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Discrimination and Phylogeny of Solenogaster Species Through the Morphology of Hard Parts (Mollusca, Aplacophora, Neomeniomorpha)

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Abstract. Ten species in five genera and three families from continental shelf and deep-sea collections of neomenioid Aplacophora (Mollusca) are described, emphasizing external anatomy and hard parts—body shape, radula, epidermal spicules, and copulatory spicules—as well as the reproductive system. One genus and seven species are new: *Plawenia* n.g., *Plawenia sphaera, P. argentinensis, Dorymenia tortilis, Eleutheromenia bassensis, E. mimus, Kruppomenia levis,* and *K. delta.* Also included are redescriptions of three published species, emphasizing hard parts for comparisons with the new species and genus: *Dorymenia sarsii* (Koren & Danielssen), *Simrothiella margaritacea* (Koren & Danielssen), and *Plawenia schizoradulata* (Salvini-Plawen). A cladistic analysis of species described here demonstrates the usefulness of hard parts for phylogeny. Specimens came from collections made in the southwest Pacific and the southwest and northeast Atlantic.

Introduction

Aplacophora are vermiform, spicule-covered molluscs that are most numerous and have the greatest diversity of species at depths greater than 200 m in the sea. But their internal anatomy seems to be primitive for the Mollusca, and the vermiform shape derived, a combination thought to be the result of progenesis (Scheltema, 1993, 1996). Aplacophora comprise two taxa, the Neomeniomorpha (=Solenogastres) and the Chaetodermomorpha (=Caudofoveata). Most neomenioids creep by means of a narrow foot on mud bottoms or on hydroids and octocorals upon which they feed; they are hermaphrodites. Chaetoderms are burrowers, feeding upon foraminifera or organic detritus; they are dioecious.

Of the two Aplacophora taxa, we believe the neomenioids are the less derived (Scheltema, 1993, 1996; Scheltema *et al.,* 1994; Ivanov, 1996), and are thus particularly important in considerations of the phylogeny of molluscs. However, the opposite view—that they are more derived—has been expressed (Salvini-Plawen, 1985; Salvini-Plawen and Steiner, 1996).

There are at present fewer than 250 described neomenioid species. However, every deep-sea and continental shelf sample taken with modern equipment, and processed by elutriating the collected sediment through fine screens (<0.4 mm mesh size), will contain at least a few, and sometimes more than a dozen, neomenioid species. Moreover, in regions never before sampled, many or most of these species will be new. By our present estimates, which are based both on the number of undescribed species already collected and on the vast areas of the deep-sea benthic fauna that have yet to be sampled, there are probably some 1000 species worldwide.

Although the works of Salvini-Plawen have raised important evolutionary issues (especially 1972, 1985; also, Salvini-Plawen and Steiner, 1996), aplacophorans have not received broad attention, owing in large part to the difficulty of obtaining living specimens (but see Salvini-Plawen, 1968; Morse, 1979; Morse and Norenberg, 1992; Scheltema and Jebb, 1994). Also, we suggest that the inadequate taxonomic characterization, particularly of neomenioids, has prevented most biologists from becoming seriously involved with them. Authors of most monographs of neomenioids have concentrated on internal anatomy as understood from histology (*e.g.,* Nierstrasz, 1902; Heath, 1911, 1918; Odhner, 1921; Salvini-Plawen, 1978). An important consequence of histological preparation is that hard structures are

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dissolved or destroyed, and have thus been poorly illustrated. Moreover, careful drawings and photographs of entire organisms have seldom been published (but see Scheltema and Kuzirian, 1991). A few isolated epidermal spicules may have been drawn, but at too small a scale for comparisons with other species. Radulae have not been isolated for illustration; the radular teeth have either been drawn as part of a histological section or reconstructed from sectioned material. Copulatory spicules, which dissolve during histological preparation, have practically never been illustrated at all, yet they are often the most important structures for species determination (*e.g., Eleutheromenia* species; see below). The absence of hard-part and external morphology from neomenioid descriptions reduces the value of the characterization—like describing the soft anatomy of a gastropod, but not its shell or isolated radula. As deep-sea ecologists collect more neomenioids, they are thus unable to identify them from the literature.

This paper therefore focuses on external anatomy and on the morphology of isolated hard parts. Descriptions of genera and species are arranged as follows: *Diagnoses* of genera are arranged in the following order: appearance, spicule type, cuticle, epidermis, radula, and particulars of anatomy from anterior to posterior. Species *Descriptions* are divided into Appearance, Cuticle and epidermis, Epidermal spicules, Radula, Copulatory spicules, Notes on anatomy, and Reproductive system. Following both diagnoses and descriptions are *Remarks* on particulars for species discrimination, problems of classification, and notable anatomical features or puzzles. We expect that specialists and nonspecialists alike will be able to use these descriptions to identify similar species at least to genus.

A second aim of this paper was to perform a preliminary phylogenetic analysis based on both the hard-part morphologies and the soft anatomy briefly described here (particularly the reproductive system). We hope that, as new deep-sea collections become available, this paper will serve as a useful model for describing neomenioid species and for investigating their phylogenetic relationships.

General Anatomy of Neomeniomorpha

Recent accounts of aplacophoran anatomy are given in Salvini-Plawen (1985) and Scheltema *et al.* (1994). A generalized illustration of a neomenioid may be found in Figure 1.

The first characteristics one notices in a neomenioid are the size and shape of the body, and the attitude of the myriad, usually shining aragonite spicules covering the animal—that is, the outer *appearance* (Fig. 11C, E). Body shape varies from almost spherical (Fig. 19D) to greatly elongate (Fig. 6A), and the length of mature individuals varies from 1 or 2 mm to 10 cm or more (Fig. 11C, F). A neomenioid may be spiny, smooth, or rough (Figs. 6, 11).

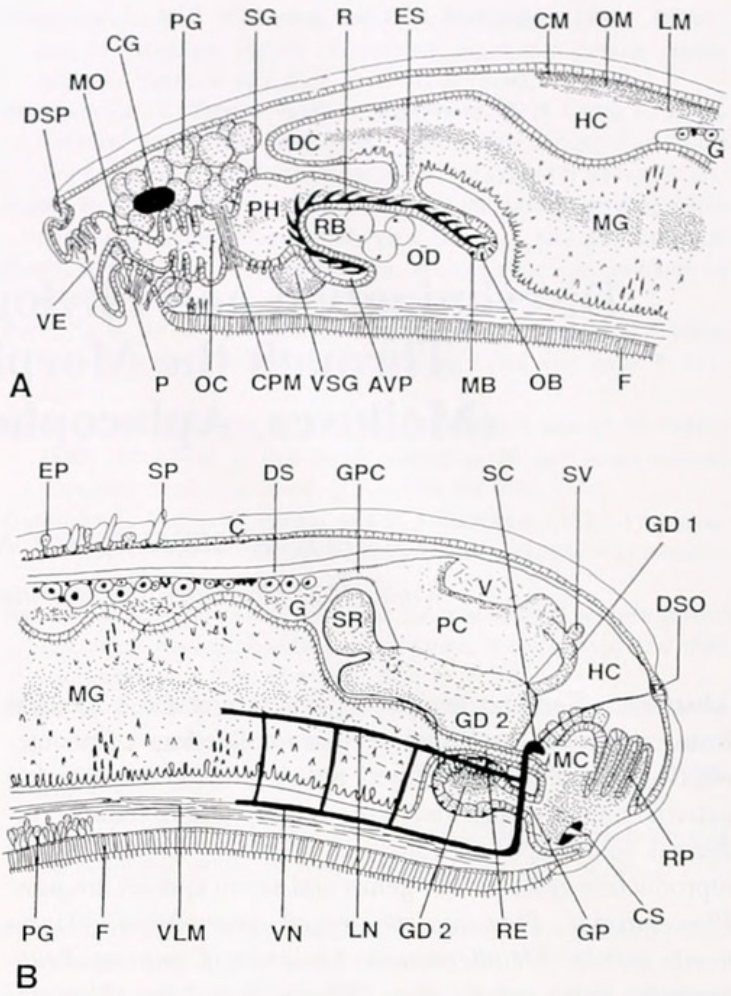

Figure 1. Anatomy of generalized Neomeniomorpha. (A) Anterior. (B) Posterior. AVP anteroventral radular pocket, C cuticle, CG cerebral ganglion, CM circular bodywall muscles, CPM circumpharyngeal muscle, CS copulatory spicule, DC dorsal cecum, DS dorsal sinus/aorta, DSO dorsoterminal sense organ, DSP dorsofrontal sensory pit, EP epidermal papilla, ES esophagus, F foot, G gonad, GD1 upper gametoduct, GD2 lower gametoduct, GP gametopore, GPC gonopericardial duct, HC haemocoel, LM longitudinal bodywall muscles, LN lateral nerve cord, MB membranoblast, MC mantle cavity, MG midgut, MO mouth opening, OB odontoblast, OC oral cavity, OD odontophore, OM oblique bodywall muscles, P pedal pit, PC pericardial cavity, PG pedal gland cell, cells greatly enlarged and numerous anteriorly, PH pharynx, R radula, RB radula bolster, RE rectum, RP respiratory papilla, SC suprarectal commissure, SG salivary gland cell, SP epidermal spicule, SR seminal receptacle, SV seminal vesicle, V ventricle, VE vestibule, VLM ventral longitudinal muscle, VN ventral nerve cord, VSG ventral salivary gland. (Modified from Scheltema *et al.*, 1994.)

The shape of retracted mouth and mantle-cavity openings may be diagnostic (Fig. 15C, H).

The *cuticle* and *epidermis* can be either thick or thin relative to the size of the species. A thick cuticle can occur with a thin epidermis, or a thin cuticle with a thick epidermis, or they may be the same thickness. Gland cells of the epidermis, termed *papillae,* may have long stalks or be unstalked (Fig. 1B, EP); their function has not been determined.

The *epidermal spicules* can be (1) *skeletal* (=tangen-

tial)—the spicules lie within the cuticle, at right angles to each other, in one or more layers, spiraling from ventroanterior to dorsoposterior and from dorsoanterior to ventroposterior (Fig. 20A); (2) *upright* (=radial)—arranged in a single layer, more or less erect, usually with the distal ends extending beyond the cuticle (Fig. 19); and (3) *adpressed,* with a single layer of overlapping spicules lying flat against the body wall cuticle (*e.g., Tegulaherpia;* see Scheltema, 1999a, fig. 3A). Species may exhibit one arrangement, a combination of (1) and (2) (Fig. 12A, D), or a combination of (2) and (3) (*e.g., Acanthomenia;* see Scheltema, 1999b, fig. 2). Spicules may be rounded and hollow with a wall surrounding a single space, or solid and flat or rounded, and encompass a variety of shapes and sizes; several types may occur within a single species. The spicules beside the pedal groove are somewhat arcuate, or at least convexly curved on one side, and are arranged in a single longitudinal row on each side of the pedal groove; they often bear a "handle," or *root* (Fig. 8B spicule 5, and Fig. 20G). Most neomenioids have a few to numerous specialized spicules at the entrance to the mantle cavity; these are presumably used in copulation (Fig. 4K, L).

The *radula* of neomenioids may have two teeth per row (*distichous*) (Figs. 11B, 21A), one tooth per row (*monostichous*) (*e.g., Acanthomenia,* see Scheltema, 1999b, fig. 3A, B), or many teeth per row (*polystichous*) (Fig. 2E, F). The terms "biserial" and "monoserial" are ambiguous, having been applied to both a divided radular membrane and a radula with two teeth per row (Scheltema, 1981); these terms are not used here. Distichous radulae are of two types: they are formed of (1) *bars* entirely attached to the radular membrane and bearing denticles or serrations (Figs. 12F, G, 19E, G), or (2) denticulate *hooks* mostly free of the radular membrane (Fig. 11D). A radula is lacking in 20% of known species. Both distichous and polystichous radulae lack a central, median tooth like the rachidians in gastropod radulae, the only exception being in some species of Proneomeniidae (*e.g.,* García-Alvarez *et al.,* 1998). In distichous radulae, the largest denticles are lateral (Figs. 7H, J, 17A, 21F); during growth, denticles are added either medially or by the bifurcation of a pre-existing denticle (Fig. 7H). In many species, the radula passes into, and is enclosed by, an anteroventral radular pocket, or pair of pockets (Figs. 1 AVP; 6B, 19F).

One or more *copulatory spicules* are found in many species of neomenioids (Fig. 14). They are largely or entirely calcitic (Figs. 4A, 9) and secreted in deep, usually paired pockets of the mantle cavity; they are thus of epidermal origin. Accessory spicules may be present (Figs. 20C, 22B, D). The exact function of copulatory spicules has never been determined. They are deciduous or become resorbed in some species, and some may be one-third the total length of an individual.

Notes on anatomy are given here for various species, according to their importance to that species for discrimination or for defining membership in higher ranks. The *tetraneural nervous system,* not described here, is morphologically quite constant among neomenioids. Examples may be found in Salvini-Plawen (1985) and Scheltema *et al.* (1994).

Salivary glands are associated with the radula or, if the radula is absent, with some part of the pharynx (Fig. 1, VSG, SG). In this work, the types of ventral salivary glands were determined according to Welsch and Storch (1973), rather than according to Salvini-Plawen (1978). The glands are usually ventrally paired, simple, multicellular, tubular glands that are elongate or saclike (Figs. 5A, 6B). They are sometimes acinar, or occur in groups of single goblet gland cells, or are compound.

The *midgut* dominates the midregion of the body and is extensive in elongate species. It is *sacculate* (*i.e.,* with lateral pouches) in those species where the midgut wall is interrupted by serially repeated, lateroventral muscles (see Scheltema *et al.,* 1994, fig. 13C). A dorsal cecum may extend anteriorly above the pharynx (Fig. 1A, DC; Scheltema *et al.,* fig. 8C).

The *mantle cavity* contains one or two gametopores, the anus, openings of the copulatory spicule sacs, and usually respiratory folds or papillae. There is usually a dorsoterminal sense organ on the outer dorsal wall of the mantle cavity.

For most species herein, the *reproductive system* is described. As in the chaetoderms, it is unique among molluscs, because the gonads, with only a single exception, empty through paired *gonopericardial ducts* directly into the pericardial cavity (Fig. 1B, GPC); in other molluscs, the gonads empty through gonoducts that bypass the pericardium. The gametes thus pass through the pericardium before entering the (usually) U-shaped, paired, upper and lower gametoducts (=pericardioducts and spawning ducts or shell glands; Stachowitsch, 1992) (Fig. 1B, GD1, GD2). The lower gametoducts, in turn, empty into the small posterior or posteroventral mantle cavity through paired gametopores; or the lower gametoducts unite before opening through a single gametopore. Usually, one or more paired seminal receptacles are found near the union of the upper and lower gametoducts (Figs. 1B, SR; 5A, 5). Seminal vesicles are uncommon; where they do occur, they are found in conjunction with either the gonopericardial ducts or the upper gametoducts (Fig. 6C). Internal fertilization is inferred from the presence of seminal receptacles, from introsperm morphology (Buckland-Nicks and Scheltema, 1995), and from observation of living *Epimenia* (Scheltema and Jebb, 1994).

Materials and Methods

Species were selected from the following collections of Aplacophora: West European Basin (INCAL, 15 July to 11 August, 1976, Centre National de Tri d'Océanographie Bio-

logique [CENTOB]; and RV *Chain* Cruise 106, 15 August to 6 September, 1972, Woods Hole Oceanographic Institution); off Gibraltar (BALGIM, 25 May to 22 June, 1984, CENTOB); Bass Strait (Bass Strait Survey 1979–1984, Museum of Victoria, Australia); and Argentine Basin (RV *Atlantis II* Cruise 60, 10.iii–30.iii.1971).

Taxonomy. Holotypes were drawn under a dissecting microscope equipped with an ocular drawing tube and then photographed. Measurements were made on drawings, either with a map wheel or with dividers. The *length* of a specimen in lateral view is measured along the axial midline; two diameters, the dorsoventral *height* and lateral *width,* are measured in lateral and either dorsal or ventral view, respectively.

Epidermal spicules were dislodged with a needle, either into glycerine in a depression slide or into distilled water on a flat slide; in the latter case, they were then air dried and covered with a coverslip and mountant. These isolated spicules were then illustrated with the aid of an ocular drawing tube. Solid spicules were examined under cross-polarized light, which is broken up into birefringent color bands by the aragonite crystals of the spicules; selected isochromes were drawn and their thickness determined.

Radulae and copulatory spicules were isolated and prepared as follows. The anterior and posterior ends of an individual were cut off and placed in a depression slide with a drop of commercial hypochlorite solution (household bleach), which dissolves the tissue. The radula or copulatory spicules were then teased away from the remaining cuticle and epidermal spicules. The preparations were washed several times by carefully adding and drawing off distilled water with a pipette, and a drop of glycerine was then added. When radular teeth were to be examined with an oil immersion lens, either a temporary or permanent slide was made. In the first case, the radula was transferred into glycerine on a flat slide, and a coverslip was added. To make a permanent slide, the radula was washed in distilled water, then pipetted into a drop of a water-miscible mountant (CMCP-10) on a slide and a coverslip added. After drawings had been made of copulatory spicules in glycerine on a depression slide, permanent slides were prepared. The spicules were washed with distilled water and transferred to a slide with the aid of a micropipetter, which can pick up and release individual spicules. After air-drying, a mountant and coverslip were added. Measurements of radulae, epidermal spicules, and copulatory spicules were made with an ocular micrometer.

Histologic sections were cut at 7 μm (paraffin embedded) or at 1.5 or 3.0 μm (Epon embedded). The former were stained with hematoxylin and Gray's double contrast or with Mallory-Heidenhain trichrome; the Epon sections were stained with azure II and methylene blue. All drawings of sections have the following conventions: (1) *double lines, no stippling, cell walls not indicated:* gonopericardial ducts, seminal receptacles, copulatory spicule sacs; (2) *single line:* dorsal sinus, pericardium, heart; (3) *double lines, stippling only:* seminal vesicles; (4) *double lines, cell walls, no stippling:* upper gametoducts, rectum, mantle cavity; (5) *double lines, stippling, cell walls:* lower gametoducts.

Holotypes, paratypes, and voucher specimens are deposited in, or were borrowed from, the following museums: MNHNP, Muséum National d'Histoire Naturelle, Paris; MV, Museum of Victoria, Melbourne; UIB.Z.M, University of Bergen Zoological Museum, Norway; USNM, National Museum of Natural History, Washington, DC.

Phylogeny. The data matrix for a cladistic analysis was created with MacClade version 3.04 (Maddison and Maddison, 1992). The exhaustive search option in PAUP version 4.0b1 (Swofford, 1998) was used to reconstruct the phylogeny, and MacClade was used for subsequent analysis and interpretation of trees. Decay values (Bremer, 1988, 1994) were calculated with AutoDecay version 4.0 (Eriksson, 1998), and bootstrap and jacknife values were calculated with PAUP version 4.0b1 with 1000 replicates.

Systematic Account

NEOMENIOMORPHA Pelseneer, 1906

Ventroplicida Boettger, 1956; Solenogastres Gegenbaur, 1878 [*partim*], Salvini-Plawen, 1967. *Non* Neomeniamorpha Salvini-Plawen, 1978.

Diagnosis: Aplacophoran molluscs with a narrow footfold in a ventral, longitudinal pedal groove and without a cuticular oral shield or mantle cavity ctenidia; midgut as a combined stomach and digestive gland; monoecius.

Remarks: The telltale ventral groove in a spicule-covered, cylindrical organism immediately identifies it as a neomenioid mollusc.

PRONEOMENIIDAE Simroth, 1893

Type genus. Proneomenia Hubrecht, 1880.

With two genera, *Proneomenia* Hubrecht and *Dorymenia* Heath.

Dorymenia Heath, 1911

Type species. Dorymenia acuta Heath, 1911, by monotypy [Bull. Zool. Nom. 38:185].

Known distribution. Reported from the northeast, southeast, and southwest Pacific Ocean, northeast and northwest Atlantic Ocean, Mediterranean Sea, off East Indies, and Antarctica; 21 species are described from 50 to 3200 m depth.

Diagnosis. Body elongate, slender, smooth, to 10 cm long, with or without posterior fingerlike projection; skeletal spicules hollow, in several layers; upright spicules, if present, solid, paddle-shaped, small; cuticle thick; epidermis thin, with long, stalked epidermal papillae extending through the cuticle; radula polystichous, largest teeth in

each row lateral, tooth rows on each side of median line mirror images, some species with a median tooth; anteroventral radular pocket single (Fig. 6B); ventral salivary glands tubular, long, ducts paired or single; midgut sacculate; with one or more dorsoterminal sense organs; paired seminal receptacles single; gametopore single; with paired copulatory spicules; gill folds greatly reduced; mantle cavity with one or more deep anterior pockets.

Remarks. Proneomenia and *Dorymenia* may be synonyms. The sole criterion for separating the two genera is the presence (*Dorymenia*) or absence (*Proneomenia*) of copulatory spicules (see, *e.g.,* Salvini-Plawen, 1978). Dissolution of copulatory spicules is evident in some individuals of both *D. sarsii* and *D. tortilis,* but it is not known whether empty copulatory spicule sacs are retained. However, Hubrecht's (1881) description of the type species *Proneomenia sluiteri* includes illustrations of paired, ventral mantle cavity pockets that appear to be empty copulatory spicule sacs.

Dorymenia sarsii (Koren & Danielssen, 1877)
(Figs. 2C, E, 3A, B, 4E, G, H, J, L)

Neomenia sarsii Koren and Danielssen, 1877; *Proneomenia sarsii* (Kor. & Dan.), Hansen, 1889; *Simrothiella sarsii* (Kor. & Dan.), Pilsbry, 1898; *sarsi* of authors.

Lectotype (Odhner, 1921 [as "prototype"]). UIB.Z.M 2074 (alcohol specimen, anterior and posterior ends missing, removed before Odhner's [1921] investigations; spicule slide): Length >40 mm, height 1.5 and 1.2 mm at anterior end and midbody, respectively. Kristianiafjord [Oslo Fjord], 190–225 m, coll. G. O. Sars.

Voucher specimens. UIB.Z.M 19850: Length ~32 mm, height 2.0 and 1.5 mm at anterior end and midbody, respectively. Herløfjord, 150 m (alcohol specimen, posterior end dissected; spicule slide). UIB.Z.M 53025: Length 46 mm, height 1.9 and 1.4 mm at anterior end and midbody, respectively. Osefjord, 60°30′30″N, 6°55′40″E, 206 m (alcohol specimen, anterior and posterior ends dissected; spicule, radula, and copulatory spicule slides).

Material examined. Lectotype and three lots from the Bergen Museum (UIB.Z.M 53024, 53025, 19850).

Description.

Appearance: With characters of the genus; with posterior fingerlike projection (Fig. 2C). Lengths of examined specimens to 46 mm, height at midbody to 1.5 mm (53 mm by 2.3 mm, Odhner [1921]; 70 mm by 3 mm, Koren & Danielssen [1877; trans. 1879]); anterior height to 2.0 mm; posterior projection to 2.0 mm long, height to 0.5 mm.

Cuticle and epidermis: Cuticle 40 to 50 μm thick, epidermis thinner.

Epidermal spicules: Skeletal spicules to 330 μm long, 19 μm wide, curve shallow, solid distal tips to 25 μm long, wall thickness to 6 μm, proximal end straight, to 45 μm long; spicules < 110 μm in length few (Fig. 3A, B). Upright paddle-shaped spicules sparse, to 103 μm long, 11 μm wide, curved, distal end rounded, bases narrow to wide (Fig. 3B, spicules 1, 2). Spicules from beside pedal groove solid, of two types: (1) flat, thin spicules, one margin straight, the other convex, with narrow root, to 120 μm long, 13 μm wide, <3 μm thick (spicule 4); (2) curved spicules lateral to type 1 round in cross-section with narrow base, to 135 μm long, 9 μm wide (spicule 3).

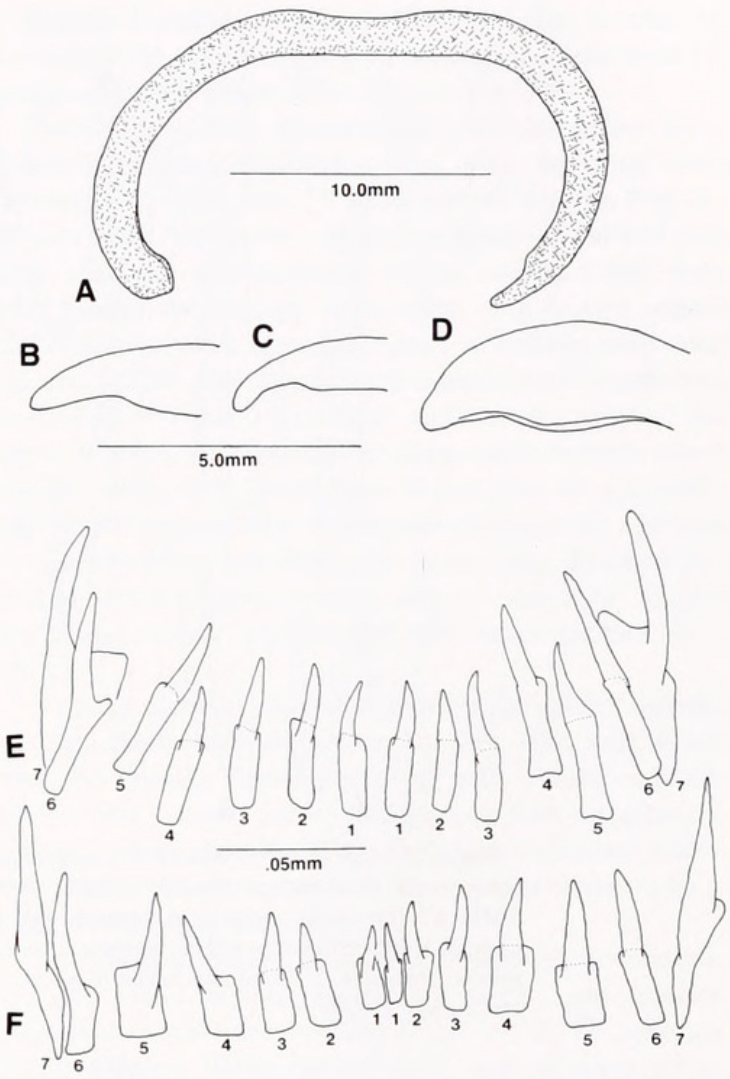

Figure 2. *Dorymenia* species. (A) *Dorymenia tortilis* n. sp. holotype, anterior to left. (B–D) Narrow posterior extension of: (B) *D. tortilis;* (C) *D. sarsii* (Koren & Danielssen); and (D) *cf. D. peroneopsis* Heath. (E) Radula tooth row of *D. sarsii* (voucher UIB.Z.M 53025), and (F) radula tooth row of *D. tortilis* paratype 1; mirror-image teeth numbered on each side of median line.

Radula (one examined, numbers in parentheses from Odhner [1921]): With 14 (16) teeth per row, rows about 28 (>30), with median furrow, length of teeth from 48 μm at median furrow to 93 μm at lateral margin, tooth bases narrow, 10 μm or less (Fig. 2E).

Copulatory spicules (2 individuals examined): Spicules undergoing dissolution in one individual, but accessory copulatory spicules and mantle cavity edge spicules intact; copulatory spicules (Fig. 4E, G) with a short, flaccid hyaline region below a solid, calcium carbonate distal end 500 μm

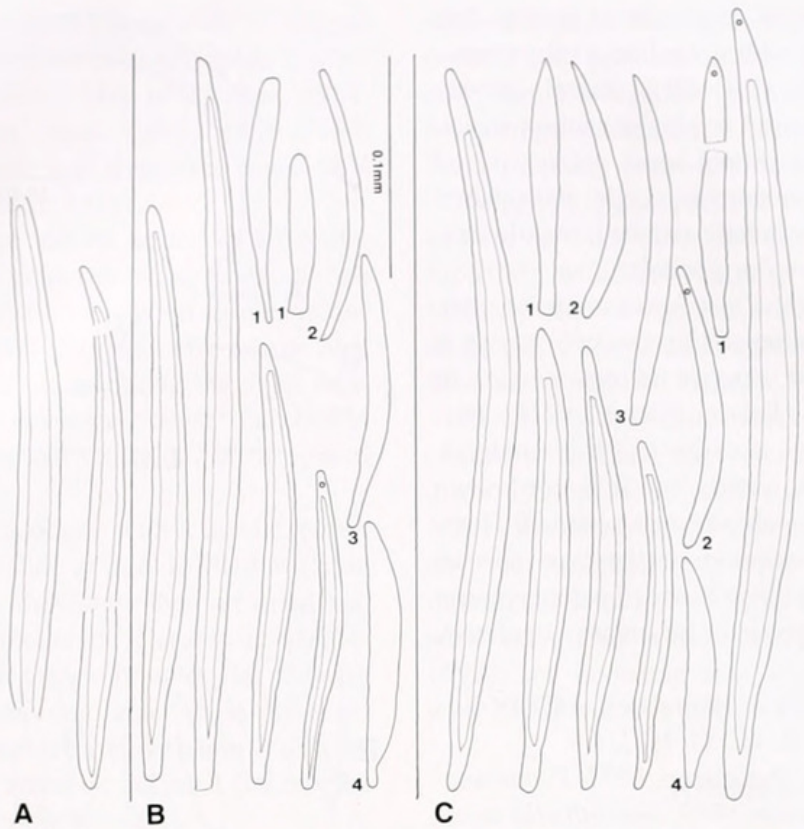

Figure 3. Epidermal spicules of *Dorymenia* species. (A) *Dorymenia sarsii* (Koren & Danielssen) from holotype. (B) *D. sarsii* from voucher UIB.Z.M 19850 and, with small circle at distal end, voucher UIB.Z.M 53025. (C) *Dorymenia tortilis* n. sp., spicules with a small circle at distal end from holotype, all others from paratype 1. Skeletal spicules without numbers; 1 upright paddle-shaped spicules en face; 2 upright paddle-shaped spicules from side; 3 curved rods lateral to 4, overarching pedal groove, and 4 flat spicules from single row beside pedal groove.

long by 90 μm wide; bent, pointed tip 70 μm long, 20 μm at its widest; calcitic portion medially grooved; accessory copulatory spicules to 315 μm long by 28 μm wide, rounded at both ends, triradiate in cross-section (Fig. 4J); epidermal spicules at opening of mantle cavity truncated distally at an angle, to 95 μm long, 8 μm wide (Fig. 18L); in second individual no copulatory spicules present, accessory copulatory spicules undergoing dissolution (Fig. 4H), and mantle cavity edge spicules not found.

Reproductive system: Not re-examined here.

Remarks. The spelling of this species is sometimes found in the literature as *sarsi,* an unnecessary emendation of *sarsii* (for Sarsius: Bull. Zool. Nom. 38:185–186). The exceptional dimensions given by Koren and Danielssen (1877, 1879)), greater than reported or seen since for this species, may be a twofold measuring error; the greatest height of the lectotype is 1.5 mm, reported as 3 mm by Koren and Danielssen. The authors also reversed anterior and posterior ends in their verbal description of body shape. That the lectotype was properly chosen by Odhner (1921) seems to be in no doubt, as it was collected by Sars and is from the type locality.

Dorymenia sarsii appears to be a continental shelf species from Scandinavian waters. The attribution of *Dorymenia* sp. in Scheltema *et al.* (1994) to *D. sarsii* is not correct (Salvini-Plawen, 1997), and does not extend the geographic distribution of *D. sarsii* to the Iberian shelf region.

Dorymenia tortilis sp. n.

(Figs. 2A, B, F, 3C, 4A–D, F, K, 5, 6A–E)

Dorymenia sp., Scheltema *et al.,* 1994 [not *D. sarsii,* Salvini-Plawen, 1997, p. 48], figs. 5c, 7b, 10c, 11c, 13a, b, d–f, 18c, 22e, 23f, 24e, g.

Holotype. MNHNP (alcohol specimen, spicule slide): Length 36.1 mm, height 1.7 mm at anterior end and midbody. NW of Gibraltar, 36°50.4′N, 9°14.9′W, 681 m, BALGIM [CENTOB] CP-03.

Illustrated paratypes 1, 2. MNHNP (no. 1, dissected alcohol specimen; radula, spicule slides); (no. 2, dissected alcohol specimen; spicule, copulatory spicule slides). Type locality.

Material examined. Eight individuals from type locality.

Description.

Appearance: With the characters of the genus; with a posterior fingerlike projection (Figs. 2A, B, 6D); holotype largest individual examined.

Cuticle and epidermis: Cuticle thick, 116 μm; epidermis thin, 12 to 14 μm, with oval to quadrate papillae borne on long, slender stalks.

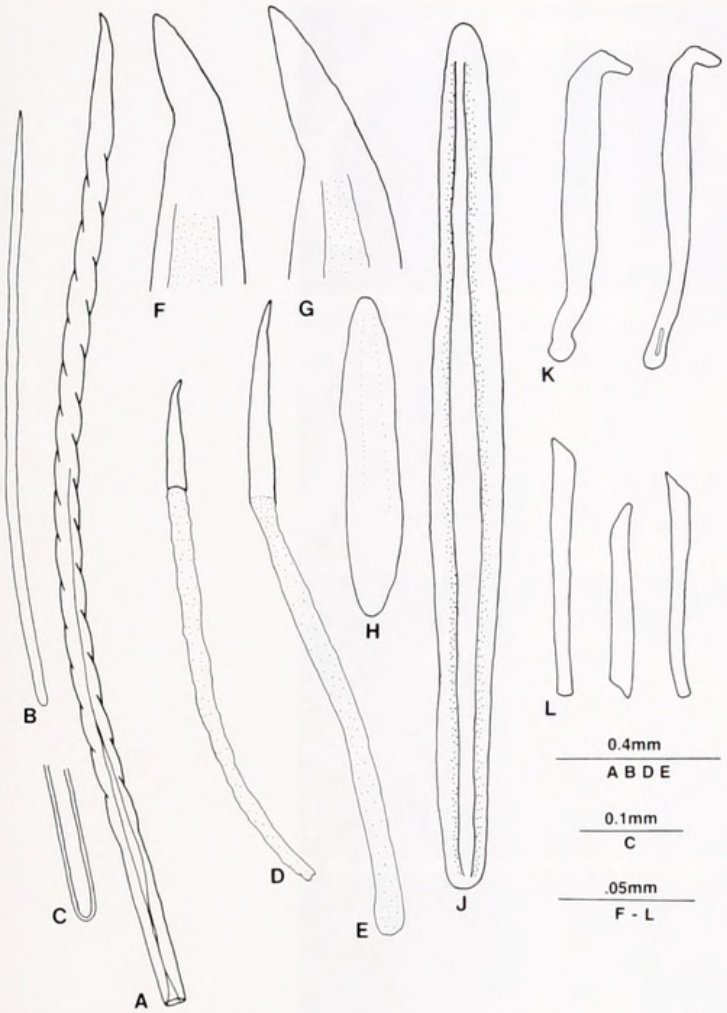

Figure 4. *Dorymenia tortilis* n. sp. and *D. sarsii* (Koren & Danielssen), copulatory spicules. (A) Fully formed spicule of *D. tortilis* (paratype 2) with short, solid distal end and long, twisted, hyaline, proximal end stiffened by crystals of calcium carbonate. (B) Isolated hollow, stiff hyaline rod that will form inner core of a fully developed spicule (paratype 2). (C) Enlarged proximal end of (B). (D, E) Flaccid copulatory spicules undergoing dissolution, with proximal hyaline matrix lacking core and calcium carbonate crystals: (D) *D. tortilis* (paratype 1); (E) *D. sarsii* (voucher UIB.Z.M. 53025). (F, G) Solid distal ends, enlarged, of (A) (*D. tortilis*) and (E) (*D. sarsii*), respectively. (H, J) Triradiate accessory copulatory spicules of *D. sarsii;* (J) fully formed from same individual as (E); and (H) spicule undergoing dissolution from an individual without copulatory spicules (voucher UIB.Z.M 19850). (K, L) Spicules from opening of mantle cavity: (K) *D. tortilis* (paratype 1); (L) *D. sarsii* (voucher UIBZ.M 53025).

Epidermal spicules: Skeletal spicules to 325 μm long, 18 μm wide, curve pronounced, solid tip to 24 μm long, wall thickness to 5 μm, proximal end straight, length to 45 μm; short hollow spicules <110 μm numerous (Fig. 3C). Upright paddle-shaped spicules deeply curved, distally pointed, to 117 μm long, 13 μm wide, base broad (Fig. 3C, spicules 1, 2). Spicules from beside pedal groove solid, of two types: (1) flat spicules, one margin convex, the other concave, to 128 μm long, 13 μm wide, <3 μm thick, with root (spicule 4); (2) lateral to type 1, curved spicules round in cross-section, base narrow to broad, to 153 μm long, 9 μm wide (spicule 3).

Radula (2 examined) with 14 teeth per row, number of rows about 44, length of medial teeth 28 μm, lateral teeth 85 μm, tooth bases broad, 10 to 15 μm (Fig. 2F).

Copulatory spicules (2 examined): Spicules in one individual undergoing dissolution (Fig. 4D), the other with intact spicules (Fig. 4A, F); intact spicule 2.4 mm long by 60 μm wide, with solid, calcium carbonate distal end and long, stiffened, hyaline region twisted around a stiff, hollow, hyaline rod forming a core (Fig. 4A); twisted region stiffened by densely scattered crystals of calcium carbonate aligned with the turns and at angle to each other, spicule less twisted proximally; solid distal end broadly grooved on opposite sides, 270 μm long, 55 μm greatest width in intact spicule, with a bent, pointed tip 38 μm long, 18 μm wide. An isolated, presumably developing solid end not attached to a proximal hyaline portion, tip 50 μm long, 20 μm wide, and an isolated, hollow hyaline core 1.5 mm long, 21 μm wide, also present in individual with intact spicules (Fig. 4B, C).

Notes on anatomy: Anteroventral radular pocket extending posteriorly beneath radular sac (Fig. 6B), with distal teeth undergoing dissolution (Fig. 6E). Paired salivary glands with united ducts opening into base of pharynx beneath radular sac (Fig. 6D). Radular sac divided proximally (Fig. 6B). Dorsoterminal sense organ single, with a large dorsal blood vessel.

Reproductive system: In common with other *Dorymenia* species, paired seminal receptacles single, and anterior pockets of mantle cavity deep (Fig. 5A, B, G; see also Salvini-Plawen, 1978). Dorsal, distal ends of upper gametoducts with three pockets appearing to function as seminal vesicles (Fig. 5A, C, D, 6C). In common with *D. sarsii* (Hansen, 1889), a large, distal, ventral lobe present on each lower gametoduct just before paired gametoducts unite (Fig. 5E, F). Gametoduct opening into the mantle cavity single (Fig. 19G). Distal ends of copulatory spicules borne on papillae.

Remarks. Dorymenia tortilis differs from *D. sarsii* in its (1) broader radular tooth bases, (2) more numerous tooth rows, (3) greater curvature of the skeletal spicules, (4) more numerous short epidermal spicules, (5) greater length and curvature of the paddle-shaped spicules, (6) shape of spicules beside the pedal groove, (7) shorter solid distal ends of the copulatory spicules, (8) spicules at the entrance to the mantle cavity hooked and larger, and (9) absence of accessory copulatory spicules.

Only one other north Atlantic species, *D. peroneopsis* Heath, has a fingerlike terminal extension of the body (Heath, 1918). The type material is unknown, but two recently collected individuals from the North American Basin probably belong to this species. They differ from both eastern Atlantic species in larger size, broader anterior and posterior ends (Fig. 2D), lack of paddle-shaped upright spicules, and presence of paired, fanlike arrays of either

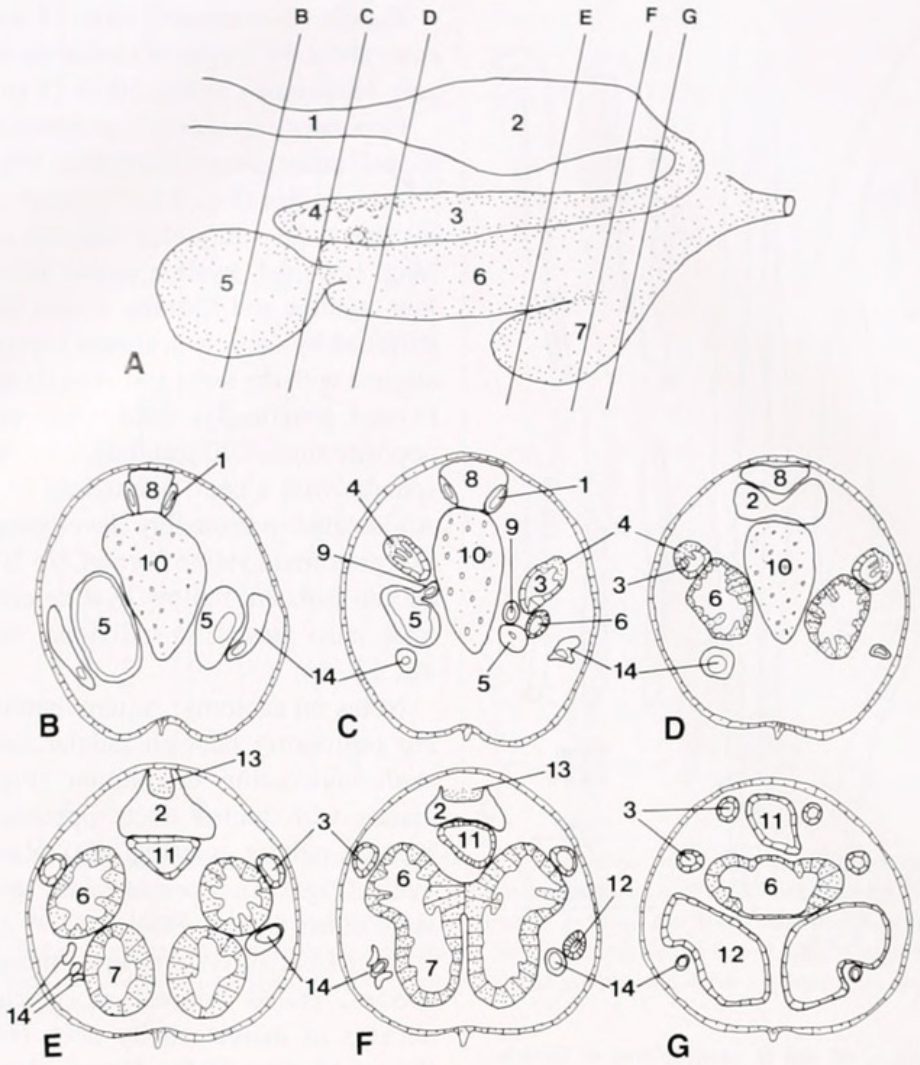

Figure 5. *Dorymenia tortilis* n. sp., reproductive system. (A) Reconstruction from histologic sections, anterior to left. (B–G) Cross-sections indicated in (A) semischematic (see text for description). 1 gonopericardial duct, 2 pericardium, 3 upper gametoduct, 4 region of upper gametoduct serving as seminal vesicle, 5 seminal receptacle, 6 lower gametoduct, 7 ventral lobe of lower gametoduct, 8 dorsal sinus, 9 duct of seminal receptacle, 10 midgut, 11 rectum, 12 mantle cavity pocket, 13 heart, 14 copulatory spicule sac.

copulatory spicules or accessory spicules seen within the open mantle cavity.

PRUVOTINIDAE Heath, 1911

Pruvotiniidae Heath, 1911. Pararrhopaliidae Salvini-Plawen, 1972.

Type genus. Pruvotina Cockerell, 1903.

Remarks. The taxon is poorly defined. Taxa with a combination of hollow upright barbed epidermal spicules, curved hollow skeletal and upright spicules, and a distichous radula with denticulate hooks include *Pruvotina, Pararrhopalia* Simroth, 1893, *Eleutheromenia* Salvini-Plawen, 1967, *Labidoherpia* Salvini-Plawen, 1978, and *Gephyroherpia* Salvini-Plawen, 1978; they were divided into two subfamilies on the basis of salivary gland morphology (Salvini-Plawen, 1978). *Lophomenia* Heath, 1911, *Halomenia* Heath, 1911, *Metamenia* Thiele, 1913, *Hypomenia* van Lummel, 1930, and *Forcepimenia* Salvini-Plawen, 1969, included in two other pruvotinid subfamilies (Salvini-Plawen, 1978), lack barbed spicules.

Eleutheromenia Salvini-Plawen, 1967

Paramenia Pruvot, 1890 [*non* Brauer & Bergenstamm, 1889] [*partim*]; *Pruvotina* Cockerell, 1903 [*partim*]; *Perimenia* Nierstrasz, 1908.

Type species. Paramenia sierra Pruvot, 1890, by monotypy.

Known distribution. Bass Strait and off southeast Australia; western Mediterranean; at depths of 50 to 400 m.

Diagnosis. Small, spiny, stout, with hollow, barbed, upright spicules; with or without dorsal carina; cuticle and epidermis thin, without stalked papillae; radula with distichous hooks; multicellular dorsal salivary glands not opening through a papilla; ventral salivary glands saclike with tubular ducts; midgut not sacculate or indistinctly so; with an elongate pericardial cavity forming an anterior glandular sac ("sac ovigère" of Pruvot [1891]); pericardial glands present; seminal receptacles as saclike extensions of

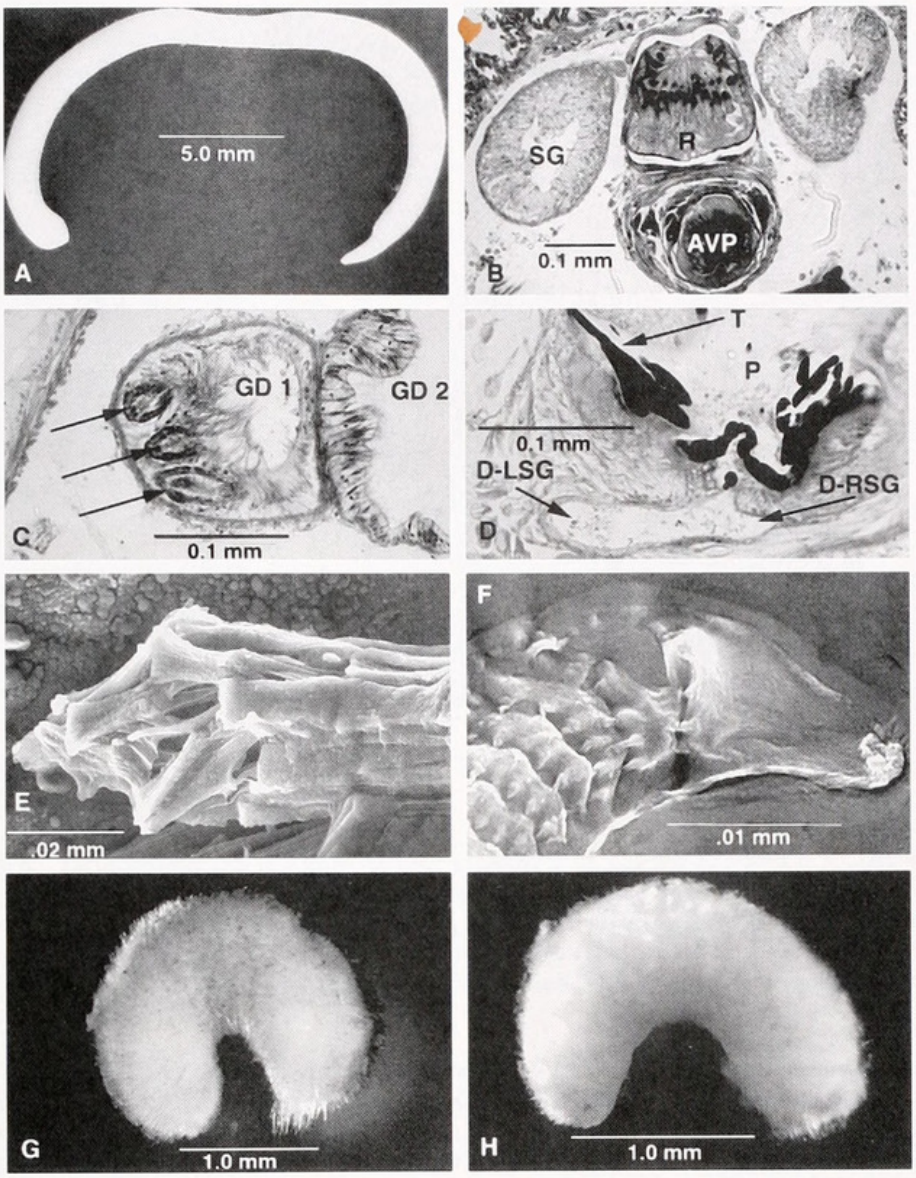

Figure 6. (A–E) *Dorymenia tortilis* n. sp.: (A) Holotype. (B) Cross-section showing single anteroventral radular pocket (AVP), ventral salivary gland (SG), and radula within radular sac (R). (C) Seminal vesicles (arrows) in pockets of upper gametoduct, GD1; GD2, lower gametoduct. (D) Joined ducts of left (D-LSG) and right (D-RSG) ventral salivary glands just before emptying into pharynx (P) beneath radular sac; tooth, T. (E) Anterior end of polystichous radula from anteroventral radular pocket undergoing dissolution. (F, H) *Kruppomenia levis* n. sp.: (F) First-formed triangular tooth retained within anteroventral radular pocket. (H) Holotype. (G) *Kruppomenia delta* n. sp., holotype. In (A, G, and H), anterior is to left and dorsal above.

lower gametoducts; with copulatory spicules; mantle cavity with numerous long respiratory papillae; dorsoterminal sense organ present.

Remarks. When new collections of *E. sierra* from the type locality (Mediterranean) become available, the relationship between *E. sierra* and the two new species described here can be reevaluated.

Eleutheromenia bassensis sp. n.

(Figs. 7E–H, 8A, 9A–D, 11F)

Holotype. MV F83480 (alcohol specimen, spicule slide): Length 2.3 mm, height 0.6 mm, width of anterior end 0.7 mm. Bass Strait, Australia, 38°56.0′S, 145°16.6′E, 70 m (RV *Tangaroa* Stn BSS-S 55 [epibenthic sled], 12.xi.1981).

Illustrated paratypes. MV F83481 (dissected alcohol specimen; slides of epidermal and copulatory spicules); MV F83482 (dissected alcohol specimen; copulatory spicule slide). Type locality.

Material examined. 52 individuals, Bass Strait Survey November 1981, RV *Tangaroa* (number in parentheses; BSS-S, epibenthic sled samples; BSS-G, Smith-MacIntyre grab samples): BSS-S 155, 38°56.0′S, 145°16.6′E, 70 m (25); BSS-G 155, 38°55.5′S, 145°17.0′E, 70 m (1); BSS-S 156, 39°45.9′S, 145°33.5′E, 74 m (1); BSS-S 157, 40°10.9′S, 145°44.3′E, 75 m (1); BSS-S 162, 40°09.4′S, 147°32.6′E, 51 m (7); BSS-G 181, 38°39.8′S, 144°18.2′E, 79 m (2); BSS-S 195, 39°38.2′S, 143°07.2′E, 127 m (2);

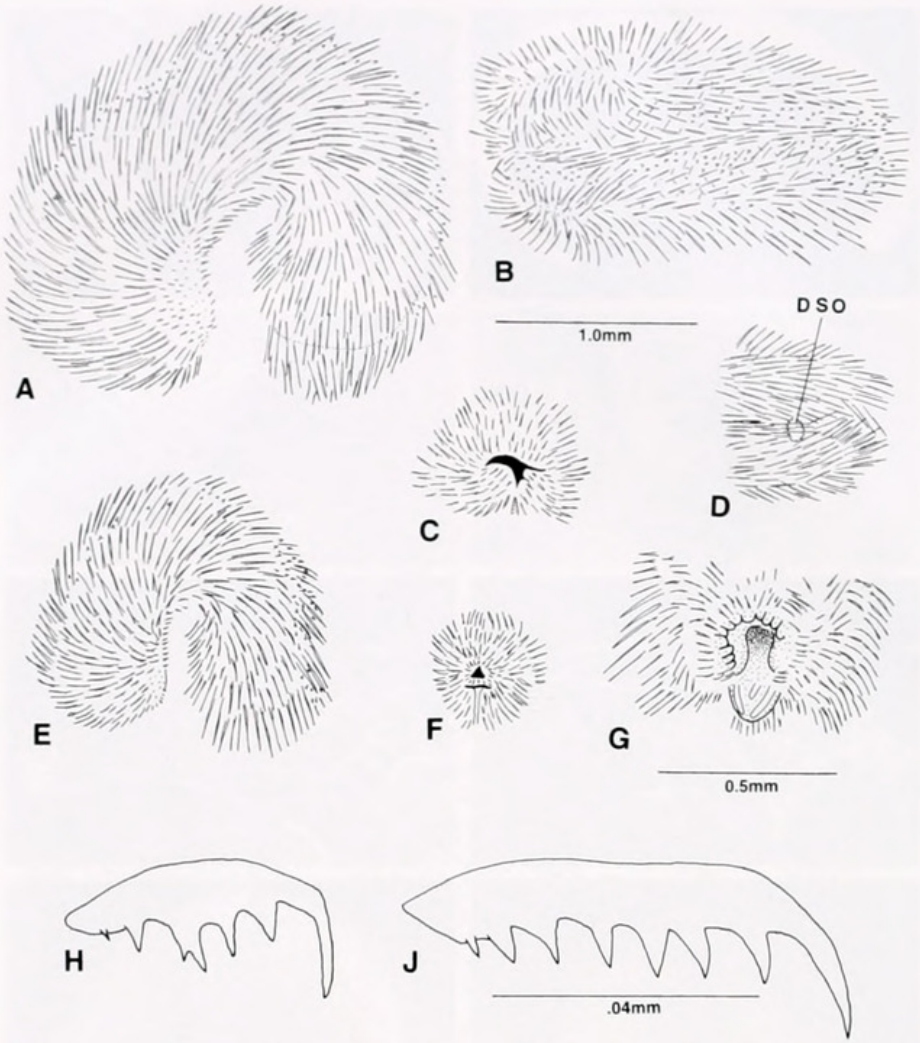

Figure 7. *Eleutheromenia mimus* n. sp. (A–D, J) and *E. bassensis* n. sp. (E–H). (A, E) Holotypes, anterior to left; barbed spicules indicated by small checks. (B) Dorsal view of (A) showing longitudinal rows of barbs. (C) Anterior view of (A). (D) Posterodorsal view of (A), dorsoterminal sense organ (DSO) obvious. (F) Anterior view of individual from type locality showing triangular appearance of contracted mouth opening and horizontal slit of contracted pedal pit. (G) Posterodorsal view of (E) at twice the magnification, open mantle cavity showing copulatory spicules; because the mantle cavity is open, the posterior spicules in (E) are fanned out, unlike those in (A) with mantle cavity opening contracted. (H, J) Single radular teeth from 6th row from formative end of radular sac, lateral denticles on right: (H) *E. bassensis* with 5 denticles, shows incipient 6th denticle forming on the middle denticle (paratype MV F83481); (J) *E. mimus* (paratype MV F83475).

BSS-G 195, 39°38.2′S, 143°07.2′E, 127 m (1); BSS-S 201, 39°08.3′S, 144°43.9′E, 66 m (2); BSS-S 202, 39°00.2′S, 144°33.9′E, 74 m (8); BSS-S 205, 39°13.6′S, 143°55.6′E, 85 m (2).

Description.

Appearance: Very spiny, to 3 mm in length (Figs. 7E, 11F); anterior width to 0.7 mm, height 0.6 mm or less; rounded anteriorly, somewhat truncated posteriorly; retracted mouth opening triangular; pedal pit a lateral slit (Fig. 7F); pedal groove covered by numerous long epidermal spicules; mantle cavity opening subterminal, spicules in brushes on each side, copulatory spicules often protruded (Fig. 7G), dorsoterminal sense organ often externally visible.

Cuticle and epidermis: Cuticle < 25 μm thick, epidermis about 10 μm thick.

Epidermal spicules: Both skeletal and upright spicules numerous, narrow, evenly curved, tapered at both ends, often slightly recurved at base (Fig. 8A); upright spicules to 400 μm long and 9 μm wide, with solid tips usually to 55 μm, a few to >60 μm (Fig. 8A spicules 3); skeletal spicules less than 200 μm long and to 8 μm wide, hidden externally under thickly set, upright spicules; barbed spicules numerous, upright, in longitudinal bands on each side of middorsal crest of crossed upright spicules, to 145 μm long and 9 μm wide, shortest anteriorly, sharply recurved twice at base (spicule 2); upright spicules from anterior end near mouth serrate (spicules 1); spicules along pedal groove to

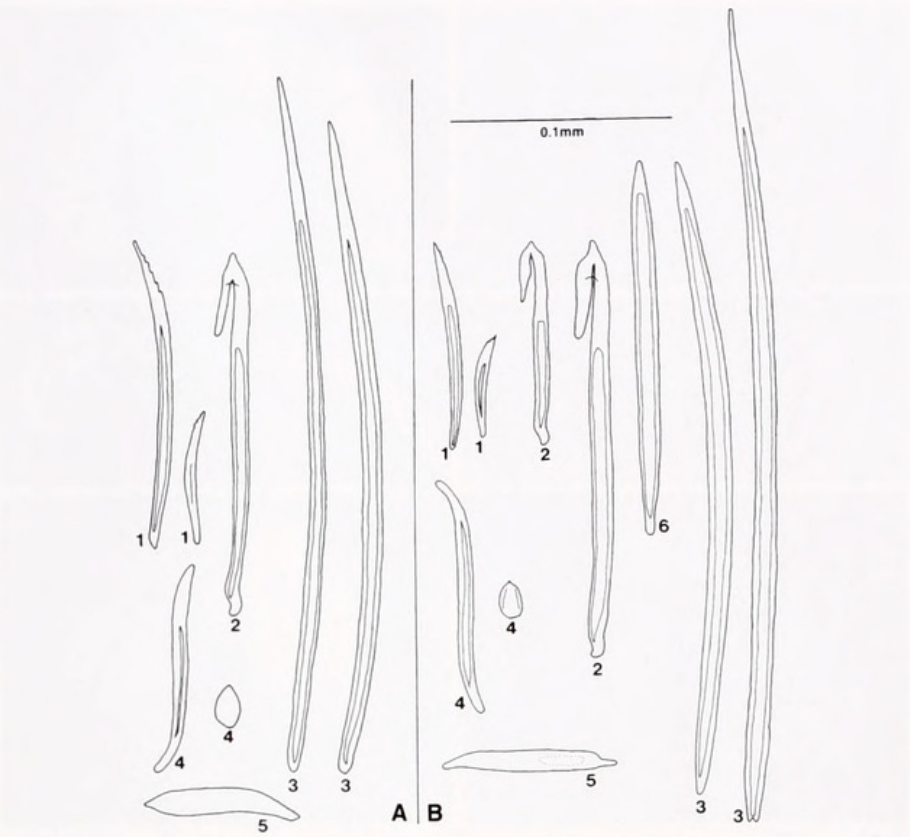

Figure 8. Epidermal spicules of *Eleutheromenia bassensis* n. sp. (A) and *E. mimus* n. sp. (B). 1 serrated spicules from above mouth, 2 barbed spicules and 3 long upright spicules from mid-dorsal region, 4 S-shaped and pointed ovate spicules from edge of mantle cavity, 5 spicules from beside pedal groove, 6 skeletal spicule. In (A), spicules from paratype (MV F83481) except upright spicule on right from another specimen from type locality. In (B), spicules from paratype (MV F83476) except upright spicule on right from another specimen from type locality.

100 μm in length, with a short, narrow base (spicule 5); spicules from opening of mantle cavity S-shaped and pointed ovals (spicules 4).

Radula (2 specimens examined): With 21 to 22 rows, teeth 40 to 45 μm by 10 μm, with 4 to 6 denticles (Fig. 7H).

Copulatory spicules (7 specimens examined): copulatory spicules paired, 2 per sac; one long, rodlike, distally tapered and curved, to 750 μm long by 25 μm wide; the other nearly as long, the distal half flared into a hood with a thickened distal ridge, width 104 μm (Fig. 9A–D).

Notes on anatomy: Large dorsal sinus present, extending far anteriorly. Midgut cecum paired anteriorly, becoming single at level of radula. Mantle cavity surrounded by subepithelial goblet cells.

Reproductive system. As in *E. mimus*.

Remarks. Morphological differences between *E. bassensis, E. mimus,* and *E. sierra* are discussed under Remarks for *E. mimus*.

Eleutheromenia mimus sp. n.

(Figs. 7A–D, J, 8B, 9E–G, 10, 11D, E)

Eleutheromenia sp., Scheltema *et al.,* 1994, figs. 3a, c, 7a, 16c, 20a (identification in caption in error), e, 24d.

Holotype. MV F83474 (alcohol specimen, spicule slide): Length 3.1 mm, height 0.8–0.9 mm, width 1.0 mm. Bass

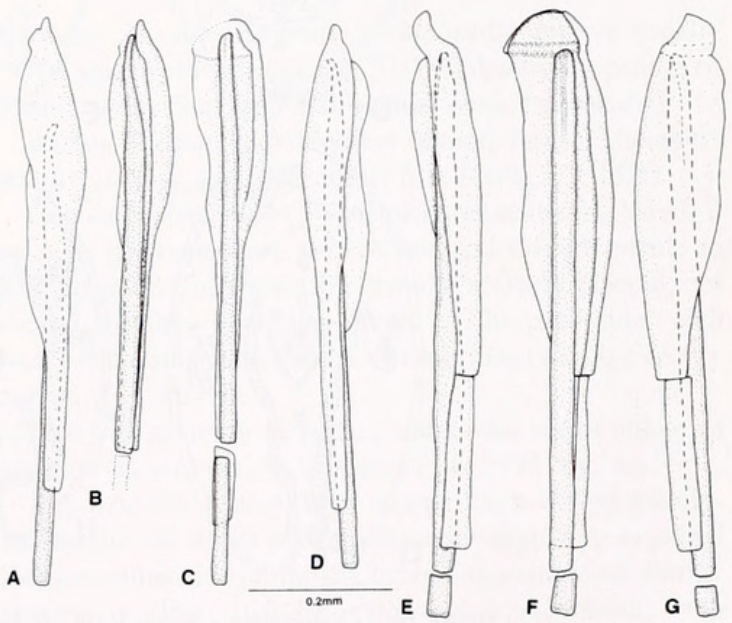

Figure 9. Copulatory spicules of *Eleutheromenia bassensis* (A–D) and *E. mimus* (E–G). The longer, rod-shaped spicule is narrow, tapered, and curved in *E. bassensis;* it is scarcely curved or tapered in *E. mimus* but has a medial groove distally. The hoodlike spicule bears a ridge distally; it is curved above the ridge, more so in *E. mimus* than in *E. bassensis*. The two spicules can move relative to each other; *cf.* spicules (A) and (B). [(A, D) Paratype MV F83481; (B, C) paratype MV F83482; (E–G) paratype MV F83477.]

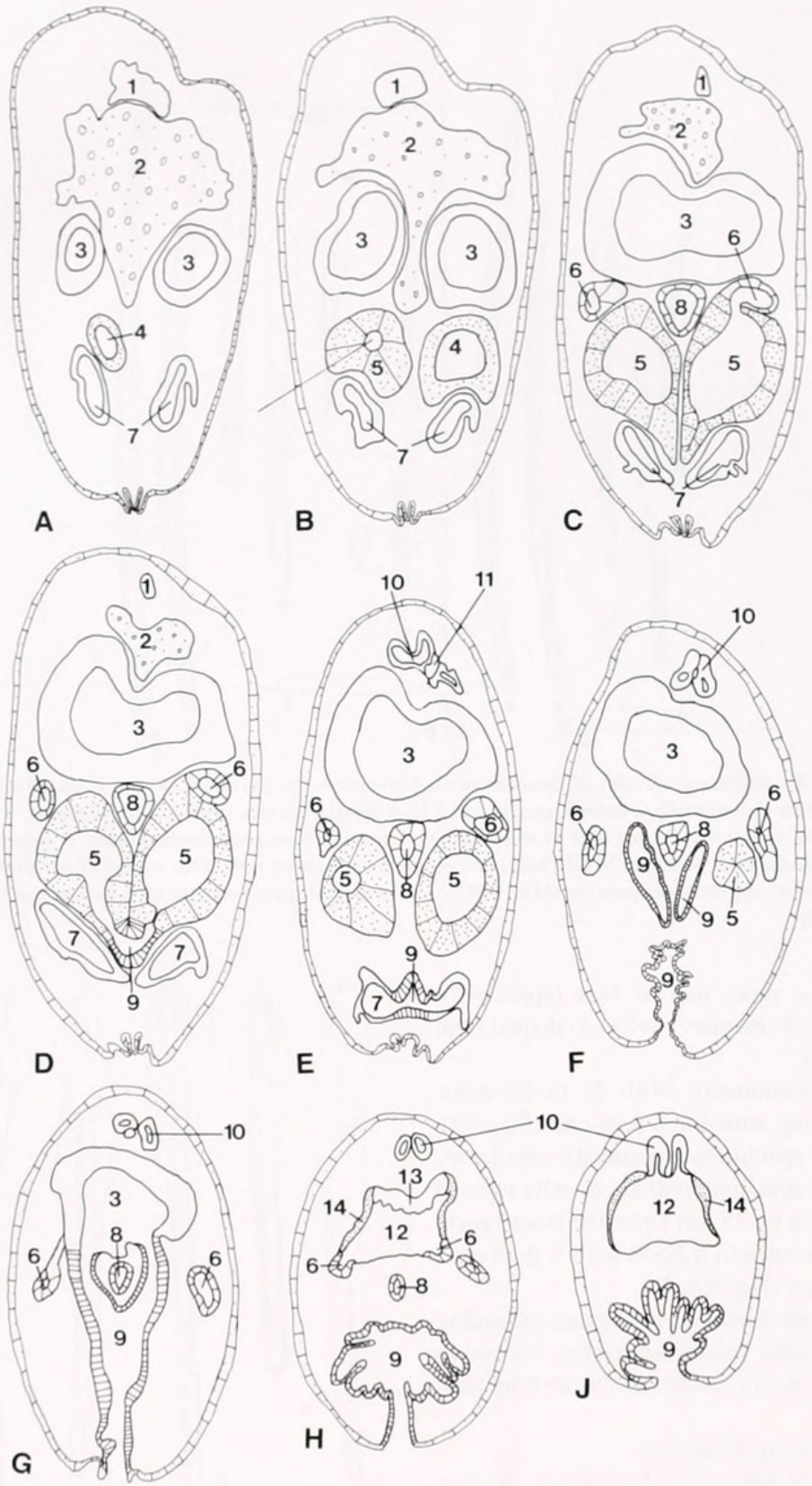

Figure 10. *Eleutheromenia mimus* n. sp., reproductive system, semischematic histologic sections from anterior (A) to posterior (J) (see text for description; reconstruction not attempted owing to obliqueness of sections). 1 gonad, 2 midgut, 3 glandular sac of pericardial cavity, 4 seminal receptacle, 5 lower gametoduct, 6 upper gametoduct, 7 copulatory spicule sac, 8 rectum, 9 mantle cavity, 10 gonopericardial duct, 11 dorsal aorta, 12 pericardium, 13 heart, 14 pericardial glands. Line in B, opening of seminal receptacle into lower gametoduct.

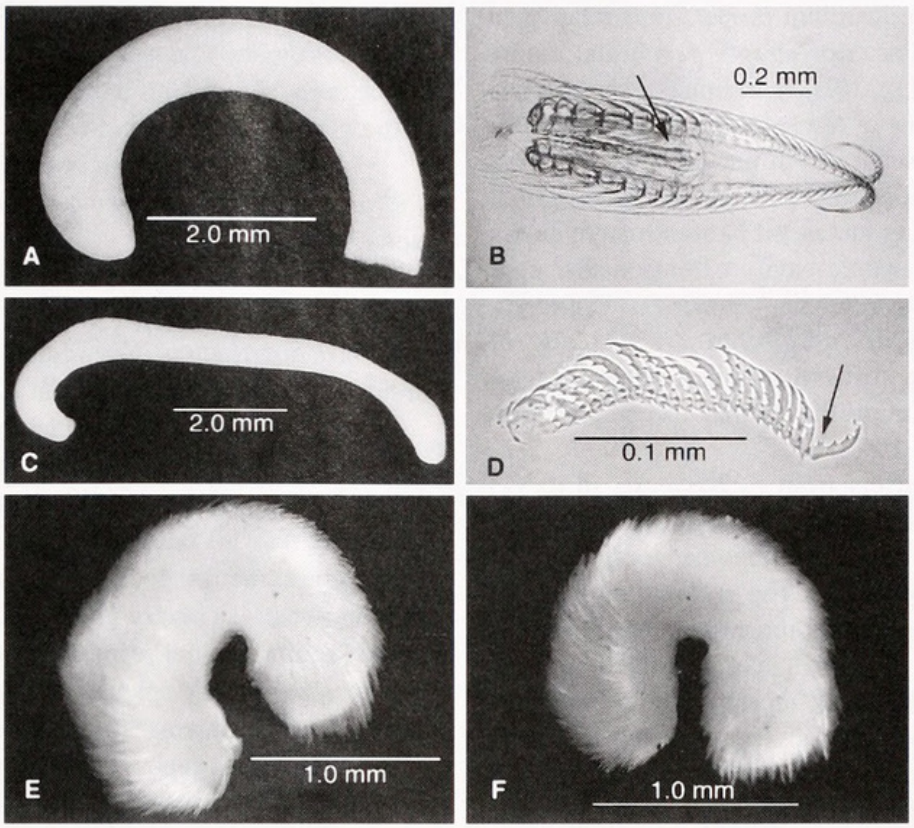

Figure 11. (A–C) *Simrothiella* (=*Solenopus*) *margaritacea* (Koren & Danielssen): (A) *Solenopus margaritaceus* Koren & Danielssen, lectotype. (B) dorsal view of entire radula, short section from radula sac indicated by arrow, greatest length of radula from within anteroventral radular pocket, anterior to left. (C) Voucher 1 (USNM). (D, E) *Eleutheromenia mimus* n. sp.: (D) Radula, one longitudinal row of the distichous radula; arrow, oldest tooth with bifurcating denticle. (E) Holotype. (F) *E. bassensis* n. sp., holotype. In (A, C, E, and F), anterior is to left, dorsal above.

Strait, Australia, 38°52.6′S, 148°25.2′E, 140 m (RV *Tangaroa* Stn BSS-S 170 [epibenthic sled], 15.xi.1981).

Illustrated paratypes. MV F83475 (dissected alcohol specimen, epidermal and copulatory spicule slides); MV F83476 (dissected alcohol specimen, epidermal spicule slide, radula slide); MV F83477 (dissected alcohol specimen, copulatory spicule slide). Type locality.

Material examined. 33 individuals (number in parentheses; all samples from epibenthic sled): Bass Strait Survey, November 1981, RV *Tangaroa* stations BSS-S 169, 38°57.8′S, 148°26.5′E, 120 m (3) and BSS-S 170, 38°52.5′S, 148°25.2′E, 140 m (20); RV *Franklin* July 1986, Slope station 40, 38°17.7′S, 149°11.3′E, 400 m (10).

Description.

Appearance: Similar to *E. bassensis* (Figs. 7A–D, 11E); to 4.4 mm long, height and width to 0.9 mm except width to 1.2 mm at anterior end.

Cuticle and epidermis: Cuticle to 23 μm thick, epidermis thinner, to 16 μm thick.

Epidermal spicules: Types and shapes as in *E. bassensis* (Fig. 8B); upright spicules to nearly 600 μm long and 13 μm wide, solid tips to 55 μm (spicules 3); many skeletal spicules < 200 μm long and to 11 μm in width (spicule 6); barbed spicules to 185 μm by 9 μm, shortest anteriorly (spicules 2); spicules from beside pedal groove usually <100 μm by 14 μm (spicule 5); spicules from opening of mantle cavity S-shaped and pointed ovals (spicules 4).

Radula (2 examined): Number of tooth rows 23, teeth 65 μm by 10 μm, denticle number 5 to 9 (Fig. 7J, 11D).

Copulatory spicules (5 specimens examined): Paired, 2 spicules per copulatory spicule sac, rod-shaped spicule to 830 μm by 32 μm, grooved distally, scarcely tapered, not curved distally; hoodlike spicule >120 μm wide, with heavy distal ridge and portion of hood distal to ridge deeply curved (Fig. 9E–G).

Notes on anatomy: A pedal commissure sac of unknown function present (see Scheltema *et al.,* 1994, fig. 2c).

Reproductive system: With a large, thick-walled, glandular anterior sac of the pericardial cavity beginning as paired lobes on either side of midgut, becoming a single sac further posteriorly (Fig. 10A–F); cells large, vacuolated, with small, deeply staining granules; sac connecting with mantle cavity through a long, tubelike, dorsoanterior extension of mantle cavity, just anterior to beginning of heart and pericardium proper (Fig. 10F, G); tubelike mantle cavity extension passing around rectum. Gonads emptying into pericardium through unusually long, paired gonopericardial ducts that open into posterior, rather than anterior, part of peri-

cardium (Fig. 10E–J). Pericardium proper short relative to anterior glandular sac. Posterior end of pericardial cavity with pericardial glands (Fig. 10H, J). Seminal receptacles as saclike anterior extensions of the lower gametoducts, without distinct ducts, but separated from gametoducts by a short, tubelike constriction (Fig. 10B, line). Lower gametoducts paired until uniting just as they reach mantle cavity anterior to the tubelike mantle cavity extension that connects with glandular pericardial sac (Fig. 10D). Upper gametoducts arising as usual from ventroposterior end of pericardium and leading forward, joining lower gametoducts just posterior to union of seminal receptacles with lower gametoducts (Fig. 10C–H).

Remarks. *E. mimus* differs from *E. bassensis* in its (1) larger size, (2) longer and wider epidermal spicules, (3) longer radular teeth, (4) more denticles per tooth, and (5) copulatory spicule morphology. The morphology of the copulatory spicules differentiates the two species unequivocally. The rod-shaped spicule in *E. bassensis* is curved distally and is narrower and more tapered than in *E. mimus,* whereas the hoodlike spicule in *E. mimus* bears a heavier ridge and is more deeply curved distally than in *E. bassensis.* It is likely that *E. bassensis* also has a pedal commissure sac, but this structure was seen only in 1.5-μm sections of *E. mimus.* Depth ranges of the two species differ but overlap: *E. bassensis* has been collected from 70 to 127 m, and *E. mimus* from 120 to 400 m. They did not occur together in samples, however. Both species differ from *E. sierra* in size and epidermal spicule morphology and lack the distinct dorsal carina of *E. sierra.* Seminal receptacles were considered to be lacking in *E. sierra* (Pruvot, 1891).

The function of the large, glandular pericardial sac at the anterior end of the pericardium is not clear. The sac is only indirectly connected with the gonads through the long gonopericardial ducts that enter the pericardial cavity at its posterior end. Other species of Pruvotinidae are known to have brood chambers, but these are extensions of the mantle cavity, not the pericardium (Salvini-Plawen, 1978).

SIMROTHIELLIDAE Salvini-Plawen, 1978

Type genus. *Simrothiella* Pilsbry, 1898.

Diagnosis. Neomenioids with body shapes from stout to elongate; epidermal spicules solid or hollow, with or without skeletal spicules; radula distichous with many rows, denticles on a barlike base entirely attached to radular membrane; with paired anteroventral radular pockets either long and spiraled, or short, retaining initial teeth in some taxa.

Remarks. The taxon is currently constituted primarily on the basis of radula morphology (*Simrothiella* Pilsbry, 1898, *Cyclomenia* Nierstrasz, 1902, *Kruppomenia* Nierstrasz, 1903, *Uncimenia* Nierstrasz, 1903 [lacking a radula], *Biseramenia* Salvini-Plawen, 1967, *Birasoherpia* Salvini-Plawen, 1978, *Sialoherpia* Salvini-Plawen, 1978, *Helicoradomenia* Scheltema & Kuzirian, 1991, and *Plawenia* n.g., herein). From the diagnosis above, monophyly of the taxon can be seen to be doubtful and is not reflected in the results of the cladistic analysis below.

Kruppomenia Nierstrasz, 1905

Type species. *Kruppomenia minima* Nierstrasz, 1905, by monotypy.

Simrothiella Pilsbry, 1898 (*partim*), Salvini-Plawen, 1972.

Known distribution. Norwegian fjords, West European Basin, and the Mediterranean from 100 m or less to >4000 m.

Diagnosis. Stout, small; epidermal spicules hollow, both skeletal and upright; epidermis and cuticle thick; radula ribbon broad with many distichous tooth rows, teeth as extremely narrow bars bearing numerous tiny denticles; anteroventral radular pocket retaining first-formed, triangular tooth; ventral salivary glands short, tubular, paired; with paired saclike seminal receptacles; copulatory spicules 2 or more per copulatory spicule sac; respiratory mantle-cavity folds present; a dorsoterminal sense organ present.

Remarks. This genus is represented by several undescribed species in the West European Basin and adjacent waters. A second species, besides the type, has previously been described (*K. borealis* Odhner, 1921). Copulatory spicules tend to be numerous and elaborate in this genus and serve to distinguish species.

Kruppomenia levis sp. n.

(Figs. 6F, H, 12A–C, F, G, 13A, 14A–D)

Holotype. MNHNP (alcohol specimen, spicule slide): Length 3.3 mm, heights 0.7, 0.9, and 0.9 mm anteriorly, at midbody, and posteriorly, respectively; widths 0.7, 1.1, and 0.9 mm. Bay of Biscay 47°29.8′N, 9°39.2′W, 4327 m (INCAL [CENTOB] OS-08, 11.viii.1976).

Paratypes. No. 1, MNHNP (dissected alcohol specimen, epidermal and copulatory spicule slides), Bay of Biscay 47°34.8′N, 9°33.3′W, 4228 m (BIOGAS VI [CENTOB] DS-76, 23.x.74); no. 2, MNHNP (dissected alcohol specimen, copulatory spicule slide), West European Basin 47°29.8′N, 9°33.4′W, 4268 m (INCAL [CENTOB] DS-16, 9.viii.1976); no. 3, MNHNP (dissected alcohol specimen, epidermal spicule slides), type locality.

Material examined. 22 individuals; see Table 1, with two additional stations: BIOGAS VI (CENTOB) DS-76 (4) and BIOGAS VI DS-77, 4240 m, 47°31.8′N, 9°34.6′W, 24.x.74 (4).

Description.

Appearance: Small, stout, length to 3.9 mm, height to 1.3 mm, height and width greatest at midbody, rounded at both ends (Figs. 6H, 12A); appearance somewhat spiny when epidermal spicules intact, but usually appearing smooth (*levis*) to rough owing to broken state of upright spicules and sediment held between spicules; skeletal spicules form-

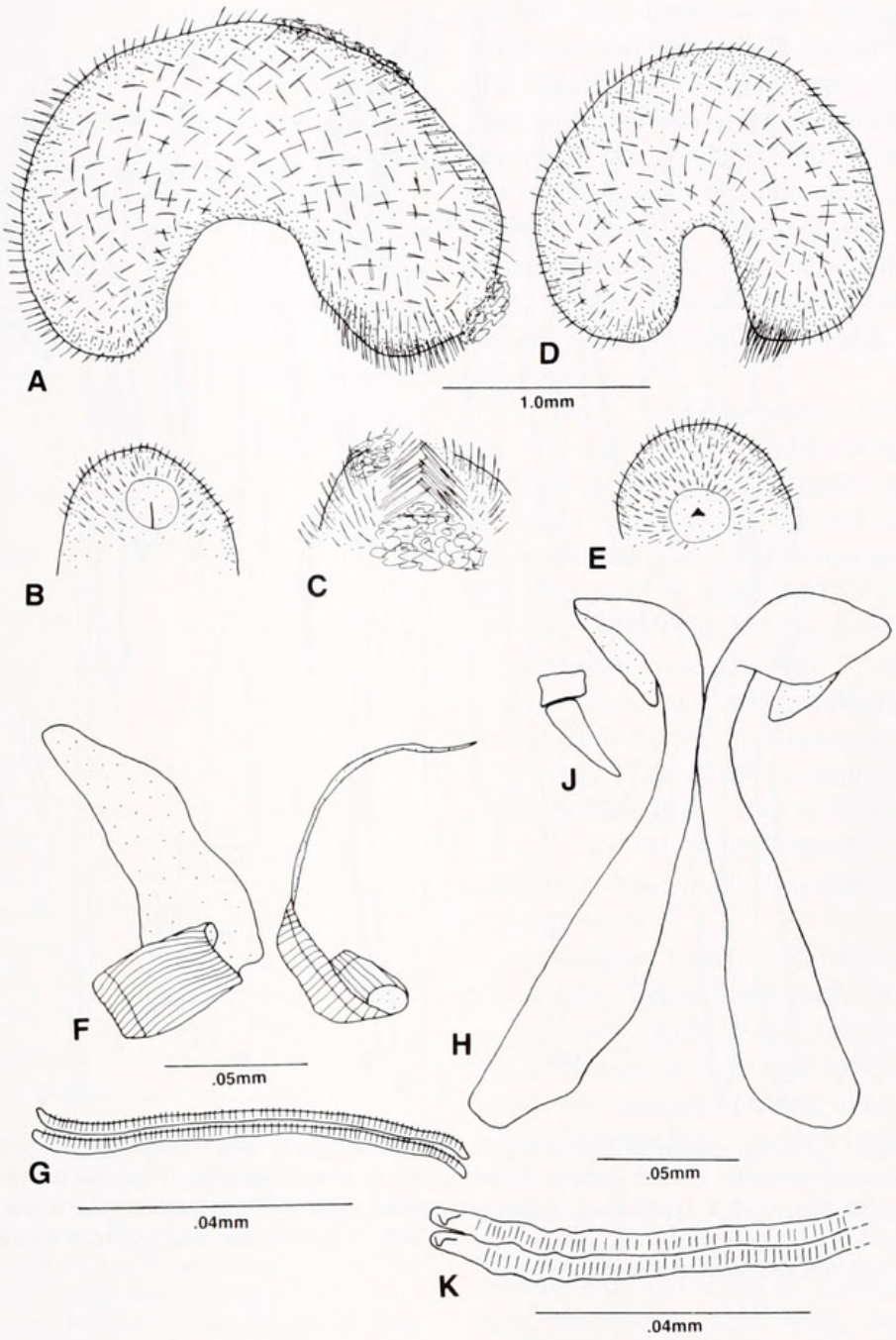

Figure 12. *Kruppomenia levis* n. sp. (A–C, F, G) and *K. delta* n. sp. (D, E, H–K). (A) Holotype of *K. levis,* anterior to left, many upright spicules masked by adhering sediment and with distal ends broken off. (B, C) Ventral views of mouth and spicules covering mantle cavity, respectively, of (A). (F) *K. levis,* entire radula of paratype 1, distal end above, tooth rows indicated sketchily; stippling indicates radular membrane viewed from below. (G) Two adjacent teeth from (F), lateral to left, denticles indicated sketchily; note lateral bend, which appears as longitudinal line in (F). (D, E) *K. delta,* holotype, as in (A, B). (H) *K. delta,* entire radula, paratype 2, distal end above, oblique view, tooth rows not sketched. (J, K) *K. delta,* paratype 3: (J) Two first-formed teeth, scale as in (K) (*cf.* Fig. 24E). (K) Two adjacent teeth, lateral to left, medial portion not illustrated.

ing an open meshwork; contracted mouth opening a vertical slit in flat, circular area without spicules (Fig. 12B); with raised ridge on each side of pedal groove; terminal spicules long and brushlike, meeting at angle above mantle cavity opening (Fig. 12C); cuticle easily torn.

Cuticle and epidermis: Cuticle thick, up to 38 μm; epidermis from thin to thick, 13 μm anteriorly to 38 μm posteriorly, with large, juxtaposed papillae.

Epidermal spicules: Asymmetric, fragile, hollow (Fig. 13A), walls about 2 μm, removable from cuticle only with difficulty; skeletal and upright spicules could not be differentiated, probably similar; many spicules long, to 290 μm anteriorly and 365 μm posteriorly; most distinctive spicules (Fig. 13A, spicules 1, 2, 4, 6, 9) curved from distal end to an abrupt bend 25 to 80 μm above base, widest at bend, to 18 μm, solid tips short, most 11 μm long but to 23 μm, often

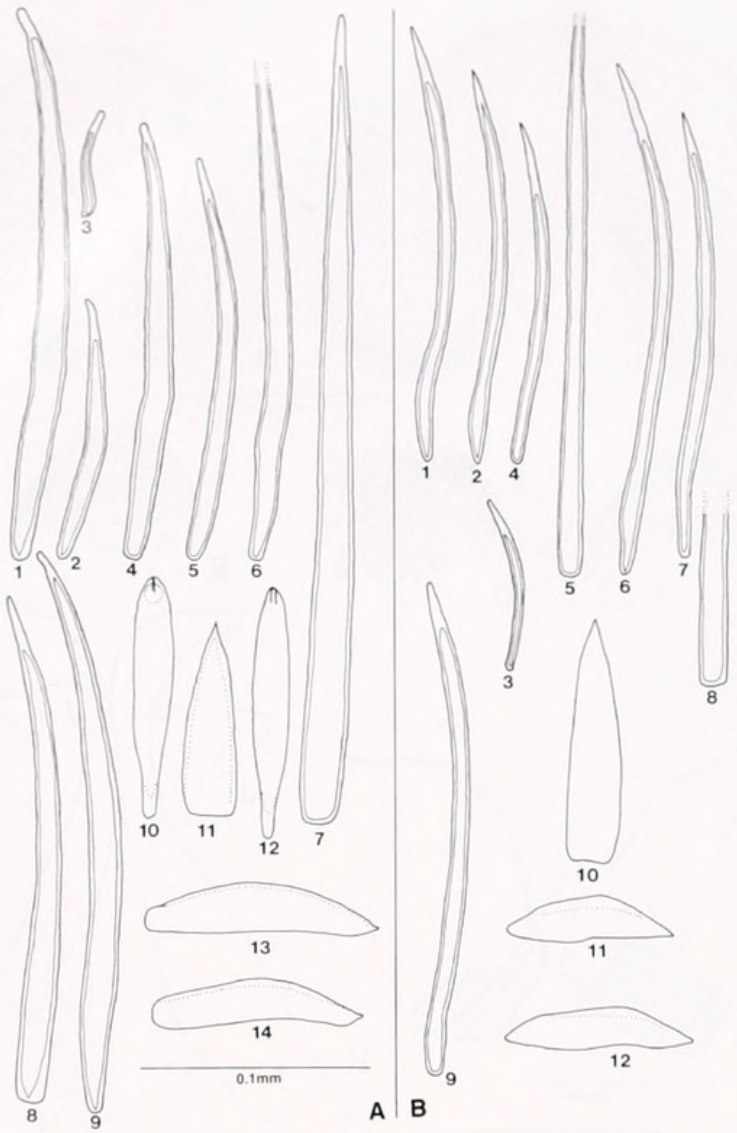

Figure 13. Epidermal spicules of *Kruppomenia levis* n. sp. (A) and *K. delta* (B). Spicules A1–5, 10, 11, 13 from paratype 1; A6–9, 12, 14 from paratype 3; spicules B1–6, 11 from paratype 1; spicules B7–10, 12 from paratype 3. Spicules A1–3, 8, 9 and B1–4, 9 from anterior end, spicule A3 and B3 from near mouth, spicules A4–7 and B5–8 from posterior end, spicules A10–14 and B10–12 from beside pedal groove, A10–12 and B10 probably from area next to mantle cavity opening.

constricted and bent beyond hollow space that fills most of spicule from tip to base; other spicules evenly curved from tip to base (spicule 8), or recurved proximal to bend (spicule 6); spicules from beside pedal groove 1–2 μm thick, base truncated, with distal nipple, to 106 μm long and 23 μm wide, thickest along outside curve and at base (spicules 13, 14); triangular and paddle-shaped, solid, thin (1–2 μm) spicules present posteriorly, to 100 μm and 115 μm long, respectively, probably from beside pedal groove near mantle cavity opening (spicules 10–12).

Radula (3 examined): About 185 μm long, with about 88 rows of narrow, distichous bars bearing numerous tiny (2 μm) denticles and a lateral thickening seen only in histologic sections; teeth bending about one-quarter of the distance from lateral margin, making an axial ridge along length of radula (Fig. 12F, G); most recent teeth 2 μm wide and to 74 μm from lateral to medial margin; first-formed tooth triangular (Fig. 6F); radular apparatus with large bolsters, anteroventral radular pocket broad, paired; proximal end of radular sac divided.

Copulatory spicules (3 individuals examined): 4 per pocket (Fig. 14A–D, spicules 1–4): spicule 1 hollow, elongate, length to >575 μm, distally pointed, basally tapered, curved, twisted around long axis and appearing either proximally broad and distally narrow or proximally narrow and distally broad (*cf.* spicules 1, Fig. 30A, B), distal points of paired number 1 spicules held in close proximity *in situ;* spicules 2 and 3 hollow, distally hooked, narrow, widest just below hook, greatest lengths >412 μm and 273 μm, respectively; spicule 4 shortest, proximally broad and partially wrapped around spicule 1, recurved twice and axially twisted, to 260 μm long; a fifth, very short (46 μm) hook in

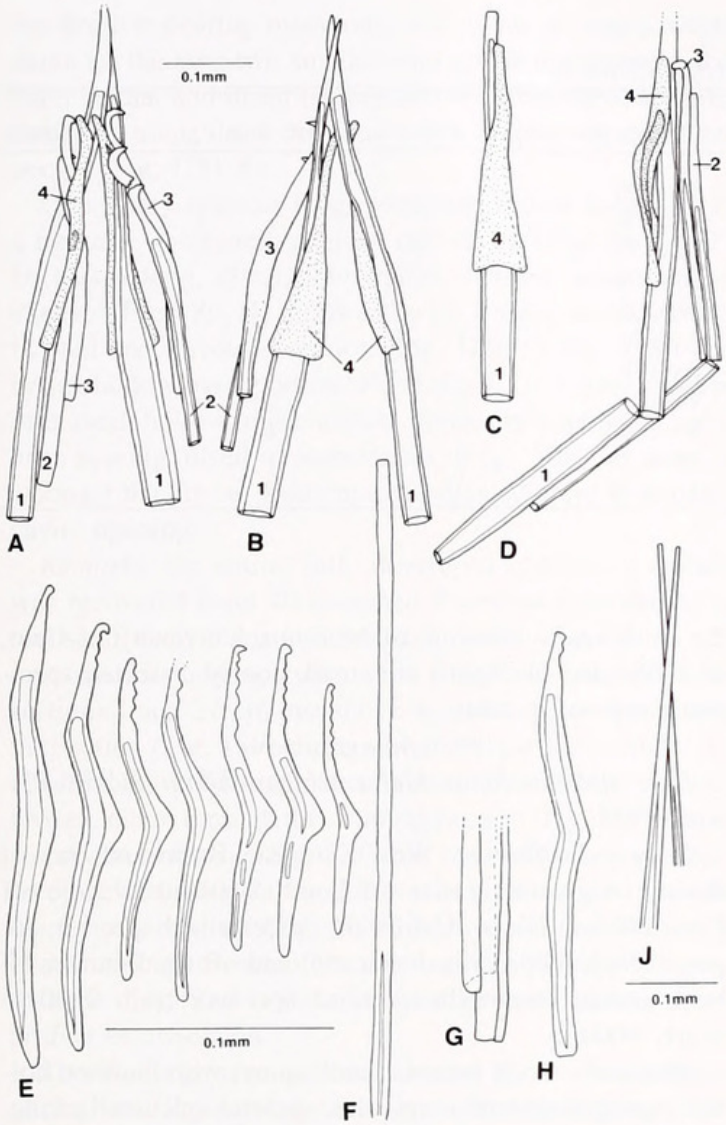

Figure 14. Copulatory spicules of *Kruppomenia levis* n. sp. (A–D) and *K. delta* n. sp. (E–J). (A, B) From paratype 2, ventral and dorsal views, respectively, proximal ends of spicules 1 and 2 broken off, spicules 2 and 3 not shown in (B). (C, D) From paratype 1, distal ends of spicules 1, 2, and 4 broken off; view of spicules C1 and C4 at 90° angle from view (D). (E) Accessory copulatory spicules, teased apart, from paratype 1. (F, G) One of paired main copulatory spicules from paratype 1, distal and proximal ends, respectively, showing two spicules wrapped around each other proximally and a single spicule distally. (H) One of seven accessory copulatory spicules from paratype 3. (J) Distally crossed pair of main copulatory spicules from paratype 3, drawn at same scale as (A–D); *cf.* spicule (F) at larger scale.

one of paired groups (Fig. 14A) may be new spicule in formation.

Notes on anatomy: Pedal pit large, not obvious externally in contracted state. Anterior pharynx a long, narrow tube; midgut not sacculate, with single dorsal cecum. Dorsoterminal sense organ present, not obvious. Mantle cavity with about 46 elongate, slender respiratory papillae.

Reproductive system (not illustrated): Paired seminal vesicles present at posterior ends of gonopericardial ducts. Paired, elongate seminal receptacles empty through long ducts into the unpaired lower gametoduct, which empties dorsally into mantle cavity. Pericardial cavity extending as a narrow, inverted U, both laterally and posteriorly, far over the mantle cavity. Paired upper gametoducts leave the lateral, posterior ends of the pericardial cavity as narrow tubes; anteriorly their relationship to seminal receptacles and lower gametoduct was unclear in examined specimen.

Remarks. Some individuals of *Kruppomenia levis* have numerous epidermal spicules with constricted tips (Fig. 13A, spicules 4, 9), whereas in others they are scarce. For differences between *K. levis* and *K. delta,* see remarks under *K. delta.*

Kruppomenia delta sp. n.
(Figs. 6G, 12D, E, H–K, 13B, 14E–J)

Holotype. MNHNP (alcohol specimen, spicule slide): Length 2.7 mm, heights 0.6, 0.9, and 0.7 mm anteriorly, at midbody, and posteriorly, respectively, widths 0.9, 0.9, and 0.8 mm. Bay of Biscay 47°27.3′N, 9°36.2′W, 4307 m (INCAL [CENTOB] OS-06, 9.viii.1976).

Illustrated paratypes. No. 1, MNHNP (dissected alcohol specimen, epidermal spicule slide); no. 2, MNHNP (dissected alcohol specimen, epidermal spicule slide); type locality. No. 3, MNHNP (dissected alcohol specimen, copulatory spicule slide); Bay of Biscay 47°29.8′N, 9°39.2′W, 4327 m (INCAL [CENTOB] OS-08, 11.viii.1976).

Material examined. 10 individuals; see Table 1.

Description.

Appearance: Small, stout, similar to *Kruppomenia levis,* but smaller; largest individual 2.8 mm, greatest height 0.9 mm, greatest width 0.9 mm; rounded at both ends (Figs. 6G, 12D); appearance somewhat spiny when epidermal spicules intact, but upright spicules often broken, with sediment lodged between them; skeletal spicules forming loose meshwork, cuticle easily torn; contracted mouth triangular in flat, circular area (Fig. 12E); with raised ridge on each side of pedal groove; terminal spicules just above mantle cavity opening long and brushlike, forming tuft (Fig. 12D); otherwise, posterior spicules shorter than in *K. levis.*

Cuticle and epidermis: Not examined.

Epidermal spicules: Asymmetric, fragile, hollow (Fig. 13B), walls about 2 μm; removable from cuticle with difficulty; longest spicules > 225 μm; greatest width to 14 μm (Fig. 13B, spicule 8), but most commonly 7 μm; greatest distance from bend to base 56 μm, most <50 μm (spicules 2, 6, 7, 9); solid tips slender, curved, sometimes with slight distal bend, from 9 to 45 μm long, many > 20 μm (spicules 1, 4, 6); some spicules evenly curved from base to tip, or straight (spicules 4, 5); spicules from beside pedal groove with tapered base, outer margin flattened, to 101 μm long by 20 μm wide (spicules 11, 12), paddle-shaped spicules not observed, but posterior triangular, solid spicules large (spicule 10), to >135 μm long.

Radula (3 examined): Length to 230 μm long, similar to that in *K. levis* but larger (Fig. 12H), teeth to about 78 μm

Table 1

Material examined, Kruppomenia levis, K. delta, *and* Plawenia sphaera *(INCAL [CENTOB])*

Sample	Depth (m)	Lat N	Long W	Date	*K. levis*	*K. delta*	*P. sphaera*
DS-01	2091	57°59.7′	10°39.8′	15.vii.76			16*
DS-02	2081	57°58.8′	10°48.5′	16.vii.76			26
CP-01	2068	57°57.7′	10°55.0′	16.vii.76			3
CP-02	2091	57°58.4′	10°42.8′	16.vii.76			1
DS-05	2503	56°28.1′	11°11.7′	18.vii.76			1
DS-14	4254	47°32.6′	9°35.7′	7.viii.76	1		
DS-15	4211	47°33.4′	9°39.1′	8.viii.76		1	
DS-16	4268	47°29.8′	9°33.4′	9.viii.76	3	1	
OS-06	4316	47°27.3′	9°36.2′	9.viii.76		6*	
OS-07	4249	47°31.8′	9°34.3′	10.viii.76	7		
OS-08	4327	47°29.8′	9°39.2′	11.viii.76	3*	2	

* Type locality.

by 4 μm with a lateral denticle larger than remaining little denticles (Fig. 12K); first-formed tooth triangular (Fig. 12J).

Copulatory spicules (3 individuals examined): Paired, two per sac, one spicule elongate, hollow, to 845 μm long, slender (about 22 μm wide), distal tip straight, solid tip to 255 μm long above hollow space (Fig. 14F, J); second spicule proximal, not seen in its entirety, wrapped part way around elongate spicule (Fig. 14G); distal ends of elongate spicules in close proximity *in situ* (Fig. 14J). With paired groups of seven accessory copulatory spicules (Fig. 14E, H) held tightly together in order of length, from >200 μm (range 205–211 μm) to about 100 μm (range 90–110 μm); spicules hollow, but smaller ones nearly solid; both ends curved, meeting medially at bulge with sharp bend, with none to several little bumps at one end below slight hook, fewest bumps on largest spicules; relationship to elongate copulatory spicules not determined.

Notes on anatomy: Neither pedal pit nor dorsoterminal sense organ obvious externally.

Reproductive system: Not examined.

Remarks. Copulatory spicules unequivocally differentiate *K. delta* and *K. levis* (Fig. 14). Further differences are: epidermal spicules of *K. delta* are (1) more slender and more deeply curved, (2) the largest spicules are shorter, (3) the solid tips are longer and without a constriction, and (4) the distance from the base to the bend is less. (5) Spicules from beside the pedal groove in *K. delta* are basally tapered and the outside margin bent; in *K. levis,* the base is truncated and the outside margin smoothly curved. (6) Terminal spicules, if still present after processing through sieves, are long and brushlike over entire posterior end in *K. levis,* but form a tuft over the mantle cavity opening in *K. delta.* (7) The radula of *K. delta* is larger than in *K. levis,* and the teeth bear a lateral denticle distinctly larger than the comblike denticles. Both species differ from *K. minima* and *K. borealis* by their occurrence at abyssal depths greater than 4000 m, and by body shape from *K. minima.* Unfortunately the types for *K. borealis* (Zoological Museum, University of Oslo, D 25654 and D 28676) are small, poorly dissected specimens without spicules.

Plawenia gen. nov.

Type species. Simrothiella schizoradulata Salvini-Plawen, 1978.

Known distribution. West European Basin and Bay of Biscay; Argentine Basin; off South Shetland Islands; off Peru; off San Diego, California (undescribed species); Japan Trench (undescribed species); and off La Réunion Island, Indian Ocean (undescribed species); from 2000 to nearly 6000 m.

Diagnosis. Body rotund, small, spiny; with thickset, hollow, upright epidermal spicules, skeletal spicules lacking; cuticle and epidermis thick; radular teeth with a strong, lateral buttress beneath large, lateral denticles; long, spiral anteroventral radular pockets retaining initial, triangular teeth; with two pairs of pharyngeal salivary glands, the dorsalmost acinar; seminal receptacles paired, bilobed; lower gametoducts first uniting and then becoming bilobed before emptying into mantle cavity through a papilla; copulatory spicules single, paired; a dorsoterminal sense organ present.

Description.

The following applies to all three species herein described: Epidermal spicules long, thin-walled (2 μm or less), gently curved or straight above an often bent and recurved base (Fig. 16); hollow internal space running from close to base nearly to tip in most spicules; proximal ends flat in widest spicules, flat to rounded in narrower spicules.

Paired anteroventral radular pockets remarkable, with numerous contained rows of teeth spiraled into flat, platelike structures positioned perpendicular to dorsoventral axis of the body; left pocket spiraled counterclockwise, right one clockwise in ventral view (Fig. 19E, F). Teeth with distinctive parts (Fig. 17C, D): (1) a bar thickened laterally into a thick buttress; (2) a serrated or scalloped distal margin of

the denticle-bearing membrane; (3) a pair of large, lateral denticles flanking two smaller ones above the buttress; and (4) a medial and distal hemispherical extension of the bar. Original, triangular tooth retained in anteroventral radular pocket (Fig. 17H–K).

Copulatory spicules long, with four distinct sections: (1) a terminal, thickened, conical, curved tip (Fig. 18A–C, F, H); (2) a long, distal, thin-walled, twisted hemispherical channel (Fig. 18F, H) followed by (3) a short, narrow, solid, twisted and furrowed section (Fig. 18E, G, H); and (4) a broad, hollow basal portion (Fig. 18D, E, G). Paired bundles of curved, hollow, thick-walled, accessory copulatory spicules bearing distal protuberances (Fig. 18J, K) present amongst thickly set epidermal spicules adjacent to mantle-cavity opening.

Remarks. No entire, fully developed copulatory spicule was recovered from 10 dissected *Plawenia* individuals. In two small individuals (1.5 mm in *P. sphaera,* 1.4 mm in *P. argentinensis*) the spicules were composed only of distal sections 1 and 2 from just above the solid, yet-to-be-formed midsection (Fig. 18F). In five of six larger individuals, the distal sections of the spicules were missing and the spicules broken, either through the solid midsection (Fig. 18D, G), or somewhat above it (Fig. 18E). In one individual of intermediate size, the basal section was beginning to form while the tip was retained (Fig. 18H). Such a constancy between body size and absence of the distal section perhaps indicates that the distal end is deciduous rather than missing as an artifact of dissection.

The biogeographic questions raised by the distributions of the three *Plawenia* species herein described are provocative. *P. schizoradulata* lives at 4758 m on the Pacific side of the great eastward-bending parabolic arc that stretches from the southern tip of South America through the Scotia Ridge to the islands lying northeast of the Antarctic Peninsula; the benthos is therefore part of the Pacific fauna. The species is also represented by a single individual from the Atacama Trench off Peru at 5821 m (Salvini-Plawen, 1978; specimen not examined by authors). The Scotia Ridge effectively cuts off the deep stenobathyal bottom fauna of the Pacific from the Atlantic. That *P. argentinensis* from the Atlantic Argentine Basin at >4000 m depth shows morphological differences from *P. schizoradulata* is therefore not surprising; what is puzzling is the close similarity between *P. schizoradulata* and *P. sphaera* from only 2091 m in the West European Basin in the northeast Atlantic.

Plawenia schizoradulata (Salvini-Plawen, 1978)
(Figs. 15A–C, 16 spicules 1, 4–7, 17A, B, H, 18C, 19A, B)

Simrothiella schizoradulata Salvini-Plawen, 1978.

Lectotype (herein designated). USNM 749767 (alcohol specimen, spicule slide): Length 2.6 mm, midbody height and width 1.6 and 1.4 mm, respectively (specimen compressed). Drake Passage off South Shetland Islands, 61°45′S, 61°14′W, 4758 m (USARP 4-127, 1.viii.62).

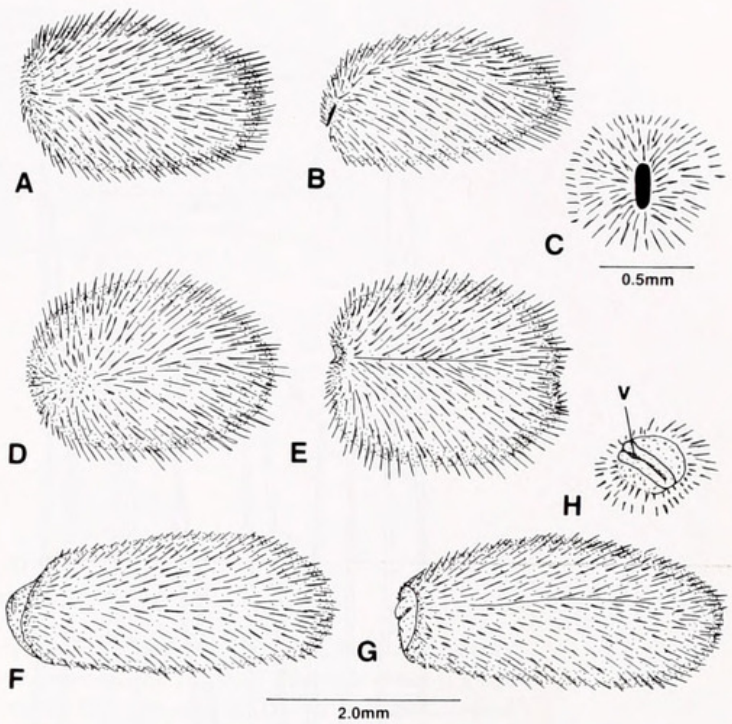

Figure 15. (A–C) *Simrothiella schizoradulata* Salvini-Plawen, lectotype (=*Plawenia schizoradulata*) (A, B) and paralectotype (C). (D, E) *Plawenia sphaera* n. sp., holotype. (F–H) *P. argentinensis* n. sp., holotype. (A, D, F) Lateral views, anterior to left. (B, E, G) Ventral view, (B) Oblique and somewhat compressed. (C, H) Contracted mouth opening. v opening to vestibule.

Paralectotypes. USNM 880322 (dissected alcohol specimen, spicule, radula slides): Length 1.1 mm, width and height 0.6 and 0.8 mm, respectively (specimen compressed), type locality. USNM 880323 (alcohol specimen): Length 1.3 mm, width and height both 0.9 mm, type locality.

Description.

Appearance: Small, rotund, length to 3.5 mm, diameter to 1.6 mm, posterior body narrower than anterior end; contracted mouth long, oval, on a broad, circular, flattened anteroventral area; pedal groove nearly hidden by spicules (Figs. 15A–C, 19A).

Cuticle and epidermis: Cuticle thick, 70–80 μm, epidermis thinner, 25 μm (Salvini-Plawen, 1978).

Epidermal spicules of lectotype and paralectotype: Almost all broken (Fig. 16, spicules 4–7; measurements, Table 2); many bent about one-quarter distance or less from base (spicules 6, 7); widest just above bend, base narrowest just below bend, then widening proximally; spicules beside pedal groove pointed distally, base rounded, without root (spicule 1).

Radula (one examined, small 1.1-mm paralectotype): Rows about 25 between proximal end of radular sac and pharynx, and 35–40 within anteroventral radular pockets; pockets with 2.5 whorls (3.5 whorls, Salvini-Plawen [1978], probably from a larger individual) (Fig. 19B; measurements, Table 2); morphology of distal extension of denticle-bearing

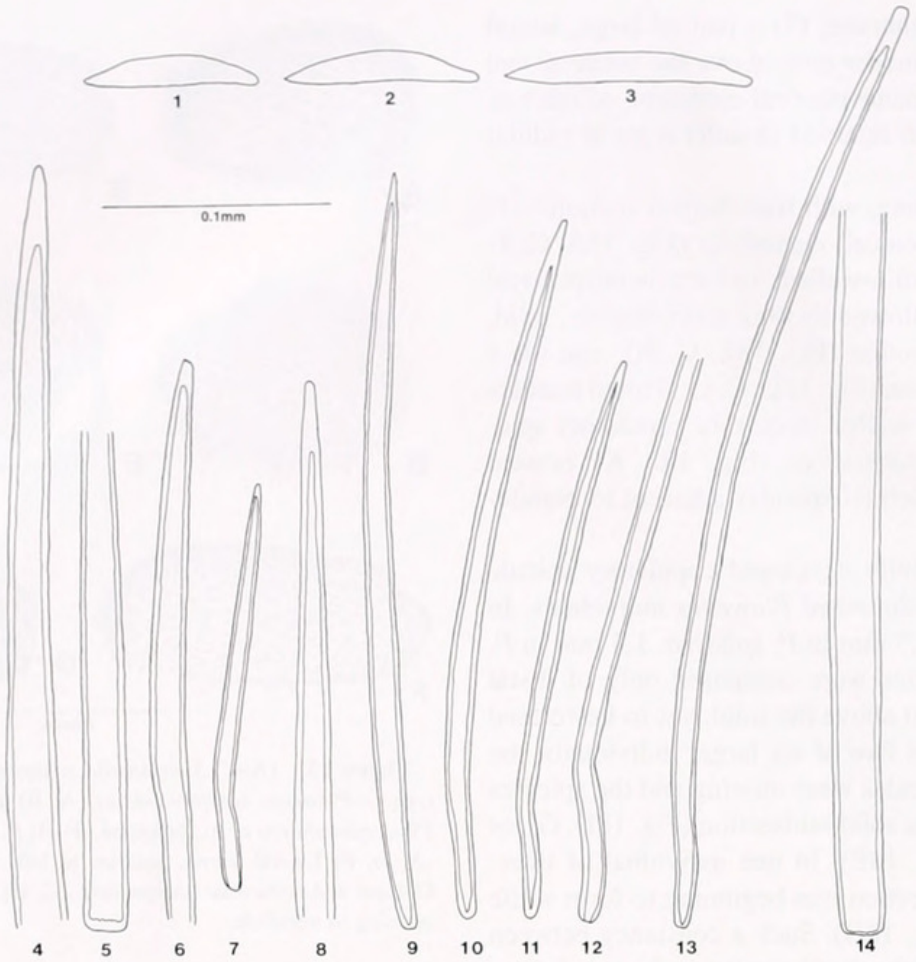

Figure 16. Epidermal spicules of *Plawenia* species. 1, 4–7, *Simrothiella schizoradulata* Salvini-Plawen (=*Plawenia schizoradulata*): spicules 4–6, lectotype; 1, 7, paralectotype. *Plawenia sphaera* n. sp.: spicules 2, 8–11, paratype 1. *P. argentinensis* n. sp.: spicules 3, 12–14, paratype USNM 880319. Spicules 1–3 from beside pedal groove; all other spicules incomplete except 7, 9–11, 13.

membrane not determined (Fig. 17A, B); number of denticles on lateral buttress 4.

Copulatory spicules (one examined): Distal tip dissected from small paralectotype, broadly conical, curved, and furrowed, 20 μm wide at distance of 45 μm proximal to tip (Fig. 18); remainder of spicule either not recovered or not yet formed; accessory copulatory spicules, if present, overlooked.

Notes on anatomy: The internal anatomy of *P. schizoradulata* has been published (Salvini-Plawen, 1978).

Reproductive system: See Salvini-Plawen (1978).

Remarks: For differences from other species, see Remarks under *P. sphaera* and *P. argentinensis* and Table 2.

Plawenia sphaera sp. n.

(Figs. 15D, E, 16 spicules 2, 8–11, 17C, D, J, 18B, G, H, K, 19D–G)

Scheltema *et al.,* 1994, fig. 18e.

Holotype. MNHNP (alcohol specimen, spicule slide): Length 2.4 mm, greatest height and width 1.7 and 1.9 mm, respectively. West European Basin, 57°59.7′N, 10°39.8′W, 2091 m (INCAL [CENTOB] DS-01, 15.vii.1976).

Illustrated paratypes. No. 1, MNHNP (epidermal, copulatory spicule slides; radula slide) and no. 2, MNHNP (epidermal, copulatory spicule slides); type locality. No. 3, MNHNP (epidermal, copulatory spicule slides; radula slide) and no. 4, MNHNP (dissected alcohol specimen, copulatory spicule slide), West European Basin, 57°58.8′N, 10°48.5′W, 2081 m (INCAL [CENTOB] DS-02, 16.vii.76).

Material examined. 68 individuals. See Table 1, also the following: Bay of Biscay, RV *Sarsia* (National Institute of Oceanography, Plymouth, UK): stn 44, 43°40.8′N, 3°35.2′W, 1739 m, 16.vii.67 (20 individuals), and stn 50, 43°46.7′N, 3°38′W, 2379 m, 18.vii.67 (1 individual).

Description.

Appearance: Small, rotund, similar in external appearance to *P. schizoradulata* but smaller; greatest length, height, and width, 2.9, 1.8, and 1.9 mm, respectively (Figs. 15D, 19D); with slight taper posteriorly; with a cleft in long posterior spicules indicating position of dorsoterminal sense organ (Fig. 15E).

Cuticle and epidermis: Cuticle thick, 45 to 50 μm, epidermis thin, 11 to 12 μm.

Epidermal spicules: Long, slender to broad, thin-walled (Fig. 16, spicules 8–11), shape as in *P. schizoradulata* but

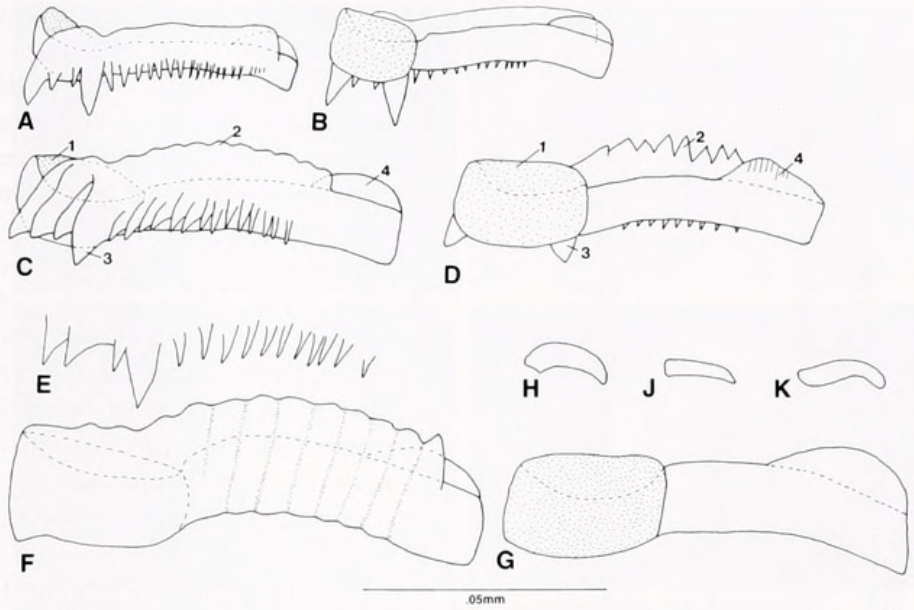

Figure 17. Radular teeth of *Plawenia* species, medial edge to right, distal edge above. (A, B, H) *Simrothiella schizoradulata* Salvini-Plawen, paralectotype (=*Plawenia schizoradulata*). (C, D, J) *Plawenia sphaera* n. sp. (paratypes 1, 3); in (C), distal edge of denticle-bearing membrane (2) serrated as in (D), but serrations covered by adjacent tooth. (E–G, K) *P. argentinensis* n. sp., paratype USNM 880319 (G, K) and USNM 880320 (F). (A, C, E, F) View from above. (B, D, G) View from beneath radular membrane; buttress with stippling. (E) 3rd tooth from proximal end of radular sac, denticles present, lost by 4th tooth as in (F). (H–K) Initial tooth retained at distal end of anteroventral radular pocket. 1 lateral buttress, 2 distal extension of denticle-bearing membrane, 3 large, lateral denticle above buttress, 4 medial and distal hemispherical extension of bar.

largest spicules longer (Table 2); spicules beside pedal groove with a sharp, distal point and proximally narrowed to a slight stem (spicule 2).

Radulae (7 examined, 4 by light microscopy, 3 by SEM, in individuals ranging in length from 1.5 to 2.7 mm; Figs. 17C, D, J; 19E–G; measurements, Table 2): Number of denticles on lateral buttress 4. Tooth structures locking both adjacent and opposed teeth closely to each other, with tips of denticles proximally overlying serrated, distal membrane of next adjacent tooth (Figs. 17D, 2; 19G), and hemispherical medial margin of bar finely denticulate (Fig. 17D, 4), holding opposed teeth in zipperlike arrangement (Fig. 19E).

Copulatory spicules (examined from 6 individuals 1.5 to 2.5 mm long, Fig. 18B, G, H, K; Table 2): Paired, single spicules, proximal two-thirds of spicule hollow, with wall thickened in two longitudinal bands; distal tip narrow, curved, bluntly pointed; accessory copulatory spicules S-shaped with up to 7 distal protuberances, with hollow extending from base up to 4th protuberance; number of accessory spicules per bundle not determined.

Remarks. Histologic descriptions of *P. schizoradulata* (Salvini-Plawen, 1978) are also descriptive of *P. sphaera,* with the additional observation that the more dorsal of the paired pharyngeal glands are acinar. The differences between *P. sphaera* and *P. schizoradulata* are as follows: In *P. sphaera* (1) small individuals are more nearly spherical than small *P. schizoradulata,* with length:height ratios of 1.0 and 1.4, respectively, in individuals less than 1.6 mm long; (2) many epidermal spicules are longer and broader than most of those in *P. schizoradulata;* (3) the distal tips of the copulatory spicules are narrower and more pointed; (4) there are fewer denticles per tooth; (5) there are more rows of teeth; (6) the initial radular teeth are shorter; and (7) the cuticle and epidermis are about one-half the thickness of those in *P. schizoradulata.* Finally, although the differences enumerated here and in Table 2 may seem minor, *P. schizoradulata* belongs to the abyssal Pacific fauna and *P. sphaera* to the upper slope fauna of the northeastern Atlantic. That they could be the same species is not likely given their morphological and biogeographic differences.

Plawenia argentinensis sp. n.

(Figs. 15F–H, 16 spicules 3, 12–14, 17E–G, K, 18A, D–F, J, 19C)

Holotype. USNM 880318 (alcohol specimen, spicule slide): Length 3.4 mm, midbody height and width 1.4 and 1.5 mm, respectively. Argentine Basin, 38°16.9′S, 51°56.1′W, 4382 m (RV *Atlantis II* Cruise 60, Stn 242, 13.iii.1971).

Illustrated paratypes. USNM 880319 and USNM 880320 (both as dissected alcohol specimens, epidermal and copulatory spicule slides, and radula slide); USNM 880321 (dissected alcohol specimen, copulatory spicule slide); type locality.

Material examined. 23 individuals from type locality.

Description.

Appearance: Largest, most elongate and least spiny *Pla-*

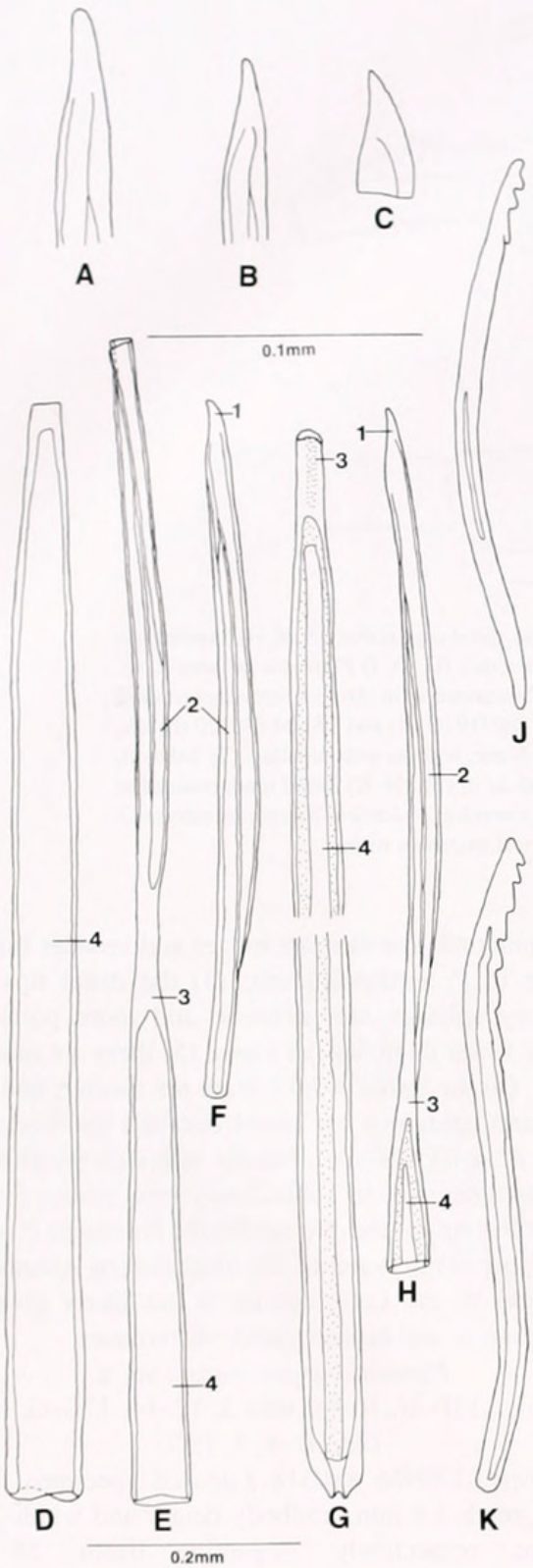

Figure 18. Copulatory spicules of *Plawenia* species; see text for description of sections 1–4. (A, D–F, J) *Plawenia argentinensis* n. sp. (B, G, H, K) *P. sphaera* n. sp. (C) *Simrothiella schizoradulata* Salvini-Plawen, paralectotype (=*Plawenia schizoradulata*). Spicules (A–C) distal tip (section 1): (A) enlargement of tip in (F), turned slightly. (B) Enlargement of tip in (H). (D) completely formed basal portion (section 4); entire distal portion above solid midsection (section 3) missing from 5.0-mm individual (paratype USNM 880320). (E) Incompletely formed basal portion (section 4), narrow, solid midsection (section 3), and proximal part of twisted, hemispherical channel (section 2), distal portion of section 2 and solid tip (section 1) missing from 3.8-mm individual (paratype USNM 880319). (F) Complete distal portion (sections 1, 2) of 1.4-mm individual, solid midsection and basal portion yet to be formed (paratype USNM 880321). (G) Completely formed basal portion (section 4) with thickened areas of spicule wall shown by stippling; solid midsection (section 3) showing furrow (stippling); entire distal portion (sections 1, 2) missing from 2.4-mm individual (paratype 3) (spicule broken during preparation; upper part rotated 90° from lower part). (H) Entire distal portion and midsection (sections 1–3) with basal portion (section 4) just beginning to form, in 2.2-mm individual (paratype 2). (J, K) Accessory copulatory spicules (paratype USNM 880320, paratype 4, respectively). Upper scale refers to spicules (A–C, J, K); lower scale, to spicules (D–H).

wenia species herein described, length to 5.0 mm, height to 1.8 mm, width to 1.6 mm (Figs. 15F, G, 19C); tapered anteriorly, mouth usually protruded with pair of lateral protuberances, contracted vestibule opening often distinct above mouth (Fig. 15H); line of pedal groove distinct.

Cuticle and epidermis: Not examined.

Epidermal spicules: Similar to other two species, but longer and broader (Fig. 16, spicules 12–14; Table 2); spicules from beside pedal groove elongate, distally pointed, without or with slight root (spicule 3).

Radula (2 examined): Teeth without distinct denticles except for the three most recently formed (Fig. 17E, F; measurements, Table 2), otherwise denticles appearing only as rows of slight protuberances; distal margin of denticle-bearing membrane scalloped except medially angular (Fig. 17F).

Copulatory spicules (3 examined): As in *P. sphaera,* but longer and wider, and solid tip longer (Fig. 18A, D–F; Table 2); accessory copulatory spicules about 19 per bundle, short, narrow, curved but not S-shaped, nearly solid or with hollow in central portion of spicule only, protuberances 1 to 3 (Fig. 18J; Table 2).

Remarks. P. argentinensis differs more from the other two *Plawenia* species than they do from each other in (1) size and shape of body, (2) erectness and size of epidermal spicules, (3) morphology of radula, (4) size of copulatory spicules, and (5) size and morphology of accessory copulatory spicules.

Simrothiella Pilsbry, 1898

Type species. Solenopus margaritaceus Koren & Danielssen, 1877, by subsequent designation [1981 Bull. Zool. Nom. 38, Op. 1185].

Known distribution. Between about 70 and 2000 m depth off Ireland and in Norwegian fjords.

Diagnosis. Elongate, smooth; epidermal spicules skeletal, hollow, uprights either not obvious or lacking; cuticle thick, epidermis thin with stalked papillae (Odhner, 1921); radula large, with long anteroventral pockets parallel to long axis of body, spiral restricted to proximal end. Monotypic, but with a second undescribed species from the West European Basin.

Remarks. The type species is described here on the basis

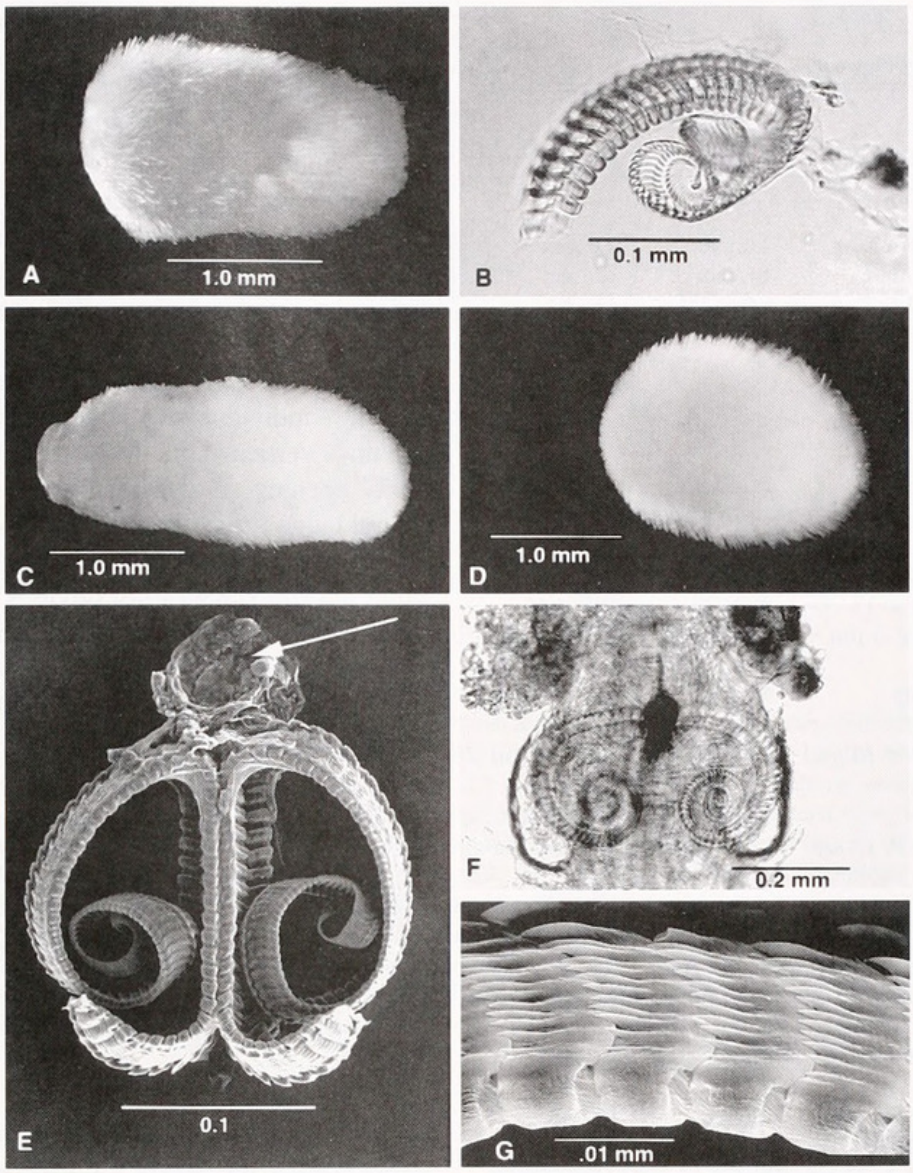

Figure 19. Three species of *Plawenia* n. g. (A, B) *Simrothiella schizoradulata* Salvini-Plawen (=*Plawenia schizoradulata*). (A) Lectotype. (B) Distichous radula, distal spiral with several turns, paralectotype. (C) *Plawenia argentinensis* n. sp., holotype. (D–G) *Plawenia sphaera* n. sp.: (D) Holotype. (E) Entire radula, pharyngeal cuticle indicated by line. (F) Ventral view of radula *in situ* within buccal mass. (G) Interlocking teeth of distichous bars. In (A, C, and D) anterior is to left and dorsal above.

of external morphology and, for the first time, on hard parts isolated from specimens recently collected in the West European Basin and from a museum specimen collected near the type locality. The internal anatomy was described by Odhner (1921).

Simrothiella margaritacea (Koren & Danielssen, 1877)
(Figs. 11A–C, 20–22)

Lectotype. UIB.Z.M 2075. Two incomplete specimens are labeled as G.O. Sars material from the type locality, Kvitingsog [Norway], 75–115 m (as Hvidingsöerne, Stavanger, 40–60 fm [=72–108 m] in Koren & Danielssen (1877 [trans. 1879]) and appear to be syntypes; Odhner (1921) called these specimens "prototype." Chosen here as lectotype is the more complete specimen with the anterior end intact; the second specimen is a paralectotype, UIB.Z.M 66806. Other G.O. Sars specimens from 75–95 m off Kopervik near the type locality are not considered syntypes (UIB.Z.M. 2078).

Illustrated voucher specimen. UIB.Z.M 66807: Length 9.5 mm, heights at anterior, midbody, just anterior to the posterior bulge, and posterior, 0.8, 1.0, 0.8, and 0.8 mm, respectively. Kopervik near type locality, 75–95 m.

Illustrated voucher specimens. USNM 894261 (entire alcohol specimen), length 9.5 mm, heights of anterior, midbody, anterior to posterior bulge, and posterior, 0.6, 0.8, 0.5, and 0.7 mm, respectively; USNM 894262 (dissected alcohol specimen, copulatory spicule slide); USNM 894263 (dissected alcohol specimen, radula slide); USNM 894264 (dissected alcohol specimen, radula slide, copulatory spicule slide); USNM 894265 (dissected alcohol specimen, radula

Table 2

Comparison of three species of Plawenia

	P. schizoradulata	*P. sphaera*	*P. argentinensis*
Body dimensions			
Maximum length	3.5 mm[1]	2.9 mm	5.0 mm
Maximum height	1.6 mm[1]	1.8 mm	1.8 mm
Length:height (range)	1.4–2.2	1.0–2.2	1.8–3.1
Length:height (mean)	1.7	1.6	2.3
Epidermal spicules			
Maximum length, midbody	>458 μm	>528 μm	>725 μm
Maximum length, posterior	—	>700 μm	>766 μm
Maximum width	21 μm	20 μm	23 μm
Length of solid tip, most spicules	≤18 μm	≤18 μm	≤22 μm
Pedal groove, max. l × w × thickness	90 × 13 × 2–3 μm	86 × 14 × 4 μm	108 × 15 × 3.5 μm
Radula[2]			
Number of rows	~65	95–145	146
Number of whorls	3.5[1]	2.5–3.5	2.8
Tooth bar	60 × 10 μm	74 × 10 μm	86 × 13 μm
Number of denticles above bar	19	11–15	11–13[3]
Buttress	19 × 13 μm	27 × 17 μm	35 × 20 μm
Number of denticles above buttress	4	4	4[3]
Length initial tooth	18 μm	14 μm	18 μm
Copulatory spicules			
Length of base	n.d.	890 μm	1,000 μm
Maximum width of base	n.d.	60 μm	80 μm
Length solid midsection	n.d.	180 μm	180 μm
Length distal section	n.d.	520 μm	678 μm
Maximum width distal section	n.d.	30 μm	35 μm
Total length[4]	n.d.	1,590 μm	1,858 μm
Length conical tip above channel	n.d.	36 μm	50 μm
Maximum width conical tip	20 μm	17 μm	20 μm
Max. 1. accessory copulatory spic.	n.d.	234 μm	196 μm
No. protuberances accessory cop. spic.	n.d.	7	3

[1] Salvini-Plawen (1978).

[2] Radula measurements in *P. schizoradulata* from small paralectotype 1.1 mm long.

[3] Present only in first three most recently formed teeth.

[4] Estimated total length before presumed loss of deciduous distal section.

slide, copulatory and epidermal spicule slides); USNM 894266 (dissected alcohol specimen); West European Basin, 50°58.7′N, 13°01.6′W, 2173 m (RV *Chain* 106, Stn 316,18.viii.72).

Material examined. 38 individuals: type material (2); UIB.Z.M. 2078(6), Kopervik, 75–95 m; UIB.Z.M 15852, 62°01′N, 0°08′E, ~1400 m (*Armauer Hansen* Stn 3, 10–11.v.1914)(4); RV *Chain* 106 Stn 316, 2173 m (26).

Description.

Appearance: Slender, length to 12.0 mm, rounded posteriorly and somewhat pointed subterminally at anterior end (Figs. 20A, B, 11A, C); greatest diameter anterior, to 1.1 mm in height, narrowing to 0.8 mm or less just before the posterior end which swells to 0.9 mm; greatly contracted individuals with constant diameter (*cf.* Figs. 11C, 20A); immature individuals without posterior swelling; contracted mouth a vertical slit, pedal pit small; contracted mantle cavity opening an anterior-posterior slit commencing on a ventral bulge (Fig. 20A); dorsoterminal sense organ present, not obvious; skeletal spicules obvious as an open meshwork, upright spicules not obvious.

Cuticle and epidermis: Not examined.

Skeletal spicules: Hollow, heavy-walled, to 280 μm long by 18 μm wide, walls 5 μm thick (Fig. 20D); lectotype spicules eroded, >144 by 16 μm, walls 5 μm (Fig. 20J);

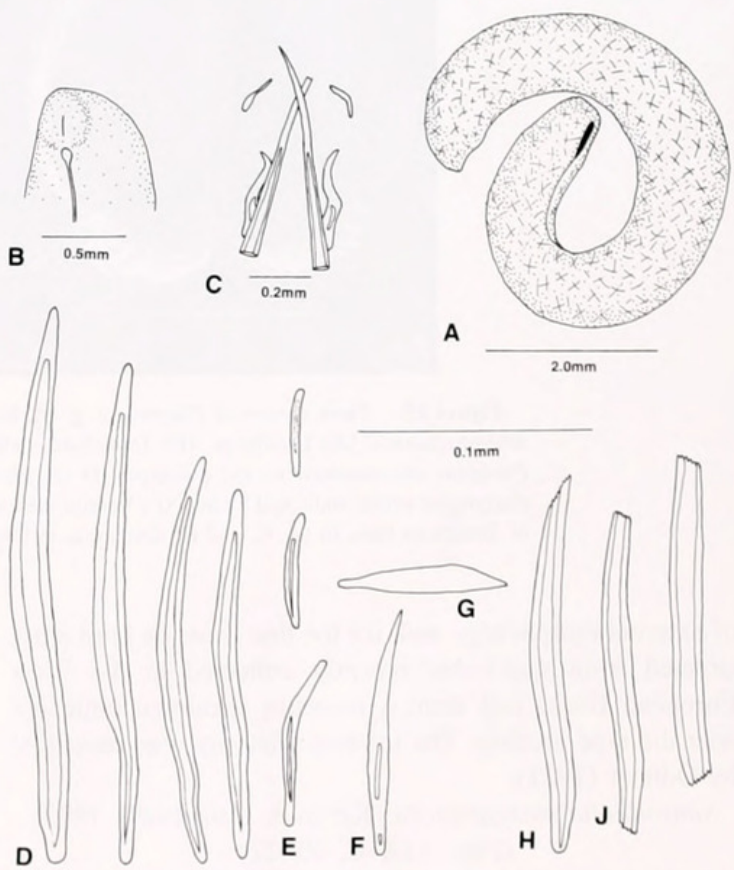

Figure 20. *Simrothiella margaritacea* (Koren & Danielssen). (A) Individual from Kopervik near type locality (voucher specimen before dissection, UIB.Z.M 66807). (B) Pointed anterior end of (A), anteroventral view. (C) Copulatory spicules *in situ* drawn as tissue dissolved in bleach (voucher USNM 894264, West European Basin). (D–G) Epidermal spicules from midbody (voucher USNM 894265, West European Basin): (D) Four skeletal spicules. (E) Upright spicules (vertical row). (F, G) From beside pedal groove, (F) lateral to (G). (H) Spicule from voucher UIB.Z.M 66807, tip eroded. (J) Two spicules, eroded, from lectotype.

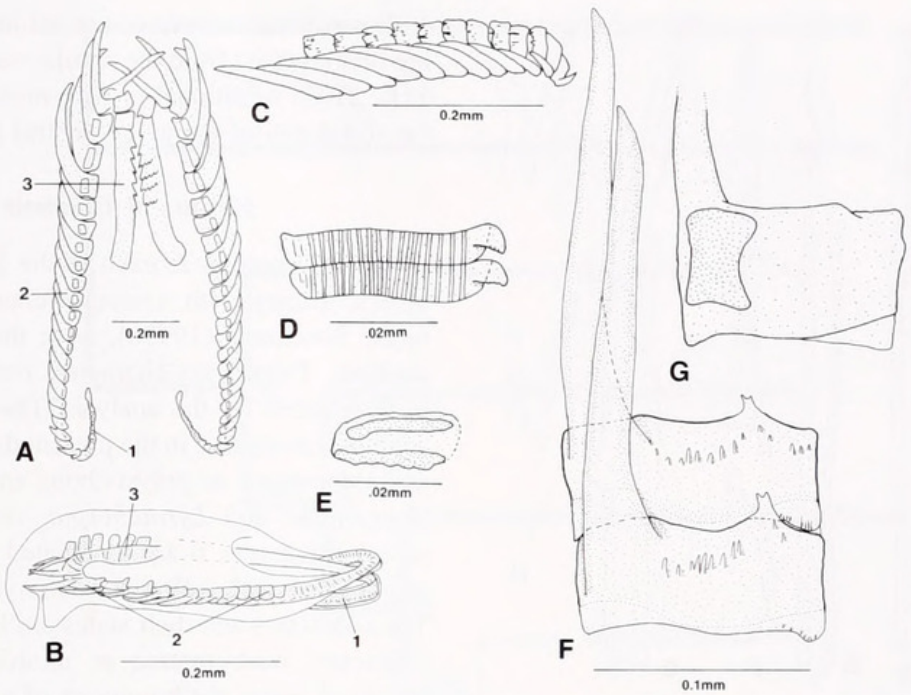

Figure 21. Radula of *Simrothiella margaritacea* (Koren & Danielssen) drawn from three individuals from West European Basin, vouchers USNM 894263 (A, G), USNM 894264 (B–D, F), and USNM 894266 (E); anterior is toward the top in all figures except (B) and (C). (A) Entire radula seen from above; sections 1 and 2 from anteroventral pocket, section 3 from radular sac (*cf.* Fig. 11C). (B) The same in lateral view, anterior to left, showing relation of teeth to buccal mass tissue; drawn during tissue dissolution in bleach. (C) First 12 proximal teeth of section 2 in lateral view, anterior to left. (D) Two teeth from region 1, comblike denticles schematic, medial edge to left; buttress, but not lateral denticles, forming on right (lateral) edge as a downturned hook. (E) First two teeth of anteroventral radular pocket, presumably the original teeth, with denticles not yet formed. (F) Two adjacent teeth ventral and just posterior to pharynx from near the anterior end of the anteroventral radular pocket, viewed from above. (G) Bar portion of tooth similar to those in (G) viewed from beneath radular membrane, showing buttress.

Kopervik voucher, spicules eroded, 170 by 16 μm, walls 5 μm (Fig. 20H); spicules evenly curved and widest above proximal straight or recurved basal section; base up to 67 μm long, solid distal tips to 27 μm long, proximal end rounded; skeletal spicules somewhat shorter anteriorly and posteriorly, to 225 μm; upright spicules small, to 95 μm long by 7 μm wide, curved or bent, hollow space narrow, distal end solid and rounded (Fig. 20E); spicules along pedal groove solid, flat, thin (2 μm), with proximal narrow root, distally pointed, length to 74 μm, greatest width to 14 μm (Fig. 20G); spicules just lateral to these shaped much like skeletal spicules in outline but nearly solid, sharply pointed distally, and shorter, to 106 μm long by 7 μm wide, proximal straight portion to 14 μm long (Fig. 20F).

Radula (6 examined: 1 from Kopervik voucher; 5 from *Chain* 106 Stn 316): Up to nearly 2 mm long, turning 180° so that short radular sac and long anteroventral radular pocket parallel each other and long axis of body, with 3 discrete sections (Figs. 11B, 21A, B): section 1, proximal anteroventral radular pocket as 0.2-mm loops, one lying over the other, initial teeth nondenticulate bars 20 by 3 μm (Fig. 21E); next teeth comblike bars about 45 by 9 μm at center of section 1, denticle number 14–18 (Fig. 21D); section 2, main part of anteroventral radular pocket and longest section of radula, about 1 mm long, proximal teeth with bar 50 by 15 μm bearing 17 comblike denticles and a lateral denticle 27 μm long, laterally buttressed (Fig. 21C); teeth of section 2 gradually enlarging anteriorly, largest tooth with bar 130 by 90 μm, lateral denticle to 280 μm long, heavily buttressed, other denticles of bar scattered, small, and varying in pattern and number among individuals (Fig. 21F, G); section 3, radular sac 0.5 to 0.6 mm long with 7–9 developing teeth, long lateral denticles ill-defined, with proximal stretch of membrane 0.2 mm long without defined teeth (Figs. 11B, 21A); at ventral bend of radula from the sac into the pharynx, lateral teeth obvious, pointing anteriorly (Figs. 11B, 21A).

Copulatory spicules (5 examined): Paired, 2 per sac (Fig. 22C); one spicule long, curved, hollow, to 1.2 mm long, 93 μm wide in curved view (Fig. 22G), narrower in view where spicule appears straight (Fig. 22C); solid distal ends pointed and approximated *in situ* (Fig. 20C), with thick core surrounded by added thin layer of calcium carbonate, perhaps as "wings" (Fig. 22E); second spicule shorter, hollow, to 370 μm long, S-shaped, base partially wrapped around long spicule, from 90 μm in widest view to 30 μm in

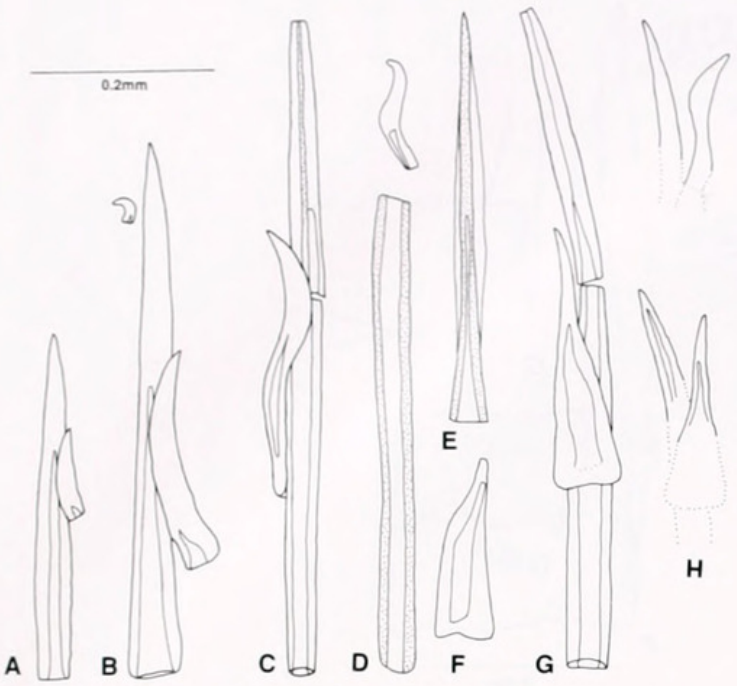

Figure 22. Copulatory spicules of *Simrothiella margaritacea* (Koren & Danielssen) (see also Fig. 20C). (A, B) growth stages, (A) from 8.3 mm individual (voucher USNM 894263), (B) from individual <7 mm (voucher USNM 864262) with accessory spicule above. (C–G) Paired spicules from voucher 5 (voucher USNM 864265), specimen length not known: (C and G) two views of one of pair, proximal end broken off; (D–F) second of pair, (D) proximal to and broken off from distal portion (E) of long spicule, wall and solid distal portion with stippling, accessory spicule above. (H) Above and below, paired, mostly (decalcified spicules of voucher specimen from Kopervik near type locality (UIB.Z.M 66807); solid lines indicate part still calcified, dotted lines indicate remaining uncalcified thin membrane. Decalcification due to dissolution during preservation.

narrowest, axially twisted such that solid distal end widest in narrowest view of base and narrowest in widest view of base (Fig. 22C, G); single, short accessory spicules paired, to 152 μm, base straight, slightly hollowed proximally, distally solid, deeply curved into distal hook (Fig. 22B, D); growth stages of copulatory spicules (Fig. 22A, B, D, E) imperfectly correlated with size of individual.

Reproductive system: See Odhner (1921).

Remarks. The recently collected material from the West European Basin was identified as *Simrothiella margaritacea* by comparing the following: (1) epidermal spicule width and wall width with the lectotype and Kopervik voucher spicules (Fig. 20D, H, J); (2) width and shape of the anterior end of the body with the lectotype (Fig. 11A); (3) shape and size of the anterior and posterior ends of the body with the Kopervik voucher; (4) radula with the radula of the Kopervik voucher; and (5) size and shape of copulatory spicules with those from the Kopervik voucher (Fig. 22H).

Elements of copulatory spicules of *S. margaritacea* are much like those in *Kruppomenia levis* (*cf.* Fig. 14A). The comblike denticles of early teeth are similar to those in *Kruppomenia* and *Plawenia* radulae, but the original tooth in *S. margaritacea* is a nondenticulate bar, not a triangle.

The radular teeth have not achieved full size when they are first released from the radular sac into the pharynx (Figs. 11B, 21A). Additional growth must therefore take place at the distal end of the anteroventral pocket.

Results of Cladistic Analysis

A single species in each of the 5 genera described here, plus a species with a monostichous radula, *Lyratoherpia incali* Scheltema (1999b), were the subjects of a cladistic analysis. Twenty-six characters from an original set of 42 were selected for the analysis. The 16 excluded characters were uninformative in the present data set and included such autapomorphies as polystichous and monostichous radulae (*Dorymenia* and *Lyratoherpia,* respectively). Of the selected characters, 6 are associated with the radula, 5 with spicules, 11 with soft-part anatomy, and 4 with body shape. The characters and their states are listed in Appendix 1. All characters were treated as unordered and were equally weighted. Since the homology of a number of characters is unknown or disputable, we chose to use presence-absence coding. This type of coding is simple and intuitive, and it has the added advantage that exact homologies between character states need not be known (Pleijel, 1995).

The resulting phylogenetic trees were rooted by outgroup analysis (*e.g.,* Nixon and Carpenter, 1993), with *Helicoradomenia juani* Scheltema & Kuzirian as the outgroup, since it possesses characters that are considered to be less derived. Among these characters are the radula, which is similar to the radula of the Middle Cambrian *Wiwaxia* (see Schander and Scheltema, in press), and spicules that are solid, a condition known through ontogeny to be plesiomorphic to hollow spicules (Scheltema and Jebb, 1994).

The cladistic analysis resulted in one shortest tree, 46 steps long (Fig. 23). The overall consistency and retention indices (CI, RI) are 0.5652 and 0.5349, respectively. One clade has a decay index of 4, and the others of 1. The character transformations are found in Appendix 2.

Discussion

The external and hard-part morphologies of the 10 species and 5 genera of neomenioid aplacophorans described here provide a basis for aplacophoran taxonomy (*i.e.,* discrimination of taxa), as well as for phylogeny (*i.e.,* the evolutionary relationships among taxa).

Taxonomy

We conclude that histologic preparations by themselves will not provide morphological evidence adequate for discriminating with certainty among closely related species. For example, the two species of *Eleutheromenia* are indistinguishable from their soft anatomy, yet hard parts, particularly the copulatory spicules (Fig. 9), do distinguish them,

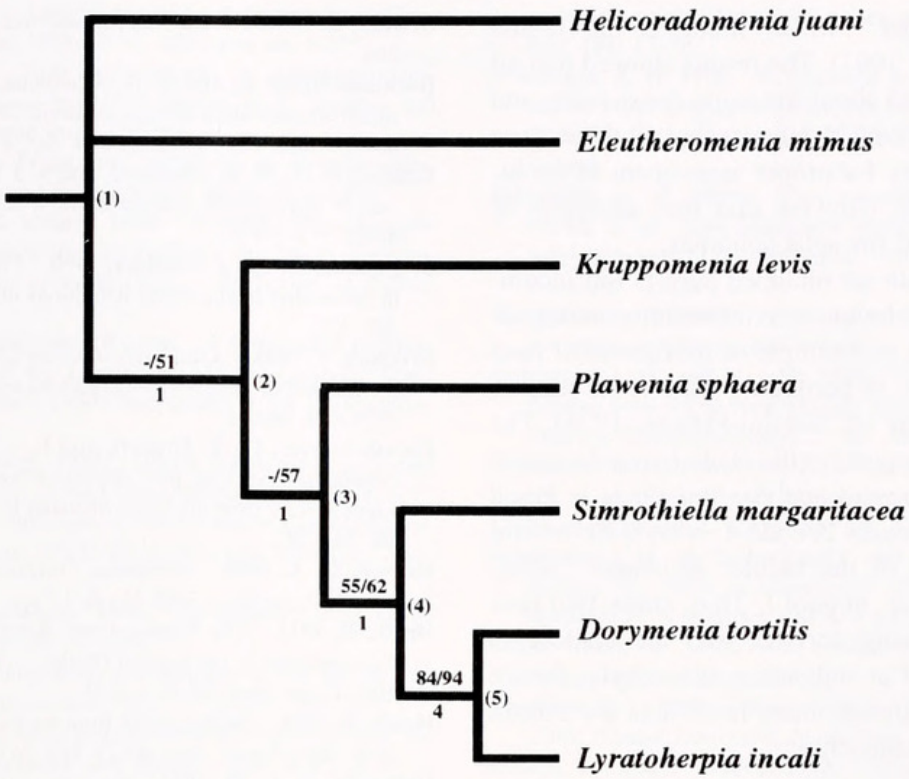

Figure 23. The single shortest tree, 46 steps long, obtained from an exhaustive search of the data matrix in Appendix 1; CI 0.5652, RI 0.5349. Numerals within parentheses are references to the nodes indicated in Appendix 2. Numerals above branches are bootstrap/jacknife values, and numerals below are decay values.

and the differences in size of their epidermal spicules and radular teeth are species related, and not due simply to variation within a species. Only measurements of the largest epidermal spicules were useful for species recognition. Analysis of a large number of spicules from a single individual would be meaningless in this regard, for it would hide the truly distinctive character—the size of the largest epidermal spicules produced in each species.

The two closely related *Kruppomenia* species are distinguished here on hard parts alone, that is, the differences in radula and copulatory spicule morphology (Figs. 12F–K, 14). Even though the differences in epidermal spicules are subtle, one can, with practice, quickly discern the differing lengths between the base and proximal bend (Fig. 13). Although *K. levis* and *K. delta* co-occur in some epibenthic sled samples (Table 1), they should not necessarily be considered sympatric; sled trawls, particularly those taken at abyssal depths, often traverse a mile or so of ocean floor and probably collect organisms from several populations.

Dorymenia sarsii and *D. tortilis* can be differentiated by the spicules at the opening of the mantle cavity (Fig. 4K, L), as well as by the differences listed under Remarks for *D. tortilis*. Finally, species of *Plawenia* are differentiated by a combination of hard-part and external morphologies (Table 2).

Higher taxa can also be determined from hard parts and body shape. Thus, although members of both genera are elongate and smooth, *Dorymenia* and *Simrothiella* species have very different radulae (Figs. 2E, F, 21). *Plawenia* species are immediately recognizable by their nearly spherical bodies with long, hollow spicules that are upright, but not skeletal (Fig. 15, 19A, C, D). *Kruppomenia* species are brought together by their distinctive, long, broad, ribbonlike radula bearing narrow, serrated teeth, as well as by their short, blunt bodies (Fig. 12). *Eleutheromenia* species belong to a taxon with hollow, barbed spicules and a radula with distichous hooks.

Soft internal anatomy will always be important for phylogeny and often for the determination of higher ranks. What is emphasized here is that identification of species should not depend on histology, and higher taxa should reflect external and hard-part morphologies.

Phylogeny

Because the bootstrap values were relatively low, and few genera and species were included, we refrain from defining clade names (de Queiroz and Gauthier, 1990; Schander and Thollesson, 1995; Cantino *et al.*, 1997). Although the figured tree (Fig. 23) cannot define clades, the usefulness of characters from hard parts in phylogenetic analyses is clear from the average consistency indexes: for radula characters, 0.58; for soft-part anatomy, 0.59; for spicule characters, 0.47; and for external appearance, 1.

In a reanalysis of 22 published phylogenetic studies of Gastropoda, three types of characters were compared: shell,

soft anatomy, and "other," which included the radula (Schander and Sundberg, 1997). The results showed that all three character groups had about the same consistency and retention indices, and the conclusion was that all three types of characters are necessary for proper assessment of evolutionary relationships. We likewise find that all types of characters should be used for aplacophorans.

Although the small data set included here is too incomplete to shed light on evolutionary relationships among all neomenioids, it serves as an example of usefulness of hard parts in cladistic analysis. In particular, there is no support for a clade Simrothiellidae (*cf.* Salvini-Plawen, 1978). The indices do give strong support for the clade *Lyratoherpia* + *Dorymenia,* but in the present analysis this clade is based mostly on absences (Appendix 2, node 4 → node 5), several arising from derivations of the radular apparatus (Scheltema, Kerth, and Kuzirian, unpubl.). Thus, these two taxa share a condition of being derived, and the cladogram should not be interpreted as indicating monophyly. Future phylogenetic analyses utilizing many more taxa are certain to suggest a different relationship.

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Literature Cited

Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* **42:** 795–803.

Bremer, K. 1994. Branch support and tree stability. *Cladistics* **10:** 295–304.

Buckland-Nicks, J., and A. H. Scheltema. 1995. Was internal fertilization an innovation of early Bilateria? Evidence from sperm structure of a mollusc. *Proc. R. Soc. Lond. Ser. B* **261:** 11–18.

Cantino, P. D., R. G. Olmstead, and S. J Wagstaff. 1997. A comparison of phylogenetic nomenclature: a botanical case study. *Syst. Biol.* **46**(2): 313–331.

de Queiroz, K., and J. Gauthier. 1990. Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. *Syst. Zool.* **39:** 307–322.

Eriksson, T. 1998. *AutoDecay. Version 4.0.* Hypercard stack distributed by the author. http://www.bergianska.se/personal/TorstenE/AutoDecay/AD4.stack.sea.hqx

García-Alvarez, O., V. Urgorri, and L. v. Salvini-Plawen. 1998. *Dorymenia troncosoi* sp. nov. (Mollusca Solenogastres: Proneomeniidae), a new species from the South Shetland Islands (Antarctica). *Polar Biol.* **20:** 382–387.

Hansen, G. A. 1889. Neomenia, Proneomenia, und Chätoderma. *Bergens Mus. Aarsber. 1888* No. 6, 12 pp.

Heath, H. 1911. The Solenogastres. Reports on the scientific results of the expedition to the tropical Pacific . . . by the "Albatross" . . . . *Mem. Mus. Comp. Zool.* **45**(1): 1–179.

Heath, H. 1918. Solenogastres from the Eastern Coast of North America. *Mem. Mus. Comp. Zool.* **45**(2): 185–263.

Hubrecht, A. A. W. 1881. *Proneomenia sluiteri* gen. et sp. n., with remarks upon the anatomy and histology of the Amphineura. *Niederl. Arch. Zool. 1881,* Suppl. 9, 75 pp.

Ivanov, D. L. 1996. Origin of Aculifera and problems of monophyly of higher taxa in molluscs. Pp. 59–65 in *Origin and Evolutionary Radiation of the Mollusca,* J. D. Taylor, ed. Oxford University Press, Oxford.

Koren, J., and D. C. Danielssen. 1877. Beskrivelse over nye arter, henhørende til slaegten *Solenopus,* samt nogle oplysninger om dens organisation. *Arch. Math. Naturvid.* [Christiana] **2:** 120–128.

Koren, J., and D. C. Danielssen. 1879. Descriptions of new species belonging to the genus *Solenopus,* with some observations on their organization. *Ann. Mag. Nat. Hist. Ser. 5* **3:** 321–328.

Maddison, W. P., and D. R. Maddison. 1992. *MacClade: Analysis of Phylogeny and Character Evolution.* Version 3.0. Sinauer Associates, Sunderland, MA.

Morse, M. P. 1979. *Meiomenia swedmarki* gen. et sp. n., a new interstitial solenogaster from Washington, USA. *Zool. Scr.* **8:** 249–253.

Morse, M. P., and J. L. Norenburg. 1992. Observation and descriptions of *Meiomenia arenicola* Salvini-Plawen 1985 (Mollusca: Aplacophora), an interstitial Solenogaster from Fort Pierce, Florida. *Proc. Biol. Soc. Wash.* **105:** 674–682.

Nierstrasz, H. F. 1902. *The Solenogastres of the Siboga-Expedition. Siboga-Exp.* Vol. 47. E. J. Brill, Leyden. 46 pp.

Nierstrasz, H. F. 1905. *Kruppomenia minima* und die Radula der Solenogastren. *Zool. Jahrb., Abt. Anat. Ont.* **21:** 655–702.

Nixon, K. C., and J. M. Carpenter. 1993. On outgroups. *Cladistics* **9:** 413–426.

Odhner, N. H. 1921. Norwegian Solenogastres. *Bergens Mus. Arb. 1918–1919, Natur. raekke* No. 3: 1–86.

Pleijel, F. 1995. On character coding for phylogeny reconstruction. *Cladistics* **11:** 309–315.

Pruvot, G. 1891. Sur l'organisation de quelques néoméniens des côtes de France. *Arch. Zool. Expér. Gén. Ser. 2* **9:** 699–805.

Salvini-Plawen, L. v. 1968. Über einige Beobachtungen an Solenogastres (Mollusca, Aculifera). *Sarsia* **31:** 131–142.

Salvini-Plawen, L. v. 1972. Zur Morphologie und Phylogenie der Mollusken: Die Beziehungen der Caudofoveata und der Solenogastres als Aculifera, als Mollusca und als Spiralia. *Z. Wiss. Zool.* **184:** 205–394.

Salvini-Plawen, L. v. 1978. Antarktische und subantarktische Solenogastres (eine Monographie: 1898–1974). *Zoologica* **44:** 1–315.

Salvini-Plawen, L. v. 1985. Early evolution and the primitive groups. Pp. 59–150 in *The Mollusca Vol. 10 Evolution,* E. R. Trueman and M. R. Clarke, eds. Academic Press, Orlando.

Salvini-Plawen, L. v. 1997. Fragmented knowledge on West-European and Iberian Caudofoveata and Solenogastres. *Iberus* **15:** 35–50.

Salvini-Plawen, L. v., and G. Steiner. 1996. Synapomorphies and plesiomorphies in higher classification of Mollusca. Pp. 29–51 in *Origin and Evolutionary Radiation of the Mollusca,* J. D. Taylor, ed. Oxford University Press, Oxford.

Schander, C., and A. H. Scheltema. In press. An alternative interpretation of the affinities of the Lower and Middle Cambrian fossil *Wiwaxia corrugata* (Matthew, 1899) from studies of the Aplacophora. *Am. Malacol. Bull.*

Schander, C., and P. Sundberg. 1997. Useful characters in gastropod phylogeny—soft information or hard facts? Chapter IV, Pp. 1–6, in C. Schander, *Taxonomy and phylogeny of the Pyramidellidae (Mollusca, Gastropoda, Heterobranchia).* Ph.D. thesis, Göteborg University, Sweden.

Schander, C., and M. Thollesson. 1995. Phylogenetic taxonomy—some comments. *Zool. Scr.* **24:** 263–268.

Scheltema, A. H. 1981. Comparative morphology of the radulae and alimentary tracts in the Aplacophora. *Malacologia* **20:** 361–383.

Scheltema, A. H. 1988. Ancestors and descendents: relationships of the Aplacophora and Polyplacophora. *Am. Malacol. Bull.* **6:** 57–68.

Scheltema, A. H. 1993. Aplacophora as progenetic aculiferans and the coelomate origin of mollusks as the sister taxon of Sipuncula. *Biol. Bull.* **184:** 57–78.

Scheltema, A. H. 1996. Phylogenetic position of Sipuncula, Mollusca and the progenetic Aplacophora. Pp. 53–58 in *Origin and Evolutionary Radiation of the Mollusca,* J. D. Taylor, ed. Oxford University Press, Oxford.

Scheltema, A. H. 1999a. Two solenogaster molluscs, *Ocheyoherpia trachia* n. sp. from Macquarie Island and *Tegulaherpia tasmanica* Salvini-Plawen from Bass Strait (Aplacophora, Neomeniomorpha). *Rec. Aust. Mus.* **51:** 23–31.

Scheltema, A. H. 1999b. New eastern Atlantic neomenioid aplacophoran molluscs. *Ophelia* **51**(1): 1–28.

Scheltema, A. H., and M. Jebb. 1994. Natural history of a solenogaster mollusc from Papua New Guinea, *Epimenia australis* (Thiele) (Aplacophora, Neomeniomorpha). *J. Nat. Hist.* **28:** 1297–1318.

Scheltema, A. H., and A. M. Kuzirian. 1991. *Helicoradomenia juani* gen. et sp. nov., a Pacific hydrothermal vent Aplacophora (Mollusca: Neomeniomorpha). *Veliger* **34:** 195–203.

Scheltema, A. H., M. Tscherkassky, and A. M. Kuzirian. 1994. Aplacophora. Pp. 13–54 in *Microscopic Anatomy of Invertebrates Vol 5: Mollusca,* F. W. Harrison and A. J. Kohn, eds. Wiley-Liss, New York.

Stachowitsch, M. 1992. *The Invertebrates: An Illustrated Glossary.* Wiley-Liss, New York. 676 pp.

Swofford, D. L. 1998. *Phylogenetic Analysis Using Parsimony.* Version 4.0b1. Sinauer Associates, Sunderland, MA.

Welsch, U., and V. Storch. 1973. *Comparative Animal Cytology and Histology.* Seattle, University of Washington Press.

Appendix 1

Data matrix and list of characters: 0 absent, 1 present

Taxon/node	1111111112222222 12345678901234567890123456
Dorymenia tortilis	00000101?0101111001010110 1
Eleutheromenia mimus	10000?01?10101011110010010
Helicoradomenia juani	11000010010100101110010110
Kruppomenia levis	11111010110101010010110010
Plawenia sphaera	11101010110100011001001110
Simrothiella margaritacea	11111010001011011001?01101
Lyratoherpia incali	00000100?0101010010110011 0

1. Distichous radula: with 2 teeth per row (Figs. 11B, D, 12F, H, 19B, E, F, 21)
2. Bar base: radula on a bar entirely attached to radular ribbon (Figs. 6F, 12G, K, 19G, 21)
3. Original tooth: retained in anteroventral radular pocket (Figs. 6F, 12J, 21E)
4. Serrate teeth: denticles as fine serrations (Figs. 6F, 12F, G, H, K, 21D)
5. Tooth buttress: thickened radula base beneath lateral denticles (Figs. 17, 21G)
6. Unipartite membrane: radular membrane not divided (Scheltema, 1988)
7. Paired anteroventral pocket (Fig. 19F, 21A)
8. Single anteroventral pocket (Fig. 6B)
9. Original tooth triangular (Fig. 6F)
10. Stout body shape (Figs. 6G, H, 11E, F, 19A, C, D)
11. Elongate body shape (Figs. 6A, 11C)
12. Rounded body ends (Figs. 7A, E, 12A, D, 15)
13. Pointed or lobate body ends (Figs. 2A–D, 11C)
14. Skeletal spicules: spicules within cuticle, at right angles to each other (Figs. 2A, 12A, D, 20A)
15. Solid spicules (Fig. 3 spicules 1–3)
16. Hollow spicules (Figs. 3 [except spicules 1–4], 8, 13, 16, 20D–J)
17. Accessory copulatory spicules (Figs. 18J, K, 20C, 22B and D small spicules)
18. Copulatory spicule hood: main spicule with a second spicule wrapped around it (Fig. 9)
19. Single seminal receptacle (Figs. 5A, 10A, B)
20. Multiple seminal receptacles (Scheltema *et al.,* 1994, fig. 24h, i)
21. Seminal vesicle (Fig. 6C)
22. Respiratory papillae (Scheltema *et al.,* 1994, fig. 11d)
23. Respiratory folds (Scheltema *et al.,* 1994, fig. 11c)
24. Midgut sacculations (Scheltema *et al.,* 1994, fig. 13c)
25. Single-cell epidermal glands (Scheltema *et al.,* 1994, fig. 5d–g)
26. Multiple cell epidermal glands (Scheltema *et al.,* 1994, fig. 5a, c)

Appendix 2

List of character transformations

Branch	Character	Change	Branch	Character	Change
node 1 → node 2	3 (Original tooth)	0 → 1	node 5 → *Dorymenia*	8 (Single anteroventral pocket)	0 → 1
	5 (Tooth buttress)	0 → 1		19 (Single seminal receptacle)	0 → 1
	9 (Triangular original tooth)	0 → 1		20 (Multiple seminal receptacles)	1 → 0
	18 (Copulatory spicule hood)	1 → 0	node 5 → *Lyratoherpia*	14 (Skeletal spicules)	1 → 0
	21 (Seminal vesicle)	0 → 1		16 (Hollow spicules)	1 → 0
node 2 → node 3	19 (Single seminal receptacle)	1 → 0		18 (Copulatory spicule hood)	0 → 1
	20 (Multiple seminal receptacles)	0 → 1		23 (Respiratory folds)	1 → 0
	22 (Respiratory papillae)	1 → 0		25 (Single-cell epidermal glands)	0 → 1
	23 (Respiratory folds)	0 → 1		26 (Multiple-cell epidermal glands)	1 → 0
	24 (Midgut sacculations)	0 → 1	node 4 → *Simrothiella*	4 (Serrate teeth)	0 → 1
node 3 → node 4	9 (Triangular original tooth)	1 → 0	node 3 → *Plawenia*	14 (Skeletal spicules)	1 → 0
	10 (Stout body shape index < 5)	1 → 0		21 (Seminal vesicle)	1 → 0
	11 (Elongate body shape index ≥ 5)	0 → 1	node 2 → *Kruppomenia*	4 (Serrate teeth)	0 → 1
	12 (Rounded body ends)	1 → 0		17 (Accessory copulatory spicules)	1 → 0
	13 (Pointed or lobate body ends)	0 → 1	node 1 → *Eleutheromenia*	2 (Bar base)	1 → 0
	25 (Single-cell epidermal glands)	1 → 0		7 (Paired anteroventral pocket)	1 → 0
	26 (Multiple-cell epidermal glands)	0 → 1		8 (Single anteroventral pocket)	0 → 1
node 4 → node 5	1 (Distichous radula)	1 → 0	node 1 → *Helicoradomenia*	14 (Skeletal spicules)	1 → 0
	2 (Bar base)	1 → 0		15 (Solid spicules)	0 → 1
	3 (Original tooth)	1 → 0		16 (Hollow spicules)	1 → 0
	5 (Tooth buttress)	1 → 0		24 (Midgut sacculations)	0 → 1
	6 (Unipartite membrane)	0 → 1			
	7 (Paired anteroventral pocket)	1 → 0			
	15 (Solid spicules)	0 → 1			
	17 (Accessory copulatory spicules)	1 → 0			