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Oversized enchytraeids (Annelida, Clitellata): a comparative study, with a revised description of *Lumbricillus maximus* (Michaelsen)

Emilia Rota

Dipartimento di Biologia Evolutiva, Università di Siena, Italy

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Abstract

Syntypes of the circum-Antarctic *Lumbricillus maximus* (Michaelsen, 1888) are re-examined, and a giant *Fridericia* worm referable to *F. hegemon* (Vejdovský, 1878) sensu lato is described from Greece. Their anatomical features are compared to those of two other gigantic representatives of the Enchytraeidae: *Mesenchytraeus antaeus* Rota & Brinkhurst, 2000 and *Henlea yukonensis* Tynen & Coates, 1991, both Canadian. Besides disclosing the structural peculiarities of the four genera, the observed differences are shown to reflect specific adaptations to particular environments, as exemplified by certain traits of the chaetae and body wall. In all four species, the nephridial apparatus is well developed and distributed along the body. The scheme of the vascular system follows the basic pattern of the family, with neither blood supply to the nephridia nor intraepidermal capillary networks, in spite of the increased respiratory needs imposed by a larger body and greater muscular activity. This and other design constraints imply limitations with regard to the geographical and ecological distribution of giant species within this family.

Key words: giant Enchytraeidae, *Lumbricillus*, *Mesenchytraeus*, *Fridericia*, *Henlea*, *Grania*, design constraints, geographical distribution

Introduction

In the Enchytraeidae, adult body sizes range more widely than usually reported. The smallest species, most of which fall in the genus *Marionina* Michaelsen s.l., can be just 1 mm long and 0.1 mm wide (e.g., the Italian *M. eleonorae* Rota, 1995, measured alive and compressed under a cover-slip), whereas the absolute giants of the family (some north-western American representatives of *Mesenchytraeus* Eisen) can surpass that length by two orders of magnitude. Eisen (1904) described the Alaskan *Mesenchytraeus grandis* from a preserved specimen 170 mm long and 2.25 mm in diameter (behind the clitellum), and his second largest species from that region, *M. harrimani*, can exceed 60 × 2.5 mm. Another giant, *M. magnus* Altman, 1936 from the State of Washington, was reported to commonly attain 72 mm in length and 2 mm in diameter (Altman 1936). The most recent addition to these 'world records' is *M. antaeus* Rota & Brinkhurst, 2000, living in the temperate rainforest of Vancouver Island, Canada: preserved specimens reach 61 mm in length and 2.9 mm in uncompressed diameter at midbody, with up to 127 segments, the highest count ever scored in the family (Rota & Brinkhurst 2000).

No other genus contains species comparable in size to those giants, although relatively oversized worms have been described in *Henlea* Ude, with the record holder, the Canadian *H. yukonensis* Tynen & Coates, 1991, measuring up to 27 × 2.5 mm after fixation and 60 mm in length when alive and extended (Tynen et al. 1991). Within *Fridericia* Michaelsen, members of the European species *F. magna* Friend, 1899 and *F. gigantea* Dequal, 1912 can have up to 90–95 segments and attain lengths of 45–50 mm in vivo; their diameters, however, do not surpass 0.7–0.8 mm (Nielsen & Christensen

***Corresponding author:** Emilia Rota, Dipartimento di Biologia Evolutiva, Università di Siena, Via P. A. Mattioli 4, I-53100 Siena, Italy, e-mail: rota@unisi.it

1959). Among the marine enchytraeids, the longest species is the circum-Antarctic, littoral *Lumbricillus maximus* (Michaelsen, 1888), which measures up to 45 mm in length and over 1 mm in width.

Investigating such extraordinarily large worms can be very rewarding, because by combining dissection, sectioning and conventional light-microscopy one can easily discriminate structural details, commonly neglected, that are peculiar to the respective genera. I am indebted to Dr. Ralph O. Brinkhurst for involving me in such an experience with *M. antaeus* (see Rota & Brinkhurst 2000), which inspired me to extend these investigations to other enchytraeid lineages.

Besides contributing to a comparative anatomy of the family, these studies may help to establish whether species much larger than average have a different arrangement of the body systems than their smaller relatives. And if not, what types of habitats can support the physiological requirements of these giants, including their increased respiratory needs imposed by a larger body and greater muscular activity? Do these giants have a slower development and delayed maturation? Further development of this research theme should provide some answers to these and other questions.

In this paper, I present a revised description of *L. maximus* based on some of the original specimens collected on the shore of South Georgia Island in 1883 (Michaelsen 1888), and I describe a giant *Fridericia* worm, referable to *F. hegemon* (Vejdovský, 1878) s.l., collected by myself in Greece. The anatomy of the two species is discussed in comparison with that of *M. antaeus*, *H. yukonensis*, the Holarctic *H. nasuta* (Eisen, 1878), and the northeast Pacific *Enchytraeus pugetensis* Altman, 1931 (= *Lumbricillus annulatus* Eisen, 1904: Coates & Ellis 1981).

Material and methods

Six specimens in alcohol, labelled "*Lumbricillus maximus* (Mich.); Süd-Georgien; u. d. Steinen leg. (Cotype)", Oligochaeta 120, were borrowed from the Museo Regionale di Scienze Naturali di Torino (MZUT), Turin, Italy. All specimens were carefully investigated under a stereomicroscope. One adult was cut into 4 pieces, sectioned at 7 µm and stained with haematoxylin (sections showed no affinity for eosin). The two anterior pieces, comprising 17 and 19 segments, were sectioned longitudinally; the following two pieces, comprising 12 and 19 segments, were cut transversely.

An adult specimen of *Fridericia hegemon* (Vejdovský) s.l., from 2 km N of Paranesti (Nomos Drama, Greece), 41° 20′N, 24° 36′E, on the right bank of River Remasecerovas, at the confluence with a tributary stream, in the shadow of alders, oaks and fig trees, coarse sand on granite, 170 m a. s. l., 9 May 1990, was divided into 4 pieces, sectioned at 7 µm and stained with haematoxylin and eosin. The first two pieces (20 and 9 segments) and the tail (25 segments) were cut longitudinally. The remaining piece was cut transversely.

For comparative purposes, a specimen of *Henlea nasuta* (Eisen) from Villa Patrizia, Siena, Italy, collected by the author on 3 April 1995, was cut into two halves, sectioned transversely and longitudinally and prepared with the same methods as above. Sections of *Mesenchytraeus antaeus* Rota & Brinkhurst were borrowed from the Museo Civico di Zoologia di Roma (MCZR), Italy (Oligochaeta 0077, adult specimen, anterior 65 segments sectioned longitudinally; Oligochaeta 0078, subadult specimen, 103 segments, anterior 25 and posterior 22 segments sectioned transversely, midbody partly sectioned longitudinally).

Supplementary observations were carried out on material of *Enchytraeus pugetensis* Altman (= *Lumbricillus annulatus* Eisen) borrowed from the Burke Museum, Invertebrate Section, University of Washington, Seattle, which included two preserved whole worms from the syntype series, Sucia Island, 1918, T. Kincaid leg., and 20 microscope slides containing sections, organs, and a dissected whole worm. One of the preserved whole worms was divided into two pieces, sectioned longitudinally at 7 µm and stained with haematoxylin and eosin. Sections of unpublished material of *Grania* Southern from Sardinia (prepared and kindly loaned by Prof. Christer Erséus) were also utilized.

All photographs were taken with Ilford Pan F Plus using a Leitz Dialux microscope.

Abbreviations used in the figures

ag	accessory spermathecal glands
b	brain
c	chaetae
chl	chloragogen cells
cl	clitellar cells
cm	circular muscle fibres
co	coelomocytes
cu	cuticle
di	spermathecal diverticula
du	spermathecal ectal duct
dv	dorsal blood vessel
e	epidermis
ed	efferent duct of nephridium
eg	epidermal glands
fd	female duct
i	intestinal lumen
lm	parietal longitudinal muscle layer(s)
l_1	outer layer of longitudinal muscle fibres
l_2	inner layer of longitudinal muscle fibres

mu chaetal muscles
nc nerve cord
ne nephridium
np nephridial pore
ns nephrostome
os ovisac
p prostomium
pe somatopleura
pg pharyngeal glands
pp pharyngeal pad
sa spermathecal ampulla
sd sperm duct (vas deferens)
se septum
sf sperm funnel
si periintestinal blood sinus
to tongue-like organ
vv ventral blood vessel

Descriptions

Lumbricillus maximus (Michaelsen, 1888)

Pachydrilus maximus Michaelsen, 1888: 4–13, fig. 1a–e; Michaelsen (1889: 26).

Lumbricillus maximus, Michaelsen (1905: 10–11); Stephenson (1932: 252–254, fig. 6).

Anatomy: Colour of alcohol-preserved worms white-yellowish. Body cylindrical, posterior region nearly quadrangular in cross section. Fixed length of the largest syntype 34.5 mm, diameter at V 1.0 mm, at clitellum and midbody 1.1 mm. Prostomium rounded (Fig. 1A). Segments 62–68. Intersegmental furrows shallow. No secondary annulation visible. Epidermal gland cells (Figs 1B-D, 3B) numerous, large (25–28 µm), round to ovoid, scattered irregularly all over the body including the clitellar region, colourless in alcoholic specimens, staining deeply in haematoxylin. Clitellum not prominent, extending from posterior of XI to whole of XIII, interrupted ventrally between male pores; granular gland cells refringent, oval, 10–13 µm long, forming an irregular pattern. Three copulatory glands (bunches of epidermal gland cells projecting inwards to enclose nerve cord) midventral at chaetal level in XIV–XVI, the two anterior glands larger than that in XVI; glands adhering only to ventral and lateral sides of nerve cord.

Head pore a small oval slit at 0/1. Spermathecal pores in 4/5, aligned with lateral lines. Male pores as paired longitudinal slits in middle of XII, with protruding lateral lips (squared folds of body wall), aligned with ventral chaetal lines. Female pores in 12/13, as small circular hollows. Nephropores conspicuous all along body, located midway between anterior septum and ventral chaetal bundle (Fig. 1C).

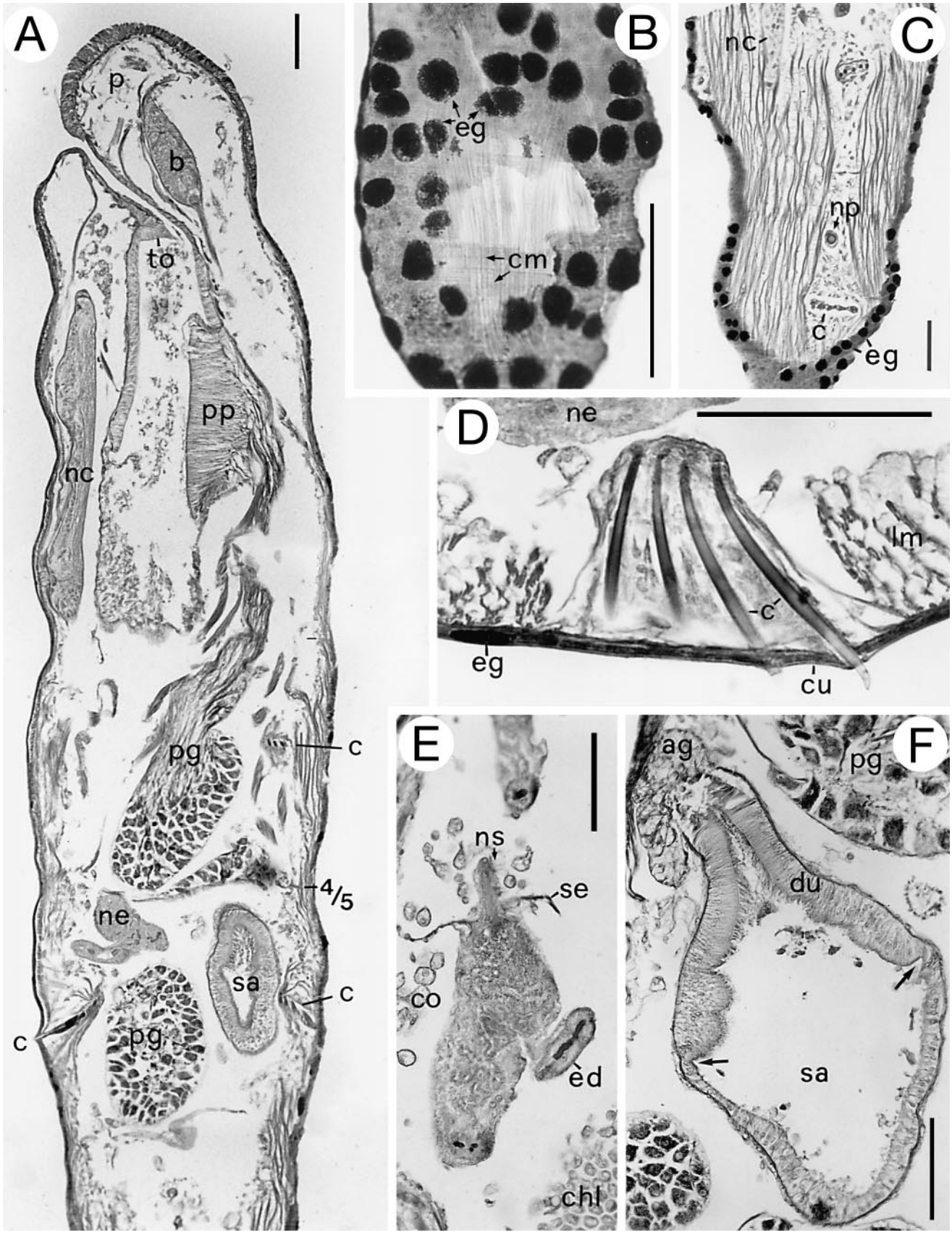
Chaetae (Fig. 1A,D) sigmoid, maximally 145 µm long (ventrally in X), 100 µm long caudally, slender, thickest just above shaft midpoint: 6–7.5 µm; arranged fanwise, 5–6 : 5–3 / 5–7 : 5–3; present (3 per bundle) dorsally in XII. Ectal tips generally pointing caudad, except for posteriormost segments where they project perpendicular to body wall. Around circumference of postclitellar segments (Fig. 2B), interval between the two dorsolateral bundles (DD) as great as that between two homolateral bundles (DV) and twice the distance between the two ventral bundles (VV), (DD = DV = 2VV).

No pigment in body wall. Cuticle (Fig. 1D) 0.8–1.2 µm thick. Epidermis 4–6 µm thick. Circular muscle fibres flattened, each 18–22 µm wide and 2 µm thick, together forming a virtually uninterrupted sheath around body circumference (Fig. 1B). Longitudinal muscles not broken up radially into distinct bands, but always thicker ventrally; comprising several layers of small fibres (each up to 12.5 µm high) arranged in a spike-like or feather-like manner (Figs 2B, 3B; Table 1). Epidermis of clitellum 15 µm thick dorsally, 12 µm ventrally; here total thickness of musculature only 20–28 µm. In postclitellar segments, total thickness of body wall 24–40 µm middorsally, 60–70 µm ventrally.

No thickened septa. A pair of postpharyngeal bulbs. Pharyngeal glands three pairs, at 4/5–6/7; lobes of the last pair bulging into VII, sometimes touching septum 7/8. Nephridia present in all segments from 3/4, namely including 9 preclitellar and one intraclitellar pair. Anteseptal portion 60 µm long, consisting solely of nephrostome; postseptal portion flat, elongate oval (320 µm long in postclitellar region), with posterior end giving off an even longer efferent duct directed anteriorly. Hindmost coils of canal in postseptal portion and efferent duct enlarged and stainable, even more so towards nephropore (Fig. 1A,C,E).

Coelomocytes (Fig. 1E) up to 38 µm long, with hyaline cytoplasm and granular periphery. Chloragogen cells (Figs 1E, 2B, 3B) cylindrical, up to 60 µm high, dense from VII, filled with finely granular material. Blood yellow-orange in alcoholic specimens. Dorsal vessel from XV, bifurcating beneath front of brain; for most of its course, stalked parietal cells are seen to hang from all sides towards its lumen. Four pairs of thin lateral commissures connecting dorsal vessel with circumoesophageal commissures and ventral vessel in III-V. Capillary vessels not detected in peripheral blood system.

Testes and ovaries poorly preserved in sectioned specimen, thus details of their structure were unobtainable. Sperm sac and egg sac unpaired, former arising from septum 11/12 and extending backwards within egg sac to XIII, latter arising from septum 12/13 and extending to XIV. Sperm funnels maximally 250 µm broad; ental ends (collars) flared, 360 µm in diameter. Sperm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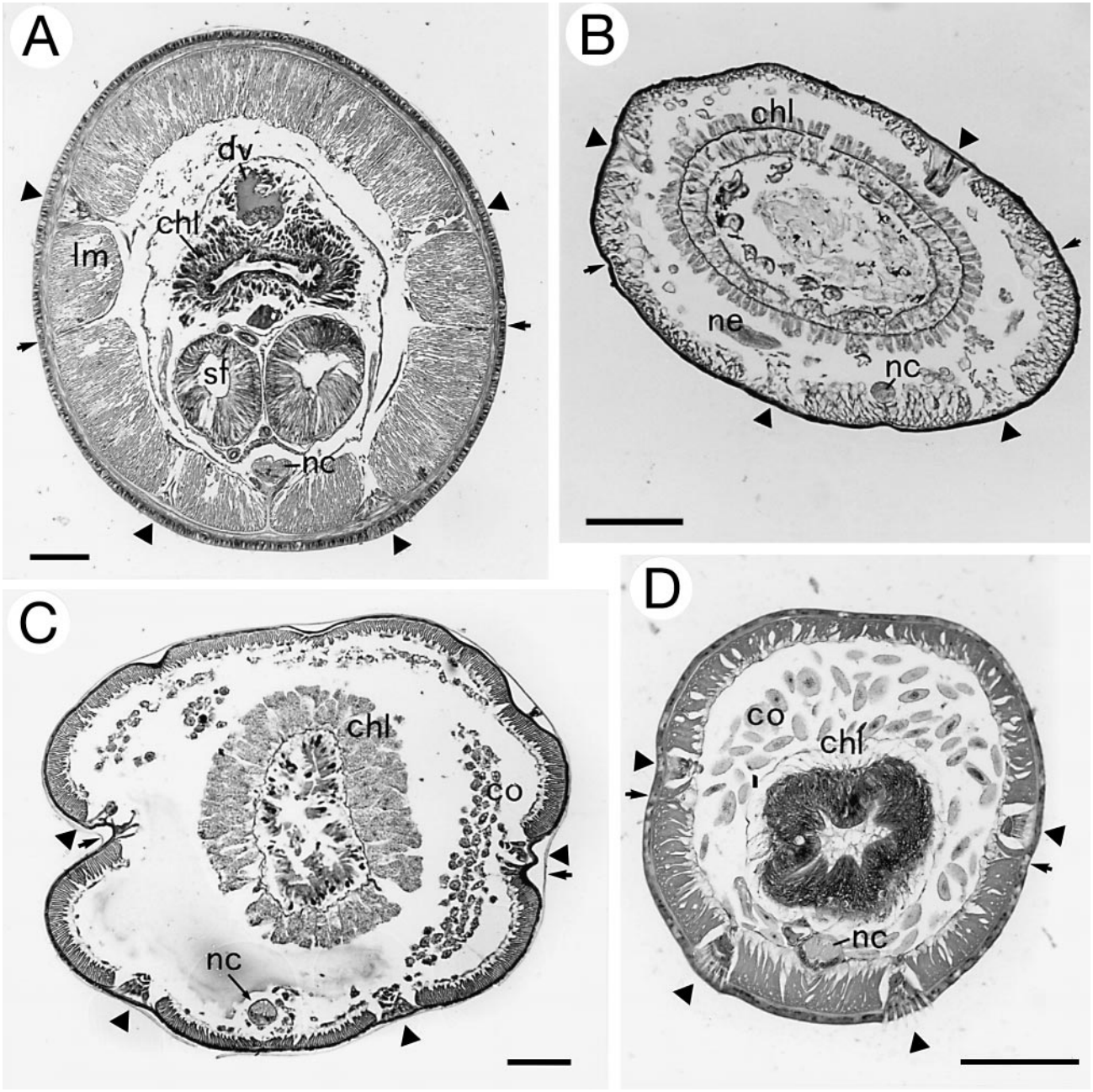


Fig. 2. Cross sections through the postclitellar regions of **A.** *Mesenchytraeus antaeus* Rota & Brinkhurst; **B.** *Lumbricillus maximus* (Michaelsen); **C.** *Fridericia hegemon* (Vejdovský) s.l.; **D.** *Henlea nasuta* (Eisen). Triangles indicate the arrangement of the four chaetal bundles around the body circumference. Note the high position of the dorsolateral bundles in *M. antaeus* and *L. maximus* and the midlateral position of these same bundles, just above the lateral lines (arrows), in *F. hegemon* and *H. nasuta*. In *H. nasuta*, the chloragogen tissue exhibits a typical 'empty' appearance behind the clitellum. All scale bars: 150 µm.

Fig. 1. *Lumbricillus maximus* (Michaelsen). **A.** Oblique longitudinal section through the anterior segments. The second anteriormost nephridium can be seen in the spermathecal segment (nephridia occur uninterruptedly from 3/4 to the last body segment). **B.** Tangential section of the body wall, showing the large epidermal gland cells. **C.** Shallow longitudinal section of the body wall (ventrolateral), showing size and positional relationships of chaetae, epidermal gland cells and nephridial pores. **D.** Left ventral chaetal bundle of XLVIII (cross section). **E.** Postclitellar nephridium. **F.** Longitudinal section through the spermatheca. Arrows indicate the boundary between the entally expanded ectal duct and the ampulla. All scale bars: 100 µm.

Table 1. Body wall construction in five large enchytraeids

Species Character	*Mesenchytraeus antaeus* Rota & Brinkhurst	*Lumbricillus maximus* (Michaelsen)	*Fridericia hegemon* (Vejdovský) s.l.	*Henlea yukonensis* Tynen & Coates	*Henlea nasuta* (Eisen)
Cuticle thickness	2–2.5 µm	0.8–1.2 µm	3 µm	11–11.5 µm	1 µm
Epidermis thickness	20–40 µm	4–6 µm	3–5 µm	*10–20 µm	7.5 µm
Circular muscles					
height of fibres	20 µm	2 µm	2.5 µm		2 µm
Longitudinal muscles					
total thickness	160–200 µm	25–50 µm	35–55 µm	*50–75 µm	35–45 µm
outermost fibres	triangular	triangular	flat cylindrical		triangular
height		2.5 µm	5 µm		
inner fibres	ribbon-shaped	ribbon-shaped	ribbon-shaped	ribbon-shaped	ribbon-shaped
arrangement	side by side, in many	spike-like or irregular echelons	palisade-like feather-like		irregular fringes
height	each max. 49 µm	each max. 12.5 µm	each max. 50 µm		each max. 40 µm

* Author's estimates from micrographs in Tynen et al. (1991).

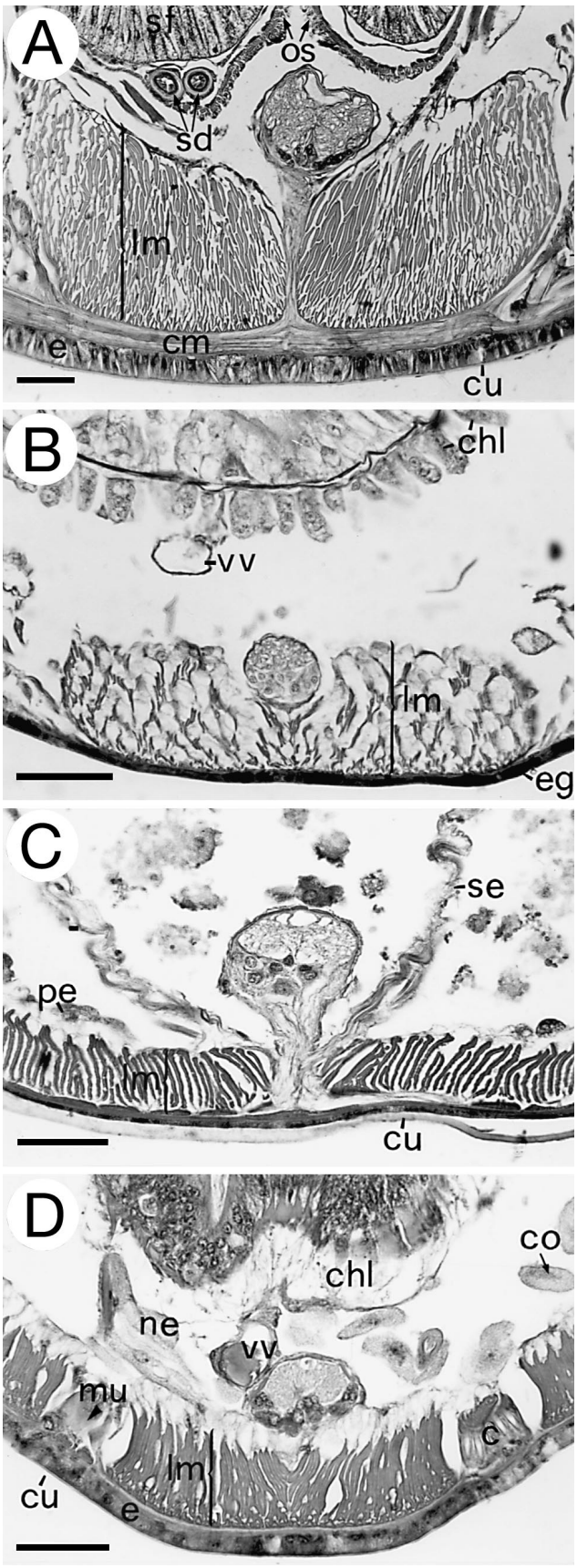
ducts 15–17 µm thick, extending backwards to XIV within egg sac. Each penial bulb with a 205–215 µm long glandular body, comprising two distinct layers of gland cells.

Spermathecae paired, connected to gut entally. Walls of ectal ducts consisting of tall (32–35 µm) columnar cells. Duct in its distal one-third (120 µm) cylindrical, 80–90 µm wide and with an inner canal of 10 µm, then duct and canal gradually expand to merge with a cup-shaped ampulla lined by a low (13–15 µm high), cubical epithelium. Ampulla 450 µm long, at its maximum width (300–350 µm) when joining ectal duct (Fig. 1F). Ampulla gradually narrowing entally into 75 µm wide, 175 µm long stalk which opens into oesophagus at 5/6. A rosette of fused ectal glands (Fig. 1F) associated with each spermatheca, this glandular structure being 125 µm high and 162 µm in diameter.

Taxonomic relationships: The new information concerning the structure of the chaetae, nephridia and spermathecae allows to better explore the taxonomic affinities of *L. maximus*. The size of this species is approached in the genus only by *L. reynoldsoni* Backlund, 1948. The two species also share the convex anterior end of the brain; however, *L. reynoldsoni* has straight, club-shaped chaetae and shows a completely different anatomy of the sperm funnels and spermathecae (Backlund 1948). Instead, the marked expansion of the spermathecal ectal ducts before their junction with the cup-shaped ampullae (which implies a sudden change in tallness of the inner epithelium where the spermatheca is approaching its maximum diameter) and their equipment with a basal crown of glands make *L. maximus* close to *L. macquariensis* Benham, 1905 (see Stephenson 1932) and *L. arenarius* (Michaelsen, 1889) (see Nielsen & Christensen 1959). It is also remarkable that all these three species possess an abundance of gland cells in the epidermis, and large and complex nephridia (see Stephenson 1932, Knöllner 1935), although similarities in the latter aspects may be related to the common euryhaline habits.

The high number and uninterrupted distribution of nephridia in *L. maximus*, with eight preclitellar pairs (3/4–10/11), two intraclitellar pairs (11/12, 12/13), and postclitellar pairs from 13/14 to the prepygidial segment, is a unique feature among enchytraeids (see also "Comparative remarks" below). Altman (1931) described his *E. pugetensis* (= *L. annulatus*) as having "nephridia, or organs that replace them, in all segments except the first few and possibly the last". However, my re-examination of part of the syntype series has shown that nephridia occur only at 7/8–9/10 and behind the clitellum.

Habitat and distribution: The Turin syntypes, like all original material, were collected in February 1883 near the German Station 1882–1883 at Royal Bay, South Georgia. The species was later also recorded from other sub-Antarctic islands (South Orkneys, Crozets, Kerguelen), as well as from the Palmer archipelago off the Antarctic Peninsula (Michaelsen 1905, Stephenson



1932). The habitat records include the algal debris and stones along the seashore and the banks of glacial streams (Michaelsen 1888, 1889). The species produces cocoons as large as 1.75 × 1.40 mm, each containing up to 33 eggs (Michaelsen 1905).

Fridericia hegemon (Vejdovský, 1878) sensu lato

Enchytraeus hegemon Vejdovský, 1878: 303; Vejdovský (1879: 60, pl. XI fig. 1, pl. XII figs 1–5).

Fridericia hegemon, Michaelsen (1889: 44); Cernosvitov (1937b: 199); Nielsen & Christensen (1959: 88–89, fig. 87).

Fridericia cf. *hegemon*, Rota (1994: 252–253, fig. 6A–C).

Anatomy: Live colour whitish-yellow, somewhat darker after storage in alcohol. Body cylindrical, tapering at both ends, broadest in mid and posterior regions. Fixed length 42 mm, diameter at V 1.3 mm, at clitellum 1.6 mm, at midbody 1.7 mm. Segments 68. Intersegmental furrows deep in anteclitellar region, shallow but clearly visible posterior to clitellum. Secondary furrows produce seven distinct annuli per segment; those of anteriormost segments arranged as three double annuli plus one simple. Clitellum annular, from 11/12 to chaetae of XIII, opaque but not elevated; gland cells polygonal, 8–20 µm across, arranged irregularly (Fig. 4B). Four copulatory glands midventral at chaetal level in XIII-XVI, the two central glands larger than those in XIII and XVI; all glands leaving dorsal surface of nerve cord free.

Dorsal pores from VII. Spermathecal pores in 4/5, aligned with lateral chaetal bundles. Male pores as Y-shaped slits, in middle of XII, aligned with ventral chaetae. Female pores in 12/13, as simple transverse slits anterior to ventral chaetae of XIII. Nephropores inconspicuous, located midway between anterior septum and ventral chaetal bundles.

Chaetae 4–6 : 4–2 / 4–6 : 6–2, those in the outer pairs with pronounced ental hooks. Ectal tips pointing caudad in anterior half of body, cephalad from segment XXV onwards. In fore- and midbody bundles, chaetae maximally 125 µm long; posteriormost segments with bundles of two chaetae, 150 µm long. Chaetal shafts at most 15 µm thick. Around circumference of postclitellar segments (Fig. 2C), interval between the two dorsolateral bundles (DD) 3.5 times both that between homolateral

Fig. 3. Cross sections through the midventral area of a postclitellar segment in **A.** *Mesenchytraeus antaeus* Rota & Brinkhurst; **B.** *Lumbricillus maximus* (Michaelsen); **C.** *Fridericia hegemon* (Vejdovský) s.l.; **D.** *Henlea nasuta* (Eisen), to show the difference in overall thickness and depth of the various layers. (Note that magnification is roughly the same for B, C and D). All scale bars: 50 µm.

bundles (DV) and that between the two ventral bundles (VV) (0.28DD = DV = VV).

No pigment in body wall. Total thickness of latter 50–60 µm in VI, 70–80 µm in XII, 60–70 µm in XX. Cuticle (Figs 3C, 4A,C) about 3 µm thick. Epidermis 3–5 µm thick. Circular muscle fibres flattened, each 25–28 µm wide, at most 2.5 µm thick, together forming an almost uninterrupted sheath around body circumference (Fig. 4B-D). Longitudinal muscles not broken up radially into distinct bands; comprising an outer layer of flattened cylindrical fibres (each 30 µm wide and 5 µm thick) constituting a sheath perpendicular to the circular muscles (Fig. 4A,B), and an inner layer of tall ribbon-shaped fibres, each up to 50 µm high (Figs 3C, 4A). Epidermis of clitellum as much as 53 µm thick dorsally, 35 µm ventrally; here total thickness of longitudinal muscle layers (Fig. 4B) only 25 µm.

Septa 4/5–6/7 moderately thickened, 7/8 and 8/9 strongly muscularized.

Peptonephridia of type *c* (sensu Nielsen & Christensen 1959), giving off many thin branches in V. Pharyngeal glands four pairs, at 4/5–7/8, the two halves of last pair not merging dorsally and at no point contiguous to septum (Fig. 5A).

Five pairs of preclitellar nephridia (6/7–10/11). Next nephridia from 13/14. In segments behind clitellum, anteseptal portion 210–225 µm long, postseptal about 400 µm long. Efferent ducts always arising anteroventrally and without terminal expansions.

Coelomocytes: nucleated cells rounded, up to 40 µm wide, with granular cytoplasm (Fig. 2C); anucleated corpuscles small (5 µm), round or slightly oval. Chloragogen cells tall (up to 110 µm), club-shaped, attached to gut wall by narrow stalks (Fig. 2C), filled with refractile orange granules (latter maximally 3 µm in diameter). Gut wall poorly preserved in segments immediately behind clitellum, to the point that neither origin of dorsal vessel nor chylus cells could be recognized. Dorsal vessel bifurcating beneath front of brain; circumoesophageal commissures first projecting forward in a characteristic 'Y' pattern, then turning backwards to merge ventrally in IV. Four pairs of thin lateral commissures connect dorsal vessel with circumoesophageal commissures and ventral vessel: one pair in III (above the pharynx), two in IV and one in V, with latter running over spermathecal ampullae. No capillary vessels in peripheral blood system.

Testes in XI, attached ventrolaterally to posterior side of 10/11 around point where nephridia cross the

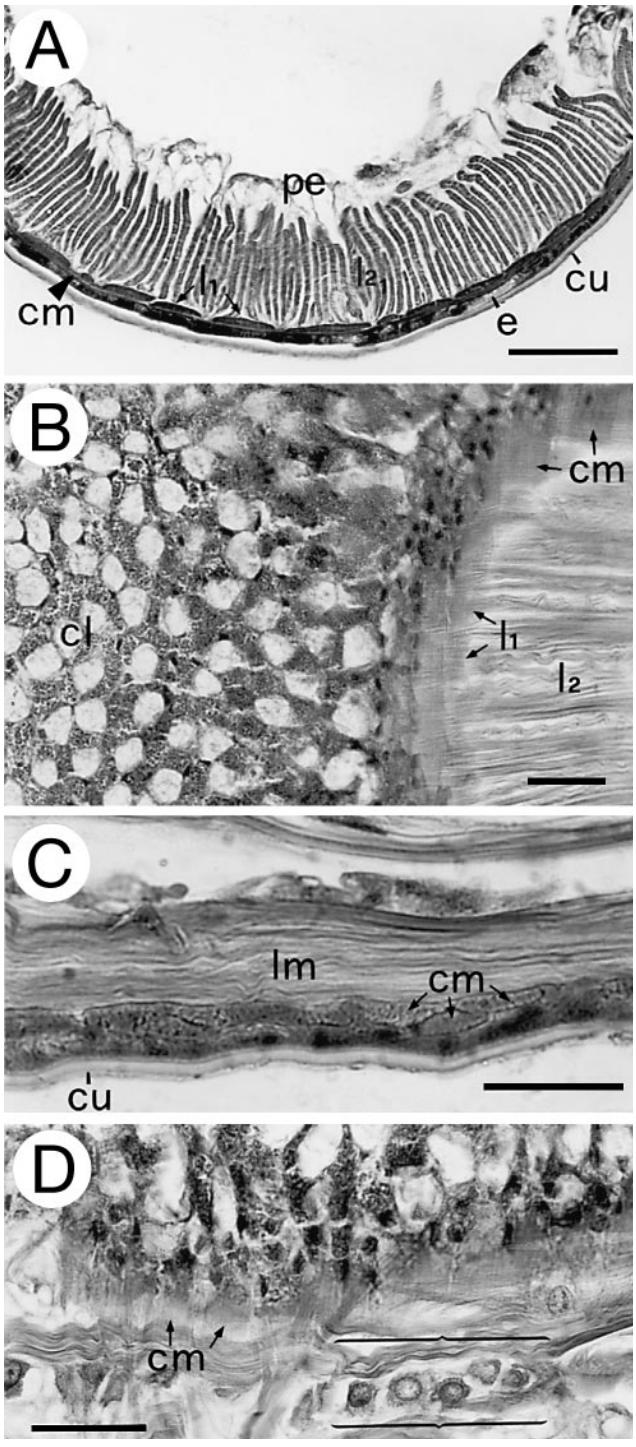


Fig. 4. Body wall organization in *Fridericia hegemon* (Vejdovský) s.l. **A.** Cross section through the ventrolateral aspect, showing the layering of the longitudinal muscles typical of the genus; **B.** Tangential section at the level of the clitellum showing the flattened fibres of the outer longitudinal layer (l_1) and the circular muscle fibres forming two adjacent (perpendicular), almost uninterrupted sheaths around the body circumference; **C.** Sagittal section through an anterior segment, showing some overlapping of the circular fibres; **D.** Tangential section of the clitellar region showing the circular muscle layer and the nuclei of the lateral line (marked off by double brackets). All scale bars: 50 µm.

septum; ovaries occupying a similar position of 11/12, close to where sperm funnels join sperm ducts and penetrate septum. Seminal vesicles paired, extending backwards within ovisac to XIII. Sperm funnels maximally 450 µm broad, confined to XI. Ental ends (collars) 300 µm broad, 37 µm high. Sperm ducts 15–17 µm thick, irregularly coiled, confined to anterior of XII. Each penial bulb with a 330 µm long glandular body. Ovisac unpaired, arising from septum 12/13 and extending to XIV.

Spermathecae paired, connected to gut entally. Ectal ducts 700 µm long and 50–60 µm thick, each with a coat of 20 longitudinal (spiral) muscle bands; duct canal 8 µm wide. At junction with ampulla, each duct expands into a cuticle-lined disk, 120 µm wide and 35 µm thick. Between this region and the elongate (320 µm) ampulla, a 280–300 µm wide crown of about 20 peripheral diverticula intervenes (Fig. 5B). Epithelium lining diverticula thin (12–20 µm), whereas epithelial cells lining ampulla down to junction with oesophagus are tall, about 50 µm, and have basal nuclei. At least two muscle fibres, each 6 µm thick, surround and constrict ampulla at one fourth of its length, giving it the shape of an amphora. No glands associated with spermathecae.

Taxonomic relationships: Although comprising only 68 segments, the body of this *Fridericia* has the largest proportions ever recorded for the genus. Segment number, multi-diverticulate spermathecae and multi-branched peptonephridia make this worm referable to *F. hegemon* (Vejdovský) s.l., a taxon (probably a species group) of which several different accounts exist in the literature. By combining an irregular arrangement of the clitellar glands, hooked chaetae numbering up to 6 in preclitellar and up to 4 in postclitellar dorsal bundles, four pairs of pharyngeal glands, the lack of spermathecal ectal glands, nephridial efferent ducts arising anteriorly in all body regions, and the possession of four copulatory glands (midventrally at chaetal level in XIII–XVI), the Greek worm differs from both Vejdovský's (1878) and Nielsen & Christensen's (1959) descriptions, based on Bohemian and Danish material, respectively. Chaetal numbers and clitellar pattern are more consistent with those of Bulgarian worms (see Cernosvitov 1937b). Material from Turkey that I tentatively referred to *F. hegemon* (see Rota 1994) was also aberrant, in having an extra pair of pharyngeal glands at 7/8 and the spermathecal diverticula arranged in a single peripheral ring. These worms had as many as five copulatory glands, lo-

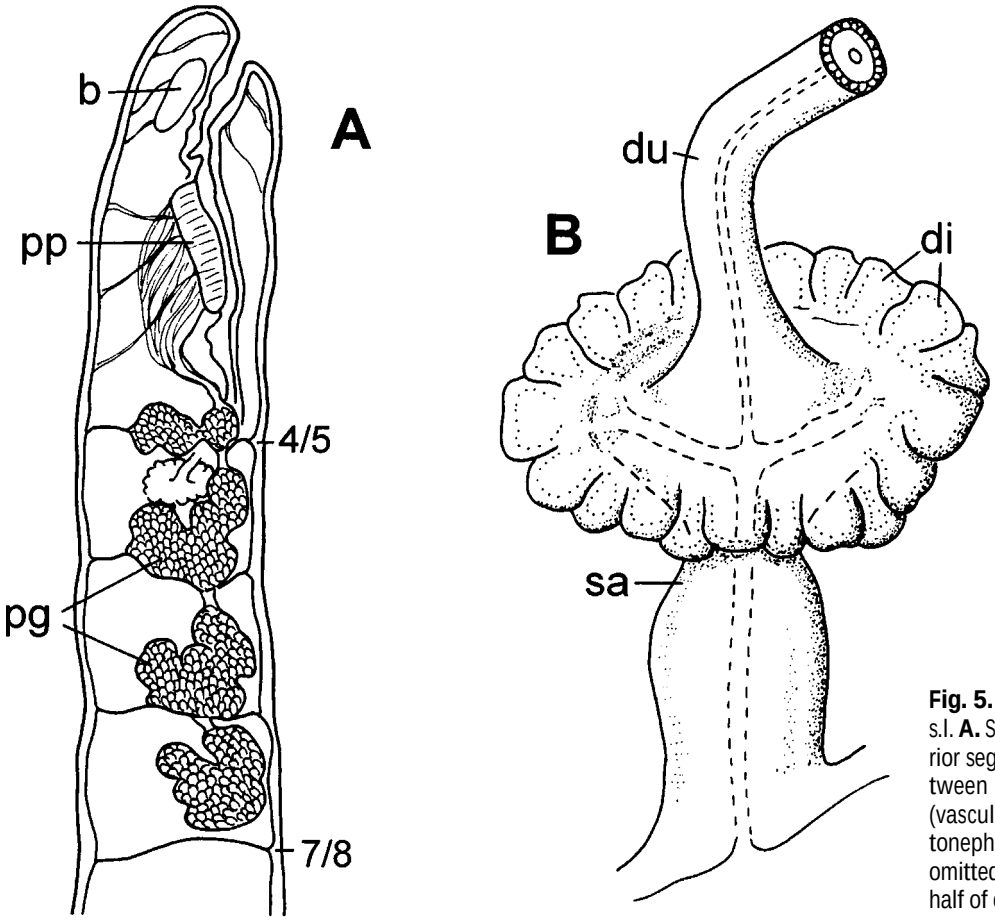


Fig. 5. *Fridericia hegemon* (Vejdovský) s.l. **A.** Schematic lateral view of the anterior segments, showing relationships between pharyngeal glands and septa (vascular apparatus, nerve cord, peptonephridia, oesophagus, and nephridia omitted); **B.** Spermatheca (only proximal half of ectal duct shown).

cated in the posterior of XI, the anterior of XII, and in the middle of XIV, XV and XVI.

Habitat and distribution: This taxon is found in northern and central Europe under a range of moisture conditions (Graefe & Schmelz 1999). In Greece and in Turkey, it appears confined to the northernmost zones, in habitats where moisture is available throughout the year, like the river banks of Aegean Macedonia (present material) and the moderately cool and humid forests around the Ulu Dag massif (Rota 1994). It had never been reported from Greece before.

Comparative remarks

Chaetae

Cross sections through the postclitellar regions of *M. antaeus*, *L. maximus*, *F. hegemon* s.l. and *H. nasuta* (Fig. 2A–D) reveal different arrangements of their chaetal bundles around the body circumference. The dorsolateral bundles occupy a high position in *L. maximus* and *M. antaeus*, whereas they lie midlaterally, just above the "lateral lines", in *F. hegemon* s.l. and *H. nasuta*. (The lateral lines are longitudinal interruptions of the parietal musculature along the sides of the body, where the lateral nerves meet the peripheral nerves in each segment forming a series of small ganglia; Beklemishev 1969: 105). From a preliminary screening, it appears that these different arrangements are characteristic of the respective genera. The more dorsal position of the upper bundles in *Lumbricillus* and *Mesenchytraeus* recalls the condition in the limicolous microdrile families (Lumbriculidae, Tubificidae, Naididae and Alluroididae; Cekanovskaja 1962: figs 13, 210, 220; Jamieson 1968), as well as that of the primarily aquatic megadriles (*Alma* Grube, *Criodrilus* Hoffmeister, etc.; Omodeo 2000), which also have a quadrangular outline of the mid and posterior body regions. A symmetrical cross-sectional profile of the body is probably better adapted for life in loose, water-saturated, organic-rich substrates, as it is also found in *Eiseniella* Michaelsen, a secondarily aquatic lumbricid genus.

If the shape and number of the chaetae reflect a phylogenetic pattern, their relative size may denote adaptations to locomotion on substrates of different texture and compactness, with taxa crawling in terrestrial habitats, or progressing through coarse sandy bottoms, requiring heavier chaetae than those living among algae or in soft mud. In the terrestrial *F. hegemon* s.l., the anterior and midbody chaetae reach 125 µm in length, while those in the posteriormost segments reach 150 µm; their shafts can be up to 15 µm thick. In the marine littoral *L. maximus*, chaetae (Fig. 1D) are also relatively long (up to 145 µm), but more slender (6–7.5 µm). In *H. yukonensis*, Tynen et al. (1991) observed that chaetae were reduced in number and distribution along the body but that the larger (located posteriorly) attained lengths of 240 µm; the posterior ventral bundle shown in their fig. 8 contained chaetae up to 25 µm thick. The chaetae of *M. antaeus* are numerous (up to 8 per bundle) and very large (up to 400 µm long and 33 µm thick) (Rota & Brinkhurst 2000). Nothing is known of the habitat of this species, but the stout chaetae and the thick parietal musculature may be important simply to enable movement in such a large worm, which apparently is even capable of climbing above the ground surface (Rota & Brinkhurst 2000).

Body wall

Cuticle: The thickness of the cuticle differs remarkably between the species considered in this study. The cuticle of *H. yukonensis* is 11–11.5 µm thick, 'many-layered', with 7 or more laminae visible (Tynen et al. 1991); Smith et al. (1990) suggested it may serve as protection from abrasion by ice crystals in the soil when burrowing. A similar thickness is reported for the cuticle of the nearly as large *H. udei* (Eisen, 1904) from Alaska (10 µm; Tynen et al. 1991). In *H. nasuta*, the cuticle is only 1 µm thick (Fig. 3D), and smaller species in the genus have been described, in which this layer of the body wall is barely discernible (Altman 1936). The giant *F. hegemon* s.l. has a relatively thick cuticle, but not as thick as reported for smaller *Fridericia* species (e.g., 5 µm in *F. pyrenaica* Giani, 1979; Schmelz et al. 1999). Indeed, in the enchytraeids the thickness of the body wall cuticle is not always proportional to the worm's size, but appears better correlated to the type of habitat, with thicker cuticles being encountered more often in arid environments, probably protecting against water loss. Richards (1977) investigated this and other epidermal features in small terrestrial species of *Fridericia* and *Mesenchytraeus* and in a range of body sizes of littoral *Lumbricillus* (from the small *L. georgiensis* Tynen, 1969, *L. mirabilis* Tynen, 1969 and *L. vancouverensis* Tynen, 1969 to the large *L. reynoldsoni*). She found that the small terrestrial species had cuticles nearly as thick as that of a much larger lumbricid, the thickness being achieved either by an increased number of relatively thin collagen fibres *(Mesenchytraeus)* or by fewer layers of thicker collagen fibres *(Fridericia)*. In *Lumbricillus*, regardless of size, cuticles showed large numbers of small diameter fibres and were consistently thin (indeed, in none of the TEM micrographs shown, including that for *L. reynoldsoni*, were they more than 1.5 µm thick). If a thin cuticle is a characteristic feature of *Lumbricillus*, it should not be unexpected to find it even in stout species like *L. reynoldsoni* and *L. maximus*. Although living in a moisture-saturated environment, terrestrial giants like *M. antaeus* are certainly subject to

high mechanical stress, and thus a cuticle thickness of only 2–2.5 µm (representing just 1/100 of the total body wall; Fig. 3A) was unexpected (Rota & Brinkhurst 2000). Other giant *Mesenchytraeus* do not have a more prominent cuticle (Altman 1936), even though in them, as in *M. antaeus*, the powerful parietal musculature must lead to high values of internal pressure during locomotion. It is likely that *M. antaeus* and allied species manage to counteract such pressures by relying on a fairly abundant extracellular matrix located beneath the epidermis and among the muscle fibres.

Circular muscles: In *Fridericia*, *Lumbricillus*, *Henlea* and *Mesenchytraeus*, the circular muscles of the body wall are formed by flattened fibres lying more or less contiguous to one another, or even imbricated (*F. hegemon* s.l.; Fig. 4C), so as to form a continuous sheath. Interestingly, all the above genera differ in this respect from the marine infaunal *Grania*, whose circular musculature is weak and not compactly arranged (pers. obs.). Figure 6 shows the body wall of undescribed *Grania* material from Sardinia, with circular muscles formed by isolated cylindrical fibres, each only 1.5–2 µm thick and separated by gaps of up to 8 µm; the underlying longitudinal muscle fibres form instead a dense fence-like layer. Indeed, *Grania*'s locomotion is accomplished more by serpentine sliding than by extension and contraction of the body (Giere & Pfannkuche 1982). In that genus, thickened septa suggesting a peristaltic burrowing activity have been described so far only in the Tasmanian *G. dolichura* Rota & Erséus, 2000.

Longitudinal muscles: Variation in the composition of the longitudinal body wall musculature of enchytraeids has been known for a long time (Michaelsen 1889; Hesse 1894; Cernosvitov 1930, 1934, 1937a, b). Early authors focused attention on the double nature of the longitudinal fibres characterizing some genera (*Fridericia*, *Achaeta* Vejdovský, *Hemienchytraeus* Cernosvitov, *Guaranidrilus* Cernosvitov, *Enchytraeus* Henle, *Stephensoniella* Cernosvitov), where an outer layer of 'tubular' fibres (round, squared, or triangular in cross section) overlies an inner layer of flattened, 'ribbon-like' fibres. Only the latter would be equivalent to the fibres observed in the other genera (Michaelsen 1889: 42). The giant specimen of *F. hegemon* s.l. described herein shows the typical layering of the longitudinal muscles of *Fridericia* (Figs 3C, 4A,B), with a cross-sectional palisade of high ribbon-like inner fibres standing edgewise at right angle to the outer tubular fibres. Thus, in this worm a thickening of the longitudinal muscles is achieved by increasing the tallness of the inner fibres rather than their number. The tubular fibres of the outer longitudinal layer appear depressed and form with the circular muscle fibres two adjacent, perpendicular and almost uninterrupted coats around the body circumference. The stiff movements of *Fridericia* when compared to other enchytraeids of the same size have been attributed to the thicker collagen fibres contained in the cuticle (Richards 1977), but they may also be determined by the more restraining arrangement of the muscle fibres in the body wall. On the contrary, the multiple layering of narrow elements both in the cuticle and the parietal muscu-

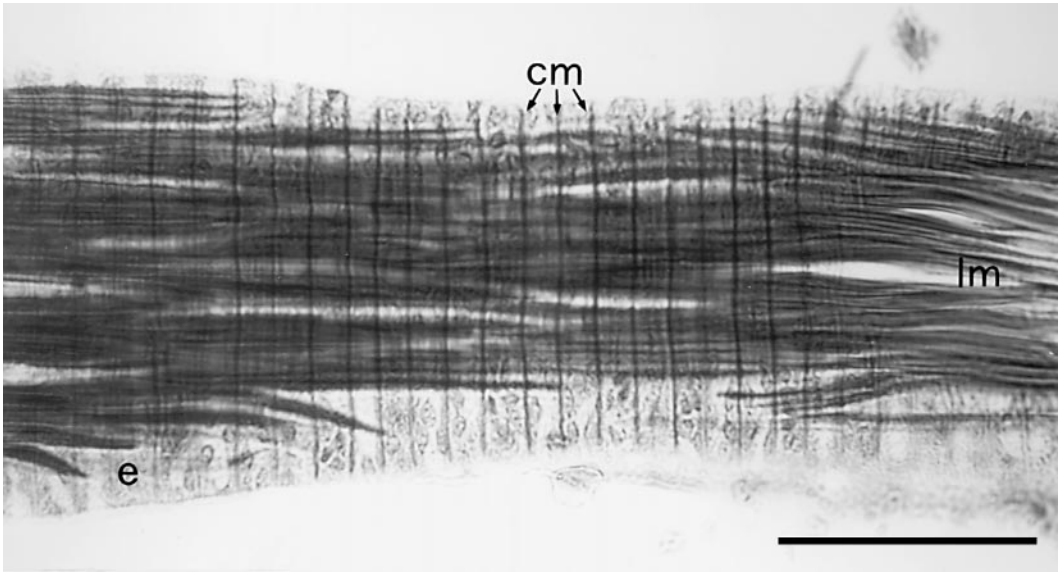


Fig. 6. Tangential section through the body wall in *Grania* Southern (material from Sardinia, unpublished), showing the widely spaced arrangement of the circular muscle fibres. Scale bar: 50 µm.

lature of *Mesenchytraeus* and *Lumbricillus* (Fig. 3A,B) concur to give these taxa a higher body flexibility than other enchytraeid genera.

Excretory and vascular systems

In *F. hegemon* s.l., *M. antaeus* and *H. yukonensis*, the distribution of nephridia follows the pattern seen in the majority of adult Enchytraeidae, with the first pair located at 6/7 (or 7/8) and nephridia absent from the genital segments. In fact, nephridia are first developed in the genital segments of immature enchytraeids, as of other microdriles, but disappear once the genital ducts start developing (Vejdovský 1884, pers. obs.). In enchytraeid species with bulky seminal vesicles, the last preclitellar nephridia (at 10/11) tend to be lacking (see Rota 1995), and the prominence of some reproductive organs (e.g., gonads, seminal vesicles, sperm funnels, male terminalia) filling the coelom of the clitellar region at full maturity may indeed be the main reason for the local nephridia to undergo regression. As noted above for *F. hegemon* s.l., testes are attached ventrolaterally to the posterior side of 10/11 exactly around the point where nephridia cross the septum. Considering the great development of the internal reproductive structures in *L. maximus*, the extended distribution of its nephridia appears all the more unusual: paired organs occur uninterruptedly from 3/4, clitellar region included; clitellar nephridia appear functional and have, like all others, prominent terminal ducts. Such a conservative development of the excretory apparatus probably reflects increased regulatory abilities required for a littoral Antarctic worm to be able to cope with a range of salinity changes determined by ice formation and melting and freshwater run-off from the land (White 1984).

In all four species, the scheme of the blood vascular system follows the basic pattern of the family, with neither blood supply to the nephridia nor parietal capillary networks, in spite of the increased respiratory needs imposed by a larger body and greater muscular activity. It is important to note here that the sole case of vascularization of the body wall reported in the Enchytraeidae, *E. pugetensis* (= *L. annulatus*) [„the hypodermis contains many blood vessels which are of value in respiration“ (Altman 1931)], has not found confirmation in my scrutiny of the type material. In *M. antaeus*, from XII-XIII to XVII, the ventral blood vessel runs within the ovisac, compressed beneath the sperm sacs: in this tract the walls of the vessel appear very stout (the longitudinal myofibrils measure 4–6 µm across).

Female pores

Sections of the clitellar region in *M. antaeus, L. maximus and F. hegemon* s.l. show the female openings to continue on the inner side as funnel-shaped invaginations of septum 12/13. This is the typical situation in the majority of enchytraeids, but in *H. nasuta* some kind of

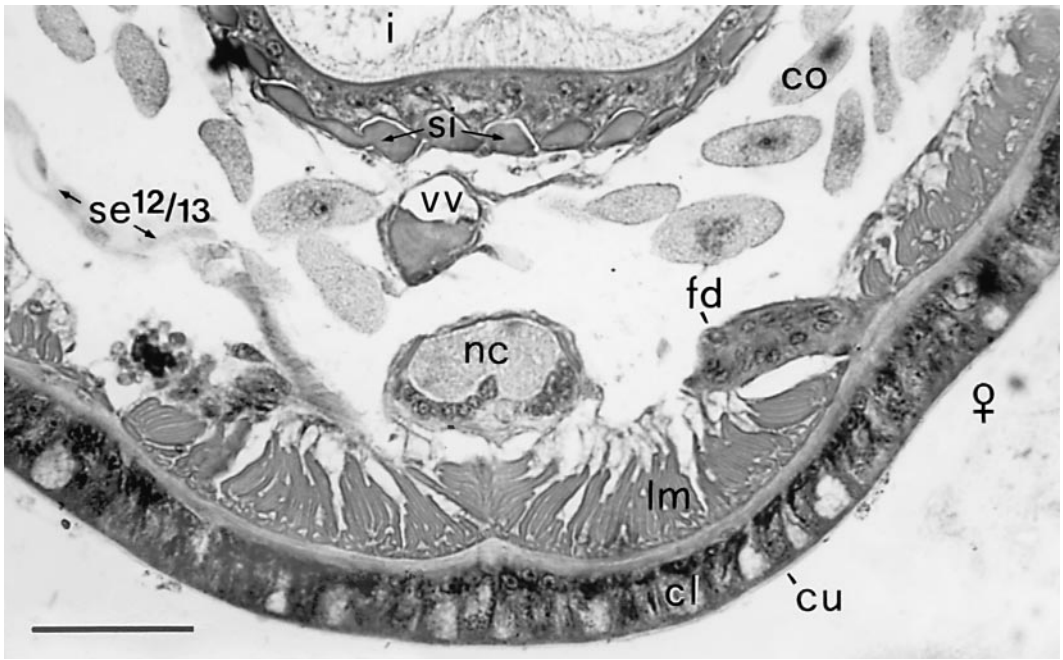


Fig. 7. *Henlea nasuta* (Eisen). Cross section (slightly oblique) of the clitellar region at the level of female pores. A female duct is seen on each side in the posterior of XII, adjacent to septum 12/13. Note the reduced thickness of the body wall muscles. Scale bar: 50 µm.

'female ducts' are seen in the posterior of XII, adjacent to septum 12/13 (Fig. 7), as also reported for *H. yukonensis* by Tynen et al. (1991).

Design constraints and ecological implications

At this stage of knowledge, it is difficult to suggest any specific selective pressure promoting enchytraeid gigantism. It is perhaps more fruitful to regard the giant species as the surviving plus-variants in a size range experienced by the respective lineages in times and places of favourable climate and food supplies.

In the oligochaetes, the body surface, or parts of it, serves as the site of gas exchange. The inner side of the body wall is often vascularized; the degree of vascularization generally varies in parallel with the thickness of the body wall (Weber 1978). In many aquatic microdriles, the parietal vessels (consisting of dorso-ventral segmental loops or a proper vascular network) are simply applied to the body wall, but in taxa where the body wall is of any considerable thickness, like in some mud-dwelling worms or in earthworms, capillary blood vessels ramify within the body wall and, in some species, penetrate between the epidermal cells so that they lie very close to the inner surface of the cuticle (Stephenson 1930, Lee 1985). In the Enchytraeidae, and the giant species are no exceptions, no parietal vessels occur behind the few paired commissures which join the dorsal and ventral vessels in the anterior segments (Stephenson 1930, see also Rota & Erséus 2000), and no capillary network has ever been ascertained in the body wall. Such a simple, invariable scheme of peripheral circulation is indeed surprising, especially when it holds for thick-walled, bulky worms like *M. antaeus*, too. Enchytraeids living in fine sediments or other poorly aerated freshwater or marine habitats enhance their respiratory exchange by an increased amount of haemoglobin in the blood (Healy & Bolger 1984, Rota & Erséus 2000), but the majority of species in the family invariably have colourless or faintly pigmented blood and prove incapable of surviving but in oxygenated substrata. The lack of a parietal vascularization in the giant species indicates two possibilities: they can perform an efficient cutaneous respiration due to an enhanced permeability of the body wall, and/or they take advantage of high oxygen tensions in their habitats. Recent studies have emphasized the importance of high oxygen availability for both terrestrial and aquatic diffusion-dependent invertebrates to overcome critical upper thresholds of body size (Graham et al. 1995, Chapelle & Peck 1999).

Indeed, *H. yukonensis* and *L. maximus* occur at latitudes where oxygen availability must rarely, if ever, become a limiting factor, while moisture and food can be abundant. The former species lives in forested and tundra sites just above the Arctic circle, within cold, moist soils characterized by thick surface accumulations of well humified organic matter (Smith et al. 1990). *Lumbricillus maximus* inhabits the seashores and glacial streams of sub-Antarctic islands, between 50°S and the Antarctic circle, where, in the absence of anthropogenic disturbances, reducing conditions are certainly uncommon; furthermore, in the summer, a decrease of seawater salinity caused by melting ice contributes to sustained high oxygen concentrations at the sediment surface (see White 1984; Dayton 1990). All giant *Mesenchytraeus* spp. are restricted to the west coast of North America, an area which, particularly where the lush temperate rainforest ecosystems persist, enjoys cool temperatures and abundant moisture in all seasons. Considering *M. antaeus*' ability to climb (Rota & Brinkhurst 2000), its respiration could be further improved by exposing the body surface to above ground oxygen levels. *Mesenchytraeus magnus* was "collected in great numbers in black humus at Martha Lake, near Seattle; from the same kind of soil at Shelton, Washington; and from the lower estuary of the Naselle River" (Altman 1936). In central Europe, *F. hegemon* is classified by Graefe & Schmelz (1999) as a dweller of the Ah (soil) horizon, with mull as the preferred humus form, but indifferent to moisture. Indeed, the habitat records for *F. hegemon* s.l. at lower latitudes (Rota 1994 and present material) indicate a preference for fresh damp soils.

In conclusion, it may well be that, owing to their respiratory requirements and other constraints, giant enchytraeids are compelled to live in environments assuring a combination of constant humidity, high oxygen availability and rich food supply. Such habitat qualities are nowadays most frequently met with at the higher latitudes but, as suggested by *F. hegemon* s.l., they can also be found in well-preserved areas of Mediterranean countries, for instance along the cool, shaded banks of rivers flowing from the Southern Rhodope range.

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