings but not true villi.
- As earlier authors, including Edmonds (1980:60) have pointed out, "It is difficult to find a satisfactory character which can be used to distinguish *P. nigrescens* from *P. puntarenae* Grube. If they are the same, *P. puntarenae* Grube, 1859 [sic] has priority." We agree with this but have been reluctant to submerge the more familiar name. The type material of *P. puntarenae* is in poor condition, lacks the introvert, and is of no value as a voucher specimen. In Copenhagen there are two specimens that appear to be part of Grube's original material. These had never been dissected nor had any hooks been removed. Our examination showed

them to be *Nephasoma* and probably *N. pelucidum*. So while there is a very poor foundation for the name *P. puntarenae*, *P. nigrescens* is represented by the type plus 13 other bottles of worms in Berlin. The single *P. nigrescens* in Poland, labeled as type, is completely dried out and had not been dissected. The older name has been used only twice in the past 125 years. Fisher (1952) used it for five worms from Panama and Mexico but commented on its similarity to *P. nigrescens*, the difference stated as the bend in the hook. Wesenberg-Lund (1959a) used this name for four worms collected off the Cape Verde Islands. Her comments about the hooks (distinct triangle, absence of swelling on clear streak in many), nephridia (longer than the trunk), and the cool water habitat cast doubt on her record. Saiz Salinas (pers. comm.), having looked at her material, concludes that it is *P. thomense* that we consider conspecific with *P. perlucens*.

The name *P. puntarenae*, based on a shaky foundation, has been avoided by most biologists for over a century, while *P. nigrescens* has been used over 60 times during that same period. Therefore, while we consider these taxa to be conspecific, we shall continue the past practice of using the familiar junior synonym to preserve nomenclatural stability and avoid confusion.

We reaffirm Cutler & Cutler's (1983) conclusion that three names, previously in other subgenera, are conspecific with this species: *P. duplicigranulatum*, *P. horsti*, and *P. minutum*.

The name *P. varians* (Keferstein, 1865a) has been used by several biologists for Caribbean worms (3 from the Pacific) with hooks having the internal structure of *P. nigrescens*, but with the tip being more bent. Most of these hooks also have a blunt secondary tooth on the concave border. Shipley (1890) made a detailed micro and macro anatomical study of *P. varians*. Many features he studied are common to all *Phascolosoma*, and they cannot be used to dif-

ferentiate *P. varians* from *P. nigrescens*. We could find no consistent differences between the two species. When one compares hooks from different populations, a continuum of curvature and secondary tooth development can be observed (Fig. 8). One possible hypothesis is that hook morphology is determined by more than one pair of genes and that allelic frequencies vary from place to place. The alleles for sharp angle and large secondary tooth occur at a high frequency in the Caribbean and a low frequency in the Indo-West Pacific. It is our conclusion that the species are conspecific and that *P. varians* is the junior name because it was described later on the page.

The reason Sluiter (1886) named one worm *P. diaphanes* seems to be the peculiar arrangement of the retractor muscles. The two ventral muscles are partially split into several strands (not uncommon in this genus), the right dorsal retractor is absent, and the left dorsal retractor has its origin atypically close to the ventral nerve cord. Such fusion and splitting of retractor muscles has been observed elsewhere (Gibbs 1973). This species (individual) with anomalous retractors is a junior synonym of *P. nigrescens*.

In the same paper Sluiter (1886) erected *P. lacteum* on the basis of one worm, with no differential diagnosis. The distal hooks are up to 90 μm tall with long points like some *P. nigrescens* from Madagascar (Fig. 8). Sluiter evidently measured the smaller (55 μm) proximal hooks. In all ways this worm fits the *P. nigrescens* morph, and we find no reason to retain it as a separate taxon.

When Sluiter (1886) erected *P. spengeli*, on the basis of two worms, he offered no differential diagnosis so it is not clear how he thought it differed from *P. nigrescens*. He counted only 22 rings of hooks, and we presume he found differences in hook and papillae morphology. Part of the introvert of the dissected worm is missing and some rings have only a few remaining hooks. A large part of each hook is hidden by folds in the

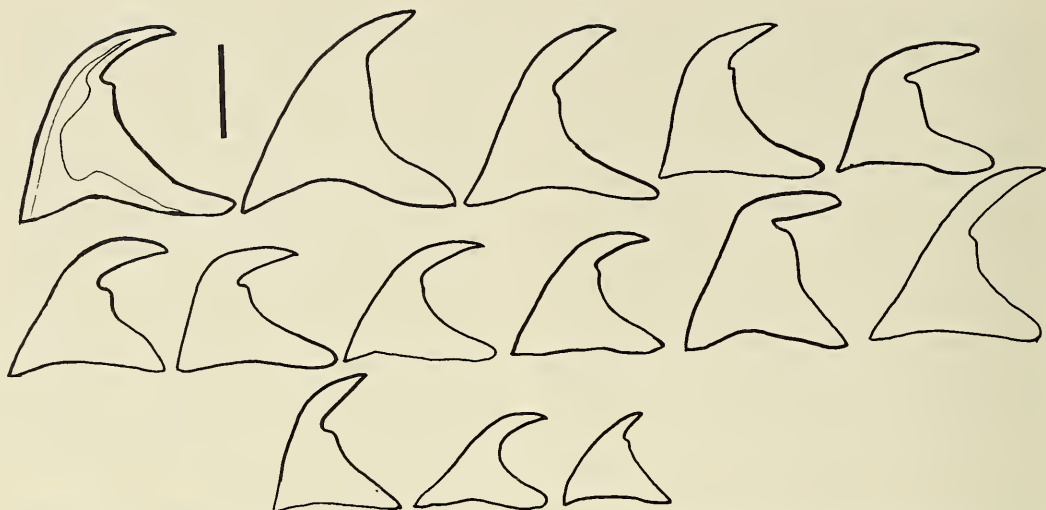


Fig. 8. Composite drawing of *P. nigrescens* hooks from different populations (internal structure same for all but only shown in first); Row one from single Japanese deme, last three from a single worm. Row two from left to right: Keferstein's type (first two), *P. puntarenae* of Fisher, type of *P. extortum* (same as Cutlers' Hawaii *P. nigrescens*), type of *P. varians*, type of *P. lacteum* (same as Cutler's Madagascar *P. nigrescens*). Row 3; types of *P. horsti*, *P. spengeli*, *P. minutum*. (Scale line = 50 μ m.)

tissue of the retracted introvert and consequently easily overlooked. The second worm has at least 50 rings of hooks. The papillae in the mid-trunk are smaller and less dense than in most worms, but overall these animals fall within the range of variation described above and *P. spengeli* becomes a junior synonym. Of the five worms Shipley (1899a) thus described, two are a species of *Themiste*, and the remaining three are *P. nigrescens*.

The putative differences used by Sluiter (1902) to differentiate *P. extortum* from *P. nigrescens* were the loosely wound gut coil and the hook morphology. Sluiter's figure of the hook matches that of *P. nigrescens* very well. The looseness of the gut coil in this single worm is not significant, and there is no reason to retain *P. extortum* as a valid specific name.

Lanchester (1905a) named *P. evisceratum* on the basis of hooks and papillae of one specimen that consisted of the epidermis only. The hook that is illustrated is clearly one from the most posterior part of the introvert. Stephen & Robertson (1952) used

this name for two complete worms but without removing any hooks. Our examination of their material convinced us that it is *P. nigrescens*.

Distribution.—The most wide spread, circum-tropical species in the genus; generally between 30°N and S in shallow water of all oceans.

Phascolosoma noduliferum
Stimpson, 1855

Phascolosoma noduliferum Stimpson, 1855: 390.—Keferstein, 1865a:423; 1865b: 198.—Baird, 1868:92.—Edmonds, 1956: 286–288; 1966:176.

Phascolosoma (Phascolosoma) noduliferum.—Stephen & Edmonds, 1972:316–317.—Cutler, 1977a:152.—Murina, 1978: 121.—Edmonds, 1980:62.

Siphunculus tuberculatus Gray, 1828:8 (part).—Rice & Stephen, 1970:52–53.

Sipunculus (Phymosomum) nodulosus de Quatrefages, 1865:621–622.

Sipunculus (Phymosomum) javanensis de Quatrefages, 1865:622 (part); Stephen &

Edmonds, 1972:339 (incertae sedis).—
Saiz Salinas, 1984b:144–148.

Phascolosoma javanense.—Baird, 1968:94
(part).

Sipunculus (Phymosomum) noduliferus de
Quatrefages, 1865:624.

Phascolosoma grayi Baird, 1868:88.—Rice
& Stephen, 1970:52.

Phymosoma japonicum Selenka et al., 1883:
76–78 (part).

Physcosoma japonicum.—Stephen, 1948:
220.

Material examined.—MNHU, specimen
listed as type but appears to be one of Ke-
ferstein's worms; S. Edmonds' specimen
from Victoria, Australia.

Discussion.—The similarities to *P. agas-
sizii* are marked, but the differences seem
real and lie in the papillae and hooks. The
introvert lacks pigment bands, and the pa-
pillae are of uniform size, more crowded
posteriorly. The uniqueness of the papillae
lies in the arrangement of platelets, i.e.,
around the central pore there is a narrow
ring of closely set units that abruptly be-
come much more dispersed, but do not ex-
tend onto the interpapillae skin. In *P. agas-
sizii* the platelets are more uniformly
distributed over the papillae surface. Illus-
trations of the hooks in the literature appear
to be of the posterior hooks (from incom-
plete rings or scattered). The more anterior
hooks are much more like *P. agassizii* (Fig.
7D, E). In general, these hooks have a more
narrow clear streak, lack a triangle, are 60–
90 μm tall, usually in more than 50 rings,
and have no secondary tooth.

Distribution.—Southern Australia and
Tasmania plus deep water records from
Philippines, New Guinea, and New Zealand
(Cutler 1977a).

Phascolosoma pacificum
Keferstein, 1866

Phascolosoma pacificum Keferstein, 1866:
8–9; 1867:49–50.—Baird, 1868:96.—Ed-
monds, 1956:291–292; 1971:146–148.—

Wesenberg-Lund, 1957b:6–7; 1959c:62–
63.—Stephen, 1967:46.—Haldar, 1976:5–
6.—Cutler et al., 1984:296–297.

Phymosoma pacificum.—Selenka et al.,
1883:63–65.—Fischer, 1895:12; 1896:
337.—Augener, 1903:310–311.

Physcosoma pacificum.—Shiple, 1898:470;
1899a:156; 1902:134.—Sluiter, 1902:
11.—Ikeda, 1904:25–26; 1905:169.—
Fischer, 1914a:6; 1922b:8; 1926:108.—
Leroy, 1942:23.—Monro, 1931:34.—
Satô, 1935:310; 1939:390–391.—Ste-
phen & Robertson, 1952:436.—Stephen,
1952:182.

*Phascolosoma (Phascolosoma) pacifi-
cum*.—Stephen & Edmonds, 1972:317–
318.—Cutler & Cutler, 1979a:965–986.—
Edmonds, 1980:62–63.—Saiz Salinas,
1984b:210–211.

Sipunculus (Phymosomum) javanensis de
Quatrefages, 1865:622 (part).—Stephen
& Edmonds, 1972:339 (incertae sedis).—
Saiz Salinas, 1984b:148–155.

Phascolosoma javanense.—Baird, 1868:94.
Phascolosoma asperum Grûbe, 1868:642–
643.

Phymosoma asperum.—Selenka et al., 1883:
61.

Material examined.—MNHU, labeled
type (6969) but only contains eggs; seven
additional bottles in this collection, at least
two named by Keferstein; MCZH, dried out
but appear to be part of the original collec-
tion and co-types (500).

Discussion.—The uniformly distributed,
tall, cone-shaped papillae give this species
a rough, sand-paper texture. It is one of the
largest species, commonly being up to 80
 μm (occasionally 125 μm), and is uniform-
ly colored. The hooks resemble those of *P.
perlucens*, have a broad base, are 70–125
mm tall, arranged in 80–200 rings, the sec-
ondary tooth is hump-like, and an irregular
clear streak with a separate triangle is pres-
ent (Fig. 6A). The nephridia are long (range
from 75–125% of the trunk length) and at-
tached for most of their length. Up to 40

anastomosing longitudinal muscle bands have been recorded.

Distribution.—From the Red Sea, throughout the Indian Ocean, and the western Pacific Ocean from southern Japan to northern Australia including Indonesia and numerous tropical islands at depths less than 3 m.

Phascolosoma perlucens Baird, 1868

Phascolosoma perlucens Baird, 1868:90–91, pl. 10, fig. 2.—Rice & Stephen, 1970:63–64.—Rice, 1975:35–48.—Rice & MacIntyre, 1979:314.—Edmonds, 1980:63–64.—Cutler et al., 1984:297.

Phascolosoma (Phascolosoma) perlucens.—Stephen & Edmonds, 1972:318–319.—Cutler, 1977a:151.—Cutler & Cutler, 1979a:987.

Sipunculus (Phascolosomum) vermiculus de Quatrefages, 1865:621.

Phascolosoma vermiculum.—Baird, 1868:85.

Sipunculus vermiculus.—Stephen & Edmonds, 1972:339 (incertae sedis).

Phascolosoma (Phascolosoma) vermiculus.—Saiz Salinas, 1984b:90–97, 203.

Phymosoma dentigerum Selenka et al., 1883:67–68.—Sluiter, 1886:500.

Phycosoma dentigerum.—Sluiter, 1891:118; 1902:11–12.—Shipley, 1898:474; 1902:134.—Augener, 1903:304–305.—Fischer, 1922a:10–11; 1922b:7.—Monro, 1931:34.

Phascolosoma dentigerum.—Fisher, 1952:432–434.—Murina, 1964:262.—Cutler, 1965:58.—Cutler & Kirsteuer, 1968:354.—Murina, 1972:306–307.

Phycosoma thomense Augener, 1903:343–344, text fig. 19.

Phascolosoma thomense.—Murina, 1967:44–45; 1968:422.

Phascolosoma (Phascolosoma) thomense.—Stephen & Edmonds, 1972:327.

Aspidosiphon insularis Lanchester, 1905b:40, pl. 2, fig. 4.—Gibbs & Cutler, 1987:56.

Paraspidosiphon insularis.—Stephen & Edmonds, 1972:247.

Phycosoma microdentigerum ten Broeke, 1925:88–89, text figs. 8–10.—Stephen, 1960:517–518.

Phascolosoma (Antillesoma) microdentigerum.—Stephen & Edmonds, 1972:280–281.—Cutler & Cutler, 1983:178.

Phycosoma scolops.—ten Broeke, 1925:86.

Phascolosoma puntarenae.—Wesenberg-Lund, 1959a:191–193.

Phascolosoma spinosum Johnson, 1971; 601–602, pl. 2, figs. 1–9.

Material examined.—BMNH, 3 type specimens; our 1988 Caribbean collections; *P. dentigerum*, MNHU, 2 type specimens (976); *P. microdentigerum*, ZMUA, type (V.Si. 111) plus additional specimens; *A. insularis*, BMNH, type (1924.3.1.80); *P. thomense*, MNHU, type (7010); specimen from Cuba identified by Murina.

Discussion.—In 1970 Rice & Stephen re-described Baird's material and reduced the more familiar *P. dentigerum* to a junior synonym. The assertion that this is the most common rock boring sipunculan in the Caribbean (Rice & MacIntyre 1979) is confirmed by our recent observations. The reddish, conical, posteriorly directed, pre-anal papillae on the dorsal base of the introvert characterize this species. The hooks are 30–60 μm tall, in 15–25 rings (8–10 in a 5 mm worm), and have a large rounded secondary tooth. The internal triangle is separate from the clear streak similar to that in *P. scolops*. The trunk is commonly up to 35 mm long (a few at 45–50 mm), and the introvert is not longer than the trunk, usually with patches of reddish pigment on the dorsal surface.

In 1984b Saiz Salinas reintroduced the name *P. vermiculus* de Quatrefages, 1865. He considered this a senior synonym of *P. thomense*. While we do not disagree with this, we conclude that both names are synonymous with *P. perlucens*. While strict application of the ICZN rules would allow using this older name (not used for over 120 years) we will continue applying the more familiar name to avoid confusion and preserve nomenclatural stability.

The name proposed by Augener (1903) for two worms from St. Thomas, *P. thomense*, was used twice by Murina (1967, 1968) for some Cuban material. Neither author used the name *P. perlucens* and our analysis of their specimens, especially the hook morphology, makes it clear that these two names are conspecific.

In 1983 Cutler & Cutler examined ten Broeke's *P. microdentigerum* and concluded that it is conspecific with *P. perlucens*. We reaffirm that decision. The contractile vessel exhibits only vesicular swellings, not true villi. The only record of this taxon from the eastern Atlantic is Stephen (1960) with no description or illustrations. Many specimens of *P. stephensoni* (a species also having enlarged, reddish, pre-anal papillae) have been collected there. The latter may be what Stephen saw, but we cannot confirm this since his specimens cannot be located.

Gibbs & Cutler (1987) observed that *Aspidosiphon insularis* was a *Phascolosoma* species and probably *P. perlucens*. This information was repeated in Cutler & Cutler (1989), and is reaffirmed here.

Haldar (1988) compared his Indian material to Johnson's (1971) description of *P. spinosum* and concluded that they were conspecific, and we agree.

Distribution.—Common in the Caribbean (Venezuela to southern Florida), and the western Pacific (Queensland to central Japan). Also recorded from several Indian Ocean locations and in the eastern Pacific off Panama and northern Mexico. The two eastern Atlantic records complete this circum-tropical but patchy distribution.

Phascolosoma saprophagicum Gibbs, 1987

Phascolosoma saprophagicum Gibbs, 1987: 135–137, fig. 1.

Material examined.—Several worms identified by P. Gibbs from type collection.

Discussion.—The single known population was collected from a decaying whale skull. The worms have small (20–25 μm) bluntly rounded hooks with a simple nar-

row internal clear streak (Fig. 6H) and small inconspicuous papillae. The nephridiopores are anterior to the anus by up to 10% of the trunk length, and the ventral retractor muscles originate in the posterior quarter of the trunk.

Distribution.—Chatham Island, New Zealand, 880 m.

Phascolosoma scolops

(Selenka, de Man & Bülow, 1883)

Phymosoma scolops Selenka et al., 1883: 75–76, pl. 2, fig. 17, pl. 10, figs. 138–144. (For synonymy between 1883 and 1965 see Stephen & Edmonds, 1972:321 and Saiz Salinas, 1984b:206–208.) (Not *Physcosoma scolops* ten Broeke, 1925:86.)

Phascolosoma scolops.—Stephen, 1965:83; 1966:148; 1967:46–47.—Cutler, 1965: 57.—Stephen & Cutler, 1969:116.—Murina, 1971:83.—Haldar, 1975:61; 1976: 6–7.—Edmonds, 1980:55–60.

Phascolosoma (Phascolosoma) scolops.—Cutler, 1977a:152–153.—Murina, 1978: 121.—Cutler & Cutler, 1979a:987–988; 1979b:108–109.—Cutler et al., 1984:298–299.—Saiz Salinas, 1984b:206–208; 1986: 62–63.

Phascolosoma (Phascolosoma) scolops scolops.—Stephen & Edmonds, 1972:321–323.

Phymosoma scolops var. *mossambiciense* Selenka et al., 1883:76, pl. 10, fig. 144.

Physcosoma scolops var. *mossambiciense.*—Sluiter, 1898:444.—Leroy, 1936: 424.—Stephen, 1942:249.—Edmonds, 1956:285 (not Augener, 1903:339).

Phascolosoma (Phascolosoma) scolops mossambiciense.—Stephen & Edmonds, 1972:324.

Phascolosoma carneum Rüppell & Leuckart, 1828:7.—Diesing, 1859:764.—Baird, 1868:85.—Stephen & Edmonds, 1972: 321.—Saiz Salinas, 1989:210–211.

Phascolosoma longicolle.—Grübe, 1840:47. *Phymosoma psaron* Sluiter, 1886:505; 1891: 118.

Physcosoma psaron.—Sluiter, 1902:13.

- Phascolosoma (Phascolosoma) psaron*. — Stephen & Edmonds, 1972:319.
- Physcosoma spongicola* Sluiter, 1902:16–17, pl. 1, figs. 11–12.
- Phascolosoma (Phascolosoma) spongicolum*. — Stephen & Edmonds, 1972:325–326.
- Physcosoma scolops* var. *adenticulatum* Hérubel, 1904b:563.
- Phascolosoma (Phascolosoma) scolops adenticulatum*. — Stephen & Edmonds, 1972:323–324.
- Phymosoma nahaense* Ikeda, 1904:29–31, figs. 8, 59–62.
- Phascolosoma (Rueppellisoma) nahaense*. — Stephen & Edmonds, 1972:274. — Cutler & Cutler, 1981:85–86; 1983:180.
- Physcosoma socium* Lanchester, 1905b:37–38, pl. 2, fig. 1 (not *Phascolosoma socium* Lanchester, 1908:1 = *Golfingia socia* (Lanchester) = *Golfingia margaritacea* (Sars)).
- Phascolosoma (Phascolosoma) socium*. — Stephen & Edmonds, 1972:324–325.
- Physcosoma agassizii*. — Fischer, 1919:280; 1922a:7–9 (part).
- Phascolosoma rotnnesti* Edmonds, 1956:282–284, text figs. 1–4.
- Phascolosoma (Phascolosoma) rotnnesti*. — Stephen & Edmonds, 1972:320–321. — Edmonds, 1980:64–65.
- Phascolosoma dunwichi* Edmonds, 1956:292–293, text figs. 12–13; 1980:65–66.
- Phascolosoma (Phascolosoma) dunwichi*. — Stephen & Edmonds, 1972:300–301.
- Phascolosoma riukiensis* Murina, 1975:55–57, fig. 2.
- Phascolosoma (Antillesoma) pelmum*. — Cutler, 1977a:150.
- maniense*, ZMUH, type (V5407); *P. psaron*, ZMUA (V.Si. 83); *P. rotnnesti*, AMSS, type (W3598); *P. socium*, BMNH, type; *P. spongicolum*, ZMUA, type (V.Si. 128–7).

Discussion. — These are usually pale worms with reddish-brown mammiform to dome-shaped pre-anal papillae. While the mid-trunk papillae are small and widely scattered, their size, color, and density increases towards the posterior end. The introvert is commonly shorter than the trunk and exhibits pigmented bands. The hooks are arrayed in less than 25 rings, are 20–60 μm tall, and if a secondary tooth is present it is small (Fig. 7F). The clear streak is separate from the distinct triangle.

Apart from hook morphology there are two minor internal differences from the similar *P. albolineatum*: the rectal caecum is present in more than half the worms (vs. 10%), and the retractor origins are closer to the posterior end of the trunk by about 10% (ventral retractors around 60% vs. 50%).

Previous action by Cutler & Cutler (1981) reduced *P. nahaense* to a junior synonym of *P. scolops*, and we reaffirm that decision.

The two subspecies in Stephen & Edmonds (1972) have characters well within the range we observe in the nominate form and are here considered to have no distinct status. In 1980 Edmonds reduced his *P. dunwichi* to a junior synonym of *P. scolops* and we concur.

When Sluiter (1886) described *P. psaron* he asserted that it lacked hooks and had only fine spines. Our examination revealed rows of normal hooks and papillae of the *P. scolops* type. Thus we place this name in synonymy.

The single 25 mm worm Sluiter (1902) described as *P. spongicolum* had unusually puffy, thickened skin, but over time this must have changed because it now appears rather normal. The papillae are mammiform to cone-shaped and while large, not outside the *P. scolops* range. Figure 33Q in Stephen & Edmonds (1972), presented as

Material examined. — MNHU, Selenka's material (960, 977, 978); ZMUA, ten Broeke's 1925 material (V.Si. 119); our Indian, Pacific, Atlantic Ocean material (Cutler 1965, 1977a, Cutler & Cutler 1979a, 1979b); *P. scolops mossambiciense*, MNHU, type material (956, 958); *P. scolops tas-*

Sluiter's *P. spongicolum* hook, is really Sluiter's fig. 14 of an *Aspidosiphon cylindricus* conical hook. Sluiter did illustrate these hooks as fig. 11, which do not show a separate clear steak and triangle. Our observations show the hooks to have the *P. scolops* attributes, and these are considered conspecific taxa.

Lanchester (1905b) described *P. socium* as lacking hooks. Of the three specimens, two lack introverts while the third has rings of *P. scolops* hooks. He compared this to *P. psaron*, but we can find nothing to distinguish this from *P. scolops*.

Examination of *P. rotnesti* material convinced us that Edmonds' (1956) distinctions (papillae platelets and presence of caecum) overlooks the variation within *P. scolops*. While some authors contend that *P. scolops* lacks a caecum, we observed one in 57% of those we examined.

Another hookless worm was given the name *P. riukiuensis* by Murina (1975). The distal end of the introvert is hookless, but it is also white and gives the impression of a regenerating body part. On the basis of other attributes, we conclude that this is an anomalous individual *P. scolops* and not a distinct species.

Saiz Salinas (1989) reexamined *P. carneum* that Stephen & Edmonds (1972) placed in incertae sedis. He concluded that it is conspecific with *P. scolops* and is the most senior available name. However, because the name has been unused for over 120 years, we would again appeal to the logic of ICZN article 79b to preserve nomenclatural stability and conserve the very often used junior synonym in this case.

Distribution.—Common throughout the Indo-West Pacific area including the Red Sea, up to northern Japan, down to northern Australia, and out to Hawaii. The several records from west Africa (Gulf of Guinea and south) cannot all be verified, but we suspect that some of these are *P. stephensoni* as well as the one Bermuda record (Rice

1986). The single Caribbean worm (ten Broeke 1925) is *P. perlucens*.

Phascolosoma stephensoni
(Stephen, 1942)

Physcosoma stephensoni Stephen, 1942:250, pl. 11, figs. 3–5.

Phascolosoma stephensoni.—Wesenberg-Lund, 1963:121–126.

Phascolosoma (Phascolosoma) stephensoni.—Stephen & Edmonds, 1972:326–327.—Cutler, 1977a:153.—Edmonds, 1980:67–68; 1987:197.—Saiz Salinas, 1982:197–199; 1984b:205–206; 1986:63–70; 1988a:166.—Haldar, 1988:127–130.

Phascolosoma laeve.—Keferstein, 1863:38–39 (part).

Sipunculus (Phymosomum) spinicauda de Quatrefages, 1865:621.

Phascolosoma spinicauda, Baird, 1868:93.

Physcosoma lanzarotae Harms, 1921:307 (part).

Physcosoma agassizii.—Fischer, 1922a:7 (part).

Physcosoma scolops.—Monro, 1931:35.

Phascolosoma heronis Edmonds, 1956:293–295, text fig. 14.

Phascolosoma (Phascolosoma) heronis.—Stephen & Edmonds, 1972:309.

Phascolosoma granulum.—Wesenberg-Lund, 1959a:193–194 (part); Cutler & Cutler, 1979b:108.

Material examined.—RSME, type material (1958:23:17); recent east Atlantic material (Saiz Salinas 1982 and as *P. granulum*, Cutler & Cutler 1987a); *P. laeve*, MNHU, Keferstein's 1863 worms (6991).

Discussion.—The large smooth cone-like pre-anal and posterior papillae distinguish *P. stephensoni* from the similar *P. granulum* that shares part of its range. When viewed under the microscope these papillae show none of the platelets typical of this genus. The smaller papillae in the mid-trunk exhibit only very small, uniform size granules, not platelets. The introvert has irreg-

ular pigmented bands and over 40 rings of hooks, 60–110 μm tall. There may be only 10–20 complete rings, the remainder represented by dorsal patches only. Internally, the clear streak is smooth, the triangular space is clear, and posterior to the clear streak is a distinct crescentic clear area (Fig. 1). This figure shows that the clear areas are hollow spaces within a more solid matrix. The shape of the hooks varies from distal to proximal, the latter are more scattered, blunter, smaller (30–45 μm), more triangular, and the crescentic clear area is not often present. In most hooks the secondary tooth is present and distinct.

Edmonds (1980) synonymized *P. heronis* and Fischer's (1922a) Port Jackson *P. agassizii* under *P. stephensoni*, and we concur. For many years *P. laeve* Keferstein, and *P. spinicauda* de Quatrefages, have been considered synonyms of *P. granulatum*. Keferstein's (1863) material is a mixture, some from Sicily is *P. stephensoni* while another portion from the Adriatic is *P. granulatum*. Saiz Salinas has reexamined de Quatrefages single worm and transfers it here, and we concur. As noted above, other biologists have confused these two species (see also Saiz Salinas 1986). An example of this is Harms (1921). Based on his figures *P. lanzarotae* is clearly a mixture of these.

Distribution.—Mediterranean Sea (Sicily and southern Spain), east Atlantic (Azores, Canaries, Gulf of Guinea to South Africa), Indian Ocean (Durban, Mozambique, southwest India), and western Pacific (northern Australia, Solomon Islands, and Hawaii).

Phascolosoma turnerae Rice, 1985

Phascolosoma turnerae Rice, 1985:54–60, figs. 1–4.

Phascolosoma (Phascolosoma) kapalum Edmonds, 1985:43–44, 2 figs.

Material examined.—USNM, type (96687). Six worms from Gyre cruise 87-G-2, sta. EJ-87-127, in cluster of vestimen-

tiferans, 600 m, Bush Hill, off Louisiana, two deposited at USNM (118769).

Discussion.—The sharply bent hooks (45–80 μm tall) have up to 10 long, posterior, basal processes/rootlets (Rice 1985, fig. 2). In light microscope preparations these appear as warts (Fig. 6C). The anterior base is drawn out into a thin prong-like extension. The clear streak is close to the anterior side and often narrows towards the base. The papillae are large and mammillate with “prominent apical protuberances.”

The Bush Hill material differed from Rice's in minor ways: the papillae in the middle of the trunk are almost as large as those at the extremities, and the nephridia are slightly anterior to the anus (not at the same level) and only 50% attached vs. 75%. The introvert is 1.7 (vs. up to 1.4) times the trunk length in a 19 mm worm with an extended introvert.

Edmonds' (1985) *P. kapalum* while geographically separated is also from deep water and the putative differences can be explained by the larger size (hook size) and retracted introverts (shorter than trunk). Edmonds (pers. comm.), after looking at specimens of *P. turnerae*, agrees with this synonymy.

Distribution.—Two of the records are from the Gulf of Mexico; off Florida and Alabama at 366–1184 m in wood, and off Louisiana at 600 m near a cold water seep. In both cases these were in close association with Pogonophora. The third record, from 710 m off New South Wales does not include comparable ecological data.

Zoogeographical Summary

Four of the 16 *Phascolosoma* species appear to have very restricted ranges, three in specialized habitats: *P. meteori* from the Red and Arabian Seas (warm, high salinity, low oxygen tension), *P. turnerae* from the Gulf of Mexico and off Australia (deep cold water in wood or near cold-water seeps), and *P. saprophagicum* from New Zealand (deep

cold water from rotting whale skull). *Phascolosoma maculatum* is from more typical habitat off Indonesia.

The most striking feature of the remaining 12 species is that 11 of these occur in the waters between the Indian and Pacific Oceans (Australia/Indonesia/Philippines). Adding the two local endemic species and *P. turnerae* means that 88% live here. This species richness is unparalleled by other sipunculan genera. Eight of these (50% of species in the genus) are widespread throughout the Indo-West Pacific (IWP). Only *P. granulatum* (from cooler waters of the northeastern Atlantic Ocean and the Mediterranean Sea) and *P. meteori* are not found in this part of the world.

A second noteworthy feature is that only three species live in the Caribbean basin (the circum-tropical *P. perlucens*, and *P. nigrescens*, plus the restricted *P. turnerae*). This situation contrasts sharply with that found in *Aspidosiphon*, the other burrowers in hard substrata, and this suggests a different evolutionary history.

In the eastern Pacific one finds the two shallow water Caribbean species just mentioned, plus *P. agassizii* (cool water), and *P. scolops* (warm water); these four also are found throughout the IWP. *Phascolosoma stephensoni* extends eastward only as far as Hawaii, but also westward to the Mediterranean and the eastern Atlantic. Four species do not extend outside the IWP (*P. albolineatum*, *P. arcuatum*, *P. glabrum*, and *P. pacificum*), while *P. noduliferum* and *P. anulatum* are restricted to the boundary between the Indian and western Pacific Oceans.

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Appendix.—Comparative morphological data.

Trunk length in mm.	Introvert length as % trunk	Number of hook rings	Longitudinal muscle bands		Retractor origins as % of trunk dorsal : ventral		Nephridia length & % attached		Rectal caecum
			anter.	post.					
<i>P. agassizii</i> —California									
8	188	20	14	20	50	62	75	83	N
10	300	18	17	22	50	70	40	75	N
10	90	14	14	18	50	60	50	60	Y
13	154	14	99	21	46	69	46	50	Y
13	108	16	22	24	54	69	53	57	N
15	107	23	18	21	40	60	40	67	N
18	78	18	17	20	44	67	44	50	Y
19	142	24	26	30	47	68	37	43	N
20	60	18	23	24	55	75	50	50	N
23	109	19	21	25	52	65	57	77	Y
26	100	19	17	18	50	58	69	72	N
26	65	12	22	22	54	69	46	67	Y
27	78	24	22	22	44	63	37	70	Y
28	71	20	20	21	54	71	48	?	Y
32	56	22	22	21	47	69	47	73	N
34	103	24	25	28	59	74	47	63	N
35	80	20	20	23	43	57	37	?	N
40	125	?	23	24	45	62	45	72	N
43	70	20	19	22	53	70	47	70	N
45	100	18	18	24	49	60	67	67	N
50	72	22	21	19	52	68	44	77	N
63	63	23	20	25	48	63	51	69	N
65	69	20	22	23	63	78	57	59	N
69	67	22	20	25	54	68	41	71	Y
<i>P. agassizii</i> —Japan									
5	140	16	20	21	50	70	100	80	N
7	143	10	16	18	57	64	71	60	N
7	71	12	20	20	57	71	71	40	N
11	136	37	24	26	55	73	45	40	Y
12	100	16	21	24	42	58	75	50	Y
17	118	15	18	26	47	71	41	57	N
18	117	54	21	24	50	72	44	50	N
19	95	16	24	26	53	63	37	86	N
21	129	16	20	25	62	71	33	57	N
22	73	56	22	22	45	64	45	?	N
23	87	18	20	25	43	57	57	38	N
24	88	27	26	28	46	67	29	71	N
30	73	20	17	99	53	67	50	67	Y
<i>P. albolineatum</i> —West Pacific									
7	114	17	22	22	43	57	57	50	N
9	56	18	16	16	56	67	33	67	N
10	50	16	18	20	50	60	40	75	N
11	91	18	16	18	27	45	36	50	N
12	58	16	16	18	42	50	33	75	N
14	43	18	20	18	50	64	29	75	N
14	50	18	18	20	43	57	50	71	N
15	67	18	20	14	33	47	20	67	N
17	82	20	20	22	29	41	41	43	Y

Appendix.—Continued.

Trunk length in mm.	Introvert length as % trunk	Number of hook rings	Longitudinal muscle bands anter. post.		Retractor origins as % of trunk dorsal : ventral		Nephridia length & % attached		Rectal caecum
<i>P. granulatum</i> —Spain									
18	122	35	18	23	61	72	56	50	N
24	133	74	20	28	46	67	62	40	N
28	86	44	15	24	43	61	46	54	Y
31	113	68	19	30	48	58	39	67	Y
<i>P. nigrescens</i> —I.W.P.									
12	267	150	20	26	58	75	67	50	N
14	71	?	?	26	36	57	50	71	N
15	167	125	24	30	47	60	40	50	Y
21	129	100	22	26	33	52	48	?	?
23	187	200	26	28	39	52	?	?	N
26	131	100	28	24	42	54	54	57	N
27	159	125	20	28	30	44	44	50	N
27	93	100	24	30	33	56	33	?	N
30	117	125	26	28	40	63	60	56	N
30	83	70	30	32	37	53	40	42	N
33	148	200	20	26	30	45	67	55	Y
40	112	150	26	32	40	55	55	68	N
<i>P. nigrescens</i> —Caribbean									
5	160	45	?	?	40	60	30	67	N
6	217	60	20	28	33	67	50	33	N
7	171	150	18	?	29	43	71	?	N
10	140	150	16	22	50	70	70	57	N
11	127	70	?	24	45	64	45	60	N
13	169	133	26	36	31	46	46	50	N
15	133	50	16	24	47	67	47	57	N
19	142	150	22	32	37	74	47	56	N
<i>P. perlucens</i> —Caribbean									
7	114	14	20	18	43	57	57	75	N
10	90	17	18	18	40	50	40	50	Y
12	58	16	19	21	42	58	25	67	N
13	62	18	18	23	46	62	38	40	N
14	93	14	18	20	50	57	43	50	N
16	56	18	20	18	44	56	38	83	N
16	88	19	18	20	44	50	44	29	N
17	88	18	18	23	35	41	35	50	N
19	74	18	16	18	37	53	26	60	N
22	82	22	18	20	41	50	36	?	N
24	54	20	18	22	38	50	25	67	N
25	96	16	17	23	36	48	40	70	N
26	65	24	19	23	35	42	23	33	Y
29	66	20	16	19	41	52	38	73	N
54	43	16	20	20	44	56	37	55	Y
<i>P. scolops</i> —I.W.P.									
5	100	10	16	20	60	80	40	50	Y
6	67	10	16	18	50	67	50	67	N
7	57	14	16	18	57	86	29	50	Y
7	57	10	18	18	29	43	29	50	N

Appendix.—Continued.

Trunk length in mm.	Introvert length as % trunk	Number of hook rings	Longitudinal muscle bands anter. post.		Retractor origins as % of trunk dorsal : ventral		Nephridia length & % attached		Rectal caecum
8	88	10	16	18	50	62	75	67	Y
9	89	12	20	20	56	67	56	80	Y
10	100	12	18	18	50	60	50	60	N
11	82	12	18	20	55	64	27	67	Y
24	67	15	19	22	38	50	33	88	Y
27	93	14	19	21	52	59	37	60	Y
<i>P. stephensoni</i> —Hawaii									
11	91	16	20	24	36	45	45	80	N
19	105	20	20	22	63	74	53	70	N
21	62	20	22	26	57	71	57	83	N
22	114	18	18	26	59	41	64	71	Y
27	96	18	22	20	48	63	48	54	N