IMEROHERPIA LAUBIERI, A NEW SOLENOGASTER FROM THE BAY OF BISCAY

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ABSTRACT

A new bathyal solenogaster species of the hitherto monotypic genus and monogeneric family *Imeroherpia* (Pachytegmentaria: Sterrofustia: Imeroherpiidae) is described from the Bay of Biscay. *Imeroherpia laubieri* shows a distinctive configuration of the internal organs of the posterior body, where the entire space between the organs of the gonopericardial complex is occupied by large lumina, instead of connective tissue as in most species of Solenogastres. The epithelium of these lumina is thin and delicate, resembling coelomic epithelium. However, the lumina are actually voluminous posterior midgut sacculations, which clearly open into the midgut.

INTRODUCTION

There are 57 species of Solenogastres and 32 species of Caudofoveata currently recorded in European seas [Check List of the European Marine Molluscs (CLEMAM), 2001]. Although this number may appear high compared to other, less investigated parts of the world, our knowledge of the systematic composition and distribution of these small, worm-like molluscs is still far from adequate. Even in Europe, most species are still known only from their type locality (often the vicinity of marine stations) and as many as 34% of them were described in the last 20 years.

The Bay of Biscay has been the subject of deep-sea biological investigations since the early days of oceanography, resulting in numerous papers and monographs on its shelled mollusc fauna. By contrast, the literature on Solenogastres and Caudofoveata is quite scanty (see Table 2). The purpose of the present paper is to describe a new species in the hitherto monotypic genus and monogeneric family *Imeroherpia* Salvini-Plawen, 1978, and to summarize what is known on the Solenogastres and Caudofoveata from the Bay of Biscay.

MATERIAL AND METHODS

The specimens were collected during the POLYGAS cruise, conducted on board R.V. *Jean-Charcot* between 23 October and 4 November 1972 under the direction of Dr Lucien Laubier. The cruise was part of the broader BIOGAS (for BIOlogie GAScogne) programme of the French Research Institute for Exploitation of the Sea IFREMER (formerly CNEXO), aimed at investigating the composition and functioning of deep-sea biological communities in the Bay of Biscay (Laubier, 1985).

Spicules from the body cover were extracted and mounted in resin. Serial sections of the animals were made at 8 and 5 μm, and stained with AZAN (Heidenhain).

Terms for the general anatomy of Solenogastres are based on the works of Salvini-Plawen (1972, 1978, 1985), Scheltema, Tscherkassky & Kuzirian (1994), Scheltema (1999), Scheltema & Schander (2000) and the Aplacophora Home Page (terminology). However, a clarification of terminology is needed for the ventral pharyngeal depressions or diverticula near the radula. In German literature [Claus, Grobben & Kühn, 1932 (reprint 1971); Hennig, 1984; Kilias, 1993; Storch & Welsch, 1997] there is a confusion concerning the terms *Radulascheide, Radulasack* and *Radulatasche* that have been used in general molluscan anatomy by different authors in different ways: for either the diverticulum containing the proximal end of the radula (with odontoblasts and younger teeth) or for the anteroventral diverticulum enclosing the distal end of the radula (older teeth).

In recent literature on Solenogastres, mainly contributed by Salvini-Plawen and Scheltema, the diverticulum containing the proximal end of the radula is called *radula sac* by Scheltema, but *radula sheath* (*Radulascheide*) by Salvini-Plawen. The anteroventral diverticulum, or pair of diverticula, enclosing the distal end of the radula is called the anteroventral *radula pocket* by Scheltema, but *radula sac* (*Radulasack*) by Salvini-Plawen. Herein, these terms are used *sensu* Scheltema.

SYSTEMATIC DESCRIPTION

Supraorder Pachytegmentaria Salvini-Plawen, 1978
Order Sterrofustia Salvini-Plawen, 1978
Family Imeroherpiidae Salvini-Plawen, 1978

Diagnosis: Tetraseriate radula (four teeth per row), ventral foregut glandular organs subepithelial-epithelial (= type B after Salvini-Plawen, 1978); copulatory stylets with associated glands. Included genera: *Imeroherpia* Salvini-Plawen, 1978

Imeroherpia Salvini-Plawen, 1978

Diagnosis: Cuticle thick, with solid needles; fused atriobuccal opening; ventral midgut with lateral pouches; cerebral connectives separate; dorsoterminal sense organ present; secondary gonopore paired; copulatory stylets with associated glands; with (?) respiratory elaborations.

Type species: *Imeroherpia quadridens* Salvini-Plawen, 1978, by original designation. Known only from the type locality: South East Atlantic off South Africa: 33°36′ S, 16°15′ E, 2785–2870 m.

Imeroherpia laubieri new species

Etymology: This species is named for Dr Lucien Laubier, then head of the French BIOGAS-programme and principal investigator of the POLYGAS cruise, now Professor at l'Institut Océanographique (Paris).

Material examined: Sta. DS 15: 47°35.2′ N, 8°40.1′ W; 2246 m; three specimens: two mature, one juvenile. Sta. DS 16: 47°36.1′ N, 8°40.5′ W; 2325 m; one specimen, without mature gonads.

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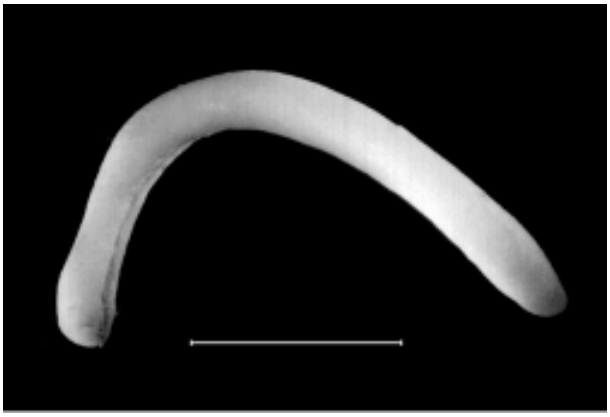

Figure 1. *Imeroherpia laubieri* n. sp. Habit, anterior to left. Scale bar = 5.0 mm.

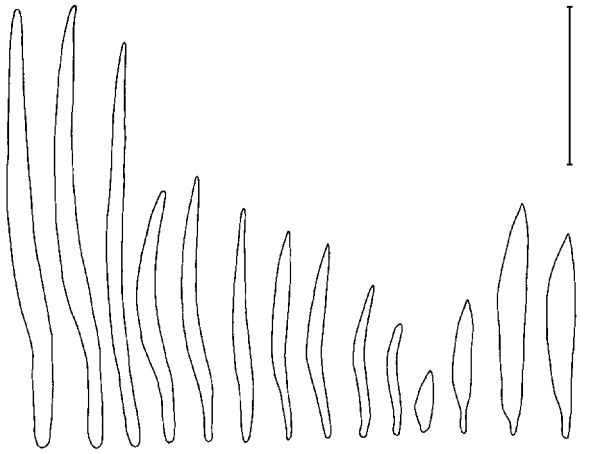

Figure 2. *Imeroherpia laubieri* n. sp. Epidermal spicules. Scale bar = 100 μm.

Holotype (serially sectioned): MNHN (no catalogue number assigned), a mature specimen from POLYGAS Sta. DS 15, labelled for the present study: DS 15/2/1.

External aspects (Figs 1 and 2): The largest specimen is about 2 cm long. In cross-section the animals are nearly round, measuring 0.9–1.3 mm in height by 0.8–1.1 mm in width. The juvenile animal is half this size. The anterior end is somewhat wider and higher than the rest of the body, with a distinct opening of the atriobuccal cavity. The posterior body is slightly tapered and rounded terminally (Fig. 1). The calcareous bodies of the body cover (Fig. 2) are solid, arranged cross-wise (nearly at right angles) and skeletal (i.e. lying within the cuticle). The slightly curved solid needles are up to 240 μm long and 12–16 μm wide, many with a nearly straight base. Knife-shaped scales are present beside the pedal fold.

Mantle: The cuticle is thick (100–140 μm) and regularly pierced by large epidermal papillae (Fig. 3A, B). The epidermis (Fig. 4A) is thin, only 4–8 μm. The body musculature varies from 4 to 16 μm thickness.

Pedal groove and pallial cavity: The pedal pit (Fig. 3A) is as usual in Solenogastres; in cross section the pedal glands extend slightly above the mid-lateral plane, to the sides of the cerebral ganglion. The single foot fold (Figs 3B, D and 4C, D) originates in the longitudinal midline of the pedal pit and ends at the opening of the pallial cavity. At the opening of the pallial cavity a bundle of 7–10 calcareous spicules is present on each side (Fig. 4E). The cross-section of each spicule (lumina left after decalcification) shows a slight tongue and groove, probably a structure for holding the spicules together. Behind these abdominal spicules, the paired secondary gonopores open into the pallial cavity. More terminally, between the secondary gonopores and anus, the epithelium of the pallial cavity forms regular, low, longitudinal folds, probably too small for respiratory elaborations, but ensuring great flexibility of the pallial cavity. Behind the anus, closely packed suprapallial glands (Fig. 5B) fill all the space between pallial cavity and body wall. A large anteroventral pouch of the pallial cavity bears the paired opening of the glandular organs that are associated with the copulatory stylets (Fig. 4D). The epithelium of this pallial pouch bears some single gland cells. Anteriorly, the pouch is lined with collagenous fibres.

Musculature: The dorsoventral muscle system produces the lateral pouches of the midgut, as in many Solenogastres. The paired musculi longitudinales ventrales of the ventral body wall musculature are strong. Remarkably strong circular and longitudinal musculature surrounds the whole radula complex. The radula bolster consists only of musculature; vacuolated cells are absent. At each side of the foregut in the radular region, a muscle inserts and runs backward to the lateral body wall. Other muscles serve as protractors and retractors of the copulatory stylets.

Cerebral and sensory system: The cerebral ganglion is oval in cross-section and about 120 μm long. The cerebral connectives are separated from each other. The foremost pedal ganglia are large, measuring more than 100 μm in length (Fig. 3B). The buccal ganglia directly adjoin the opening of the radula pocket and the opening of the foregut glandular organs. The main nerve cords have a large diameter (~30 μm) and are clearly visible. The suprarectal commissure is also easily discernible above the hindgut, in the loop formed by the transition of the pericardium into the pericardial ducts. The atrial sense organ is delimited by a horseshoe-shaped ledge of high-prismatic, ciliated cells running along the front, and lateral edges of the atrium before bending dorsally and fusing in front of the mouth opening. The atrium bears a number of basally bundled, long, slender papillae. In front of the atrium a small sac-like invagination with a homogeneous glandular and ciliated epithelium is present. A dorsoterminal sense organ is located medially above the posterior end of the pallial cavity.

Alimentary tract (Fig. 5A): The mouth lies in the atriobuccal opening and leads into the foregut. The foremost part of the foregut does not show any special folds or pouches. Behind the cerebral ganglion the foregut flattens and bends dorsally. Here, a longitudinal retractor inserts on each side of the terminal part of this foregut 'knee', runs backward along the outer side of the foregut glandular organs and attaches to the lateral body wall. The ascending part of the foregut is surrounded by distinct musculature and by many large, single, pharyngeal gland cells (Fig. 3A). The foregut then curves to become horizontal, where the radula complex and the ventral foregut glandular organs are located. The radula is tetraseriate (Fig. 3B); the four teeth per row are arranged two by two with a space in the middle. Each tooth is 15–20 μm high, 22–32 μm broad and triangular with a somewhat curved base and a small hook at the tip. (The juvenile specimen has smaller teeth.) The opening of the radula pocket is elongated so that the transition between the radula sac and the radula pocket projects like a tube into the lumen of the foregut (Fig. 3C). The epithelium of the radula pocket is gland-

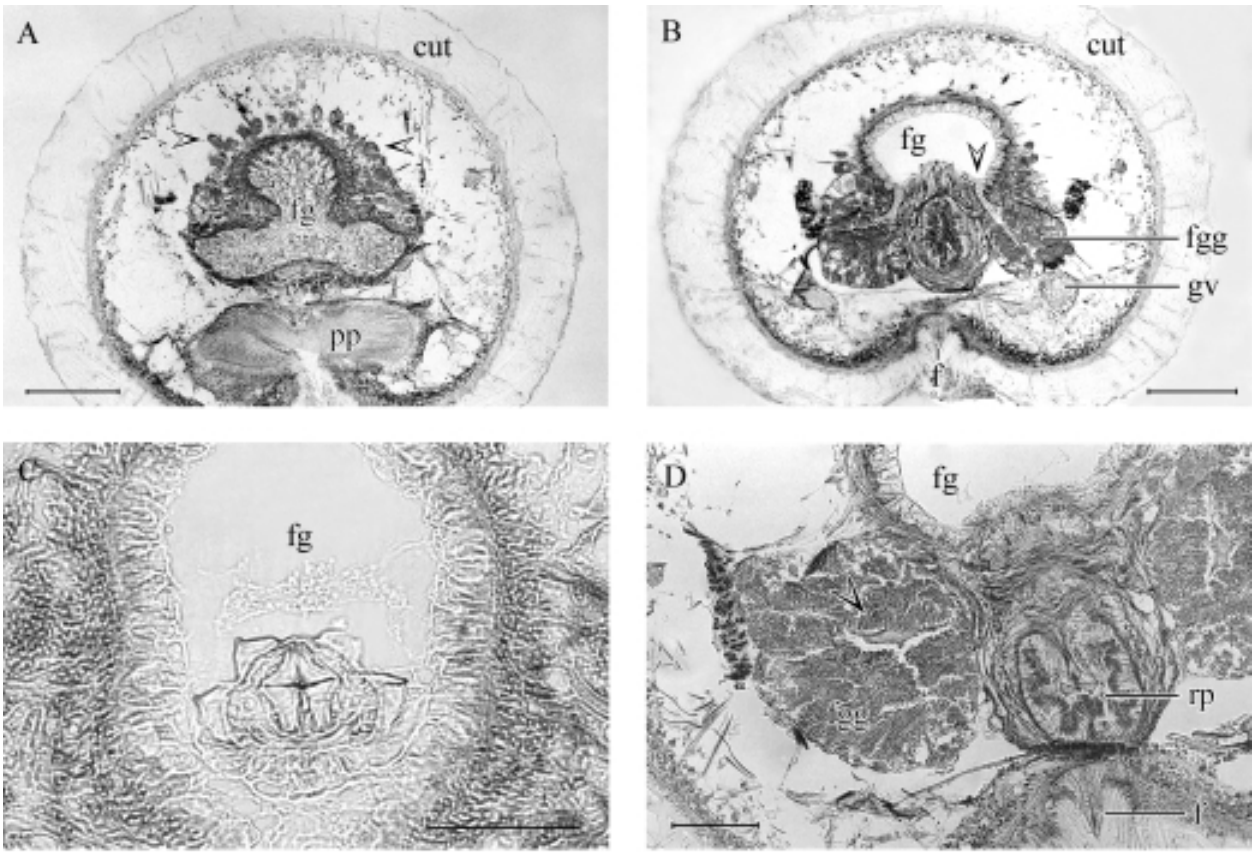

Figure 3. *Imeroherpia laubieri* n. sp. Cross-sections of the anterior body. **A.** Foregut with single foregut glands (arrows); scale bar = 200 μm. **B.** Foregut and opening of the foregut glandular organs (arrow); scale bar = 200 μm. **C.** Radula with four triangular teeth per row; teeth of another row visible inside the radula pocket; scale bar = 50 μm. **D.** Foregut glandular organ with glandular epithelium (arrow) and subepithelial glands as well (= Type B); scale bar = 100 μm. Abbreviations: cut, cuticle; f, foot; fg; foregut; fgg, foregut glandular organ; gv, foremost ventral ganglion; pp, pedal pit; rp, radula pocket.

ular (Fig. 3D). The paired foregut glandular organs are nearly spherical and lined with a thin layer of connective tissue. Each gland consists of subepithelial gland cells along an equally glandular epithelial duct (Fig. 3D) opening from lateroventral into the foregut next to the opening of the radula pocket (Fig. 3B). Behind the radula complex the foregut merges into the midgut. In one of the four specimens a distinct anterodorsal midgut caecum is formed. Towards the rear body end the gut shows a very distinctive configuration: the midgut forms large lateral and ventrolateral pouches which accompany the organs of the rear body end along their full length. The most posterior midgut pouch ends behind the anus. The pouches fill the space between the organs, which is usually filled by connective tissue and sinuses of the circulatory system in most Solenogastres. The epithelium of the midgut pouches is firmly attached to the other organs, forming secondary pouches and vaults, depending on the extent of the other organs (Fig. 4B, C, F). The straight main limb of the midgut narrows ventrally to form the hindgut, which shows distinct longitudinal folds and then opens dorsally into the pallial cavity.

Gonopericardial system (Fig. 5B): The paired gonad has lateral pouches, the most posterior of which serve as reservoirs for fully developed spermatids. From the gonad, the paired gonopericardial duct leads into the pericardium, which bears broad lateral ciliary tracts. The heart, both the auricle and ventricle, is tubular and not attached to the dorsal pericardial wall (Fig. 5B). Directly behind the auricle, the pericardium merges into the two pericardial ducts, which immediately bend and run anteriorly along the lateral body wall. They are equipped with a very high medial ledge of ciliated epithelial cells, a continuation of the pericardial ciliation. After one-third of the entire length of each pericardial duct, the ciliary ledge flattens just in front of a tiny medial pouch, probably serving as a small seminal vesicle (Figs 4F and 5B). Further anteriorly the pericardioducts are evenly ciliated. They open laterally into the anteriormost ends of the limbs of the spawning ducts. At this position a stalked seminal receptacle is located on each side as a prolongation of the spawning ducts. The spawning ducts are paired throughout, with high-prismatic, ciliated epithelium anteriorly, becoming glandular towards the posterior end. The paired secondary gonopores lead into the pallial cavity. The paired copulatory glands (Fig. 4B, C, D) are located below the spawning ducts. Each of these glands has two parts: the first is a long duct with a high-prismatic, glandular epithelium, similar to the epithelium of the spawning duct. The second, partly equipped with a high-prismatic, glandular epithelium, is smaller and lies lateroventral and more terminal to the first part. The first and second parts fuse, before opening laterally through a short duct into the pouch of the pallial cavity (Fig. 4D). Another opening of the smaller part of the copulatory gland leads into the sheath of the copulatory stylets on each body side (Fig. 4C). The copulatory stylets are paired structures, with one needle and one groove-shaped element in one collagenous sheath (Fig. 4A). Their proximal ends are connected with a retractor consisting of muscle and collagenous fibres inserting into the lateral body wall of the midbody region. Two protractor muscles insert at each stylet sheath and run posteriorly to the body wall, one medio-ventrally to the body wall above the pedal fold, the other one to the lateroventral body wall. The whole stylet complex is

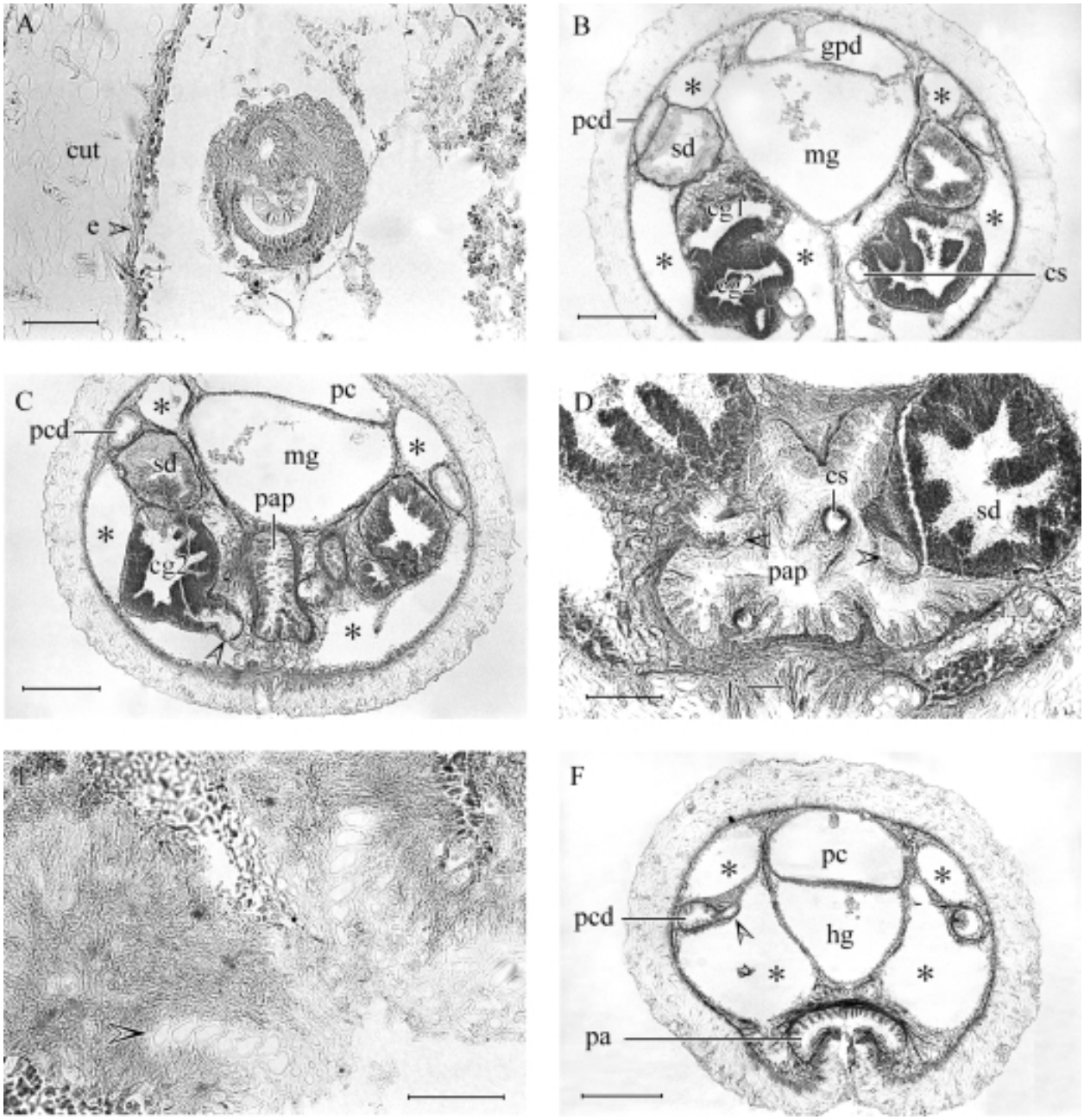

Figure 4. *Imeroherpia laubieri* n. sp. Cross-sections of the posterior body. **A.** Lumina of the copulatory stylets (a round one and a groove-shaped one) of one side of body; scale bar = 50 μm. **B.** Spawning ducts, copulatory glands and posterior midgut pouches (asterisks); scale bar = 200 μm. **C.** Posterior midgut pouches (asterisks), copulatory glands with duct to copulatory stylet (arrow); scale bar = 200 μm. **D.** Opening of copulatory gland into pouch of pallial cavity (arrow); scale bar = 100 μm. **E.** Lumina of abdominal spicules (arrow); scale bar = 50 μm. **F.** Posterior midgut pouches (asterisks) and seminal vesicle (arrow) emerging from the pericardial duct; scale bar = 200 μm. Abbreviations: cg1, upper part of copulatory gland; cg2, lower part of copulatory gland; cs, lumen of copulatory stylets; cut, cuticle; e, epidermis; gpd, gono-pericardial duct; hg, hindgut; mg, midgut; pa, pallial cavity; pap, pouch of pallial cavity; pc, pericardium; pcd, pericardial duct; sd, spawning duct.

more than 1.3 mm long. In its terminal region, the copulatory gland opens into the sheath, then the stylet projects into the lumen of the pallial pouch. As in most Solenogastres with copulatory stylets, the stylets of the two body sides seldom lie symmetrically; one is more dorsal than the other. Because of the voluminous midgut pouches that occupy most of the space in between the organs, the copulatory stylets, copulatory gland organs, nerve cords and longitudinal muscle bundles are connected to the body wall only by narrow, longitudinal tissue cords.

DISCUSSION

The characters of the present animals from the Bay of Biscay are in accordance with the generic diagnosis of *Imeroherpia*. However, *Imeroherpia quadridens* and *I. laubieri* differ by several discrete characters that are here interpreted as species-specific (Table 1).

Before the present paper, only five species of Solenogastres, two of them of uncertain classification, were known from the Bay of Biscay. This is clearly an under-representation of the local

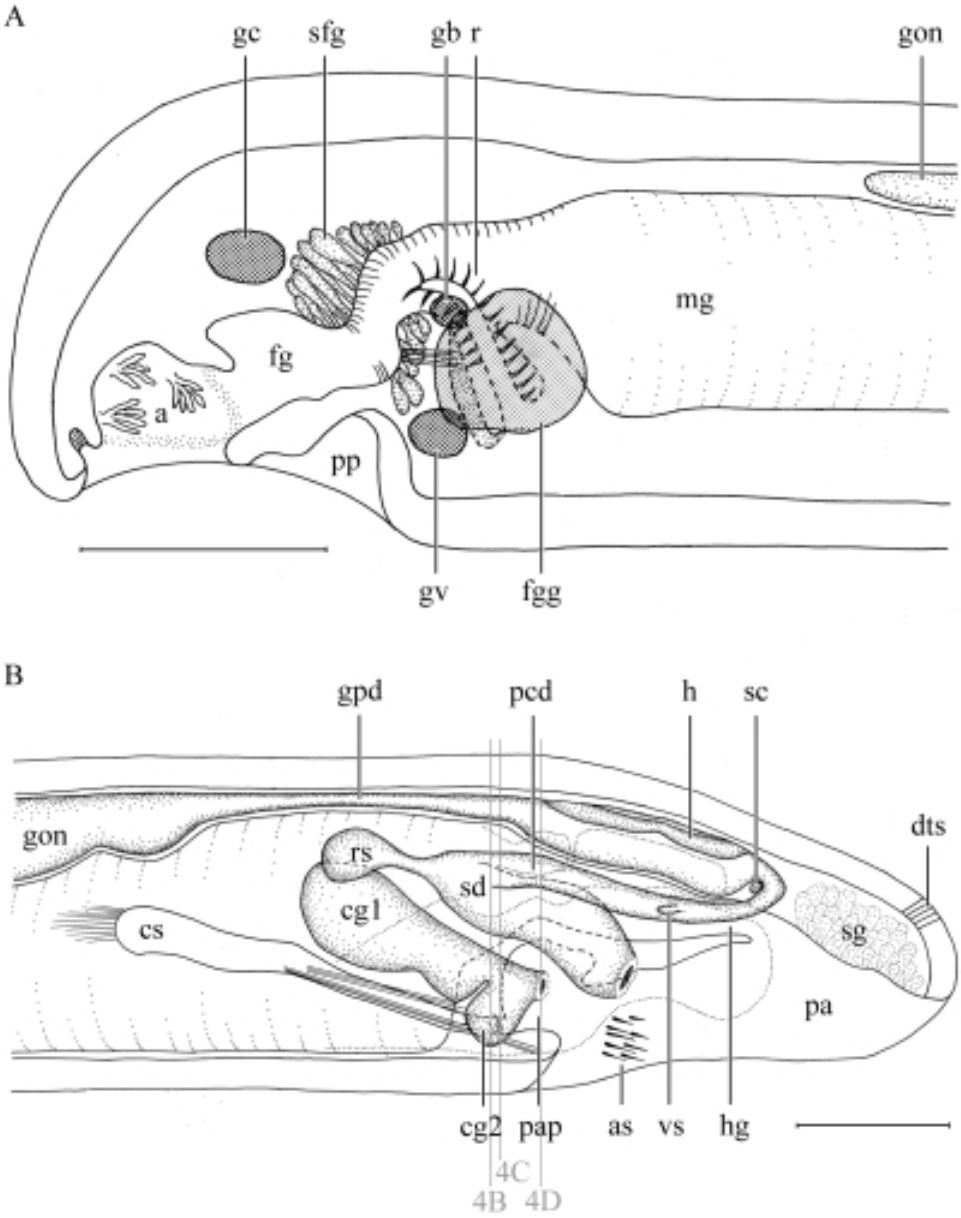

Figure 5. *Imeroherpia laubieri* n. sp. Reconstruction. **A.** Anterior body; scale bar = 500 μm. **B.** Posterior body; dotted line indicates extent of posterior midgut pouches; grey lines indicate histological sections of Figure 4B, C, D; scale bar = 500 μm. Abbreviations: a, atrium; as, abdominal spicules; cg1, upper part of copulatory gland; cg2, lower part of copulatory gland; cs, lumen of copulatory stylets; dts, dorsoterminal sense organ; fg, foregut; fgg, foregut glandular organ, gb, buccal ganglion; gc, cerebral ganglion; gon, gonad; gpd, gono-pericardial duct; gv, foremost ventral ganglion; h, heart; hg, hindgut; mg, midgut; pa, pallial cavity; pap, pouch of pallial cavity; pcd, pericardial duct; pp, pedal pit; r, radula; rs, seminal receptacle; sc, suprarectal commissure; sd, spawning duct; sfg, single foregut glands; sg, suprapallial glands; vs, seminal vesicle.

Table 1. Specific characters separating *Imeroherpia laubieri* from *I. quadridens*.

Character	*Imeroherpia quadridens*	*Imeroherpia laubieri*
Pre-atrial pit	Absent	Present
Origin of the pedal fold	In the posterior fusion of lateral rims of pedal pit	In the middorsal line of the pedal pit
Musculus longitudinalis ventralis	Slightly thickened ventral part of body musculature	Massively thickened ventral body musculature
Heart	Atrium attached to the dorsal wall of pericardium	Tubular, not attached to the pericardial wall
Posterior midgut pouches	Absent	Present
Copulatory stylets	Three elements (a round and two flattened needle-shaped) in one sheath per body side	Two elements (a needle-shaped and a groove-shaped) in one sheath per body side
Respiratory elaborations	Present (?)	Absent
Size of radula teeth	20 μm broad, 12 μm high	22–32 μm broad, 15–20 μm high

Table 2. Known records of Caudofoveata and Solenogastres from the Bay of Biscay.

Taxon	Depth range in the Bay of Biscay	Reference
CAUDOFOVEATA		
CHAETODERMATIDAE		
Falcidens vasconiensis Salvini-Plawen, 1996	164–300 m	Salvini-Plawen (1996, 1997, 1999)
PROCHAETODERMATIDAE		
Claviderma gladiatum (Salvini-Plawen, 1992)	1739–2379 m	Scheltema & Ivanov (2000)
Claviderma iberogallicum (Salvini-Plawen, 1999)	101–135 m	Salvini-Plawen (1999), Scheltema & Ivanov (2001)
Chevroderma turnerae (Scheltema, 1985)	2124–4825 m	Scheltema (1985), Scheltema & Ivanov (2000)
Prochaetoderma boucheti Scheltema & Ivanov, 2000	101–860 m	Scheltema & Ivanov (2000, 2001)
Prochaetoderma yongei Scheltema, 1985	1175–2006 m	Scheltema (1985)
Spathoderma alleni Scheltema & Ivanov, 2000	610–1175 m	Scheltema & Ivanov (2000)
Spathoderma clenchi Scheltema, 1985	1913–2885 m	Scheltema (1985)
LIMIFOSSORIDAE		
Scutopus ventrolineatus Salvini-Plawen, 1968	350–543 m	Salvini-Plawen (1996, 1997, 1999)
SOLENOGASTRES		
LEPIDOMENIIDAE		
(?) *Tegulaherpia myodoryata* Salvini-Plawen, 1985	860–1150 m	Salvini-Plawen (1997)
IMEROHERPIIDAE		
Imeroherpia laubieri n. sp.	2246–2325 m	this paper
ACANTHOMENIIDAE		
Acanthomenia arcuata Scheltema, 1999	4211–4327 m	Scheltema (1999)
(?) AMPHIMENIIDAE		
Meromenia hirondellei Leloup, 1949	166 m	Leloup (1949), Salvini-Plawen (1972, 1997)
SIMROTHIELLIDAE		
Kruppomenia delta Scheltema & Schander, 2000	4211–4327 m	Scheltema & Schander (2000)
Kruppomenia levis Scheltema & Schander, 2000	4249–4327 m	Scheltema & Schander (2000)

diversity; indeed, my own unpublished results on the Solenogastres from the POLYGAS cruise indicate that at least a further eight species are present in the area. In addition, nine species of Caudofoveata have so far been recorded from the Bay of Biscay (Table 2). The specimens of *Imeroherpia laubieri* were collected in zone 1 of the BIOGAS programme, situated on Mériadzek Terrace on the continental rise of the northern part of Bay of Biscay, and characterized by sediments with a high content of carbonates (45–60%) and an important coarse fraction consisting of planktonic Foraminifera (Auffret, 1985).

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