

Contributions to West European Cavibelonia (Mollusca, Solenogastres) with two new species

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Salvini-Plawen L. von 2008. — Contributions to West European Cavibelonia (Mollusca, Solenogastres) with two new species. *Zoosystema* 30 (4): 873-897.

ABSTRACT

New records of Solenogastres Cavibelonia from French and Spanish coasts, belonging to the West European Atlantic fauna, are presented. They include four species classified within different families of the order Cavibelonia. Two of them are new to science: *Simrothiella vasconiensis* n. sp. from the southeastern Bay of Biscay and *Alexandromenia gulaglandulata* n. sp. from the West European basin. The finding of *Pararrhopalia pruvoti* Simroth, 1893, from off Galicia (Spain) significantly enlarges its geographic range, and the record of *Dorymenia sarsii* (Koren & Danielssen, 1877) from the southeastern Bay of Biscay bridges a former gap in distribution. These records improve our fragmented knowledge on the biodiversity of Solenogastres of the Northeast Atlantic fauna.

RÉSUMÉ

Les Cavibelonia (Mollusca, Solenogastres) d'Europe occidentale, avec description de deux nouvelles espèces.

De nouveaux signalements de Solenogastres Cavibelonia des côtes françaises et espagnoles appartenant à la faune atlantique d'Europe occidentale, sont présentés. Cela comprend quatre espèces appartenant à différentes familles de l'ordre Cavibelonia. Deux d'entre elles sont nouvelles pour la science: *Simrothiella vasconiensis* n. sp. du sud-est du golfe de Gascogne et *Alexandromenia gulaglandulata* n. sp. du Bassin européen occidental. La découverte de *Pararrhopalia pruvoti* Simroth, 1893 au large de la Galice (Espagne) accroît considérablement son aire géographique, et la mention de *Dorymenia sarsii* (Koren & Danielssen, 1877) du sud-est du golfe de Gascogne comble une lacune dans sa distribution. Ces signalements améliorent notre connaissance fragmentaire de la biodiversité des Solenogastres de la faune nord-est atlantique.

KEY WORDS

Mollusca,
Solenogastres,
Cavibelonia,
Simrothiella,
Alexandromenia,
Pararrhopalia,
Dorymenia,
zoogeography,
biodiversity,
new species.

MOTS CLÉS

Mollusca,
Solenogastres,
Cavibelonia,
Simrothiella,
Alexandromenia,
Pararrhopalia,
Dorymenia,
zoogéographie,
biodiversité,
espèces nouvelles.

INTRODUCTION

Within the Mollusca, the Solenogastres (neomeniomorphs) represent one of the two aplacophoran clades (the second one being the Caudofoveata or chaetodermomorphs). Both are externally characterised by a mantle with chitinous cuticle as well as unicellularly produced aragonitic sclerites. They reflect conservative levels of molluscan configuration (Salvini-Plawen & Steiner 1996; Haszprunar 2000; Salvini-Plawen 2003a, 2006a). The Solenogastres are hermaphroditic, freely moving predators and currently include about 250 nominal species (between 0.8 and 300 mm in length), all from marine environments with records between 1 and 6850 m depth (mostly below 50 m).

Though more intensive research over the last 40 years has distinctly enlarged our knowledge on their organization and evolutionary significance (summarised in Salvini-Plawen 1985; Scheltema *et al.* 1994), the presently known array of Solenogastres (and of Caudofoveata) by no means reflects their actual biodiversity. The available information is still fairly fragmentary, not only with respect to biological, developmental and physiological features, but also regarding pure faunistics (diversity, biogeography, etc.). This holds true even for the West European Atlantic, which is currently stated to have a low solenogaster biodiversity. Only 16 species are known from this biogeographic area (Salvini-Plawen 1997, 2006b). This contribution presents records of four Solenogastres species from the West European Atlantic; three of them are new for this area. They belong to different families within the order Cavibelonia (mainly characterised by hollow, acicular sclerites; Salvini-Plawen 1978, 2003a). Two of these species are new to science. Their examination and identification points to a higher biodiversity and to a still poorly known geographic distribution of Solenogastres species.

ABBREVIATIONS

MNCN	Museo Nacional de Ciencias Naturales, Madrid;
MNHN	Muséum national d'Histoire naturelle, Paris;
SMNH	Svenska Naturhistoriska Riksmuseet, Stockholm;
cs	cross sections;
ls	longitudinal sections.

SYSTEMATICS

Family SIMROTHIELLIDAE Salvini-Plawen, 1978

DIAGNOSIS. — Solenogastres with biserial radula (rows of paired denticulate radula plates or bars), anteroventral radula sack (when present) paired; ventral foregut glandular organs variously configured, but not of the so-called type A (paired duct with subepithelially or exoepithelial-extraepithelially arranged glandular cells; Salvini-Plawen 1972, 1978); sclerites hollow-acicular or solid-elongate to scaly.

Genus *Simrothiella* Pilsbry, 1898

TYPE SPECIES. — *Solenopus margaritaceus* Koren & Danielssen, 1877 (Odhner 1921; ICZN 1981).

DIAGNOSIS. — With thick cuticle and acicular hollow sclerites (spicules) in two or more intercrossing layers; mouth opening within common atrio-buccal cavity, biserial radula with heterogeneous denticulation, ventral radula sack paired. Lateroventral foregut glandular organs bulbous with elongate epithelial glands interspersed by low supporting cells (modified type C; Salvini-Plawen 1972, 1978; Todt 2006). Secondary genital opening single. With copulatory stylets, dorso-terminal sense organ and respiratory organs.

Simrothiella vasconiensis n. sp.

(Figs 1-9)

HOLOTYPE. — Sclerites, section series on slides; midbody 2 × in araldite (MNHN 9833).

PARATYPES. — 1) Cap Breton 88, stn DE 07, section series on slides, midbody 2 × in araldite (MNCN 15.02/0017); 2) Cap Breton 88, stn DE 07, section series on slides; midbody in araldite (MNHN 9834).

TYPE LOCALITY. — Southwestern France, Atlantic coast, Cap Breton 88, stn DE 05.

ETYMOLOGY. — Referring to the ancient name *Vasconia* for the Basque area bordering the southeastern golfe de Gascogne (Bay of Biscay).

OTHER MATERIAL EXAMINED. — **France.** Cap Breton 88, stn DE 05, 43°57.42'N, 02°05.16'W, 164 m, 5.VII.1988, Jean-Claude Sorbe and Serge Gofas, 11 specimens (incl. 6 larger fragments), mostly rolled up (MNHN). — Same data, stn DE 07, 43°58.65'N, 02°05.27'W, 170 m, 8 specimens (incl. a fragment).

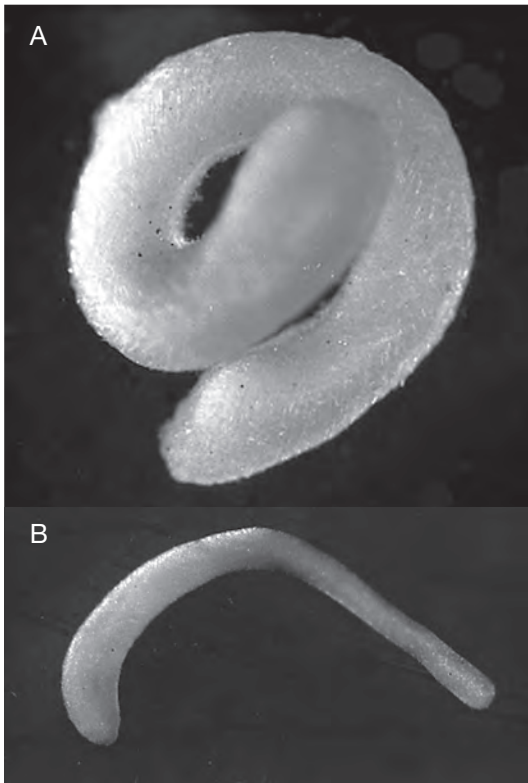


FIG. 1. — *Simrothiella vasconiensis* n. sp.: **A**, holotype in preserved state (posterior end below), 6.5 mm long; **B**, submature paratype 2 in preserved state (anterior end left), 5 mm long.

The body ends of two specimens from each station were serially cross-sectioned (cs 1-1.5 μm) in araldite and stained with toluidine blue. One fragment from DE 05 was manually dissected for preparation of the radula apparatus by histolysing tissues with bleach (hypochlorite solution).

Material examined for comparison: *Simrothiella margaritacea* (Koren & Danielssen, 1977) of Odhner's (1921) section series (SMNH 4731) was examined: 4731:1 (half anterior end, cs 5 μm), 4731:2a-c (cs 10 μm), 4731: 3a-c (posterior body, cs 5 μm) and 4731:4a, b (ls 5 μm and 10 μm); the series 4731:1 and 4731:3 are not complete, but series 4731:2 and 4731:4 should be regarded as part of the type material of this species (cf. Salvini-Plawen 2004).

DIAGNOSIS. — Up to 7.5 mm long. Mantle with epidermis papillae. Single pedal fold does not enter mantle cavity; a strong pallial hook at both sides of anterior cavity opening; mantle cavity with paired ventro-anterior pouch or sack, respiratory organs papilla-like or missing. Radula plates

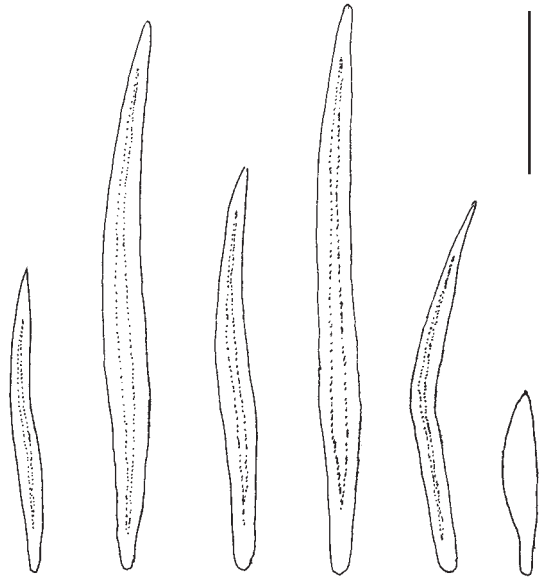


FIG. 2. — *Simrothiella vasconiensis* n. sp., mantle sclerites. Scale bar: 50 μm .

with 15 heterogeneous distal denticles; radula support (bolster, odontophore) with turgescent vesicles; midgut caecum frontally paired. Supra-rectal commissure short. Spawning ducts with a blind central portion before their junction. At each side a long copulatory stylet and a short, more scaly element.

DESCRIPTION

External appearance

Up to 7.5 mm long, fairly tubular, but anterior part of the body somewhat wider, posterior part may be club-shaped; in preserved state often rolled up (Fig. 1A). Sclerites almost adjacent but causing a slightly uneven outline. Closer inspection reveals multilayered, intercrossing spicules; body openings inconspicuous, pedal groove visible.

Mantle

Epithelium 6-12 μm thick; with several slender papillae, distal "head" up to 10 μm diam.; cuticle 30 μm (ventrally) to 50 μm thick. Sclerites consisting of acicular hollow needles, slightly curved or straight or bent, 70-170 \times 7-14 μm (Fig. 2); they are thick-walled (2.5-3.5 μm) in cross section, yielding only a 4-7 μm wide cavity, and intercross in two or three layers. Ventrally, lateral to the pedal groove, the hollow

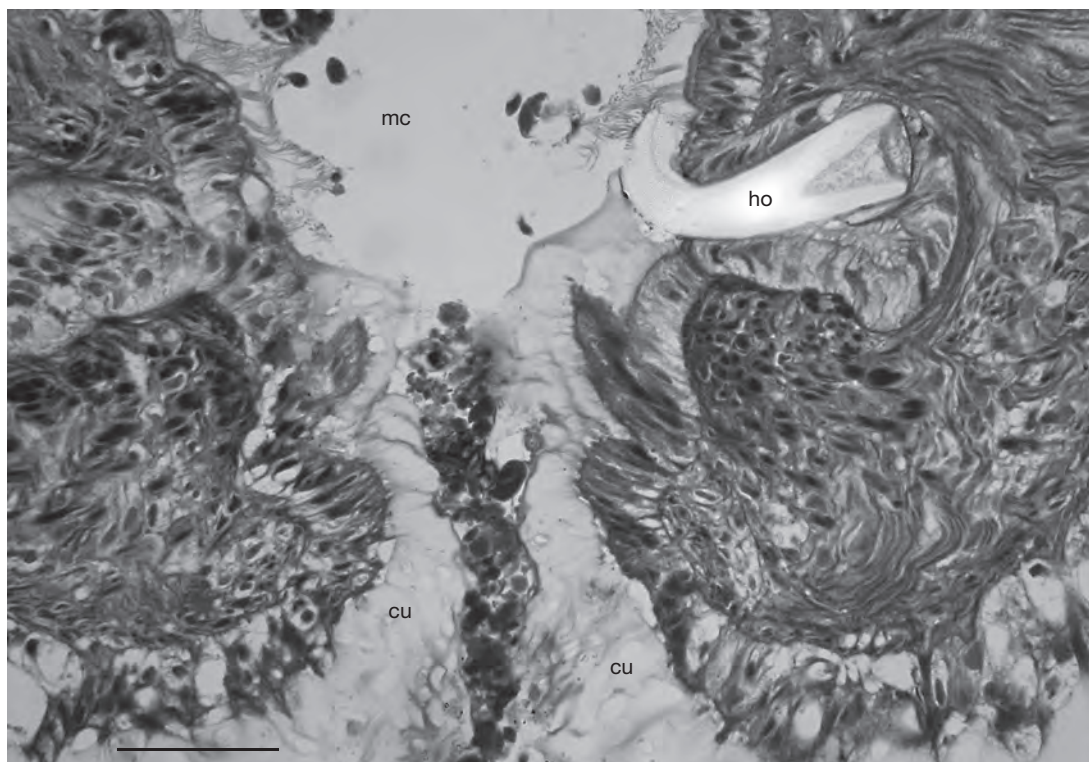


FIG. 3. — *Simrothiella vasconiensis* n. sp., cross section through beginning mantle cavity opening showing the calcareous pallial hook (paratype 2). Abbreviations: **cu**, mantle cuticle; **ho**, pallial hook; **mc**, mantle cavity. Scale bar: 25 μ m.

needles measure only $40 \times 5 \mu\text{m}$; adjacent to the foot, there are knife-blade scales ($45\text{--}60 \times 10 \mu\text{m}$).

Foot and mantle cavity

Pedal pit shallow, posteriorly bilobed; middorsal roof continues into one low pedal fold, which ends anterior to the opening of the mantle cavity proper, separated by a small pit with folded epithelium (not continuous with the pedal fold). Pedal gland consists of two different glandular cell types densely grouped together: first, pale-stained cells of reticulate appearance, which open frontally and laterally into pedal pit; second, cells with dense, deeply stained granula opening dorsally into pit. The latter type continues in paired arrangement as smaller sole glands along pedal groove, where they open intercellularly within the pedal fold.

Mantle cavity opening entirely ventral, epithelium in posterior half of mantle cavity of submature

specimens (DE 07) ciliated and provided with symmetrical arrangement of 11–15 lateral and dorso-terminal, stout and rather papilla-like respiratory organs (Fig. 7A). These are about $60 \mu\text{m}$ long and have a $30\text{--}40 \mu\text{m}$ basal diameter, and are distally and laterally ciliated; each organ has two intruding muscle strands. This area is loosely overlain by suprapallial glands. In the two fully mature specimens (DE 05), however, only the terminal cavity shows – over a short distance – what appear to be free papillae (Fig. 7B). The epithelium of the latter, however, consists of large gland cells and no ciliation is visible; these gland cells are anteriorly continuous with the densely packed suprapallial glands (extending to the pericardium). These mature specimens, therefore, lack true respiratory organs. Central mantle cavity without lateral ciliation and forming a pair of lateral, dorso-ventrally oval pouchings (Fig. 7, pp); in the two fully mature

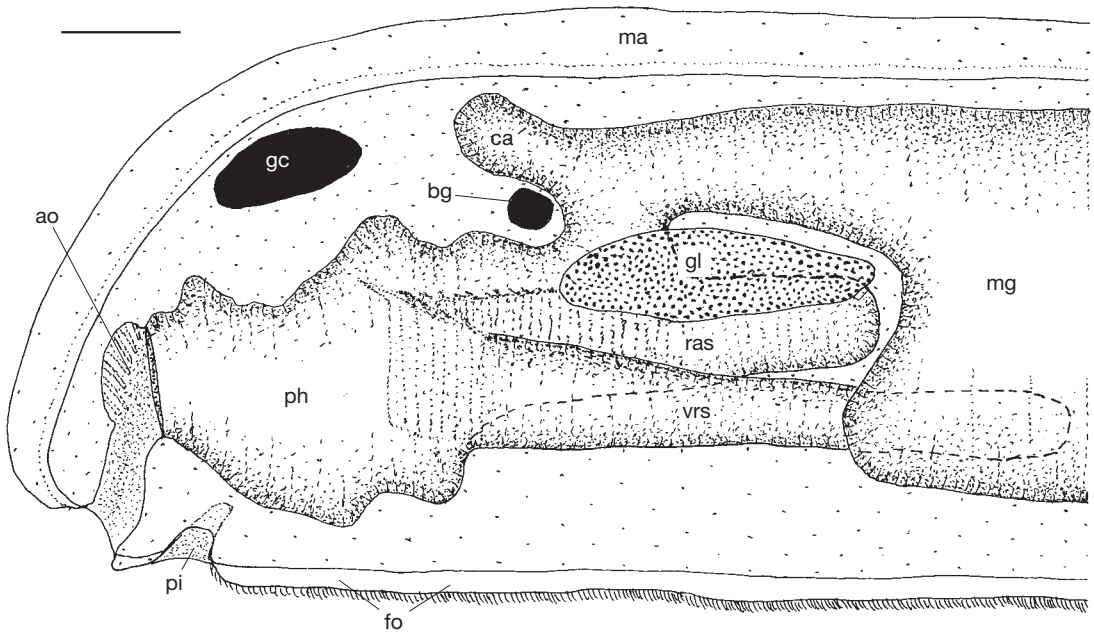


FIG. 4. — *Simrothiella vasconiensis* n. sp., organization of the anterior body viewed from left. Abbreviations: **ao**, atrial sense organ; **bg**, buccal ganglion; **ca**, midgut caecum; **fo**, pedal fold (foot); **gc**, cerebral ganglion; **gl**, lateroventral foregut glandular organ; **ma**, mantle; **mg**, midgut; **ph**, pharynx; **pi**, pedal pit; **ras**, radula sheath; **vrs**, ventral radula sack. Scale bar: 100 μ m.

specimens these are lined by 15–20 μ m high epithelial glands (the “sac-formed glands” in Odhner 1921: 19, yet not really glandular in SMNH 4731). The ciliated rectum opens medio-dorsally. A strong, calcareous pallial hook with proximal excavation is differentiated at both sides of the anterior cavity opening (Fig. 3).

The mantle cavity continues anteriorly to its opening, and the dorsal space forms a short, transversely separated (genital) pouch; the copulatory stylet sheaths open laterally. Ventrally, a characteristic, paired pouch or paired irregular sack opens; this paired sack extends anteriorly (Figs 7; 9, vp). The dorsal (genital) pouch is dorsally ciliated only; at its anterior end it receives, from ventral, the narrow opening of the central portion of the unpaired spawning duct (Fig. 9).

Musculature

Body wall musculature inconspicuous, paired ventral reinforcement of longitudinal layer (used to roll up) distinct, wide. Dorso-ventral bundles moderate,

close to body wall. Strong and voluminous radula musculature; copulatory stylets with strong muscle bundles (Fig. 8).

Sensory system

The unpaired cerebral ganglion (160–180 μ m wide, 75 μ m high) is slightly bilobed posteriorly and releases laterally the three pairs of connectives separately; two pairs of latero-frontal cerebral nerves begin with a distinct ganglionic swelling. Each (first) lateral ganglion is voluminous and located close to the cerebral ganglion. Elongate ventral ganglia (diam. 40 μ m) behind the pedal pit interconnected by two commissures. Buccal ganglia (diam. 30–35 μ m) lateral to opening of the pharynx into the midgut (Fig. 4); their commissure runs between midgut and beginning radula sheath. The lateral cords are sparsely, the ventral cords more regularly provided with nuclei (medullar). Medullar suparectal commissure rather short (60–80 μ m \times diam. 15–20 μ m), positioned directly behind the anus.

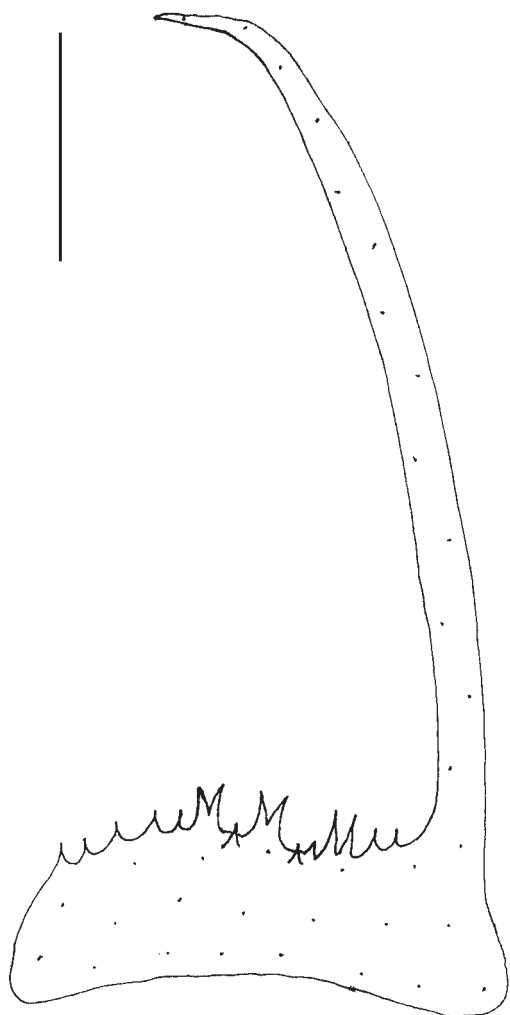


FIG. 5. — *Simrothiella vasconiensis* n. sp., radula, one right plate. Scale bar: 50 μ m.

Atrial (vestibular) sense organ short with densely arranged slender papillae (diam. 7-10 μ m), basally united in groups of up to four. "Horseshoe-shaped" ciliary tract incomplete: it begins unpaired at mid-point of organ extension and then runs pairedly postero-ventrally to end of the common atrio-buccal opening; ventral tracts patchy, anteriorly missing.

Dorso-terminal sense organ prominent at dorsal end of body (behind end of mantle cavity; Fig. 7).

Alimentary tract

The foregut epithelium begins immediately adjacent to the atrial ciliary tract, dorso-posteriorly within the common atrio-buccal cavity. Due to longitudinal folding, the foregut epithelium (with moderate cuticle) appears to be papillate; it is loosely underlain by circular, longitudinal and radial muscles. Pharynx widened and strongly cuticularised, antero-laterally pouched to house the distal portion of the strong lateral radula denticles. Anterior pharynx underlain by subepithelial, intercellularly opening glandular cells (pharyngeal glands), most densely latero-dorsally; posterior pharynx with increased dorsal and lateral (radula-)musculature. Radula apparatus consists of sheath (400-450 μ m) and paired, ventro-posteriorly bending sack, which exceeds the sheath by about 150-300 μ m (Fig. 4; total length of radula apparatus in the investigated specimens therefore 500-750 μ m); ventral sacks embedded in radula musculature along almost their entire length. In the sectioned specimens, the ventral sacks show an additional transverse leg (about 270°) distally in the U-shaped medial bend (of about 180°); the bends at each side are arranged above each other. Radula sheath paired for most of its extension towards pharynx, proximally unpaired (in cs U-shaped). Plates of biserial radula in pharynx 90-100 μ m wide and 25-40 μ m high, with a maximum of 15 denticles (Fig. 5): a strong lateral denticle up to 170 μ m long, 12 heterogeneous denticles at the distal border (not being precisely aligned and two of them possess a double cusp which is poorly visible in sections), and two small denticles somewhat below the border at the face (Fig. 5). In distal ventral sacks, the radula plates measure 30-40 \times 10 μ m and still have about 15 rather homogeneous, small denticles. Radula support (bolster, odontophore) muscular, posteriorly with four pairs of differently sized turgescent cells.

Lateroventral foregut glandular organs are elongate-bulbous, surrounded by a thin lamina (reinforced basal membrane?) and embedded within radular musculature. Elongate gland cells epithelial, with main cell bodies longitudinally arranged (modified type C; cf. Todt 2006); secretion of large granula or droplets. Each organ distally with distinct central lumen; narrow duct

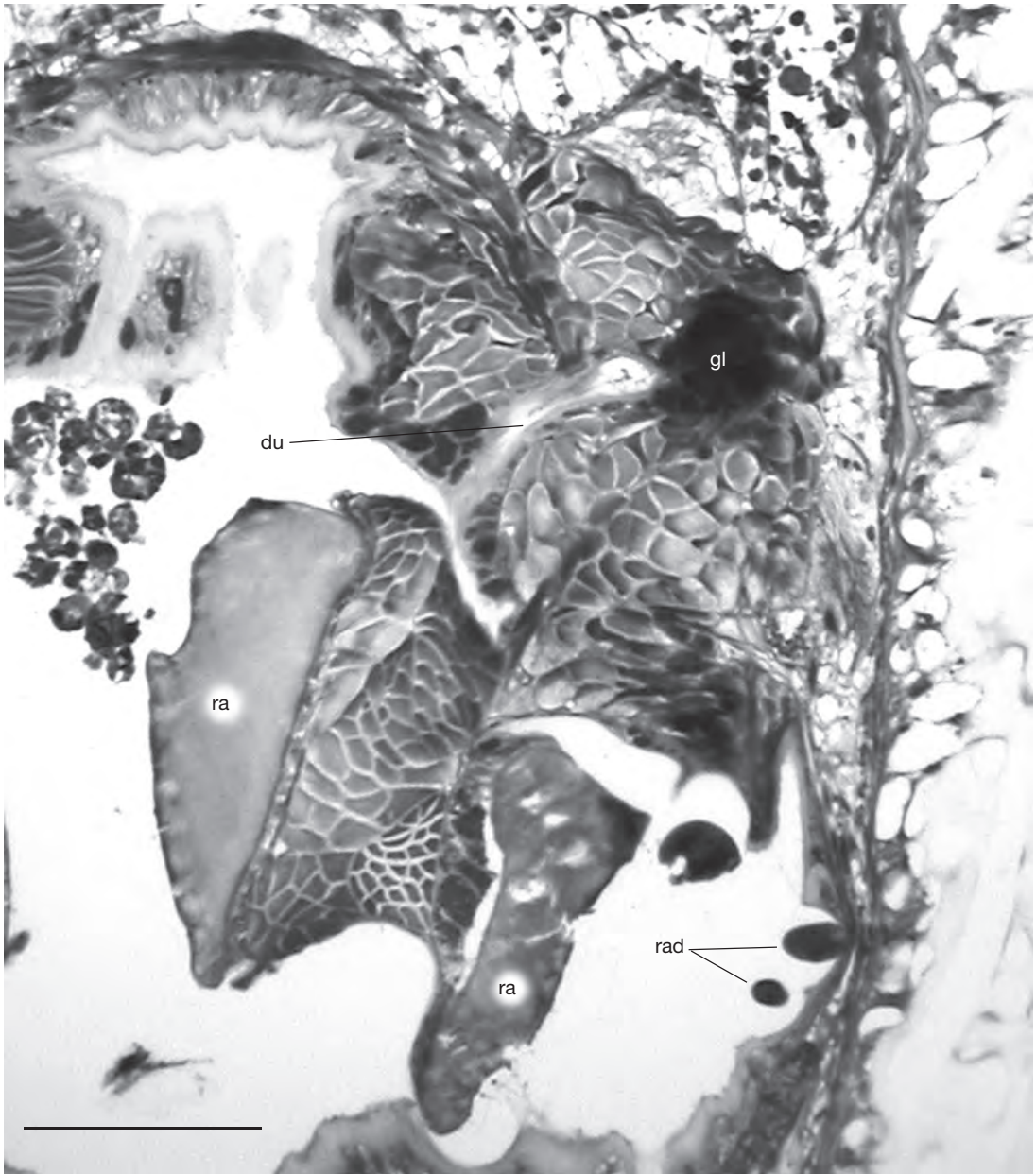


FIG. 6. — *Simrothiella vasconiensis* n. sp., right portion of cross section through pharynx just anterior of its transition into midgut with narrow duct of latero-ventral foregut glandular organ opening laterally (paratype 1). Abbreviations: **du**, outleading duct of foregut glands (**gl**); **ra**, radula plate; **rad**, cross sectioned long, lateral radula denticles. Scale bar: 50 μ m.

(about 50 μ m long) of pharyngeal epithelium opens laterally just anterior of pharynx transition into midgut (Fig. 6).

Oesophagus lacking. Pharynx opens directly into midgut above beginning of the radula sheath. Midgut with short caecum, anteriorly paired. Dorsoventral

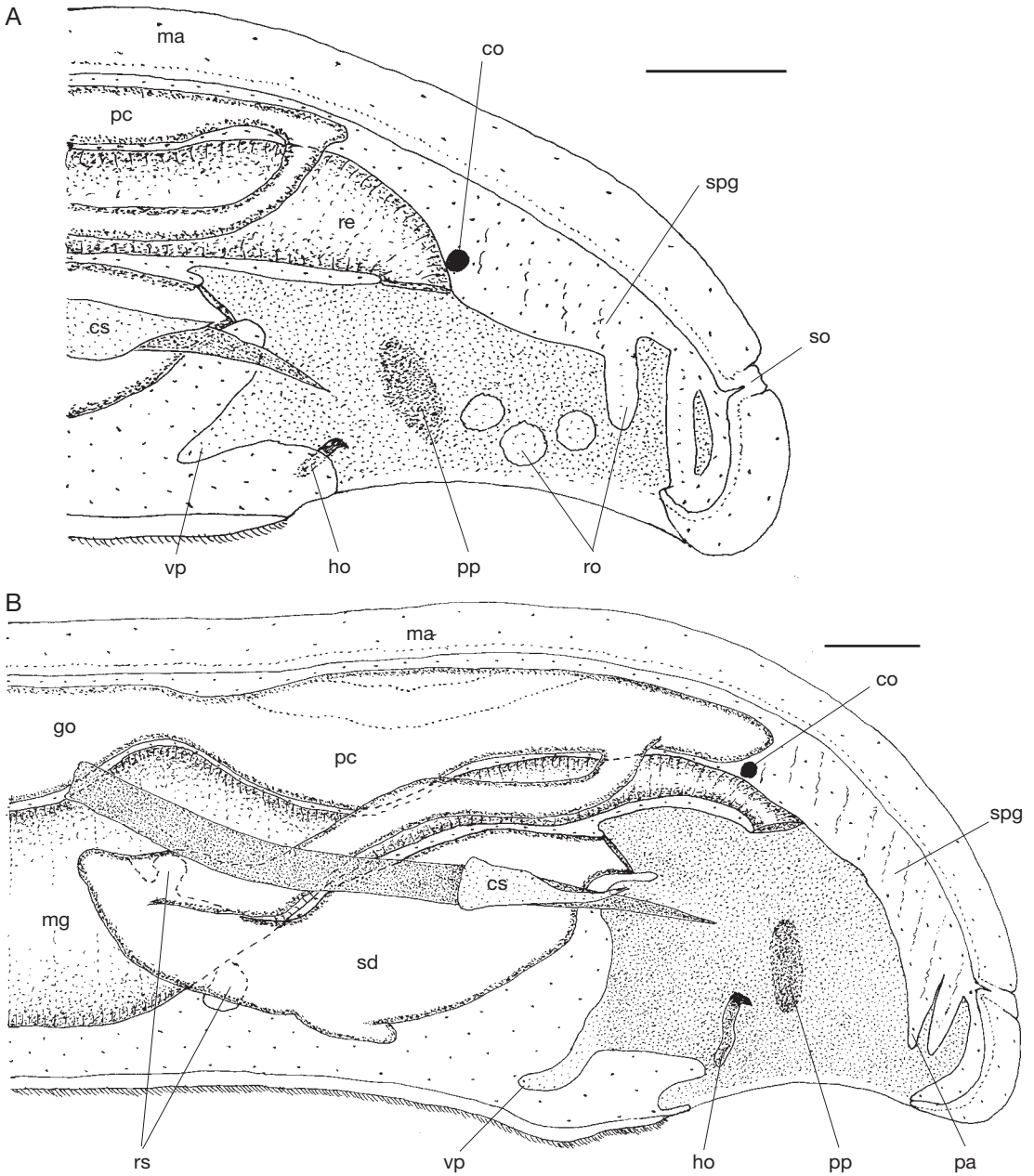


FIG. 7. — *Simrothiella vasconiensis* n. sp., organization of the posterior body: **A**, of a submature specimen viewed from left; **B**, of a fully mature specimen viewed from left. Abbreviations: **co**, suprarectal commissure; **cs**, copulatory stylet sheath; **go**, gonad; **ho**, pallial hook; **ma**, mantle; **mg**, midgut; **pa**, papillae; **pc**, pericardium (with heart); **pp**, lateral pallial pouch; **re**, rectum; **ro**, respiratory organs; **rs**, receptaculum seminis; **sd**, spawning duct; **so**, dorsoterminal sense organ; **spg**, suprapallial glands; **vp**, ventro-anterior pallial pouch. Scale bars: 100 μ m.

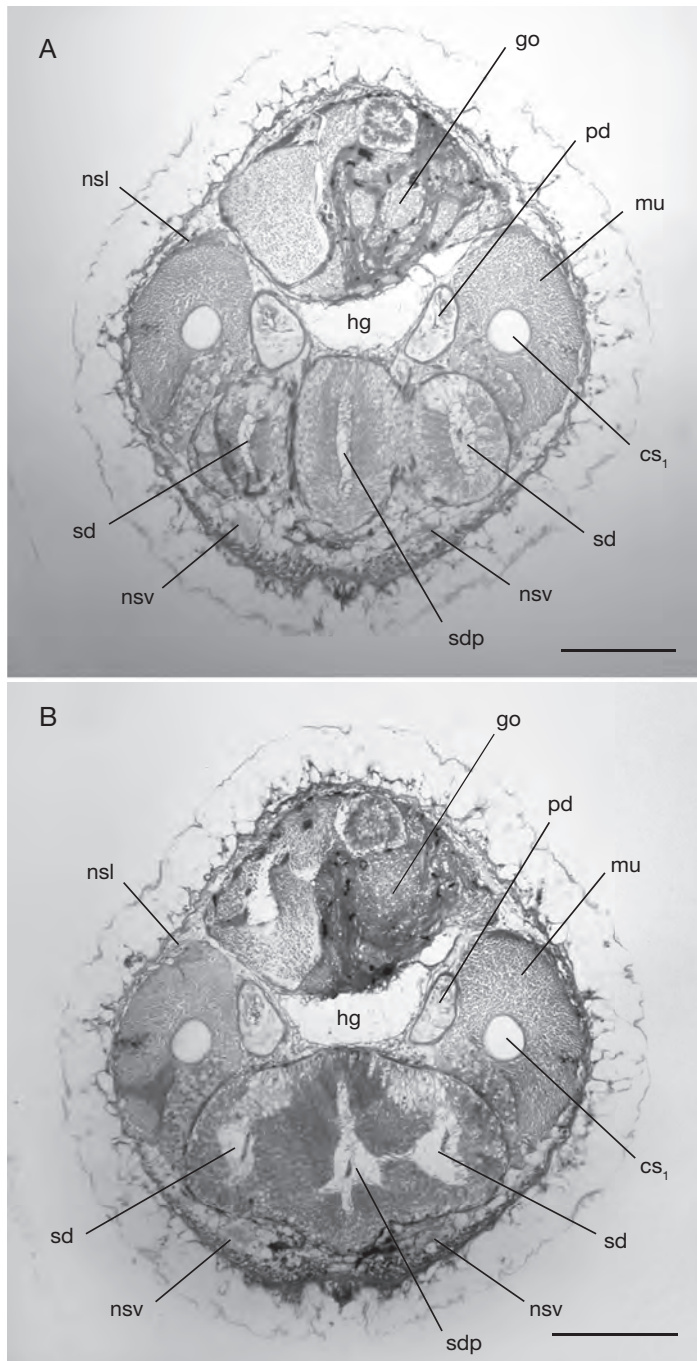


FIG. 8. — *Simrothiella vasconiensis* n. sp., two cross sections through junction of spawning ducts (holotype): **A**, three-part configuration with blind middle portion; **B**, fusion of spawning ducts with middle portion. Abbreviations: **cs₁**, strong copulatory stylet; **go**, gonad; **hg**, hindgut; **mu**, musculature of copulatory stylets; **nsl**, lateral nerve cord; **nsv**, ventral nerve cord; **pd**, pericardio-duct; **sd**, spawning duct; **sdp**, blind anteriorly directed middle portion at junction of spawning ducts. Scale bars: 100 µm.

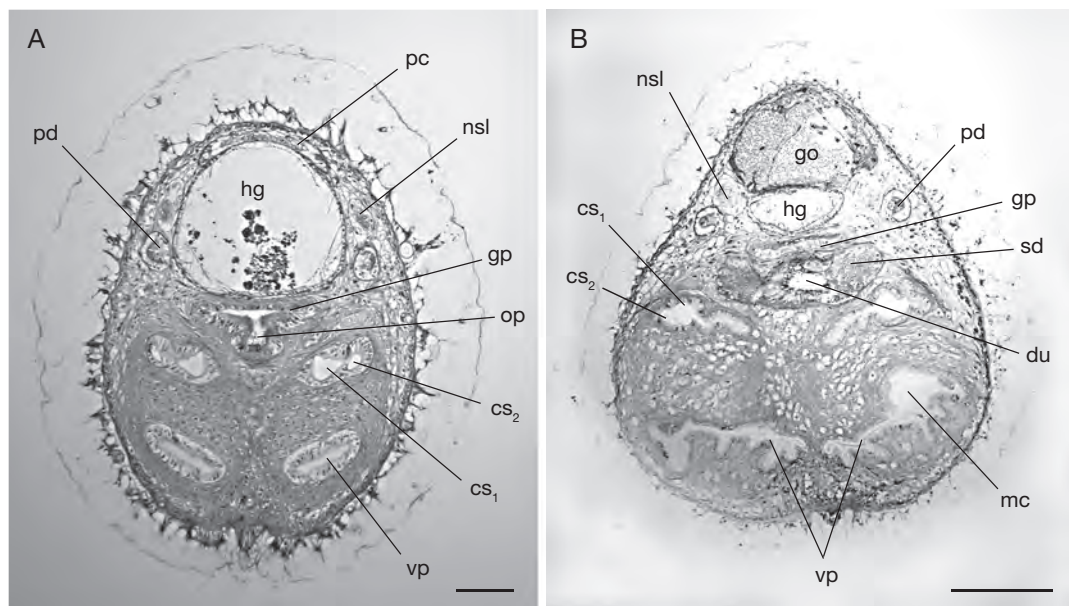


FIG. 9. — *Simrothiella vasconiensis* n. sp., cross sections through posterior body in the region of the outlet of the spawning duct: **A**, in the submature paratype 2; **B**, in the holotype. Abbreviations: **cs₁**, strong, inner copulatory stylet; **cs₂**, lateral, short copulatory stylet; **du**, central outlet (short duct) of spawning duct; **go**, gonad; **gp**, genital pouch of mantle cavity; **hg**, hindgut; **mc**, mantle cavity; **nsI**, lateral nerve cord; **op**, opening of central portion of spawning duct into genital pouch; **pc**, pericardium; **pd**, pericardioduct; **sd**, spawning duct; **vp**, paired ventro-anterior pouch of mantle (pallial) cavity. Scale bars: A, 50 μ m; B, 100 μ m.

muscle bundles run close to body wall, forming only weak midgut pouches. Middorsal ciliary tract continues in ciliation of hindgut. Posterior lumen of midgut and hindgut in one specimen of station DE 07 (paratype 1) was filled with an elongate, compact, non-cnidarian piece of prey.

Gonopericardial system

The two sectioned specimens of station DE 05 were fully mature. Gonad paired, not extending into anterior body; eggs up to 130 μ m in diameter. Paired gonopericardioducts open frontally into spacious pericardium (Fig. 7B), with heart largely unattached. Pericardioducts emerge laterally; in fully mature animals, pericardium (filled with genital products) continues somewhat further posteriorly (Fig. 7B). Pericardioducts ciliated except medially, no vesiculae seminales; they run anteriorly, each opening into the spawning duct. Paired spawning ducts with tall, ciliated epithelium; in fully mature animals, behind opening of pericardioducts, each

duct has a dorsal and ventral sacculation (probable receptacula seminis; Fig. 7B), posteriorly with increasing glandular contents. Junction of spawning ducts is not a simple fusion but a paired opening into an anteriorly blind-ending central portion; in cross section this yields for a short distance a characteristic, three-parted aspect (Fig. 8). The united spawning ducts continue posteriorly as a voluminous, unpaired, glandular and ciliated organ, extending almost up to the (genital) pouch of the mantle cavity; here, only the central portion of this wide spawning duct opens from ventral into the pouch (Fig. 9).

Paired copulatory stylet apparatus, each with two elements (Figs 7-9) within a common sheath: 1) a very strong stylet that may extend (max. length 650 μ m, max. diameter 50 μ m) close to the beginning gonad. This stylet has a cavity along most of its length; the cavity is proximally wider and is filled by a tissue plug at the proximal end; and 2) a much shorter, entirely solid element (about 225 μ m long) adjoining the stylet. It is proximally

flattened and scale-like (up to 65 μm wide) and tapers distally to a point that ends earlier than the strong stylet. Sheath at each side surrounded (particularly at its proximal portion) by a strong envelope of musculature (protractors, retractors) up to 60 μm thick (Fig. 8).

COMPARISONS

Based on the organization, the present specimens belong to the Simrothiellidae. Among the nine defined genera (see Scheltema & Schander 2000; Salvini-Plawen 2004), they must be classified within *Simrothiella* Pilsbry, 1898. Herein, they are very similar to the type species *Simrothiella margaritacea* (Koren & Danielssen, 1877) from Norway at 75–115 m (Odhner 1921; Salvini-Plawen 2004; not Scheltema & Schander 2000), particularly with respect to the hard parts (radula, etc.).

The differences between the two subadults and the two fully mature specimens pertain to respiratory organs and to the (probable) receptacula seminis. Other features of the secondary genital apparatus, however, are typically differentiated in the submature specimens, allowing determination to the species level (see also Salvini-Plawen & Paar-Gausch 2004). All four specimens of the new species differ in certain characters from *S. margaritacea* (see Odhner 1921; Salvini-Plawen 2004) and also from the specimens from off Galicia, Spain (cf. Todt 2006). These characters include: 1) the configuration of the mantle cavity with the differentiation of a paired ventro-anterior pouch or sack (Figs 7; 9, vp) and the peculiar condition of the respiratory organs (Fig. 7; in *S. margaritacea* there is at most an unpaired ventro-anterior pouch and the gills show lateral foldings); 2) the denticulation at the distal border of the radula plates in adults (also contrasting the position of the denticles in *S. abyseuropaea*; cf. Salvini-Plawen 2004), as well as the ventral radula sacks extending far behind (in *S. margaritacea* the sacks exceed the sheath by about 50–130 μm); 3) the presence of turgescer cells in the radula support or bolster (absent in *S. margaritacea*); 4) the frontally paired midgut caecum (unpaired in *S. margaritacea*); 5) the short supra-rectal commissure (in *S. margaritacea* up to 250 μm); and 6) the configuration of the spawn-

ing ducts: before their junction they have a blind central portion into which the ducts open (Fig. 8; in *S. margaritacea* the ducts simply fuse). These differences clearly define the new species.

These characters underline that solenogaster species should not be determined predominantly based on hard parts (Scheltema & Schander 2000). Specific characterisations using that approach fail in two respects: 1) hard parts are only superficially similar (see *S. margaritacea* vs. *S. abyseuropaea* in Scheltema & Schander 2000 and Salvini-Plawen 2004); and 2) hard parts (including the radula) are fairly identical in shape in species with different internal organization (present contribution).

Family PRUVOTINIDAE Heath, 1911¹

Parameniidae Simroth, 1893b: 225 (type genus preoccupied by the insect genus *Paramenia* Brauer & Bergenstamm, 1889).

Parameniidae – Pruvot 1902: XXII (incorrect subsequent spelling).

Perimeniidae Nierstrasz, 1909: 298 (as Nierstrasz bases this family on his new genus *Perimenia*, consciously created as a junior synonym of *Pruvotina* Cockerell, 1903 [Nierstrasz 1909: 291, 292], it cannot be regarded as valid; see Salvini-Plawen [2003b: 48] and ICZN [1999: Art. 23.9.1]).

Pruvotiniidae Heath, 1911: 47 (incorrect original spelling, corrected and available according to ICZN [1999: Art. 35.4.1]; Pruvotiniidae).

Pararrhopaliidae Salvini-Plawen, 1972 (based on the oldest genus name, but formally not in accordance with ICZN [1999: Art. 13.2]).

Pararrhopaliidae Salvini-Plawen, 1978 (based on the oldest genus name, but a junior synonym of Pruvotiniidae above).

¹ According to Dr P. Bouchet (pers. comm.), the name Pruvotiniidae is a junior objective synonym of Perimeniidae Nierstrasz, 1908, based on *Perimenia* Nierstrasz, 1908 (a replacement name for *Paramenia* Pruvot, 1890, non Brauer & Bergenstamm, 1889 [Diptera] and a junior objective synonym of *Pruvotina* Cockerell, 1903). However, the present author cannot follow such a purely formalistic treatment which ignores the familiar use of “pruvotinids” or “*Pruvotina*-group” since Heath (1911) established the name Pruvotiniidae, and he will present a case to the ICZN to suppress the name Perimeniidae in favour of Pruvotiniidae.



FIG. 10. — *Pararrhopalia pruvoti* Simroth, 1893, preserved specimen, 3 mm long (anterior end above).

DIAGNOSIS. — Solenogastres with acicular sclerites as hollow spicules (needles); radula in each transverse row a pair of erect teeth (= distichous), or without radula; ventral foregut glandular organs generally as subepithelially arranged glands opening into a paired duct (type A); with hooked mantle sclerites and/or a middorsal papillose foregut gland and/or respiratory organs (see Salvini-Plawen 1978, 2003b).

Genus *Pararrhopalia* Simroth, 1893

TYPE SPECIES. — *Pararrhopalia pruvoti* Simroth, 1893.

DIAGNOSIS. — Solenogastres with thick cuticle and hollow sclerites in more than one layer, also including hooked ones; mouth opening separated from atrial sense organ; distichous radula present; with dorsal papillose foregut gland; unpaired secondary genital opening, with copulatory stylets; with dorsoterminal sense organ, without respiratory organs.

Pararrhopalia pruvoti Simroth, 1893 (Figs 10-12)

Pararrhopalia pruvoti Simroth, 1893a: 325.

Proneomenia vagans – Pruvot 1891: 723 (not *Proneomenia vagans* Kowalevsky & Marion, 1887).

MATERIAL EXAMINED. — Specimens collected during the Spanish DIVA-Artabria I project in September 2003 off Galicia (Spain) were used by Christiane Todt for special investigations (Todt 2006). 2 specimens from about 43°33'N, 8°35'W, at 150 m; 1 individual (5.5 mm) not clearly conspecific from about 43°48'N, 8°53'W, at 600 m. Serial semithin (cs 2 µm) sections stained by Richardson's solution, and ultrathin sections.

DIAGNOSIS. — Up to 5 mm long. Mantle with intercrossing tangential spicules *plus* radial spicules. With small pre-atrial sense organ, atrial sense organ terminally bilobed; Radula teeth with distal hook and 2 or 3 median denticles. With oesophagus; midgut caecum anteriorly paired, without regular midgut pouchings. With one pair of seminal vesicles, no receptacula seminis; fused part of spawning ducts with a paired, posteriorly directed lateral pouch; copulatory apparatus paired, each with a bundle of stylets in body axis.

DESCRIPTION

External appearance

Specimens 3 mm long. Body round, without keel; body outline uneven due to radial spicules (Fig. 10).

Mantle

Cuticle 35-40 µm, dorsally up to 60 µm. Sclerites (Fig. 11; not figured by Pruvot 1891, but referred to the sclerites of *Pruvotina impexa* (Pruvot, 1890) are hollow tangential spicules intercrossing in three layers, with several (somewhat obliquely positioned) radial spicules extending far beyond cuticle, all 80-120 × 5-8 µm; along pedal groove, knife-blade scales (35-45 × 8 µm) and adjoining slender needles (90-120 × 3-5 µm); radial, hooked sclerites (about 40 µm long) dorsally, more dense posteriorly. Pluricellular epidermis papillae distinct.

Foot and mantle cavity

One pedal fold reaching the ciliated, narrow mantle cavity which lacks respiratory organs.

Sensory system

Unpaired cerebral ganglion with three pairs of frontal nerves with distal swelling above atrium. Buccal ganglia small (diam. about 20 µm), to each side of pharynx. Medullar suprarectal commissure at end of pericardium about 50 µm long.

Atrial sense organ terminally bilobed and delimited by a horseshoe-shaped ciliary tract, middorsally fused for a short distance only; most papillae of atrium basally bundled into groups of three. With circular (sense) organ close to anterior rim of atrial sense organ, and with terminally located dorsoterminal sense organ.

Alimentary tract

Mouth opening distinctly separated from atrium; anterior pharynx with strong circular musculature, behind this a narrow dorsal pouch includes the papilla of the dorsal foregut gland (cf. Todt 2006). Radula teeth about 25 µm long with distal hook and 2 or 3 median denticles; ventral foregut glandular organs with subepithelially positioned glands opening into a paired duct (type A in Salvini-Plawen 1972, 1978), these ducts opening separately below radula. Distinct post-radular foregut (oesophagus) opening ventrofrontally into midgut. Midgut caecum anteriorly paired. Dorsoventral muscle bundles not causing distinct regular lateral pouchings of the midgut due to the wide distance of the gut to the body wall; middorsal ciliary tract present.

Gonopericardial system

Pericardium wide with heart ventricle as a free tube, auricle as dorsal invagination. Smaller specimens with one posteriorly directed, lateral seminal vesicle at the beginning curve of each pericardioduct, the latter opening dorsolaterally into spawning ducts; no receptacula seminis. Spawning ducts paired for a short distance only; more posteriorly the single spawning duct exhibits a paired, posteriorly directed lateral pouch, which makes the organ three-parted (Fig. 12), with the central duct portion opening ventrofrontally into the mantle cavity. Paired copulatory stylet apparatus with a bundle of 6-8 stylets each (Fig. 12), proximally with muscular sheath, opening laterally of terminal pedal fold at rim of mantle cavity opening.

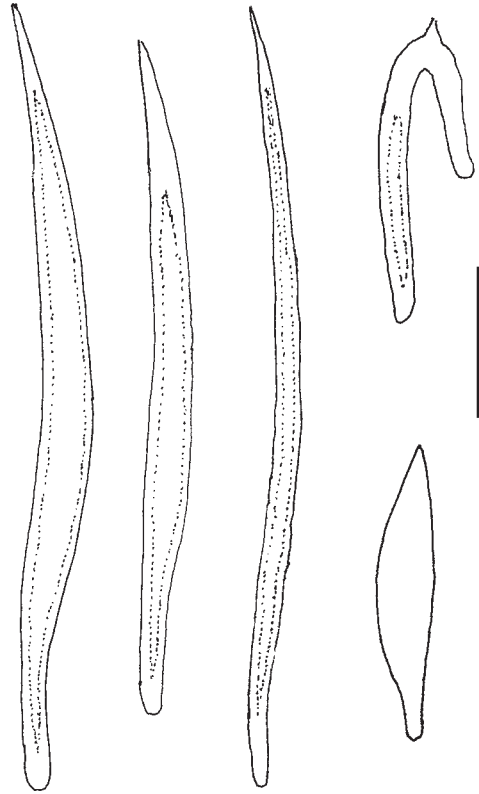


FIG. 11. — *Pararrhopalia pruvoti* Simroth, 1893, mantle sclerites. Scale bar: 20 µm.

DISCUSSION

The organization of the present specimens (hollow, hooked sclerites; papillose dorsal foregut gland, etc.) clearly corresponds to the Pruvotinidae and all essential characters coincide with *Pararrhopalia* Simroth, 1893 (see Salvini-Plawen 2003b). Two species are known, the type species *P. pruvoti* (misidentified as “*Proneomenia vagans*” in Pruvot 1891) from off Banyuls-sur-Mer (S France) and *P. (?) fasciata* Salvini-Plawen, 1978, from the South Shetland Islands. Several characters differ in *P. (?) fasciata* (no oesophagus, short midgut caecum unpaired, with receptacula seminis, copulatory stylets in transversal position). A detailed comparison of the new 3 mm specimens with Pruvot’s (1891) description of the type specimen (5 mm) revealed a clear correspondence (e.g., Pruvot 1891: fig. 55

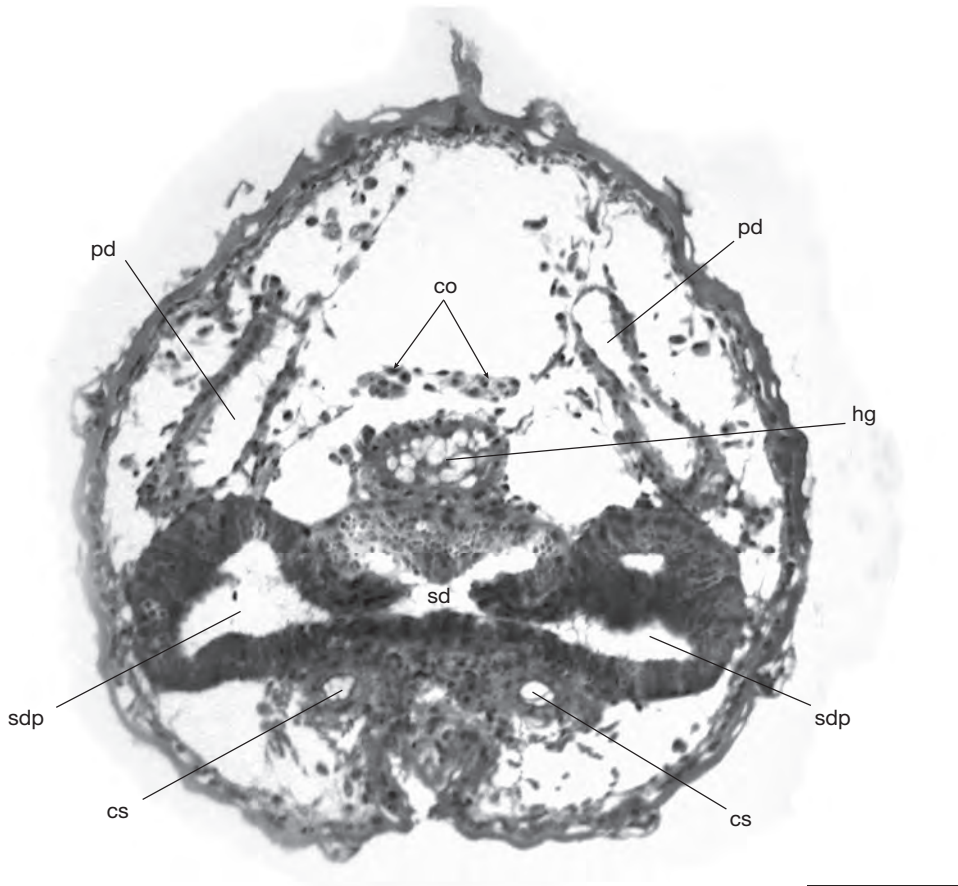


FIG. 12. — *Pararrhopalia pruvoti* Simroth, 1893, cross section through posterior body showing the three-parted spawning duct due to a paired, posteriorly directed lateral pouch. Abbreviations: **co**, supra-rectal commissure; **cs**, bundle of copulatory stylets; **hg**, hindgut; **pd**, pericardioduct (posterior curve); **sd**, spawning duct; **sdp**, pouch of spawning duct. Scale bar: 50 μ m.

and Todt 2006: fig. 6A). This holds true also for the pre-atrial sense organ (see Pruvot 1891: fig. 86) and in particular for the configuration of the spawning ducts and the bundles of 5-7 copulatory stylets (see Pruvot 1891: figs 60, 60a). The pouchings along the pericardioducts – to form multiple vesiculæ seminales – in Pruvot's specimen (Pruvot 1891: 772, fig. 60) obviously refer to full-grown animals only and are absent in the smaller specimen investigated here (150 m depth, 3 mm long; eggs still in development with diam. 10-20 μ m). Hence, the present animals are conspecific and represent the first findings after the

original description of *Pararrhopalia pruvoti*. They thus enlarge the geographical range of this species to the NW-Iberian Atlantic.

The larger, 5.5 mm long, specimen shows an identical organization of the anterior body. The posterior body is somewhat damaged terminally and the paired bundle of 12 copulatory stylets opening laterally of terminal pedal fold is the only coincidence; there are no discernible eggs, the characteristic tripartition of the spawning duct(s) is at most indicated and other organs are not satisfactorily visible. Consequently, this specimen from 600 m depth cannot be definitively attributed to *P. pruvoti*.

Family PRONEOMENIIDAE Simroth, 1893²

DIAGNOSIS. — Solenogastres with thick mantle cuticle, sclerites acicular as hollow spicules (needles); radula polyserial/polystichous; ventral foregut glandular organs with epithelial gland cells (= type C). One pair of receptacula seminis.

Genus *Dorymenia* Heath, 1911

TYPE SPECIES. — *Dorymenia acuta* Heath, 1911 by original designation (ICZN 1981).

DIAGNOSIS. — Acicular hollow spicules in two or more intercrossing layers, with epidermis papillae; mouth opening within common atrio-buccal cavity. Secondary genital opening single. With copulatory stylets and dorso-terminal sense organ; no respiratory organs.

Dorymenia sarsii (Koren & Danielssen, 1877)
(Figs 13-15)

Solenopus sarsii Koren & Danielssen, 1877: 128.

Simrothiella sarsi auct.

Dorymenia sarsi auct.

Dorymenia tortilis Scheltema & Schander, 2000: 126 (cf. Handl & Salvini-Plawen 2002)

DIAGNOSIS. — Up to 53 mm long, slender, with dorso-posterior finger-like projection. Mantle with epidermis papillae, tangential hollow spicules (needles) interspersed with delicate, slender, solid, radial, paddle-like sclerites. Opening of mantle cavity antero-laterally with numerous distally hooked abdominal spicules. One pedal fold, not extending into mantle cavity. Radula with 14 teeth per transverse row, symmetrically arranged, tooth length increasing towards lateral; with unpaired ventral radula sack surrounded by strong musculature. Radula sheath proximally bifid. Longitudinal musculature with paired ventral reinforcement, in part distinctly separated as paired musculus longitudinalis ventralis. Midgut caecum unpaired, extending far anterior. Heart as a dorsally open



FIG. 13. — *Dorymenia sarsii* (Koren & Danielssen, 1877), specimen of 27 mm length (posterior end with "bill" below).

invagination of pericardium. Prior becoming fused, each spawning duct with a prominent ventral enlargement (ampulla, lobe); unpaired opening of fused duct with a sphincter. Paired ventro-anterior pouch of mantle cavity encircling copulatory stylets. One pair (rarely two or three pairs) of copulatory stylets, distally three- or four-edged.

DISTRIBUTION. — Scandinavian to Lusitanic waters, 164-681 m.

MATERIAL EXAMINED. — France. Cap Breton 88, DE 05, 43°57.42'N, 02°05.16'W, 164 m, 5.VII.1988, Sorbe & Gofas, 2 specimens and a fragment, size 27 mm × max. 1.3 mm, and 23 mm × max. 1 mm. After removing sclerites, the body ends of the longer specimen were histologically investigated by serial cross sections of 10 µm; these series (and the midbody in alcohol) are deposited as voucher material in MNCN (no. 15.02/0016).

Material examined for comparison: *D. sarsii*, holotype (SMNH 4737), paratype (SMNH 4738).

DISCUSSION

The present specimens, with their characteristic dorso-posterior extension of the body (Fig. 13), are organizationally identical with *Dorymenia sarsii*; all important specific characters (see diagnosis; Odhner 1921; Scheltema & Schander 2000, including *D. tortilis*; Handl & Salvini-Plawen 2002) are

² The name Proneomeniidae is traditionally attributed to Simroth (1893), but according to Dr P. Bouchet (pers. comm.) the name Proneomenidae introduced by Mitchell (1892: 58) is available and is to be considered as the valid name for this family. The present author, however, is of the opinion that Mitchell used the name Proneomenidae instead of the missing genus name as a plural noun rather than as a family name (cf. Salvini-Plawen [2004]; ICZN [1999: Art. 11.7.1.2]).

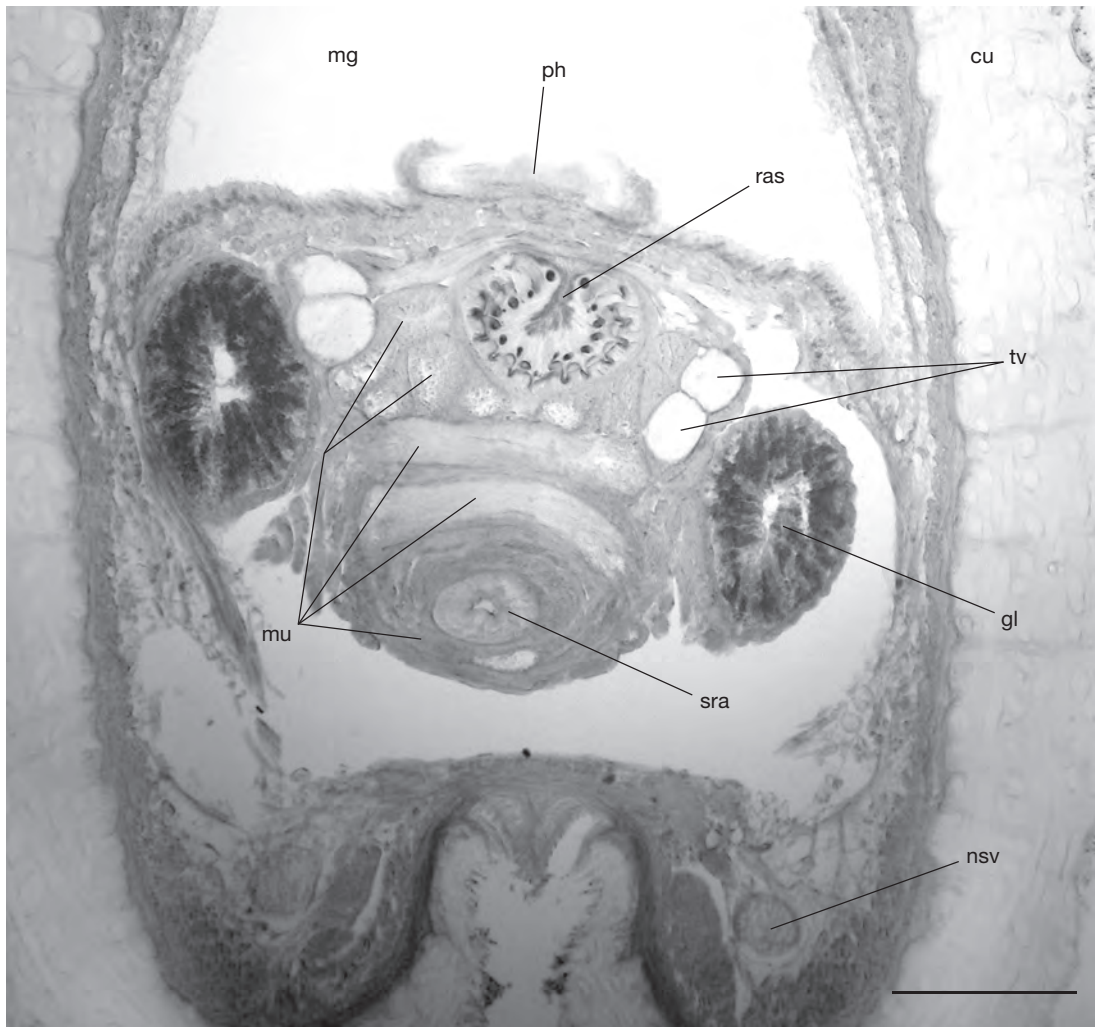


FIG. 14. — *Dorymenia sarsii* (Koren & Danielssen, 1877), cross section through region of radula bolster. Abbreviations: **cu**, mantle cuticle; **gl**, ventral foregut glandular organ; **mg**, midgut; **mu**, bolster musculature; **nsv**, ventral nerve cord; **ph**, terminal portion of pharynx opening; **ras**, radula sheath; **sra**, subradular sack; **tv**, bolster vesicles. Scale bar: 100 μ m.

present in the specimen examined; this is mature (egg diam. 100 μ m), the pericardioducts show small pouches (vesiculae seminales) surrounded by the common muscular layer (Fig. 15), the spawning ducts have ventral ampullae close to their fusion and there is one pair of copulatory stylets. Neither Odhner (1921) nor Handl & Salvini-Plawen (2002), however, mention the existence of two pairs of bolster vesicles within the radula support (big “chondroid

cells”; Fig. 14; region not retained in the type material). In the sectioned specimen at hand, each pair is differentiated at the end of two lateral radula support or bolster muscles; in addition, the ventral sack retractors are attached to four vesicles.

The body dimensions of 70 \times 3 mm given by Koren & Danielssen (1877) are most probably erroneous (cf. Scheltema & Schander 2000: 126); the records of three fragments in the Arctic Ocean at

71°25'N, 15°41'E in 1134 m depth (Odhner 1921) neither geographically nor bathymetrically fit into the known range and are thus doubtful (Salvini-Plawen 1997). As already underlined (Salvini-Plawen 1997; Handl & Salvini-Plawen 2002), the geographical range of *D. sarsii* (including *D. tortilis*) thus includes the Scandinavian waters from the Trondheimfjord to the Skagerrak on the one hand, and the Gorringe Bank (off Cap São Vicente, Portugal) on the other. The geographical gap in the records is now bridged by the present findings in the southeastern Bay of Biscay at 164 m.

Family AMPHIMENIIDAE Salvini-Plawen, 1972

DIAGNOSIS. — Solenogastres with thick mantle cuticle, sclerites acicular as hollow spicules (needles). Radula monoserial (or lacking); antero-ventral radula sack (when present) unpaired. Foregut glandular organs typically as ramified ducts with terminally arranged clusters of gland cells (= type D). Spawning ducts with subepithelially arranged, intercellularly opening glands.

Genus *Alexandromenia* Heath, 1911

TYPE SPECIES. — *Alexandromenia agassizi* Heath, 1911.

DIAGNOSIS. — Spicules arranged tangentially and radially in several layers; with common atrio-buccal cavity; radula present; foregut glandular organs typically with common, cone-shaped pre-radular outlet into pouch; midgut with serial lateral constrictions. Secondary genital opening unpaired, no copulatory stylets. With dorsoterminal sense organ and respiratory organs.

Alexandromenia gulaglandulata n. sp. (Figs 16-19; 20A; 21-24)

HOLOTYPE. — Sclerites, section series on slides; midbody in alcohol (MNHN 9835).

TYPE LOCALITY. — *Thalassa* Cruise 73 Z, stn Z 435.

MATERIAL EXAMINED. — **West European Basin.** *Thalassa* Cruise 73 Z (CENTOB), stn Z 435, 48°40'N, 09°53'W, 1050 m, 26.X.1973, 1 specimen, 21 mm long, without keel formation (Fig. 16). The preserved animal has a rounded, coiled body, somewhat higher (2.8-3.5 mm) than broad (2.4-2.8 mm), and is thicker anteriorly.

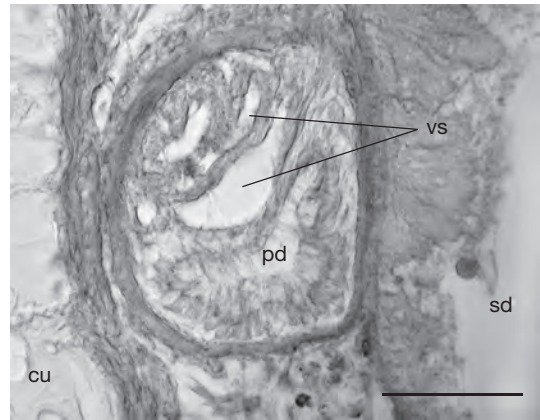


FIG. 15. — *Dorymenia sarsii* (Koren & Danielssen, 1877), cross section through anterior pericardioduct. Abbreviations: **cu**, mantle cuticle; **pd**, pericardioduct; **sd**, spawning duct; **vs**, small pouches of vesicula seminalis. Scale bar: 50 μ m.

Both body ends of the specimen were serially cross sectioned in paraffin of 10 μ m and stained with Azan.

ETYMOLOGY. — Latin: *gula*, gullet, throat, pharynx; *glandula*, small gland; *-atus*, provided with. Referring to the different types of foregut glands.

DIAGNOSIS. — 21 \times max. 3.5 mm, without keel formation. Mantle papillae long-stalked with most distal swellings at the same level. With 18-11 (terminally 4) pedal folds that do not enter the mantle cavity; mantle cavity posteriorly with 16 respiratory folds, anteriorly with irregular, slender sacculations; with suprapallial glands. Transverse body wall musculature embedded in matrix. Atrial papillae slender, single. With four sets of foregut glands: pharyngeal glands, pre-radular packages of glands, paired lateroventral foregut glandular organs with duct leading into pouch through ductule-less cone and not opening on a papilla, and oesophageal glands. Radula plates 55-65 μ m wide, with one denticle at each side; radula support (bolster, odontophore) symmetrically arranged turgescens cells; midgut caecum short, unpaired throughout. Fused section of spawning ducts anteriorly still with glands, muscular opening ventral at anterior border of mantle cavity opening. Suprarectal commissure long; dorsoterminal sense organ above mantle cavity.

DESCRIPTION

Mantle and body wall

The 150-250 μ m thick cuticle with densely arranged, long-stalked epidermis papillae, whose distal swellings are nearly all at the same level (Fig. 18). The sclerites are mostly eroded, but fragments and negatives in the



FIG. 16. — *Alexandromenia gulaglandulata* n. sp., holotype in preserved state (anterior end upper left), 21 mm long.

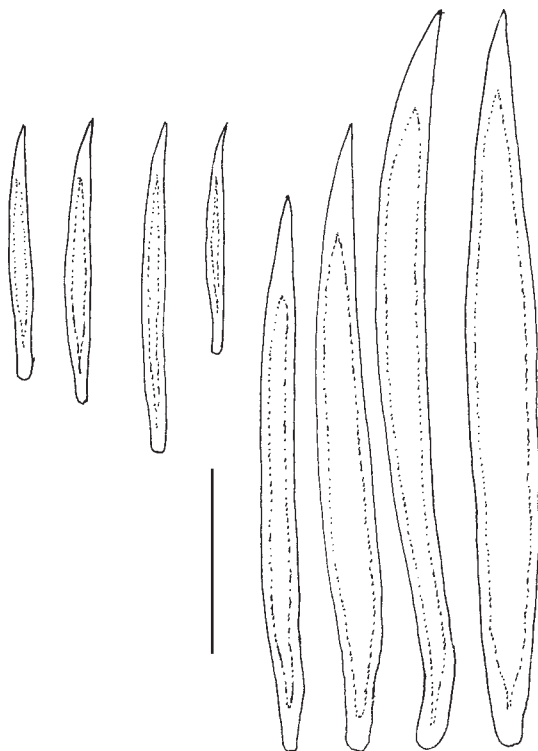


FIG. 17. — *Alexandromenia gulaglandulata* n. sp., mantle sclerites. Scale bar: 50 μ m.

cuticle show two kinds of acicular, slightly curved, hollow spicules (Fig. 17): small, 60-90 \times 4-8 μ m long, tangential needles, densely arranged in several layers,

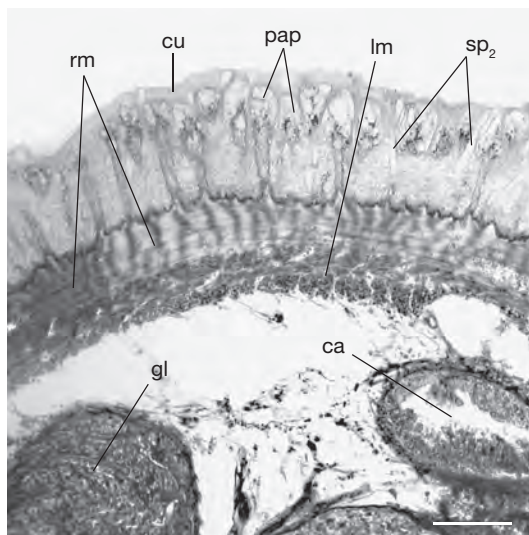


FIG. 18. — *Alexandromenia gulaglandulata* n. sp., cross section through mantle. Abbreviations: **ca**, anterior caecum of midgut; **cu**, cuticle; **gl**, lateroventral foregut glands; **lm**, longitudinal musculature; **pap**, epidermal papillae; **rm**, matrix with transverse musculature of body wall; **sp₂**, radial spicules. Scale bar: 150 μ m.

and strong radial spicules (Fig. 18, **sp₂**) measuring 120-200 \times 10-15 μ m (the shorter and more slender ones towards ventral), some up to 225 \times 25 μ m. The low epidermis (only 4-8 μ m) is underlain by a 70 μ m thick matrix. This contains the transverse (“circular”) musculature (Fig. 18), which is rather scattered in the anterior body. The longitudinal musculature of the body wall is indistinctly grouped into bundles; bundles somewhat enlarged ventrally without, however, forming a distinct, paired musculus longitudinalis ventralis.

Foot and mantle cavity

The posterior half of the pedal pit shows 18 slender folds which enter the pedal groove and extend along the oesophageal region; in the posterior body, 11 of these folds are reduced to eight below the anterior mantle cavity, ultimately to four folds directly in front of the opening of the mantle cavity. The mantle cavity forms 16 symmetrically arranged respiratory folds. Anterior to the ventral opening, these are replaced by peripheral, irregular, slender diverticula (up to 200 μ m long) or sacculations of the roof (Fig. 24);

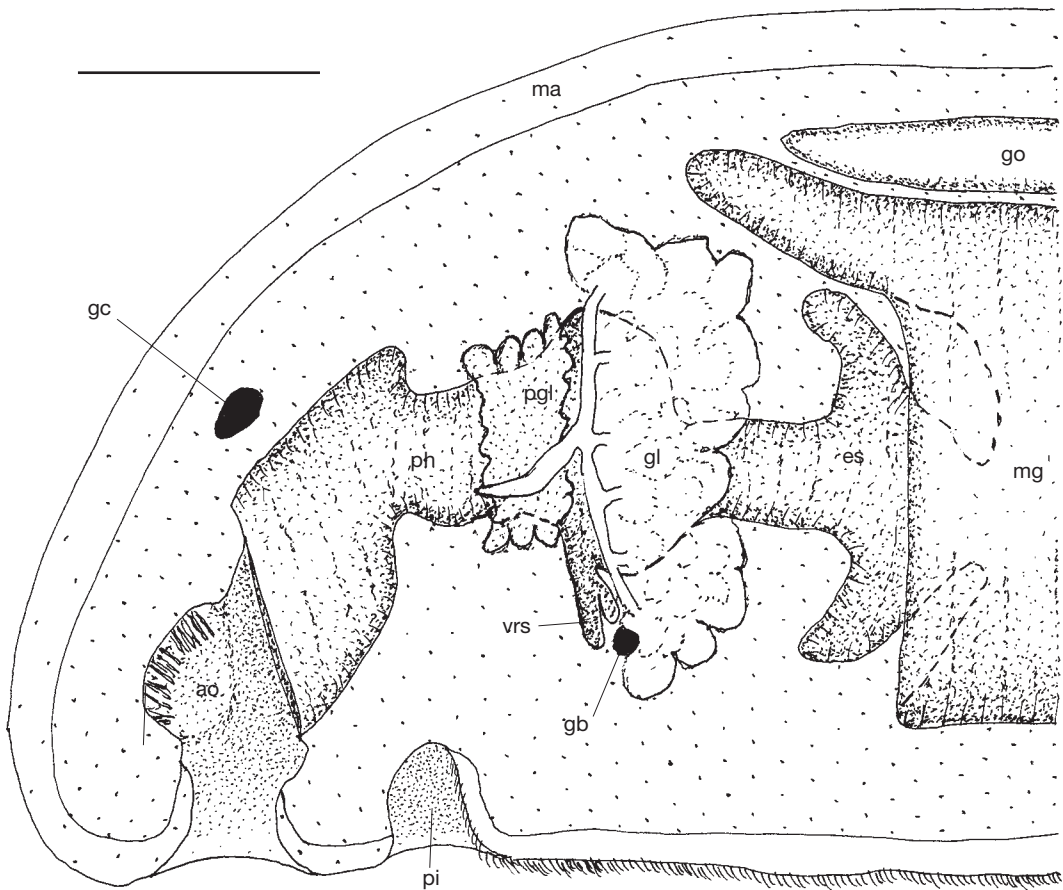


FIG. 19. — *Alexandromenia gulaglandulata* n. sp., organization of the anterior body viewed from left. Abbreviations: **ao**, atrial sense organ; **es**, oesophagus; **gb**, buccal ganglion; **gc**, cerebral ganglion; **gl**, lateroventral foregut glandular organ; **go**, gonad; **ma**, mantle; **mg**, midgut; **pi**, pedal pit; **pgl**, peripheral packages of pre-radular glands; **ph**, pharynx; **vrs**, ventral radula sack. Scale bar: 1000 μ m.

they delimit the mantle cavity against the circular hindgut; the 800 μ m long supra-rectal commissure is located near the end of the pericardium. The muscular terminal portion of the unpaired spawning duct opens at the anterior border of the mantle cavity opening. From the supra-rectal commissure backwards, the whole mantle cavity is coated by a dense mass of suprapallial glands. The terminal sense organ lies above the central mantle cavity (Fig. 23).

Alimentary tract

The anterior sense organ is located within the common atriobuccal cavity and is delimited by the

horseshoe-shaped ciliary tract; the atrial papillae are single and slender. The cerebral ganglion (400 μ m broad, 200 μ m long, 200 μ m high) is located above the buccal cavity between atrium and mouth opening; it has three pairs of cerebral nerves, each with a small basal swelling and a separate lateral origin of the connectives. The wide anterior pharynx shows several irregular foldings and is surrounded by distinct, but loosely arranged musculature as well as by indistinct pharyngeal glands. More posteriorly, the lumen becomes X-shaped and the musculature more distinctly circular; ventro-laterally, the paired foregut glandular organ opens pre-radularly

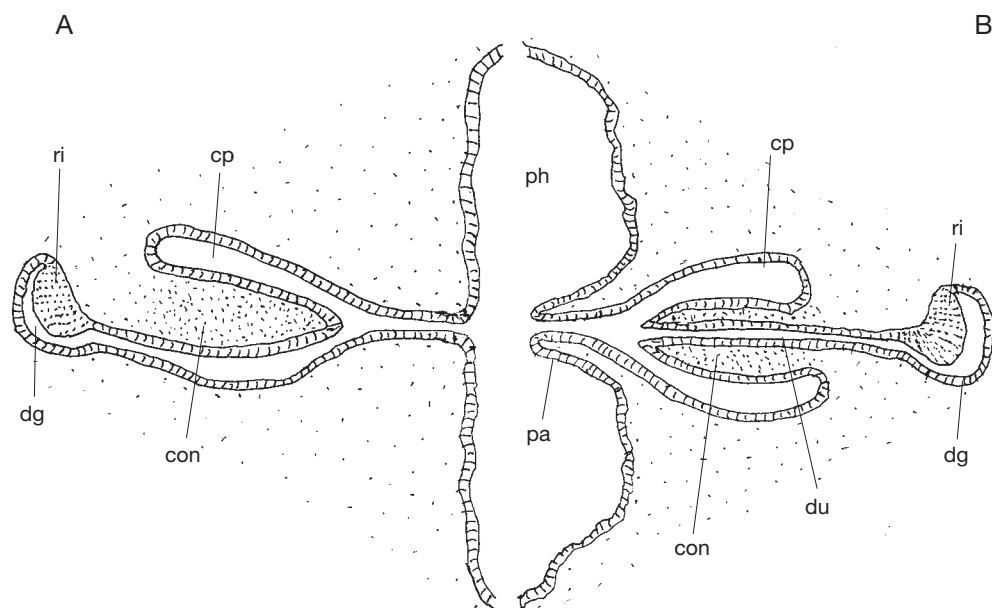


FIG. 20. — Two types of the outlet of the lateroventral foregut glandular organs with terminal cone (and opening papilla) within Amphimieniidae (schematised): **A**, simple cone as in *Alexandromenia gulaglandulata* n. sp.; **B**, cone with internal ductule such as in *A. antarctica* Salvini-Plawen, 1978. Abbreviations: **con**, cone; **cp**, cone pouch (sheath); **dg**, duct of glandular organ; **du**, ductule of cone; **pa**, opening papilla; **ph**, pharyngeal cavity; **ri**, median ridge of duct.

(Fig. 19). The region between these openings and the radula is widened and characterised by peripheral packages of an additional type of strongly stained glands; the cells of each package empty together via slender stalks into the pharynx (Figs 19; 21). These packages differ distinctly from those of the paired lateroventral foregut glandular organs; both types partially overlap in the radula region (Fig. 21). The ducts of the paired foregut glandular organs show a median ridge and are encircled by musculature. The anterior-most portion of each duct curves medially and widens to a pouch. The median ridge of the pouch is enlarged to form a cone (Fig. 20A) which, in this species, has no ductule. Both pouches open directly into a deep, slender cleft (“duct”) of the pharynx; no protruding opening papilla is developed. Each of the paired ducts of the glandular organs is, in the radula region, continuous with the dorsal and ventral limb of a collecting duct. This duct, in turn, receives the often ramified outleading ductules of the gland clusters; these clusters are thus more

or less semicircularly arranged at both sides of the postradular foregut.

The radula bends into an unpaired antero-ventral sack containing the radula plates. The plates are basally 65 μm , distally 50 μm broad and about 30 μm high with a 27–30 μm long denticle at both lateral borders (Fig. 22); no central denticles were detected. The radula support consists of a paired bolster of at least five turgescient cells each. The buccal ganglia (diam. 150 \times 100 μm) closely adjoin (distance 50 μm) and are located ventro-posterior to the radula sheath. The postradular foregut (oesophagus) initially narrows without structural change and is provided with circular musculature as well as several strong radial muscle bundles. It is surrounded by densely arranged, small groups of long-necked oesophageal glands. More posteriorly, this portion telescopically intrudes into the wide second oesophageal region, which has a weak circular musculature and groups of gland cells. The oesophagus narrows again and axially intrudes into the midgut. The anterior caecum of the midgut

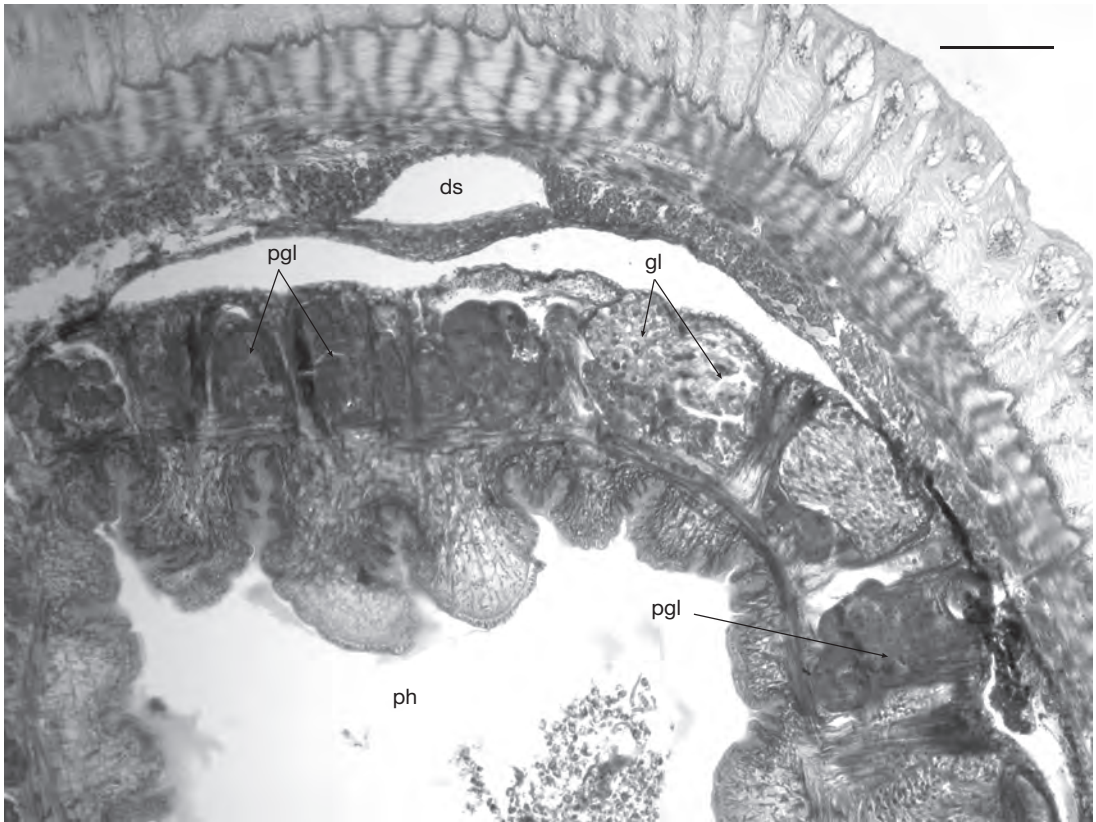


FIG. 21. — *Alexandromenia gulaglandulata* n. sp., cross section through posterior pharynx, just anterior to radula. Abbreviations: **ds**, dorsal sinus; **gl**, lateroventral foregut glands; **pgl**, pre-radular packages of glands; **ph**, pharynx. Scale bar: 150 μ m.

is short, extending above the oesophagus only. The midgut enlarges laterally to flank both sides of most of the oesophagus. Both the midgut and caecum have a middorsal ciliary tract. The dorsoventral muscle bundles, about 300 μ m apart, cause regular ventro-lateral midgut pouches. Below the pericardium and between the spawning ducts, the midgut continues into the hindgut, which is ciliated throughout; the anterior hindgut is surrounded by loose longitudinal muscles, posteriorly by both longitudinal and circular musculature. The 800 μ m long, medullar suprarectal commissure (diam. 90 μ m) is located below the end of the pericardium (Fig. 23).

Gonopericardial system

The animal is mature, with the paired gonad extending to the second oesophageal region; the eggs are

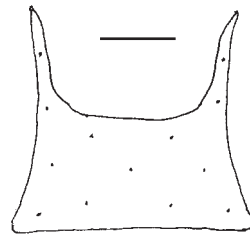


FIG. 22. — *Alexandromenia gulaglandulata* n. sp., one radula plate. Scale bar: 20 μ m.

up to 150 μ m in diameter. The gonopericardioducts are continuous with the dorso-frontal pericardium, which shows a paired anterior pouch. Both the ventricle and the single auricle of the heart are a free tube within the pericardium; the connection

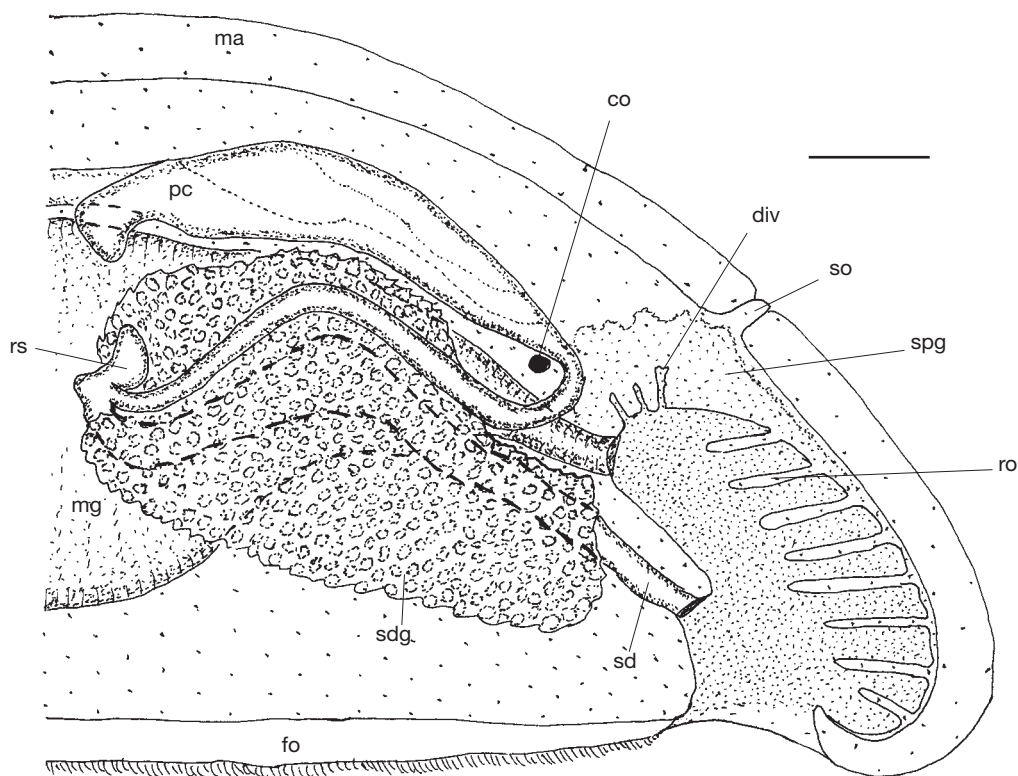


FIG. 23. — *Alexandromenia gulaglandulata* n. sp., organization of the posterior body viewed from left. Abbreviations: **co**, supra-rectal commissure; **div**, diverticula; **fo**, pedal folds (foot); **ma**, mantle; **mg**, midgut; **pc**, pericardium; **ro**, respiratory organs; **rs**, receptaculum seminis; **sd**, spawning duct; **sdg**, spawning duct glands; **so**, dorsoterminal sense organ; **spg**, suprapallial glands. Scale bar: 500 μ m.

of both portions is strongly narrowed. The two pericardioducts emerge laterotermally. There are no vesiculae seminales. A small, posteriorly directed receptaculum seminis is laterally differentiated at the opening of each pericardioduct into the anteriormost, lateral spawning duct (Fig. 23). The ciliated, simple spawning ducts are paired along most of their length and fuse near the end region of the pericardium. The subepithelially arranged, elongate and slender spawning glands are aggregated; they surround the ducts as a dense mass and open intercellularly. The unpaired spawning duct is provided with circular musculature and anteriorly (region of rectum) still shows openings of glands. The posterior portion of the unpaired spawning duct (below anterior mantle cavity) has a sphincter and radial muscles within a bulge at the bottom of the mantle cavity (Fig. 24);

the ventro-terminal outlet opens into the beginning mantle cavity opening.

COMPARISONS

All organizational characters of the single specimen classify it as a member of the Amphimeniidae. The key features here include the configuration of the lateral foregut glandular organs, the monoserial radula and the organization of the spawning ducts (see Salvini-Plawen 1972, 1978). Except in *Plathymenia* Schwabl, 1961, and *Alexandromenia* (?) *crassa* Odhner, 1921, all members of the family show a pre-radular outlet of the ventro-lateral foregut glandular organs. In most species this organ possesses a terminal cone within a pouch or sheath (Fig. 20) that opens by formation of a papilla intruding into the pharynx (Fig. 20B). The details of the outleading

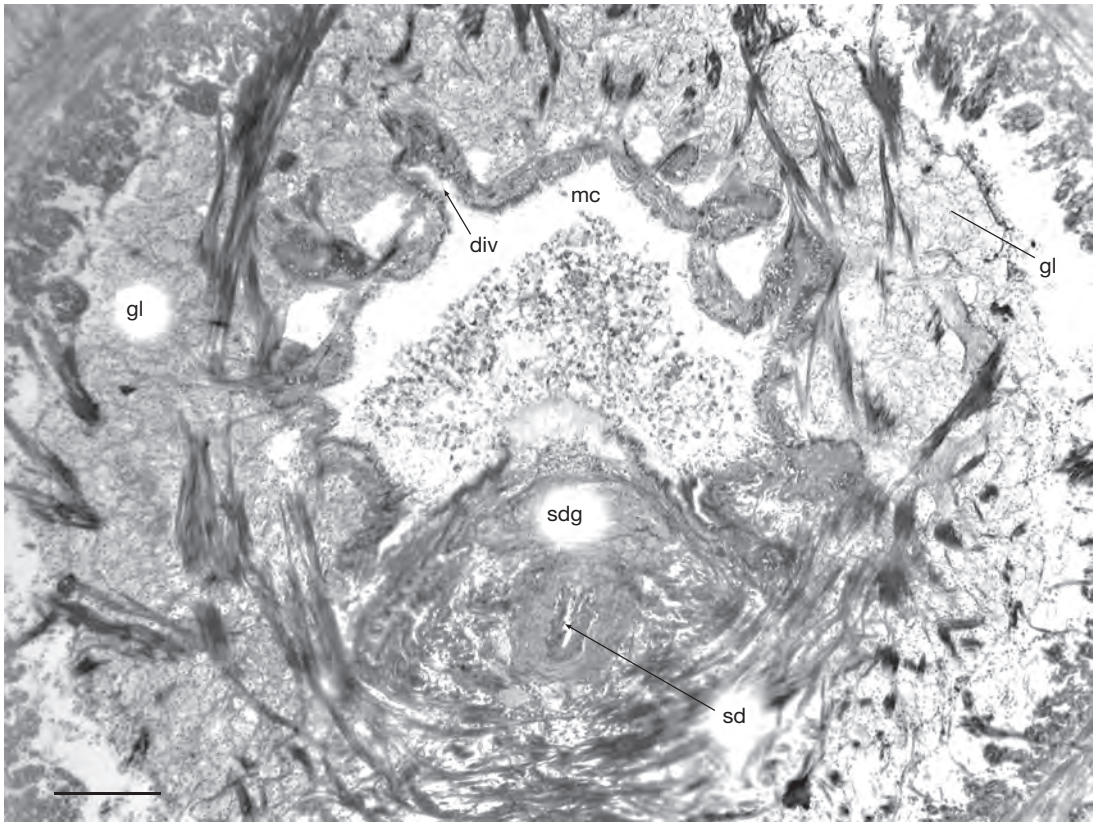


FIG. 24. — *Alexandromenia gulaglandulata* n. sp., cross section through anterior mantle cavity with irregular, slender diverticula. Abbreviations: **div**, diverticle; **gl**, suprapallial glands; **mc**, mantle cavity; **sd**, spawning duct; **sdg**, spawning duct glands. Scale bar: 150 μ m.

duct, however, differ: this may open directly, without cone formation, into the pharynx (with or without a papilla), such as in *Alexandromenia pilosa* Handl & Salvini-Plawen, 2002; the duct may open into the pouch (sheath) of the cone (Fig. 20A), such as in the present species (no papilla); the outleading duct may be directly continuous with a (somewhat eccentric) internal ductule of the cone (Fig. 20B), such as in *A. antarctica* Salvini-Plawen, 1978. Several species exhibit both a connection with the pouch and a ductule within the cone (Salvini-Plawen 1978); in some species, several slender ductules pass through the cone (Heath 1911).

Within the Amphimeniidae, the present specimen clearly belongs to the genus *Alexandromenia* (see diagnosis above and the comparative tables in Salvini-Plawen 1978 as well as García-Álvarez *et al.*

2000). An identity with the incompletely known *Meromenia* (*M. hirondellei* Leloup, 1949, from the Bay of Biscay) can be excluded based on the lack of respiratory organs and midgut pouches. Eight *Alexandromenia* species are currently known. The present specimen differs from these by the packages of additional foregut glands in the region between the outlets of the lateral glandular organs and the radula apparatus. This also includes the three known Atlantic representatives: *A. crassa* Odhner, 1921, from the Hjeltefjord (Bergen area, Norway) at 100-200 m, *A. grimaldii* Leloup, 1946, from off the Azores at 1250 m, and *A. pilosa* Handl & Salvini-Plawen, 2002, from the Trondheimsfjord (Norway) at 180-240 m.

The poorly described *A. crassa*, apart from its “pair of small salivary glands opening into the radula sac”

(Odhner 1921: 22) – which casts doubt on the generic classification – also differs from the animal at hand by the dorso-median keel of spicules, by the fairly stout body (10 × 3–3.3 mm) with 9 pedal folds, by the 160 µm broad radula plates of different outline, by the long midgut caecum extending beyond the cerebral ganglion, and by the dorsally extended receptacula seminis.

Alexandromenia grimaldii measures 20 × 2.3 mm with an about 140 µm thick cuticle; it differs from the present specimen in the number (7–3) of pedal folds, whereby the median fold connects with the mantle cavity, in the voluminous midgut caecum, in the hindgut being continuous with the ventral midgut only, as well as in the receptacula seminis being enlargements of the distal pericardioducts (Leloup 1946). It is particularly characterised by the U-shaped radula teeth (Salvini-Plawen 1972).

Alexandromenia pilosa, measuring 9 × 1.2–1.4 mm, has only 5–3 pedal folds, club-shaped epidermis papillae, sclerites of one type only, a subepithelial matrix outside the transverse musculature, an anteriorly bilobed midgut caecum, a short suprarectal commissure (about 100 µm), and anteriorly directed receptacula seminis; it lacks suprapallial glands and no turgescer cells of the radula support or bolster are mentioned (Handl & Salvini-Plawen 2002).

The present specimen is thus organizationally well separated and represents a proper, new species: *A. gulaglandulata* n. sp.

Acknowledgements

The author is very grateful to Christian Szaeffich (Vienna) for preparing the photographs and to Dr Michael Stachowitsch (Vienna) for polishing the English text.

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*Submitted on 12 April 2007;
accepted on 27 November 2007.*