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New genus of Lumbriculidae (Annelida, Clitellata) from a karst spring in the Cantabrian Mountains, northern Spain

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Abstract

The groundwater worms of the family Lumbriculidae exhibit high diversity and endemism in southern Europe. All stygobiont lumbriculid species known so far in this region belong to six genera. In the present study, a new stygobiont lumbriculid *Fendia cantabrica* **n. gen. n. sp.** is described, mainly based on distinct characteristics of the male duct structure. The male duct is semiprosoporous and the spermathecae (two pairs) are postatrial, starting in the ovarian segment. These characteristics are shared with only two lumbriculid genera: the Nearctic *Eremidrilus* and Holarctic *Trichodrilus.* The new genus is clearly distinguished from the former by the absence of proboscis, and from both genera by a remarkably complex structure of the atrium: a very strong musculature organized in several crossed layers, a protrusible penis with a singular hydrostatic skeleton, and two prostate glands, which join separately to the atrial ampulla by short stalks.

Key words: *Fendia*, stygobiont, oligochaete, Iberian peninsula, groundwater

Introduction

Springs are ecotones between surface and subterranean waters and are useful to collect groundwater species from less accessible subterranean habitats. In previous studies of the Cantabrian region (northern Spain), oligochaete taxa from springs have been included in the lists of subterranean species (e.g. Giani *et al.* 2001; Achurra *et al.* 2015). Members of the family Lumbriculidae (Annelida, Clitellata) represent one of the groups with the highest diversity among the aquatic oligochaetes in subterranean waters of Europe (Giani *et al.* 2001; Dumnicka 2014; Martinez-Ansemil *et al.* 2016). Out of 32 genera of Lumbriculidae in the world (Martin *et al.* 2023), a total of 12 genera have been reported in groundwater (Martin *et al.* 2008). The number of stygobiont lumbriculid species, i.e., living exclusively in groundwaters, represents about one quarter of the total known taxa in the family, however, most of them are classified into a relatively small number of genera. To be specific, European stygobiont lumbriculids belong to only 6 genera (*Cookidrilus* Rodriguez & Giani; *Dorydrilus* Piguet, *Guestphalinus* Michaelsen, *Rhynchelmis* Hoffmeister, *Stylodrilus* Claparède and *Trichodrilus* Claparède). In the Iberian peninsula, in addition to the genus that is described here, a total of 6 stygobiont and stygophilic (inhabiting subterranean waters but found sometimes also in surface waters) lumbriculid species have been reported so far, belonging to only two genera, *Stylodrilus* and *Trichodrilus* (Rodriguez & Núñez 2023). One of the reasons for this low diversity at the genus level may be the fact that the main taxonomic characters used for the generic classification in the family Lumbriculidae are based on not more than the position of the spermathecae relative to the male ducts plus the general characteristics of the male duct organization, which is prosoporous (*Rhynchelmis*), semiprosoporous (*Cookidrilus, Guestphalinus, Stylodrilus, Trichodrilus*), or plesioporous (*Dorydrilus*). However, different structures of the male duct (e.g., penis, atrial musculature or prostate glands) may also be relevant for the taxonomy at the genus level, as well as other non-reproductive characters, such as nephridia, chaetae, presence of proboscis, accessory glands, etc., although they appear normally subordinate to the two main characters mentioned above, widely considered diagnostic at a generic level.

The aims of the present study are (a) the description of a new stygobiont genus and species of freshwater

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oligochaete and (b) to contribute to the enrichment of taxonomic criteria for genus demarcation in the family Lumbriculidae.

Material and methods

All specimens were sampled at the waters of the resurgence that flow under the entrance of a cave, at the karstic headwaters of the Cabra River, a short coastal river of only 5 km long, in La Borbolla, Llanes, Asturias (Cantabrian Mountains, Spain). Five individuals were sampled on July 7, 2008 and fixed in formaldehyde, and subsequently another 14 individuals were sampled on February 25, 2012 and fixed in FAA (formalin-acetic acid-alcohol solution). All specimens were preserved afterwards in 70% ethyl alcohol. Two specimens of the second sample were used for histological sections made at the Laboratory of Animal Cell Biology (University of Basque Country, UPV/EHU). An additional specimen was sent to the author by Ana Camacho from the Cave El Pindal (Rivadedeva, Asturias). Permanent preparations were mounted in Canada balsam, after being stained in Harris' or Ehrlich's hematoxylin, dehydrated using alcohol series and cleared in methyl salicylate.

A Nikon SMZ1500 stereoscopic microscope was used for dissections, wet-mounts and permanent preparations. Photography and measurements were made under an Olympus BX50 microscope with Differential Interference Contrast (DIC), equipped with a Nikon DS camera.

Abbreviations

a: atrium, aa: atrial ampulla, ad: atrial duct, al: atrial lumen, am: atrial musculature, ff: female funnel, mp: male pore, mpg: male pore glands, ov: ovary, p: penis, pb: penial bulb, sf: sperm funnel, ph: pharynx, pr: prostate, pr1: anterior prostatic gland, pr2: posterior prostatic gland, prj: prostate gland junction, sp1: first pair of spermathecae, sp2: second pair of spermathecae, spp: spermathecal pore, sv: spermathecal vestibulum, t: testis, v: vacuoles, vd: vas deferens.

In the description, Roman numbers indicate the order of the segment; intersegments are given as Arabic numerals, e.g., "9/10" for the intersegment of IX and X.

RESULTS

Class Clitellata

Order Lumbriculida

Family Lumbriculidae

Fendia n. gen.

Diagnosis

Small worms, with a short prostomium and secondary annulation in the pre-clitellar segments. Muscular pharynx well developed both dorsal and ventrally. Posterior lateral blood vessels absent. Nephridia with long postseptal duct, present from segment XIII. Testes paired in both IX and X. One pair of ovaries in XI. Male pores open in X, posterior to ventral chaetae, surrounded by a ring of glandular cells. One pair of atria in X with cross-hatched musculature, and a muscular penial bulb where penis protrudes from the inner epithelium of the atrial duct. Two clusters of prostatic cells, connected to opposite sides of the atrium by stalks. Small sperm funnels on 9/10 and 10/11. Spermathecae paired in segments XI (ovarian) and XII (post-ovarian). Spermathecal pores posterior to ventral chaetae. Female pores in 11/12.

Type species : *Fendia cantabrica* **n. sp.**

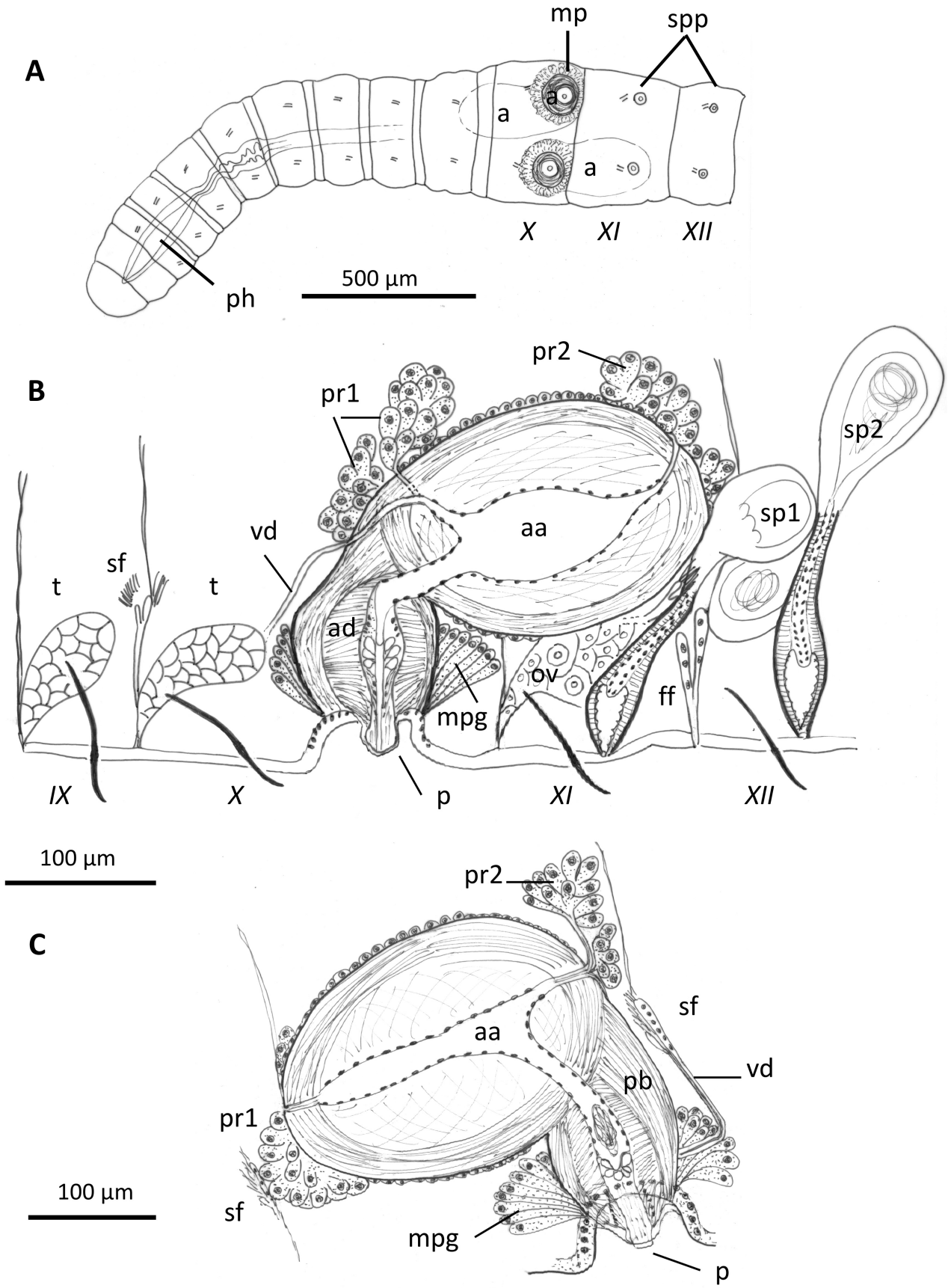

FIGURE 1. *Fendia cantabrica* **n. gen. n. sp. A.** Anterior body segments in paratype. **B.** Reproductive system in the holotype. **C.** Male duct in paratype. (The anterior part of the worm is always on the left side of the drawings).

Remarks

There are only two lumbriculid genera that share with *Fendia* n. gen. the semiprosoporous condition of the male duct together with the presence of two pairs of spermathecae in the postatrial segments: *Trichodrilus* Claparède, 1862 and *Eremidrilus* Fend & Rodriguez, 2003. The absence of a filiform proboscis, and the irregular shape and structure of the atrium clearly separate *Fendia* n. gen from the Nearctic genus *Eremidrilus*. The main distinction of *Fendia* **n. gen.** from *Trichodrilus*, as well as from other semiprosoporous taxa, is the complex male duct structure (cross-hatched, thick atrial musculature, muscular penial bulb, protrusible penis, a ring of glandular cells at the male pore), and in particular the presence of prostatic glands forming well-separated clusters joining opposite sides of the atrium through thick passages. Specifically, the covering of the atria by prostatic cells, either in a diffuse and continuous manner, or forming several small clusters of prostatic cells that join the atrial ampulla separately, is the common condition in Lumbriculidae. The prostatic glands organized in few bundles that join the atrium by short stalks were previously described by Fend & Ohtaka (2004) in the prosoporous lumbriculid *Yamaguchia* Fend & Ohtaka.

Fendia cantabrica **n. gen., n. sp.**

(Figs 1–3)

Dorydrilus sp.1: Achurra 2012. Tables 1, p.54; Table 2, p.56; Appendix 2, p.223.
Lumbriculidae gen. sp.: Achurra *et al.* 2015.Table 1, p. 151.

Holotype. MNCN16.03/3155, 25 February 2012 (Pilar Rodriguez coll.)

Paratypes. 6 sexually mature individuals, all from the type locality, sampled on 25 February 2012; 3 dissected (MNCN16.03/3156-16.03/3158), and two whole mounted (MNCN16.03/3159-16.03/3160), all Stained in hematoxylin, dehydrated and mounted in Canada balsam; two specimens sectioned (MNCN16.03/3161-16.03/3171), stained in eosin-hematoxylin and mounted in DPX. (Pilar Rodriguez coll.)

Other material. One dissected individual, stained in hematoxylin, from Cave El Pindal, Piniango, Rivadedeva, Asturias (Spain), located at 24 m asl. Coordinates: 30T 4806099N 375873E (Ana Camacho coll.), 18 March 1989.

Four individuals from the type locality, sampled 7 July 2008 (Ainara Achurra and Pilar Rodriguez coll.): one whole mounted and 3 dissected, sexually mature individuals, Stained in hematoxylin, dehydrated and mounted in Canada balsam. Seven sexually mature individuals sampled 25 February 2012 (Pilar Rodriguez coll.): 4 dissected, 2 whole-mounted, Stained in hematoxylin, dehydrated and mounted in Canada balsam; 3 individuals sectioned, stained in eosin-hematoxylin and mounted in DPX, all Stained in hematoxylin, dehydrated and mounted in Canada balsam. One half-mature individual, whole-mounted, 25 February 2012.

Type locality. La Borbolla, springs of the Cabra River, Cantabrian Mountains, Llanes, Asturias (Spain). Coordinates: 30T 4802519 N, 0367630 W, at about 100 m asl.

Etymology. The genus is dedicated to Steven V. Fend, in recognition of his important contribution to the knowledge of the family Lumbriculidae, and for the opportunity he gave to the author for establishing a fruitful collaboration in the study of the aquatic oligochaetes from the Nearctic region. The species name refers to the Cantabrian Mountains.

Description. Complete specimens up to 77 segments. Width of the body 240–500 µm at the clitellum. Prostomium short and rounded, 90–124 µm long, 200 µm wide at the base. Male pores paired, posterior to, and in line with ventral setae of segment X, in circular depressions 104–106 µm diameter (Figs. 1A; 2E). Spermathecal pores paired, 30 µm diameter, posterior to, and in line with ventral setae of segments XI and XII. One pair of female pores open ventrally, in 11/12 (Fig. 1B). Secondary annuli present from segment III to segment IX. Two chaetae per bundle, sigmoid, single-pointed (Fig. 2B). Anterior ventral chaetae (II to X) 60–123 µm long, shortest in segment II, and progressively longer up to VI; ventral chaetae in segment X usually somewhat shorter than those of adjacent segments (91–112 µm long). Dorsal chaetae in anterior segments 59–92 µm long, 0.6–0.9 times as long as the ventral ones of the same segment; shorter in II, and progressively longer up to VII. Posterior chaetae gradually shorter, down to 82–93 µm long. Ratio tip-nodulus/total length of chaetae = 0.35–0.42.

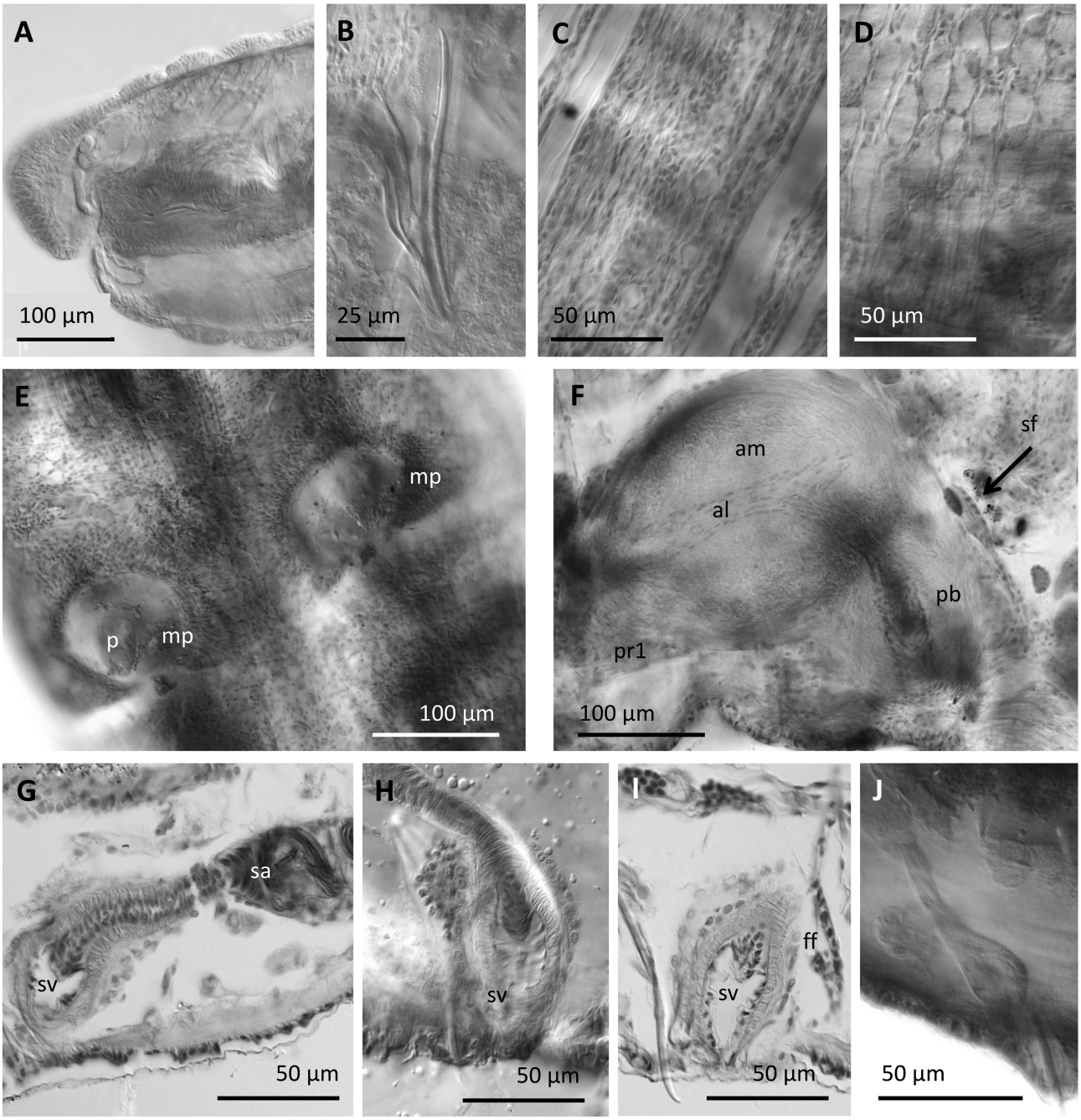

FIGURE 2. *Fendia cantabrica* **n. gen. n. sp.**, photographs from the type series. **A**–**F**, **H**, **J** specimens whole mounted or dissected; **G**, **I** histological sections. **A**. Pharynx and prostomium. **B**. Postclitellar chaeta. **C**. Epidermis in segment VIII. **D**. Epidermis in clitellum. **E**. Male pores and penes. **F**. Atrium. **G**. Second spermatheca. **H**. Spermathecal duct and vestibulum. **I**. Vestibulum in the first spermatheca and female funnel (composed by 2 photos). **J**. Nephridial efferent duct forming an ampulla before opening to the nephridiopore.

Body wall with epidermis 10–24 µm high and muscle layers up to 22 µm thick, measured in the anterior body section. Pharynx well developed dorsally and ventrally, to segment III (Fig. 2A). Clitellar epithelium weakly developed from X to XII (or to anterior part of XIII), but well distinguished from non-clitellar epithelium (Fig. 2C) and formed by squared glandular cells, ordered in lines (Fig. 2D). Pharyngeal glands present in segments (IV) V to VII (VIII). Chloragogen cells inconspicuous, beginning in segment VI. Blind posterior lateral blood vessels absent. Nephridia from 12/13, forming long tubes in the ventral side of the segments; the ectal efferent duct forms a small vesicle, observed only in a few segments, and the nephridiopores open just in front of the ventral bundle of

chaetae (Fig. 2J). Sperm sacs forward to segment (VIII) IX and backward to segment XI or XII. Egg sac backward to segment XIII.

Two pair testes, in IX and X, and one pair ovaries in XI. Two pairs of tiny sperm funnels are located on septa 9/10 and 10/11 (Figs. 1B, C; 2F). Vasa deferentia narrow (8–14 μm in diameter), barely visible in some cases. The posterior vas deferens does not penetrate the postatrial segment. Atria very large and heavily muscular, with both the duct and the ampulla covered by very thick musculature (35–100 μm) forming several crossing layers, the outer longitudinal (Figs. 1B, C; 3A, B). Both atria are always oriented in opposite directions, one forward and the other backwards, and the latter can cross into segment XI (Fig. 1B). The junction of the vas deferens to the atrium is not clearly seen due to the extraordinary thickness of the atrial musculature, but it appears to join through the base of the ampulla (Figs. 1B; 3E, F). Atrial ampullae 120–325 μm long, 106–198 μm wide, covered by a layer of one-cell thick peritoneal (?) cells, and two well-separated clusters of prostatic glands, each formed by several cells, joined to the atrial ampulla by a single stalk which crosses the atrial musculature through a well-defined, straight passage (5–7 μm diameter). Two prostatic passages are shown at opposite poles of the ampulla joining the two-branched atrial lumen (Figs. 1B, C; 2F; 3A, C). The lumen of the atrial ampulla (30–50 μm wide) is lined by a poorly defined layer of epithelial cells (Figs. 2F; 3C, D); in some individuals, there is sperm within the atrial lumen. Atrial duct very thick (127–162 μm long, 106–111 μm wide), forming a muscular penial bulb with outer longitudinal (to 22 μm thick) and inner circular (to 15 μm) layers of muscles (Figs. 1B, C; 3A, E–I). Large vacuoles in the penial epithelium (Fig. 3G, H), probably providing a hydrostatic skeleton. It is a "type-2 penis", as defined by Cook (1967) and Rodriguez & Giani (1994); it may protrude through the wide male pore to about 25 μm (Figs. 2E; 3F). A dense ring of gland cells, up to 27–80 μm high, surrounds the base of the atrial duct, around the male pore (Figs. 1B, C; 3A, E, F).

Spermathecae paired in segments XI and XII. They have sac-like, simple ampullae (first pair: 54–114 μm long, 38–72 μm wide; second pair: 55–111 μm long, 50–88 μm wide), and a narrow-duct (82–100 μm long, 11–23 μm diameter) that gets thinner toward the junction with the ampulla, and forms an ectal vestibulum (47–62 μm long, 38–43 μm wide, internal lumen 22 μm wide covered by a thin cuticle) (Figs. 1B; 2G–I). The spermathecal vestibulum and the duct are covered by circular muscles (to 12 μm thick), and an outer longitudinal muscle layer (ca. 5 μm thick) (Fig. 2H, I). Female funnels small, attached to the septum 11/12 (Fig. 2I).

Taxonomic remarks. The species was originally attributed to the genus *Dorydrilus* Piguet, since only the anterior vas deferens was visible in the first collection of 2008. New material found in the later collection made it possible to observe the tiny anterior and posterior sperm funnels, thus establishing the semiprosoporous male duct pattern of the species.

Fendia cantabrica **n. gen. n. sp.** shows a unique combination of the following characters: very thick atrial musculature organized in several cross-hatched layers, protrusible penis assisted by both muscular and vacuolar (hydrostatic) systems, and petiolate prostatic glands forming clusters joined to the atrium through two opposite passages. Only the two latter characters can be considered as apomorphies of the new genus relative to the family Lumbriculidae (see discussion, below).

Among the semiprosoporous lumbriculid species with spermathecae in the ovarian and postovarian segments, the presence of atrial musculature with muscle bundles organized in a crossing pattern, a long protrusible penis and prostatic cells in few clusters is also known in *Trichodrilus longipenis* Rodriguez & Giani, 1994 (Giani & Rodriguez 1994). That species presents a spherical atrium covered by a continuous layer of small prostatic cells and a few large clusters of prostatic glands attached to the atrium in a diffuse manner (not by common stalks). This species has a penis which also extends from the inner epithelial layer of the atrial duct through the male pore; however, there is not a vacuolar system in the penis nor glandular cells at the male pore.

Ecological remarks. *Fendia cantabrica* **n. gen. n. sp.** inhabits the unpolluted karst springs of the Cabra River, at La Borbolla and a small stream in the cave El Pindal. Those sites are only 9 km apart. Water characteristics and sediment particle distribution in the spring of the Cabra River were measured in only one occasion (7th July, 2008), showing pH= 7.4, 12.4 °C, > 97% dissolved oxygen, 296 μS cm^{-1}, 2.7% loss on ignition, and 1.6 % silt-clay in the < 1mm sediment fraction (Achurra 2012). The gut content included organic detritus and large sand grains.

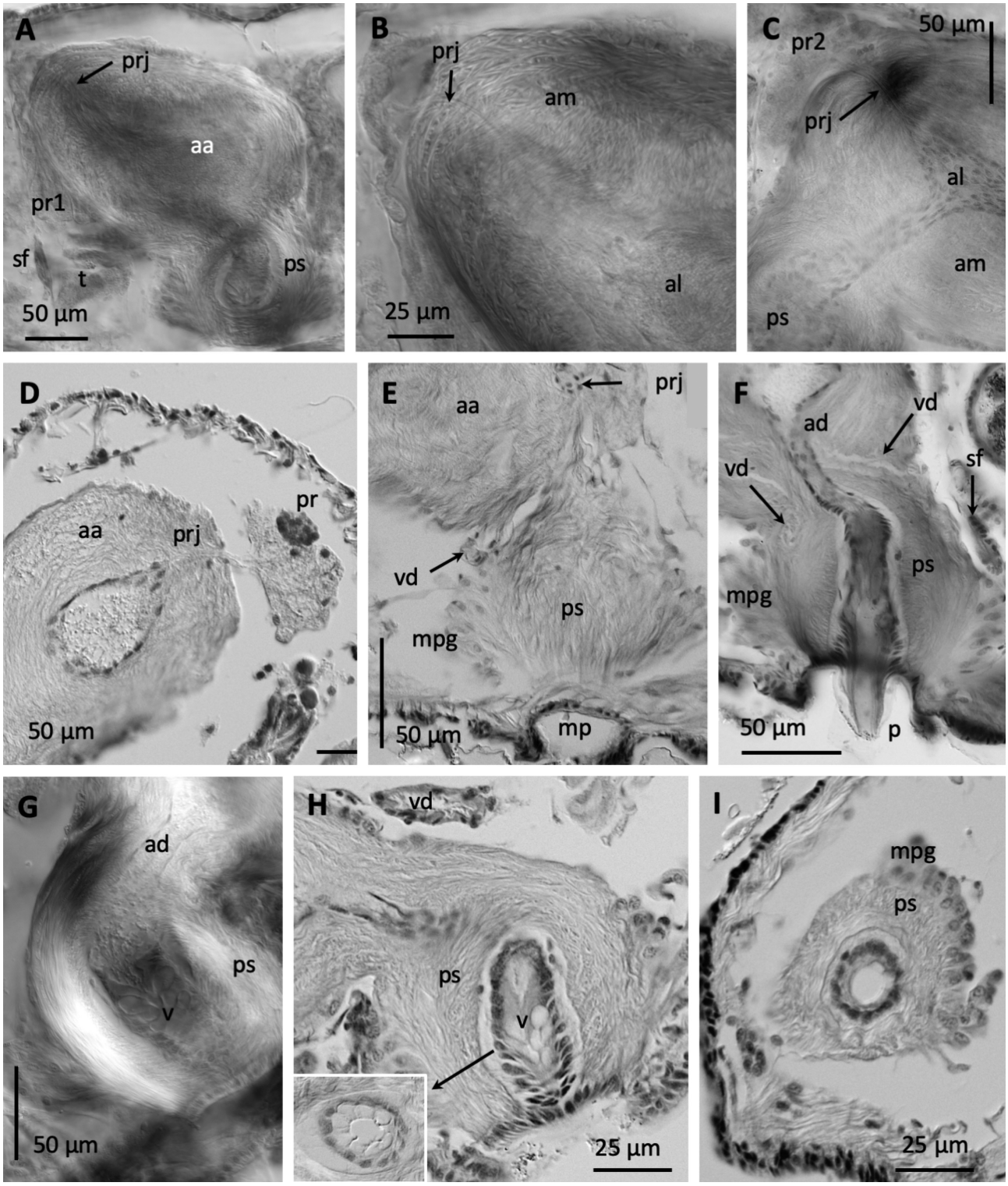

FIGURE 3. *Fendia cantabrica* **n. gen. n. sp.**, individuals of the type series; details of the atrium. **A**–**C**, specimens whole mounted or dissected and **D**–**F**, **H**, **I** histological sections. **A.** Atrium in holotype. **B**. A detail of the previous photograph, showing prostate junction to atrial ampulla and cross-hatched atrial muscles. **C**. Prostate junction to atrial ampulla and two-branched atrial lumen. D, transverse section of atrium showing the petiolate prostatic gland junction. **E**. Muscular penial bulb and gland cells at the male pore. **F**. Atrial duct, penial bulb and penis protruded through the male pore, posterior sperm funnel, and junction of vasa deferentia are also shown. **G**, **H**. Penis within penial bulb, showing the vacuoles at proximal end. **I**. Penis, transverse section of distal end.

Discussion

The semiprosoporous male duct pattern is the most common among the Palearctic lumbriculids, and this character together with the postatrial spermathecae beginning in the ovarian segment is shared by *Trichodrilus, Eremidrilus* and *Fendia* **n. gen.** Some species of *Lumbriculus* Grube also present a similar pattern for the reproductive system, although their assignation to that genus is usually based on well-differentiated characters (e.g. bifid chaetae, male pores on porophores, atrial musculature in two perpendicular layers, penis protrusible, and spermathecal pores in lateral to dorsal position). The presence of a proboscis in the prostomium of *Eremidrilus* is the main external anatomical character to separate this exclusively North American genus from the other two, but other characteristics of the reproductive system such as the common presence of male porophores and the club-shaped or elongate atrium are usually distinctive (Fend & Rodriguez 2003, 2020). The large genus *Trichodrilus* does not have well-defined apomorphies, and the semiprosoporous arrangement of the reproductive system may constitute a basal state in the phylogeny of the family (Brinkhurst 1989). In addition, the position of gonads in *Trichodrilus* is variable, as well as the structure of the male duct, e.g. atrium size and shape, atrial musculature simple or organized in crossed muscular layers, diffuse or clustered prostatic cell cover, and several penis types (see Rodriguez & Giani 1994; Giani & Rodriguez 1994). The peculiar arrangement of the prostatic cells and the male duct characteristics in *Fendia cantabrica* n. sp. are unknown in other lumbriculid genera and they are, therefore, regarded here as diagnostic features at genus level. Future molecular analysis will provide insight into the phylogenetic relationships with other lumbriculids.

Prostatic cells organized in clusters that are attached to the atrium by a single stalk seems to be a derived character in Lumbriculidae, which might improve the survival of spermatozoa. The secretion from the prostatic cells to a narrow atrial lumen, possibly better regulates the nutritional function and lubrication of the spermatozoa (Jamieson 1981) in an atrium devoid of a glandular internal epithelium. The reduction in the number of the prostatic glands and their position in the opposite ends of the antero-posterior axis of the atrium can also be partly related to the space limitation of the body cavity in a small worm with relatively large atria.

The Cantabrian region has proved to be a hotspot of biodiversity for groundwater oligochaetes (Achurra *et al.* 2015). Although there has also been a greater study effort focused on the subterranean fauna of this region, new lumbriculid taxa have yet to be discovered or described, as can be inferred from the species lists published elsewhere (i.e. Dole-Olivier *et al.* 2009, Achurra *et al.* 2015), where several undetermined species of the family Lumbriculidae are reported in the Cantabrian region, specially of the genus *Trichodrilus*.

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