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A guide to European terrestrial and freshwater species of Enchytraeidae (Oligochaeta)

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Abstract

A guide to European terrestrial and freshwater enchytraeid species is presented, designed for the identification of living specimens. Altogether 206 species are included. Recent taxonomic advances regarding new species, revisions, and improved standards of description are integrated. Marine and exotic species are excluded. The illustrated keys are preceded by introductions into the taxonomic traits, the general anatomy of enchytraeids, and the technique of handling living worms during the identification process. Due to persistent taxonomic problems in many groups, a 'sensu lato' approach is adopted in the circumscription of several common species. ***Bryodrilus ehlersi glandulosus*** Dózsa-Farkas, 1990 and ***Enchytraeus christenseni bisetosus*** Rota & Healy, 1994 are elevated to species rank; the latter receives a new name, ***Enchytraeus dichaetus***, due to homonymy with ***Enchytraeus bisetosus*** Levinsen, 1884, now ***Fridericia bisetosa***. ***Marionina libra*** Nielsen & Christensen, 1959 is transferred to ***Bryodrilus***. ***Marionina serbui*** Botea, 1984 is synonymised with ***Buchholzia simplex*** Nielsen & Christensen, 1963. ***Mesenchytraeus franzi*** Nurminen, 1977, ***Euenchytraeus bisetosus*** Bretscher, 1906 and ***Cognettia clarae*** Bauer, 1993 are probably one species. The youngest name is maintained here, pending a systematic revision of the group. The purpose of this key is to facilitate and to stimulate work with enchytraeids.

Keywords: Clitellata, enchytraeids, key, species identification, taxonomy

Contents

1. Introduction

This guide to European enchytraeids started with a plain text key handed out to the participants at a taxonomic workshop held during the 8th Symposium on Enchytraeidae in Durham, U.K., in July 2008. The response to this key motivated us to develop a more comprehensive and illustrated guide. Half a century after the publication of the seminal work on European enchytraeids by Nielsen & Christensen (1959), and more than 20 years after the encyclopedic compilations of Wilcke (1967) and Kasprzak (1986), the time may be right for a new key that incorporates recent advances – new species, taxonomic revisions, improved standards of description – making them available for students and researchers who work with enchytraeids at the species level.

The key includes species recorded from terrestrial and freshwater sites in Europe. Excluded are species restricted to marine or marine littoral habitats and aliens known only from greenhouses, botanical gardens or laboratory cultures of unknown origin. The exclusion of the marine littoral fauna will be disappointing for those who work 'by the sea', but we hope to deliver a marine supplement to this key in the near future. A list of marine enchytraeid species is available in Erséus & Healy (2001). Freshwater enchytraeids are also included in a comprehensive and richly illustrated guide to aquatic oligochaetes of Northern and Central Europe (Timm 2009).

In taxonomic terms the key is an interim report of our ongoing revisionary work. Apart from the many new species that are to be discovered or described, taxonomic problems are still considerable in many groups. Only one genus has been critically revised recently (Schmelz 2003). We would have preferred to await the revision of at least the more common taxa before publishing a key, but that would have meant a delay of several years. Species distinctions are therefore not always as clearcut as they should be, or they may not work for all specimens found in the field. In several frequently cited species we adopted a 'sensu lato' approach (e.g., ***Enchytraeus albidus***, ***Enchytraeus buchholzi***, ***Enchytronia parva***, and ***Lumbricillus lineatus***) which allowed us to subsume similar species with unresolved identity under the more common names. The new synonymies will be dealt with critically in future contributions.

Enchytraeids are mostly identified ***in vivo*** (Fig. 1) and the work with living material has requirements of its own, quite different from the more straightforward work with dead specimens. Therefore we start with a description of the handling of worms during the identification process, and we give a list of recommendations, results of 'troubleshooting' experiences during introductory courses. Furthermore, enchytraeid taxonomy uses outer and inner structures, profiting from the transparency of most forms. A general understanding of the enchytraeid 'bauplan' is absolutely necessary to recognise the structures and to distinguish the taxonomically important traits from the unimportant ones. Therefore we also give an introduction to the general anatomy of enchytraeids, and we outline the variations of those traits used to recognise genera and species. The accompanying illustrations can be studied without referring to the text. However, illustrations in the key sections are not fully labelled and require the knowledge given in the introduction. The two basic methods of extraction of enchytraeids from soils and sediments are not repeated here; they are well-covered in the literature. For the O'Connor method (wet funnel extraction with heat) see O'Connor (1955, 1962), for the Graefe method (extraction in cold water) see Graefe in Dunger & Fiedler (1997) and ISO (2008); efficiencies of both methods are compared in Didden et al. (1995), Kobetičová & Schlaghamerský (2003), and Panchenko (2006).

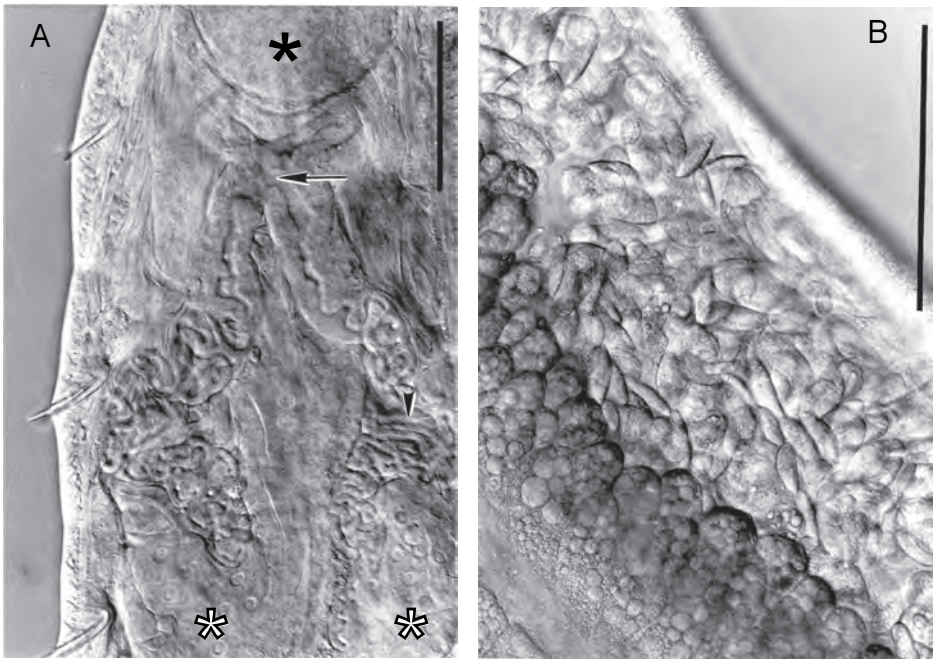

Fig. 1 Live photographs of ***Enchytraeus luxuriosus***. Enchytraeid taxonomy uses mostly inner, soft-bodied structures, best recognised in living specimens, but not always easy to distinguish. The photographs give examples of traits as seen in living specimens. A: Oesophageal appendage, dorsal view, with meandering canal characteristic of the ***Enchytraeus buchholzi*** group. Arrow: Common opening of both branches into the oesophagus, behind the pharyngeal pad (asterisk). Hollow asterisks: Pharyngeal glands of segment IV. Lateral chaetae of III, IV and V can be seen to the left. B: Chloragocytes (bottom left) and coelomocytes (top right), both in dense packages and completely filling out body cavity. Bars = 100 µm. From Schmelz & Collado (1999, Fig. 2A,C).

The keys to genera and species work best for adult specimens, i.e. those with distinct clitellum and large yolky egg (or eggs), but whenever possible we gave priority to characters that are present and alike in all age-groups. Fragmenting species with only sporadically occurring sexual specimens can be identified without referring to reproductive characters. In most other species adult specimens are found throughout the year so that after identification of the adults, the subadults and juveniles can often be identified as well, using traits constant in all age groups. Each species is described briefly in order to ensure the accuracy of the identification, and references to further useful literature are given. Please note that descriptions and illustrations are not exhaustive! When doubts remain or an observed trait is not covered in the key, the primary literature should be consulted. Notes on habitat and distribution are also added, but these entries require further elaboration. Genera can be identified either using the key, with the attached tabular comparison (p. 46), or with the genus diagnoses preceding each sub-chapter in the species section.

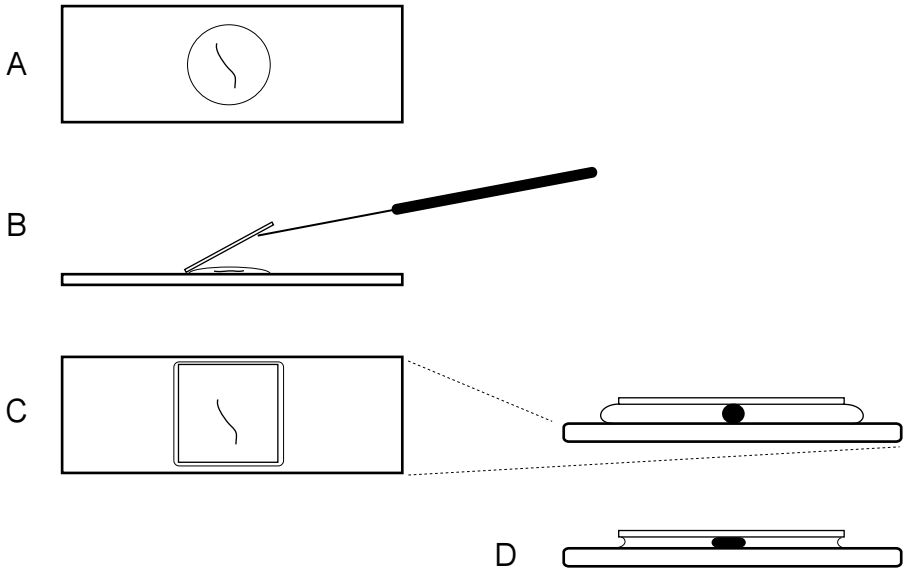

Fig. 2 Live investigation, four steps (A, B, C, D): Procedure of placing and pressing the worm under slide and coverslip.

Our purpose is to facilitate the work of those who identify enchytraeids and to motivate more students and researchers to start working with this group. Dealing with living worms may not be to everybody's taste, but it offers possibilities that are not available when studying only dead material. It may lead to a better understanding of the organism, stir scientific imagination, and even carry aesthetic appeal. We greatly appreciate comments and any kind of feedback that may help to improve the key for a future edition.

2. Techniques

Equipment. An ordinary dissecting microscope (stereolupe) is required to sort and pick up specimens, submerged in water after extraction from soil or sediment. Specimens are identified with a transmission microscope. It should be of good quality, and with four objectives, magnifications appr. x4, x10, x20, and x40. A x100 objective and oil immersion is not necessary. Most part of the identification is carried out at ca x200 magnification. A coaxial mechanical stage is indispensable. Interference contrast greatly helps to see the structures. Whenever there is such a microscope in the lab, you need it! Phase contrast is useless. Dissecting microscope and transmission microscope should have an ocular scale. Further equipment: glass or plastic dishes, small petri dishes, slides, coverslips, sizes 24 mm x 24 mm to 24 mm x 32 mm, tissue paper, pipettes, needles, tweezers, soft steel forceps.

Handling. Two or three drops of water are applied on a slide. A specimen is picked up from the water with a curved needle, a pipette, or with tweezers, and placed into the water on the slide (Fig. 2A). A coverslip is gently placed on the specimen (Fig. 2B,C). Surplus water is removed with a tissue paper (e.g. bathroom tissue, lint-free); this increases the pressure on the worm (Fig. 2D). Pressure is released by placing a drop of water at the edge of the coverslip with a pipette. The worm must be pressed in order to reduce body movements and to see the inner structures, but too much pressure damages the worm. The right amount of water (and pressure) is crucial for a successful study of the worms; it varies from species to species, and a bit of practice and patience is required here. Larger worms may be anaesthetised in diluted carbonated (sparkling) mineral water, but too much of it leads to complete relaxation, pressure displaces the organs, and body fluid is expelled. However, most worms recover from such treatment when returned to non-carbonated water.

Fixation and preservation. Specimens are fixed and preserved with 70% ethanol. For detailed morphological studies, a fixation with hot Bouin's fluid is preferrable, details can be found in Schmelz (2003) and Beylich (2005). We do not recommend fixation in formaldehyde. A routine fixation in ethanol has the advantage that specimens can be used for morphological studies and for DNA sequencing.

Recommendations

1. Pick out the adult worms first, i.e. those with a large white spot – the egg – somewhere in the anterior body half.

2. Take notes about the worms as seen under the stereolupe under top light: body colour, approximate length and diameter, body movements.

3. Start the microscopical investigation with a surplus of water. When the coverslip is applied, water should leak at the edges (Fig. 2C).

4. Remove only surplus water. If the worm continues to move, put the tissue close to the edge, this will suck more water from below the coverslip.

5. If the worm has moved to an edge, add water again, lift the coverslip at one side with a needle (Fig. 5B), and repeat the procedure. To lift the coverslip from a pressed worm without adding water may damage it.

6. 'Give it some time'! Don't press too much at the beginning. Body movements often slow down after a while. Try to 'chase' the worm using the two mechanical stage knobs.

7. When the worm is more or less immobilised, control the state of the worm with the microscope. Pressure is too strong when inner organs are barely distinguishable, when inner organs are displaced (for example, when the egg is in preclitellar segments), when there is no back and forth movement of body fluid in the interior, or when body fluid is expelled either from the head pore or from an injury. Add a drop of water immediately to avoid further damage.

8. If during observation the worms stays immobilised for more than 3 minutes, add a drop of water. Slight body movements facilitate the observation of structures and reduce the risk of damaging or killing the worm.

9. Don't spend much time with a damaged worm. When the body is injured and fluids or organs leak out, throw it away or fix it, and take a new one.

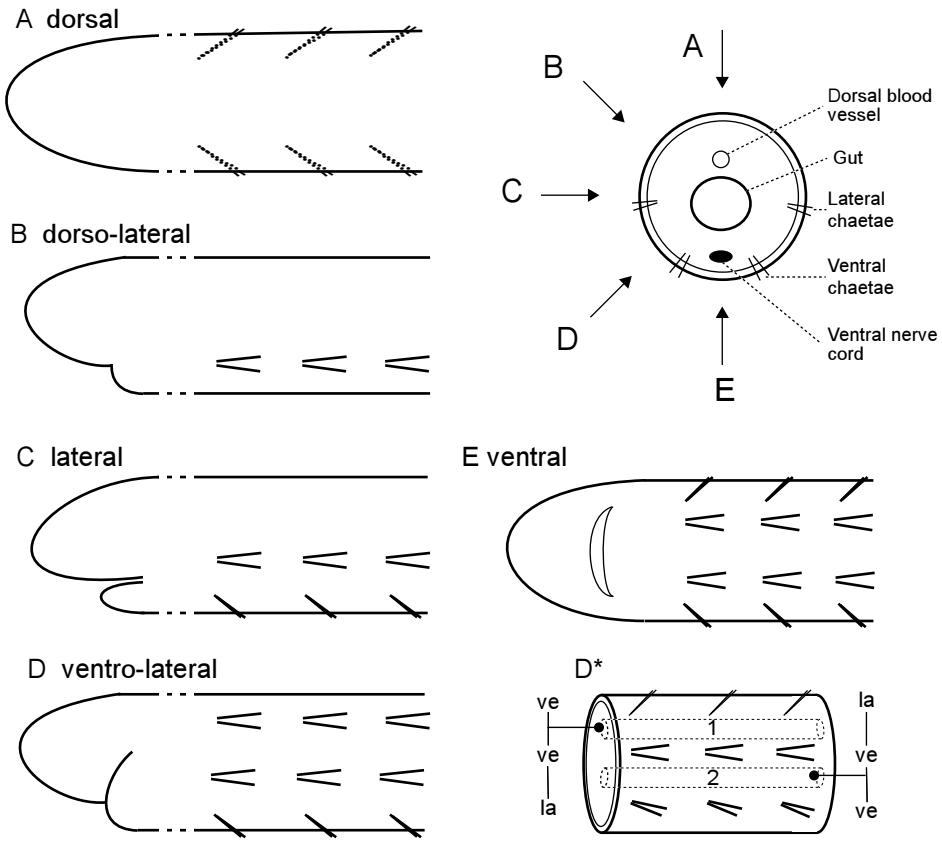

Fig. 3 Establishing the position of the worm during live investigation, using either the prostomium and mouth opening (A–D, left) or the chaetae. The scheme at top right indicates the angles of vision in A–E, respectively. When three rows of chaetae are visible (D), the middle row must be a ventral row, and the ventral nerve cord can be used to establish which of the outer rows is lateral and which is ventral. When the nerve cord is seen above the middle row of chaetae (D* '1'), the bottom row of chaetae is the lateral row (la) and the other two are ventral rows (ve). In turn, when the nerve cord is seen below the middle row of chaetae (D* '2'), the top bottom row of chaetae is the lateral row and the other two are ventral rows. The scheme works only for species with chaetae in all 4 rows (2 laterals, 2 ventrals).

10. Start the microscopical investigation with low magnification to distinguish front end and rear end and to establish whether the worm is complete and intact. Further traits to be noted at the start: state of maturity (egg, clitellum); transparency or opacity of body interior, colour and coverage of chloragocytes; origin of dorsal blood vessel: pulsations are often more conspicuous at the beginning of the investigation.

11. Move to the anterior end, switch to higher magnification, move the objective down (or the mechanical stage up) until the upper body surface is focused.

12. Establish the position of the worm: dorsal, lateral, ventral, or intermediates, using either prostomium and mouth opening or the lines of chaetal bundles (Fig. 3). To know the position of the worm is crucial for recognising the structures!

13. Count the segments again and again using the chaetae, beginning at the anterior end and starting with number '2' (the first segment has no chaetae). You should always know whether you are counting lateral or ventral rows. When localising inner structures, mind that inner segments are often pushed backwards and forwards, especially in preclitellar segments.

14. Use the focusing screw constantly, moving the optical focusing plane up and down through the body; this helps to recognise form and arrangement of organs.

15. Establish a routine in using simultaneously the focusing screws (with one hand) and the mechanical stage screws (with the other).

16. Make notes and sketches of recognised structures. The worm may not be in the right position to see the characters required in the key. For example, the maximum number of chaetae require a ventral or ventro-lateral position; nephridia are best seen in lateral or ventro-lateral position; brain shape and head pore are recognised only in perfectly dorsal position.

17. Don't expect to identify all animals.

18. Make an effort and try to fix as many of the identified specimens as possible, and to store them in a well-labelled reference collection. Only reference material gives validity to your identification results! With interference contrast optics many characters can be observed even in ethanol-preserved material; at least the accuracy of an identification can be checked. Furthermore, the unsettled taxonomy and the lack of biogeographical data in most species require larger collections of reference specimens. Your specimens may also be useful for DNA-based taxonomic or biogeographical studies.

3. General enchytraeid morphology

In the following overview, numbers in brackets refer to Fig. 4, and terms in brackets refer to synonyms used in the literature. Segments are conventionally indicated by Roman numerals (e.g., X = 10th segment), and segment boundaries by Arabic numerals (e.g., 6/7 = boundary between segment VI and VII; may refer to the septum or nearby structures).

Enchytraeids share the general body plan of oligochaetes as segmented, bilaterally symmetrical, hermaphroditic, clitellate annelids with a spacious **coelom** (the body cavity), a pre-oral, pre-segmental **prostomium** (1), an anterior ventral **mouth** (3), and a posterior post-segmental **pygidium** with anus.

Full-grown individuals are usually between 2 and 30 mm long and between 0.1 and 1 mm wide. In cross-section they are cylindrical. The number of segments is rarely below 20 or above 70.

From segment II on there are four discrete bundles of single-pointed **chaetae** (= setae) (44) in each segment, two ventral (46) bundles and two lateral (45) or latero-dorsal bundles. Chaetae are always absent on the prostomium, the pygidium, and on the first segment, the

peristomium (4), which surrounds the mouth opening. Most European species further lack ventral chaetae in segment XII, the segment of the gonopores; lateral chaetae are often absent here as well. Chaetae are absent completely in ***Achaeta*** and in some marine species of ***Marionina***; in species of other genera chaetae may be absent in specific bundles. The number of chaetae per bundle varies between 1 and 16 within species-specific limits and according to the body region; most often there are 2–8 chaetae in a bundle. Detached chaetae, often compiled to packages, are seen in the body cavity of some species, mostly ***Fridericia*** (Fig. 57C right).

The **body wall** is composed of cuticle, epidermis, a layer of circular muscles, longitudinal muscles, and peritoneum. A small mid-dorsal, slit-like **head pore** (2) is situated on the prostomium or right between prostomium and peristomium; coelomic fluid can be issued here. Segmental **dorsal pores** from VII on are a distinctive feature of ***Fridericia***.

Epidermal gland cells (= cutaneous glands) (20) are present in each segment, more or less distinct, mostly more numerous in preclitellar than in postclitellar segments. In many species of ***Achaeta***, glands are enlarged into pyriform glands (= setal follicles), projecting flask-like into the coelom.

At maturity, the epidermis of segments XII and XIII is thickened into secretory cells that form the **clitellum** (39), the cocoon-building organ. The two main types of secretory cells, **granulocytes** (41) and **hyalocytes** (40), often form a distinctive pattern. In some species, **subneural glands** (Fig. 12C) are present between the ventral chaetae of XIII or following segments.

Outer segment boundaries are marked by the intersegmental grooves exactly at half length between the chaetae. In living animals they are often invisible. Inner segment boundaries are marked by the **septa** (24), present from 4/5 on; more anterior segments are without apparent inner segmentation. The septa are elastic and they have clefts that allow the coelomic fluid to pass back and forth across segments. Septa insert slightly anterior to the intersegmental grooves, resulting in a forward shift of inner segmentation with respect to the outer.

A medullar or more or less segmentally ganglionic **ventral nerve cord** (6) extends through the length of the body mid-ventrally and connects with the dorsal and unpaired **brain** (= cerebral ganglion, supraoesophageal ganglion) (5) via circumoesophageal connectives (not shown in Fig. 4). The brain lies in segments I and II. Immediately behind the pharyngeal pad, a pair of oval **post-pharyngeal bulbs** (9) is closely attached to the oesophagus dorsally; a further outer pair is often visible on the afferent fascicles of the pharyngeal glands (see below). These bulbs are probably ganglia of the stomatogastric nervous system.

The gut extends through the entire body and is connected with the body wall by the intersegmental septa and also by additional intrasegmental ventral or dorsal ligaments. The functional gut regions pharynx, oesophagus and intestine are light-microscopically not well-distinguished. In segment III, the dorsal gut epithelium is much raised and forms the **pharyngeal pad** (7), which by a dense and complicated system of **pharyngeal muscles** (8) is everted and retracted for food uptake.

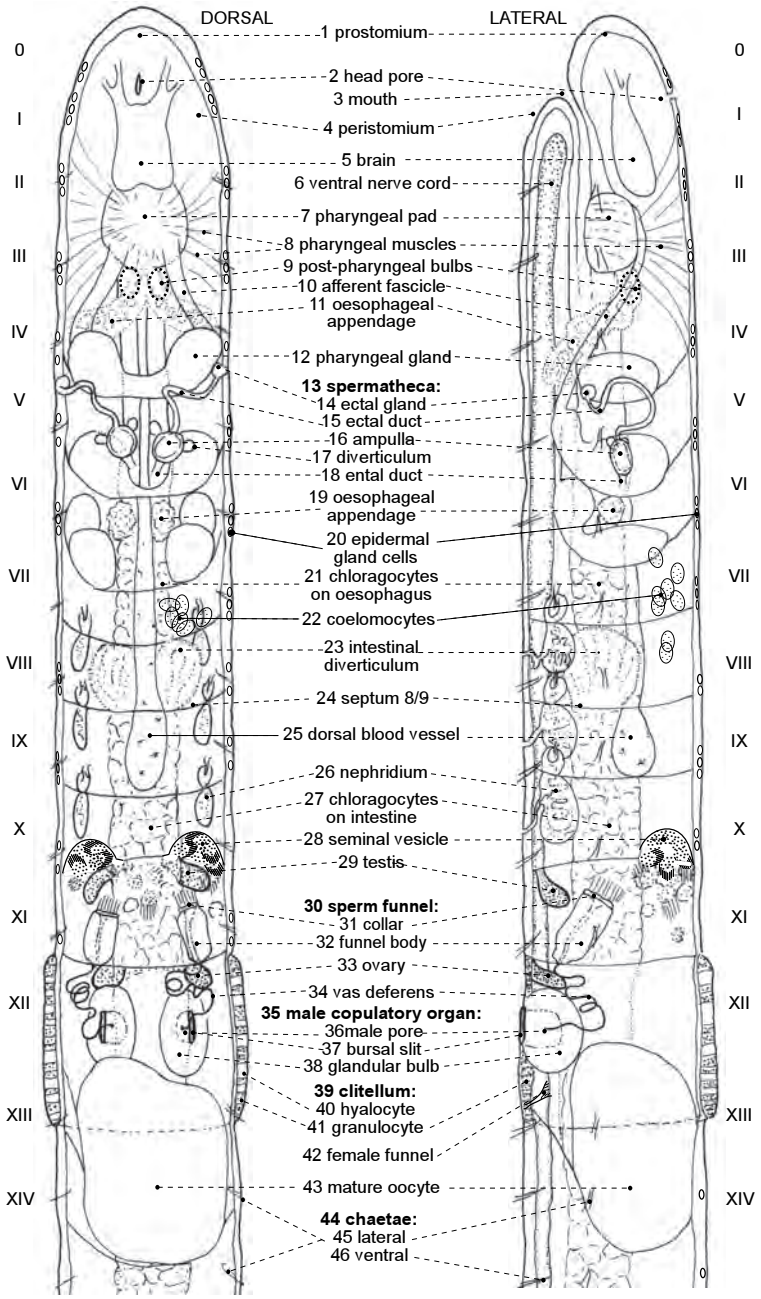

Fig. 4 Overview of enchytraeid anatomy, anterior 14 segments. Left dorsal view, right lateral view. Traits as shown here represent several possibilities and do not occur in one and the same animal.

Pharyngeal glands (= septal glands) (12) are present from IV on, occupying usually 3, sometimes more consecutive segments. They are solid, i.e. without lumen, compact, segmentally paired, and usually attached to the posterior septum in a segment. Mucous proteins and digestive enzymes are produced here. The glandular lobes of each side are longitudinally interconnected by a ventro-lateral strand, the **afferent fascicle** (10); the two fascicles are conspicuous in segments III and IV where they rise and connect with the dorsal side of the pharyngeal pad.

Oesophageal appendages (= peptonephridia) (11, 19) are often present in definite body regions between segments III and VII. Their lumen is often continuous with that of the oesophagus. Shape and position vary among genera and species. The oesophagus merges gradually or abruptly into the intestine. The transition may be marked by **intestinal diverticula** (23), situated in VI, VII or VIII, varying among taxa, or by specialised cells, e.g. the canalised **chylus cells** in ***Fridericia***. **Chloragocytes** (27) are present on the outer intestinal surface from segment IV or V on; they form a dense layer around the gut from segment V, VI or VII on, except in segment XII.

From segment IV or V on, the gut is entirely surrounded by blood sinus, situated between gut epithelium and chloragocyte layer. The **blood** is usually colourless but may be reddish or yellowish in some species. There is a ventral and a **dorsal blood vessel** (25). The ventral vessel extends through the entire body; the pulsating dorsal blood vessel is present only in the anterior body region, it rises posteriorly from the peri-intestinal blood sinus. In segment I, rarely in III, it bifurcates into a pair of circumoral connective vessels that extend postero-ventrad to reunite in segment IV into the ventral blood vessel. Dorsal and ventral vessel communicate also by three or four pairs of thinner commissural vessels in the foremost six segments. Capillary blood vessels are absent.

The segmentally paired, ventrolateral **nephridia** (26) are metanephridia with an entally open **funnel**, the nephrostome; the following efferent duct is usually compacted into a laterally flattened **nephridial body** with much interstitial tissue; the nephroporus is situated ventro-laterally in line with and anteriorly of the ventral chaetal bundles. Gonadal segments and a varying number of foremost and other segments are without nephridia.

The coelom is more or less filled with free-floating, flat, and disc- to spindle-shaped **coelomocytes** (= lymphocytes) (22). Two types are light-microscopically distinguishable: **mucocytes**, nucleate cells with a textured cytoplasma, are present in all species; **lenticytes**, smaller anucleate and completely hyaline bodies, are restricted to and diagnostic of ***Fridericia***, ***Buchholzia*** and ***Hemifridericia***.

The **male reproductive system** consists of one pair each of testes and sperm funnels in segment XI, and one pair of vasa deferentia and male pores in segment XII. Each male pore is usually encompassed by a glandular and muscular **male copulatory organ** (35). **Testes** (29) are jointly attached ventrally to septum 10/11, extending postero-dorsad; in ***Achaeta*** the testis is unpaired. Spermatogonia (= morulae, cysts, developing sperm) are usually released early from the testes and develop freely in the coelom of segment XI, the lumen of which is

often enlarged by a paired or unpaired, sac-like anterior extension of the dorsal peritoneum between segments X and XI, the **seminal vesicle** (28). In ***Lumbricillus*** and ***Enchytraeus***, the developing sperm remains enclosed with the testes by a common membrane, forming **testis sacs**, until maturity. Mature **spermatozoa** align in parallel on top of the sperm funnels. The **sperm funnel** (30) consists of a ciliated **collar** (31) and a subsequent and closely attached **funnel body** (32), a glandular inflation of the funnel wall epithelium. At the transition from segment XI to XII the funnel merges into the **vas deferens** (plural: vasa deferentia) (34), a long and narrow tube, wound in regular or irregular spirals. In ***Cernosvitoviella*** and ***Mesenchytraeus***, the vas deferens often widens distally into an **atrium** with thickened epithelia; prostate glands may or may not be attached. The **male pores** (36) are either on the body surface or hidden in an eversible epidermal invagination, the **bursa**, which opens on the body surface by a **bursal slit** (37). In almost all enchytraeids the male pore is surrounded by a compacted **glandular bulb** (= penial bulb) (38). Bursa, glands and accompanying musculature form the **male copulatory organ** (35).

The **female reproductive system** consists of the clitellum and of one pair each of ovaries, female funnels and spermathecae. **Ovaries** (33) arise ventrally at the anterior margin of segment XII, attached to septum 11/12, and extending postero-dorsad. In ***Achaeta*** there is one unpaired ovary. The inconspicuous **female funnels** (42) open to the exterior at the posterior margin of segment XII, in line with the ventral chaetae and the male openings. Eggs develop in the coelom, in a posterior extension of septum 12/13. Several oogonia (pale, with large nucleus) are usually compacted in front of the large yolky **oocytes** (43), which may extend over 2–3 segments.

The **spermatheca** (plural: spermathecae) (13) consists of an **ectal duct** (15) and a proximal sperm-containing chamber, the **ampulla** (16), to which a varying number of **diverticula** (singular: diverticulum) (17) may be attached; these are peripheral outgrowths of the ampulla, and most often sperm-containing; their lumen connects with the ampullar lumen.

The ectal duct opens to the exterior by a usually minute **ectal pore**, situated laterally at the intersegmental furrow of 4/5, halfway between and slightly ventrally of the lateral chaetae. Many species of ***Achaeta*** have ventral ectal pores. The ampulla is either blind-ending, or proximally connected with the oesophagus, directly or by means of an **ental duct** (18), so that spermathecal and oesophageal lumen are continuous. The spermathecae of both sides may unite before communicating with the oesophagus. Spermathecae with attached ampullae are almost always confined to segment V, spermathecae with blind-ending ampullae may extend backwards through several segments; they are without diverticula in European species. The ectal duct epithelium is either smooth or glandular; at the ectal pore, one or more **ectal glands** (14) may be present.

In some species the entire set of reproductive organs in XI–XIII is shifted one or more segments forward. A forward shift by several segments is characteristic of species with fragmentation (= architomy) as main reproductive mode: ***Cognettia sphagnetorum***, ***C. glandulosa***, possibly ***C. cognettii***, ***Buchholzia appendiculata***, ***Enchytraeus bigeminus***. A forward shift by only one segment is known in species of ***Achaeta*** and may be present in other genera as well.

4. Taxonomic characters

4.1. Age groups, positional and directional terms

Age groups. The key is designed for the identification of adult specimens, but very often subadults and juveniles can be identified as well. The three age groups mentioned are distinguished as follows:

Adults: Clitellum fully developed, usually thicker than epidermis of adjacent segments, granulocytes and hyalocytes clearly distinguished. Large yolky egg or eggs present.

Subadults: Clitellum not fully developed, flat and/or without distinguishable glands cells, or absent. Yolky eggs absent or small. Other sexual organs (spermathecae, sperm funnels, male glands etc.) more or less fully developed. Fully developed spermathecae contain spermatozoa, and fully developed sperm funnels have spermatozoa attached to the collar.

Juveniles: No clitellum, no sexual organs, or organs in early stage of development.

The following non-sexual traits refer to adults only:

– Body dimensions – non-adults are smaller than indicated;
– Segment numbers – non-adults have fewer segments than indicated;
– Numerical patterns of chaetae – in species with more than 3 chaetae per bundle, non-adults have fewer chaetae per bundle than adults. However, in species with 1–3 chaetae per bundle the pattern is often the same in all age groups.
– Locations of some structures related to the intestine (dorsal vessel origin, chylus cells) – located more anteriorly in non-adults.

In fragmenting species these traits apply also to juveniles. Traits that apply to all age groups are: body colour and epidermal gland cells (including pyriform glands of ***Achaeta*** species), position of head pore, shape of chaetae and brain, coelomocyte texture, shape and position of pharyngeal glands, nephridia, oesophageal appendages, and intestinal diverticula.

Positional terms. Several terms are used to describe position and arrangement of structures in the worm body. **Anterior** or **posterior** refer to the longitudinal axis of the worm. **Distal** or **proximal** refer to the worm radius in cross section; the distal part of a structure is closer to the body surface or the body wall, and the proximal part is closer to the centre of the worm. The distinction is important in elongate structures attached to the body wall. The proximal part of the vas deferens, for example, is closer to the sperm funnel, and its distal part closer to the male pore. A synonymous pair is also in use: **ectal**=distal and **ental**=proximal. **Dorsal**, **ventral**, **lateral** and intermediates refer to the xy axis in cross section, see Fig. 3. All terms can be converted into **directional terms**, using the ending '-ad' instead of '-al'. For example, 'sperm funnel widening proximad' means, 'sperm funnel gradually widening towards its proximal end'.

4.2. External characters

Body size varies among species, among specimens of the same species – depending on age and other factors – and even within the same animal, depending on its state of contraction, but always within species- or taxon-specific limits. Very small forms (2–3 mm long), when sexually mature, comprise: ***Enchytronia***, ***Hemifridericia***, ***Cernosvitoviella***, many ***Marionina***

species, a few ***Achaeta*** species, and some ***Enchytraeus*** species of the ***buchholzi***-group. Very large forms (> 18 mm long) are found among ***Fridericia***, ***Henlea***, ***Mesenchytraeus***, ***Lumbricillus*** and ***Enchytraeus***; the latter two only in aquatic habitats or in compost. Usually body length and body diameter co-vary, i.e. longer specimens are also thicker. For example, a small ***Marionina*** with 2–3 mm body length is about 0.1–0.15 mm wide, and a large ***Fridericia*** with 22 mm body length may be 0.5–0.8 mm wide. Fixed specimens are shorter than living ones, and the body is strongly contracted, unless the worms have been anaesthetised before. Length and diameter refer to a specimen in a drop of water on a slide, not pressed by a coverslip.

Segment number varies within species-specific limits. The maximum number is more informative than the minimum number, because specimens that have lost posterior segments and regenerated a new hind end have fewer segments. Segments are counted using the chaetal bundles, starting with '2' (the first segment, the peristomium, is without chaetae). Counting segments in living ***Achaeta*** is difficult; here the segmental ventral nerve cord ganglia may be used, starting with '4', which is the large suboesophageal ganglion; it unites the ganglia of segments I–IV. Ganglia from V on are much smaller and restricted to one segment. The dorsal pyriform glands may also help, although their beginning varies between segments II and IV.

Body colour, ascertained with the dissecting microscope under top light, is usually pale white, occasionally with a yellowish tinge. It is influenced by gut contents, size of chloragocytes, amount and texture of coelomocytes, and blood colour. Some species are distinctly opaque-white due to coelomocytes or chloragocytes; in others the reddish blood gives an overall rose tinge (***Lumbricillus***), which however is never as strong as in the aquatic tubificids or lumbriculids. A distinct white spot, as wide as the body diameter, and somewhere in the anterior half of the worm, is the mature oocyte (or an assemblage of several of these), indicating full sexual maturity. Directly anterior to it a more irregular whitish mass may be present, indicating larger amounts of developing and mature sperm.

Chaetae (Fig. 5) are simple-pointed sticks protruding with their distal ends outside the body. Within a bundle, the proximal ends of the chaetae (those inside the body) are closer to each other than the distal ends (those outside the body). Taxonomically important traits are (1) shape and (2) numerical pattern. The shape can be used also in juvenile specimens, whereas the numerical pattern often applies only to adult or subadult specimens, see above (4.1).

(1) Chaetae are either **straight distally** and with a more or less pronounced proximal bend (= ental hook), or bent distally and proximally, resulting in an overall **sigmoid** shape. Very rarely chaetae are bent distally and straight proximally. Sigmoid chaetae may have a **nodulus**, a swelling at about 2/5 length from the distal tip; distally straight chaetae are always without nodulus. Both distinctions (i.e. straight/sigmoid, and with/without nodulus) are not always clearcut; ambiguous cases are reflected in the key to genera.

Sigmoidity can be recognised beyond doubt in all species of ***Cernosvitoviella***, ***Mesenchytraeus***, and ***Buchholzia***. In other genera only some species have sigmoid chaetae (***Bryodrilus***, ***Lumbricillus***, ***Marionina***). In cases of doubt, chaetae in side view should be focused, i.e. those seen sticking out of the body.

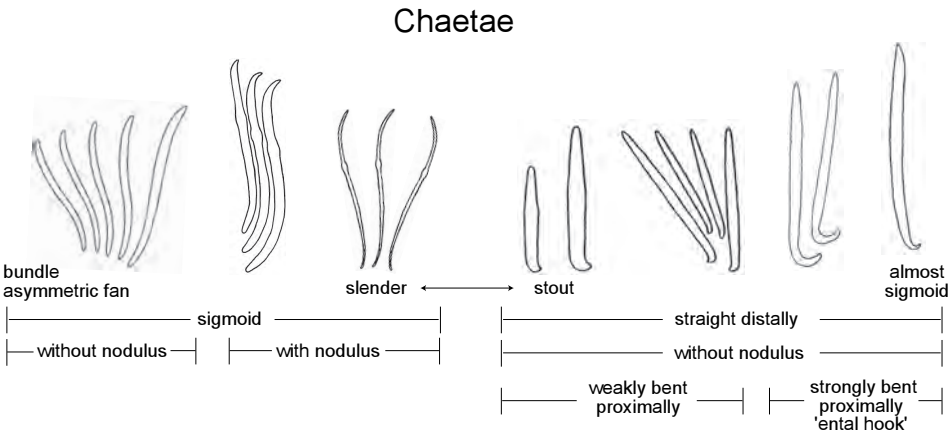

Fig. 5 Variation of shape of chaetae in enchytraeids. From 2nd to left to right: Timm & Popčenko (1978, Fig. 11-4); Černosvitov (1928, textfig. 3-5, altered); Chalupský (1991, Fig. 10 right); Schmelz (1999, Fig. 4B); Schmelz et al. (2008, Fig. 1E); Schmelz (2003, 64G).

A nodulus is present only in three genera: In ***Cernosvitoviella*** it is conspicuous in all species; in ***Mesenchytraeus*** and ***Stercutus*** the nodulus may be not more than an abrupt proximal thickening of the chaeta, or it is absent. Light diffractions in the body wall region may fake a nodulus in other genera!

(2) The number of chaetae per bundle varies among species, and also among bundles of an animal. Lateral bundles never have more chaetae than ventral bundles in the same body region, and posterior bundles rarely have more chaetae than anterior bundles. This means, the maximum number of chaetae is usually found in ventral preclitellar bundles. The numerical chaetal pattern is traditionally summarised in the formula

A – B : C – D

with

A = lateral preclitellar, (i.e. from II to XI),
B = lateral postclitellar,
C = ventral preclitellar,
D = ventral postclitellar.

For example, 2,3 – 3 : 2–4 – 2,3 means: 2 or 3 chaetae in lateral preclitellar bundles, 3 chaetae in all lateral postclitellar bundles, 2, 3, or 4 chaetae in ventral preclitellar bundles, 2 or 3 chaetae in ventral postclitellar bundles. In the literature the formula is often specified by figures in brackets, meaning numbers of chaetae per bundle present only in some specimens, or by emphasised figures (bold, italics, underlined), meaning the predominant number of chaetae in bundles of a given body region; here we use underlined figures in several descriptions.

The study of the chaetae over the entire body often provides elegant shortcuts to species or species groups.

A. Chaetae sigmoid:

– Distinctly more chaetae in ventral than in lateral bundles (e.g., 4–6 vs 2–4, or 6–9 vs 3–5): ***Mesenchytraeus*** (all species except ***M. sanguineus***, ***M. lusitanicus***, and ***M. flavidus***).
– Some preclitellar chaetae (ca IV–VII) distinctly larger than the rest, about 2x as thick or more: ***Cognettia cognettii*** (lateral, 2–3 segments), ***Mesenchytraeus armatus*** (lateral, 2–3 segments), ***Buchholzia simplex*** (ventral, in IV), ***B. subterranea*** (ventral, in IV), ***Mesenchytraeus monochaetus*** (ventral, V–VII), ***M. tetrapodus*** (ventral, VI, VII).
– Chaetae arranged in a distinctly asymmetrical fan of 5 or more: several species of ***Lumbricillus***.

B. Chaetae straight distally:

– Chaetal bundle arranged as a symmetrical fan, with inner chaetae pairwise smaller than outer: ***Fridericia*** (many but not all species), ***Oconnorella cambrensis*** (many specimens). A symmetrical fan with inner chaetae almost as large as outer occurs also in many species of ***Henlea***. In ***H. perpusilla*** the innermost pair is often distinctly smaller than the outer pairs.
– Lateral chaetae absent in II, present from III on, 2 in all bundles: ***Marionina argentea***, ***Marionina southerni***.
– Lateral chaetae absent in segments immediately before clitellum (IX–XI), present in all other bundles, not more than 2 per bundle: ***Enchytronia*** spp. (2 chaetae throughout), ***Marionina clavata*** (1 chaeta in lateral postclitellar bundles).
– Lateral chaetae absent in segments before clitellum, ventrally 3 chaetae in several preclitellar bundles, small worms: ***Marionina hoffbaueri***, ***M. rubens***.
– Chaetae absent in many lateral bundles of anterior and posterior segments, not more than 2 chaetae in ventral bundles: ***Marionina minutissima***, ***M. subterranea*** (small worms, < 5 mm); ***Fridericia*** spp. (larger enchytraeids, > 7 mm long, see shortcut after the key to species).

The **head pore** is located on the prostomium in ***Achaeta***, ***Cernosvitoviella***, ***Mesenchytraeus***, ***Guaranidrilus***, and ***Hemienchytraeus***; in the rest it lies at the transition from prostomium to peristomium (0/1). It is conspicuous in larger species and inconspicuous in small species; under pressure body fluid is expelled through the head pore, this may ascertain its position in smaller forms. ***Stercutus niveus*** is the only known species that lacks a head pore. Usually it is not necessary to recognise the head pore since other traits are more evident. However, juvenile specimens of ***Mesenchytraeus*** can be distinguished from ***Lumbricillus*** or ***Cognettia*** using this trait. The pore is often slit-like; in ***Fridericia*** the slit is longitudinal while in ***Henlea*** and ***Bryodrilus*** it is transverse; this may serve as an additional character to separate ***Fridericia*** from ***Henlea***, when the chaetal pattern is ambiguous. Most species of ***Fridericia*** have also segmental **dorsal pores**, present from VII on (Fig. 50). They are difficult to see, and not necessary to recognise the genus.

Epidermal gland cells stand out against the surrounding epidermis by its hyaline, rarely granular, texture. They are arranged in several transverse rows, in varying densities, more dorsally than ventrally, more in anterior than in posterior segments, and more in the middle of a segment, at the level of the chaetae, than near the segment boundaries. Though often conspicuous, they rarely provide clearcut distinctions for the identification of taxa.

Glands are especially conspicuous in ***Bryodrilus***, ***Buchholzia*** (Fig. 48A), ***Mesenchytraeus***, and ***Lumbricillus***; they are inconspicuous or scarce in ***Enchytraeus***, ***Cernosvitoviella***, and ***Cognettia***.

Epidermal gland cells are distinctly yellow-brownish in ***Marionina riparia*** (Fig. 41A), ***M. vesiculata***, ***M. minutissima*** (Fig. 39C), ***Achaeta seminalis***, ***Bryodrilus ehlersi***, and in several species of ***Fridericia*** (see shortcut after the key to species).

The genus ***Achaeta*** is peculiar in possessing two types of epidermal glands, **pyriform glands**, flask-shaped and more or less hyaline bodies that project into the body cavity, and flat **lentiform glands** (lens-shaped glands) with a circular or oval outline. Both types have a fixed and segmentally repetitive pattern, which can be used to distinguish species groups and species (Fig. 24). The old term 'setal follicles' should not be used any more for pyriform glands, because these structures are demonstrably not remains or replacement structures of the chaetae (Graefe 2002).

In the mainly tropical ***Guaranidrilus*** epidermal glands are elongate, transverse stripes, often with yellow-brown colour (Fig. 29A).

The **clitellum** (Fig. 6), a glandular modification of the epidermis, is present in segments XII and XIII, sometimes also in parts of XI. Its total longitudinal extension varies among taxa between 1 and 2.5 segment lengths. The clitellum is rich in taxonomic details; here we use two traits, (1) circumferal extension (Fig. 6, top row) and (2) gland cell pattern (Fig. 6, bottom row).

(1) The clitellum is either (a) girdle-shaped, i.e. developed on all sides, (b) saddle-shaped, i.e. not developed ventrally, or (c) it is only laterally developed, i.e. ventral and dorsal sides are without clitellum. This useful trait is still unknown in many species. Very rarely the dorsal side is free and the ventral side developed. A ventrally and dorsally interrupted clitellum is found in species of ***Enchytronia***, ***Cernosvitoviella***, ***Achaeta***, possibly ***Marionina***, and in a few species of ***Fridericia*** (see shortcut after the key to species). Two intermediate states are known: Dorsally the clitellum may be interrupted only in a narrow area (Fig. 25F); ventrally the clitellum may be partly developed, e.g., present posteriorly, absent anteriorly (Fig. 59B).

(2) In a fully developed clitellum, two types of cells can be distinguished. **Granulocytes** are cells densely packed with globular bodies. **Hyalocytes** appear as free interspaces between the granulocytes. Further, clitellar gland cells are either arranged in transverse rows or in a reticulate pattern (= 'irregular' in the literature). Transverse rows are either separate from each other, dense, or indefinite; the latter is a transitional stage between 'transverse' and 'reticulate'. Differences among reticulate patterns (see Fig. 6 bottom left) are not used in this key. Hyalocytes may be restricted to a distinct region of the clitellum, for example they may be absent ventrally in an otherwise girdle-shaped clitellum, or they are present only in the dorso-lateral half of a saddle-shaped clitellum. In ***Achaeta***, hyalocytes are often concentrated in distinct baguette-shaped longitudinal rows that project into the body cavity (Figs 25C, 26B).

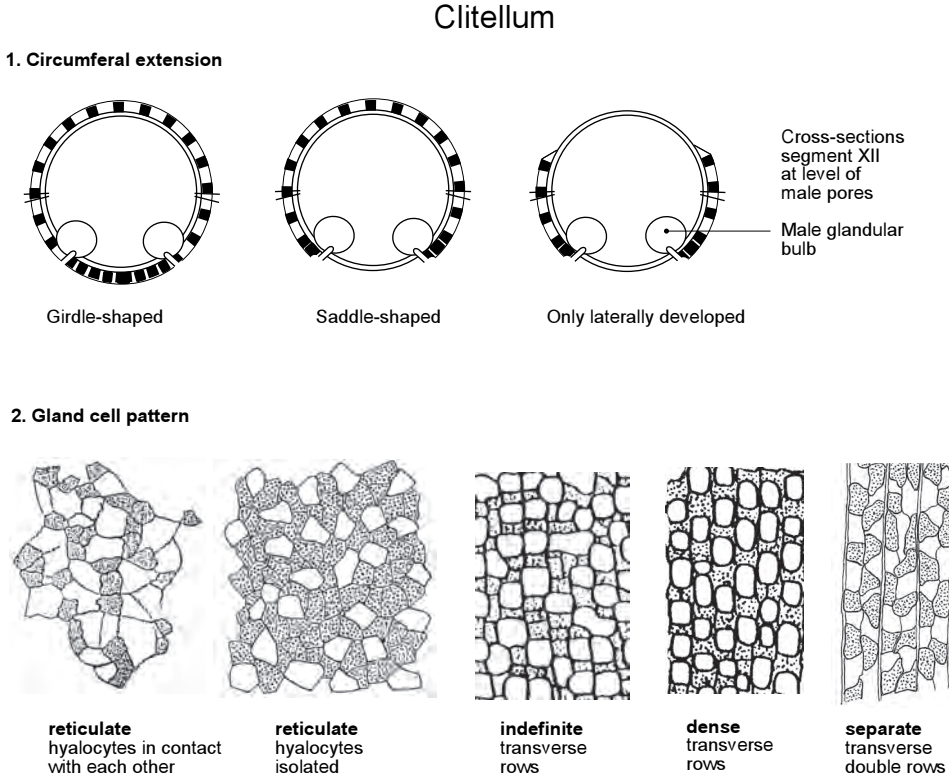

Fig. 6 Clitellum, taxonomic traits. Bottom (left to right), from Issel (1905a, Pl. XIII Fig. 8); Rota et al. (1998, Fig. 5E); Rota & Healy (1999, Figs 5G, 6F); Rota et al. (1998, Fig. 3A).

Between the male pores or the bursal slits (see below), i.e. on the ventral side and in the anterior half of the clitellum, the glandular pattern is often different from the rest. For example, gland cells may be absent here and present everywhere else (Fig. 12C). This trait is usually not covered in the key, except for species of the ***Enchytraeus albidus*** group (Fig. 34F): Here a more or less rectangular area, the **genital field**, is distinguishable against the surrounding clitellum by its lowered surface and by cells that differ from ordinary clitellum cells; its borders are marked by lip-like extensions of the clitellum that bulge inwards.

Apart from the clitellar region, other regions of the epidermis may undergo a glandular modification. For example, the epidermis around the spermathecal ectal pores is often thick and warty in some species of ***Achaeta***, ***Fridericia***, and others. A circular field between the ventral chaetae behind the clitellum may be glandularly thickened in some species of ***Fridericia*** (Fig. 12B).

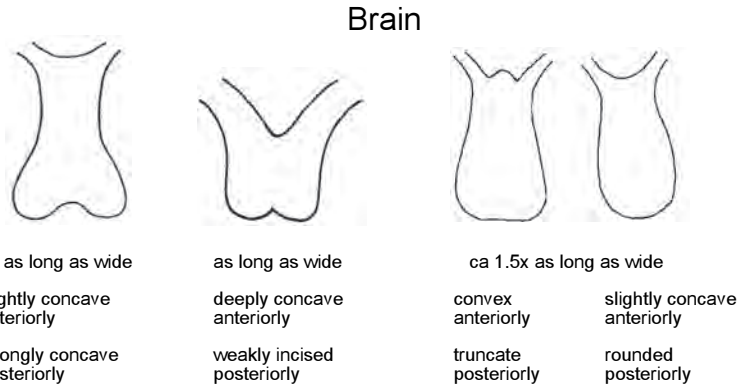

Fig. 7 Brain (= supraoesophageal or cerebral ganglion), taxonomic traits.

4.3. Internal characters, general

The outline of the **brain** (Fig. 7) helps to distinguish genera. It is usually longer than wide; only in ***Mesenchytraeus*** it seems to be as wide as long, due to a strong anterior incision. The posterior margin of the brain is either convex, i.e. rounded, or concave, i.e. incised or indented. This distinction is useful in some species, but in many others there are transitions. The brain is distinctly concave in ***Cernosvitoviella***, ***Cognettia***, ***Enchytronia***, ***Stercutus***, ***Hemienchytraeus***, ***Guaranidrilus***, and ***Hemifridericia***. In ***Fridericia***, ***Enchytraeus***, ***Achaeta***, ***Oconnorella*** and ***Bryodrilus*** the brain is posteriorly convex. In other genera, especially ***Marionina***, ***Lumbricillus***, and ***Henlea***, the trait is variable or little marked. The trait is recognised only with an animal in perfectly dorsal position (Fig. 3A).

Pharyngeal glands (Figs 8, 9) are usually present in IV–VI and sometimes also in following segments. They are compact bodies without lumen, composed of large, pale, and hyaline cells with distinctly visible nucleus in the centre (Fig. 1A). In living specimens this aspect is always the same, although its representations in line drawings of taxonomic descriptions may differ considerably (comp. Figs 25C–E, 31A,C, 37A, 38A). The glands are often lobed. Posteriorly they are attached to the septa; these extend backwards by about one segment, forming a ‘U’ inside the worm body. Accordingly, the pharyngeal glands are shifted backwards as well; for example, glands of segments VI are at the level of the chaetae of segment VII; this is the normal position (comp. Fig. 51A). Under pressure the glands may be pushed further back or further to the front. In order to determine the segmental position of inner anterior organs, it is convenient to use the most anterior pair of pharyngeal glands as reference, situated without exception in segment IV.

The gland lobes are usually symmetrical, i.e. they are alike on the left and the right side of the body. Asymmetry indicates injury or malformation. Usually dorsal lobes and ventral lobes are distinguished, with ventral lobes lying more anteriorly than dorsal lobes. Dorsal lobes are widely connected with the septum, while ventral lobes extend forwards into the body cavity,

surrounding the afferent fascicles; posteriorly they merge into the dorsal lobes of the same side and the same segment. The two dorsal lobes of a segment are either continuous with one another mid-dorsally, or they are separate. The dorsal connection may be either narrow or wide; sometimes both dorsal lobes are completely fused into one unpaired mid-dorsal lobe (Fig. 8E). The typical pattern of glands in IV–VI with paired dorsal and ventral lobes is found in many genera and species (Fig. 8A-D, 9B–G).

In some species, additional glands occur, separate from the other glands (comp. Figs 9G, H, 23, 25C, 31D); they lie usually ventro-laterally in a segment, close to the anterior septum, and sometimes attached to it; in ***Mesenchytraeus*** they may extend dorsally (Fig. 17B). These additional glands are termed 'secondary', and the others ones accordingly 'primary'. In the literature, ventral lobes of primary glands are often erroneously described as secondary glands. In some species both primary and secondary ventral gland lobes occur together (Fig. 23 left). In Figs 8 and 9, all glands are primary except in 9G and 9H; here the secondary glands are easily distinguished from the primary glands; compare also the figures in the ***Cernosvitoviella*** and ***Mesenchytraeus*** sections.

Peculiar traits:

– Small species, especially of ***Marionina*** and ***Enchytronia***, often have two unpaired dorsal glands, one in IV, one in V, and two elongate ventral glands in VI (Figs. 8E, 37A).
– Secondary glands occur in all species of ***Cernosvitoviella*** (Figs 19A, 20E, 21A, 22) and ***Mesenchytraeus*** (Figs 16C, 17B,C, 18C,D,F), in all species of ***Cognettia*** except ***C. sphagnetorum*** (Fig. 31A,C,D) and in several species of ***Achaeta*** (Figs 23, 25C, 26A). They are also found in ***Hemienchytraeus*** (Fig. 9G) and ***Guaranidrilus*** (Figs 9H, 29A,B).
– Glands in VII or further back are found in some species of ***Fridericia*** (see shortcut after the key to species), in ***Cognettia*** (Fig. 30B–D), ***Mesenchytraeus*** (Fig. 18C,D), and often in fragmenting species (***Enchytraeus bigeminus***, ***Buchholzia appendiculata***, ***Cognettia sphagnetorum***, ***C. glandulosa***).
– ***Cernosvitoviella*** has a characteristic 2 + 2 pattern: paired and separate dorsal glands in IV and V, and paired secondary ventral glands of the same size in V and VI (Figs 19A, 20E, 21A, 22A,C–E). One species is said to have a 3 + 3 pattern.
– ***Mesenchytraeus*** has a characteristic 2 + n pattern: Dorsal glands are attached posteriorly to the septa in IV and V, and pairs of secondary ventral glands are present in a varying number of segments, down to X in some species (Figs 16C, 17B,C, 18C,D,F). They are irregularly lobed, closely attached to the oesophagus, and sometimes very large, occupying much space in the segment; their distinction from the primary dorsal glands may be difficult.

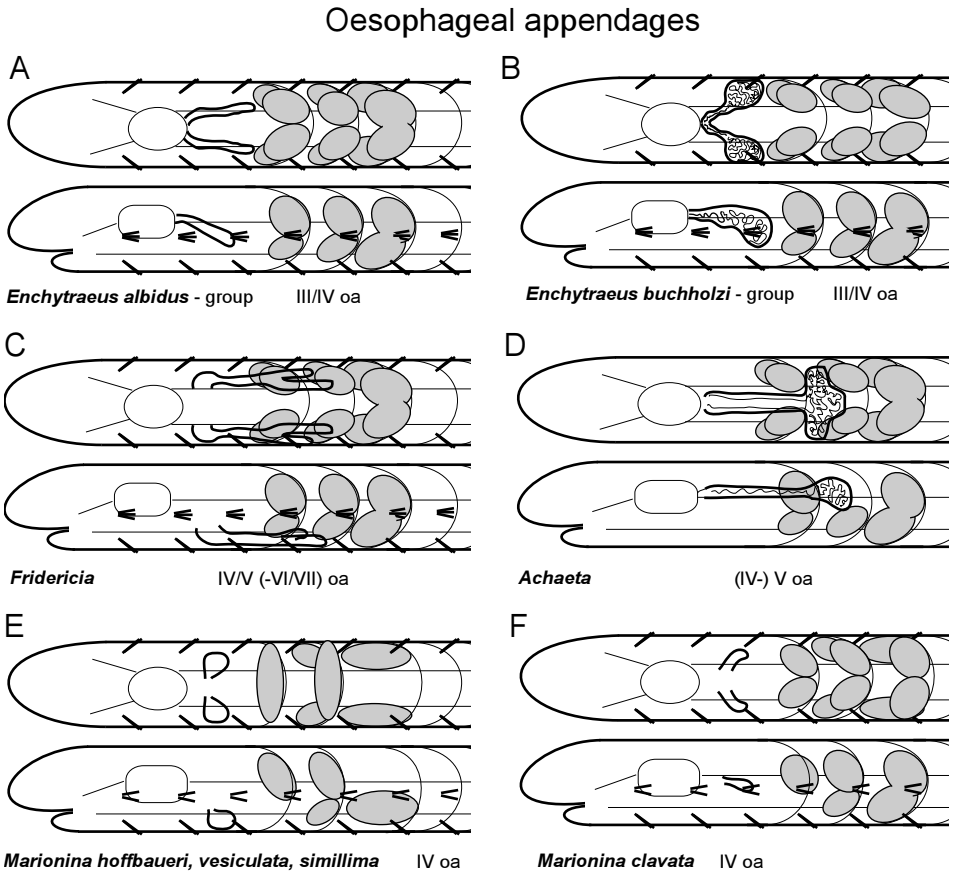

Fig. 8 Oesophageal appendages (oa), taxonomic traits, with pharyngeal glands (shaded grey).

The two following paragraphs deal with structures closely associated with the anterior gut. Their distinction into ‘oesophageal appendages’ and ‘intestinal diverticula’ is not always clearcut, and some structures may fall into either category in some groups with a gradual transition from the oesophagus into the intestine. There is also large variation in each category, see Figs 8 and 9. However, neither a lumping into one category nor a further subdivision seemed appropriate for the purposes of this key. Oesophageal appendages are located more anteriorly (III–VII), and intestinal diverticula more posteriorly (VI–VIII). Note that there are taxa with both oesophageal appendages and intestinal diverticula, but no taxa with two types of oesophageal appendages or two types of intestinal diverticula. Many taxa are without any kind of gut attachment or outgrowth.

Oesophageal appendages (Figs 8, 9) are hollow blind-ending organs, usually paired, attached to and opening into the oesophagus; in some species an opening has not been demonstrated. They often characterise genera. They are found in segments III to VII. Those of anterior segments (III–IV) are tube-or pouch-like and they connect with the oesophagus only at the junction; the rest extends freely into the body cavity. Those of posterior segments (IV–VII) are bean-shaped or of irregular outline, and they are closely and widely attached to the oesophagus. They often have a spongy consistency; a lumen and a connection with the oesophageal lumen is not always evident. Both types have been distinguished in the literature as 'pharyngeal peptonephridia' and 'oesophageal peptonephridia/appendages', respectively. Oesophageal appendages are absent in all European species of ***Mesenchytraeus***, ***Cernosvitoviella***, ***Stercutus***, ***Cognettia***, ***Lumbricillus***, ***Enchytronia***, ***Hemifridericia***, and in several European species of ***Achaeta*** and ***Marionina***.

The following gives an overview of the types of oesophageal appendages and their distribution among European taxa.

- Segment III, paired, short, straight, not winded, not tapering, free tubes inserting jointly immediately behind pharyngeal pad: ***Enchytraeus albidus***-group (Fig. 8A).
- Segment III, paired, elongate, free, much winded and distally tapering tubes inserting immediately behind pharyngeal pad, extending posteriad: ***Enchytraeus buchholzi***-group (Fig. 8B), ***Hemienchytraeus*** (Fig. 9G).
  - ***Enchytraeus buchholzi***-group: tubes not branched, meandering but not compacted into a solid body, outline irregular and changing with body movements, united immediately before opening into oesophagus.
  - ***Hemienchytraeus***: Meandering tubes compacted into a body, most often bifurcating once or twice, or branching distally. Tubes proximally uniting into a common trunk with vesicle before opening into oesophagus.
- Segment IV, short and paired appendages, finger-, globe-, or sac-like, with distinct lumen, inserting at half-distance between pharyngeal pad and pharyngeal glands in IV, respectively: ***Buchholzia*** (sac, insertion dorso-lateral, Fig. 9B), ***Marionina clavata*** (finger, dorso-lateral, Fig. 8F), ***M. hoffbaueri***, ***M. vesiculata***, ***M. simillima*** (globe/sac, ventro-lateral, Fig. 8E).
- Elongate tubes with distinct lumen, not meandering, free, inserting ventro-laterally in IV, anteriorly of pharyngeal glands, extending into V(VI), branched or unbranched; very long unbranched tubes often coiled into a mass in IV: ***Fridericia*** (Fig. 8C).
- Segments IV or V, unpaired organs closely attached dorsally to oesophagus, appearance spongy, similar to nephridia, often bi-lobed in V and with a meandering canal in IV: many species of ***Achaeta*** (Fig. 8D).
- Segments IV–VI, spongy masses closely attached to oesophagus in VI, with free lobes, usually two dorsally and two ventrally, with two anterior canals, one dorsal, one ventral, extending into IV, and forming a loop before connecting with oesophagus: ***Henlea*** (Fig. 9D).
- Segment VI, spongy masses closely attached to oesophagus, with free lobes, usually two dorsally and two ventrally: ***Henlea*** (Fig. 9D).

– Segment VI, two pairs of small, oval bodies, an antero-dorsal pair and a postero-ventral pair: ***Bryodrilus*** (Fig. 9C).
– Segment VI: one pair of small oval bodies dorso-laterally; ***Guaranidrilus*** (Fig. 9H).
– Segments IV–VI; one pair ventrally of small bodies in VI, united medially and with a winding canal that projects anteriorly into IV, closely attached to the ventral surface of the oesophagus: ***Oconnorella cambrensis*** (Fig. 9E).
– Segment VII: one pair of bean-shaped bodies laterally: ***Oconnorella tubifera*** (Fig. 9F).

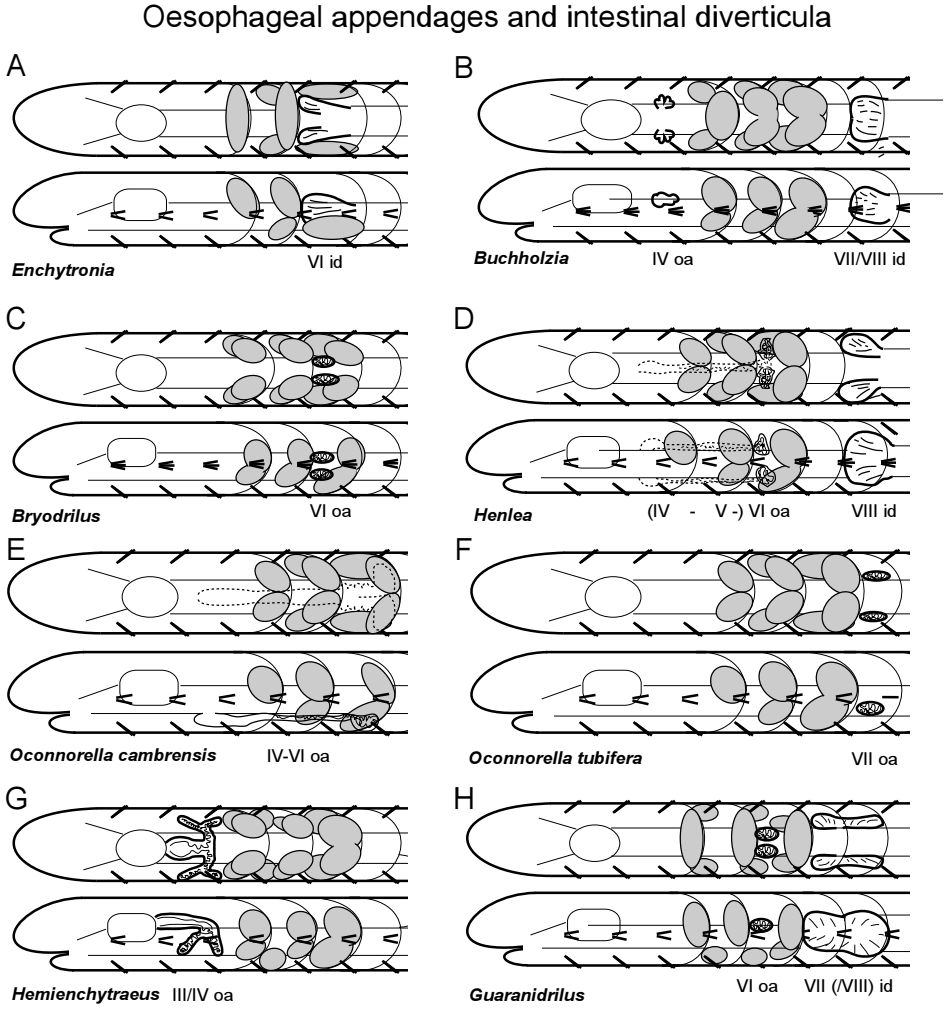

Fig. 9 Oesophageal appendages (oa) and intestinal diverticula (id), taxonomic traits, with pharyngeal glands (shaded grey).

Intestinal diverticula (Fig. 9) are sac-or pouch-like outgrowths of the intestinal epithelium directed forwards; their lumina are posteriorly continuous with that of the intestine. The gut widens often abruptly at the level of the intestinal diverticula or closely behind. Intestinal diverticula are characteristic of the genera ***Henlea***, ***Buchholzia***, ***Enchytronia***, the (sub)tropical ***Guaranidrilus***, and the monospecific ***Enchylea***, known only from a laboratory culture (Nielsen & Christensen 1963) and not included here.

Enchytronia: In VI, a lateral pair, framed by the last pair of pharyngeal glands (Fig. 9A).

Buchholzia: In VII/VIII, a dorsal organ that may extend ventrally (Fig. 9B).

Henlea: In VIII(–IX), two or four lateral pouches (Fig. 9D).

Guaranidrilus: A lateral pair of large and hollow vesicles in VII that may extend into VIII, inserting with a small pore laterally in the posterior of VII Fig. 9H).

Curiously, all four genera have also species without intestinal diverticula; in the case of ***Guaranidrilus*** a new genus, ***Tupidrilus***, has been erected for this type.

Dorsal blood vessel. Blood in the dorsal vessel runs from the rear to the front, so its origin is the posterior end, where it rises from the peri-intestinal blood sinus. The origin of the dorsal blood vessel varies from VI in some ***Achaeta*** species to beyond XX in large species of ***Fridericia*** or ***Mesenchytraeus***. The further behind it originates, the more intraspecific variation is present. A preclitellar origin of the dorsal blood vessel is a useful taxonomic trait because of its segment-constancy; it is often well-marked by large and strong pulsations of the blood vessel in the first posterior 2 or 3 segments. The following taxa have a preclitellar origin of the dorsal blood vessel:

Segment VI: ***Achaeta aberrans***, ***A. bohemica.***
Segment VII: several ***Achaeta*** species, ***Buchholzia***, ***Marionina eleonorae***.
Segment VIII: ***Achaeta camerani***, ***Henlea*** spp.
Segment IX: ***Henlea*** spp., ***Stercutus niveus.***

This trait applies only to adult specimens, because in juveniles of other species the dorsal blood vessel may originate in an anterior segment as well. A preclitellar origin of the dorsal vessel is often, but not always correlated with the presence of intestinal diverticula.

An intra- or postclitellar origin may be inconspicuous when the blood vessel remains embedded in the layer of chloragocytes over several posterior segments. In this case it is useful to observe the waves of gut contractions, which always run forwards. At the point where the blood vessel begins (somewhere between XII and XXV) the movement of contraction is suddenly continued only in the mid-dorsal part of the gut, and it runs slightly faster than before.

In almost all species, the dorsal blood vessel ends in segment I, the peristomium, below and slightly in front of the brain, where it bifurcates into the two circumoral connectives (Fig. 10 right). In some smaller species of ***Marionina*** the bifurcation point lies behind the pharynx. i.e. in segment III (Fig. 10 left). In the literature terms like ‘marionine’ or ‘pharyngeal’ denote the bifurcation in III, and ‘lumbricilline’ and ‘prostomial’ the bifurcation in I (Giere 1974, Rota 1995). We have described a bifurcation in III in fragmenting ***Enchytraeus*** species (Schmelz et al. 2000), but in recent investigations (unpublished) we found it to be in I as usual.

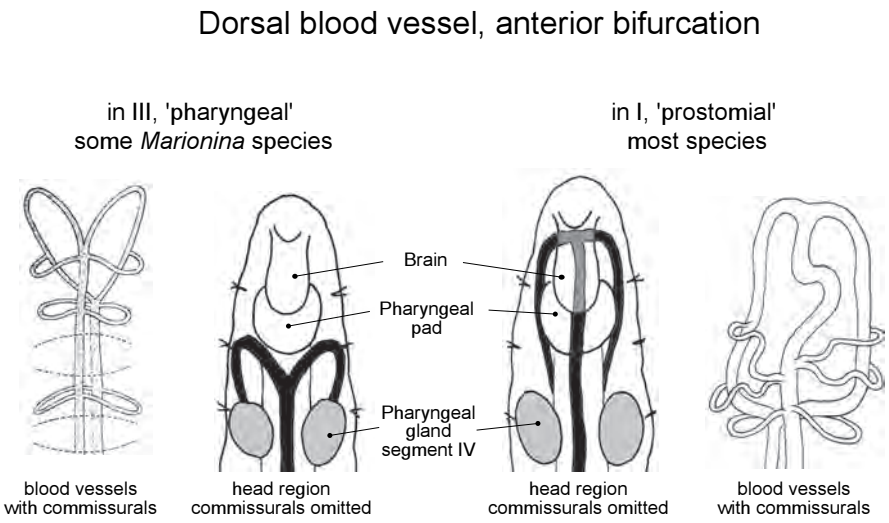

Fig. 10 Dorsal blood vessel, bifurcation in I (left), or III (right). Left from Hesse (1893, Pl. 1 Fig. 1); right from Vejdovský (1879, Pl. 8 Fig. 8).

The **blood** is colourless in most species. A red, reddish, yellowish, or greenish tinge is present in ***Lumbricillus*** spp., ***Fridericia magna***, ***F. ilvana***, ***Mesenchytraeus sanguineus***, ***Cognettia sphagnetorum*** (partim), ***C. clarae*** (partim), some species of ***Cernosvitoviella***, ***Enchytraeus albidus*** (partim), ***Marionina riparia***, ***M. filiformis***, and ***M. rubens***. The trait is variable in several species.

Other gut structures. Pharyngeal pad, pharyngeal muscles, afferent fascicles of pharyngeal glands, and the oesophagus are without taxonomically useful differences, but the structures should be recognised to avoid confusion with other traits. For example, afferent fascicles or pharyngeal muscles may be confused with oesophageal appendages, or the pharyngeal pad may be confused with the brain or pharyngeal glands.

The intestine consists of two epithelial layers: outer mesodermal peritoneum, and inner entodermal gut epithelium. Both layers are separated by a circumferal cavity, the peri-intestinal blood sinus, which extends throughout the body from segment IV or V on. Both outer and inner layer are with taxonomically useful traits.

Outer layer: From segment V on, peritoneal cells are differentiated into **chloragocytes**. The chloragocyte layer (chloragogenous tissue) which covers the intestine is among the most conspicuous traits in living worms but of little taxonomic value. Cells are filled with vesicles that often give a tinge that differs from the rest of the body, somewhat darker, greenish-yellowish, or brownish-grey (Fig. 1B). The coverage of the intestine is usually denser in anterior than in posterior segments. In well-fed species of ***Enchytraeus*** the chloragocytes can fill out almost the entire body cavity. The distinctly white body colour of ***Stercutus niveus*** is caused by a dense layer of very tall chloragocytes.

Some chloragocytes are frequently found detached and floating in the coelomic fluid. They may be mistaken as coelomocytes, but the texture of both types of cells is always different (Fig. 1B).

Inner layer: The intestinal epithelium of all ***Fridericia*** species has canalised cells in a region that may mark the transition from oesophagus to intestine, so-called '**chylus cells'**. Each cell is perforated by a thread-like, ciliated, incurved, blind-ending canal that opens into the intestinal lumen. Chylus cells form together a characteristic repetitive pattern in the intestinal wall (Fig. 50, 59B, 62A). Their approximate segment location is species-specific, and location of the chylus cell region in pre-clitellar segments is a good taxonomic character in adult specimens.

In almost all enchytraeids, the ventral epithelium of the posterior intestine is conspicuously thickened over several segments; this structure has been termed 'ventral intestinal ridge' (Rota 1995), 'pars tumida' (Schmelz et al. 2008), or incorrectly 'ventrally inflated gut endothelium' (Schmelz 2003). The trait is conspicuous only in properly fixed material and not used here.

Coelomocytes (e.g., Figs 19D, 32F, 48J, 60H) are flattened in enchytraeids. Taxonomically useful are quantity, size, shape, and texture. Specifics are well-known only in recently described or re-described species.

The nucleate **mucocytes** are either circular in outline, oval, rhomboid or spindle–shaped. In order to ascertain the shape it is important (1) to choose the largest cells – in species with oval mucocytes the smaller ones are often circular in outline – and (2) to choose only cells that are oriented perfectly in the focusing plane – cells in oblique or vertical position appear to be spindle- or even rod-shaped (comp. Fig. 48J) when in fact they are oval or circular. Rhomboid or spindle-shaped mucocytes are found only in species of ***Cernosvitoviella***, ***Lumbricillus***, and ***Mesenchytraeus***. Mucocytes are ca 20–60 µm long; their texture, created by organelles or bodies in the cytoplasma, is taxon-specific. Often the entire cell is filled with globular vesicles, more or less distinct, and all the same size. Or no vesicles are seen but rather grooves or some kind of irregular undulation. Möller (1971) has introduced a typology, widely used in the literature (type 'a': vesicles blurred, 'b': vesicles refractile; 'c': vesicles pale, distinct). The description of the mucocyte texture is difficult to standardise, since the aspect changes with the optical properties and adjustments of the microscope; but used in comparison it is of great help in routine identification of larger samples of specimens. For example, vesicles in ***Henlea*** and ***Bryodrilus*** are especially fine and regular, compared to those of ***Fridericia***, ***Buchholzia***, or ***Enchytraeus***.

Most conspicuous and taxonomically useful is the presence of light-refractile vesicles or granules (the terms are roughly synonymous); they are often concentrated at the cell periphery but may occupy the entire cell area. Aggregations of such cells may be dark and opaque in transmittent light and they give the worm a distinct white body colour under the dissecting microscope.

Lenticytes are completely hyaline and oval plates of 3–12 µm length. Size and quantity (in relation to mucocytes) are taxon-specific. Large and very abundant lenticytes are characteristic of ***Buchholzia appendiculata***. Small lenticytes are often attached to the margins of mucocytes. Lenticytes are present in all species of ***Fridericia***, ***Buchholzia*** and ***Hemifridericia***, and absent in all other European species. In a few species of ***Fridericia*** they are sparse and appear to be absent.

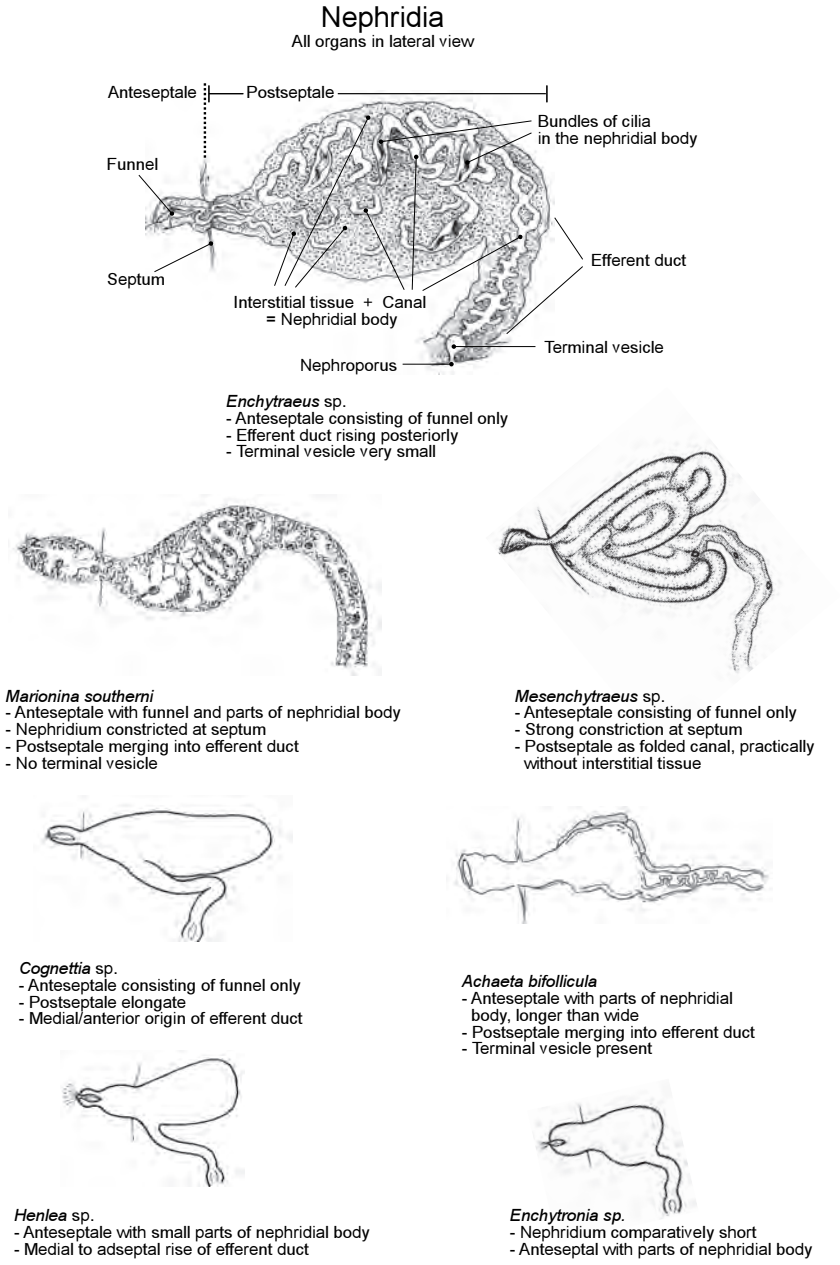

Fig. 11 Nephridia, structure and variations. From (top to bottom and left to right) Goodrich (1897, Pl. 5 Fig. 2); Knöllner (1935a, Fig. 15); Michaelsen (1897, Pl. 21 Fig. 1d); Nielsen & Christensen (1959, Fig. 28); Chalupský (1992, Fig. 5D); Nielsen & Christensen (1959, Figs 50, 36).

Peculiar traits:

- Mucocytes and lenticytes present: ***Fridericia***, ***Buchholzia***, ***Hemifridericia***.
- Apparently only lenticytes present, mucocytes rare, inconspicuous: ***Buchholzia appendiculata***, ***Fridericia profundicola***.
- Mucocytes dark in transmittent light, completely filled with refractile vesicles: ***Cernosvitoviella*** and ***Mesenchytraeus*** (several species)***, Marionina argentea***, ***M. southerni***, ***Fridericia nix***, ***F. granosa***, ***F. pyrenaica***, ***Enchytraeus norvegicus***, ***E. bulbosus***, ***E. buchholzi*** s.l.
- Coelomocytes rhomboid or spindle-shaped, with distinct tips at both ends: several species of ***Lumbricillus***, ***Mesenchytraeus***, and ***Cernosvitoviella***.

Nephridia (Fig. 11) are inter- or bisegmental organs, attached to ventro-lateral strands of the septa. The anterior part, the **anteseptale**, comprises always the funnel and often also parts of the nephridial body (= canal + interstitial tissue). The posterior part, named **postseptale**, consists of the nephridial body and the efferent duct, which opens by a nephroporus on the body surface. The efferent duct may be widened into a bladder-like terminal vesicle right beneath the porus. The canal in the nephridial body is much winded, somewhat diffuse, and with short branches or lacunae. In ***Mesenchytraeus*** the canal is unbranched and conspicuous throughout and resembles the nephridia of aquatic oligochaetes (tubificids and lumbriculids); interstitial tissue is practically absent here.

Nephridia are best observed in lateral or ventro-lateral view. In living specimens they can be distinguished from other structures by the undulating movements of the cilia: a fan of cilia outside the funnel, and a 'flame' inside the funnel; further 'flames' (2–4) are undulating in the postseptal nephridial body. The most anterior part of the nephridial body is often darker than the rest; the tinge is often the same as in the chloragocytes, probably due to the resorption of remnants of detached chloragocytes.

In this key we use three traits: (1) Shape and size of the anteseptale, useful at the genus level, and (2) number and location of nephridia in anterior (= preclitellar) segments, used to distinguish species. (3) In a few instances the insertion of the efferent duct is also included.

(1) The anteseptale may consist only of the ciliated funnel, while the rest of the nephridial body lies behind the septum: All species of ***Mesenchytraeus***, ***Cernosvitoviella***, ***Cognettia***, ***Lumbricillus***, ***Enchytraeus***, and ***Oconnorella***, some species of ***Henlea*** and ***Bryodrilus***, ***Achaeta abulba***. Anteseptale rather short, with only small parts of the nephridial body: ***Buchholzia***, ***Henlea***, ***Bryodrilus***, ***Achaeta bibulba***.

(2) A very useful taxonomic trait is the distribution of nephridia in preclitellar segments. The first nephridium is usually at 6/7 (which means that the anteseptale with funnel is in segment VI, and the postseptale + nephroporus in segment VII), and two to five preclitellar pairs are usually present, but there is wide variation among taxa. ***Henlea ventriculosa*** has 7 pairs, from 4/5 to 10/11, and ***Oconnorella tubifera*** has 6 pairs, from 5/6 to 10/11. ***Achaeta abulba*** and ***A. bibulba*** have only one pair, at 6/7. In ***Cognettia clarae*** the most anterior nephridium is in the head region at about segment II, whereas in fragmenting species nephridia begin as far back as 8/9 or 9/10. Single specimens may blur the pattern, because sometimes not all nephridia are developed, or some are resorbed or necrotic. The nephridial distribution pattern is unknown in several species.

(3) The efferent duct rises from the ventral side of the postseptale, either anteriorly, close to the septum, or posteriorly, at the end of the postseptale, or somewhere in between. Often the distinction between postseptale and efferent duct is not marked and there is a gradual transition from one into the other.

4.4. Internal characters, reproductive system

Seminal vesicles are open sacs created by a paired forward bulging of septum 10/11 dorsally (Fig. 4: '28'). They are present in species with large amounts of developing sperm. However, sperm masses are not only present in the vesicles but also in the rest of segment XI, which further may extend its volume over several segments by a bulging of the septa that delimit segment XI (Fig. 12B, 42M), i.e. a forward bulge of 10/11 and a backward bulge of 11/12. Therefore in the literature any large mass of spermatogonia is usually equivalent with a seminal vesicle. Taxonomically useful here is presence/absence and its extension (1, 2 or 3 segments). In species without seminal vesicle developing sperm is scarce and restricted to the dorsal part of XI. There is some intra-specific variation that may depend on the stage of maturity. In ***Mesenchytraeus***, septum 11/12 may be bulged backwards by several segments, and masses of sperm can be seen behind the clitellum. This is called **sperm sac** in the literature, although there is no structural difference to seminal vesicles.

Testis sacs are a peculiar feature of ***Lumbricillus*** and ***Enchytraeus***. Here developing sperm remains enclosed by a common membrane that also encloses the testes. Fully mature sperm is seen outside the sacs, attached to the sperm funnel collar as in other taxa. ***Enchytraeus*** has two testis sacs, one on each side (Fig. 32G,H). In ***Lumbricillus***, testis sacs of the larger species (with more than 3 chaetae per bundle) are arranged in a bouquet of pear-shaped lobes that may extend into X or IX. They are best seen in lateral view (Fig. 35A). In smaller species the lobes are inconspicuous or absent.

Sperm funnel (= male funnel). Shape and size offer useful taxonomic traits (Fig. 12): (1) length of funnel body relative to the worm body diameter (when pressed); (2) length : width ratio; (3) width of collar relative to the funnel body; (4) overall shape (e.g., cylindrical, or pear-shaped), and sometimes, texture (size and distribution of vesicles in the funnel body). Large sperm funnels (ca 2x as long as body diameter or even more) are found in some species of ***Enchytraeus***, ***Lumbricillus***, ***Fridericia***, and ***Achaeta*** (comp. Fig. 23 right), usually in species with abundant sperm. Large funnels are quite floppy and vary much in shape according to their position. The smallest funnels are found in some species of ***Cernosvitoviella*** (comp. Fig. 20D). The funnel may be as wide as long or up to 10 to 15 times as long as wide. The collar can be as narrow as 1/3 of the funnel body or more than twice as wide (Fig. 12D).

Vas deferens (= sperm duct, spermioduct) (Fig. 12D). The vas deferens is usually a thin and isodiametric tube, longer than the body diameter and wound in numerous irregular loops ventrally in XII, between sperm funnel and male pore. In ***Achaeta***, ***Guaranidrilus*** and ***Hemienchytraeus*** contraction of its muscles leads to a series of closely attached spirals of equal diameter (Fig. 28A). In ***Cernosvitoviella*** and some species of ***Mesenchytraeus*** and ***Achaeta*** the vas deferens is comparatively short, with few loops or no loops at all. In ***Cernosvitoviella*** and in species of the ***Enchytraeus albidus*** group, the vas deferens may be widened in determined regions. In some species of ***Mesenchytraeus***, an atrium-like dilatation

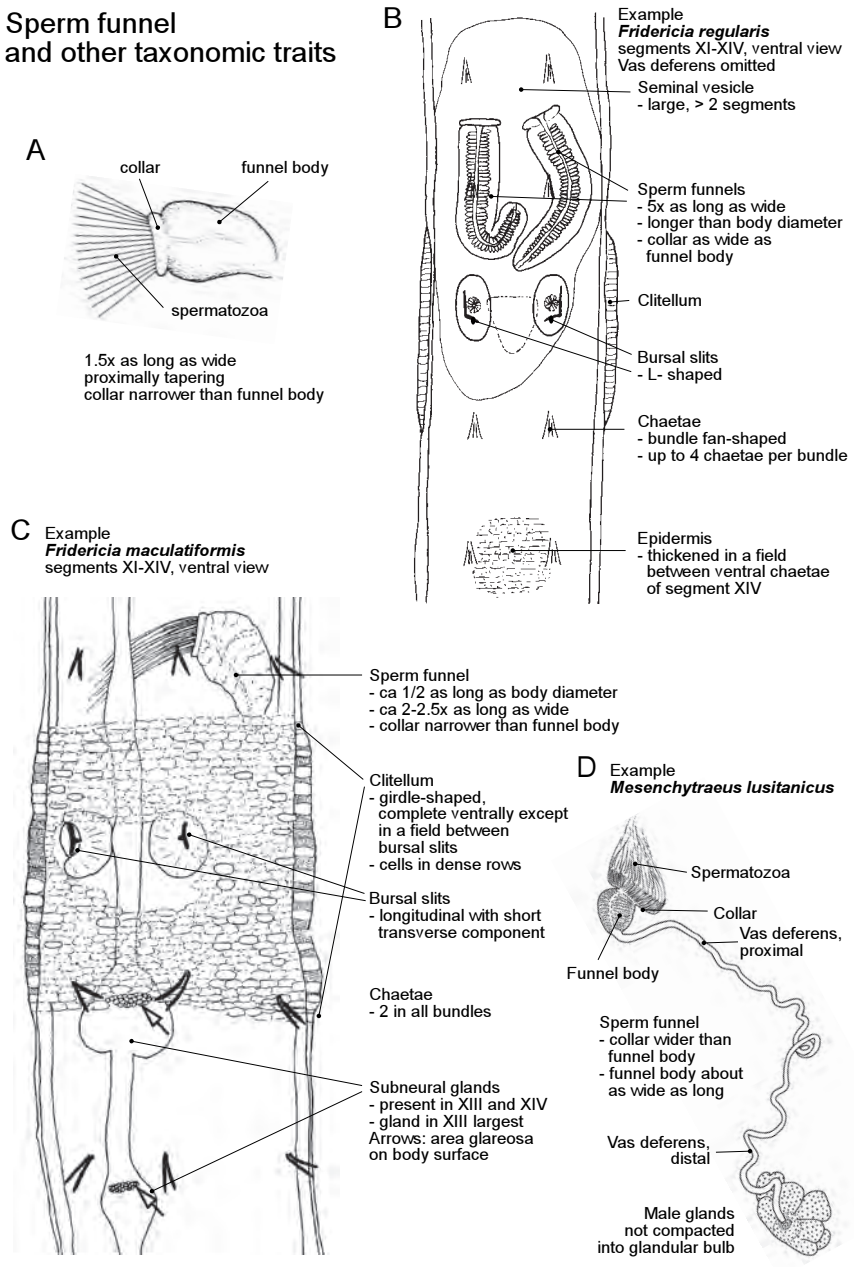

Fig. 12 Sperm funnel and other taxonomic traits. A from Chalupský (1994, Fig. 12). B from Schmelz (2003, Fig. 61B). C from Schmelz (2003, Fig. 45B). D from Collado & Martínez-Ansemil (1993, Fig. 3E).

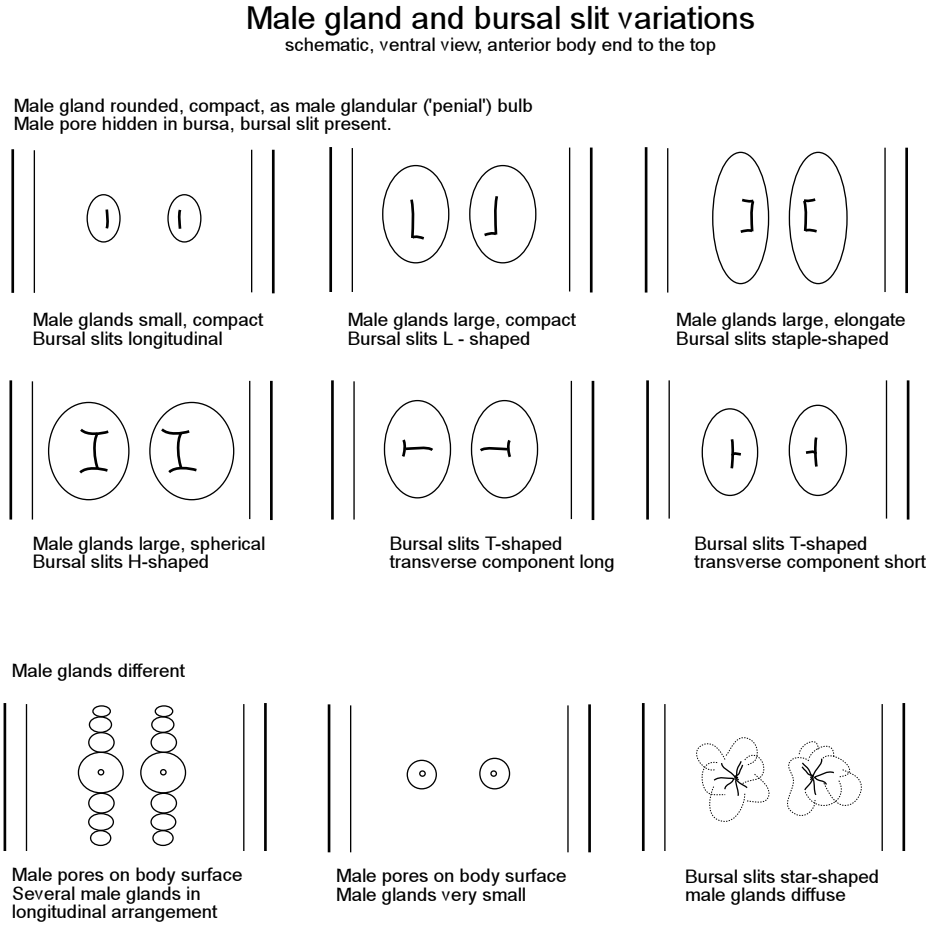

Fig. 13 Male glands and bursal slit, variations.

occurs at the ectal end of the vas deferens, and glands are attached, somewhat similar to the atria in tubificids and naidids. Although restricted to segment XII, loops of the vas deferens may be seen in segments posterior to the clitellum, due to a bulging backward of septum 12/13 by several segments (***Enchytraeus albidus*** and some species of ***Mesenchytraeus***).

The **male copulatory organ** (Figs 12B–D, 13) surrounds the male pore, it consists of (1) glands, (2) bursa, and (3) musculature. One or several components may be missing in some species; the musculature is of little taxonomic importance.

(1) Glands around the male pore are either compacted into a single body, the male glandular bulb (= penial bulb), or several glandular bodies are arranged in a longitudinal row anteriorly and posteriorly of the male pore, with the central body usually being the largest. Glandular bulbs are present in most of the taxa. Their size and outline is taxonomically useful, although

intraspecific variations occur. Rows of gland cells are found in many species of ***Achaeta*** and in ***Enchytraeus albidus*** and related species. Glands are rarely absent completely (e.g. ***A. abulba***). In ***Cernosvitoviella*** and ***Mesenchytraeus*** glands around the male pore are not compacted, or they are absent.

(2) Each male pore lies either on the body surface (***Achaeta***, ***Guaranidrilus***, perhaps ***Cernosvitoviella***), or it is hidden in an epidermal invagination or bursa. The bursa is eversible and morphologically equivalent to what in aquatic oligochaetes is termed 'pseudopenis'. The bursa opens slit-like on the body surface; form and orientation of the slit is used in ***Fridericia*** to distinguish species. In most other species it has not yet been adequately described. In ***Enchytraeus*** species of the ***buchholzi***-group the slit is longitudinal. In ***Mesenchytraeus*** the bursal opening is not a slit but rather a hole with irregular outline. The bursa is often partly or fully everted due to the pressure on the worm during live investigation or as a fixation artefact. Bursal slit shape can be ascertained only when the bursa is fully retracted.

(3) Musculature usually encloses the male glandular bulb, giving it a compact shape. Glandular bulbs without muscular coating are floppy and irregular in shape. Further dorso-ventral muscle strands – copulatory muscles – are arranged in parallel on each side of the body, anteriorly and posteriorly of the male pore. For further details see Schmelz (2003).

The **spermathecae** (Fig. 14) are best studied with the worms in lateral to dorsal position, and investigation starts conveniently with the localisation of the ectal pore, situated at half-length and slightly below the lateral chaetae of IV and V. The pore is minute (diameter ca 1 µm) but due to its exact position it can be localised without too much difficulty. In ***Lumbricillus*** the pore is enlarged. Several species of ***Achaeta*** have ventral pores. Starting with the pore, the course of the organ is now followed focusing inside the body. Five basic distinctions should be recognised and noted:

(1) The ectal duct is either smooth and non-glandular, or wavy-bushy, i.e. glandular.

(2) Ectal glands, close to the ectal pore, and different from the ectal duct, are present or absent.

(3) The ampulla, the central sperm-containing chamber, is with or without diverticula.

(4) The ampulla is proximally attached to the oesophagus, or the ampulla is proximally blind-ending, not attached to oesophagus, and floating freely in the coelomic cavity. In the key we use the pair **attached** / **free** to designate this alternative.

(5) Attached spermathecae have either separate connections with the lateral or dorso-lateral sides of the oesophagus, or the spermathecae are united proximally and connect jointly with the oesophagus dorsally. We use the pair **separate** / **fused** to designate this alternative.

Apart from these distinctions, size proportions of the constituent parts are most important (e.g., ectal duct shorter or longer than ampulla, diverticula longer than wide or shorter, etc.). In some species of ***Fridericia***, the diverticula have two chambers, an apical sperm-containing one and a basal subchamber equipped with cilia (Figs 63B, 65B).

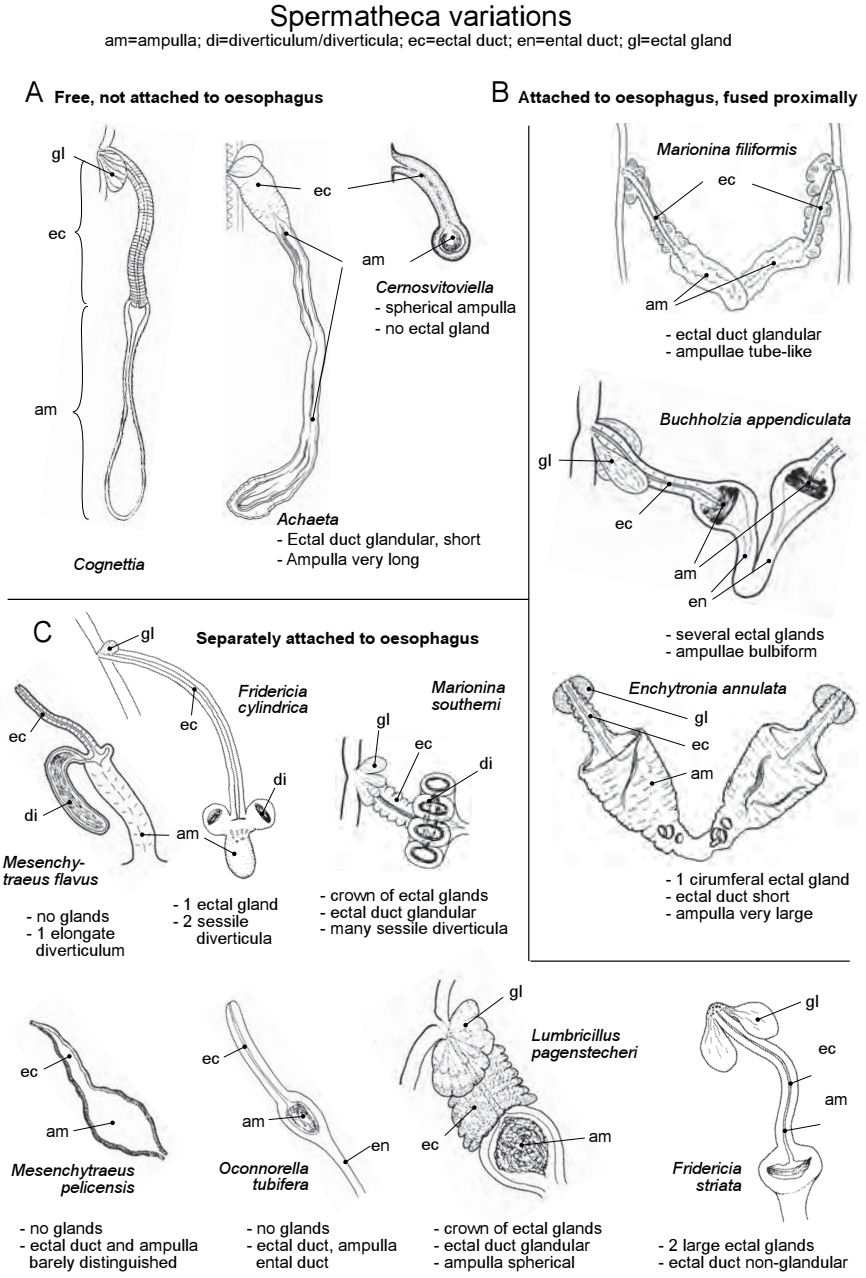

Fig. 14 Spermatheca, structure and variations. A from Černosvitov (1945, Fig. 69), Chalupský (1992, Fig. 2A); Dózsa-Farkas (1990, Fig. 14). B from Schmelz et al. (2008, Fig. 1F); Nielsen & Christensen (1959, Fig. 62); Chalupský (1994, Fig. 8). C from Nielsen & Christensen (1959, Fig. 10); Schmelz (2003, Fig. 30F); Nielsen & Christensen (1959, Fig. 135); Issel (1905a, Pl. 13 Fig. 12); Rota (1995, Fig. 17F); Erséus (1976, Fig. 8); Schmelz (2003, Fig. 64H).

Two further anomalies deserve mentioning:

In a few species, the spermathecae are completely absent in the adult stage, while other parts of the male reproductive system including the male parts are completely developed. These populations apparently reproduce by parthenogenesis but the function of the male system is obscure unless the switch from bisexuality to parthenogenesis is a very recent event. The **athecate** condition is characteristic of ***Fridericia christeri*** and ***Achaeta affinis***; their thecate counterpart is unknown. Athecate forms occur in several other species (see ***Enchytraeus buchholzi*** and ***E. dichaetus***), which include bisexual species and parthenogenetic lineages.

Occasionally, an extra pair of spermathecae may be present in IV or VI. We consider this **quadrithecate** condition as a developmental anomaly, and the two species erected on this criterium – ***Henlea puteana*** and ***Enchytraeus polonicus*** – are not accepted here.

Subneural glands (Fig. 12C) are closely attached to the ventral nerve cord in segments XIII–XV or XVI. In living specimens they appear as an enlargement of the nerve cord itself, but in fact they are a compact mass of epidermal cells that project into the body cavity, thereby sourrounding the ventral nerve cord; on the body surface an 'area glareosa' makes their glandular nature evident: hyaline and cobble-like accumulations of gland cell apices. Subneural glands are described in more detail in Schmelz (2003). Presence, size, and location are often taxon-specific, within certain limits; these limits are not yet established in all species. Subneural glands are found in: ***Lumbricillus*** (many if not all species), ***Fridericia*** (see shortcut after the species key), ***Buchholzia subterranea***, ***Marionina southerni***, and in several other marine or non-European taxa, not included in this key.

Oocytes (= eggs). Usually there are only 1–2 fully mature eggs at a time, recognisable by large amounts of yolk. ***Stercutus niveus*** and species of ***Enchytraeus***, ***Lumbricillus***, ***Mesenchytraeus*** may have more than 3 mature oocytes, sometimes up to 12.

Egg sacs occur in ***Mesenchytraeus***, caused by a bulging backwards of septum 12/13 over several segments: oogonia and yolky oocytes extend often as far back as segment XVIII or XX.

5. Species list

This key includes 206 accepted species. Compare also the online-list in the Fauna Europaea 3.1 (http://www.faunaeur.org), which reflects the state-of-the-art until 2002 (accessed March 2010). Asterisk: new taxonomic proposal.

Achaeta aberrans Nielsen & Christensen, 1961

Achaeta abulba Graefe, 1989

Achaeta affinis Nielsen & Christensen, 1959

Achaeta afolliculata Sesma & Dózsa-Farkas, 1993

Achaeta antefolliculata Dózsa-Farkas & Boros, 2005

Achaeta bibulba Graefe, 1989

Achaeta bifollicula Chalupský, 1993

Achaeta bohemica (Vejdovský, 1879)

*= ***Achaeta microcosmi*** Heck & Römbke, 1991

*= ***Achaeta vesiculata*** Nielsen & Christensen, 1959

Achaeta brevivasa Graefe, 1980

Achaeta bulbosa Nielsen & Christensen, 1961

Achaeta camerani (Cognetti, 1899)

Achaeta danica Nielsen & Christensen, 1959

Achaeta diddeni Graefe, 2008

Achaeta eiseni Vejdovský, 1878

(***Achaeta etrusca*** Rota, 1995: see ***A. iberica***)

Achaeta hallensis Möller, 1976

Achaeta iberica Graefe, 1989

*= ***Achaeta etrusca*** Rota, 1995

Achaeta matritensis Sesma & Dózsa-Farkas, 1993

(***Achaeta microcosmi*** Heck & Römbke, 1991 see ***A. bohemica***)

Achaeta minima Southern, 1907

Achaeta pannonica Graefe, 1989

= ***Achaeta petseri*** Dózsa-Farkas, 1998

Achaeta seminalis Kasprzak, 1972

Achaeta unibulba Graefe, Christensen & Dózsa-Farkas, 2005

Achaeta parva Nielsen & Christensen, 1961

Achaeta urbana Heck & Römbke, 1991

(***Achaeta vesiculata*** Nielsen & Christensen, 1959 see ***A. bohemica***)

Bryodrilus ehlersi Ude, 1892

(***Bryodrilus ehlersi*** ssp. ***glandulosus*** Dózsa-Farkas, 1990 see ***B. glandulosus***)

Bryodrilus diverticulatus Černosvitov, 1929

****Bryodrilus glandulosus*** Dózsa-Farkas, 1990 new rank

****Bryodrilus librus*** (Nielsen & Christensen, 1959), new combination, ex ***Marionina***

Bryodrilus parvus Nurminen, 1970

Buchholzia appendiculata (Buchholz, 1862)

Buchholzia fallax Michaelsen, 1887

Buchholzia simplex Nielsen & Christensen, 1963

*= ***Marionina serbui*** Botea, 1984

Buchholzia subterranea (Černosvitov, 1937b)

Cernosvitoviella aggtelekiensis Dózsa-Farkas, 1970

*= ***Cernosvitoviella goodhui*** Healy, 1975

Cernosvitoviella ampullax Klungland & Abrahamsen, 1981
Cernosvitoviella atrata (Bretscher, 1903)
*= ***Cernosvitoviella microtheca*** Rota & Healy, 1999
Cernosvitoviella briganta Springett, 1969
Cernosvitoviella bulboducta Martínez-Ansemil & Collado, 1996
Cernosvitoviella carpatica Nielsen & Christensen, 1959
Cernosvitoviella crassoductus Dózsa-Farkas, 1990
(***Cernosvitoviella estaragniensis*** Giani, 1979 see ***C. palustris***)
(***Cernosvitoviella goodhui*** Healy, 1975 see ***C. aggtelekiensis***)
Cernosvitoviella immota (Knöllner, 1935)
(***Cernosvitoviella microtheca*** Rota & Healy, 1999 see ***C. atrata***)
Cernosvitoviella minor Dózsa-Farkas, 1990
Cernosvitoviella omodeoi Rota, 1995
Cernosvitoviella palustris Healy, 1979
= ***Cernosvitoviella estaragniensis*** Giani, 1979
Cernosvitoviella parviseta Gadzińska, 1974
Cernosvitoviella sphaerotheca Healy, 1975
Cernosvitoviella tatrensis (Kowalewski, 1916)
Cernosvitoviella tridentina Dumnicka, 2004
Cognettia clarae Bauer, 1993
*= ***Mesenchytraeus franzi*** Nurminen, 1977
*= ***Euenchytraeus bisetosus*** Bretscher, 1906
Cognettia cognettii (Issel, 1905)
Cognettia glandulosa (Michaelsen, 1888)
Cognettia hibernica Healy, 1975
Cognettia lapponica Nurminen, 1965
Cognettia sphagnetorum (Vejdovský, 1878)
*= ***Cognettia anomala*** (Černosvitov, 1928a)
*= ***Cognettia paxi*** (Moszyński, 1938)
Enchytraeus albidus Henle 1837
Enchytraeus bigeminus Nielsen & Christensen, 1963
Enchytraeus bohemicus Dumnicka, 1996
Enchytraeus buchholzi Vejdovsky, 1879
*= ***Enchytraeus florentinus*** Bell, 1947
*= ***Enchytraeus polonicus*** Dumnicka, 1977
Enchytraeus bulbosus Nielsen & Christensen, 1963

Enchytraeus capitatus v. Bülow, 1957

*= ***Enchytraeus irregularis*** Nielsen & Christensen, 1961

Enchytraeus christenseni Dózsa-Farkas, 1992, replacement name for ***E. minutus*** Nielsen & Christensen, 1961

(***Enchytraeus christenseni bisetosus*** Rota & Healy, 1994 see ***E. dichaetus***)

Enchytraeus coronatus Nielsen & Christensen, 1959

Enchytraeus crypticus Westheide & Graefe 1992

*= ***E. variatus*** Bouguenec & Giani 1987

* ***Enchytraeus dichaetus*** new name and new rank for ***E. christenseni bisetosus*** Rota & Healy, 1994

Enchytraeus doerjesi Westheide & Graefe, 1992

*? = ***Enchytraeus dominicae*** Dumnicka, 1976

(***Enchytraeus florentinus*** Bell, 1947 see ***Enchytraeus buchholzi***)

(***Enchytraeus irregularis*** Nielsen & Christensen, 1961 see ***Enchytraeus capitatus***)

Enchytraeus lacteus Nielsen & Christensen, 1961

Enchytraeus luxuriosus Schmelz & Collado, 1999

Enchytraeus mariae Kasprzak 1973

Enchytraeus norvegicus Abrahamsen, 1969

(***Enchytraeus variatus*** Bouguenec & Giani 1987 see ***E. crypticus***)

Enchytraeus varithecatus Bouguenec & Giani 1987

(***Enchytraeus polonicus*** Dumnicka, 1977 see ***Enchytraeus buchholzi***)

Enchytronia annulata Nielsen & Christensen, 1959

Enchytronia hellenica Dumnicka, 1980

Enchytronia longispermatheca Chalupský, 1991

(***Enchytronia minor*** Möller, 1971 see ***E. parva***)

Enchytronia oligosetosa Sesma & Dóza-Farkas, 1993

Enchytronia parva Nielsen & Christensen, 1959

= ***Marionina diverticulata*** Nurminen, 1970b

= ***Enchytronia minor*** Möller, 1971

*= ***Enchytronia christenseni*** Dózsa-Farkas, 1970

Enchytronia pratensis Chalupský, 1994

(***Euenchytraeus bisetosus*** Bretscher, 1906 see ***Cognettia clarae***)

Fridericia alata Nielsen & Christensen, 1959

Fridericia anomala Košel, 1975

Fridericia argillae Schmelz, 2003

Fridericia asymmetricoides Kasprzak, 1972

Fridericia aurita Issel, 1905

Fridericia auritoides Schmelz, 2003
Fridericia baskini Černosvitov, 1937
Fridericia benti Schmelz, 2002
Fridericia berninii Dózsa-Farkas, 1988
Fridericia bisetosa (Levinsen, 1884)
Fridericia brachiata Rota, 1994
Fridericia bretscheri Southern, 1907
Fridericia brunensis Schlaghamerský, 2008
Fridericia bubalus Sesma & Dózsa-Farkas, 1993
Fridericia bulboides Nielsen & Christensen, 1959
(***Fridericia caprensis*** Bell, 1947 see ***F. pretoriana***)
Fridericia christeri Rota & Healy, 1999
Fridericia conculcata Dózsa-Farkas, 1986
Fridericia connata Bretscher, 1902
Fridericia crassiductata Dózsa-Farkas & Cech, 2006
Fridericia cusanica Schmelz, 2003
Fridericia cylindrica Springett, 1971
= ***Fridericia sohlenii*** Rota et al., 1998
Fridericia deformis Möller, 1971
Fridericia discifera Healy, 1975
Fridericia dozsae Schmelz, 2003
Fridericia dura (Eisen, 1879)
(***Fridericia eiseni*** Dózsa-Farkas, 2005 see ***Fridericia ratzeli***)
Fridericia florentina Dequal, 1914
Fridericia gamotheca Issel, 1905
Fridericia galba (Hoffmeister, 1843)
Fridericia gigantea Dequal, 1912
Fridericia glandifera Friend, 1911
Fridericia globuligera Rota, 1995
(***Fridericia gracilis*** von Bülow, 1957 see ***F. minor***)
Fridericia granosa Schmelz, 2003
Fridericia healyae Schmelz, 2003
Fridericia hegemon (Vejdovský, 1878)
Fridericia humicola Bretscher, 1900
Fridericia ilvana Issel, 1905
Fridericia isseli Rota, 1994
Fridericia lacii Dózsa-Farkas, 2009

Fridericia larix Schmelz & Collado, 2005
Fridericia lenta Schmelz, 2003
Fridericia maculata Issel, 1905
= ***Fridericia renatae*** Möller, 1971
= ***Timmodrilus oligoseta*** Dózsa-Farkas, 1997
Fridericia maculatiformis Dózsa-Farkas, 1972
Fridericia magna Friend, 1899
Fridericia minor Friend, 1913
= ***Fridericia gracilis*** von Bülow, 1957
Fridericia monochaeta Rota, 1995
Fridericia monopera Cognetti, 1903
Fridericia montafonensis Schmelz, 1998
Fridericia nemoralis Nurminen, 1970
Fridericia nielseni Möller, 1971
Fridericia nix Rota, 1995
Fridericia parasitica Černosvitov, 1928
Fridericia parathalassia Schmelz, 2002
Fridericia paroniana Issel, 1904
Fridericia perrieri (Vejdovský, 1878)
Fridericia pretoriana Stephenson, 1930
= ***Fridericia caprensis*** Bell, 1947
Fridericia profundicola Dózsa-Farkas, 1991
Fridericia pyrenaica Giani, 1979
Fridericia ratzeli (Eisen, 1872)
*= ***Fridericia eiseni*** Dózsa-Farkas, 2005
Fridericia reducata Dózsa-Farkas, 1974
Fridericia regularis Nielsen & Christensen, 1959
Fridericia rendsinata Dózsa-Farkas, 1972
Fridericia sardorum Cognetti, 1901
Fridericia semisetosa Dózsa-Farkas, 1970
Fridericia schmelzi Cech & Dózsa-Farkas, 2005
Fridericia singula Nielsen & Christensen, 1961
(***Fridericia sohlenii*** Rota et al., 1998 see ***F. cylindrica***)
Fridericia stephensoni Moszyński, 1933
Fridericia strenua Rota, 1995
Fridericia striata (Levinsen, 1884)
Fridericia sylvatica Healy, 1979

Fridericia terrarossae Sesma & Dózsa-Farkas, 1993
Fridericia tuberosa Rota, 1995
Fridericia tubulosa Dózsa-Farkas, 1972
Fridericia ulrikae Rota & Healy, 1999
Fridericia viridula Issel, 1904
Fridericia vixdiverticulata Sesma & Dózsa-Farkas, 1993
Fridericia waldenstroemi Rota & Healy, 1999
Guaranidrilus europaeus Healy, 1979
Hemienchytraeus bifurcatus Nielsen & Christensen, 1959
Hemifridericia parva Nielsen & Christensen, 1959
Henlea andreae Rodriguez & Giani, 1986
(***Henlea balcanica*** Černosvitov, 1930 see ***H. perpusilla***)
Henlea nasuta (Eisen, 1878)
Henlea perpusilla Friend, 1911
Henlea glandulifera Nurminen, 1970
Henlea heleotropha Stephenson, 1922
Henlea jutlandica Nielsen & Christensen, 1959
Henlea montana Rota, 1994
Henlea perpusilla Friend, 1911
= ***Henlea brucei*** Stephenson, 1922
= ***Henlea balcanica*** Černosvitov, 1930
Henlea similis Nielsen & Christensen, 1959
Henlea ventriculosa (d'Udekem, 1854)
Lumbricillus arenarius (Michaelsen, 1889)
Lumbricillus buelowi Nielsen & Christensen, 1959
Lumbricillus fennicus Nurminen, 1964
Lumbricillus kaloensis Nielsen & Christensen, 1959
Lumbricillus lineatus (Müller, 1774)
Lumbricillus pagenstecheri (Ratzel, 1869)
Lumbricillus rivalis Levinsen, 1883
Marionina argentea (Michaelsen, 1889)
Marionina brendae Rota, 1995
Marionina clavata Nielsen & Christensen, 1961
Marionina communis Nielsen & Christensen, 1959
Marionina eleonorae Rota, 1995
Marionina filiformis Nielsen & Christensen, 1959
Marionina hoffbaueri Möller, 1971

(***Marionina libra*** Nielsen & Christensen, 1959 see ***Bryodrilus***)
Marionina magnaglandulosa Nurminen, 1970
Marionina minutissima Healy, 1975
Marionina riparia Bretscher, 1899
Marionina rubens Rota, 1995
Marionina sexdiverticulata Dózsa-Farkas, 2002
Marionina simillima Nielsen & Christensen, 1959
(***Marionina serbui*** Botea, 1984 see ***Buchholzia simplex***)
Marionina southerni (Černosvitov, 1937)
Marionina subterranea (Knöllner, 1935)
Marionina vesiculata Nielsen & Christensen, 1959
Mesenchytraeus armatus (Levinsen, 1884)
Mesenchytraeus beumeri (Michaelsen, 1886)
Mesenchytraeus celticus Southern, 1909
Mesenchytraeus flavidus Michaelsen, 1887
Mesenchytraeus flavus (Levinsen, 1884)
(***Mesenchytraeus franzi*** Nurminen, 1977 see ***Cognettia clarae***)
Mesenchytraeus gaudens Cognetti, 1903
Mesenchytraeus glandulosus (Levinsen, 1884)
Mesenchytraeus kuehnelti, Dózsa-Farkas, 1991
Mesenchytraeus lusitanicus Collado, Martínez-Ansemil & Giani, 1993
Mesenchytraeus monochaetus Bretscher, 1900
Mesenchytraeus ogloblini Černosvitov, 1928
Mesenchytraeus pelicensis Issel, 1905
Mesenchytraeus sanguineus Nielsen & Christensen, 1959
Mesenchytraeus straminicolus Rota, 1995
Mesenchytraeus viivi Timm, 1978
Mesenchytraeus tetrapodus Timm, 1978
Oconnorella cambrensis (O'Connor, 1963)
= ***Marionina asymmetrica*** Nurminen, 1970
Oconnorella tubifera (Nielsen & Christensen, 1959)
= ***Oconnorella chalupskyi*** Rota, 1995
Stercutus niveus Michaelsen, 1888
(***Timmodrilus oligoseta*** Dózsa-Farkas, 1997 see ***Fridericia maculata***)

6. Key to genera

1 Chaetae absent (check ventral anterior bundles) . . . . . ***Achaeta***, p.64

1* Chaetae present **2**

2 Chaetae sigmoid **3**

2* Chaetae distally straight, proximally often bent (side view!) **16**

3 Chloragocytes tall, 3x as long as wide or longer, body cavity most often entirely filled with chloragocytes; animals stout, ca 10x as long as wide, strongly tapering anteriorly; not more than 3 or 4 chaetae per bundle; head pore and coelomocytes absent; one species, in non-acidic forest soil . . . . . ***Stercutus***, p. 77

3* Character combination different **4**

4 Not more than 2 or 3 chaetae per bundle (check ventral anterior bundles) **5**

4* More than 3 chaetae in ventral anterior bundles **8**

5 Nephridial anteseptale consisting of funnel only; max. 2 or 3 chaetae per bundle . . **6**

5* Nephridial anteseptale with parts of nephridial body; 2 chaetae per bundle throughout **7**

6 Nephridial postseptale gradually merging into short and thick efferent duct (Fig. 35B); pharyngeal glands in IV–VI, no secondary lobes, no glands behind segment VI; marine littoral species, rare at inland sites . . . . . ***Lumbricillus***, p. 92

6* Nephridial efferent duct long, thin, rising close to septum (Fig. 30E); pharyngeal glands in IV–VI and further back (VII, VIII), secondary ventral lobes often present; species abundant at acidic sites . . . . . ***Cognettia***, p. 77

7 Oesophageal appendages in III–IV dorsally (Fig. 9G); intestinal diverticula absent . . . . . ***Hemienchytraeus***, p75

7* Oesophageal appendages in VI (Fig. 9H), or absent; intestinal diverticula in VII(–VIII), a pair of hollow pouches . . . . . ***Guaranidrilus***, p. 75

8 Chaetae with nodulus; nephridial anteseptale consisting of funnel only, nephridial body (postseptale) without or with little interstitial tissue, canal often conspicuous . **9**

8* Chaetae without nodulus; nephridia variable **10**

9 Small worms, ca 2–5 mm long and 0.1 mm thick, chaetae thin and slender, nodulus conspicuous, body wall thin and transparent . . . . . ***Cernosvitoviella***, p. 56

9* Larger worms, usually > 6 mm long; chaetae often stout; body wall often thick, but animals not stiff . . . . . ***Mesenchytraeus***, p. 48

10 Dorsal blood vessel origin in VIII or IX, pulsating; intestine mostly widening abruptly and/or with diverticula at or near VIII **11**

10* Origin of dorsal blood vessel more posteriorly or indistinct; no abrupt gut widening in VII–IX **12**

11 Chaetae distinctly sigmoid, two types of coelomocytes, mucocytes and lenticytes; a pair of short, sac-like oesophageal appendages present dorso-laterally in IV . . . . . ***Buchholzia***, p. 118

11* Chaetae faintly sigmoid; one type of coelomocytes, only mucocytes; oesophageal appendages sponge-like at VI, inconspicuous . . . . . ***Henlea***, p. 112

12 Four sessile, hollow or compact oesophageal appendages in VI . . . ***Bryodrilus***, p. 116

12* No oesophageal appendages in VI **13**

13 Nephridial anteseptale consisting of funnel only **14**

13* Nephridial anteseptale with parts of nephridial body **15**

14 Testes subdivided into several pear-shaped lobes (‘testis sacs’, lateral view !), very rarely unlobed; head pore at 0/1, dorsal and ventral pharyngeal gland lobes in IV, V, VI, of regular outline; nephridial body (behind septum) with well-developed interstitial tissue . . . . . ***Lumbricillus***, p. 93

14* No testis sacs; head pore at tip of prostomium, dorsal pharyngeal gland lobes in IV and V, (secondary) ventral lobes in (IV,) V, VI, or further back, outline often irregular; nephridial body (behind septum) without interstitial tissue, canal conspicuous . . . . . ***Mesenchytraeus***, p. 48

15 Two types of coelomocytes, mucocytes and lenticytes (genus with distally straight chaetae, occasionally chaetae faintly sigmoid, e.g. in ***F. striata***) . . . ***Fridericia***, p. 124

15* Only one type of coelomocytes, mucocytes (only ***Marionina riparia***, or marine littoral species, not included here) . . . . . ***Marionina***, p. 96

16 (2*) Two types of coelomocytes, mucocytes and lenticytes **17**

16* Only one type of coelomocytes, mucocytes; lenticytes absent **18**

17 Medium-sized to large worms (length 4–25 mm); a pair of tubiform oesophageal appendages present in IV–V–(VI) ventro-laterally, branched or unbranched; segmental dorsal pores from VII; beginning of intestine marked by canalised cells ('chylus cells'); brain not incised posteriorly, mostly rounded or truncate, sometimes slightly concave . . . . . ***Fridericia***, p. 124

17* Animals small (ca 2–3 mm long); oesophageal appendages, intestinal diverticula, dorsal pores, chylus cells absent; brain deeply incised posteriorly . . . . . ***Hemifridericia***, p. 121

18 More than 3 chaetae in ventral preclitellar bundles **19**

18* Not more than 2 or 3 chaetae in ventral preclitellar bundles **24**

19 Dorsal blood vessel origin in a preclitellar segment (VIII or IX) with conspicuous pulsations; in the same region, abrupt gut enlargement or intestinal diverticula mostly present . . . . . ***Henlea***, p. 112

19* Dorsal blood vessel beginning in intra- or postclitellar region (XII–XIV), often inconspicuous or difficult to see; no abrupt gut enlargement in preclitellar segments, no intestinal diverticula **20**

20 Oesophageal appendages present in III/IV, VI or VII **21**

20* Oesophageal appendages absent **23**

21 Oesophageal appendages in III–IV, a pair of short unbranched tubes with wide lumen, opening into oesophagus dorsally behind pharyngeal pad . . . . . ***Enchytraeus***, p. 84

21* Oesophageal appendages in VI or VII **22**

22 Oesophageal appendages either paired in VII, kidney-shaped, or unpaired in IV–VI, closely attached to oesophagus ventrally . . . . . ***Oconnorella***, p. 109

22* Four compact oesophageal appendages in VI . . . . . ***Bryodrilus***, p. 116

23 Nephridial anteseptale consisting of funnel only, testes subdivided into several pear-shaped lobes ('testis sacs', lateral view !) . . . . . ***Lumbricillus***, p. 92

23* Nephridial anteseptale with parts of nephridial body, testes not subdivided into several lobes . . . . . ***Marionina***, p. 96

24(18*) Three chaetae present in several ventral preclitellar bundles **25**

24* Not more than 2 chaetae in ventral preclitellar bundles **27**

25 Oesophageal appendages present in III–IV (between pharyngeal pad and first pair of pharyngeal glands), a pair of much winding tubes with spongy appearance . . . . . ***Enchytraeus***, p. 84

25* Oesophageal appendages absent **26**

26 Nephridial anteseptale consisting of funnel only, seminal vesicle large, extending over > 1 segment . . . . . ***Lumbricillus***, p. 92

26* Nephridial anteseptale with parts of nephridial body, seminal vesicle smaller or absent . . . . . ***Marionina***, p. 96

27 Chaetae missing in several lateral bundles (see especially II and IX–XI) **28**

27* Lateral chaetae present throughout, absent only at XII **29**

28 Lateral chaetae absent in VIII–XI, rest with two chaetae per bundle; intestinal diverticula in VI, or abrupt gut enlargement at 5/6; rarely absent . . . . . ***Enchytronia***, p. 106

28* No intestinal diverticula, chaetal pattern different . . . . . ***Marionina***, p. 96

29 Nephridial anteseptale consisting of funnel only, oesophageal appendages present in III–IV, a pair of much winding tubes with spongy appearance, not branching (Fig. 1A), spermathecae attached . . . . . ***Enchytraeus***, p. 84

29* Nephridial anteseptale with parts of nephridial body, oesophageal appendages absent in III or, when present, branched on each side **30**

30 Large hollow intestinal diverticula in VII or VII–VIII . . . . . ***Guaranidrilus***, p. 75

30* No intestinal diverticula in VII–VIII **31**

31 Unpaired dorsal oesophageal appendage present in III–IV, bifurcating twice, distal branches spongy, spermathecae not attached to oesophagus, head pore on prostomium . . . . . ***Hemienchytraeus***, p. 75

31* Oesophageal appendages in III–IV absent or short, tube-like, not branching, spermathecae attached to oesophagus, head pore at 0/1 (see also ***Enchytronia***, when intestine in VI widening abruptly or with diverticula) . . . . . ***Marionina***, p. 96

Table 1 gives an overview of key traits in enchytraeid genera recorded from Europe, and also the order in which the genera appear in the following. They have been grouped according to similarities in characters that we consider to be phylogenetically significant at a suprageneric/subfamilial level (mainly traits 1–4).

Tab. 1 Overview of key traits in terrestrial and freshwater enchytraeid genera occurring in Europe. Species numbers in brackets behind genus name. Rounded brackets in rest of columns = trait not present in all species. Square brackets = trait rare. Roman numerals give segment position. Abbreviations: 1: 0 = prostomium; 0/ 1= furrow between prostomium and peristomium. 3: att = attached; fus = fused; sep = separate; free=not attached proximally to oesophagus. 4: F = funnel; NB = parts of nephridial body; nb = small parts of nephridial body. 5: max. = highest number of chaetae per bundle in each specimen. 6: sig = sigmoid = distally bent; str = distally straight. 7: U=rounded proximally; W = concave/incised proximally.

	1 Head pore	2 Secondary pharyngeal glands	3 Spermathecae proximally	4 Nephridial anteseptale	5 Number (max.) of chaetae	6 Shape of chaetae	7 Brain posteriorly	8 Oesophageal appendages	9 Intestinal diverticula	10 Dorsal vessel, anterior origin	11 Peculiar coelomocytes
Mesenchytraeus (16)	0	+	free/att+sep	F	> 3	sig(+nod)	U/W	–	–	–	(rhombus)
Cernosvitoviella (15)	0	+	free	F	> 5	sig+nod	U	–	–	–	(spindle)
Achaeta (23)	0	+/(–)	free	F + NB	0		U	(IV, V)	–	VI-VII	
Guaranidrilus (1)	0	+	free	F + NB	2	str/sig	W	VII	VII-VIII	–	
Hemienchytraeus (1)	0	+/(–)	free	F + NB	2	str/sig	W	III-IV	–	–	
Stercutus (1)	–	+	free	F + nb	2–4	sig+nod	W	–	–	IX	
Cognettia (6)	0/1	+/(–)	free	F	2–4	sig	W	–	–	–	
Enchytraeus (16)	0/1	–	att+sep.	F	2,3(–5)	str	U	III-IV	–	–	
Lumbricillus (7)	0/1	–	att+sep	F	var	str/sig	U/W	–	–	–	
Marionina (16)	0/1	–	var	F + NB	var	str/sig	U/W	[IV]	–	–	
Enchytronia (6)	0/1	–	att+fus [free]	F + NB	2	str	W	–	(VI)	–	
Oconnorella (2)	0/1	–	att+fus	F	> 2	str	U	IV-VI / VII	–	-	
Henlea (10)	0/1	–	att+fus	F + nb	> 2	str(/sig)	U	(IV-) VI	(VIII)	VIII, IX	
Bryodrilus (5)	0/1	–	att+fus [free]	F + nb	> 2	str/sig	U	VI	–	–	
Buchholzia (4)	0/1	–	att+fus	F + nb	> 2	sig	W	IV	(VIII)	VIII	lenticytes
Hemifridericia (1)	0/1	–	att+fus	F + NB	2,3	str	W	–	–	–	lenticytes
Fridericia (76)	0/1	–	att+fus/sep [free]	F + NB	var	str	U	IV-V(-VII)	–	–	lenticytes

7. Keys to species

Technical notes: Traits used in the key path are not repeated in the descriptions. Only some of the most conspicuous characters are mentioned, for more information on the morphology of the species see the references given behind the species names, and those listed under 'Lit.:' at the end of a species description. Papers with different focus (cytology, reproduction, molecular taxonomy) are not listed completely. Regarding cytology read the monograph of Christensen (1980). Paired organs (e.g. spermathecae, sperm funnels, male copulatory organs) are often described in the singular form; this does not mean that only one organ is present. 'L' = live body length, 'fix' = fixed specimen, 'D' = body diameter, 'S' = segment number. Figures are oriented with the head region to the top (dorsal or ventral view) or to the left (lateral view). References in the figure captions are given in the order left to right, top to bottom. Not referenced figures are original drawings.

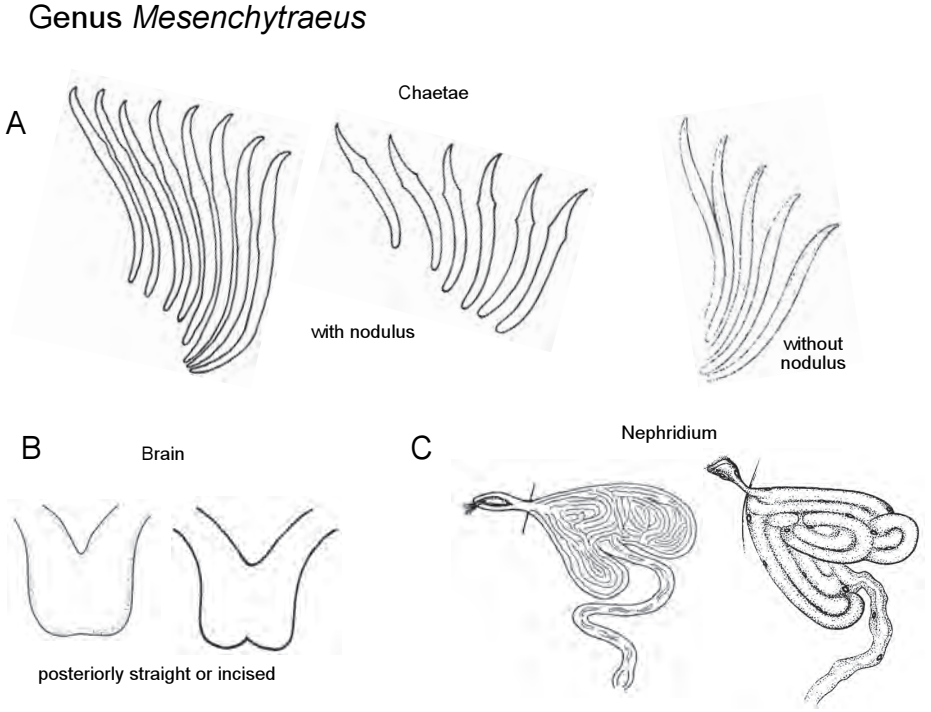

Fig. 15 Genus ***Mesenchytraeus***, some taxonomic traits. A from Timm & Popchenko (1978, Fig. 11-5), Nielsen & Christensen (1959, Fig. 5), Michaelsen (1887, Pl. 21 Fig. 1A). B from Rota (1995, Fig. 6A), Nielsen & Christensen (1959, Fig. 12). C from Nielsen & Christensen (1959, Fig. 11), Michaelsen (1887, Pl. 21 Fig. 1D).

7.1. ***Mesenchytraeus*** Eisen, 1878 (Fig. 15)

Medium-sized to large forms. Head pore at tip of prostomium. Chaetae sigmoid, with or without nodulus, more than three in at least several bundles; lateral bundles often shifted dorsally. Brain short, with deep anterior incision, posteriorly truncate or slightly concave. Body wall often not stiff, worms with soft consistency. Oesophageal appendages and intestinal diverticula absent. Primary pharyngeal glands in IV and V, attached to septa posteriorly in position of dorsal lobes, secondary pharyngeal glands not attached to septa, often diffuse, lobed, closely attached to oesophagus, over various segments. Dorsal blood vessel origin from XIII or further back, blood usually pale, sometimes reddish/yellowish. Nephridial anteseptale consisting of funnel only, postseptale with conspicuous and folded canal, interstitial tissue practically absent. Coelomocytes often spindle-shaped, with distinct vesicles or refractile bodies. Developing sperm and eggs often in several segments posterior to clitellum (sperm sacs, egg sacs). Clitellum extending over more than 1.5 segments, girdle-shaped, cells small and in reticulate pattern. Sperm funnel often small, vas deferens usually widening distally into a thick-walled atrium, often with atrial glands. Bursa present, often surrounded by diffuse glands; bursal slit irregular, star-shaped. Spermathecae without ectal glands, proximally free or attached separately to oesophagus, diverticula 2, 1 or 0. – Genus holarctic, species-richest in boreal regions. Mostly terrestrial, few species aquatic. The largest enchytraeids are found in this genus (L > 60 mm, > 100 segments, non-European fauna). Lit.: Rota & Brinkhurst (2001).

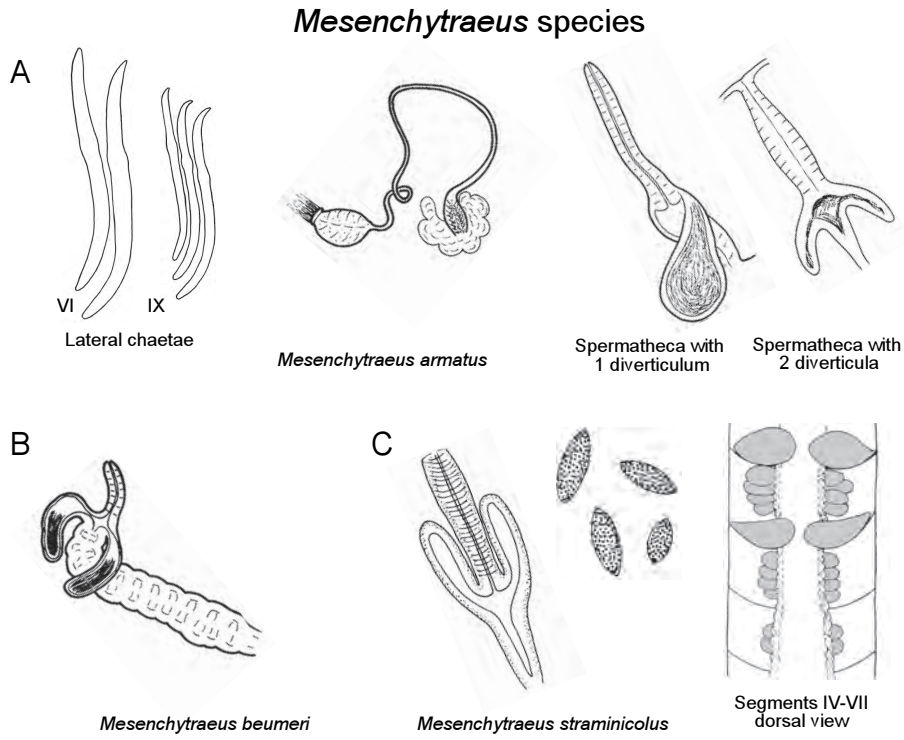

Fig. 16 ***Mesenchytraeus*** species. A: ***M. armatus***, from Timm & Popchenko (1978, Fig. 11-3, 11-4), Nielsen & Christensen (1959, Figs 6,7), Nurminen (1970a, Fig. 1). B: ***M. beumeri***, from Nielsen & Christensen (1959, Fig. 13). C: ***M. straminicolus***, from Rota (1995, Fig. 6F,E,D).

1 Lateral or ventral chaetae enlarged in V–VII **2**

1* Chaetae in V–VII not larger than the rest **4**

2 Enlarged chaetae in lateral bundles; Fig. 16A . . . . . ***Mesenchytraeus armatus*** (Levinsen, 1884)

L 9–16 mm. S 42–55. Body greyish-yellow-brownish. Chaetal pattern 1-4 – 3-8 : 7-12 – 6-11. Enlarged chaetae only 1–2 per bundle; nodulus conspicuous. Secondary pharyngeal glands in V, VI. Dorsal vessel from XVI–XX, blood colourless. Coelomocytes spindle-shaped, small, pale, with a few additional refractile granules. Spermathecae with elongate ectal duct, narrow ampulla and one large asymmetrical diverticulum; rarely with two diverticula. Gonadal segments may be shifted 2 segments anteriad. – Common and widespread at wet terrestrial or semi-aquatic sites. Lit.: Michaelsen (1888, as ***M. setosus***), Černosvitov (1928a, as ***M. setosus***), Nielsen & Christensen (1959), Nurminen (1970a), Kasprzak (1986), Chalupský (1992).

2* Enlarged chaetae in ventral bundles **3**

3 Coelomocytes spindle-shaped; enlarged chaetae thicker but only slightly longer than ordinary chaetae . . . . . ***Mesenchytraeus monochaetus*** Bretscher, 1900

L 7–10 mm, S 40 (juveniles!). Chaetae 2–3 dorsally, 5–7 ventrally. In V–VII ventrally only 1(2) chaeta per bundle, enlarged, twice as thick but little longer than regular chaetae. Body wall thick. Blood light yellow. Coelomocytes spindle-shaped, weakly granulated. – Ill-known species, described from juvenile specimens. Only known from original description, one site, a lake shore in Switzerland. Doubtful species according to Nielsen & Christensen (1959), accepted by Kasprzak (1986).

3* Coelomocytes oval; enlarged chaetae distinctly longer (1.5x) than ordinary chaetae . . . . . ***Mesenchytraeus tetrapodus*** Timm, 1978

L 10–17 mm (fix?), S 55–67. Body colour pinkish-white. Chaetae sigmoid with nodulus, 2–6 per bundle, except ventrally in VI and VII; here one enlarged chaeta per bundle, up to 220 µm long and 20 µm thick. Primary pharyngeal glands in IV and V, secondary glands in V–VI (-VII). Dorsal vessel from XX. Six preclitellar pairs of nephridia, 5/6 – 10/11. Vas deferens with thickened part and atrium, a large gland attached to the latter. Spermathecae each with 1 or 2 small tubular diverticula and long and winding ampulla, communicating separately with oesophagus in IX or X (!). – Russia, Kola Peninsula, alpine stream. Only known from original description, specimens subadult.

4 In anterior segments distinctly more chaetae in ventral bundles than in dorsal bundles (e.g., 4–6 vs 2–4, or 6–9 vs 3–5); spermathecae connected with oesophagus **5**

4* Number of ventral and lateral chaetae more or less alike; spermathecae free, not attached to oesophagus (attached in 1 species, see 14*) **14**

5 Spermathecae with diverticula **6**

5* Spermathecae without diverticula **11**

6 Spermatheca with two diverticula of equal size **7**

6* Spermatheca with one asymmetrical diverticulum, or with one large and another one rudimentary **9**

7 More than 50 segments; up to 8 or 9 chaetae per bundle; animals mostly large, > 20 mm long (the rare ***M. viivi*** is smaller); collar of sperm funnel not narrower than funnel body **8**

7* Not more than 50 segments, up to 11 chaetae per bundle; worms up to 15 mm long, collar of sperm funnel narrower than funnel body; Fig. 16C . . . . . ***Mesenchytraeus straminicolus*** Rota, 1995

L 9–15 mm, S 41–50. Chaetae 1-4 – 3-8 : 4-11 – 3-11. Body colour whitish or yellow. Secondary pharyngeal glands in V–VII. Preclitellar nephridia from 6/7. Dorsal vessel from XVI. Coelomocytes lemon- to spindle-shaped, transparent, vesicles pale, cell aggregations reddish-brownish. Sperm funnel shorter than 1/2 body diameter, ca 2x as long as wide. Vas deferens very long (ca 4 mm). Spermatheca with narrow and tube-like ampulla and paired elongate diverticula, all of equal length, shorter than ectal duct. – Italy, soils in Tuscany. Only known from original description.

8 Worms longer than 20 mm; spermathecal ampulla longer and wider than diverticula; sperm only in diverticula; Fig. 16B . . . ***Mesenchytraeus beumeri*** (Michaelsen, 1886)

L ca 22–30 mm, S 55–65. Chaetae 2-4 – 3-7 : 5-8 – 4-8. Body opaque, white-yellow. Secondary pharyngeal glands in (V), VI, (VII). Preclitellar nephridia from 6/7. Dorsal blood vessel from XVI–XX. Coelomocytes ellipsoid, with sparse, colourless inclusions of varying shape. Sperm funnel shorter than 1/2 body diameter, ca 2–3x as long as wide, vas deferens long with several coils. Spermatheca with narrow ectal duct; ampulla cylindrical, 3–4x as long and 2x as wide as ectal duct, with inner epithelial protrusions, outer surface often wrinkled; two elongate diverticula of same length as ectal duct, narrower than ampulla. – Widespread, moist soils. Lit.: Issel (1905a, as ***M. rhabdogenus***), Backlund (1946, as ***M. valvifer***), Nielsen & Christensen (1959).

8* Worms shorter than 20 mm; spermathecal ampulla and diverticula of equal shape and length, all filled with sperm . . . . . ***Mesenchytraeus viivi*** Timm, 1978

L 10–14 mm, S 59–61, body colour white or whitish. Chaetae 3-5 – 5-8 : 6-9 – 6-9. Secondary glands in V, VI, (VII). Dorsal blood vessel from XVI–XVII. Five pairs of preclitellar nephridia, from 6/7 to 10/11. Sperm funnel shorter than 1/2 body diameter, ca 1.5x as long as wide, collar wider than ectal duct. Vas deferens very short, with few or no coils. Spermathecal diverticula elongate, of same shape as ampulla. Ampulla, diverticula and ectal duct of about same length, ectal duct ca 1/2 as thick as diverticula or ampulla. Occasionally only one diverticulum present (?); a small ectal gland anteriorly of ectal duct (?). – Mountain lake shores in Kola peninsula, Russia. Only known from original description.

9 Chaetae 10–13 in ventral preclitellar bundles; pharyngeal glands over 7 segments, from IV–X; coelomocytes with dark vesicles; Fig. 17A . . . . . ***Mesenchytraeus celticus*** Southern, 1909

L 12–25 mm (same animal !), S unknown. Large animals, dark under transmittent light except in foremost segments, due to coelomocytes. Ventral preclitellar bundles with 10–11, occasionally 12–13 chaetae; lateral bundles with 5–7 chaetae. Brain incised posteriorly. Dorsal vessel from XIII (?). Coelomocytes numerous, oval, full of dark granules. Vas deferens with atrium and several stalked glands around ectal pore. Spermathecal ectal duct short; ampulla thin-walled, ca 3x as long as wide and 3x as long as ectal duct; distally with one oval, sperm-filled diverticulum. – Ireland, Scotland, moist soils. Only known from original description.

9* Usually less than 10 chaetae per bundle, pharyngeal glands in 3 or 4 segments, from IV to VI or VII; coelomocytes with intensely yellow granules (unknown in ***M. ogloblini***) **10**

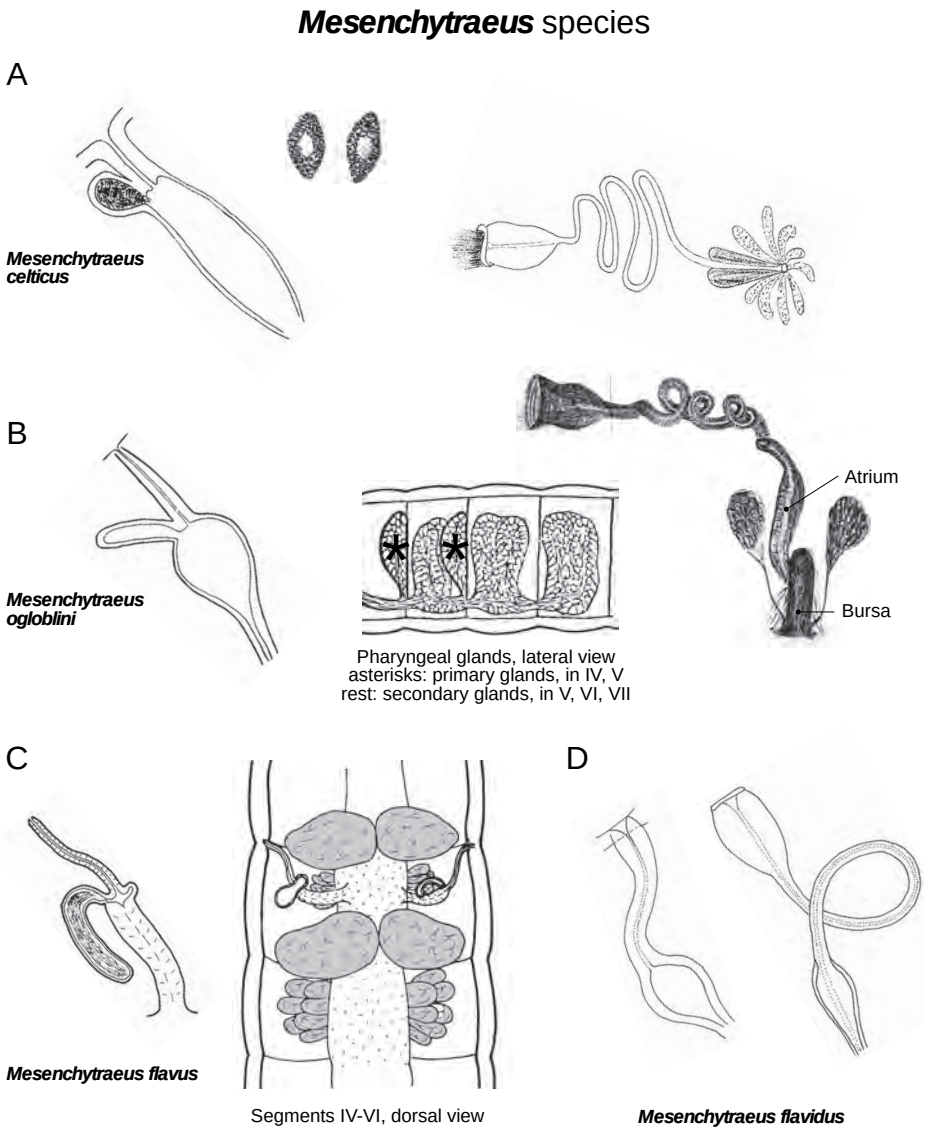

Fig. 17 ***Mesenchytraeus*** species, continued. A: ***M. celticus***, from Southern (1909, Pl.11 Fig. 13F, C, G). B: ***M. ogloblini***, from Černosvitov (1928a, text fig. 4B3, 4B2, Pl. 1 Fig. 5). C: ***M. flavus***, from Nielsen & Christensen (1959, Figs 10, 9). D: ***M. flavidus***, from Michaelsen (1887, Pl. 21 Fig. 2A,D).

10 Not more than 7 chaetae per bundle; secondary pharyngeal glands about twice as large as primary glands, in V–VII; body colour and coelomocytes unknown; dorsal vessel from XIV–XV; Fig. 17B . . . . . .***Mesenchytraeus ogloblini*** Černosvitov, 1928a

L 10–15 (fix), S 54–62. Body yellowish (fix). Chaetal pattern 2-3(4) – 5-6(7) : 5-7 – 6-7. Brain straight posteriorly. Secondary pharyngeal glands in V–VII, as large as or larger than primary glands. Coelomocytes small, ca 15 µm long. Sperm funnel trumpet-shaped, vas deferens short, atrium without glands, bursa with 2 large stalked glands. Spermathecae with short and narrow ectal duct; ampulla large, pear-shaped, ca 3x as wide as ectal duct, with one elongate diverticulum distally. – Eastern Carpathians, river sediment. One unconfirmed find from forest soil in Germany.

10* Up to 9–13 chaetae in ventral bundles; secondary pharyngeal glands not larger than primary glands, in V and VI; body colour intensely yellow; coelomocytes with intensely yellow granules; dorsal vessel from XVII–XVIII; Fig. 17C . . . . . .***Mesenchytraeus flavus*** (Levinsen, 1884)

L ca 20–30 mm, S 59–66. Chaetal pattern 3-5 – 5-8 : 6-9 – 4-10, larger worms with up to 13 chaetae per bundle. Secondary pharyngeal glands in V and VI, smaller than primary glands. Dorsal blood vessel from XVII–XVIII. Coelomocytes rather small, not wider than diameter of chaetae, but conspicuous by their yellow refractile granules. Spermathecal ectal duct and asymmetrical diverticulum of about equal length, the latter brown when filled with sperm, ampulla slightly longer; occasionally a stump-like second diverticulum present. – Widespread. Lit.: Nielsen & Christensen (1959), Nurminen (1970a).

11 Pharyngeal glands in 7 segments, secondary glands from V–X; coelomocytes pale when isolated, dark-grey in aggregations; Fig. 18A . . . . . .***Mesenchytraeus glandulosus*** (Levinsen, 1884)

L 10–15 mm, S (31)-42-45-(60). Body stout but soft, flat-worm-like. Colour yellowish to light red. Chaetal pattern 3-5 – 5-7 : 6-10 – 6-10. Numerous irregularly shaped epidermal gland cells dorsally to latero-ventrally. Secondary pharyngeal glands at VI–X. Dorsal blood vessel from XIII, blood pale. Coelomocytes spindle-shaped, larger and smaller ones, the smaller ones less abundant, more oval and coarsely granulated. Spermathecae with short and stout ectal duct; ampulla bag-shaped, with undulating inner surface, often collapsed. – Widespread. Lit.: Stephenson (1926, as ***M. harperi***), Nielsen & Christensen (1959), Kasprzak (1986), Römbke (1989), Rota (1995).

11* Pharyngeal glands in 4 or 5 segments, secondary pharyngeal glands extending into VII or VIII; coelomocytes with refractile granules, dark in aggregations **12**

12 Pharyngeal glands in 4 segments, from IV to VII; epidermal gland cells numerous; Fig. 18B . . . . . .***Mesenchytraeus gaudens*** Cognetti, 1903b

L 6–8 mm, D 0.25 mm, S 35–50. Body colour yellowish white. Chaetal pattern 3,4 – 3-5 : 4-6 – 3,4. Epidermal gland cells large and conspicuous, not as numerous as in ***M. glandulosus***. Secondary pharyngeal glands in VI and VII. Dorsal vessel from XII or XIII. First pair of nephridia at 6/7. Coelomocytes few in number, oval, with refractile granula. Clitellum from 1/2 XI–XIII. Sperm funnel ca 1.5x as long as wide, collar wider than funnel body, vas deferens short, atrium elongate (without glands?). Spermathecae spongy, with rugose or undulating outer surface; ectal duct gradually widening into ampulla; ampulla with irregular diverticula-like protrusions, often seen pulsating; a small ectal gland often present. – Apparently widespread, but still insufficiently known. Lit.: Ditlevsen (1904, as ***M. parva***), Nielsen & Christensen (1959).

12* Pharyngeal glands in 5 segments, from IV to VIII; epidermal gland cells sparse . .**13**

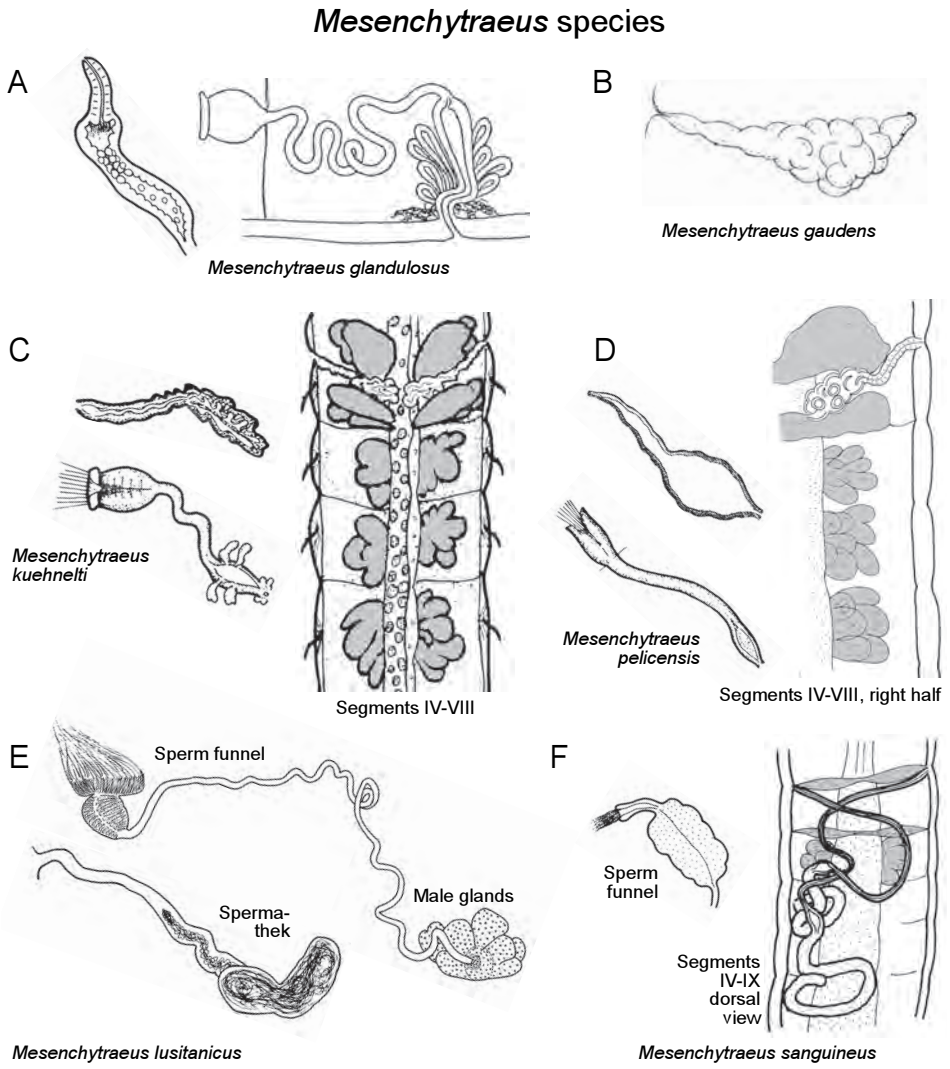

Fig. 18 ***Mesenchytraeus*** species, continued. A: ***M. glandulosus***, from Nielsen & Christensen (1959, Fig. 3), Stephenson (1926, Fig. p. 87). B: ***M. gaudens***, from Cognetti (1903b, Fig. p. 3). C:***M. kuehnelti***, from Dózsa-Farkas (1991b, Fig. 1G,F,B). D: ***M. pelicensis***, from Issel (1905a, Pl. 13 Fig. 12), Nielsen & Christensen (1959, Fig. 4), Dózsa-Farkas (1991, Fig. 2C). E: ***M. lusitanicus***, from Collado et al. (1993, Fig. 2E,1G). F: ***M. sanguineus***, from Nielsen & Christensen (1959, Figs 2,1).

13 Sperm funnel pear-shaped, collar about as wide as funnel body; vas deferens ca 3x as long as sperm funnel, atrium with four well-developed glands; Fig. 18C . . . . . .***Mesenchytraeus kuehnelti*** Dózsa-Farkas, 1991b

L ca 9–15 mm, D 0.4–0.6 mm, S (30)–40–50. Colour whitish-yellow. Chaetal pattern 2-5 – 2-5 : 4-6 – 4-7. Epidermal gland cells scarce. Brain rounded or truncate posteriorly. Dorsal vessel from XIII (XIV). Coelomocytes granulated, black in transmittent light. Sperm funnel with regular collar, distinctly wider than vas deferens; atrium well-demarcated, ca 2x as wide as vas deferens. Spermathecae as in ***M. pelicensis***, often seen pulsating. – Hungary, boglands. Only known from original description.

13* Sperm funnel bell-shaped, widest diameter at proximal end; vas deferens 1.5–2x as long as sperm funnel, atrium only slightly wider than ectal duct, without glands; Fig. 18D . . . . . .***Mesenchytraeus pelicensis*** Issel, 1905a

L 12–17 mm, S 36–56. Chaetae 2-4 – 2-4 : 4-6 – 4-6. Dorsal vessel from XIII. Coelomocytes spindle-shaped, completely packed with fairly large granules. Sperm funnel without regular collar, hardly wider than vas deferens, atrium indistinct. Spermatheca with rugose outer and inner surface, ectal duct 4–5x as long as wide, ampulla of same length, little wider than ectal duct, often seen pulsating. – Widespread. Lit.: Černosvitov (1945), Nielsen & Christensen (1959), Kasprzak (1986), Rota (1994, 1995).

14 Spermathecae extending over several segments, winded, not attached to oesophagus **15**

14* Spermathecae confined to V, attached to oesophagus; Fig. 17D . . . . . .***Mesenchytraeus flavidus*** Michaelsen, 1887

L ca 12 mm, S 41–52. Chaetae 2–4 in lateral bundles, 3–5 in ventral bundles. Preclitellar nephridia 5 pairs, from 6/7 to 10/11. Dorsal vessel from XIII, blood colourless. Clitellum 1/2XI – XIII. Sperm funnel short, vas deferens short, up to 5x as long as sperm funnel, atrium elongately pear-shaped, narrow end distally; small floppy glands around male pore. Spermathecal ectal duct with slight distal swelling, ampulla pear-shaped, with smooth inner and outer surface. – Germany, two sites.

15 Coelomocyte granula elongate; first nephridia at VIII; blood reddish; Fig. 18F . . . . . .***Mesenchytraeus sanguineus*** Nielsen & Christensen, 1959

L 10–14 mm, S ca 45. Chaetae 2–5 in preclitellar bundles, 2,3,(4) in postclitellar bundles; nodulus inconspicuous but distal part abruptly thinner than proximal part. Pharyngeal glands in IV and V dorsally connected, secondary ventral lobes in VI (–VII, VIII). Sperm funnel with narrow and elongate collar, or widened as in ***M. lusitanicus***. Spermathecal ectal duct about as long as ampulla, ampulla sausage-like, of same diameter throughout. – Semi-aquatic, acidic sites, common in bogs. Widespread.

15* Coelomocyte granula almost spherical, first nephridia at VII; blood colourless; Fig. 18E . . . . . .***Mesenchytraeus lusitanicus*** Collado, Martínez-Ansemil & Giani, 1993

L 9–13 mm, S 43–52. Chaetae 4–6 in preclitellar bundles, 2–4 in postclitellar bundles; nodulus inconspicuous but distal part abruptly thinner than proximal part. Pharyngeal glands in IV and V dorsally separate, secondary glands in V–VIII. Sperm funnel collar wider than funnel body. Spermathecal ectal duct shorter than ampulla, ampulla widened proximad, club-shaped. – Semi-aquatic, wet acidic sites. Common in North-West of Iberian Peninsula.

The key is unsatisfactory, because often only a few juvenile or submature specimens appear in a sample, and inner structures in adults are obscured by body thickness and coelomocytes. An improvement could be achieved if the position of preclitellar nephridia and the coelomocyte texture were known in more species. The distribution of secondary pharyngeal glands may be subject to some intraspecific variation. The differences between ***M. monochaetus*** and ***M. tetrapodus*** are not convincing, but Bretscher's species is very poorly known. Some of the differences between ***M. sanguineus*** and ***M. lusitanicus*** were established comparing living material. Several details in the descriptions of ***M. flavidus*** and ***M. viivi*** are based on type reinvestigation; more detailed descriptions are in preparation. Question marks in the description of ***M. viivi*** refer to traits originally described but not seen in the types. ***M. celticus*** may have been misidentified several times as ***M. glandulosus*** (Schlaghamerský 1998). We do not include ***M. franzi*** Nurminen, 1977, described from the Austrian Alps, and indistinguishable from ***Cognettia clarae***, see chapter 7.7. The transfer of ***M. franzi*** to ***Cognettia*** makes the genus diagnosis of ***Mesenchytraeus*** more precise: it had been the only species in the genus with only two chaetae per bundle; all other species have more.

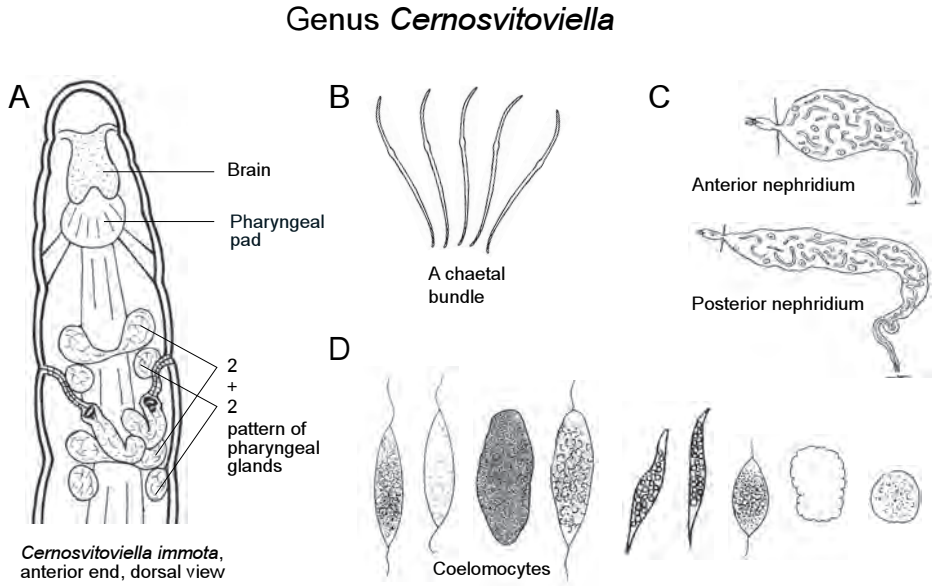

Fig. 19 Genus ***Cernosvitoviella***, some taxonomic traits. A from Nielsen & Christensen (1959, Fig. 19). B from Černosvitov (1928a, Text Fig. 3.5) C from Černosvitov (1928a, Text Fig. 3.2, 3.6). D from Chalupský (1992, Fig. 7A,D); Dózsa-Farkas (1970, Fig. 3G).

7.2. *Cernosvitoviella* Nielsen & Christensen, 1959 (Fig. 19)

Small worms (2–5 mm, rarely longer), active, contractile, with peristaltic body movements. 18–35 segments. Chaetae slender, sigmoid, with distinct nodulus. Number of chaetae per bundle variable, about 5–8–(10) ventrally before clitellum, fewer in other body regions, down to 2. Head pore on prostomium (at 0/1 in two species, requiring confirmation), brain incised posteriorly. Oesophageal appendages and intestinal diverticula absent. Pharyngeal glands alike in all species (except one): two primary pairs dorsally, at IV and V, with or without dorsal connection, and two pairs of secondary ventral glands, at V and VI ('2+2 pattern'). Blood pale or slightly rose/yellow. Nephridial anteseptale with funnel only, postseptale compact but canal conspicuous, efferent duct short, terminal. Nephridia often unpaired, first one usually at 6/7, positions unknown in most species. Coelomocyte shape and texture variable, from oval to spindle-shaped, and from pale over brown, dark-brown to black under transmittent light; often different types in anterior and posterior body region of the same animal. Clitellum insufficiently known in most species. Seminal vesicle absent, present in ***C. immota***. Vas deferens often widened in determined regions. Glands surrounding male pore loose or compact; no accessory glands. Spermathecae free, not attached to oesophagus, consisting of ectal duct and ampulla; ectal glands absent. – Holarctic. Moist and wet soils, frequent in bogs and moorlands, also oxygen-rich freshwater sediments; ***C. immota*** in brackish habitats.

1 Pharyngeal glands 2+2: a dorsal pair each in IV and V before septum, a ventral pair each at V and VI behind septum **2**

1* Pharyngeal glands 3+3: dorsal pairs in IV–VI, ventral pairs in V–VII; Fig. 20A . . . . . ***Cernosvitoviella carpatica*** Nielsen & Christensen, 1959

L 3–4 mm, S 25–28. Up to 7 chaetae in ventral preclitellar bundles. Coelomocytes with refractile granula. Dorsal vessel from XII, blood colourless. Sperm funnel 1.5–2x as long as wide, vas deferens 3–3.5x as long as sperm funnel. Spermathecae short, in V with spherical ampulla, ectal duct ca 2–3x as long as wide. – Poland, Switzerland, Denmark, Germany (?), small streams, damp soil. Lit.: Černosvitov (1928a, as ***Enchytraeoides atratus*** Bretscher), Kasprzak (1986).

2 Sperm funnels funnel-shaped, i.e. tapering distad (i.e. towards vas deferens), collar not narrower than funnel body (Figs 20B–D, 21A,B) **3**

2* Sperm funnels cylindrical, collar not wider than funnel body (Figs 21C–F, 22A–E) **7**

3 Spermathecae short, always confined to V **4**

3* Spermathecae elongate, extending into VII or VIII when fully extended (may be confined to V but then much coiled) **5**

4 Proximal half of vas deferens inflated and with large lumen, as wide as sperm funnel (Fig. 20B) . . . . . ***Cernosvitoviella crassoductus*** Dózsa-Farkas, 1990

L 3–4 mm, S 19–23. Up to 7 chaetae per bundle. Coelomocytes transparent, not dark, a few cells excepted. Dorsal vessel from XI–XII, blood faintly yellow. Proximal dilatation of vas deferens 2x as long as sperm funnel, longer than narrower distal part of vas deferens. – Hungary, Estonia, boglands. Only known from original description.

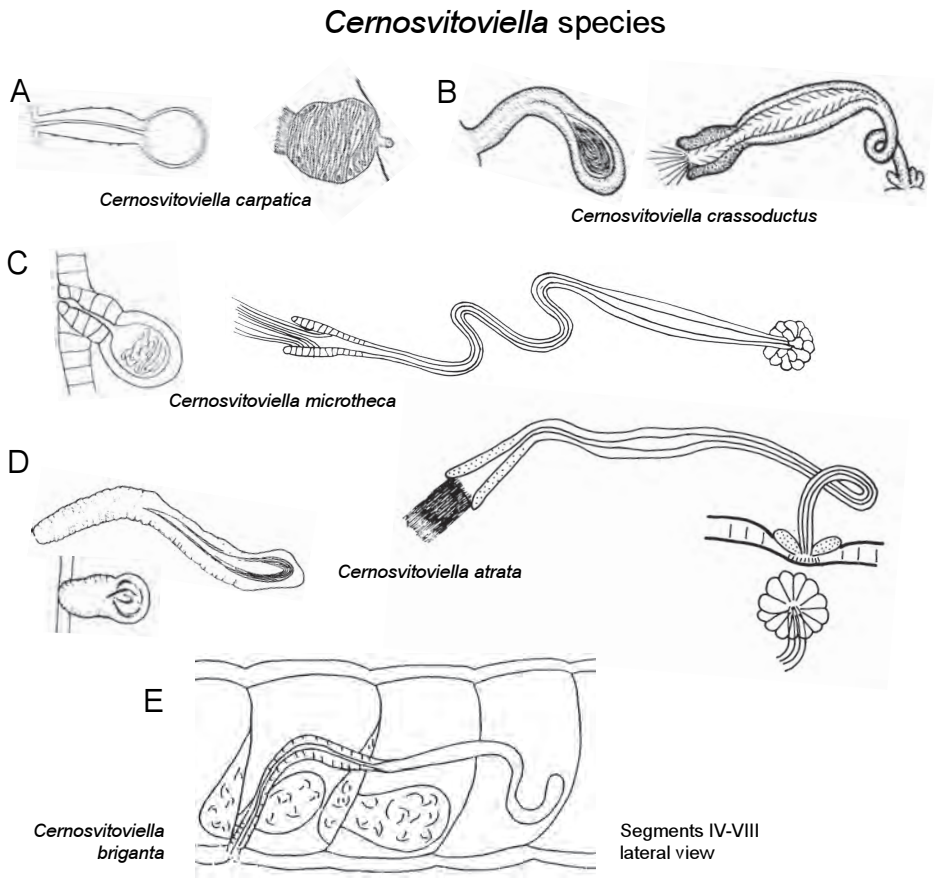

Fig. 20 ***Cernosvitoviella*** species. Left: spermatheca; right: male efferent apparatus. A: ***C. carpatica***, from Černosvitov (1928a, Text Fig. 3.1, 3.7). B: ***C. crassoductus***, from Dózsa-Farkas (1990, Figs 9, 10). C: ***C. microtheca***, from Rota & Healy (1999, Fig. 1B,C). D: ***C. atrata***. Left from Chalupský (1992, Fig. 7B,C), right from Nielsen & Christensen (1959, Fig. 18). E: ***C. briganta***, from Springett (1969, Fig. 1).

4* Distal half of mid-part of vas deferens inflated, or vas deferens not inflated at all; Fig. 20C,D . . . . . .***Cernosvitoviella atrata*** (Bretscher, 1903) sensu lato
= *Cernosvitoviella microtheca* Rota & Healy, 1999

L 2–4 mm, S 18–28. Up to 7, 8, 9, or 10 chaetae per bundle. Body colour greyish-white or intensely white due to coelomocytes. Coelomocytes variable, spindle-shaped or oval, with or without strongly refractile granules. Rosette of glands around male pore small. Spermathecae variable, in some specimens short and stump-like, ca 2x as long as wide, ampulla spherical, ectal duct about as long as wide; in other specimens up to 7x as long as wide, ampulla elongate. – Common and widespread. Probably a species complex. Lit.: Nielsen & Christensen (1959), Kasprzak (1986), Chalupský (1992), Rota (1995), Rota & Healy (1999).

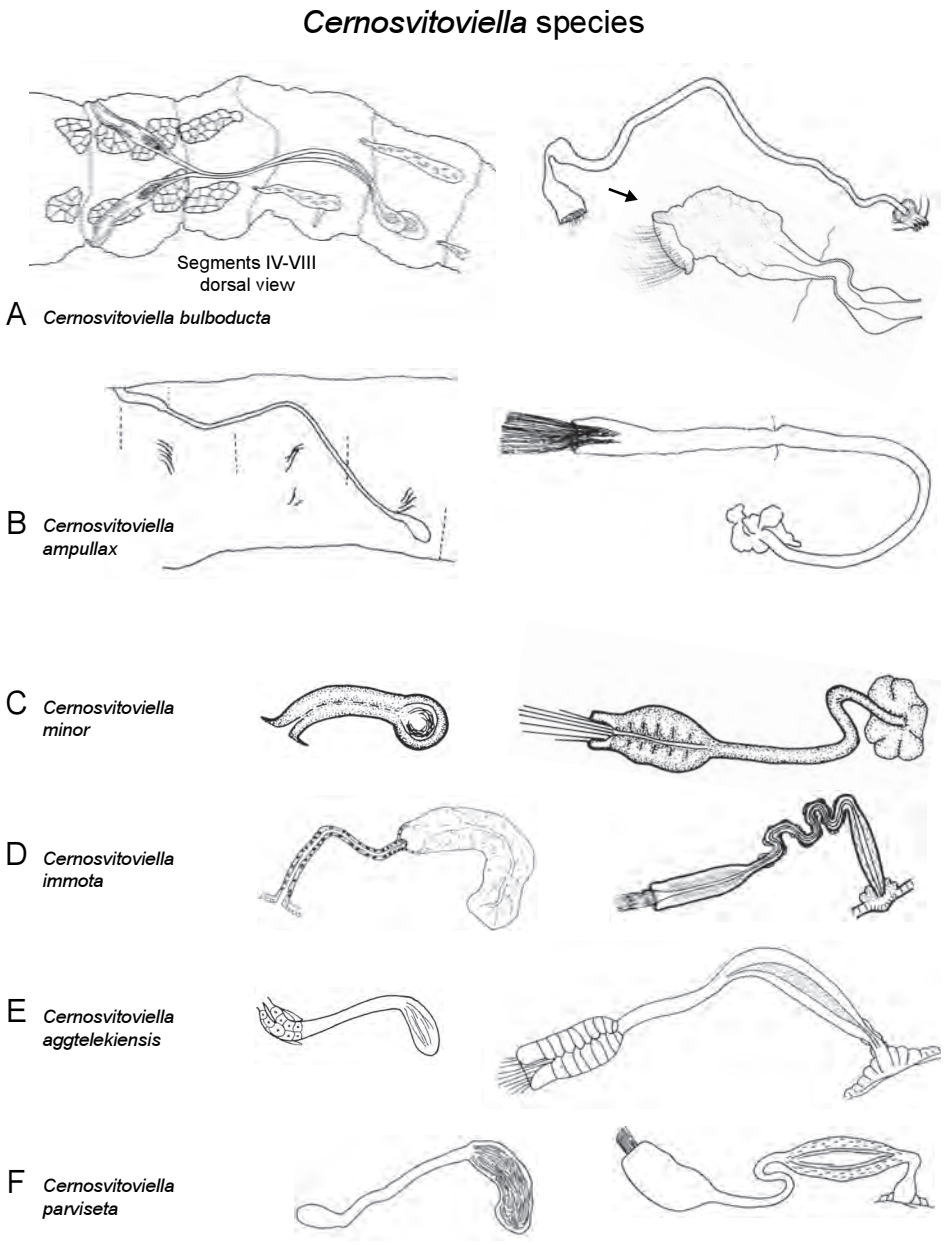

Fig. 21 ***Cernosvitoviella*** species, continued. Left: spermatheca; right: male efferent apparatus. A: ***C. bulboducta***, from Martínez-Ansemil & Collado (1996, Fig. 2C,F,G). B: ***C. ampullax***, from Klungland & Abrahamsen (1981, Fig. 1B,E). C: ***C. minor***, from Dózsa-Farkas (1990, Figs 13, 14). D: ***C. immota***, left from Knöllner (1935, Fig. 13), right from Nielsen & Christensen (1959, Fig. 22). E: ***C. aggtelekiensis***, from Dózsa-Farkas (1970, Fig. 3B,C). F: ***C. parviseta***, from Gadzińska (1974, Figs 2, 3).

5 Spermathecal ampulla without sperm-containing lumen; worms comparatively large, length > 4 mm; Fig. 20E . . . . . .***Cernosvitoviella briganta*** Springett, 1969

L 4–9 mm, S 28–35. Up to 8 chaetae per bundle. Dorsal vessel from XIII, blood colourless or faintly red. Coelomocytes oval and spindle-shaped, the latter opaque. Sperm funnel short, funnel-shaped, small separate glands at male pore. Spermathecal ectal duct ca 1 segment long, ampulla not wider than ectal duct. – England, moorland. All records from sites near the type locality.

5* Spermathecal ampulla with sperm-containing lumen; worms usually smaller, length < 4.5 mm **6**

6 Sperm funnel ca 2x as long as wide, vas deferens ca 7x as long as sperm funnel; Fig. 21A . . . . . .***Cernosvitoviella bulboducta*** Martínez-Ansemil & Collado, 1996

L 2–3 mm (fix), S 29–33. Up to 8 chaetae per bundle. Dorsal vessel from XIII. Coelomocyte texture unkown. Sperm funnel collar as wide as funnel body, proximal end of vas deferens with a short swelling right beneath sperm funnel. – North West of Iberian Peninsula, several localities; rivers.

6* Sperm funnel 5x as long as wide, vas deferens ca 2.5x as long as sperm funnel; Fig. 21B . . . . . .***Cernosvitoviella ampullax*** Klungland & Abrahamsen, 1981

L 2–4 mm, S 17–27. Up to 8 chaetae per bundle. Coelomocytes variable, brown to black-brown with refractile granules, refractile cells not dominant. Dorsal vessel from XI, blood colourless. Vas deferens 2.5x as long as sperm funnel, as wide as sperm funnel proximally, gradually tapering towards male pore. – Northern Europe, Italian Alps.

7 Body intensely white in some regions, most often in posterior half (top light); several or many coelomocytes spindle-shaped, dark-black in transmittent light due to coarse, strongly refractile granules **8**

7* Body whitish-greyish, not intensely white; coelomocytes brownish to dark-brown or pale in transmittent light, granula fine and regular; dark coelomocytes scarce **11**

8 Spermathecae short and stout, 4x as long as wide or shorter, confined to V, ampulla spherical, ectal duct canal without ectal dilatation; Fig. 21C . . . . . .***Cernosvitoviella minor*** Dózsa-Farkas, 1990

L 2–3.5 mm, S 18–24. Up to 7 or 8 chaetae per bundle. Brain only slightly concave posteriorly. Most or all coelomocytes spindle-shaped, with refractile granules. Sperm funnel cylindrical, 3x as long as wide, collar tall and narrower than funnel body, vas deferens 3–5x as long as sperm funnel, without distal dilatation (Rota & Healy (1999): a small distal dilatation present near the orifice). Spermatheca about 4x as long as wide, ampulla spherical, with sperm often arranged cross-wise in lumen. – Widespread. Lit.: Rota & Healy (1999).

8* Spermathecae more than 5x as long as wide, often extending beyond V, ectal duct with or without ectal dilatation **9**

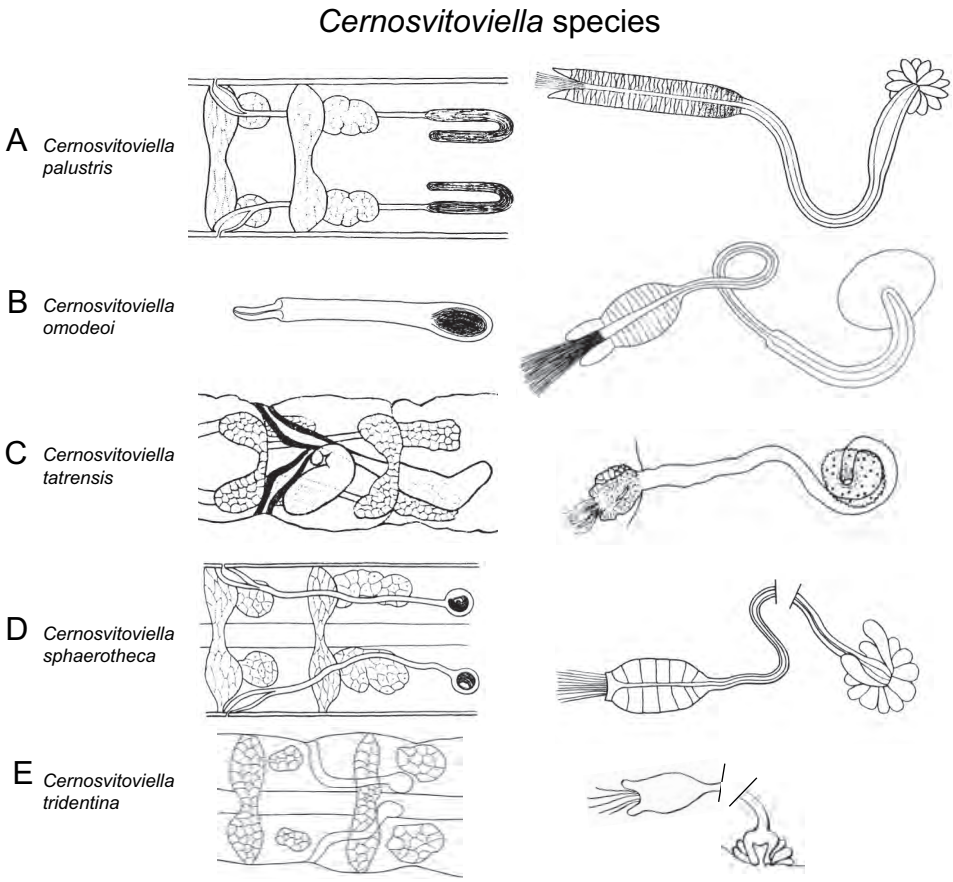

Fig. 22 ***Cernosvitoviella*** species, continued. Left: spermatheca; right: male efferent apparatus. A: ***C. palustris***, from Healy (1979a, Fig. 1A,D). B: ***C. omodeoi***, from Rota (1995, Fig. 7B,C). C: ***C. tatrensis***, left from Kowalewski (1916, Fig. 2), right from Martínez-Ansemil & Collado (1996, Fig. 3A). D: ***C. sphaerotheca***, from Healy (1975, Fig. 1A,E). E: ***C. tridentina***, from Dumnicka (2004, Figs 1C,D, 2).

9 Seminal vesicle usually large; Fig. 21D . . . . . .
. . . . . .***Cernosvitoviella immota*** (Knöllner, 1935a,b)

L 3–4 mm, S 20–28. Up to 7 chaetae per bundle. Dark coelomocytes spindle-shaped or oval, the latter fairly large, ca 1/2 worm body diameter. Sperm funnel as long as body diameter, 2–3x as long as wide, vas deferens with distal dilatation. Spermathecal ampulla elongate, sausage-shaped, longer than ectal duct and ca 3x as wide, with a distal ring of sperm; ectal duct narrower and without distal dilatation. – Widespread, marine coastal areas. Lit.: Nielsen & Christensen (1959), Kasprzak (1986), Rota & Healy (1999).

9* Seminal vesicle absent **10**

10 Chaetae >30 µm long; Fig. 21E . . . . . .
. . . . . .***Cernosvitoviella aggtelekiensis*** Dózsa-Farkas, 1970
= ***Cernosvitoviella goodhui*** Healy, 1975

L 2–3 mm, S 21–23. Up to 9 chaetae per bundle, 35–42 µm long. Dark coelomocytes spindle-shaped. Dorsal vessel from (XIII?)–XIV–XV. Sperm funnel cylindrical, ca 3x as long as wide, distal half of vas deferens widened. Male glands large. Spermathecae extending into V–VI, ectal duct canal distally widened, ampulla short, oval. – Widespread, few records.

10* Chaetae only 15 µm long; Fig. 21F . . . .***Cernosvitoviella parviseta*** Gadzińska, 1974

L 2–5 mm (fix), S 21–24. Sperm funnel cylindrical, ca 3x as long as wide, distal half of vas deferens widened. Spermathecae extending into V–VI, ectal duct canal distally widened, ampulla short, oval, about 2x as wide as mid-section of ectal duct. – Only known from type locality, a cave in the Tatra Mountains. Insufficiently known species.

11 Vas deferens widened in distal half (if enlarged in proximal half, see 4 or 7*) **12**

11* Vas deferens without widenings or widened only close to male pore **13**

12 Sperm funnel 5–7x as long as wide, spermathecae extending into VII when fully extended, vas deferens widened in distal third; Fig. 22A . . . . . .
. . . . . .***Cernosvitoviella palustris*** Healy, 1979a
= ***Cernosvitoviella estaragniensis*** Giani, 1979

L 3–6 mm, S 24–27. Up to 8–10 chaetae per bundle. Coelomocytes broadly spindle-shaped or disc-shaped, mostly not refractile. Dorsal vessel from XIII–XIV. Blood colourless or faintly red. Seminal vesicle absent, very rarely present, small. Vas deferens only little longer than sperm funnel, widened in distal third. Male pore with a large rosette of glands. Spermathecae reaching VII when fully extended, with elongate ampulla and a distal widening of ectal duct. – Ireland, French Pyrenees, North-West of Iberian Peninsula.

12* Sperm funnel 2x as long as wide, spermathecae short, confined to V, vas deferens widened over entire distal half; Fig. 22B . . . . .***Cernosvitoviella omodeoi*** Rota, 1995

L 2–3 mm, S 19–23. Coelomocytes oval, light to dark-brown. Dorsal vessel from XIII, blood colourless. No seminal vesicle. Sperm funnel small, with high collar. Male pore surrounded by a large compact gland. Spermathecae reaching VII when fully extended, with narrow and short ectal duct and wider and elongate ampulla, sperm-filled proximally. – Italy, acidic soil. Only known from original description.

13 Spermatheca with a spherical ampulla at proximal end, about 3x as wide as ectal duct; sperm funnel distinctly longer than wide **14**

13* Spermathecal ampulla elongate, less than 2x as wide as ectal duct; sperm funnel almost as wide as long; Fig. 22C . . . .***Cernosvitoviella tatrensis*** (Kowalewski, 1916)

L 5–9 mm, S unknown. Vas deferens gradually tapering distally. Male pore surrounded by a large crown of glands. Spermathecae 2 segments long, with widened ectal duct. – Poland. Lit.: Kasprzak (1986), Martínez-Ansemil & Collado (1996).

14 Spermathecae extending into VI or VII, ectal duct inflated distally; Fig. 22D . . . . . .***Cernosvitoviella sphaerotheca*** Healy, 1975

L 2.5–7 mm, S 27–31. Up to 10 chaetae per bundle. Coelomocytes variable, some or many densely dark-brown. Dorsal blood vessel from XIII, blood colourless or distinctly red, or intermediate. Sperm funnel ca 3x as long as wide, vas deferens with small distal dilatation. Male pore surrounded by a large rosette of glands. Spermathecae reaching VII when fully extended, with spherical ampulla at proximal end, widening of ectal duct distally, and a narrow and long connecting tube in between. – Ireland, several localities.

14* Spermathecae extending into V or VI, ectal duct not inflated distally; Fig. 22E . . . . . .***Cernosvitoviella tridentina*** Dumnicka, 2004

L 2–3.5 mm (fix), S 24–31. Up to 8–9 chaetae per bundle. Sperm funnel 1.5x as long as wide, vas deferens with a slight distal swelling, male pore with a small rosette of glands. Spermathecae with spherical ampulla; ectal duct elongate, of equal length throughout, without distal swelling. – Italian Alps, streams. Only known from original description.

Species diagnoses and distinctions among species are not beyond doubt and require a critical assessment of the key characters to separate species. Some traits are unknown in most species, e.g. details of the clitellum. Couplet 2/2* may not work well, so both paths should be tried.

C. aggtelekiensis, C. parviseta and ***C. goodhui*** are rather similar. ***C. parviseta*** differs from ***C. aggtelekiensis*** only in the length of the chaetae; the trait is unknown in ***C. goodhui***. ***C. goodhui*** differs in a more anterior origin of the dorsal blood vessel (XIII vs XIV–XV in ***C. aggtelekiensis***); the trait is unknown in ***C. parviseta***. These and further differences require reinvestigation of the types. Records of ***C. goodhui*** in Chalupský (1992) and Rota (1995, as 'cf.') may belong to a different species.

C. atrata sensu lato is characterised by simple spermathecae without ectal thickening, confined to V, and by minute, short, and funnel-shaped sperm funnels that merge gradually with the vas deferens. The rest appears to be variable, notably (1) coelomocytes, (2) length of the spermathecae, and (3) widening of the vas deferens; this leads to the incorporation of ***C. microtheca***, for the following reasons: (1) Coelomocytes: According to the original description of ***C. atrata***, the body is full with dark coelomocytes. According to Nielsen & Christensen (1959) only some coelomocytes are dark, and according to Rota & Healy (1999), dark coelomocytes are absent. The coelomocytes in ***C. microtheca*** are originally described as for ***C. atrata*** in Nielsen & Christensen. (2) Spermathecae: The short spermathecae of ***C. atrata*** are as in ***C. microtheca*** (see Fig. 20C,D). (3) Vas deferens: The widening of the vas deferens has never been described adequately for ***C. atrata***. In a figure by Nielsen & Christensen (1959, see Fig. 20D) there appears to be a widening in the mid-section, but the trait is not dealt with in the text. In ***C. microtheca*** the widening is in the distal half. We have seen specimens with elongate spermathecae (Fig. 20D top left) and a vas deferens widening in the distal half (see Fig. 20C), and identified them as ***C. atrata***.

C. bulboducta and ***C. briganta*** are highly similar, but the descriptions are too heterogeneous for a literature-based comparison. We hope to compare the types in the near future.

C. carpatica. The 3 + 3 pattern of pharyngeal glands has never been redescribed. According

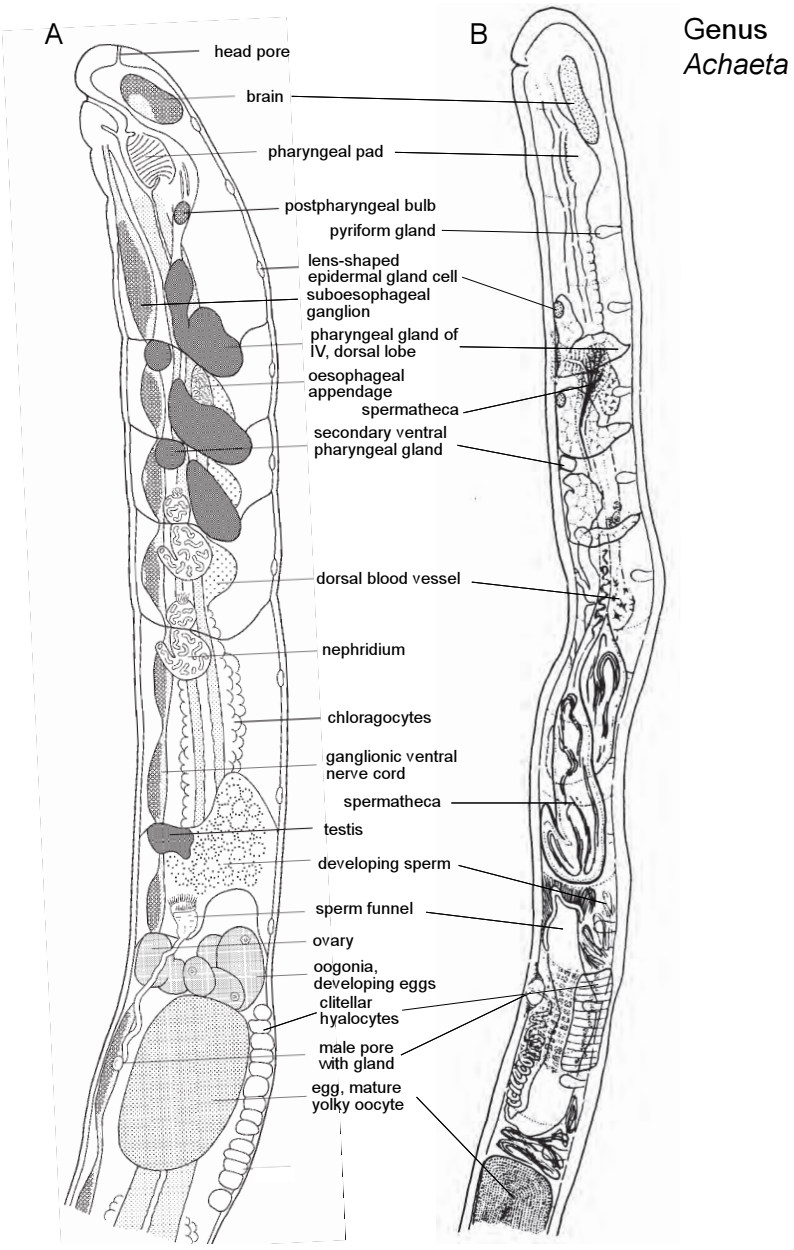

Fig. 23 ***Achaeta***, general morphology. A: ***Achaeta diddeni*** Graefe, 2005, a typical representative of the group without pyriform glands. From Graefe (2007, Fig. 1). B: ***Achaeta bifollicula*** Chalupský, 1992, species with dorsal pyriform glands and very large spermathecae, seminal vesicle and sperm funnels. From Chalupský (1992, Fig. 5J).

to Dumnicka (pers. com.) it really exists, but the secondary glands in V and VI are sometimes reduced or inconspicuous, whereas those in VII are always present. Kasprzak (1986) figures the spermatheca with a slender ectal duct, less than 1/3 as thick as the spherical ampulla, and up to 3x as long (comp. Fig. 20A).

Timm (2009) uses ***C. estaragniensis*** as valid name but ***C. palustris*** has priority; its description was effectively published in October 1979 and that of ***C. estaragniensis*** in December 1979. The synonymy was first suggested by Healy (1980).

7.3. ***Achaeta*** Vejdovský, 1878 (Fig. 23)

Chaetae absent. Head pore on prostomium. Brain ca 2x as long as wide, rounded posteriorly or slightly convex. Coelomocytes of one type only, mucocytes. Spermathecae not connected with oesophagus. – Animals often stiff, slow-moving. Pyriform epidermal glands often present, extending into coelom. Further epidermal glands lens-shaped, mostly few in number and with species-specific segmental pattern. Pharyngeal glands in IV–VI, mostly connected dorsally (rarely reduced in VI), some species with secondary ventral glands. Oesophageal appendages, when present, unpaired dorsally in V or IV–V, rarely in IV only. In European species, intestinal diverticula absent, and origin of dorsal vessel in preclitellar region; intestine often widening abruptly. Nephridial anteseptale usually with parts of nephridial body, reduced in 2 species. Clitellum variable, often absent ventrally and/or dorsally; in

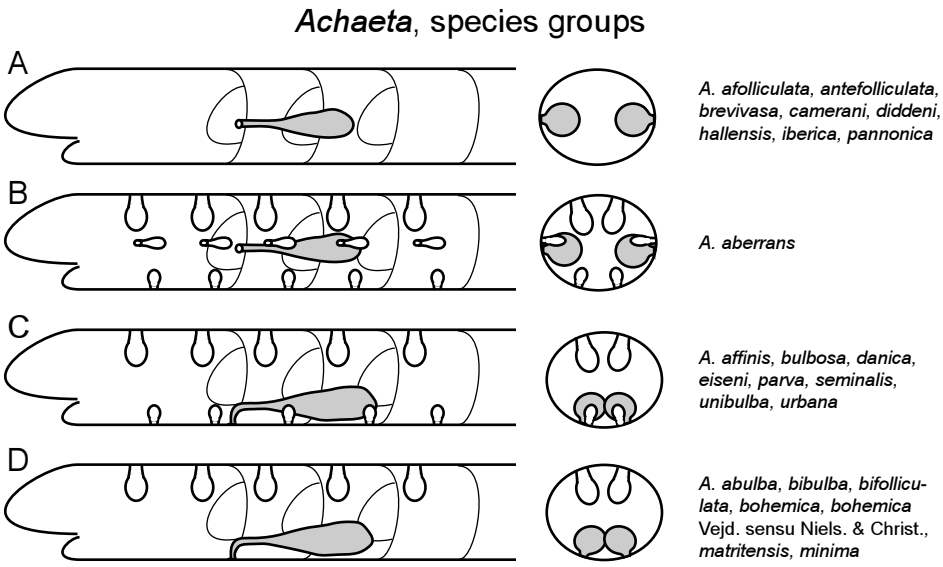

Fig. 24 Four groups of European ***Achaeta*** species, distinguished by pyriform glands and location of spermathecal ectal pores. Left: Anterior body end, lateral view, with spermatheca (grey), pyriform glands (white, bold lines), pharyngeal glands in IV, V, VI (white, thin lines), and septa 4/5-7/8. Right: Cross section, with spermathecae and pyriform glands. A: No pyriform glands; ectal pores lateral (ventral only in the marine littoral ***Achaeta littoralis*** Lasserre, 1968, not included in the key). B: Six pyriform glands per segment; ectal pores lateral. C: Four pyriform glands per segment, dorsal and ventral; ectal pores ventral. D: Two pyriform glands, dorsal; ectal pores ventral. From Schmelz et al. (2009, Fig. 3).

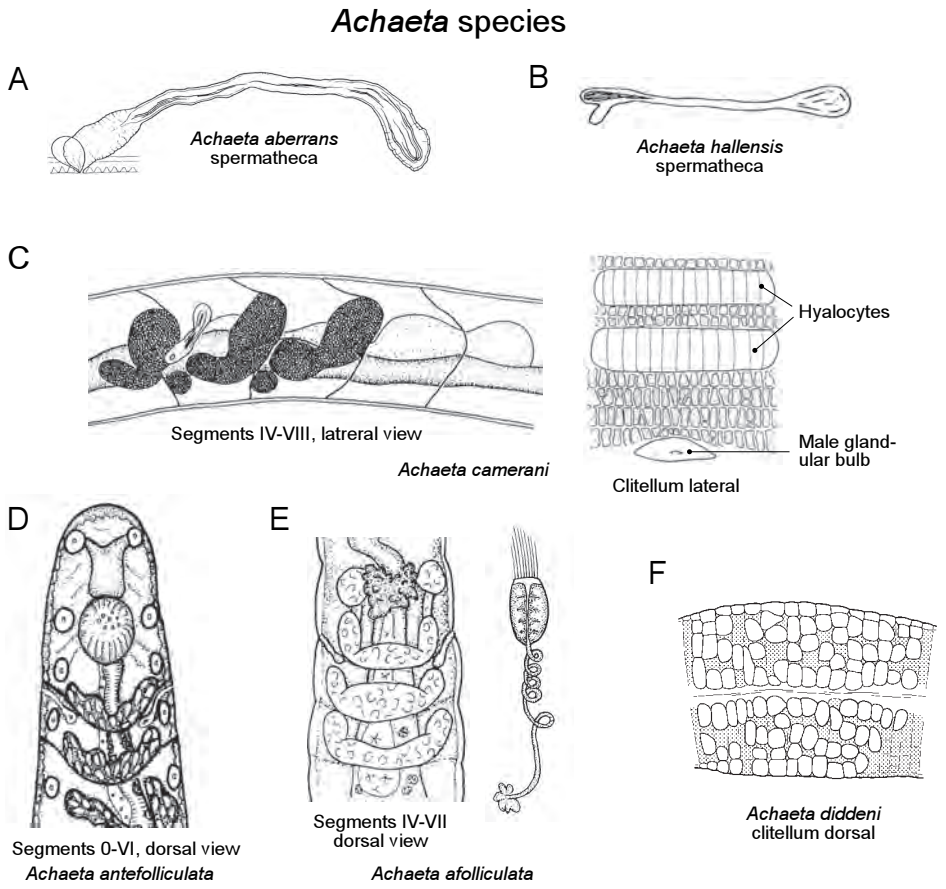

Fig. 25 ***Achaeta*** species. A: ***A. aberrans***, from Chalupský (1992, Fig. 2A.) B: ***A. hallensis***, from Möller (1974, Fig. 1G.) C: ***A. camerani***, left from Graefe (1980, Fig. 4), right from Chalupský (1992, Fig. 6B). D: ***A. antefolliculata***, from Dózsa-Farkas & Boros (2005, Fig. 1). E: ***A. afolliculata*** from Sesma & Dózsa-Farkas (1993, Figs 42, 47). F: ***A. diddeni***, from Graefe (2007, Fig. 4).

several species hyalocytes arranged in 4–6 conspicuous dorso-lateral longitudinal baguette-shaped rows, protruding into body cavity. Vasa deferentia often wound into a regular spiral. Male pore on body surface, no bursa. Male glands compact around male pore, or several glands in longitudinal row, or absent. No subneural glands. Spermathecal ectal pores lateral or ventral. Spermathecae mostly without diverticula, often with ectal asymmetry. – Several characters are only found in this genus, but they are not present in all species: pyriform glands, unpaired dorsal oesophageal appendage in (IV–)V, baguette-shaped rows of clitellar hyalocytes, ectal asymmetry of spermathecae.

1 Pyriform glands present; spermathecal ectal pores mostly ventral (lateral in 1 species, see 2*) **2**

1* Pyriform glands absent; spermathecal ectal pores lateral (Fig. 24A) (ventral in the marine littoral ***A. littoralis*** Lasserre, 1968, not included here) **4**

2 Two or four pyriform glands per segment, spermathecal ectal pores ventral **3**

2* Six pyriform glands per segment, spermathecal ectal pores lateral; Figs 24B, 25A . . . . . ***Achaeta aberrans*** Nielsen & Christensen, 1961

L 3–5 mm, S 20–23. Oesophageal appendage absent or small in V. Preclitellar nephridia two pairs, at 6/7, 7/8. Dorsal vessel from VI. Seminal vesicle and sperm funnel small; male glandular bulb compact. Spermathecae simple, extending into V or VI. – Northern, Central, Western Europe. Lit.: Chalupský (1992).

3 Two pyriform glands per segment, dorsally; spermathecal ectal pores ventral (Fig. 24D) **11**

3* Four pyriform glands per segment, 2 dorsally, 2 ventrally (Fig. 24C) **18**

4 Dorsal vessel from VIII (adults! from VII or VI in juveniles); body length > 6 mm; > 30 segments; Figs 25C, 26C . . . . . ***Achaeta camerani*** (Cognetti, 1899)

L 6–9 mm, S 32–35. Six epidermal gland cells per segment. Oesophageal appendage only in V. Pharyngeal glands with secondary ventral lobes in V and VI. Preclitellar nephridia two pairs, at 6/7, 7/8. Clitellum saddle-shaped, with 4 baguette-rows of hyalocytes dorsally. No seminal vesicle, sperm funnel half as long as body diameter, spermathecae small and short. – Widespread, common in acidic forest soils. Lit.: Černosvitov (1945, as ***Achaeta*** sp.), Nielsen & Christensen (1959), Möller (1971), Graefe (1980), Kasprzak (1986), Chalupský (1992).

4* Dorsal vessel from VII; body length < 5.5 mm, less than 30 segments **5**

5 Two pairs of preclitellar nephridia **6**

5* Three pairs of preclitellar nephridia, at 6/7, 7/8, 8/9 . . . . . **10**

6 In each segment one pair of large greenish iridescent epidermal gland cells, dorsolaterally; preclitellar nephridia at 7/8, 8/9; spermathecae long, extending into VI or VII, with diverticulum-like ectal asymmetry; Figs 25B, 26C . . . . . ***Achaeta hallensis*** Möller, 1976
New name ***for A. segmentata*** Möller, 1974 non Prabhoo, 1966

L 2.5–3.5 mm, S 18–24. Pharyngeal glands all dorsally united, small secondary ventral lobes in V, VI. Oesophageal appendage absent. Clitellar hyalocytes not in rows. Developing sperm in XI. Sperm funnel length ca 1/2 body diameter, inflated. – North-eastern Germany, Czech Republic, 3 records. Possibly subcontinental. Lit.: Schlaghamerský & Pižl (2009).

6* No greenish epidermal gland cells, or more than two per segment; preclitellar nephridia at 6/7, 7/8; spermathecae short, confined to V **7**

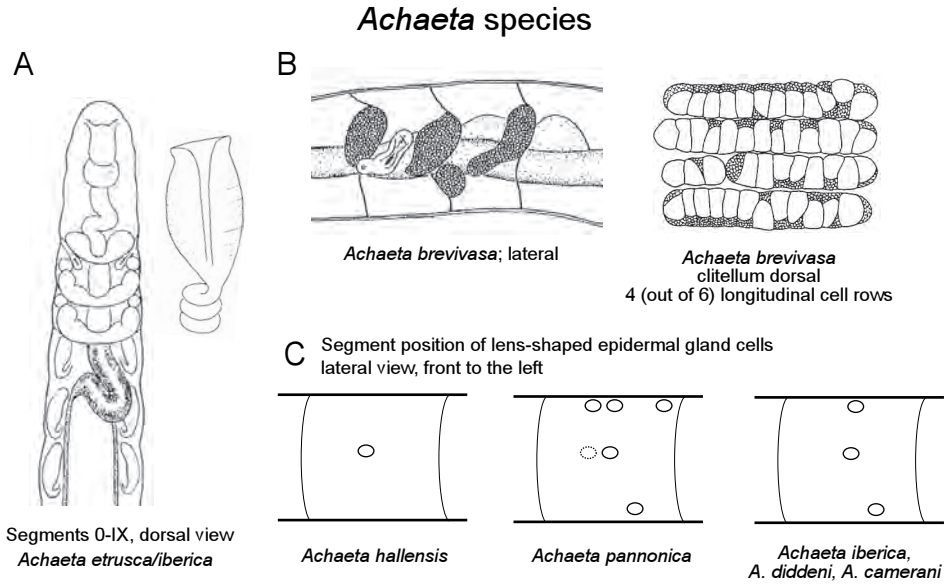

Fig. 26 ***Achaeta*** species, continued. A: ***A. etrusca*** = ***A. iberica***, from Rota (1995, Fig. 8A, C). B: ***A. brevivasa***, from Graefe 1980, Figs 1, 3.

7 In segments I, III, IV, V, and VI, one dorsal pair each of solid and knob-like glands or bodies attached to inner side of the body wall; Fig. 25D . . . . . .***Achaeta antefolliculata*** Dózsa-Farkas & Boros, 2005

L 2.4–3.5 mm, S 20–21. Pharyngeal glands with secondary ventral lobes in V. Oesophageal appendage small, in V only. Clitellar gland cells ventro-laterally in transverse rows; hyalocytes on dorsal side, often inconspicuous, in indefinite longitudinal rows. Cells absent between male pores and in a thin mid-dorsal line. No seminal vesicle. Sperm funnel 1.5–2x as long as wide, 1/4–1/3 as long as body diameter. – Hungary; Only known from original description.

7* No such glandular bodies **8**

8 Oesophageal appendage in IV, lentiform epidermal gland cells absent; Fig. 25E . . . . . .***Achaeta afolliculata*** Sesma & Dózsa-Farkas, 1993

L 3–4 mm, S 21–24. Pharyngeal glands with an additional ventral body anteriorly in IV. Dorsal vessel from VII. Clitellar gland cells dorsally not in rows. Seminal vesicle absent or small, sperm funnel ca 1.5x as long as wide, 1/4–1/3 as long as body diameter. – Spain. Only known from original description.

8* Oesophageal appendage in V, small and inconspicuous; lentiform epidermal gland cells present **9**

9 Two pairs of secondary ventral pharyngeal gland lobes, in V and VI; sexual organs except spermathecae shifted one segment forward, i.e. testes and sperm funnel in X, male pores and clitellum in XI; Figs 23A, 25F, 26C . . . . . .***Achaeta diddeni*** Graefe, 2007

L ca 4 mm, S 22–24. Six lentiform epidermal gland cells per segment. Clitellum absent ventrally, mid-dorsally a narrow cell-free line. Hyalocytes in indefinite longitudinal rows dorsally. Seminal vesicle in X. Sperm funnel ca 1/4 as long as body diameter, 1.5x as long as wide. – Northern Germany, several grassland localities; neutral to moderately acidic soils.

9* One pair of secondary ventral pharyngeal gland lobes, in VI; male pores and clitellum in usual position, at XII; Fig. 26B . . . . . .***Achaeta brevivasa*** Graefe 1980

L 3–3.5 mm, S 20–22. Six lentiform epidermal gland cells per segment. Clitellum saddle-shaped, 6 dorsal baguette-rows of hyalocytes. Sperm funnel small, funnel-shaped, ca 1.2x as long as wide, 1/4 as long as body diameter. – Northern and Central Europe. Widespread in acidic forest soils.

10 (5*) Lentiform epidermal gland cells numerous (8–12 per segment, 4–6 on each side); sexual organs except spermathecae shifted one segment forward, i.e. testes and sperm funnel in X, male pores and clitellum in XI; Fig. 26C . . . . . .***Achaeta pannonica*** Graefe, 1989
= ***Achaeta petseri*** Dózsa-Farkas, 1998

L 3–3.5 mm, S 22–29 (–39?). Oesophageal appendage small, only in V. Pharyngeal glands with secondary ventral lobes in V and VI. Clitellum not developed ventrally; mid-dorsally a narrow field without clitellum, lined by 8 longitudinal, slightly irregular rows of hyalocytes. No seminal vesicle, sperm funnel 1/3 as long as body diameter, spermathecae small and confined to V (as in A***. camerani***, comp. Fig. 25C). – Widespread, neutral to moderately acidic soils. Similar to ***A. diddeni***, comp. Fig. 23. Lit.: Schmelz et al. (2005), Schlaghamerský & Pižl (2009).

10* Lentiform epidermal gland cells less numerous (6 per segment), male pores and clitellum in usual position (XII) ; Fig. 26A,C . . . . . .***Achaeta iberica*** Graefe, 1989
= ***Achaeta etrusca*** Rota, 1995

L 3 mm, S 22. Oesophageal appendage small, only in V. Pharyngeal glands with secondary ventral lobes in V and VI. Dorsal vessel from VII. Clitellum not developed ventrally; mid-dorsally a narrow field without clitellum, lined by 4 longitudinal rows of hyalocytes. No seminal vesicle, sperm funnel 1/3 as long as body diameter, spermathecae small and short. – Spain, Italy. Only known from the original descriptions.

11 (3) Spermathecae absent. Species with often small and inconspicuous ventral pyriform glands, see 18 . . . . . .***Achaeta affinis*** Nielsen & Christensen, 1959

11* Spermathecae present **12**

12 Body length 3–5 mm; < 30 segments; preclitellar nephridia one pair, at 6/7 (trait unknown in ***A. minima***) **13**

12* Body length > 7 mm; > 30 segments; preclitellar nephridia two pairs, at 6/7, 7/8 (trait unknown in ***A. matritensis***) **15**

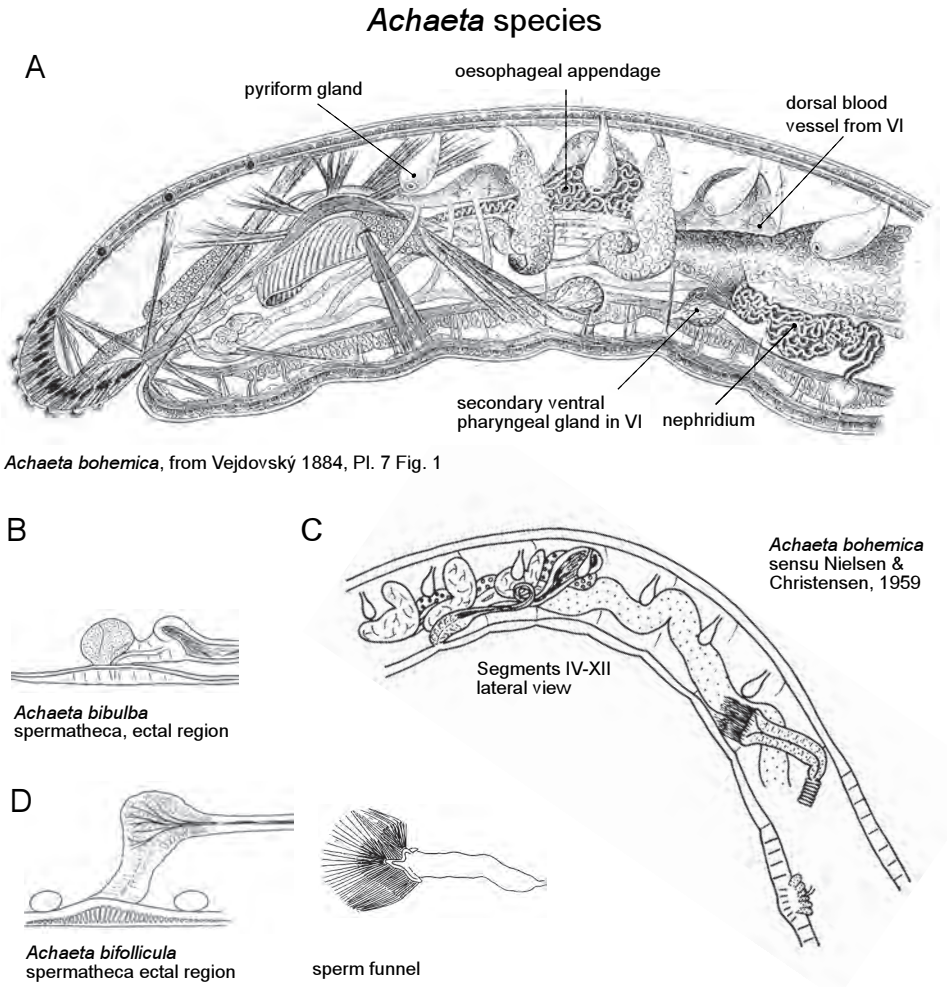

Fig. 27 ***Achaeta*** species, continued. A: ***Achaeta bohemica***, from Vejdovský (1884, Pl. 7 Fig. 1). B: ***A. bibulba***, from Graefe (1989, Fig. 8). C: ***A. bohemica*** Vejd. sensu Niels. & Christ., from Nielsen & Christensen (1959, Fig. 43). D: ***A. bifollicula***, from Chalupský (1992, Fig. 5A, E).

13 Nephridial anteseptale short or seemingly absent; sperm funnel 1.5–2x as long as wide, male pores in XI, spermathecae extending into VI-VIII **14**

13* Nephridial anteseptale as long as wide; sperm funnel 4–6x as long as wide, male pores in XII, spermathecae short, confined to V . . . . . ***Achaeta minima*** Southern, 1907

L 3 mm, S 22. Pharyngeal glands of VI larger than anterior glands. Dorsal vessel from VI. First nephridium at 6/7, with constriction at septum. Spermathecae without ectal asymmetry. – Ireland, only known from original description (1 specimen), insufficiently known species.

14 Chloragocyte vesicles conspicuously enlarged in anterior segments; male pores without glands; nephridial anteseptale consisting of funnel only . . . . . .
. . . . . .***Achaeta abulba*** Graefe, 1989

L 3–4 mm, S 20–25. Thin worms, diameter 0.1 mm and less. Pharyngeal glands all united dorsally, without secondary lobes. Oesophageal appendage in V, lobed, with canal in IV. Nephridia with terminal vesicle. Dorsal vessel from 1/2 VII. Clitellum saddle-shaped, dorsally 2 longitudinal rows of hyalocytes. Sperm funnel 2/3 as long as body diameter. Spermathecae with ectal asymmetry, short ectal duct and a gland at the orifice; ampulla extending into VII, not enlarged. – Germany, common at moderately acidic forest sites, occasionally in high numbers.

14* Chloragocyte vesicles not conspicuously enlarged in anterior segments; male pores surrounded by spherical glands; nephridial anteseptale with funnel and a very small portion of the winded canal; Fig. 27B . . . . . .***Achaeta bibulba*** Graefe, 1989

L 4–5 mm, S 24–27. Oesophageal appendage in V, lobed, with canal in IV. One pair of preclitellar nephridia, at 6/7. Dorsal vessel from 1/2 VII. Clitellum girdle-shaped, hyalocytes dorsally, not in longitudinal rows. Sperm funnel 3/4 as long as body diameter. Spermathecae with rounded ectal gland and ectal duct asymmetry, extending into VII or VIII; epidermis thickened around ectal pores. – Germany, Southern Sweden. Lit.: Chalupský (1992).

15 Glandular ectal duct continuously merging into ampulla without abrupt bend; Fig. 27C
. . . . . .***Achaeta bohemica*** (Vejdovský 1879b)
sensu Nielsen & Christensen (1959) non Vejdovský (see 16)

L ca 8 mm, S 34–38. Pyriform glands ca 1/2 as long as body diameter. Oesophageal appendage small, in V only, without canal in IV (‘absent’ in Nielsen & Christensen 1959, see remarks below). Origin of dorsal blood vessel in VII. Sperm funnel ca 1–1.5x as long as body diameter, 2–3x as long as wide. Spermathecal ectal duct 2–3x as long as wide, ampulla extending into VII, voluminous when filled with sperm. – Widespread. Lit.: Kasprzak (1986), Rota & Healy (1994), Rota (1995). ***A. matritensis*** (17*) may also key out here.

15* Spermathecae abruptly bent at transition from ectal duct to ampulla: most distal spermatozoa positioned at ca 90° to 120° with respect to longitudinal ectal duct axis (comp. Fig. 27B,D); ectal duct often asymmetrically swollen **16**

16 Two large pairs of secondary ventral pharyngeal gland lobes, in V and VI; dorsal vessel from VI; Fig. 27A . . . . . .***Achaeta bohemica*** (Vejdovský, 1879b)
= ***Achaeta vesiculata*** Nielsen & Christensen, 1959
= ***Achaeta microcosmi*** Heck & Römbke, 1991

L 8–15 mm, S 32–44. Stout specimens, truncate, as if incomplete. Cuticle thick and reflecting. Oesophageal appendage large in IV and V. Third pair of pharyngeal glands reduced and not connected dorsally, often absent. Preclitellar nephridia with large terminal vesicle. Clitellum only laterally developed; cells in transverse rows, hyalocytes not in longitudinal rows. Seminal vesicle large, several segments, sperm funnel 3(–6?)x as long as wide, as long as body diameter (up to 1.5x?). Male pores closely paired. Spermatheca extending into VII–IX, ental reservoir thin-walled, large. – Widespread. Lit.: Vejdovský (1884), Černosvitov (1928a).

16* One small pair of secondary ventral pharyngeal gland lobes, in VI; dorsal vessel from VII **17**

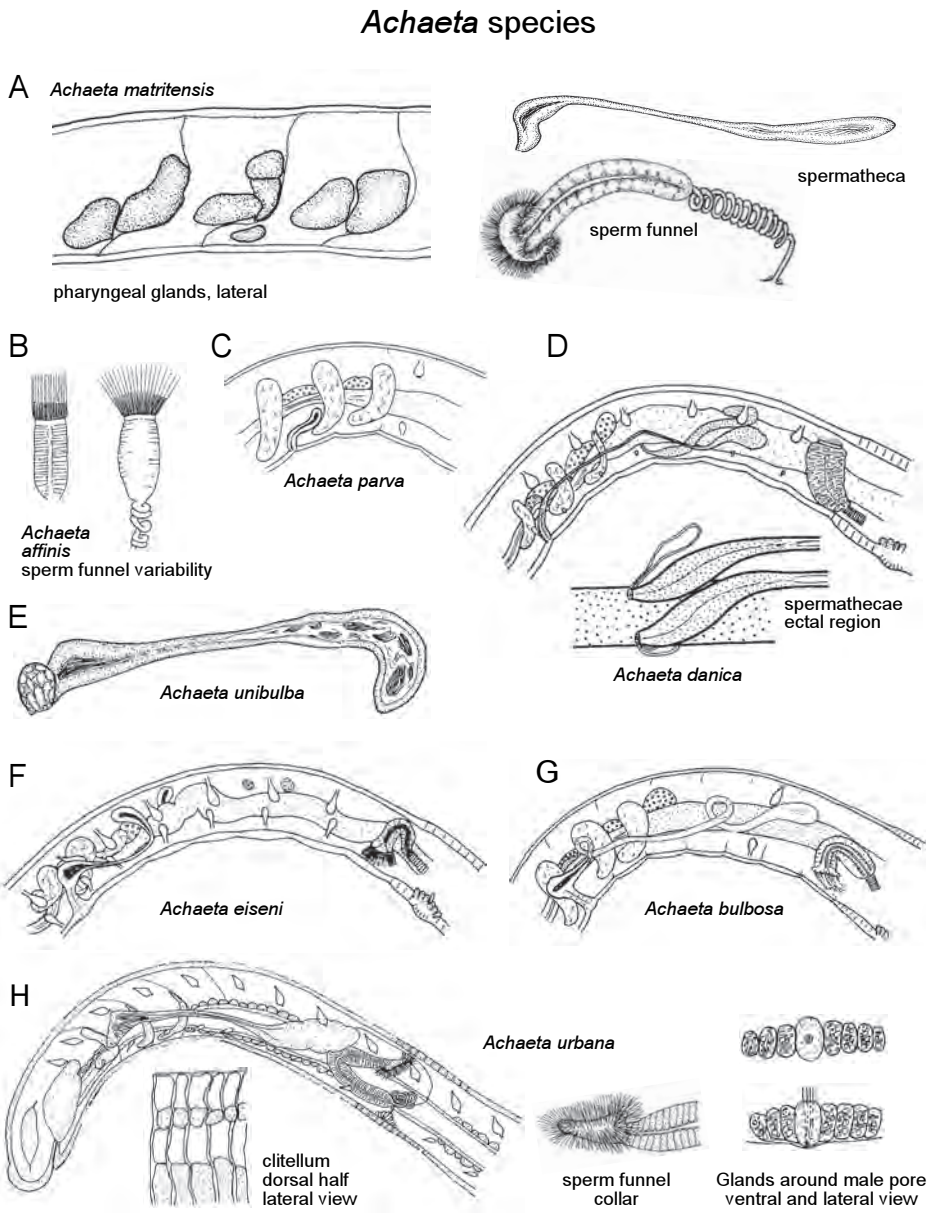

Fig. 28 ***Achaeta*** species, continued. A: ***A. matritensis*** from Sesma & Dózsa-Farkas (1993, Figs 37, 39, 40.) B: ***A. affinis***, from Chalupský (1992, Fig. 3C). C: ***A. parva***, from Nielsen & Christensen (1961, Fig. 2). D: ***A. danica***, from Nielsen & Christensen (1959, Figs 44, 45). E: ***A. unibulba***, from Graefe et al. (2005, Fig. 1A). F: ***A. eiseni***, from Nielsen & Christensen (1959, Fig. 42). G: ***A. bulbosa***, from Nielsen & Christensen (1961, Fig. 1). H: ***A. urbana***, from Heck & Römbke (1991, Fig. 2A,C,G,H).

17 Seminal vesicle over 3 or more segments; sperm funnel 8–10x as long as wide, 3–4x as long as body diameter; vas deferens very long, may extend through several segments posteriad; spermathecal ampulla filling out entire coelomic space in IX and X; Figs 23B, 27D . . . . . .***Achaeta bifollicula*** Chalupský, 1992

L 8–10 mm, S 40–46. Cuticle often thick. Two knob-like bodies attached to inner body wall in front of and behind spermathecal pore. Oesophageal appendage large in IV–V. Secondary ventral pharyngeal gland lobes in VI distinct but small. Two or three pairs of preclitellar nephridia, at 6/7, 7/8, (8/9). Clitellum mid-dorsally not developed, hyalocytes with 2 baguette-rows on each side dorso-laterally. Sperm funnel collar with asymmetrical extension. – Germany, Sweden.

17* Seminal vesicle in XI, sperm funnel 5x as long as wide, ca 1.5x as long as body diameter; maximum diameter of spermathecal ampulla 1/3 of 1/2 body diameter; Fig. 28A . . . . . .***Achaeta matritensis*** Sesma & Dózsa-Farkas, 1993

L 9 mm, S 35. Oesophageal appendage in V. Clitellar gland cells in transverse rows. Spermathecae extending into IX/X. – Spain. Known only from original description.

18 (3*)Spermathecae absent; Fig. 28B . . . . . .***Achaeta affinis*** Nielsen & Christensen, 1959 sensu lato

L 5–8 mm, S 26–32. Ventral pyriform glands often small, indistinct. Oesophageal appendage large in IV, V. Nephridia at 6/7, 7/8. Ventral pharyngeal gland lobe in IV somewhat separate from dorsal lobe. Dorsal vessel from VII. Sperm funnel 2–3x as long as wide, much varying in size, from less than half as long as body diameter to almost as long as body diameter. Male pores closely paired; male glandular body small, with anterior and posterior accessory glands (Fig. 13 bottom left). Common and widespread, often in moderately acidic soils. Probably a species complex. Lit.: Chalupský (1992), Rota (1995).

18* Spermathecae present **19**

19 Spermathecae short, only in V; dorsal vessel from VI; Fig. 28C . . . . . .***Achaeta parva*** Nielsen & Christensen, 1961

L 3–5 mm, S 18–23. Pyriform glands with refractile globules. Oesophageal appendage small, inconspicuous. No seminal vesicle. – Denmark, Germany, the Netherlands. Insufficiently known species.

19* Spermathecae longer, extending at least into VII; dorsal vessel from VII (unknown in ***A. seminalis***) **20**

20 Spermathecal ectal duct not oblique to main axis of spermatheca, more than 4x as long as wide; sperm funnel 2–3x as long as wide; Fig. 28D . . . . . .***Achaeta danica*** Nielsen & Christensen, 1959 sensu lato

L 5–7 mm, S 29–36. Ventral pyriform glands in IV often enlarged. Oesophageal appendage well-developed in IV, V. Pharyngeal glands without secondary ventral lobes. Two pairs of preclitellar nephridia, at 6/7 and 7/8. Clitellum open dorsally and ventrally. Hyalocytes dorso-laterally, in two baguette-like longitudinal packages on each side. Seminal vesicle small or absent; sperm funnel variable, flattened or inflated, almost as long as body diameter. Male glandular body small, with anterior and posterior accessory glands (Fig. 13 bottom left). Spermathecae medium-sized, ectally thickened, extending into VI–IX (X). – Widespread. Probably a species complex. Lit.: Kasprzak (1986).

20* Spermathecal ectal duct oblique to main axis of spermatheca, less than 4x as long as wide; sperm funnel 2–6x as long as wide **21**

21 Glands around both male pores united into one large common body (ventral view!), no accessory glands; 3 pairs of preclitellar nephridia; Fig. 28E . . . . . ***Achaeta unibulba*** Graefe, Dózsa-Farkas & Christensen, 2005

L 8–10 mm, S 32–40. Oesophageal appendages small, only in V. Preclitellar nephridia at 6/7 – 8/9. Clitellum absent mid-dorsally and mid-ventrally. Sperm funnel 4–6x as long as wide, about as long as body diameter. Male pores close to each other. Spermathecae with rounded ectal gland and ectal duct asymmetry, extending into VII or VIII; epidermis thickened around ectal pores (as in ***A. bibulba***, comp. Fig. 27B). – Widespread. Only European ***Achaeta*** species with 4 segmental pyriform glands and 3 preclitellar nephridia.

21* Glands of both male pores separate from each other, accessory glands present, usually two pairs of preclitellar nephridia (number unknown in several species) **22**

22 Seminal vesicle absent or poorly developed, confined to XI **23**

22* Seminal vesicle well-developed, extending over 2 segment lengths **24**

23 Spermatheca extending into VII/VIII, ental reservoir with sperm; ectal duct as long as wide; Fig. 28F . . . . . ***Achaeta eiseni*** Vejdovský, 1878

L 6–8 mm, S 30–40. Pharyngeal glands of VI occasionally reduced. Oesophageal appendage in IV and V. Coelomocytes indistinctly granulated, some of them larger than dorsal pyriform glands. Sperm funnel variable in length, 2–5x as long as wide. – Widespread. Probably a species complex. Lit.: Nielsen & Christensen (1959), Möller (1971), Rota (1994, 1995).

23* Spermatheca extending into X, ental reservoir without sperm, inconspicuous, ectal duct 3x as long as wide; Fig. 28G . . . . . ***Achaeta bulbosa*** Nielsen & Christensen, 1961

L 10–12 mm (?), S ca 37. Coelomocytes coarsely granulated, largest cells as long as pyriform glands. Oesophageal appendage well-developed in V. – Denmark. Insufficiently known species.

24 Body covered with minute, transversely elongate, epidermal gland cells; spermathecae extending into VII (rarely VIII), collar of sperm funnel symmetrical as usual . . . . . ***Achaeta seminalis*** Kasprzak, 1972

L ca 10 mm, S 40. Oesophageal appendage in V, well-developed. Clitellum girdle-shaped (?), cells in regular transverse rows. – Poland. Insufficiently known species.

24* Epidermal gland cells absent, spermathecae extending into IX or X; collar of sperm funnel asymmetrical, with lip-like extension on one side; Fig. 28H . . . . . ***Achaeta urbana*** Heck & Römbke, 1991

L 9 mm, S 36–40. Oesophageal appendage in V, with canal in IV. Pharyngeal glands with wide (IV) or narrow (V, VI) dorsal connection. Preclitellar nephridia 2 pairs, 7/8, 8/9. Clitellum absent ventrally and dorsally; gland cells in separate transverse rows. Hyalocytes in 4 longitudinal dorso-lateral rows. Glands at male pore in a longitudinal row, 7–8 per pore, gland around pore largest (Fig. 13 bottom left). Seminal vesicles large (ca 2 segments), sperm funnel 5–6x as long as wide, length ca 2x body diameter. Spermathecae with ectal glandular asymmetry, ental reservoir large, extending into IX/X–(XII). – Germany. Only known from original description.

Shortcuts to species with conspicuous characters

Only one pair of preclitellar nephridia: ***A. abulba***, ***A. bibulba***

Three pairs of preclitellar nephridia

With pyriform glands: ***A. unibulba***, ***A. bifollicula*** (partim)

Without pyriform glands: ***A. pannonica***, ***A. iberica***

Seminal vesicle large, over 2 or more segments

Only dorsal pyriform glands: ***A. bohemica***, ***A. bifollicula***, ***A. matritensis***

Dorsal and ventral pyriform glands: ***A. seminalis***, ***A. urbana***

A. iberica and ***A. etrusca***. ***A. etrusca*** is said to differ from ***A. iberica*** in the following: (1) clitellar hyalocytes and granulocytes arranged in irregular mosaic pattern, (2) nephridia of 7/8 and 8/9 apparently not attached to a septum. We reinvestigated the holotype of ***A. iberica***; the longitudinal rows of hyalocytes are not completely regular and the preclitellar septa behind 6/7 are thin and inconspicuous.

A. bifollicula as originally described (from Sweden) has 3 pairs of preclitellar nephridia. Specimens found in Germany usually have only two pairs, but the original form may occasionally be found here as well.

A. bulbosa, ***A. eiseni***, and ***A. seminalis***. The differences between these three species need reinvestigation. Christensen (1961) counted 150–160 somatic chromosomes in ***A. bulbosa***, which may thus be a polyploid form of ***A. eiseni*** or of ***A. seminalis***. Chromosome numbers of the latter two, however, are unknown. Specimens that key out as ***A. eiseni*** here may belong to more than one species. Despite numerous records (over 80), no satisfactory description of ***A. eiseni*** is currently available; in the most detailed accounts (Rota 1994, 1995) the identity is uncertain ('cf.'), and several traits differ from the (old and poor) original description. Originally the sperm funnel is 5x as long as wide. The original description of ***A. seminalis*** is inconsistent regarding the origin of the dorsal blood vessel (the text says VI and a figure shows it in VII) and probably wrong regarding the distribution pattern of clitellar gland cells. The species was never found again. Unfortunately, types of all three species are lost or inaccessible.

A. affinis and ***A. danica.*** The taxonomy of both species needs revision. On the one hand, they are quite similar and even the most conspicuous difference, presence/absence of the spermatheca, does not appear to work in all cases, since thecate specimens of ***A. affinis*** have been described (Chalupský 1992). On the other hand, each species may consist of more than one species. ***A. danica*** as originally described has (1) closely paired spermathecal pores and (2) hyaline spermathecal ectal glands; the latter are perhaps misidentified ventral pyriform glands, enlarged in IV. These two traits can be found in specimens identifiable as ***A. danica***, but never in one and the same specimen. Both forms may differ also in the sperm funnel, the pattern of male glands, and in the extension of the spermathecae. Form No. (2) (with widely paired male pores and enlarged pyriform glands in IV) appears as 'dzwilloi' in several German ecological papers, but the species is not yet formally described. ***A. affinis*** may also consist of more than one species; Healy (1979b) distinguished small and large forms. In many specimens identifiable as ***A. affinis*** the sperm funnels are almost as long as the body diameter and not less than half as long, as originally described. The informal name 'affinoides' in some German ecological papers refers to this form.

A. bohemica, ***A. vesiculata*** and ***A. microcosmi. Achaeta vesiculata*** and ***Achaeta microcosmi*** fit Vejdovský's old and often-recorded ***Achaeta bohemica*** in the following traits, derived from an instructive figure in Vejdovský (1884, Pl. VII Fig. 1, see Fig. 27A): a large oesophageal appendage in IV and V, (2) primary pharyngeal glands only in IV and V, (3) dorsal blood vessel from VI, (4) first nephridium at 6/7, (5) with large terminal vesicle. Traits (2) and (4) differ in the original description of ***A. microcosmi***, but they are present in the type material (Schmelz, unpublished). Size of sperm funnel and seminal vesicle appear to vary much and need reinvestigation. On the other hand, ***Achaeta bohemica*** as redescribed in Nielsen & Christensen (1959) differs in the first three characters from Vejdovský's descriptions (traits No. 4 and 5 are not dealt with) and is hence a different species, currently without name. Specimens identifiable as ***A. bohemica*** sensu Nielsen & Christensen have a small oesophageal appendage in V, probably overlooked by Nielsen & Christensen (1959), who state that it is absent, and the dorsal blood vessel rises in VII (not described in the monography). The informal name 'healyae' in some German ecological papers refers to this form.

The last two paragraphs use expert knowledge of U. Graefe, kindly acknowledged here.

7.4. *Guaranidrilus* Černosvitov, 1937e (Fig. 29A,B)

Prostomium short, head pore on prostomium. Two chaetae throughout, mostly straight distally. Epidermal gland cells often conspicuous as transverse stripes on body surface. Brain incised posteriorly. Pharyngeal glands all united dorsally, with secondary ventral lobes in V and VI, oesophageal appendages often present as paired bodies attached in VI dorso-laterally; one pair of intestinal diverticula present, mostly as large, hollow and thin-walled pouches laterally of intestine, in VII or VII-VIII. Dorsal vessel rising in or near clitellar region. Nephridial anteseptale with coils of canal and interstitial tissue. Male pore on body surface, no bursa. Male glandular bulb often small, inconspicuous, or absent. Spermathecae simple, without ectal glands or diverticula, not attached to oesophagus. – Species-rich and abundant in tropical and subtropical soils of South America. One species in Europe so far.

Guaranidrilus europaeus Healy, 1979c

L 3–6 mm, S 23–29. Chaetae small, only 20 µm long. Epidermal glands indistinct, in 3–5 rows per segment. Oesophageal appendages absent. Intestinal diverticula large, in VII–VIII, with narrow connection to oesophagus laterally at 7/8. Clitellar gland cells square-shaped, in 20–33 rows. Sperm funnel pear-shaped, no seminal vesicle. Spermathecae extending into VI, duct distally with slight expansion. – Southern France.

7.5. *Hemienchytraeus* Černosvitov, 1934b (Fig. 29C)

Two chaetae per bundle, straight distally or bent. Head pore on prostomium. Oesophageal appendage with unpaired stem dorsally in III, behind pharyngeal pad, extending posteriad, bifurcating into two primary branches; these branching into secondary branches; common stem with large lumen, lumina in branches often sponge-like, canals much winded. No intestinal diverticula. Nephridial anteseptale large with coils of canal. Sperm funnel usually tapering distad, male glandular bulb usually well-developed, bursa present. Spermathecae free, not attached to oesophagus, without ectal gland, ampulla without diverticula. – Common and widespread in tropical and subtropical soils. One species in Europe so far.

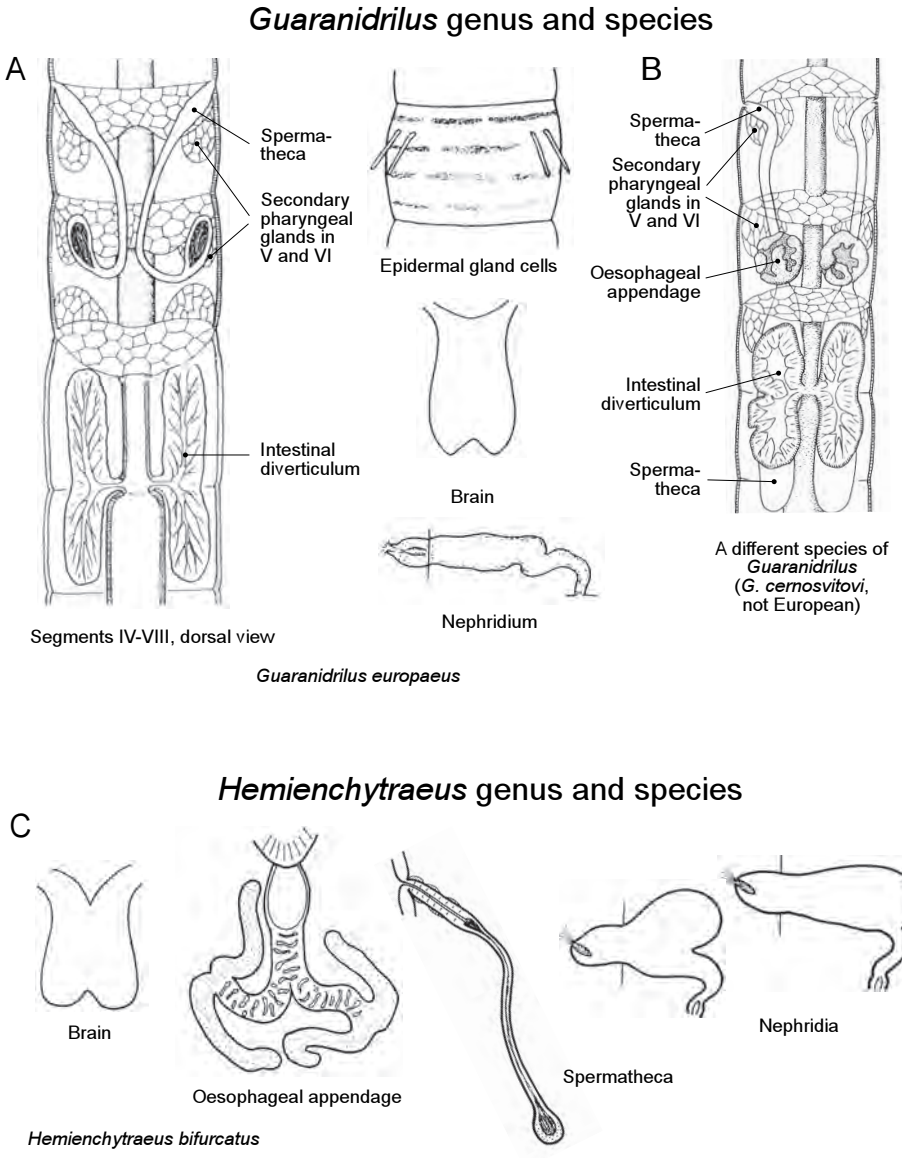

Fig. 29 ***Guaranidrilus*** and ***Hemienchytraeus***. A: ***G. europaeus***, from Healy (1979c, Fig. 2F,A,E,I). B: ***G. cernosvitovi***, from Healy (1979c, Fig. 1A). C: From Nielsen & Christensen (1959, Figs 27, 26, 23, 24, 25).

Hemienchytraeus bifurcatus Nielsen & Christensen, 1959

L 10 mm (?), S 28–32. Oesophageal appendage with two secondary branches on each side. Nephridia with terminal vesicle. Sperm funnel usually tapering distad, small, length 1/3 worm diameter, 2–3x as long as wide. Spermathecae thin, extending into VI/VII. Denmark, Germany, Poland. Insufficiently known species.

A very similar species from Amazonia has been described, and the original description of ***H. bifurcatus*** has been considered as insufficient (Schmelz et al. 2005b). Records of the species should not be published without a detailed redescription (comp. Schmelz & Collado 2007). Animals are most probably shorter than 10 mm. Body dimensions are usually exaggerated in Nielsen & Christensen (1959), for unknown reasons.

7.6. *Stercutus* Michaelsen, 1888 (Fig. 30A)

Genus probably monotypic.

Stercutus niveus Michaelsen, 1888

L 3–6 mm, diameter up to 0.5 mm, S 19–28. Animals opaque-white, stout (only ca 10x as long as wide), strongly tapering at both ends. Head pore apparently absent. White colour caused by very tall chloragocytes (not coelomocytes!) filling out entire coelomic cavity from IV on. Chaetae 2,3 – 2 : 4,3 – 4,3. Chaetae sigmoid with weak nodulus, both sigmoidity and nodulus may be inconspicuous. Chaetae robust, especially ventrally in anterior segments. Brain deeply incised posteriorly. Pharyngeal glands all separate dorsally, primary pairs in IV–VI, small secondary pairs antero-ventrally in V and VI. Oesophageal appendages and intestinal diverticula absent. Intestine seasonally degenerate (closed) posteriorly. Preclitellar nephridia 4 pairs, 6/7–9/10. Nephridial anteseptale with few coils of canal, almost consisting of funnel only. Dorsal vessel from IX or XI. Sperm funnel about as long as wide, collar wider than funnel body, male glands around male pore minute. Spermathecae free, short, with ectal glands. 1–2 or up to 10–15 large eggs at a time, extending of several segments. – In forest litter. Lit.: Černosvitov (1937d), Nielsen & Christensen (1959), Dózsa-Farkas (1973), Römbke (1989), Rota (1995), Rota & Healy (1999).

The genus has only one species, therefore no genus diagnosis is given here. (One more species has been ascribed to ***Stercutus***, ***S. ugandensis*** Bell, 1954, but it does not belong here, see Nielsen & Christensen (1959) for details.) The sigmoid chaetae, the free spermathecae and the shape of the nephridia suggest a close relationship of the species to ***Cognettia***.

7.7. *Cognettia* Nielsen & Christensen, 1959 (Fig. 30B-E)

Chaetae sigmoid, without nodulus, 2 or 3 per bundle in European species. Head pore at 0/1. Brain incised posteriorly (straight in some specimens of ***C. sphagnetorum***). Secondary ventral pharyngeal gland lobes present in all species except ***C. sphagnetorum***; ventral lobes always placed anterior to dorsal lobes in a segment. No oesophageal appendages, no intestinal diverticula. Transition from oesophagus into intestine gradual, abrupt in ***C. hibernica***. Origin of dorsal blood vessel in XII or further back, blood colour pale or yellow/rose. Nephridial anteseptale with funnel only, postseptale bulky, efferent duct rising close to septum. Coelomocytes of one type only, mucocytes. Spermathecae not attached to oesophagus, without diverticula, with rounded ectal gland.

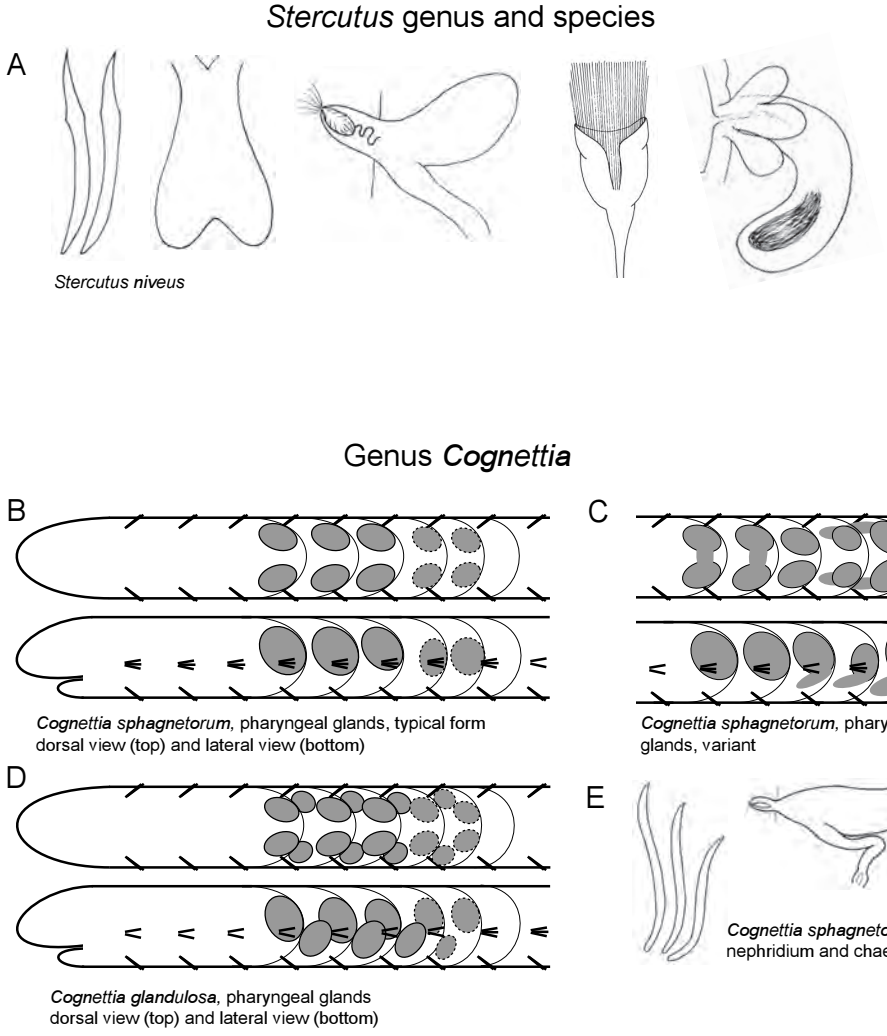

Fig. 30 ***Stercutus*** and ***Cognettia.*** A: ***S. niveus***, from Dózsa-Farkas (1973, Fig. 1A,B,C,E,D). B, C: ***C. sphagnetorum***. D: ***C. glandulosa***. E: ***C. sphagnetorum***, from Timm (1999, p. 136), Nielsen & Christensen (1959, Fig. 28).

1 Three chaetae in many or most bundles (check ventral bundles) **2**

1* Two chaetae in all or most bundles **5**

2 Enlarged chaetae in 2 or 3 lateral bundles of segments III–VII; pharyngeal glands with dorsally connected primary lobes in IV–VI; secondary lobes in V, VI, and VII; Fig. 31A,B . . . . . ***Cognettia cognettii*** (Issel, 1905) augm. Černosvitov (1945)

L 6–11 mm, 30–41 segments. Ventral bundles with three chaetae, lateral bundles with 2 or 3. Chaetae distinctly yellowish. Dorsal lobes of pharyngeal glands connected; secondary ventral lobes in VII larger than anterior ones. Preclitellar nephridia 4 pairs, 6/7 – 9/10. Coelomocytes with fine, pale, occasionally slightly yellowish or opaque granulation. Genital organs in usual position. Sexual specimens not rare. No fragmentation (?, see remarks). – Widespread, wet, slightly acidic soils, peatland. Lit.: Černosvitov (1945), Römbke (1989).

2* No enlarged chaetae, pharyngeal glands different. **3**

3 Two lobes of pharyngeal glands per segment, mostly separate dorsally; pharyngeal glands in mostly 4 or 5 segments (IV–VII or IV–VIII), occasionally in 3 or 6 segments (IV–VI or IV–IX); fragmenting species; Figs 30B,C,E, 31B . . . . . ***Cognettia sphagnetorum*** (Vejdovský, 1878)
= ***Cognettia anomala*** (Černosvitov, 1928a)
= ***Cognettia paxi*** (Moszyński, 1938)

L up to 25 mm, S up to 65 or more, down to 5 or 6. Ventral bundles with 3 chaetae, lateral bundles variable: all with 3, or in II–VIII with 2 chaetae, rest with 3, or other combinations; in single bundles 1, 2, or 4 chaetae. Pharyngeal glands in 3–6 segments, mostly separate dorsally, occasionally connected in anterior two segments; secondary lobes mostly absent; when present, restricted to posterior segments (VI–IX) and of unequal size (Fig. 30C). First nephridium at 8/9 or further back. Reproduction mostly by fragmentation, sexual specimens rare, seasonal, more common in southern than in northern regions. Gonadal segments displaced forward by 2–4 segments. Coelomocytes sparse in some animals. – Widespread, dominant in acidic organic soils (peat, bogs, mor, raw humus etc.). Lit.: Nielsen & Christensen (1959), Römbke (1989), Chalupský (1992), Rota (1995), Timm et al. (1996, as ***C***. cf. ***sphagnetorum***).

3* Four lobes of pharyngeal glands per segment at least in V and in VI, an anterior ventral pair and a posterior dorsal pair; species fragmenting or non-fragmenting **4**

4 Pharyngeal glands in more than 3 segments (i.e. also in VII or VIII), four lobes in 3 or more segments, in V-VII (-VIII); large forms; reproduction by fragmentation common, sexual specimens rare, with gonadal segments (clitellar region) shifted forwards; Figs 30D, 31B . . . . . ***Cognettia glandulosa*** (Michaelsen, 1888)

L up to 25 mm, S up to 65. All or several lateral bundles in II-VIII with 2 chaetae, rest with mostly 3. Pharyngeal glands mostly with 5 + 4 pattern: 5 dorsal lobes, in IV-VIII, and 4 ventral lobes, in V-VIII, almost as large as dorsal lobes. Posterior glands may be missing in young fragments. First nephridium at 8/9 or further back. – Common and widespread, in wet, neutral to slightly acidic soils. Lit.: Nielsen & Christensen (1959).

4* Pharyngeal glands in 3 segments only (IV–VI), four lobes only in V and VI; small forms, no reproduction by fragmentation, sexual specimens not rare, clitellar region in usual position; Fig. 31B . . . . . ***Cognettia lapponica*** Nurminen, 1965

L ca 6 mm, S 32–37. Three chaetae per bundle throughout, rarely 2 in some posterior bundles. Pharyngeal glands with 3 + 2 pattern: dorsal lobes in IV–VI, separate; secondary ventral lobes in V and VI. Position of preclitellar nephridia unknown. Sperm funnel in XI, cylindrical, 2–2.5x as long as wide, shorter than body diameter, collar as wide as funnel body. Male pores in usual position, with glandular bulb. Spermathecae short, confined to V; ental part of ampulla often bent or curved. – Arctic species, widespread in tundra soils, insufficiently described.

5 Pharyngeal glands dorsally separate, three pairs in IV, V, VI, three secondary ventral lobes in V, VI, VII; large forms; Fig. 31C . . . . . ***Cognettia clarae*** Bauer, 1993 sensu lato
= ***Mesenchytraeus franzi*** Nurminen, 1977
= ***Euenchytraeus bisetosus*** Bretscher, 1906

L 10–16 mm, S 55–67. Two chaetae in all bundles; or 3 ventrally from II/III – V/VI, 2 in the rest (Western population). First nephridia at 2/3, 'head nephridia', with very large terminal vesicle, (Fig. 31C left). Reproductive organs in normal position. Intestine widening gradually. Clitellum girdle-shaped. Sexual specimens seasonal (spring, early summer). – Holarctic, cool climates. Widespread in mountain regions of Central and Western Europe (unpublished records of Graefe, Chalupský, Schmelz & Collado). Lit.: Piper et al. (1982, as ***Marionina*** sp.).

5* Pharyngeal glands broadly united dorsally in IV and V, separate and elongate in VI; small secondary ventral lobes in V and VI; small forms; Fig. 31D . . . . . ***Cognettia hibernica*** Healy, 1975

L 3–4 mm, S ca 22. No head nephridia, preclitellar nephridia in 6/7, 7/8, and sometimes also 10/11. Reproductive organs in normal position. Intestine widening abruptly in VII. Clitellum saddle-shaped. Sperm funnel oval, short, slightly longer than wide. Sexual specimens common. – Ireland, Northern Spain. Lit.: Collado et al. (1993).

Variability in *Cognettia sphagnetorum*. *C. sphagnetorum* is most easily identified by the pharyngeal glands (one pair of dorsally separate glands in more than 3 segments, no secondary glands), but some variation has to be taken into account. (1) Some specimens, especially small ones, have only three pairs, in IV–VI. (2) Others have slight swellings on the afferent fascicles, which resemble secondary glands and appear to blur the distinction to ***C. glandulosa***. However, in ***C. glandulosa*** the secondary glands are almost as large as the primary glands; they are present and well-developed from V on and of same size at least in V and VI; from VII on they may be smaller. In ***C. sphagnetorum*** the swellings are little developed or absent in V, and they may increase in size in posterior segments. (3) In some specimens, some of the anterior pharyngeal glands are dorsally connected (Fig. 30C). In aquatic habitats dorsal connection of anterior glands seems to be the rule (Timm et al. 1996). According to Chalupský (1992), these forms have reddish blood and may represent a different species. (4) Finally, glands are usually rounded and about the same size, or diminishing in size posteriorly; but sometimes they are larger in posterior segments (VII, VIII or IX) and of irregular outline. Such forms are known as ***C. paxi*** and ***C. anomala***, species that we incorporate here into a ***C. sphagnetorum*** sensu lato.

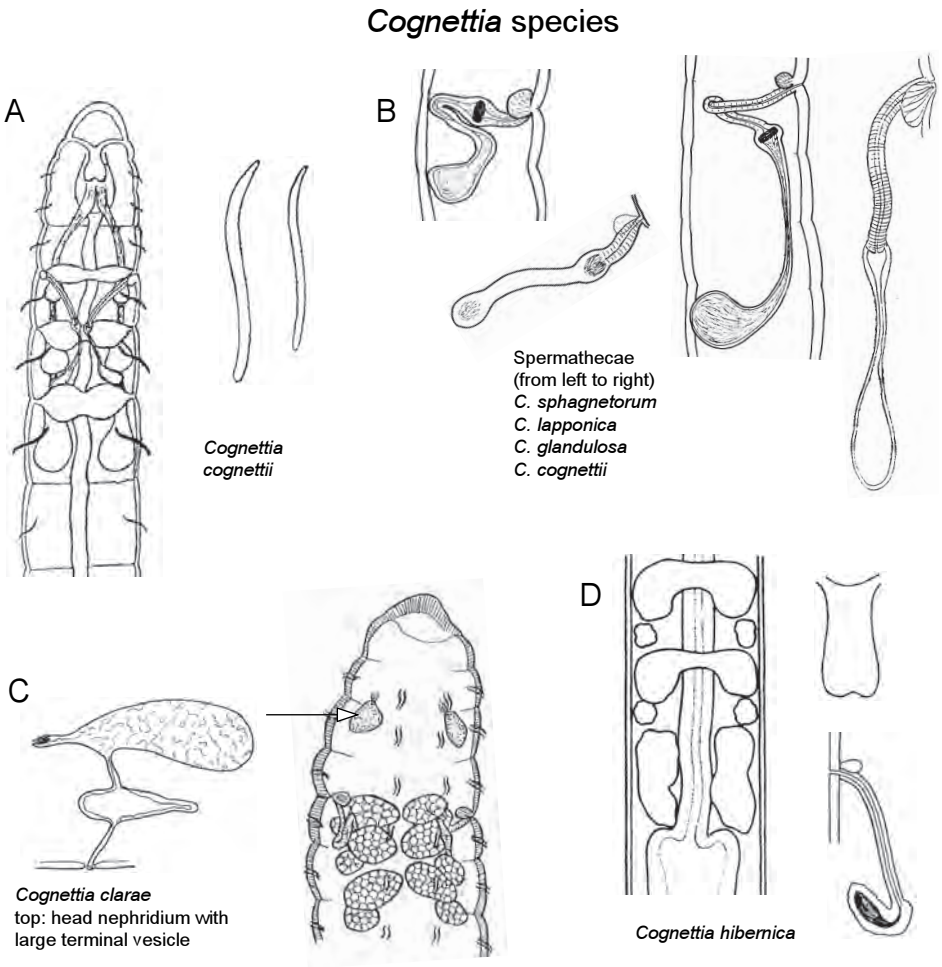

Fig. 31 ***Cognettia*** species. A: ***C. cognettii***, from Černosvitov (1945, Figs 62, 65, 66). B: Spermathecae of different species. From (left to right) Nielsen & Christensen (1959, Fig. 29), Nurminen (1965, Fig. 2A), Nielsen & Christensen (1959, Fig. 30), Černosvitov (1945, Fig. 69). C: ***C. clarae***. Left from Piper et al. (1982, Fig. 13), right from Bauer (1993, Fig. 4). D: ***C. hibernica*** from Healy (1975, Fig. 3A,B,F).

At terrestrial sites, Chalupský (1992) distinguished two forms of ***C. sphagnetorum***, separable by chaetal pattern and coelomocyte texture: Form A: two chaetae laterally in II–VIII, coelomocytes almost hyaline and with net-like texture. Form B: three chaetae laterally in II–VIII, coelomocytes with fine and regular granulation. Most of our material from Germany and Spain conforms to this distinction, which may indicate two lineages or subtaxa in ***C. sphagnetorum***. Form A prefers drier sites (e.g. pine forests) and form B wetter

sites (e.g. mors and bogs). Furthermore, adult specimens of form A have spermathecal pores in ventro-lateral position, and the supernumerary male glandular bulb described by Nielsen & Christensen (1959) is found only here, not in form B. A critical revision of ***C. sphagnetorum*** is in preparation.

Identification of *Cognettia cognettii*. The species is easily recognised by the enlarged lateral chaetae. They were first described by Černosvitov (1945), but they are not mentioned in the original description (Issel 1905a), so the trait seems to be variable. However, according to Issel, chaetae in ***C. cognettii*** reach 100 µm length and 10 µm thickness, which is in the size range of the enlarged chaetae – so they may have been present also in the original material. According to Černosvitov (1945), the size difference between normal and enlarged chaetae is not always conspicuous. We never found adult specimens of ***C. cognettii*** without enlarged lateral chaetae; they were absent only in some juvenile specimens. Therefore we maintain – as a working hypothesis and until proven otherwise – that enlarged anterior lateral chaetae are always present in adult ***C. cognettii***. Specimens without large chaetae are similar to ***C. glandulosa***, which occasionally has a similar 3 + 3 pattern of pharyngeal gland cells, but dorsal lobes are not connected in ***C. glandulosa***, and secondary lobes are not larger in VII than in the rest. The two species are also separable by the chaetal formula and the location of anterior nephridia. The same 3 + 3 pattern of pharyngeal glands is also present in ***C. clarae***, a species with only 2 chaetae per bundle.

Römbke (1989) found a few fragments of ***C. cognettii*** and adults with the clitellar region shifted 4–5 segments forward, among a larger number of 'normal' specimens, collected in a beech forest in southern Germany. This suggests either fragmentation as a rare reproductive alternative in the species, or at least strong regenerative capacities after injury or environmental stress.

Cognettia clarae* and related species**. ***Cognettia clarae differs from the other ***Cognettia*** species by its larger body diameter and a somewhat soft body wall, resembling species of ***Mesenchytraeus***. The peculiar head nephridia have very large terminal vesicles (Fig. 31C). The species as conceived here may consist of more than one species. Head nephridia were also found in the Siberian ***Cognettia piperi*** Christensen & Dózsa-Farkas, 1999 and in ***Euenchytraeus bisetosus*** Bretscher, 1906 from the Swiss Alps. Bretscher erected a new genus specifically because of the head nephridia, but the species was described on juvenile specimens, which prompted Černosvitov (1937a) to invalidate the taxon. ***Mesenchytraeus franzi*** Nurminen, 1977, described from the Austrian Alps, also resembles this group in many traits, although nephridia were not described. We have seen further material in the collections of Chalupský and Graefe, and in samples from mountain regions in Galicia, Spain (all unpublished). There are variations in the chaetal pattern (see description above), the seminal vesicle (from absent to large, extending over 2 segments), sperm funnel (5–10x as long as wide), and spermatheca (from stump-like, in V only, to long, extending into VIII). At present we do not know how many species are involved, and we maintain the name of ***Cognettia clarae*** for the entire group, although one of the older names may have priority.

Nomenclature. The genus name has two senior synonyms, (1) ***Chamaedrilus*** Friend, 1913a, a genus erected for ***Ch. chlorophilus***, a species that was later synonymised with ***Marionina sphagnetorum*** (Delphy 1921, Černosvitov 1937c), now the type species of ***Cognettia***; and (2) ***Euenchytraeus*** Bretscher, 1906, erected for ***E. bisetosus*** (see above). To conserve ***Cognettia*** as valid name a proposal towards the ICZN is necessary.

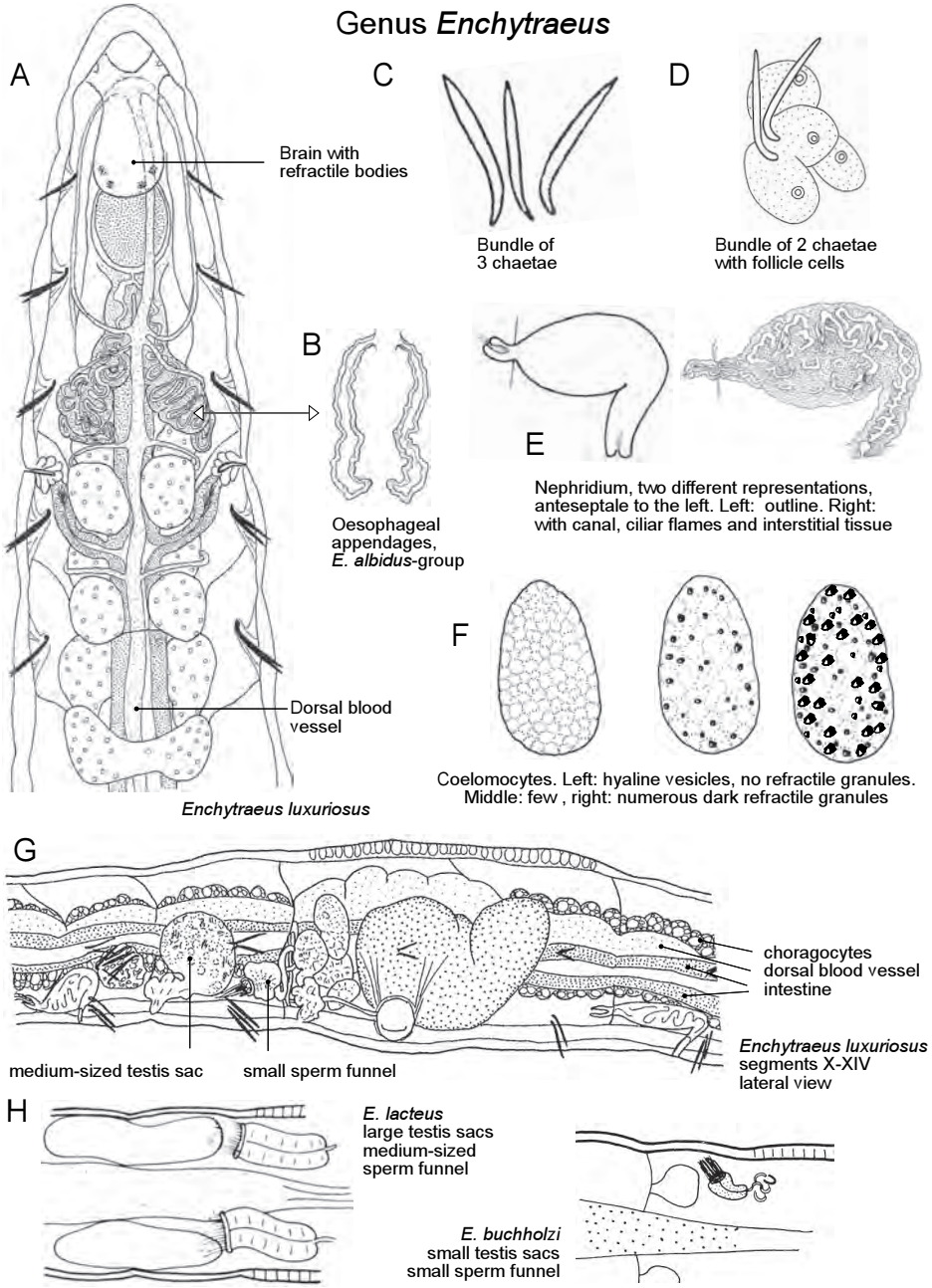

Fig. 32 ***Enchytraeus***, taxonomic traits. A: representative of the ***buchholzi***-group from Schmelz & Collado (1999 Fig. 1). B from Cejka (1913, Fig. 3). C from Bell (1947, Fig. 8). D from Westheide & Graefe (1992, Fig. 1F). E left from Nielsen & Christensen (1959, Fig. 100), right from Goodrich (1897, Pl. 5 Fig. 2). F from Schmelz et al. (1999b, Fig. 2, altered). G from Schmelz & Collado (1999, Fig. 1B). H left from Nielsen & Christensen (1961, Fig. 15), right from Nielsen & Christensen (1959, Fig. 102).

7.8. *Enchytraeus* Henle, 1837 (Fig. 32)

Chaetae straight with ental hook, mostly 2 or 3 per bundle, 4–5 in some species. Head pore at 0/1. Brain posteriorly rounded or slightly incised, often with aggregations of refractile bodies in postero-lateral part. Oesophageal appendages a pair of unbranched tubes with common opening dorsally into oesophagus in III, behind pharyngeal pad; tubes extending into IV, much winding in smaller species, and often compacted into a mass of spongy appearance. No intestinal diverticula. Dorsal vessel rising in intra- or postclitellar segments. Nephridial anteseptale with funnel only, usually four preclitellar pairs, at 6/7 – 9/10. Coelomocytes one type, mucocytes. Developing sperm enclosed by a membrane into a pair of testis sacs. Male glandular bulbs compact, rounded, or dissolved into several bodies aligned anteriorly and posteriorly of male pores. No subneural glands. Spermatheca with ectal duct, ampulla, ental duct and separate openings into oesophagus; ectal glands mostly present. diverticula mostly absent; one asymmetrical diverticulum present in some of the larger species (***E. albidus***-group).

1 Small to medium-sized forms, length 3–10–(15) mm; ventrally not more than 3 chaetae in regular bundles; if more than 3, then one chaeta attached or two bundle sets closely together; oesophageal appendages long, tubes tapering proximally, usually much winded or folded and with meandering canal (Figs 1A, 32A), often compressed into a spongy mass; pharyngeal glands usually separate dorsally or with connection in VI dorsal blood vessel rising in clitellar region, mostly XIII; clitellum most often saddle-shaped; no genital field between bursal slits: ***E. buchholzi***-group **2**

1* Large forms (> 15 mm), several ventral bundles with 4 or 5 chaetae; oesophageal appendages simple, short, with wide lumen, not winded (Fig. 32B); pharyngeal glands usually united dorsally dorsal blood vessel rising behind clitellum; clitellum girdle-shaped; a rectangular to trapezoid 'genital field' often present between elongate bursal slits or body folds that enclose the male pore (Fig. 34F): ***E. albidus***-group **16**

2 Only two chaetae per bundle (check ventral anterior and caudal bundles) **3**

2* Three chaetae in several, many or all ventral bundles **5**

3 Often four pairs of pharyngeal glands, in IV–VII; reproduction mainly by fragmentation (i.e. sexual organs usually absent) . . . .***Enchytraeus bigeminus*** Nielsen & Christensen, 1963 sensu lato

L (0.5)–3–10–(15) mm, S (2)–20–40–(80). Specimens often with incomplete anterior or posterior end. Coelomocytes without refractile granules. Sexual specimens rare, so far only known from laboratory cultures, gonadal segments shifted usually 4 segments forward, with large testis sacs in VII, male pores in VIII, and clitellum over VIII/IX. Large glandular rosettes around short spermathecal ectal duct. – Compost fields, probably common in southern Europe. Lit.: Bouguenec & Giani (1987), Schmelz et al. (2000).

3* Always three pairs of pharyngeal glands, in IV–VI; sexual reproduction **4**

4 Testis sacs large, more than 1 segment length; clitellar gland cells in reticulate pattern; Fig. 33A . . . . . ***Enchytraeus varithecatus*** Bouguenec & Giani, 1987

L 6–7.5 mm, S 25–30. Pharyngeal glands all united dorsally. Spermathecae present or absent, sometimes not fully developed; ectal duct glandular, more so distally than proximally. – France, compost. Only known from original description.

4* Testis sacs small; clitellar gland cells in separate rows . . . . . ***Enchytraeus dichaetus***

New rank and new name for ***E. christenseni*** ssp. ***bisetosus*** Rota & Healy, 1994

L 4–8 mm, S 26–34. Pharyngeal gland cells all separate dorsally. Coelomocytes filled with conspicuous, spherical, non-refractile vesicles. Spermathecae with long ectal duct, covered for half its length with small fused glands. Athecate specimens common, reproducing parthenogenetically. – Widespread.

5 Three chaetae in all bundles; Fig. 33B . . . . . ***Enchytraeus mariae*** Kasprzak, 1973

L 8 mm, S 33. Pharyngeal glands in VI dorsally connected. Clitellar gland cells in transverse rows. Testis sacs small. Sperm funnel 2x as long as wide, collar slightly wider than funnel body. Male glandular bulb small, compact. Spermathecae with a narrow ectal duct surrounded by glands in distal third; ampulla thin-walled, oval, large, about as long as and at least 4x as wide as ectal duct. – Poland, neutral forest soil. Only known from original description.

5* Two chaetae at least in anterior lateral bundles **6**

6 Spermathecal ectal duct as long as or longer than ampulla, smooth for most of its length **7**

6* Traits different: spermathecal ectal duct shorter than ampulla, glandular, or longer than ampulla and with distinctly wavy or irregular/glandular outline; or ampulla absent; or spermathecae absent **8**

7 Three chaetae in ventral preclitellar bundles; testis sacs small, < 1/2 segment length; spermathecal ectal duct about twice as long and almost as wide as ampulla; Fig. 33I . . . . . ***Enchytraeus doerjesi*** Westheide & Graefe, 1992
? = ***Enchytraeus dominicae*** Dumnicka, 1976

L 4–7 mm, S up to 37. Chaetae mostly 3 per bundle, sometimes 2, 4 or 6. Preclitellar nephridia 4 or 5 pairs, from 5/6 or 6/7 to 9/10. Coelomocytes without refractile vesicles. Sperm funnels 1.5–2x as long as wide, ca 1/4 as long as body diameter, collar about as wide as funnel body. Spermathecae with long ectal duct and a small crown of glands near orifice, as wide as ectal duct; ampulla spherical. – France, The Netherlands, compost, grassland.

7* Two chaetae in ventral preclitellar bundles; testis sacs large, > 1 segment length; spermathecae without ectal glands, ectal duct about as long as ampulla . . . . . ***Enchytraeus bohemicus*** Dumnicka, 1996

L 3–5 mm (fix), S 30–36. Chaetae 2,3 – 2 : 2 – 3. Coelomocyte texture unknown. Collar of sperm funnel narrower than funnel body. Spermathecae without glands, ectal and ental duct similar, ampulla small. – Only known from type locality, a cave in the Czech Republic. Insufficiently known species.

8 Coelomocytes with refractile granula (Fig. 32F middle, right) **9**

8* Coelomocytes pale, filled only with globular, hyaline, partly blurred vesicles (Fig. 32F left) **14**

9 Testis sacs at least 1 segment long; sperm funnel large, 1.5–3x as long as wide (Fig. 32H left) **10**

9* Testis sacs 1/2 segment long or shorter; sperm funnel small, 1–1.5x as long as wide (Fig. 32H right) **11**

10 Spermathecal ectal duct 1/3 as long as ampulla or shorter, without glands, canal not distinctly widened distally, a single ring of glands around ectal pore; Fig. 33E . . . . . ***Enchytraeus coronatus*** Nielsen & Christensen, 1959

L ca 7–9 mm, S 34–42. Testis sacs large, extending into IX. Sperm funnel ca 3x as long as wide, as long as body diameter, collar as wide as funnel body. Ampulla large, attached directly to oesophagus, no ental duct. – Widespread. Lit.: Bouguenec & Giani (1987).

10* Spermathecal ectal duct almost as long as ampulla, distal half covered with tall gland cells, ectal duct canal widened here; Figs 32H, 33F . . . . . ***Enchytraeus lacteus*** Nielsen & Christensen, 1961

L ca 7–9 mm, S 38–41. Testis sacs large, extending into X. Sperm funnel ca 2x as long as wide, not as long as body diameter, collar as wide as funnel body. Male copulatory organ small. Spermathecal ampulla large when sperm-filled, lying parallel to oesophagus; ental duct at rectangles to ampulla. – Widespread. Lit.: Kasprzak (1979), Rota & Healy (1999).

11 Male glandular bulb large, floppy; Fig. 33C . . . . . ***Enchytraeus bulbosus*** Nielsen & Christensen, 1963

L ca 4 mm, S ca 30. Chaetal formula 2 – 2 : 3 – 3. Animals white, coelomocytes dark in transmittent light due to strongly refractile granules. Spermathecae with long naked ectal duct, a few glands at ectal pore; epidermis often swollen around ectal pore. – Widespread. Lit.: Rota & Healy (1994), Rota (1994, 1995).

11* Male glandular bulb small, not floppy, diameter ca 50 µm or less **12**

12 Worms chequered white and with 2 chaetae in most lateral bundles; preclitellar nephridia (mostly?) three pairs, from 7/8 – 9/10; Fig. 33 G . . . . . ***Enchytraeus norvegicus*** Abrahamsen, 1969

L ca 3 mm, S ca 26. Chaetae 1,2 – 2,3 : 2,3 – 2,3. Coelomocytes densely filled with large, oval and strongly refractile bodies. Spermathecae with inconspicuous and narrow ampulla; small and inconspicuous ectal glands attached to distal part of ectal duct. – The only ***Enchytraeus*** species with numerous records from acidic soils. Widespread. Lit.: Kasprzak (1986), Rota (1995).

12* Worms not chequered white or with 3 chaetae in most lateral bundles behind citellum; preclitellar nephridia mostly 4 pairs, from 6/7 – 9/10 . . . . . **13**

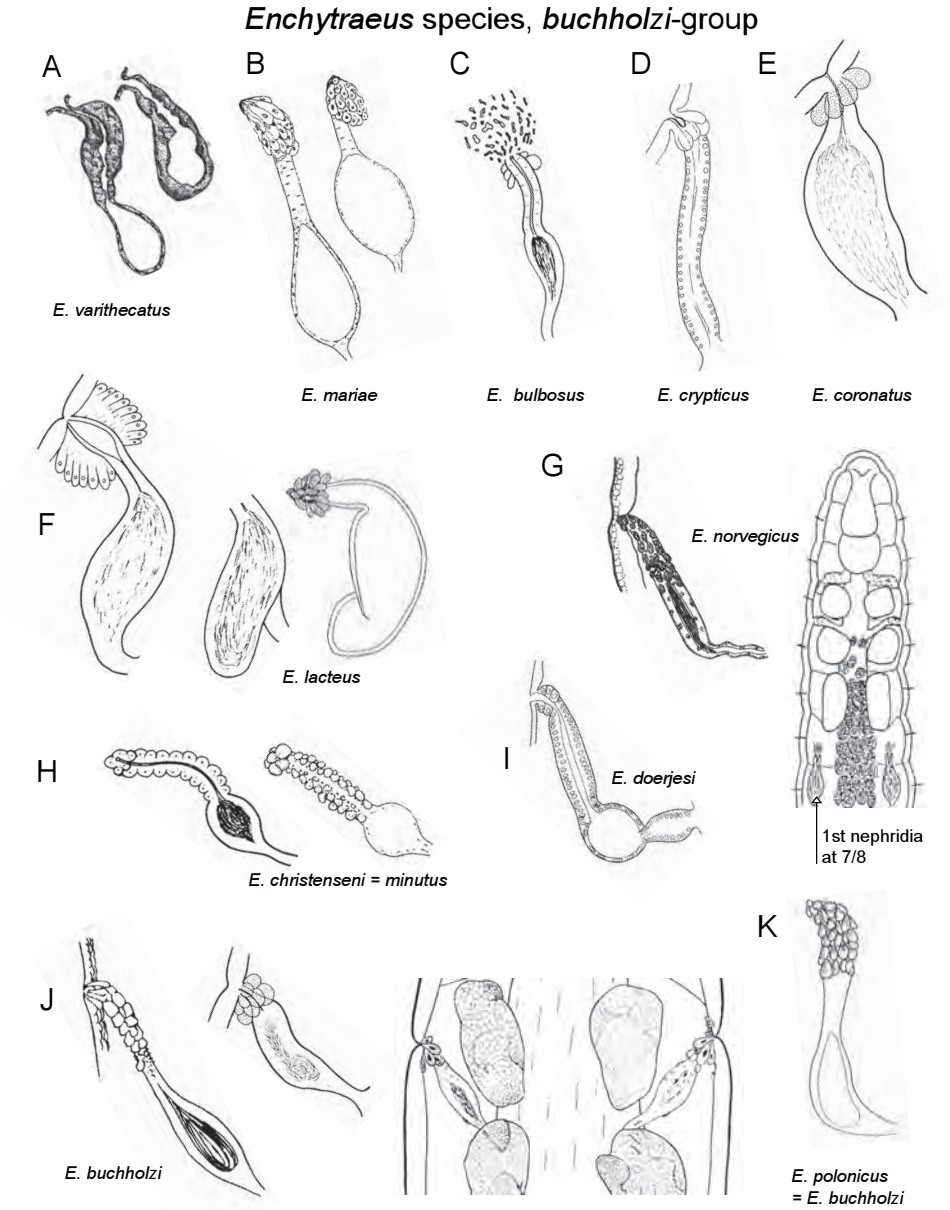

Fig. 33 ***Enchytraeus*** species, ***E. buchholzi***-group. A: ***E. varithecatus***, from Bouguenec & Giani (1987, Fig. 1H, H'). B: ***E. mariae***, from Kasprzak (1973, Figs 4, 5B). C: ***E. bulbosus***, from Nielsen & Christensen (1963, Fig. 9). D: ***E. crypticus***, from Westheide & Graefe (1992, Fig. 1B). E: ***E. coronatus***, from Nielsen & Christensen (1959, Fig. 106). F: ***E. lacteus***, from Nielsen & Christensen (1961, Figs 13, 14), Dumnicka (1977, Fig. 3). G: ***E. norvegicus***, from Kasprzak (1986, Fig. 728), Abrahamsen (1969, Fig. 2). H: ***E. christenseni***, from Nielsen & Christensen (1961, Fig. 12), Kasprzak (1973, Fig. 5C). I: ***E. doejesi,*** from Westheide & Graefe (1992, Fig. 2B). J: ***E. buchholzi***, from Chalupský (1986, Fig. 28), Nielsen & Christensen (1959, Fig. 105), Kasprzak (1986, Fig. 725). K: ***E. polonicus*** = ***buchholzi***, from Dumnicka (1977, Fig. 2).

13 Spermathecal ectal duct longer than ampulla, with slight and uniform glandular swelling of wall cells; ampulla spherical; Fig. 33H . . . . . .***Enchytraeus christenseni*** Dózsa-Farkas, 1992
Replacement name for ***E. minutus*** Nielsen & Christensen, 1961

L 3–5 mm, S 23–31, Chaetae 2 – 2,3 : (2),3 - 3. Refractile vesicles of coelomocytes small and sparse, cells not dark, not even in aggregations. Clitellar gland cells in dense rows. Sperm funnel and male copulatory organ small. Spermathecal ectal duct longer than the spherical ampulla and longer than the ental duct, with uniform glandular swelling of its wall cells throughout its entire length.– Widespread but not common, wet habitats. Lit. Kasprzak (1973, 1986, as ***E. minutus***), Rota (1995, as ***E. minutus*** ssp. ***minutus***).

13* Spermathecal ectal duct shorter than ampulla, glandular often only in distal half; Figs 32H, 33J,K . . . . . .***Enchytraeus buchholzi*** Vejdovský, 1879 sensu lato
= ***Enchytraeus florentinus*** Bell, 1947
= ***Enchytraeus polonicus*** Dumnicka, 1977

L ca 5–9 mm, S 24–34(–40?) Chaetae usually 2,3 – 2,3 : 3 – 3. Preclitellar nephridia 4 pairs, from 6/7 – 9/10. Refractile granula of coelomocytes absent or present, size and density variable. Clitellum most often saddle-shaped, cells mostly in dense rows. Sperm funnel and male copulatory organ small. Spermathecal ectal duct shorter than ampulla, length variable, usually not longer than ampulla, glands around ectal duct variable, often in irregular pattern, or a crown of glands around ectal pore; ampulla oval, ental duct often longer than ectal duct. – Not in strongly acidic soils. Widespread, very common, species complex. ***E. polonicus*** with an additional pair of spermathecae in VI. ***E. florentinus*** athecate. Lit.: Backlund (1947), Nielsen & Christensen (1959), Kasprzak (1986), Chalupský (1986, 1992), Rota (1994, 1995), Schmelz & Collado (1999), Schmelz et al. (2005).

14 (8*)Testis sacs medium-sized to large, minimum 2/3 of a segment length, up to 1.5 segments; Figs 1A,B, 32A,G . . . . . .***Enchytraeus luxuriosus*** Schmelz & Collado, 1999

L 8–13 mm. S up to 45. Chaetae 2 – 2,3 : 3 – 3. Preclitellar nephridia at 6/7 – 9/10. Clitellar gland cells in indefinite rows. Spermathecae with short ectal duct surrounded by ca 10 glands; ampulla conspicuous, thick-walled, drop-shaped, ca 2x as long as ectal duct, gradually merging into elongate ental duct. – Germany, few records.

14* Testis sacs small, not longer than 2/3 of a segment **15**

15 Spermathecae a simple elongate canal (ectal duct, ampulla and ental duct not distinguished) with indistinct lumen and a small crown of gland cells around ectal orifice; citellar gland cells in reticulate pattern; Fig. 32D, 33D . . . . . .***Enchytraeus crypticus*** Westheide & Graefe 1992
= ***Enchytraeus variatus*** Bouguenec & Giani 1987

L 3–12 mm. S up to 34. Chaetae 2,3 - 2,3 : 2,3 – 2,3. Preclitellar nephridia most often three pairs, 7/8 – 9/10, occasionally also at 6/7. Testis sacs small, 1/2 to 2/3 segment length. Sperm funnel and male copulatory organ small. Spermathecal ampulla seemingly absent but hidden among ectal glands. – Compost, fields. Standard test species in terrestrial ecotoxicology.

15* Spermathecae divided into ectal duct, ampulla and ental duct; clitellar gland cells in transverse rows (see 13*) . . . . .***Enchytraeus buchholzi*** Vejdovský, 1879a sensu lato

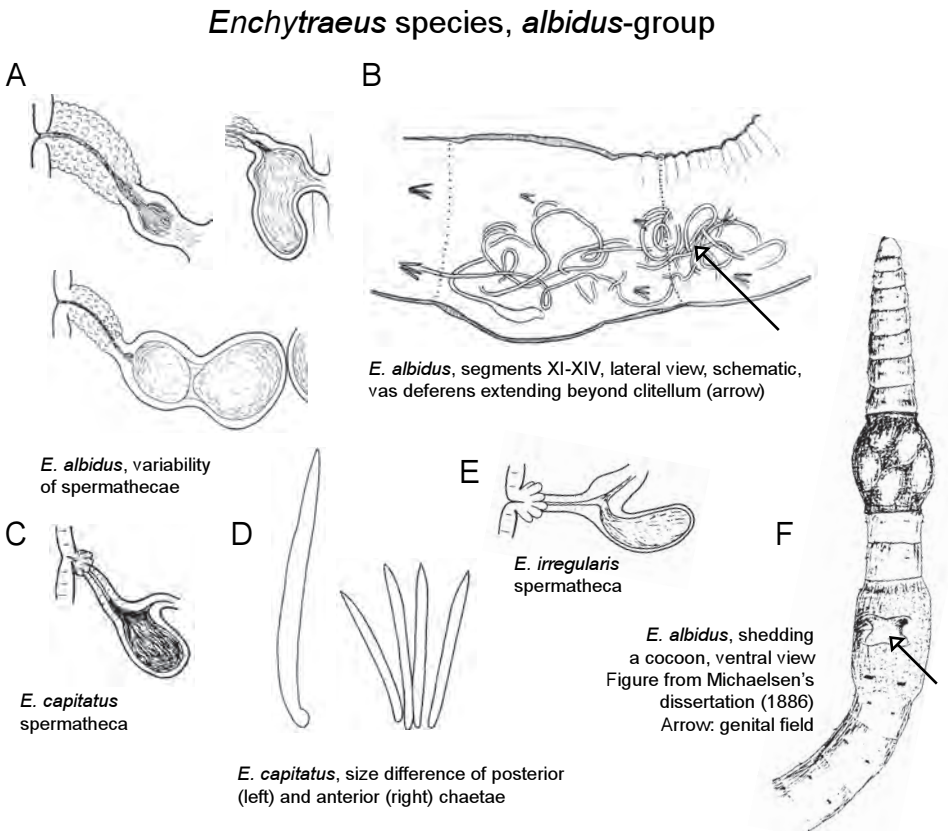

Fig. 34 ***Enchytraeus*** species, ***E. albidus*** – group. A: ***E. albidus***, from Nielsen & Christensen (1959, Figs 95–97). B: ***E. albidus***, from Backlund (1947, Fig. 5, as ***E. constrictus***). C: ***E. capitatus***, from Nielsen & Christensen (1961, Fig. 9). D: ***E. capitatus***, from von Bülow (1957, Figs 15, 17). E: ***E. irregularis***, from Nielsen & Christensen (1961, Fig. 11). F: ***E. albidus***, from Michaelsen (1886, Pl. 3 Fig. 2).

16 Vasa deferentia widened and quite long, with loops extending beyond posterior border of clitellum; spermathecal ectal duct glandular; Figs 32B, 34A,B,F . . . . . .***Enchytraeus albidus*** Henle, 1837 sensu lato

L 20–30 mm, S 40–65. Chaetae 2-4 – 2,3 : 2-5 – 2-4. All pharyngeal glands united dorsally. Preclitellar nephridia 4 pairs, 6/7 – 9/10. Coelomocytes without (or also with?) refractile granules. Dorsal blood vessel from XIV–XVIII, blood colourless or slightly yellowish. Clitellum girdle-shaped, ventrally in XII with two elongate longitudinal ridges = folds of the body wall, enclosing a 'genital field'. Testis sacs over 2-3 segments, sperm funnels large, longer than body diameter, 5–8x as long as wide. Loops of vasa deferentia extending beyond posterior border of clitellum, into XIV and XV. Male glandular bulbs compact, rounded, or dissolved into several bodies aligned anteriorly and posteriorly of male pores. Spermathecal ectal duct completely glandular, glandular cover thicker distally than proximally; ampulla large, conspicuous, variable in shape. – Widespread, marine littoral, compost, large forms. Cultivated as quality food for aquarium fishes; standard test species in terrestrial ecotoxicology. Lit.: Michaelsen (1886, as ***E. moebii***), Cejka (1913, as ***Litorea krumbachi)***, Stirrup (1913, as ***E. pellucidus***), Backlund (1947, as ***E. constrictus***), Bell (1958), Nielsen & Christensen (1959), Kasprzak (1986).

16* Vasa deferentia confined to XII; spermathecal ectal duct not glandular, a rosette of glands present around ectal pore; spermatheca always with one large asymmetrical diverticulum; Fig. 34C,D,E . . . . .***Enchytraeus capitatus*** von Bülow, 1957 sensu lato
. . . . . .augm. Nielsen & Christensen (1959, 1961)
= ***Enchytraeus irregularis*** Nielsen & Christensen, 1961

L 12–15 mm, S 50–58. Chaetae 2–4 in anterior segments, 2–3 posteriorly. Dorsal vessel from XV–XVI, blood colourless or faintly red. Clitellum girdle-shaped, ventrally in XII with two elongate longitudinal ridges = folds of the body wall. Testis sacs large, over ca 2 segments, sperm funnel 5–6x as long as wide, ca 1.5x as long as body diameter, with lobed collar. Vas deferens narrow, confined to XII. Male glandular bulbs small and compact. Spermathecae with small or large crown of ectal glands around pore, ampulla asymmetrical. – Marine coastal soils, sand dunes, compost.

Subgroups. The primary distinction into two subgroups – ***E. albidus***-group and ***E. buchholzi***-group - works well in most cases, but character mixes may occur. The ***buchholzi***-group can further be subdivided into a group with fragmenting species (here represented by ***E. bigeminus*** sensu lato) and a group with sexual reproduction (all others). Further distinctions among species are unsatisfactory, and a critical evalution of key traits is pending: chaetal pattern, shape of sperm funnel, distribution of spermathecal ectal glands. Coelomocyte texture is unknown in some species and described ambiguously in others; a standardisation is badly needed. Several species are ill-described but we still lack criteria to accept or to reject species in this group. Specimens with mixed or intermediate characters are common.

Enchytraeus bigeminus sensu lato is understood here to include ***E. bigeminus*** sensu stricto and ***E. japonensis*** Nakamura, 1993, not recorded from Europe so far. The two species differ morphologically only in a minute detail of the male copulatory organ, but sexual specimens are rare in the field. The species are distinct at the isozyme and DNA level (Schmelz et al. 2000, Collado et al., submitted). ***E. japonensis*** is widely used now in experimental research on development, regeneration and induction of sexuality. To our knowledge, all publications are based on populations that go back to a single specimen found by Nakamura (1993) in Japan. Our concept of ***E. bigeminus*** sensu lato does not invalidate ***E. japonensis***, but it allows the identification of specimens in the field. Fragmenting ***Enchytraeus*** species that do not belong to ***E. bigeminus*** sensu lato have 3 chaetae in some or all bundles, or the coelomocytes have refractile granules. Such specimens have not been recorded from Europe so far. Fragmenting forms of ***Enchytraeus*** have often been identified as ***E. fragmentosus*** Bell, 1959, but this species cannot be separated from either ***E. bigeminus*** sensu stricto or ***E. japonensis***, and was hence considered a species inquirenda in Schmelz et al. (2000).

Enchytraeus dichaetus. We give a new name to ***E. christenseni bisetosus*** Rota & Healy, 1994, since ***bisetosus*** in combination with ***Enchytraeus*** is preoccupied (***Enchytraeus bisetosus*** Levinsen, 1884, now ***Fridericia bisetosa***). 'Dichaetus' uses Greek stems to express the same as the Latin-based 'bisetosus'. The subspecies is elevated to species rank here; this restores the species rank of ***E. christenseni christenseni***. ***E. dichaetus*** differs from ***E. christenseni*** in the chaetal pattern and in the glandular cover of the spermathecal ectal duct. The species, originally described from Algeria, has been recorded several times from sites in Europe. Athecate forms are said to be common. We found the athecate form in Canadian field soils (unpublished). Details of the coelomocyte texture in the above description are from these specimens; the original description says 'light granules' (Rota & Healy 1994). Our specimens had a girdle-shaped clitellum, a trait not dealt with in the original description of ***E. dichaetus*** (= ***E. minutus bisetosus***).

E. norvegicus has an excellent distinguishing character, nephridia from 7/8, while in almost all other species except the fragmenting ones the nephridia begin at 6/7. However, we have seen specimens identifiable as ***E. norvegicus*** with nephridia at 6/7. The same variation occurs in ***E. crypticus***. In future finds of ***E. norvegicus*** this trait should be checked regularly.

Enchytraeus dominicae and ***E. bohemicus***. The coelomocyte texture is unknown in both species, described on ethanol-preserved material only. Both species are said to have a glandular ectal duct, but the figures in the original descriptions show that cell nuclei were mistaken for glands. This questions the distinctness of ***E. dominicae*** and ***E. doerjesi***, separable according to Westheide & Graefe (1992) by presence/absence of spermathecal glands. Indeed, both may be the same species, in which case the correct name would be ***E. dominicae***, but this species is too insufficiently known to establish a synonymy. At present we maintain the name ***doerjesi***, pending a reinvestigation of types or topotypic material of ***E. dominicae***. ***E. bohemicus*** is similar to ***E. globuliferus*** Nielsen & Christensen, 1963, a species described from laboratory cultures of unknown origin and not included in this key. ***E. globuliferus*** differs from ***E. bohemicus*** in: three chaetae in all lateral postclitellar bundles; testis sacs about 2 segments long; sperm funnel collar wider than funnel body; spermathecal ectal duct up to 5x as long as ampulla. Both species need reinvestigation, but types of ***E. globuliferus*** have been lost.

Enchytraeus buchholzi, one of the most widely distributed and most-often-cited enchytraeid species (together with ***E. albidus*** and ***Cognettia sphagnetorum***), is currently not more than a name for an aggregate of small and otherwise unidentifiable ***Enchytraeus*** species. In collected field material often two or more forms can be recognised, distinguishable by the presence or absence of refractile granules in the coelomocytes. Further variations concern body length, segment number, distribution pattern of clitellar gland cells, size and shape of sperm funnel and shape of the spermatheca. Variations among forms are often slight and differ among localities, so delineating species within the group is problematic. A possible explanation for these difficulties is the ability of many small ***Enchytraeus*** species to reproduce by self-fertilisation (Dózsa-Farkas 1995b), which favours morphological diversification of populations, based on single founder specimens with slight deviations. A good example may be ***E. polonicus*** (Fig. 33K), a name for a cave population with an additional pair of spermathecae in VI but otherwise conforming to ***E. buchholzi*** as circumscribed here. ***E. florentinus*** without spermathecae and with rudimentary male glandular bulbs may also be part of the complex, as a parthenogenetic lineage. Mind that also ***E. dichaetus*** comprises athecate forms. ***E. florentinus*** was found on river banks near Florence, Italy.

Enchytraeus christenseni (= ***E. minutus***) is often recorded together with ***E. buchholzi***, but from our experience the species is not very common. ***E. christenseni*** is characterised by an elongate spermathecal ectal duct that is slightly and uniformly glandular over its entire length; the duct is longer than the spherical ampulla and longer than the ental duct; furthermore, the coelomocytes have few small refractile granules embedded in a vesicular matrix (Fig. 32F middle). The latter trait is present in topotypic material and also in specimens cultured by Dózsa-Farkas and by us. However, the original description says ‘light granules’. ***E. christenseni*** prefers rather wet habitats and reproduces more slowly in the laboratory than other forms. The morphological circumscription of ***E. christenseni*** is more precise than that of ***E. buchholzi***, and the name ***E. christenseni*** should not be applied to divergent forms, e.g. to those where the glandular cover of the spermathecal ectal duct is more irregular and

developed only in the distal half, leaving the proximal part close to the ampulla naked, such as in ***E. mariae*** or ***E. dichaetus. E. dominicae*** is very similar to ***E. christenseni***, except for a slight difference in the chaetal pattern (three chaetae in all ventral preclitellar bundles).

Enchytraeus crypticus and ***E. variatus*** are light-microscopically identical, and even molecular differences (isozymes, DNA) are rather slight (Westheide & Graefe 1992, Schirmacher et al. 1998). For convenience, we treat them as one species here; a justification will be published elsewhere. Since the name ***E. variatus*** has priority, a proposal towards the Commission on Zoological Nomenclature is necessary to conserve the name of ***E. crypticus***, widely used now in terrestrial ecotoxicology. Earlier reports on fragmentation as reproductive mode in ***E. variatus*** (Bouguenec & Giani 1989) may be due to a contamination of cultures with ***E. bigeminus*** or another species from the fragmenting group.

E. albidus, ***E. capitatus*** and ***E. irregularis***. The taxonomy of the ***E. albidus*** group is confused and includes many more species from the marine littoral of Europe and elsewhere. ***E. albidus*** has a long list of synonyms; on the other hand, it consists almost certainly of several species (see Erséus & Gustafsson 2009). The distinction between ***E. albidus*** and ***E. capitatus*** may be difficult, because specimens with intermediate traits are not rare, e.g. specimens with vasa deferentia as in ***E. albidus*** and spermathecal glands as in ***E. capitatus***, or the reverse. The distinction 'spermathecal ectal duct glandular / ectal duct not glandular' is with all kinds of intermediate states. Perhaps thickness and extension of the vasa deferentia are good characters to separate the taxa. This trait is covered in the original description of ***E. albidus***, but unfortunately not in that of ***E. capitatus***. The redescription of ***E. capitatus*** in Nielsen & Christensen (1959, 1961) differs in several traits from the original account and may be based on a different species. ***E. irregularis*** Nielsen & Christensen (1961), described from a compost heap in the Copenhagen Botanical garden, is basically an ***E. capitatus*** with large accessory male glands. However, accessory male glands are common in the entire ***E. albidus*** group, although poorly dealt with in recent descriptions. The same may apply to the enlarged posterior chaetae in ***E. capitatus*** (Fig. 34D). And, as so often, types of all species in question are lost.

7.9. *Lumbricillus* Ørsted, 1844 (Fig. 35)

Chaetae sigmoid or distally straight, without nodulus, often in asymmetrical fan-shaped pattern. Body colour light to intensely red, or yellowish. Prostomium large, head pore at 0/1. Brain mostly incised posteriorly. Oesophageal appendages and intestinal diverticula absent. Gradual transition from oesophagus to intestine. Dorsal blood vessel origin intra- or postclitellar, blood coloured. Nephridial anteseptale consisting of funnel only. Coelomocytes one kind, mucocytes, often distinctly vesicular or granulate. Developing sperm usually enclosed in numerous pear-shaped and large testis sacs. Male glandular bulb compact, bursa usually present. Subneural glands often present. Spermathecae often stout, attached separately to oesophagus; a crown of glands around ectal pore; ectal duct may be glandular, ampulla without diverticula. Often many mature, yolky oocytes at a time. – Aquatic genus, mostly in the marine littoral. Lit.: Rota (2001).

1 Four and more sigmoid chaetae per bundle; testis sacs in regular pear-shaped lobes; medium-sized to large forms, often > 10 mm long **2**

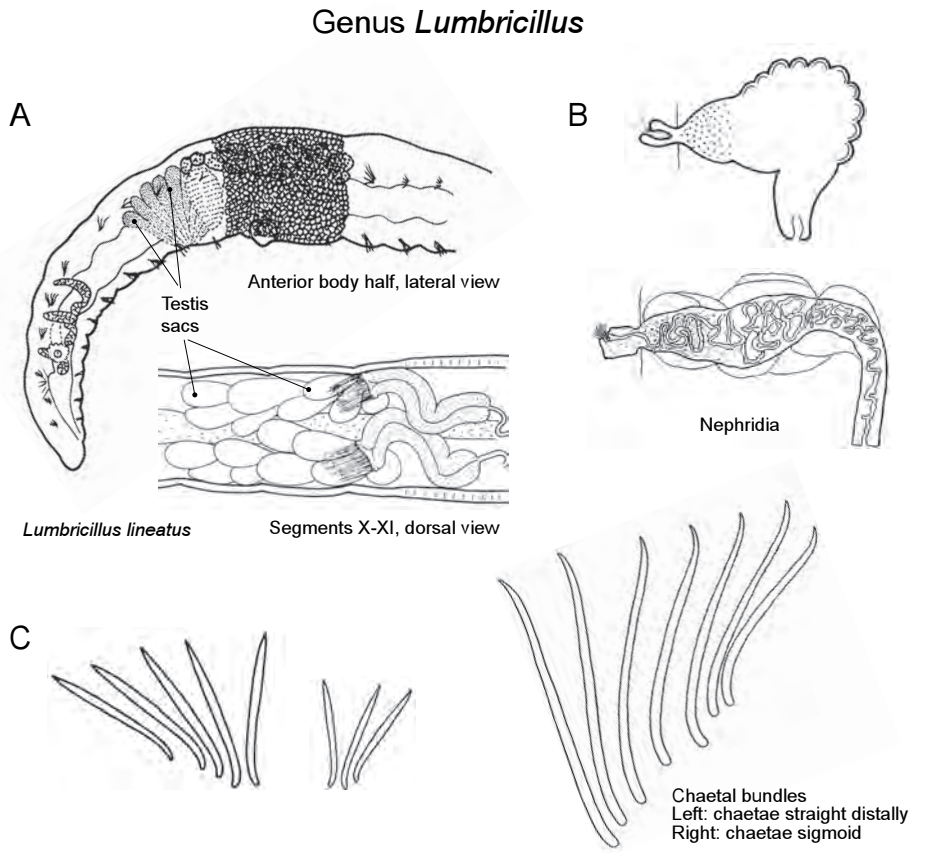

Fig. 35 ***Lumbricillus***, taxonomic traits. A from Timm (1999, Fig. p. 138), Nielsen & Christensen (1959, Fig. 111). B from Nielsen & Christensen (1959, Fig. 110), Knöllner (1935a, Fig. 7). C (left) from Nielsen & Christensen (1959, Figs 118, 104).

1* Two to three (rarely 4) chaetae per bundle, sigmoid or straight distally; testis sacs often irregularly lobed; small forms, usually ca 5–6 mm long . . . . . **.6**

2 Sperm funnel about as wide as long, ca half as long as worm diameter, pear-shaped; Fig. 36A . . . . . ***Lumbricillus fennicus*** Nurminen, 1964

L 8 mm, S 28–33. Chaetae slightly sigmoid, pattern 3–5 – 3 : 4–6 – (7)–4. Brain slightly concave posteriorly. Pharyngeal glands all with dorsal connection, connection narrow in VI. Dorsal blood vessel from XII–XIII, blood faintly reddish yellow. Sperm funnel with collar narrower than funnel body, tapering distad, superficially subdivided into 5 longitudinal, often inconspicuous lobes. Spermathecal ampulla spindle-shaped, thick-walled, with sperm centrally, embedded in walls; ectal duct short, crown of ectal glands narrow, not wider than ampulla. – Fresh- and brackish water. Scandinavia, Northern Germany. Lit.: Rota & Healy (1999).

2* Sperm funnel longer than wide, as long as body diameter or longer, cylindrical **3**

3 Spermathecal ectal duct longer than ampulla, glandularly swollen, different from large crown of ectal glands; ampulla spherical; body colour yellowish to light-brown due to brown droplets in chloragocytes; Fig. 36B . . . . . .***Lumbricillus pagenstecheri*** (Ratzel,1869), sensu lato

L 14–18 mm, S 41–47. Chaetae 4-6 – 3-5 : 5-7 - 4-6. Brain incised posteriorly. Pharyngeal glands of IV and V dorsally connected. Testis sacs over 3 segments. Sperm funnel 3–4x as long as wide. Spermathecal ectal duct glandularly swollen into a thick cloud that surrounds the canal; ampulla spherical. – Lit.: Nielsen & Christensen (1959), Erséus (1976), Timm (2005).

3* Spermathecal ectal duct short, not glandular, with crown of often fused glands around pore; ampulla large, thick-walled, spindle-shaped; body colour faintly to intensely red **4**

4 Large forms, body length > 18 mm; sperm funnel ca 10x as long as wide; Fig. 36C . . . . . .***Lumbricillus rivalis*** Levinsen, 1884 augm. Ditlevsen (1904), sensu lato

L 20–30 mm, S (50)–54–56–(60). Chaetae 6-9 – 5-9 : 7-12 – 6-10. Body intensely red. Sperm funnel ca 10x as long as wide, longer than body diameter, collar 2–3x as wide as funnel body, much lobed. Subneural glands in XIII–XV. Spermathecal ampulla spindle-shaped, thick-walled, with wide lumen, not subdivided. – Organically enriched aquatic sites compost. Lit.: Nielsen & Christensen (1959), Kasprzak (1986).

4* Medium-sized forms, body length < 16 mm; sperm funnel ca 3–5x as long as wide. **5**

5 Spermathecal ectal glands as a dense crown around ectal pore, enclosing ectal duct and distal part of ampulla; Fig. 36C,D . . . . . .***Lumbricillus lineatus*** (Müller, 1774) sensu lato

L 6.5–10 mm, S 36–46. Chaetal pattern 4-6 – 4-7 : 6-8 – 5-8. Body reddish-rose. Dorsal vessel from XIII. Pharyngeal glands in IV and V dorsally connected, separate or with narrow connection in VI. Sperm funnel ca 3–5x as long as wide, longer than body diameter, collar about as wide as funnel body, not lobed. Subneural glands in XIII, XIV, (XV), always (?) largest in XIV. Spermathecal ampulla variable, thick-walled distally when sperm accumulates in proximal half only; crown of ectal glands often asymmetrically enlarged on anterior side. – Marine littoral, freshwater. Widespread , on northern and southern hemisphere, temperate to subarctic regions. – Lit.: Welch (1917), Backlund (1947), Nielsen & Christensen (1959), Coates (1994).

5* Spermathecal ectal pore surrounded by 4 loose and stalked glands, not enclosing ectal duct; Fig. 36E . . . . . .***Lumbricillus kaloensis*** Nielsen & Christensen, 1959

L ca 10 mm, S ca 36. Chaetae 3-6 – 4-5 : 4-7 – 4-7. Blood faintly red. Dorsal vessel from XIII. Subneural glands unknown. Sperm funnel 2–3x as long as wide. Spermatheca spindle-shaped, narrowing strongly at both ends. Ectal glands all free or fused at base only, anterior gland largest. – Marine littoral, inland records rare. Lit.: Kasprzak (1986).

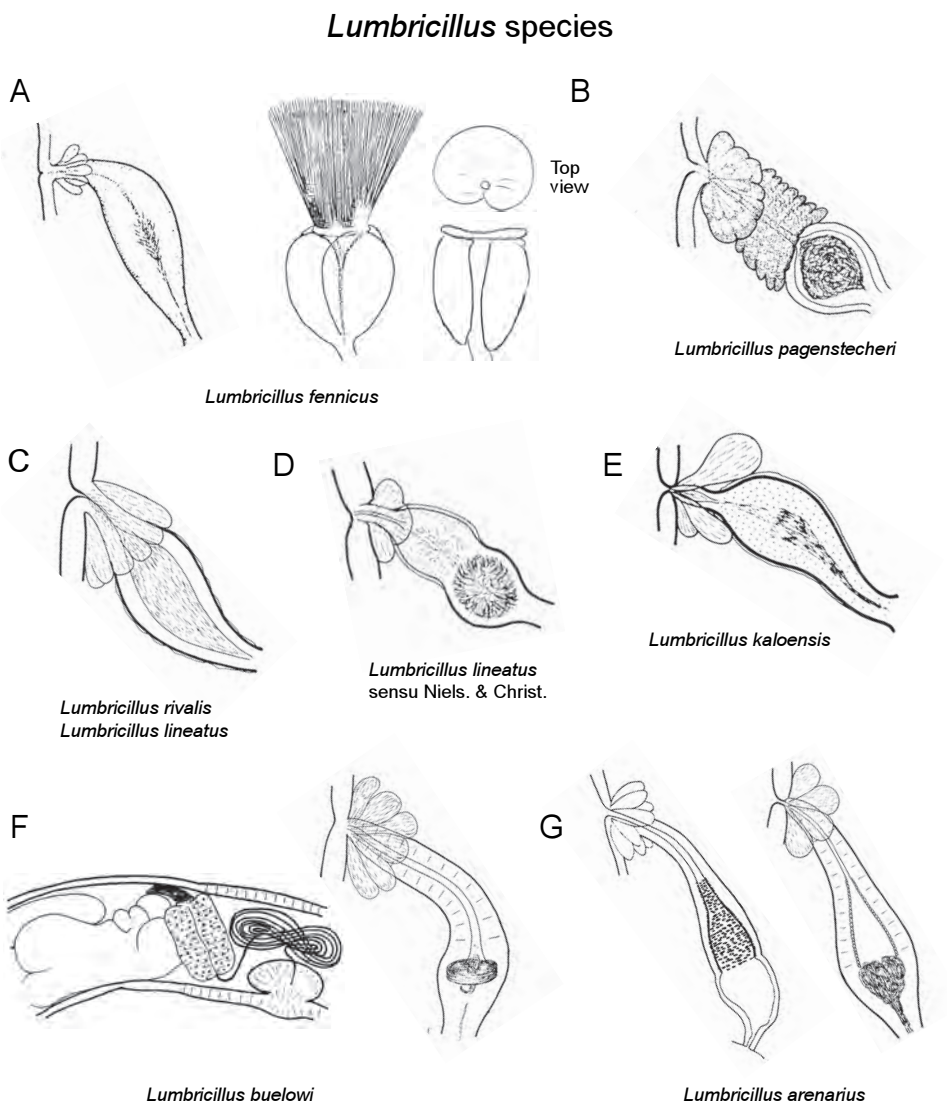

Fig. 36 ***Lumbricillus*** species. A: ***L. fennicus***, left and middle from Nurminen (1964, Fig. 2A,B). B: ***L. pagenstecheri***, from Erséus (1976, Fig. 8). C: ***L. rivalis*** and ***L. lineatus*** from Nielsen & Christensen (1959, Fig. 107, as ***L. rivalis*** only). D: ***L. lineatus***, from Nielsen & Christensen (1959, Fig. 109). E: ***L. kaloensis***, from Nielsen & Christensen (1959, Fig. 113). F: ***L. buelowi***, from Nielsen & Christensen (1959, Figs 124, 129). G: ***L. arenarius***, from Knoellner (1935a, Fig. 8), Nielsen & Christensen (1959, Fig. 128).

6 Sperm funnel ca 1.5x as long as wide, about as long as body diameter; 1 mature egg at a time; Fig. 36F . . . . . .***Lumbricillus buelowi*** Nielsen & Christensen, 1959

L 5–7 (–10?) mm, S 29–39. Body colour yellow-brown to reddish. Pharyngeal glands all united dorsally, those of VI largest. Coelomocytes oval or pear-shaped, with yellow-brown granules. Blood reddish or yellow. Testis sacs large, paired, irregularly and superficially lobed. Male glandular bulbs large. Spermatheca with crown of ectal glands; ectal duct distinct, elongate, ca 5x as long as wide, ampulla hardly wider than ectal duct, with sperm in a ring perpendicular to spermathecal long axis. – Marine littoral species, one inland record from Northern Germany. Lit.: von Bülow (1957, as ***Fridericia bulbosa***).

6* Sperm funnel up to 15x as long as wide, ca 3x as long as body diameter; 5–10 mature eggs at a time; Fig. 36G . . . . . .***Lumbricillus arenarius*** (Michaelsen, 1889a)

L ca 5–7–(10?) mm, S 31–43. Body colour light-red. Pharyngeal glands all united dorsally, those of VI largest. Coelomocytes few in number, shape variable. Blood light red. Testis sacs large, paired, distinctly or indistinctly lobed. Male glandular bulbs large. Spermatheca with crown of ectal glands, ampulla gradually widening in diameter, with characteristic structure in the middle; sperm only in proximal part. – Brackish water species, also in freshwater. Lit.: Knöllner (1935b, as ***Enchytraeoides arenarius***), Černosvitov (1937d, as ***Pachydrilus arenarius***), Nielsen & Christensen (1959), Rota & Healy (1999).

Lumbricillus is a difficult genus with over 100 described species that differ in few and often doubtful characters. Fortunately for our purposes, most species live in the marine littoral and only ***L. fennicus***, ***L. rivalis*** and ***L. lineatus*** are frequently recorded from freshwater or moist terrestrial habitats; of these, ***L. rivalis*** and ***L. lineatus*** appear to require saline or organically enriched conditions in order to survive at non-marine sites.

L. lineatus, the most-often-cited species of the genus, has been ill-defined from the very beginning (Müller, 1774), and authors disagree as to the morphological idiosyncrasies. Our diagnosis stems from a larger series of specimens from the Baltic Sea (unpublished) and the Atlantic Coast in Northern Spain (Parapar et al. 2009); it is in agreement with several authors (e.g. Welch 1917, Backlund 1947), and perhaps also with Nielsen & Christensen (1959), although they describe a subdivision in the spermathecal ampulla which we never observed in our material: a thin-walled proximal half with the bulk of sperm is separated by a constriction from a thick-walled distal half with very little sperm (Fig. 36D). Nielsen & Christensen (1959) use this character to separate ***L. lineatus*** from ***L. rivalis***, and to revalidate the latter, since both had been considered the same species for a long time. However, this trait was never described before for ***L. lineatus***, and Koßmagk-Stephan (1985) describes transitional states in the spermathecae of ***L. lineatus*** between the ***rivalis***-form and the ***lineatus***-form sensu Nielsen & Christensen (1959). Both species are best separated by the body size, number of chaetae per bundle and by the length of the sperm funnel, traits already highlighted in Nielsen & Christensen (1959).

7.10. ***Marionina*** Michaelsen, 1890 (in Pfeffer 1890) (Fig. 37)

Small worms, rarely >7 mm long, often <5 mm. Head pore mostly at 0/1. Chaetae distally straight or sigmoid. Brain shape variable. Oesophageal appendages present in some species, in IV, intestinal diverticula absent. Gradual transition from oesophagus to intestine in most species. Origin of dorsal blood vessel variable, anterior bifurcation in I or in III. Blood colourless or faintly red. Nephridial anteseptale with parts of nephridial body in European

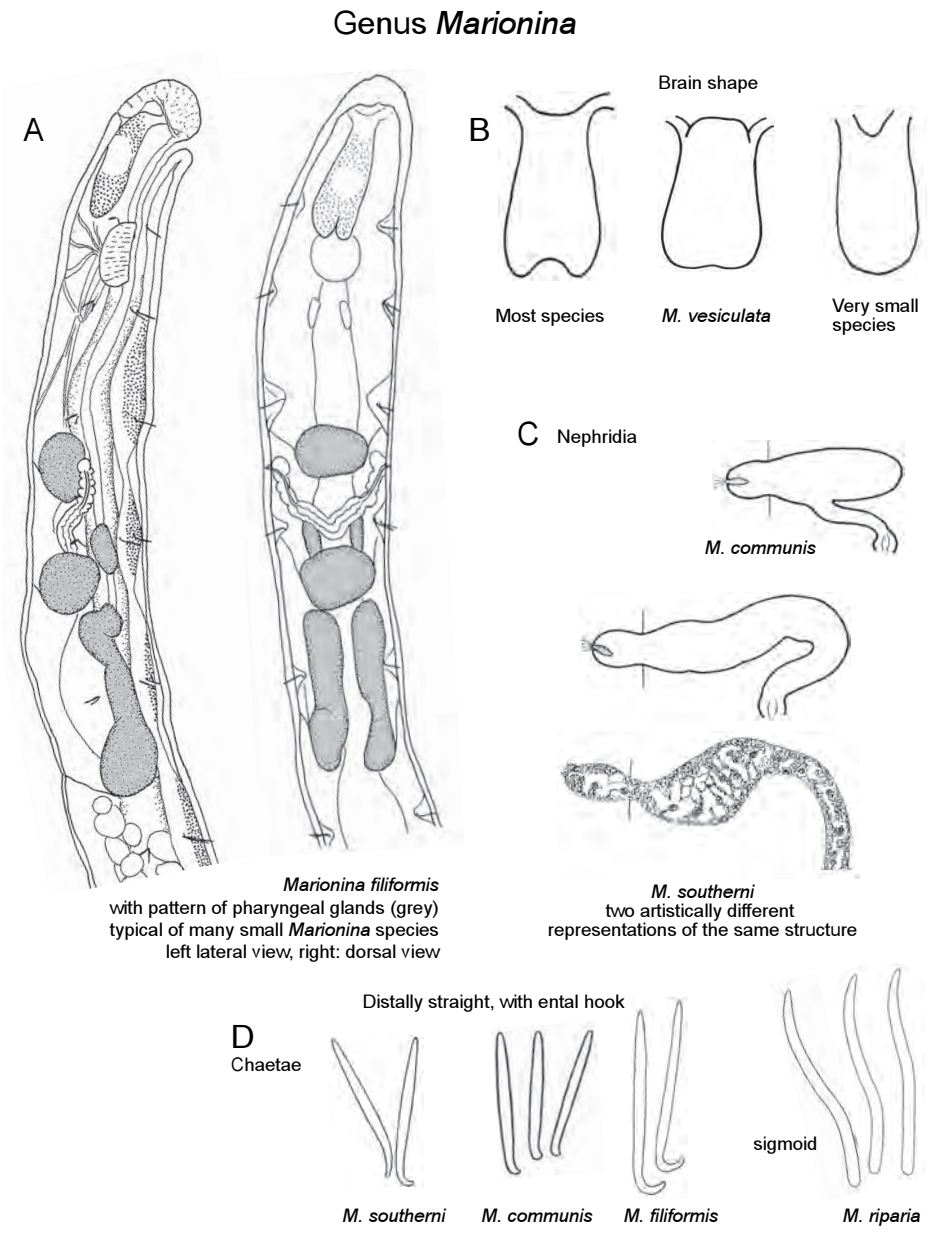

Fig. 37 ***Marionina***, taxonomic traits. A from Schmelz et al. (2008, Fig. 1A,B). B from (left, middle) Nielsen & Christensen (1959, Figs 141, 156). C from. Nielsen & Christensen (1959, Figs 136, 152), Knöllner (1935a, Fig. 15). D (left to right) from Knöllner (1935a, Fig. 14), Chalupský (1994, Fig. 9A), Schmelz et al. (2008, Fig. 1E).

species. Coelomocytes one type, mucocytes. Spermathecae attached to oesophagus, ampulla mostly without true diverticula. Subneural glands absent in most European species, present in ***M. southerni***. – All habitats, including marine littoral sediments. At present, ***Marionina*** is the residual genus for enchytraeid species that do not fit into other genera. Although the genus is problematic, the species themselves are well-defined and distinguishable, at least in the non-marine European fauna. Some of them may contain more than one species. The genus was erected by Michaelsen (1889b) under the name of ***Marionia*** (***sic!***); for reasons of homonymy he changed the name into ***Marionina*** (Michaelsen in Pfeffer, 1890). The taxonomic history of ***Marionina*** is reviewed in Rota et al. (2008); see also Schmelz & Collado (2008a).

1 Not more than two chaetae in ventral preclitellar bundles **2**

1* More than 2 chaetae in ventral preclitellar bundles **11**

2 Lateral chaetae present in all bundles (except XII), also in II **3**

2* Lateral chaetae absent in either II or in several (check IX–XI), many, or all segments **6**

3 Many lateral bundles with only 1 chaeta; 30 and more segments; a pair of hollow subspherical oesophageal appendages present in IV ventro-laterally **4**

3* All or most lateral bundles with 2 chaetae (1 chaeta occasionally); segment number below 30; no oesophageal appendages **5**

4 Spermathecal ectal duct subdivided into an elongate and narrow distal part and a swollen proximal part, the latter about half as long as distal part and with peculiar inner structure; male pores without accessory glands; Fig. 38A . . . . . ***Marionina simillima*** Nielsen & Christensen, 1959

L 4.5–8 mm, S 34–36. Ventrally two chaetae per bundle. Pattern of lateral chaetae variable: 2 in preclitellar, 1 in postclitellar bundles; or chaetae absent from IX or X until XIV to XVIII. Brain distinctly concave posteriorly. All pharyngeal glands united dorsally. Dorsal vessel from XIII, anterior bifurcation in I. Preclitellar nephridia 3 pairs, 7/8 – 9/10. No seminal vesicle. Vasa deferentia very long and narrow. Spermathecae without ectal glands, ectal duct not glandular, ampulla almost as narrow as swollen proximal part of ectal duct, ental ducts proximally fused. – Widespread, not recorded from southern Europe. Terrestrial. Lit.: Chalupský (1992), Rota (1995).

4* Spermathecal ectal duct uniform, narrow, not subdivided, with slight and regular glandular swellings. In XII often one accessory gland anteriorly, situated asymmetrically, and resembling male glandular bulbs; Fig. 38B . . . . . ***Marionina vesiculata*** Nielsen & Christensen, 1959

L 4–6 mm, S ca 30. Chaetal pattern 1,2-1,2 : 2-2. Epidermal gland cells yellow. Brain slightly concave posteriorly. All pharyngeal glands united dorsally. Dorsal vessel from XIII, anterior bifurcation in I. Preclitellar nephridia 2 pairs, at 7/8, 8/9. No seminal vesicle. Male glandular bulbs spherical. Vasa deferentia long and narrow. Spermathecal ampulla distinctly wider than ectal duct; ental ducts proximally joint. – Denmark, Germany, several records. Terrestrial.

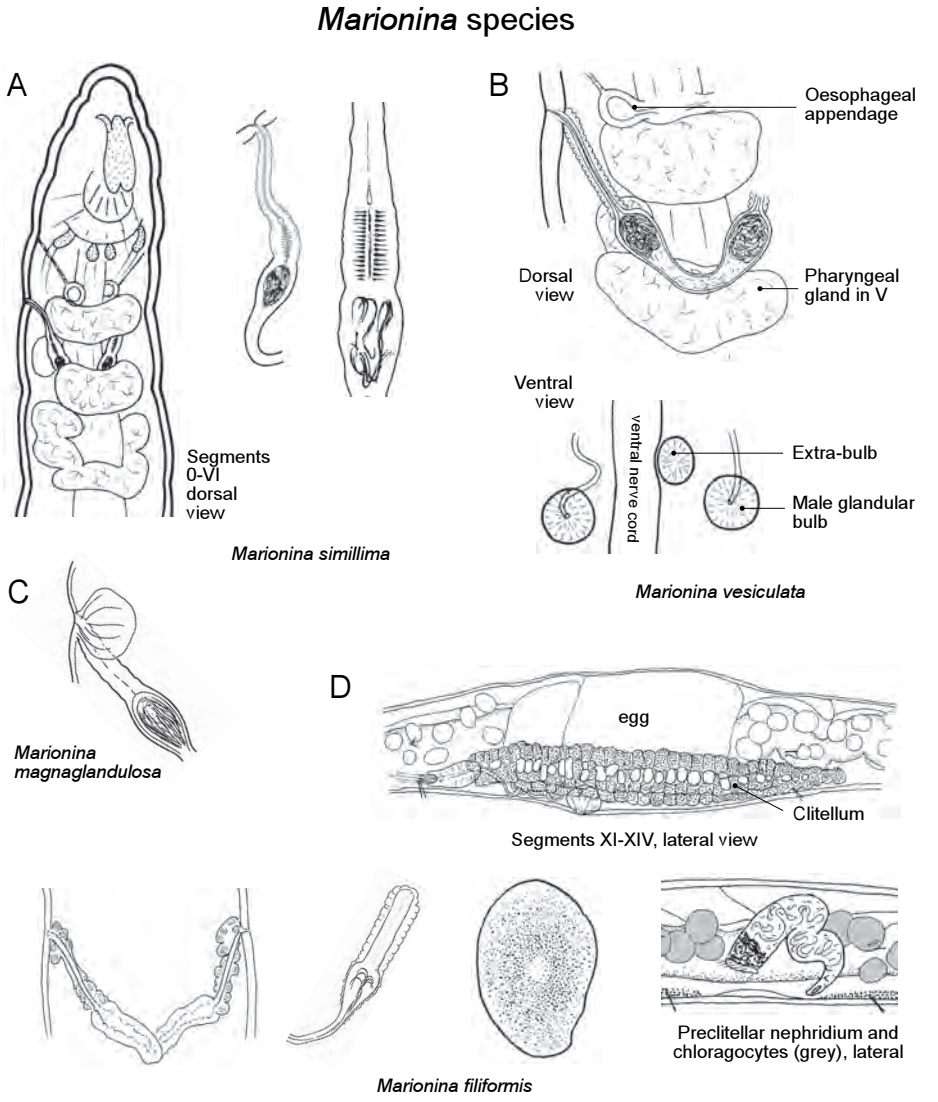

Fig. 38 ***Marionina*** species. A: ***M. simillima***, from Nielsen & Christensen (1959, Figs 159, 160), Chalupský (1992, Fig. 17). B: ***M. vesiculata***, from Nielsen & Christensen (1959, Figs 157, 158). C: ***M. magnaglandulosa***, from Nurminen (1970b, Fig. 9). D: ***M. filiformis***, from Schmelz et al. (2008, Fig. 1C,F), Chalupský (1992, Fig. 16A,B), Schmelz et al. (2008, Fig. 1A).

5 Spermathecae with very large globular ectal gland, measuring ca 1/3 of body diameter; Fig. 38C . . . . . .***Marionina magnaglandulosa*** Nurminen, 1970b

L ca 2 mm, S 23–25. Brain deeply incised posteriorly. Pharyngeal glands dorsally separate in VI. Dorsal vessel from XII. Seminal vesicle small. Spermathecal ampulla little wider than ectal duct. Separate attachments to oesophagus. – Southern Finland, nutrient-rich forest soil. Only known from original description, insufficiently known species.

5* Spermathecal ectal gland absent or much smaller; Figs. 37A,D, 38D . . . . . .***Marionina filiformis*** Nielsen & Christensen, 1959

L 4–5 mm, S 24–30. Prostomium short. Brain deeply incised posteriorly. Pharyngeal glands separate dorsally in VI. Dorsal blood vessel from XIII–XIV, anterior bifurcation in I, blood slightly reddish. Preclitellar nephridia at 7/8 and 9/10, often unpaired. Clitellum only laterally developed. Spermathecal ampullae small, elongate, fused proximally, ectal ducts glandular. – Widespread. Wet sites, in moder or raw humus. Often in deeper strata. Atlantic-subatlantic regions. Lit.: Chalupský (1992), Schmelz & Collado (2008b).

6 Lateral chaetae absent only in II (and XII), 2 per bundle in the rest **7**

6* Chaetae absent in several, many, or all lateral bundles **8**

7 Seminal vesicle small or absent; spermathecal ampulla spherical; dorsal blood vessel bifurcation in III; Fig. 39A . . . . . .***Marionina argentea*** (Michaelsen, 1889a)

L 3–4 mm, S 19–26. Body chequered white. Prostomium short. Pharyngeal glands broadly united dorsally in IV and V, separate and elongate in VI. Dorsal vessel from XIII. Preclitellar nephridia in one or two positions of 7/8, 8/9 or 9/10. Coelomocytes variable, filled with coarse refractile granula, dark-black in transmittent light, or with fine and regular vesicles, brown in transmittent light. Clitellum saddle-shaped, gland cells in separate rows. Seminal vesicle absent or small, < 1/2 segment length. Sperm funnel small, ca 1.5x as long as wide, male glandular bulb small. No subneural glands. Spermathecal ectal duct with slight glandular swellings. – Very common and widespread. Wet sites, also aquatic. In soils often in deeper strata with groundwater contact. Slightly salt-tolerant. Not at acidic sites. Species complex. Lit.: Nielsen & Christensen (1959), Möller (1971), Kasprzak (1986), Chalupský (1992), Rota (1994, 1995)

7* Seminal vesicle large; spermathecal ampulla with a ring of sessile diverticula containing the bulk of sperm; dorsal blood vessel bifurcation in I; Fig. 39B . . . . . .***Marionina southerni*** (Černosvitov, 1937a)

L 3–8 mm, S 18–36. Body chequered white. Pharyngeal glands broadly united dorsally in IV and V, separate and elongate in VI. Dorsal vessel from XIII. Coelomocytes filled with refractile granules, dark in transmittent light. Clitellum saddle-shaped, gland cells in separate rows. Sperm funnel 4x as long as wide, male glandular bulb large. Small subneural glands in XIV and XV. Spermathecal ectal duct with glandular swellings and a crown of ectal glands. – Widespread. Common in coastal marine soils. Lit.: Southern (1909, as ***Enchytraeus lobatus***), Stephenson (1911, as ***Enchytraeus nodosus***), Knöllner (1935, as ***Fridericia pseudoargentea***), Nielsen & Christensen (1959, as ***M. southerni***).

8 Lateral chaetae absent in posterior segments, no oesophageal appendages **9**

8* Lateral chaetae present in posterior segments; a pair of hollow oesophageal appendages present in IV dorso-laterally, anteriorly of pharyngeal gland **10**

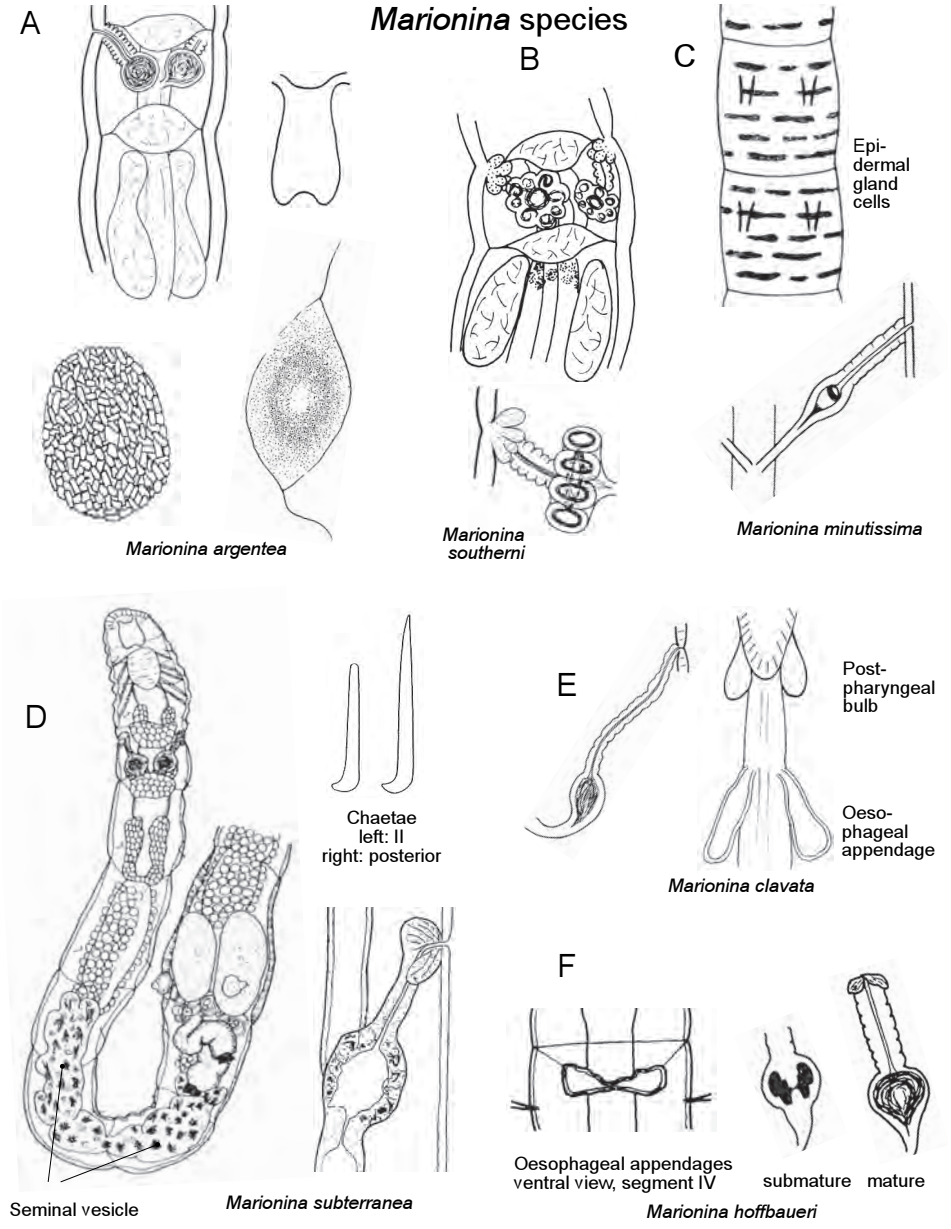

Fig. 39 ***Marionina*** species, continued. A: ***M. argentea***, Chalupský (1992, Fig. 15A,B). B: ***M. southerni***, from Nielsen & Christensen (1959, Figs 135, 137). C: ***M. minutissima***, from Healy (1975, Fig. 5A,H). D: ***M. subterranea***, from Koßmagk-Stephan (1983, Fig. 8), Knöllner (1935a, Figs 26, 28). E: ***M. clavata***, from Nielsen & Christensen (1961, Figs 19, 20). F: ***M. hoffbaueri***, from Möller (1971, Fig. 18C,F,G).

9 Lateral chaetae present in II–V, absent from VI on; Fig. 39C . . . . . ***Marionina minutissima*** Healy, 1975

L 1.5–3 mm, S 24–25. Body wall covered with conspicuous, transversely elongate, yellow epidermal gland cells in 4–5 segmental rows. Brain incised posteriorly. Pharyngeal glands united in IV and V, elongate and separate in VI. Dorsal blood vessel from XIII, blood pale. Spermathecae without glands, ampulla slightly wider than ectal duct, separate communications with oesophagus. – Ireland, Northern Germany.

9* No lateral chaetae at all; Fig. 39D . . . . . ***Marionina subterranea*** Knöllner, 1935a,b

L 4 mm, S 22–26. Body colour white. Chaetae short, stout. All pharyngeal glands dorsally united. Seminal vesicle large, 2–3 segments. Spermatheca with a crown of ectal glands, thin ectal duct and large spherical ampulla; separate attachments to oesophagus. – Marine coastal species. One inland record from Northern Germany. Lit.: Koßmagk-Stephan (1983).

10 Spermathecal ectal duct thickened proximally and with peculiar inner structure; three pairs of preclitellar nephridia, 7/8 – 9/10, oesophageal appendages subspherical, see 4 . . . . . ***Marionina simillima*** Nielsen & Christensen, 1959

10* Spermathecal ectal duct not thickened proximally; two pairs of preclitellar nephridia, 7/8, 8/9, rarely 8/9, 9/10; oesophageal appendages tubiform; Fig. 39E . . . . . ***Marionina clavata*** Nielsen & Christensen, 1961

L 4–7 mm, S 24–29. Chaetal pattern 2,1,0 – 1 : 2 – 2. Chaetae absent laterally in IX–XII. Brain incised posteriorly. A pair of short, tubiform oesophageal appendages present dorso-laterally in IV. All pharyngeal glands dorsally connected. Dorsal blood vessel from XII, anterior bifurcation in I. Coelomocytes often brownish. Clitellum saddle-shaped. Seminal vesicle small or absent. Sperm funnel and male glands small. Spermathecae fused proximally – Common and widespread in acidic soils. Lit.: Römbke (1989), Rota (1995).

11 (1*) Chaetae absent in several lateral bundles; ventrally 2 and 3 chaetae per bundle, not more **12**

11* Chaetae present in all bundles (occasionally even in XII); ventrally at least some bundles with 3 or more chaetae **13**

12 Lateral chaetae absent from VIII–XII, mostly 2 per bundle in II–VII; body colour pale-whitish; a pair of hollow oesophageal appendages present in IV ventro-laterally; Fig. 39F . . . . . ***Marionina hoffbaueri*** Möller, 1971

L 1.5–2 mm, S 18–21. Chaetal pattern (3),2,0 – 2 : 2,3 – 2. Chaetae absent laterally in VIII–XII. Brain posteriorly truncate or slightly incised. Pharyngeal glands united dorsally in IV, V, separate in VI. Dorsal vessel from XII–XIII, anterior bifurcation in III, blood colourless. Preclitellar nephridia at 7/8, 8/9. Sperm funnel 2x as long as wide. Spermathecal ectal duct glandular, ampulla thin-walled in adult specimens, subdivided into 4 subchambers in subadult specimens. – Northern Germany, moist soil. Lit.: Xie & Rota (2001).

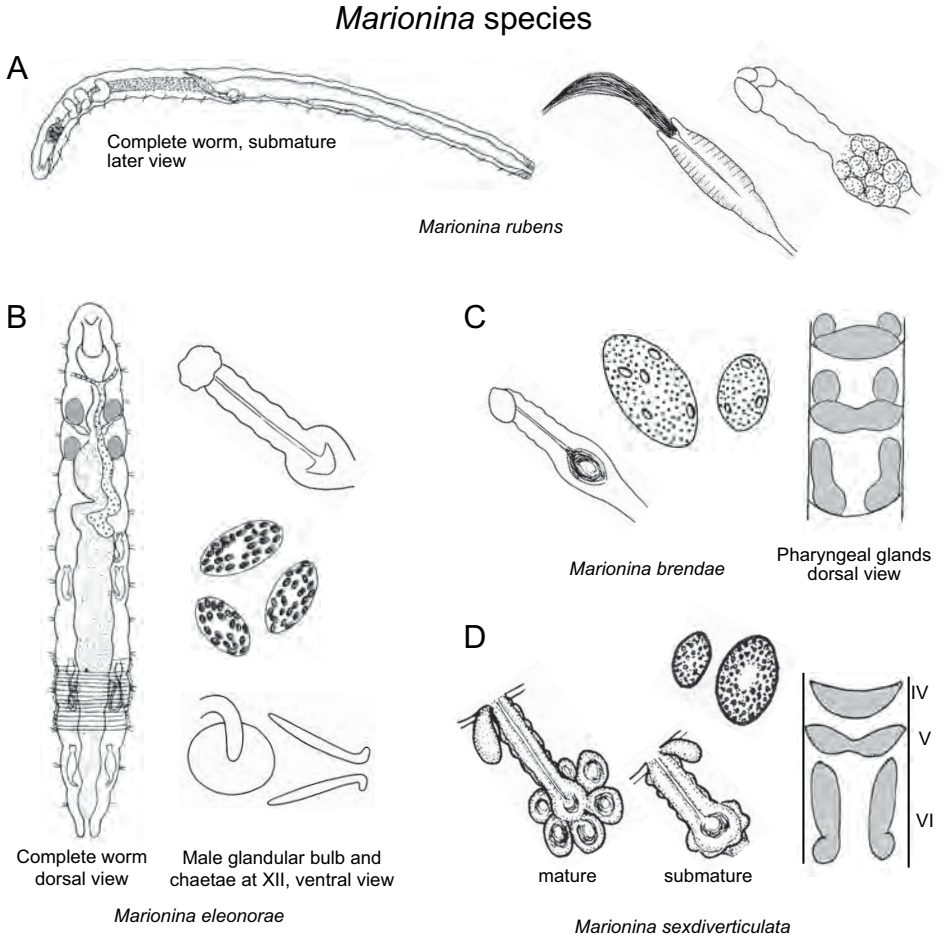

Fig. 40 ***Marionina*** species, continued. A: ***M. rubens***, from Rota (1995, Fig. 16C,D,E). B: ***M. eleonorae***, from. Rota (1995, Fig. 15A,C,D,E). C: ***M brendae***, from Rota (1995, Fig. 14F,G.D). D: ***M. sexdiverticulata***, from Dózsa-Farkas (2002, Fig. 2H,I,B,D).

12* Lateral chaetae absent from VI–XX, ventrally in II–V mostly 3 per bundle; body colour red-brown due to red blood and red-brown or yellow-brown chloragocytes, oesophageal appendages absent; Fig. 40A . . . . . .***Marionina rubens*** Rota, 1995

L 2 mm, S 24. Brain deeply incised posteriorly. Septa of last 4 caudal segments thickened. Pharyngeal glands in IV and V widely connected, in VI almost connected. Dorsal vessel from XII, anterior bifurcation in I. Preclitellar nephridia at 7/8, 8/9. Sperm funnel 3–4x as long as wide, tapering at both ends. Spermathecae with small ectal glands, ampulla only slightly wider than ectal duct, with opaque, granular epithelium. – Italy, moist soil. Only known from type locality. Lit.: Xie & Rota (2001).

13 Animals very small, max. 2 mm long; segment number mostly below 20; two pairs of preclitellar nephridia; coelomocytes mostly with refractile granula or vesicles; brain rounded posteriorly; clitellum in posterior body half **14**

13* Animals larger, 4 mm or longer; segment number > 24; four pairs of preclitellar nephridia; coelomocytes without refractile vesicles; brain posteriorly rounded or incised; clitellum in mid-body region or anterior body half **16**

14 Pharyngeal glands only 2 pairs, in IV and V, dorsally separate; spermathecae with small ectal gland, ampulla without diverticula; Fig. 40B . . . . . .***Marionina eleonorae*** Rota, 1995

L 1–1.5 mm, S 15–17. Chaetal pattern 2 – 2 : 3 – (2),3. Chaetae present at XII in all 4 bundles. Body with intensely white spots due to coelomocytes. Dorsal vessel from VII, anterior bifurcation in III, blood pale. Nephridia at 7/8, 8/9, 13/14. Coelomocytes with few large, strongly refractile granula. Clitellum in posterior half. Spermathecae with ectal gland. – Italy, several terrestrial sites.

14* Pharyngeal glands 3 pairs, dorsally connected in IV and V, separate in VI 15

15 Spermathecal ampulla without diverticula, only slightly wider than ectal duct (ca 1.2x); coelomocytes variable, often with refractile granules; Fig. 40C . . . . . .***Marionina brendae*** Rota, 1995

L 1.5–2 mm, S 18–20. Chaetal pattern 2 – 2 : 3,2 – 3,2. Brain rounded posteriorly. Dorsal vessel from VIII or IX, pulsating, anterior bifurcation in III. Coelomocytes with few large refractile granula embedded in a finely vesicular matrix. Seminal vesicle absent, sperm funnel and male glandular bulb small. Spermathecae simple, with short ectal duct and small ectal gland. – Italy, Ireland, Germany. Terrestrial.

15* Spermathecal ampulla with ca 6 sessile spherical diverticula, in total much wider than ectal duct (> 3x); coelomocytes with fine and coarse refractile granules; Fig. 40D . . . . . .***Marionina sexdiverticulata*** Dózsa-Farkas, 2002a

L 1.3–2 mm, S 15–19. Chaetal formula 2 – 2 : 3,2,(1) – 2. Brain rounded posteriorly. Pharyngeal glands united dorsally in IV, V, separate in VI. Dorsal vessel from VIII, anterior bifurcation pattern unknown. Nephridia at 6/7, 7/8, or 7/8, 8/9. Seminal vesicle large, 2 segments. Sperm funnel up to 2x as long as wide, length up to 2/3 body diameter, male glandular bulb large (D 40–50 µm). Spermatheca with one medium-sized and elongate ectal gland, ampullae with separate openings into oesophagus. – Hungary, deciduous forest soil. Only known from original description.

16 Epidermal gland cells mostly yellow-orange; sperm in spermathecal ampulla arranged in few, discrete, rounded packages; one small ectal gland; Fig. 41A . . . . . .***Marionina riparia*** Bretscher, 1899 augm. Černosvitov, 1928a

L 5 mm, S 26–30. Chaetae slightly sigmoid, up to 3,4 or 5 in ventral preclitellar bundles. Brain incised posteriorly. Pharyngeal glands all separate dorsally, sometimes with very narrow dorsal connection, all pairs of about same size. Preclitellar nephridia 4 pairs, 6/7 – 9/10. Nephridial anteseptale rather small, with small parts of nephridial body. Dorsal blood vessel from XIII or XIV, blood faintly red. Spermathecae mostly attached, sometimes free, ampulla almost spherical, with thin walls, transparent; sperm arranged distally near ectal duct in one to four regular masses, occupying only a small part of ampullar lumen; ectal gland small, sessile. – Aquatic species, also in wet soils. Widespread. Lit.: Černosvitov (1928a, as ***Enchytraeoides riparius***), Wilcke (1957, as ***Enchytraeoides maculatus***) Nielsen & Christensen (1959), Kasprzak (1986), Rota & Healy (1994), Rota (1994, 1995), Rota & Healy (1999).

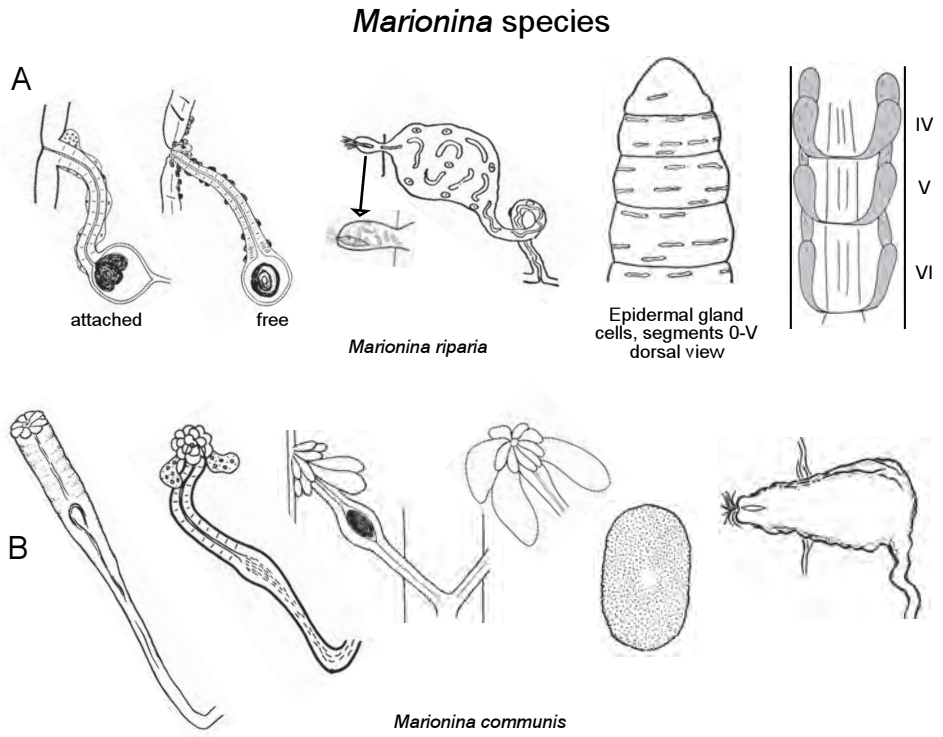

Fig. 41 ***Marionina*** species, continued. A: ***M riparia***, from Nielsen & Christensen (1959, Fig. 171), Kasprzak (1986, Fig. 588), Černosvitov (1928a, text Fig. 2–4, 2–6), Nielsen & Christensen (1959, Fig. 172). B: ***M. communis***, from Chalupský (1994, Fig. 11A), Nielsen & Christensen (1959, Fig. 149), Healy (1979b, Fig. 6A,B), Chalupský (1994, Figs 13, 10).

16* Epidermal gland cells pale; sperm not arranged in discrete packages; more than one ectal gland; Fig. 41B . . . . . .***Marionina communis*** Nielsen & Christensen, 1959

L 3–5 mm, S 25–27. Chaetae 2,3 – 2,3 : 2,3 – 2,3. Brain incised posteriorly. Not more than 3 chaetae per bundle. Pharyngeal glands all separate dorsally, all with ventral lobes; pair in VI largest, elongate. Coelomocytes ca 2x as long as wide, pale, finely vesicular. Preclitellar nephridia 4 pairs, 6/7 – 9/10. Dorsal vessel from XIII, blood pale. Spermathecae with elongate ampulla, joint proximally and attached to oesophagus, ectal pore surrounded by several glands, often fused, either floppy and large or minute and sessile, or intermediate. – Widespread, not in acidic soils. Lit.: Healy (1979b), Kasprzak (1986), Chalupský (1994).

Shortcuts to *Marionina* species with peculiar characters

Chaetae sigmoid: ***M. riparia***

Oesophageal appendages in IV: ***M. clavata***, ***M. vesiculata***, ***M simillima***, ***M. hoffbaueri***

Dorsal blood vessel originating in a preclitellar segment: ***M. eleonorae***, ***M. brendae***

Four pairs of preclitellar nephridia: ***M. communis***, ***M. riparia***

Three pairs of preclitellar nephridia: ***M. simillima***

Coelomocytes dark, with strongly refractile granula: ***M. southerni***, ***M. argentea***, ***M. eleonorae,*** ? ***M. brendae***

Seminal vesicle large: ***M. southerni***, ***M. sexdiverticulata***, ***M. subterranea***

Sperm rings in walls of spermathecal ampulla: ***M. southerni***, ***M. sexdiverticulata,*** ? ***M. subterranea***

We transferred ***Marionina libra*** to ***Bryodrilus*** and ***M. serbui*** to ***Buchholzia*** (see remarks there); the latter is probably a synonym of ***Buchholzia simplex***.

Very similar to ***Marionina subterranea*** is the marine littoral ***M. glandulifera*** (Jansson, 1961), differing from ***M. subterranea*** by thick cushions of epidermal glands at the position of the lateral chaetae and a shorter spermathecal ectal duct. The account of ***M. subterranea*** in Nielsen & Christensen (1959) refers to this species, see Koßmagk-Stephan (1983), Dózsa-Farkas (1992). There are no records of ***M. glandulifera*** from non-marine sites. In ***M. subterranea***, sperm is embedded in the ampullar walls of the spermatheca according to Knöllner (1935b), while according to Koßmagk-Stephan (1983) the ampullar lumen is filled with sperm.

Marionina riparia has a possible senior synonym, ***Marionina maculata*** (Bretscher, 1896), see Wilcke (1957) and Timm (2005). Both species are originally ill-described, and type material does not exist, so a name change makes little sense. The name ***riparia*** has come into use by the detailed description in Černosvitov (1928a), on which subsequent identifications are based. Nielsen & Christensen (1959), not knowing Wilcke's paper, consider ***M. maculata*** as species dubia. According to Timm (2007: 91), ***M. riparia*** may be ' ... a collective taxon, with several morphological and genetical variations in different water bodies.'

Marionina magnaglandulosa has been synonymised with ***Enchytronia parva*** in Coates (1989). The insufficiently known species may be a member of ***Enchytronia***, but its synonymy with ***E. parva*** is not accepted here. Coates (1989) does not provide new information on the species, although types were investigated.

7.11 ***Enchytronia*** Nielsen & Christensen, 1959 (Fig. 42A–D)

Small worms, 2–5 mm, rarely longer, 19–31 segments. Chaetae straight with ental hook, two per bundle, absent in several anterior lateral bundles, mostly VIII–XII. Head pore at 0/1. Brain incised posteriorly. Pharyngeal glands united dorsally in IV and V, separate and elongate in VI. No oesophageal appendages. Intestine in VI most often with a pair of lateral, anteriorly blind-ending diverticula, or without diverticula but with an abrupt and considerable widening behind septum 5/6, and with canal-furrows inside. Coelomocytes often finely granulated, length at least equalling length of chaetae. Nephridial anteseptale with parts of nephridial body, first pair at 7/8. Dorsal vessel from (XII/)XIII, blood colourless. Male pore with compact glandular bulb, bursa present. Spermathecae free in ***E. longispermatheca***; proximally joint and attached to oesophagus in all other species; with ectal glands and glandular ectal duct; ampulla without diverticula. – Terrestrial, not in strongly acidic soils.

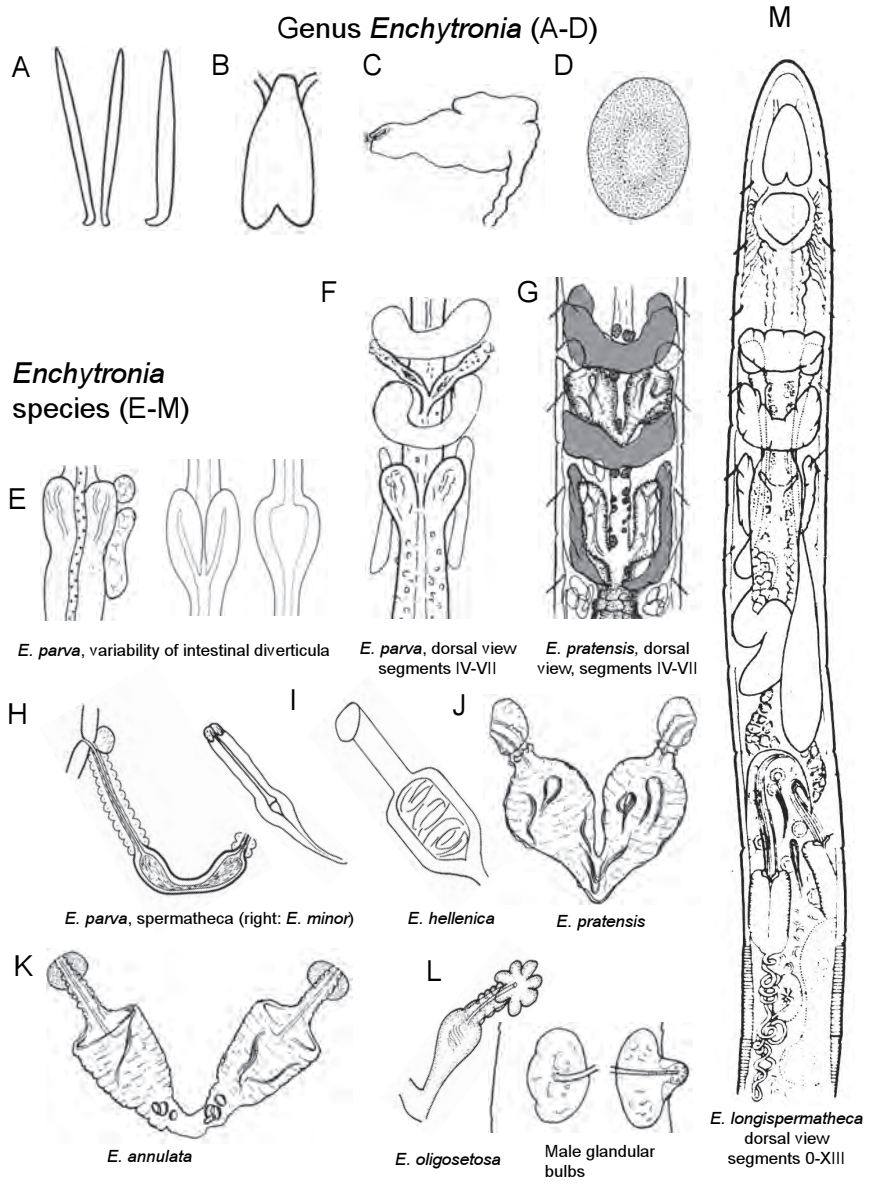

Fig. 42 ***Enchytronia***, genus (A–D) and species (E–M). A from Chalupský (1991, Fig. 4). B from Nielsen & Christensen (1959, Fig. 35). C from Chalupský (1991, Fig. 5). D from Chalupský (1994, Fig. 6). E: ***E. parva***, from Nielsen & Christensen (1959, Fig. 37), Healy (1979b, Fig. 2A,B). F: ***E. parva***, from Nurminen (1970b, Fig. 7, as ***Marionina diverticulata***). G: ***E. pratensis***, from Chalupský (1994, Fig. 1). H: ***E. parva***, from Nielsen & Christensen (1959, Fig. 38), Möller (1971, Fig. 3G, as ***E. minor***). I: ***E. hellenica***, from Dumnicka (1979, Fig. 4). J: ***E. pratensis***, from Chalupský (1994, Fig. 5). K: ***E. annulata***, from Chalupský (1994, Fig. 8). L: ***E. oligoseta***, from Sesma & Dózsa-Farkas (1993, Figs 3, 6). M: ***E. longispermatheca***, from Chalupský (1991, Fig. 1).

1 Spermathecae not attached to oesophagus, ampullae in VII–IX or –X, large sacs filled with sperm; Fig. 42M . . . . . .***Enchytronia longispermatheca*** Chalupský, 1991

L 3.5–5 mm, S ca 27–30. Abrupt widening of intestine after 5/6, with thick epithelium and inner furrows directed anteriad. Preclitellar nephridia at 7/8, 8/9. Clitellum open dorsally. Seminal vesicle extending over 3–4 segments. Spermathecal ectal gland large and compact, ampulla sac-like, extending over more than two segments. – Czech Republic. Only known from original description.

1* Spermathecae attached to oesophagus, confined to V **2**

2 Spermathecal ampulla large and conspicuous, at least 3x as wide as ectal duct **3**

2* Spermathecal ampulla small, often inconspicuous, up to 2x as wide as ectal duct . .**5**

3 Seminal vesicle absent or small; sperm in proximal part of spermathecal ampulla arranged in small regular rings; Fig. 42K . . . . . .***Enchytronia annulata*** Nielsen & Christensen, 1959

L ca 4 mm, S 28–30. Chloragocytes filling body lumen almost completely. Sperm funnel ca 2x as long as wide, almost as long as body diameter. Spermathecal ampulla ca 3x as wide as ectal duct, with abrupt widening at transition from ectal duct to ampulla. – Widespread.

3* Seminal vesicle large, extending over at least 2 segments; no small regular rings of sperm in proximal part of spermathecal ampulla **4**

4 Spermatheca with gradual widening at transition ectal duct/ampulla; sperm funnel 3–3.5x as long as wide, more than half as wide as body diameter; Fig. 42G,J . . . . . .***Enchytronia pratensis*** Chalupský, 1994

L ca 4.5–5 mm, S (19)–28–30. Coelomocytes with fine and regular granulation. Preclitellar nephridia at 7/8 and 8/9. Clitellum open ventrally. Spermatheca with large ectal gland (2x ectal duct diameter), very short ectal duct, mostly hidden by ectal gland, and club- or onion-shaped ampulla. – Czech Republic. Only known from original description.

4* Spermatheca with abrupt widening at transition ectal duct/ampulla, sperm funnel 2x as long as wide; Fig. 42I . . . . . .***Enchytronia hellenica*** Dumnicka, 1979

L 3–4 mm (fix), S 20–23. Intestine in VI with branched inner furrows (without diverticula ?). Sperm funnel 2x as long as wide, ca 1/2 as long as body diameter. Spermathecal ectal duct about as long as ampulla. – A cave in Greece. Only known from original description.

5 Lateral anterior chaetae mostly absent from VIII; Fig. 42E,F,H . . . . . .***Enchytronia parva*** Nielsen & Christensen, 1959 sensu lato
= ***Marionina diverticulata*** Nurminen, 1970b
= ***Enchytronia minor*** Möller, 1971
= ***Enchytronia christenseni*** Dózsa-Farkas, 1970

L 1.5–3 mm, S 22–26. Intestine in VI variable: distinct diverticula or neither diverticula nor abrupt widening of diameter at 5/6, or intermediates. Two or three preclitellar nephridia, at 7/8, 8/9, (9/10). Clitellum open dorsally and ventrally. Sperm funnel 1.5–3x as long as wide. Spermathecal ectal gland minute, not wider than ectal duct, or up to 1/3 as wide as body diameter, or intermediates. – Common and widespread in neutral to moderately acidic soils. Probably a complex of species. Lit.: Chalupský (1986, as ***Enchytronia*** sp.), Kasprzak (1986), Chalupský (1992), Rota (1994, 1995), Schmelz et al. (2005, as ***E. christenseni***).

5* Lateral anterior chaetae absent from VI; Fig. 42L . . . . . .
. . . . . .***Enchytronia oligosetosa*** Sesma & Dóza-Farkas, 1993

L 2.5–4.4 mm, S 17–29. Intestine in VI with diverticula. Dorsal vessel from XII. Seminal vesicle present, sperm in X, XI, sperm funnel 3–3.5x as long as wide, almost as long as body diameter. Male glandular bulb large, about half as long as body diameter. Spermatheca with onion-shaped ampulla and a crown of ectal glands, wider than ectal duct. – Spain. Only known from original description.

E. parva is generally recognised as a difficult species, although – or because – it is the most-often cited and most widely distributed species of the genus. Here we assemble all forms with small spermathecal ampullae and no lateral chaetae from VIII to XI under ***E. parva*** sensu lato. The species varies in the intestinal diverticula, number of preclitellar nephridia, size of the male reproductive structures, and size of the spermathecal ectal gland. From our experience not all of these variations are intraspecific. For example, specimens with 3 preclitellar nephridia have always conspicuous intestinal diverticula. However, to recognise species within ***E. parva***, large series of specimens from different regions should be compared and more characters should be included.

Occasionally chaetae are present laterally at VIII, VIII–IX, or even at VIII–XI. Such specimens key out as ***Marionina***, but the gut widening at 5/6 should lead to the genus ***Enchytronia***. Most similar to ***Enchytronia*** is ***Marionina magnaglandulosa***, synonymised with ***E. parva*** in Coates (1989), see ***Marionina***, remarks. The insufficiently described species has 2 chaetae throughout, data on gut enlargement are missing. Relationships between ***Marionina*** and ***Enchytronia*** are difficult and cannot be fully resolved here.

E. minor and ***E. christenseni*** are tentatively included in ***E. parva***; in ***E. minor***, the spermathecal ectal glands are smaller than in ***E.parva***, in ***E. christenseni*** they are larger. Further distinguishing characters are doubtful. For example, the spermathecae are said to be separate in ***E. christenseni***, but the connection is often very thin in ***E. parva***. ***E. minor***, included in ***E. parva*** by Coates (1989) without explanations, is said to have a large seminal vesicle, but this was not seen in the type specimens (Schmelz unpubl.). ***Marionina diverticulata*** was synonymised with ***Enchytronia parva*** by Zalesskaya (1982).

The genus, well-circumscribed at the beginning, has ‘frayed’ over time: ***E. baloghi*** Dózsa-Farkas, 1988b from Marokko has 2 chaetae in all bundles, those laterally in VIII–XI included. Such specimens can also be found in Europe (see above). ***E. longispermatheca*** has free spermathecae. Chalupský (1991) discusses the striking similarities of this species with more southern taxa such as ***Guaranidrilus*** and ***Hemienchytraeus***.

7.12 ***Oconnorella*** Rota, 1995 (Fig. 43)

More than 2 chaetae in many bundles, with inner chaetae shorter than outer, bundles asymmetrical or symmetrical. Head pore at 0/1, slit transverse in European species. No segmental dorsal pores. Brain rounded, truncate, or slightly indented at the most. Oesophageal appendages present in European species, ventrolateral and closely attached to oesophagus. Gradual widening of intestine, no intestinal diverticula. Dorsal vessel rising in clitellar region or closely behind. Nephridia consisting of funnel only. Coelomocytes of one type only. Male glandular bulb compact. Spermathecae attached to oesophagus. – The genus is an assemblage of species close to ***Henlea***, ***Bryodrilus***, and some species of ***Marionina***. Holarctic, temperate regions, terrestrial.

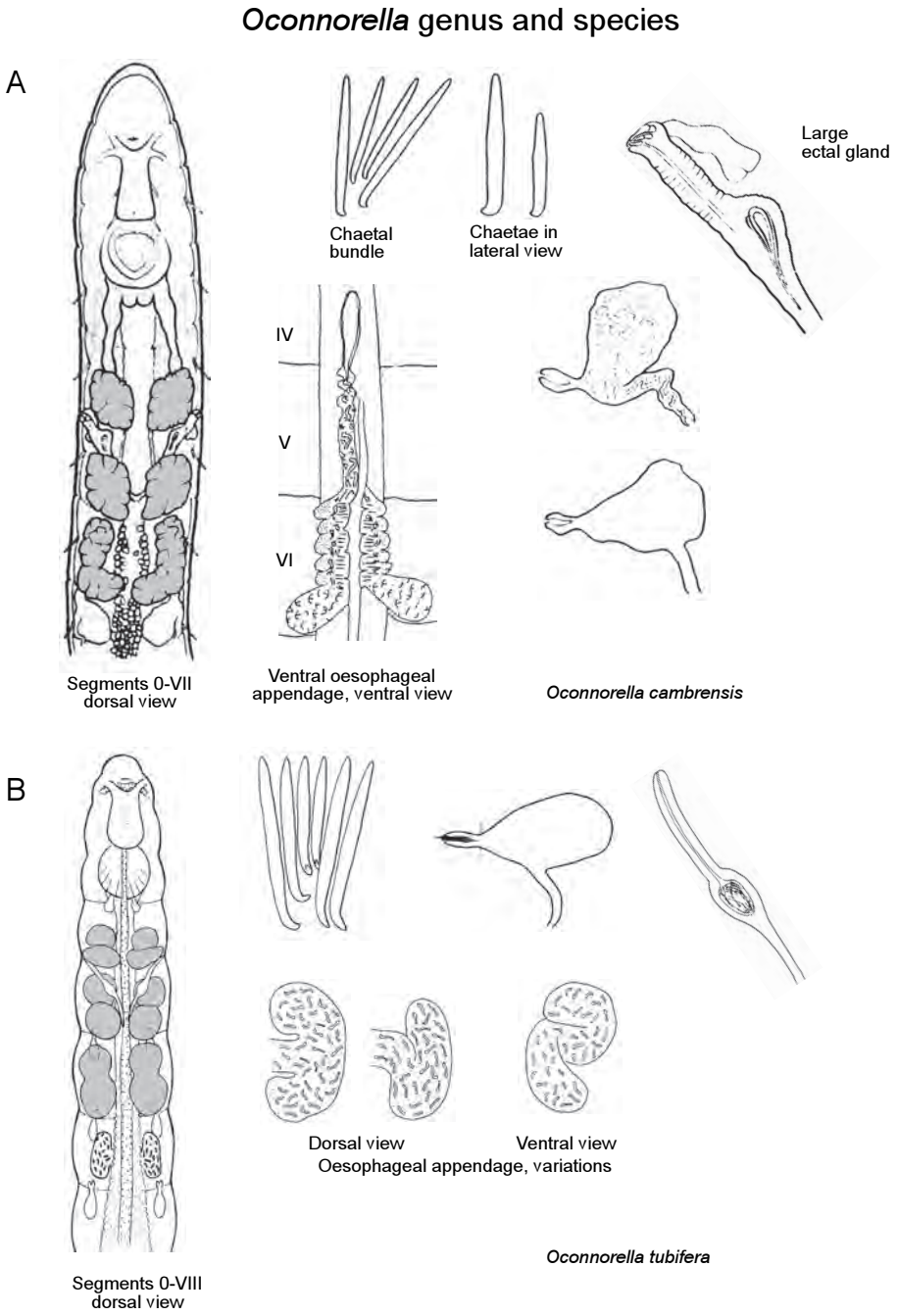

Fig. 43 ***Oconnorella***, genus and species. A: ***O. cambrensis***, from Chalupský (1991, Figs 7, 10, 8), O'Connor (1963, Fig. 4), Chalupský (1991, Fig. 9). B: ***O. tubifera***, from Rota (1995, Fig. 17A,B,C,F,G,H,L, as ***O. chalupskyi***).

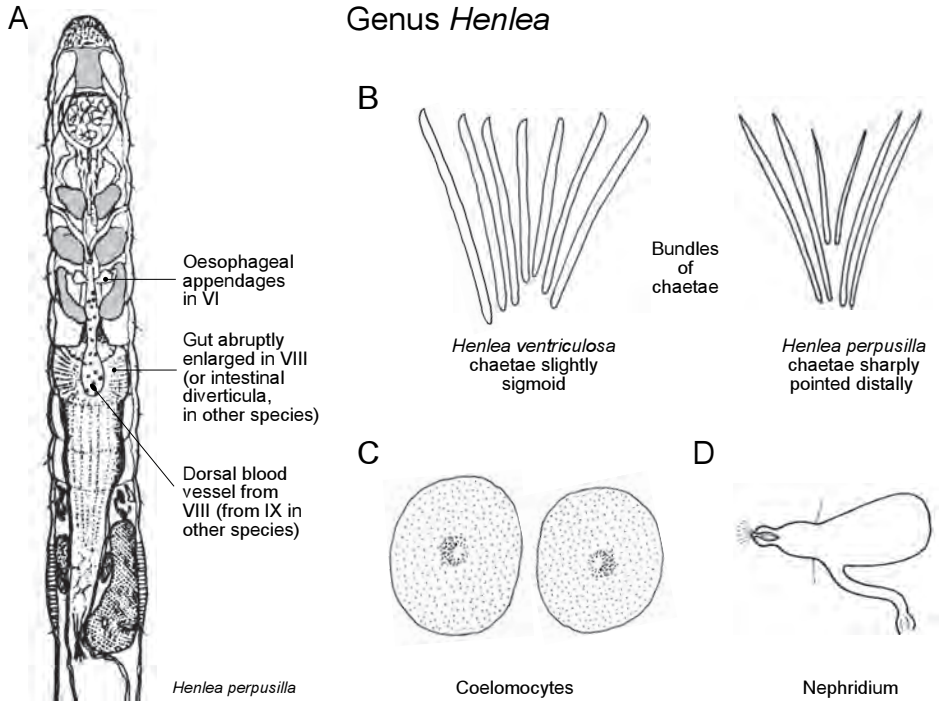

Fig. 44 ***Henlea***, taxonomic traits. A from Chalupský (1986, Fig. 29), B (right) from Timm (1999, Fig. p. 144). D from Nielsen & Christensen (1959, Fig. 50).

1 Up to 4 chaetae per bundle; oesophageal appendages in VI (below last pair of pharyngeal glands), with a canal attached ventrally to oesophagus, extending forwards to IV; Fig. 43A.....***Oconnorella cambrensis*** (O'Connor, 1963)
= ***Marionina asymmetrica*** Nurminen, 1970b

L 5–8 mm, S 31–41. Up to 4 chaetae in ventral preclitellar bundles, behind clitellum often 3 per bundle. Chaetae 3,4 – 4-2 : 4 – 4-2. Preclitellar nephridia 4 pairs, 6/7 – 9/10. Coelomocytes with fine and inconspicuous vesicles, pale. Clitellum partly incomplete mid-ventrally. Spermathecae short, proximally joint, with floppy ectal gland of varying size, and slightly asymmetrical ampulla at about half-length. – Common and widespread, abundant in moderately acidic soils. Lit.: Chalupský (1991, 1992), Römbke (1989), Rota (1995), Rota & Healy (1999), Dózsa-Farkas (2002b).

1* Up to 6 chaetae per bundle or more; oesophageal appendages in VII ventrolaterally (behind last pair of pharyngeal glands), as a pair of kidney-shaped bodies; Fig. 43B
.....***Oconnorella tubifera*** (Nielsen & Christensen, 1959)
= ***Oconnorella chalupskyi*** Rota, 1995

L 8–10 mm, S 35–41. Worms usually in a tube made of foreign matter. Up to 6 chaetae in lateral bundles, up to 6–8 in ventral bundles. Preclitellar nephridia 6 pairs, 5/6–10/11. Coelomocytes with small, pale and conspicuous vesicles, often yellowish. Clitellum partly incomplete mid-ventrally. Spermathecae short and simple, proximally joint or closely separate, without ectal gland, ampulla not asymmetrical. – Widespread, from Sweden to Italy. Moist soils. Lit.: Chalupský (1991), Dózsa-Farkas (2002b).

7.13 *Henlea* Michaelsen, 1889b (Fig. 44)

Chaetae straight distally or slightly bent, in fan-shaped arrangement. In caudal segments often as many chaetae per bundle as in preclitellar segments. Head pore at 0/1, a transverse slit. Brain posteriorly concave or straight. Pharyngeal glands all separate dorsally, rarely connected in VI. Oesophageal appendages present dorsally and ventrally in VI or in IV–VI, often difficult to see, closely attached to oesophageal walls and with free lobes in (IV +) VI. Intestinal diverticula present in VIII or absent; when present, abrupt gut widening in IX; when absent, gut widening at 7/8, abruptly or continuously; diverticula of varying shape, always blind-ending anteriorly and with widely open connection to intestine posteriorly. Dorsal vessel rising in VIII or IX in European species, usually pulsating and conspicuous, blood pale. Nephridial anteseptale with parts of nephridial body, size variable, usually small. Coelomocytes only mucocytes, finely and regularly vesicular. Clitellum girdle-shaped, cells mostly in reticulate pattern. Seminal vesicle absent in European species, male glandular bulb compact, no subneural glands. Spermathecae without diverticula in European species; ental ducts united before attachment to oesophagus. – Nordic genus, holarctic, species-richest in boreal to arctic regions. Terrestrial or semi-aquatic, not in acidic soils.

1 Intestinal diverticula present in VIII **2**

1* Intestinal diverticula absent **7**

2 Dorsal vessel rising in VIII, in between intestinal diverticula; one pair of lateral intestinal diverticula, separate from each other **3**

2* Dorsal vessel rising in IX, in segment posterior to intestinal diverticula; intestinal diverticula fused, circumferal, lobed or unlobed **5**

3 Large forms, > 20 mm long; coelomocytes almost circular, opaque, large (ca 50 µm), with yellowish or brownish granules; Fig. 45A . . . . . ***Henlea nasuta*** (Eisen, 1878)

L 15–25 mm, S 50–62 (arctic form: L 12 mm, S 48–50). Up to 6–8 chaetae in ventral anterior and posterior bundles. Brain concave posteriorly. Oesophageal appendages spongy, dorsal and ventral lobes in VI, canals in V and IV, in IV with a free loop dorsally and ventrally before entering oesophagus. Intestinal diverticula a pair of lateral, rounded bodies, confined to VIII. Preclitellar nephridia 5 pairs, from 6/7 – 10/11 (arctic form: 6 pairs, from 5/6 to 10/11), anteseptale small. Spermathecal ectal duct without glands, elongate ampulla conspicuous, pear-shaped, 3x as wide as ectal duct. – Common and widespread. Probably a species complex. At least two forms distinguishable, one of them restricted to arctic regions. Lit.: Backlund (1947), Nielsen & Christensen (1959), Kasprzak (1986), Rota & Healy (1994), Rota (1995), Rota et al. (1998), Rota (2001).

3* Smaller forms, < 20 mm long; coelomocytes oval, pale, not opaque, smaller (< 35 µm) **4**

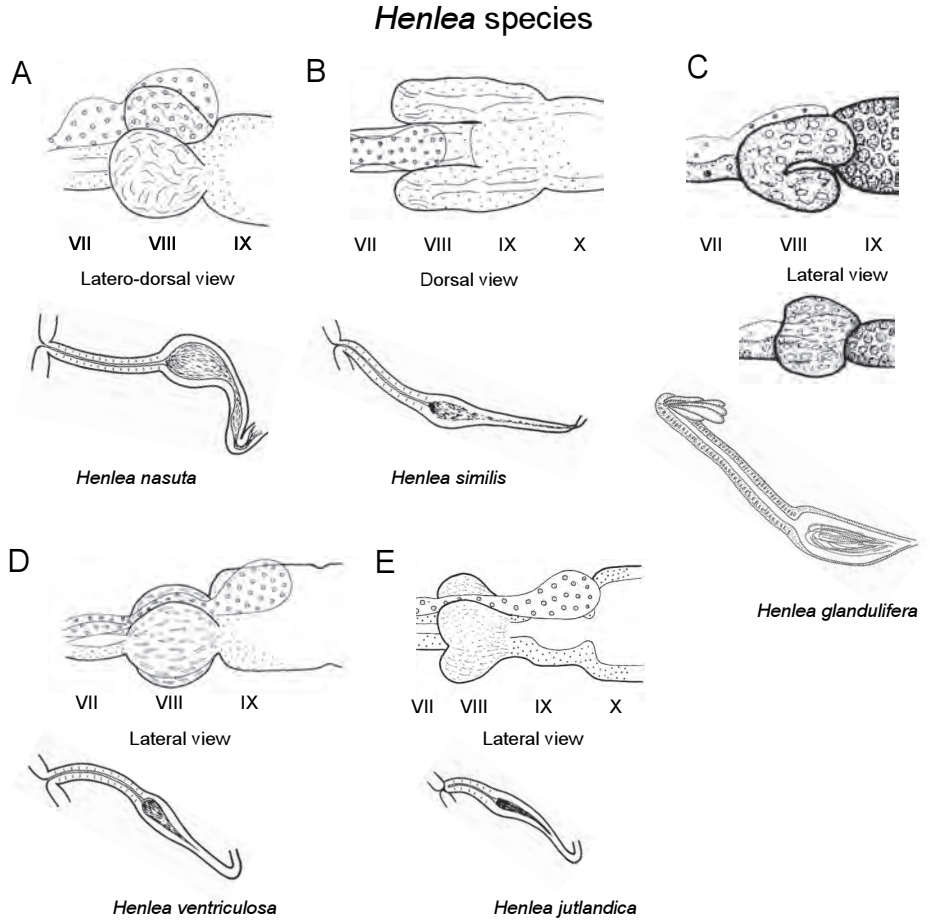

Fig. 45 ***Henlea*** species. A: ***H. nasuta***, from Nielsen & Christsensen (1959, Figs 51, 55). B: ***H. similis***, from Nielsen & Christsensen (1959, Figs 52, 56). C: ***H. glandulifera***, from Christensen & Dózsa-Farkas (1999, Fig. 15B,D), Rota et al. (1998, Fig. 4C). D: ***H. ventriculosa***, from Nielsen & Christsensen (1959, Figs. 53, 57). E. ***H. jutlandica***, from Nielsen & Christensen (1959, Figs 54, 58).

4 Intestinal diverticula extending over VIII and IX, first preclitellar nephridia at 6/7; spermathecae without ectal glands; Fig. 45B . . . . . .***Henlea similis*** Nielsen & Christensen, 1959

L ca 10–12 mm, S 39–43. Up to 8–9 chaetae in ventral preclitellar and caudal segments. Brain slightly concave posteriorly, almost straight. Oesophageal appendages only in VI. Intestinal diverticula a pair of lateral pouches in VIII, extending posteriorly and connecting with intestine in IX, whole region extending over two segments, distinguishable from rest of intestine by thicker epithelium and different texture. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Spermathecal ampulla narrow, only slightly wider than ectal duct. – Widespread. Lit.: Kasprzak (1986), Rota (1995), Rota et al. (1998).

4* Intestinal diverticula confined to VIII; first preclitellar nephridia at 5/6; spermathecae with ectal glands; Fig. 45C . . . . . .***Henlea glandulifera*** Nurminen, 1970a

L 8–10 mm, S 33–43. Up to 6 chaetae in ventral preclitellar and caudal segments. Brain concave posteriorly. A pair of rounded lateral pouches in VIII. Preclitellar nephridia 6 pairs, from 5/6 to 10/11. Spermathecal ectal glands present, slightly longer than ectal duct diameter; ampulla thin-walled, pear-shaped, about 2x as long as wide. – Alps. Widespread in Northern Europe. Lit.: Rota et al. (1998), Christensen & Dózsa-Farkas (1999).

5 Intestinal diverticula fused but lobed, surrounding gut; spermathecal ectal glands usually absent **6**

5* One cuff-like, circumferal intestinal diverticulum, not lobed; spermathecal ectal glands present . . . . . .***Henlea andreae*** Rodriguez & Giani, 1986

L 9–13 mm (fix), S 40–48. Up to 10 chaetae in ventral precitellar bundles, numbers successively reduced posteriorly, 2 chaetae in bundles of caudal segments. Intestinal diverticulum surrounding gut completely, cuff-like, large, with numerous branching canals. First pair of preclitellar nephridia at 4/5. Spermathecal ectal glands present, stalked, up to 2x as long as ectal duct diameter. – Northern Spain. Only known from original description. Similar to ***H. ventriculosa***.

6 Small animals, length < 15 mm; up to 7–9 chaetae in ventral preclitellar bundles; widening of intestine abrupt at 8/9; Fig. 45D . . . . . .***Henlea ventriculosa*** (d'Udekem, 1854)

L ca 9–13 mm, S ca (30)–40–50–(60). Up to 6–9 chaetae in ventral bundles, chaetae in caudal segments about as numerous as in anterior segments. Brain concave posteriorly. Four intestinal diverticula in VIII, closely applied to one another, difficult to distinguish. Gut widening abrupt at 8/9; intestinal cells with large pale vesicles from XX on and over several segments. Preclitellar nephridia 7 pairs, from 4/5 – 10/11. Spermathecal ectal duct longer than ampulla, usually without ectal glands. – Common and widespread, moist and dry sites, probably a species complex. Lit.: Nielsen & Christensen (1959), Rota (1994, 1995), Rota et al. (1998).

6* Large animals, length > 15 mm, up to 5–6 chaetae in ventral preclitellar bundles; gut widening gradually in IX; Fig. 45E . . . . . .***Henlea jutlandica*** Nielsen & Christensen, 1959

L ca 20 mm, S 50–60. Chaetae in caudal segments as numerous as in anterior segments. Spermathecal ectal duct short and stout. Three records, Denmark, Germany, Poland, wet sites. Probably A tetraploid cytotype of ***H. ventriculosa***.

7 Dorsal vessel from VIII, gut widening abruptly at beginning of VIII **8**

7* Dorsal vessel from IX, gut widening gradually over VII–IX; Fig. 46A . . . . . .***Henlea heleotropha*** Stephenson, 1922

L ca 10 mm, S 38–48. Up to 7 chaetae in ventral pre- and postclitellar bundles. Preclitellar nephridia 6 pairs, 5/6–10/11. Nephridial anteseptale half as long and wide as postseptale. Coelomocytes transparent, as long as the smallest chaetae. Spermatheca with narrow ampulla, ectal glands present or absent.– Widespread in Northern and Central Europe. Lit.: Nielsen & Christensen (1959).

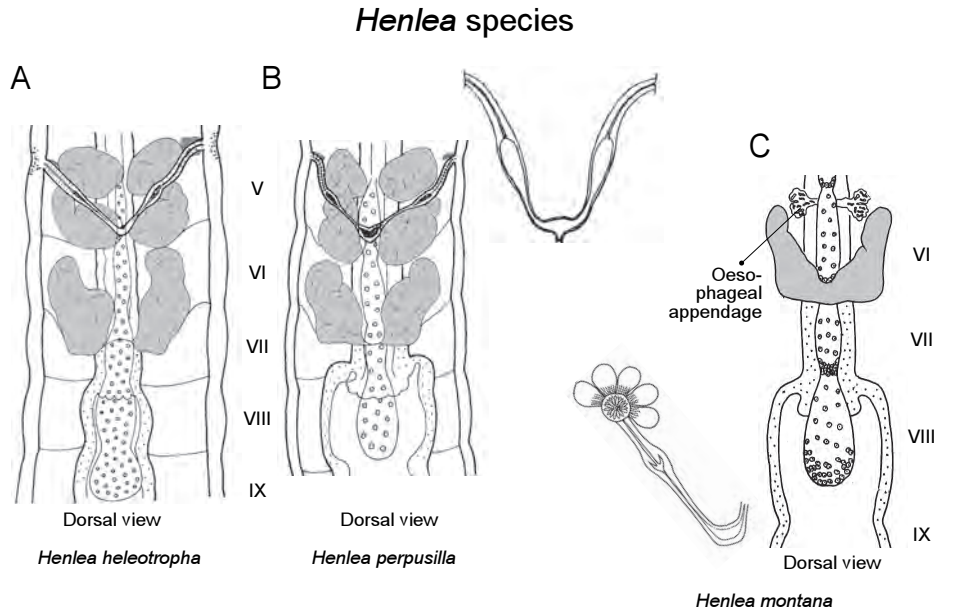

Fig. 46 ***Henlea*** species, continued. A: ***H. heleotropha***, from Nielsen & Christensen (1959, Fig. 48). B: ***H. perpusilla***, from Nielsen & Christensen (1959, Fig. 47), Černosvitov (1937c, Fig. 5). C: ***H. montana***, from Rota (1994, Fig. 3B,F).

8 Spermathecal ectal glands absent or very small, not longer than ectal duct diameter; Figs 44, 46B . . . . . .***Henlea perpusilla*** Friend, 1911
augm. Černosvitov, 1937c, sensu lato
= ***Henlea brucei*** Stephenson, 1922
= ***Henlea balcanica*** Černosvitov, 1930

L 4–9 mm, S 25–36. Up to 5–9 chaetae in ventral bundles. Brain posteriorly straight or slightly concave. Pharyngeal glands in VI occasionally connected dorsally. Intestine abruptly widened at 7/8, occasionally with slight diverticula-like lateral protrusions into VII. Preclitellar nephridia 5 pairs, 6/7–10/11. Clitellar gland cells in reticulate pattern or in dense/indefinite rows. Spermathecal ectal glands absent or present, small, not wider than ectal duct diameter; ectal duct not thickened near ectal pore, ampulla almost as narrow as ectal duct. – Very common and widespread, often at wet or almost aquatic sites. Species complex with various cytotypes. Lit.: Nielsen & Christensen (1959), Chalupský (1986), Kasprzak (1986), Rota & Healy (1994), Rota (1995), Rota et al. (1998).

8* Spermathecal ectal glands large; Fig. 46C . . . . . .***Henlea montana*** Rota, 1994

L 9–9.5 mm, S 24–37. Up to 6–8 chaetae in ventral bundles. Brain slightly concave posteriorly. Pharyngeal glands in VI occasionally connected dorsally. Spermathecal ectal glands 2–6, large (> 2x as long as ectal duct diameter), conspicuous, stalked, surrounding thickened distal end of ectal duct in a rosette-like, ‘petaloid’ fashion. – Turkey, Italy, Ireland. Lit.: Rota (1995), Rota et al. (1998).

Henlea balcanica Černosvitov, 1930 is probably a junior synonym of ***H. perpusilla***. ***H. balcanica*** was first synonymised with ***H. brucei*** Stephenson, 1922 (Černosvitov 1934a), described from Spitsbergen. Later, ***H. brucei*** was synonymised with ***H. perpusilla*** (Dózsa-Farkas 1999). It seems that Černosvitov's synonymisation of ***H. balcanica*** with ***H. brucei*** passed unnoticed by Nielsen & Christensen (1959), who include ***H. balcanica*** in a uncommented list of accepted European species, and also by Dózsa-Farkas (1999). ***H. brucei*** and ***H. balcanica***, both described on fixed material, are said to possess intestinal diverticula, but the variability reported for both species suggests that – instead of true diverticula – there is only an abrupt gut widening as in ***H. perpusilla***; at least this is the conclusion of Dózsa-Farkas (1999) after revising types of ***H. brucei***. ***H. perpusilla*** itself is heterogeneous on the cytological level, i.e. a species complex, but clearcut morphological differences among cytotypes are not evident (Nielsen & Christensen 1959).

We exclude ***Henlea puteana*** (Vejdovský, 1878), a name for ***Henlea*** worms with two pairs of spermathecal diverticula. Such specimens were first found in water pumped from a well in Moravia in 1876; the only further record is from watered moss on a wall in England (Friend 1912). We consider the quadrithecate condition as an anomaly, but it remains obscure to which species the specimens may have belonged; the descriptions (Vejdovský 1878, 1879a) are poor in detail and Friend does not give any details at all.

We further hesitate to include ***Henlea pertoserica*** Popčenko, 1988 (originally ***H. pertosericus***), described from lake shore sediments in the Kola peninsula, Russia. The original description – ignored for over 20 years and kindly brought to our attention by T. Timm – is full of exotic traits and probably flawed: Dorsal blood vessel from X, body wall transparent but about 0.1 mm thick, clitellum from XI–XV, spermathecal ectal pores ventral; spermathecal ectal duct up to 65 µm thick, about as long as body diameter, spermathecal ampulla with spherical and tubular attachments, ectal glands more than 3x as wide as ectal duct. A dorsal blood vessel origin from X is known in the Alaskan ***H. udei*** (Eisen, 1904) – all other ***Henlea*** species have the origin in either VIII or IX – but in view of the other exotic traits in the description we question that trait in ***H. pertoserica*** as well, pending a reinvestigation of the types. Probably accurate characters: Fixed specimens 11–15 mm long and up to 0.7 mm thick, 4–8 chaetae per bundle, gut dilatation sudden at VIII, without intestinal diverticula, spermathecal ampulla with large lumen. The original figure of the spermatheca of ***H. pertoserica*** is reproduced in Timm (2009).

7.14. *Bryodrilus* Ude, 1892 (Fig. 47)

Head pore at 0/1. Chaetae sigmoid or almost straight. Brain posteriorly convex. Pharyngeal glands all separate dorsally. Two pairs of kidney-shaped oesophageal appendages in VI, one dorso-lateral, one ventro-lateral. No intestinal diverticula. Dorsal vessel rising in clitellar region. Nephridial anteseptale consisting of funnel only or with small parts of nephridial body. Coelomocytes discoid, one type only, finely granulate. Spermathecae with elongate ectal duct, ampulla only slightly wider than ectal duct, without diverticula, and with joint proximal attachment to oesophagus dorsally; spermathecae free, stump-like in one species. – Nordic genus, holarctic, species-richest in arctic/subarctic regions.

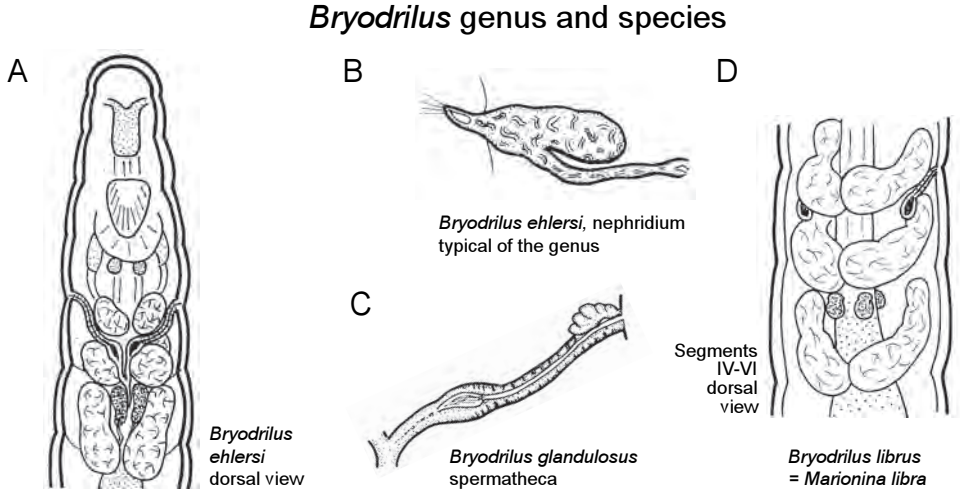

Fig. 47 ***Bryodrilus***, genus and species. A: ***B. ehlersi***, from Nielsen & Christensen (1959, Fig. 65). B: ***B. ehlersi***, from Dózsa-Farkas (1990, Fig. 6). C: ***B. glandulosus***, from Dózsa-Farkas (1990, Fig. 4). D: ***B. librus*** = ***Marionina libra***, from Nielsen & Christensen (1959, Fig. 162).

1 Body length < 12 mm; coelomocytes not abundant, or pale **3**

1* Body length > 12 mm; coelomocytes abundant, yellowish; Fig. 47A–C **2**

2 Spermathecae without ectal glands, no seminal vesicle; Fig. 47A,B . . . . . .***Bryodrilus ehlersi*** Ude, 1892

L 13–18 mm, S 41–50. Chaetae strongly sigmoid. Up to 6, rarely 7 or 8 chaetae per bundle. Coelomocytes present in large numbers, cells thick, regularly granulated, yellowish or faintly brownish. Oesophageal appendages with small but distinct lumen, thick-walled. First preclitellar nephridium at 4/5. Sperm funnel and male glandular bulb small. – Widespread. Mostly bogs and peatlands. Lit.: Černosvitov (1928a), Backlund (1947), Nielsen & Christensen (1959), Römbke (1989).

2* Spermathecae with ectal gland, seminal vesicle present, in XI or X–XI; Fig. 47B,C . . . . . .***Bryodrilus glandulosus*** Dózsa-Farkas, 1990, new rank = ***Bryodrilus ehlersi*** Ude ssp. ***glandulosus*** Dózsa-Farkas, 1990

All as in ***B. ehlsersi*** except for the traits listed above. – A ***Sphagnum***-bog in Hungary. Only known from original description.

3 Spermathecae with a crown of pear-shaped ectal glands; oesophageal appendages with lumen; body length 7–12 mm . . . . . .***Bryodrilus diverticulatus*** Černosvitov, 1929

L 7–12 mm, S 31–42. Chaetae distinctly sigmoid, 2–5 or 2–6 chaetae per bundle. Oesophageal appendages hollow, lobed, pulsating. Intestine widens abruptly in VII. Coelomocytes transparent. Seminal vesicle small or absent. Sperm funnel 3–4x as long as wide, male glandular bulb large, as long as or longer than sperm funnels, ca half as long as body diameter. Spermathecae with a crown of small, pear-shaped ectal glands. – Northern Europe. Lit.: Christensen & Dózsa-Farkas (1999, 2006).

3* Spermathecae without or with minute ectal glands; oesophageal appendages without apparent lumen; body length 4–5 mm **4**

4 Spermathecae attached to oesophagus . . . . . .***Bryodrilus parvus*** Nurminen, 1970a

L 4–5 mm, S 27–30. Body usually covered with soil particles. Chaetae slightly sigmoid, formula 3-5 – 4-6 : 3,4 – 3-5. Oesophageal appendages seemingly compact, unlobed, not pulsating; intestine widening at IX–X. Coelomocytes sparse. Sperm funnel 2x as long as wide. Spermathecae mostly without ectal glands. – Northern Europe.

4* Spermathecae not attached to oesophagus; Fig. 47D . . . . . .***Bryodrilus librus*** (Nielsen & Christensen, 1959)
New combination for ***Marionina libra*** Nielsen & Christensen, 1959

L 5 mm, S 28–36. Body usually covered with soil particles. Chaetae distally straight or slightly sigmoid, up to 4 or 5 per bundle. Nephridial anteseptale with parts of nephridial body. Dorsal vessel from XIII. Sperm funnel 2x as long as wide. Spermathecae short, free, club-shaped, without glands. – Northern and Central Europe.

Nielsen & Christensen (1959) hesitated to include ***Marionina libra*** in ***Bryodrilus*** because of the distally straight chaetae and the free spermathecae, but free spermathecae occur occasionally in genera with attached spermathecae, see ***Fridericia reducata*** and ***Enchytronia longispermatheca***, and the distal chaetal tip is variable in other genera as well, see ***Henlea*** or ***Lumbricillus***. The only other character that might question the new combination is the nephridial anteseptale, which according to the genus diagnosis of ***Bryodrilus*** in Nielsen & Christensen (1959) consists only of the funnel. However, parts of the nephridial body are present in the anteseptale of the Siberian ***B. borealis*** Cejka, 1912 (Pl. 1 Fig. 4) and in further non-European species of ***Bryodrilus*** (Xie et al. 2000), not included here.

7.15. ***Buchholzia*** Michaelsen, 1887 (Fig. 48)

Medium-sized worms, rarely > 10 mm long. Head pore at 0/1, a longitudinal slit. Chaetae sigmoid without nodulus. Epidermal gland cells usually in dense transverse rows at level of chaetae. Brain slightly concave posteriorly. Oesophageal appendages one pair in IV dorso-laterally; intestinal diverticula at VII/VIII or absent. Dorsal blood vessel from VII, anteriorly of intestinal diverticula, blood colourless. Nephridial anteseptale with funnel and small parts of nephridial body. Two types of coelomocytes, lenticytes and mucocytes. Spermathecae without diverticula, ampullae onion-shaped, proximally fused. – Terrestrial, not in acidic soils.

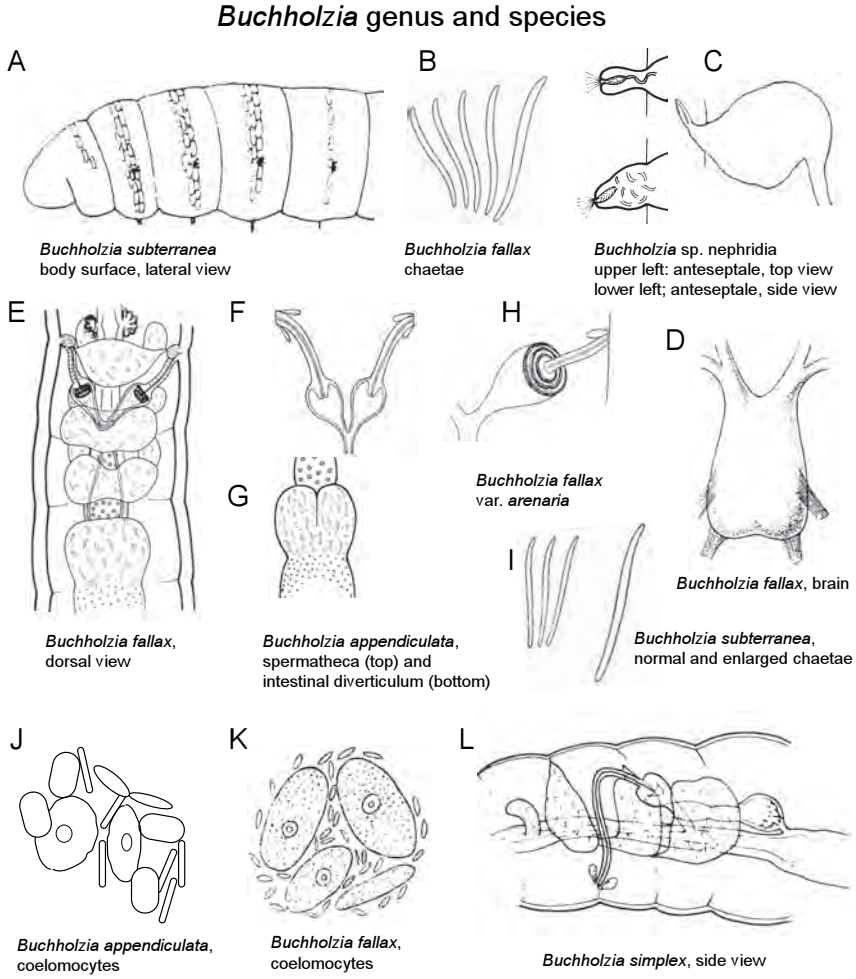

Fig. 48 ***Buchholzia***, genus (A–D) and species (E–L). A: ***B. subterranea***, from Černosvitov (1937b, Fig. 2). B: ***B. fallax***, from Michaelsen (1887, Pl. 21 Fig. 4A). C from Nielsen & Christensen (1959, Fig. 59), Černosvitov (1937b, Fig. 5). D: ***B. fallax***, from Michaelsen (1887, Pl. 21 Fig. 4D). E: ***B. fallax***, from Nielsen & Christensen (1959, Fig. 60). F: ***B. appendiculata***, from Černosvitov (1937b, Fig. 1). G: ***B. appendiculata***, from Nielsen & Christensen (1959, Fig. 64). H: ***B. fallax*** var. ***arenaria***, from Healy (1979b, Fig. 3). I: ***B. subterranea***, from Černosvitov (1937b, Figs 3, 4). K: ***B. fallax***, from Michaelsen (1887, Pl. 21 Fig. 4B). L: ***B. simplex***, from Nielsen & Christensen (1963, Fig. 1).

1 Intestinal diverticula present; more than 4 chaetae in several ventral bundles **2**

1* Intestinal diverticula absent, not more than 4 chaetae per bundle **3**

2 Coelomo-lenticytes very numerous, optically dominating, almost as large as mucocytes, the latter scarce; pharyngeal glands often with an additional pair in VII; male pores in IX or VIII; reproduction mainly by fragmentation; Figs 14B, 48F,G,J
.....***Buchholzia appendiculata*** (Buchholz, 1862)

L 3–12 mm, S up to 65. Body often with segmental rings of adhering foreign particles, attached to body surface by strongly developed epidermal gland cells. A maximum of 5 or 6 chaetae in ventral anterior bundles. Pharyngeal glands with narrow or wide dorsal connection, separate in VII. Intestinal diverticulum with a dorsal incision. Seminal vesicle large. – Common and widespread in neutral to slightly acidic soils, often abundant in litter layer. Lit.: Nielsen & Christensen (1959), Kasprzak (1986), Rota (1994, 1995), Rota & Healy (1994), Christensen et al. (2002).

2* Coelomo-lenticytes distinctly smaller than mucocytes, the latter optically dominating; no additional pharyngeal glands in VII; male pores in XII; sexual reproduction only; Fig. 48E,D,K.....***Buchholzia fallax*** Michaelsen, 1887 sensu lato

L 7–12 mm, S 37–51. Body sometimes with segmental rings of adhering foreign particles, attached to body surface by strongly developed epidermal gland cells. A maximum of 5–8 chaetae per bundle. Pharyngeal glands all widely connected dorsally. Intestinal diverticulum without incision. Seminal vesicle absent. – Widespread. Lit.: Nielsen & Christensen (1959), Rota & Healy (1994), Rota (1995).

3 Segment number below 40; subneural glands absent; enlarged chaetae ventrally in IV present or absent; Fig. 48L .....
.....***Buchholzia simplex*** Nielsen & Christensen, 1963 sensu lato
= ***Marionina serbui*** Botea, 1984

L 7 mm, S 28–43. Chaetal formula 2-4 – 2-4 : 3,4(5) – 2-4, often only 3 in many bundles. Oesophageal appendages stiff, finger-like. Pharyngeal glands all separate dorsally. Dorsal blood vessel from VII, with a heart-like expansion; gut widening in VIII. Two small spermathecal ectal glands. Some specimens with 1 or 2 enlarged chaetae in ventral bundles of IV. – Central and Eastern Europe. Lit.: Rota (1995).

3* Segment number up to 70; a subneural gland present in XIV; enlarged ventral chaetae in IV; Fig. 48A,I.....***Buchholzia subterranea*** (Černosvitov, 1937b)

L 7 mm (fix!), S ca 70. 3–4 chaetae per bundle. Dorsal blood vessel from VII, with a heart-like expansion; gut widening in VIII. Clitellum saddle-shaped. One large spermathecal ectal gland. – Caves in Bulgaria. Only known from original description.

Juvenile specimens of ***B. fallax*** sensu lato and ***B. appendiculata*** are easy to separate by the size and quantity of the coelomo-lenticytes; differences in the shape of the intestinal diverticulum (dorsally incised in ***appendiculata***, not incised in ***fallax***) are not so evident.

B. subterranea is revalidated here. Nielsen & Christensen (1959), who transferred the species from ***Henleanella*** (a previous subtaxon of ***Henlea***) to ***Buchholzia***, found the original description too insufficient to accept the species, but the description of ***B. subterranea*** is actually more detailed than the one of ***B. simplex*** given later by Nielsen & Christensen (1963) themselves. Both species are closely related.

The two variants of ***B. simplex*** – distinguished by presence/absence of enlarged ventral chaetae – occur at the same sites (Bauer 1996). In new material from the Alps, we did not find further significant morphological differences. The ill-described ***Marionina serbui*** Botea, 1984

probably also belongs here, although some traits diagnostic of ***Buchholzia*** are not described (coelomo-lenticytes, oesophageal appendages). The known traits are strikingly similar to ***Buchholzia simplex***, only the dorsal blood vessel origin differs (in XIII); ***serbui*** may therefore also be a new species of ***Buchholzia***; but we assume an observation error, pending further evidence. Enlarged ventral chaetae are present in ***serbui***, described as being in V, but a figure (Botea 1984, Fig. 1A) suggests that they are in IV, as in ***B. simplex***. The species is said to have large coelomocytes with yellow-brownish granula, which agrees with our observations in ***B. simplex*** (cells up to 60 µm long).

B. fallax appears to assemble several forms (species?) within ***Buchholzia***, characterised by intestinal diverticula and gonadal segments not shifted forward, i.e., in the usual position. One form, restricted to sand dunes, has been sorted out as a variety, ***B. fallax*** var. ***arenaria*** (Healy 1979b), with fewer chaetae (max. 4–5) and very large spermathecal ampullae (Fig. 48H); sperm is arranged in 3–4 concentric rings arranged perpendicular to the spermathecal long axis.

7.16. *Hemifridericia* Nielsen & Christensen, 1959 (Fig. 49)

Small worms. Chaetae distally straight without nodulus, proximally bent. Head pore at 0/1. Brain incised posteriorly. Pharyngeal glands in IV–VI, no secondary glands. Oesophageal appendages absent (present in one non-European species). Intestinal diverticula absent. Nephridial anteseptale with parts of nephridial body. Dorsal vessel from XII–XIII, blood colourless. Coelomocytes of two kinds, mucocytes and lenticytes. Spermathecae without ectal glands, ampullae without diverticula.

Hemifridericia parva Nielsen & Christensen, 1959

L 2–3 mm, S ca 20. Chaetal formula 2–3 : 2,3-2 (two ventral preclitellar chaetae only in II and XI). Brain deeply incised posteriorly. No oesophageal appendages. Coelomo-lenticytes very small, ca as long as diameter of chaetae. Male reproductive system small. Spermathecae with long ectal duct devoid of glands, pear-shaped ampullae, ental ducts fused, one common opening into oesophagus. – Wet soils. Widespread. Lit.: Möller (1971), Rota (1995), Rota & Healy (1999).

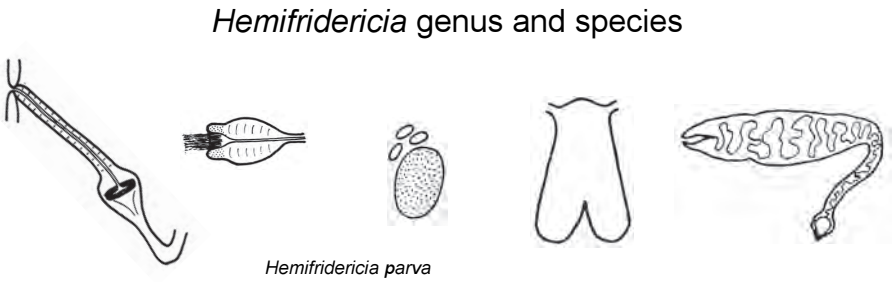

Fig. 49 ***Hemifridericia***, genus and species. ***H. parva***, from Nielsen & Christensen (1959, Figs 69, 68, 70), Möller (1971, Fig. 5A,B).

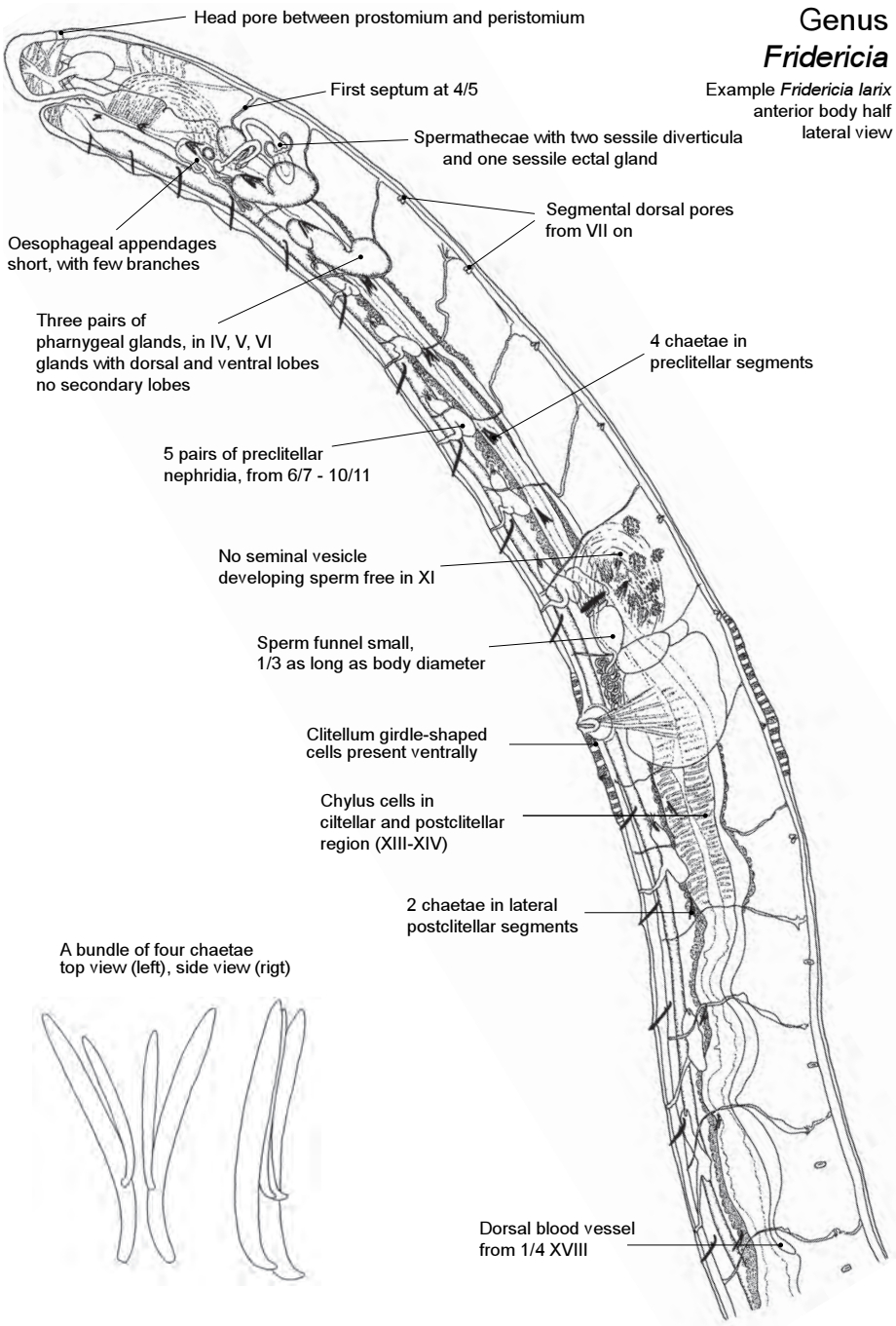

Fig. 50 ***Fridericia***, taxonomic traits. ***F. larix***, from Schmelz & Collado (2005, Fig. 1A). Schmelz (1999, Fig. 4B).

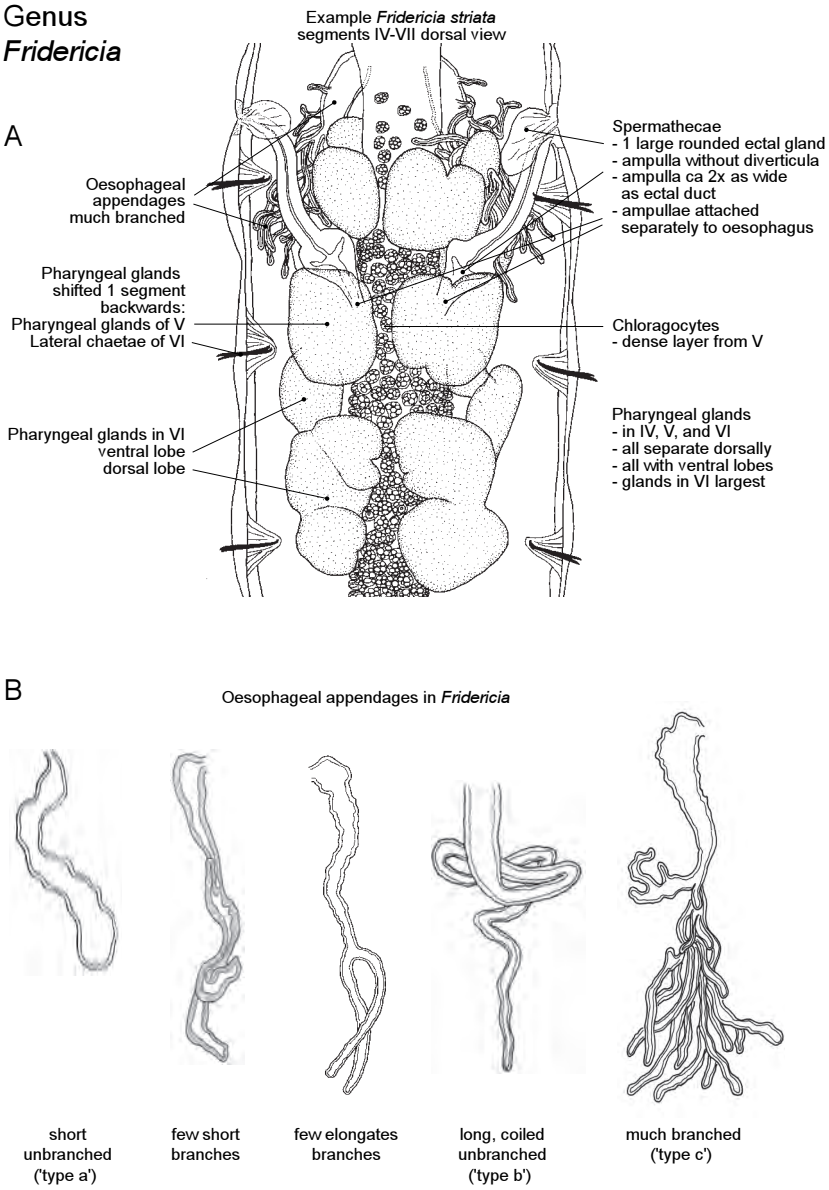

Fig. 51 ***Fridericia***, taxonomic traits, continued. A: ***F. striata***, from Schmelz (2003, Fig. 64A). B: Oesophageal appendages. From Issel (1904, Fig. 4), Schmelz (1998, Fig. 4), Issel (1905a, Pl. 14 Figs 32, 25).

7.17. ***Fridericia*** Michaelsen, 1889b (Figs 50, 51)

Medium-sized to large worms. Chaetae straight with ental hook, number per bundle variable. In bundles with 4 or more chaetae, arrangement symmetrically fan-like with inner chaetae shorter than outer. Head pore at 0/1, a longitudinal slit. Segmental dorsal pores from VII. Brain not incised posteriorly. Pharyngeal glands in IV–VI, rarely also in VII. Oesophageal appendages a pair of tubes, branched or unbranched, with distinct lumen, opening ventro-laterally into oesophagus in IV, behind pharyngeal pad. Intestinal diverticula absent. Chylus cells present, gradual transition of oesophagus into intestine. Origin of dorsal blood vessel in a postclitellar segment, blood mostly colourless. Coelomocytes of two types, mucocytes and lenticytes. Nephridial anteseptale with parts of nephridial body, first pair mostly at 6/7, rarely further back. Subneural glands present in some species. Spermathecae rarely free, mostly connected with oesophagus, with or without ectal glands and diverticula, ectal duct long, ampullae proximally joint or separate. – Cosmopolitan. Species-richest and often dominant (abundance, biomass) in moderately moist and not strongly acidic soils in temperate or mediterranean climates. Tropical, subtropical and southern species probably peregrine or introduced.

The keys are adapted and revised versions of the ones in Schmelz (2003), a critical revision of the genus. Five new species are included, ***F. larix*** Schmelz & Collado, 2005a, ***F. schmelzi*** Cech & Dózsa-Farkas, 2005, ***F. crassiductata*** Dózsa-Farkas & Cech, 2006, ***F. brunensis*** Schlaghamerský, 2007, and ***F. lacii*** Dózsa-Farkas, 2009. As to ***F. eiseni*** Dózsa-Farkas, 2005, see remarks. A very useful tabular comparison of species with two spermathecal diverticula was compiled by Dózsa-Farkas (2009). For further details on the species, synonymies, excluded species, and all literature published up to 2003, see Schmelz (2003).

Key to species groups

1 Spermathecae present in adult specimens (with clitellum), connected with oesophagus, differentiated into canalised ectal duct and a widened ampulla, with or without diverticula **2**

1* Spermathecae absent in adult specimens or reduced, not connected with oesophagus . .....**Group A**, p. 126

2 Spermathecae without diverticula (small diverticula-like protrusions may be present) .....**Group B**, p. 126

2* Spermathecae with diverticula (1 or more) **3**

3 Spermathecae each with 1 diverticulum only .....**Group C**, p. 132

3* Each spermatheca with more than 1 diverticulum.....**4**

4 Spermathecae each with 2 diverticula 5

4* Spermathecae each with more than 2 diverticula **7**

5 Two chaetae per bundle ..... **Group D**, p. 133

5* More than 2 chaetae at least in ventral preclitellar bundles **6**

6 Up to 3–5 chaetae in ventral preclitellar bundles ..... **Group E**, p. 138

6* Up to 6 and more chaetae in ventral preclitellar bundles ..... **Group F**, p. 148

7 Not more than 5 chaetae in ventral preclitellar bundles ..... **Group G**, p. 153

7* Six or more chaetae in at least some ventral preclitellar bundles ..... **Group H**, p. 156

Fridericia species

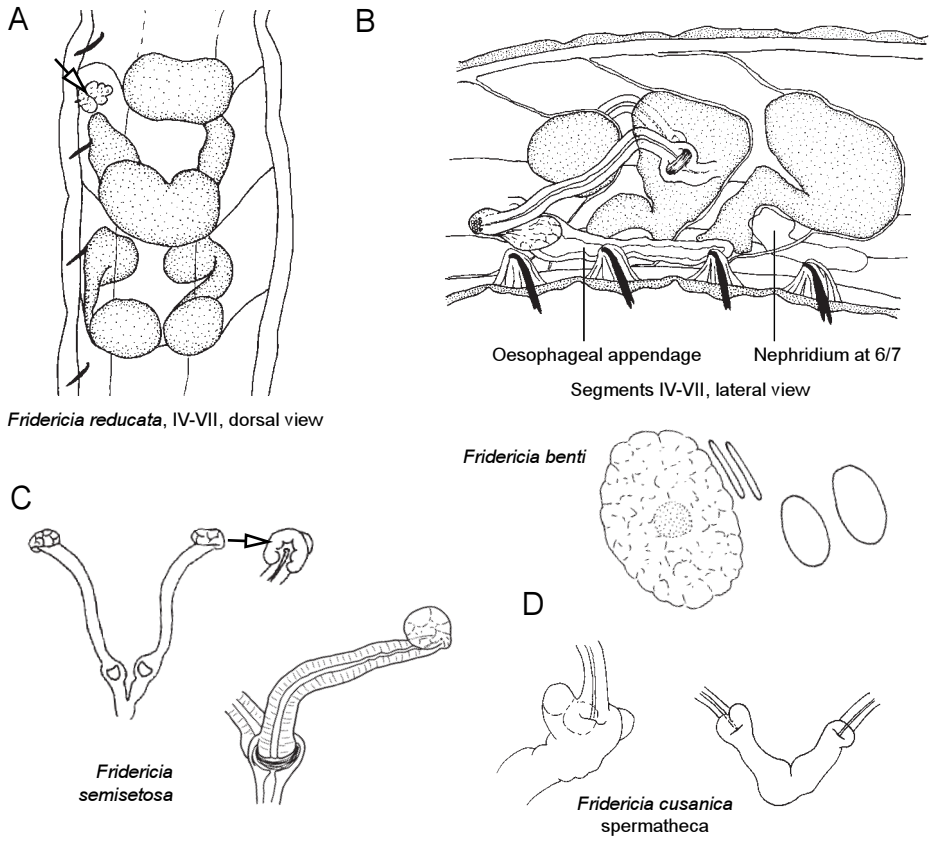

Fig. 52 ***Fridericia*** species. A: ***F. reducata***, from Schmelz (2003, Fig. 60D). B: ***F. benti***, from Schmelz (2002, Fig. 2A, lateral chaetae not shown here), Schmelz (2003, Fig. 17C). C: ***F. semisetosa***, from Dózsa-Farkas (1970, Fig. 1E), Schmelz 2003, Fig. 62B. D: ***F. cusanica***, from Schmelz 2003, Fig. 28J,K.

A. Spermathecae absent or rudimentary, not differentiated; or spermathecae differentiated but not connected with oesophagus.

1 A maximum of 4 chaetae per bundle, spermathecae completely absent.....**2**

1* A maximum of 2 chaetae per bundle (rarely 3 or 4 in single bundles), spermathecae rudimentary; Fig. 52A .....***Fridericia reducata*** Dózsa-Farkas, 1974

L 10–15 mm, S 42–54. Oesophageal appendages unbranched, short. Preclitellar nephridia 5 pairs, 6/7 - 10/11. Clitellum saddle-shaped; seminal vesicle and sperm funnel not large. Bursal slit T-shaped. Spermatheca rudimentary, not connected with oesophagus. – Northern and Central Europe.

2 Body colour speckled white, coelomocytes entirely filled with refractile vesicles, additional pair of pharyngeal gland lobes in VII, subneural glands absent; see E8 ....***Fridericia nix*** Rota, 1995

2* Body colour not speckled white, coelomocytes with pale and non-refractile vesicles, no additional pair of pharyngeal gland lobes in VII, subneural glands present..... .....***Fridericia christeri*** Rota &Healy, 1999

L 8–12 mm, S 36–46. Oesophageal appendages short, unbranched. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Clitellum saddle-shaped. Sperm funnel thick, inflated and with large, pale vesicles. Subneural glands in XIII–XV, largest in XIII, floppy. – Northern half of Europe. Very common in Germany.

Single specimens of other species may occasionally lack spermathecae.

B. Spermathecae without diverticula, small diverticula-like protrusions may be present

1 Two chaetae per bundle, also in ventral preclitellar bundles **3**

1* More than two chaetae in ventral preclitellar bundles **2**

2 A maximum of 4 chaetae in most ventral preclitellar bundles.....**6**

2* More than 4 chaetae in ventral preclitellar bundles.....**14**

3 Coelomo-mucocytes pale, without refractile vesicles at cell periphery; cuticle thin, inconspicuous.....4

3* Coelomo-mucocytes with refractile vesicles at cell periphery; cuticle often thick.....**5**

4 Spermathecae with separate openings into oesophagus, ectal gland large, floppy; male bursal slit longitudinal; coelomo-lenticytes large; Fig. 52B..... .....***Fridericia benti*** Schmelz, 2002

L 5–8 mm, S 32–39. Brain egg-shaped. Oesophageal appendages short, unbranched. Preclitellar nephridia 5 pairs, 6/7 - 10/11. Chylus cells partly in preclitellar segments, dorsal vessel from XIV–XVI. Clitellum girdle-shaped. Seminal vesicle and sperm funnel small. Spermathecal ectal ducts short (< 2/3 body diameter), ampullae with separate openings into oesophagus. – Widespread and common in northern half of Europe. Indistinguishable from ***F. paroniana*** (D8*) except for the spermathecal diverticula.

4* Both spermathecae fused proximally, ectal gland medium-sized, sessile; male bursal slit T-shaped; coelomo-lenticytes small; Fig. 52D .... ***Fridericia cusanica*** Schmelz, 2003

L 7–7.5 mm, S 32–35. Brain quasi-rectangular. Oesophageal appendages short, unbranched. Preclitellar nephridia 5 pairs, 6/7 - 10/11. Chylus cells in IX and X, dorsal vessel from XIII–XIV. Clitellum girdle-shaped. Seminal vesicle and sperm funnel small. Spermathecal ectal long short (ca 3/4 body diameter), ampullae with joint opening into oesophagus. – Germany, Greece, Italy (Graefe, Schmelz, unpubl.).

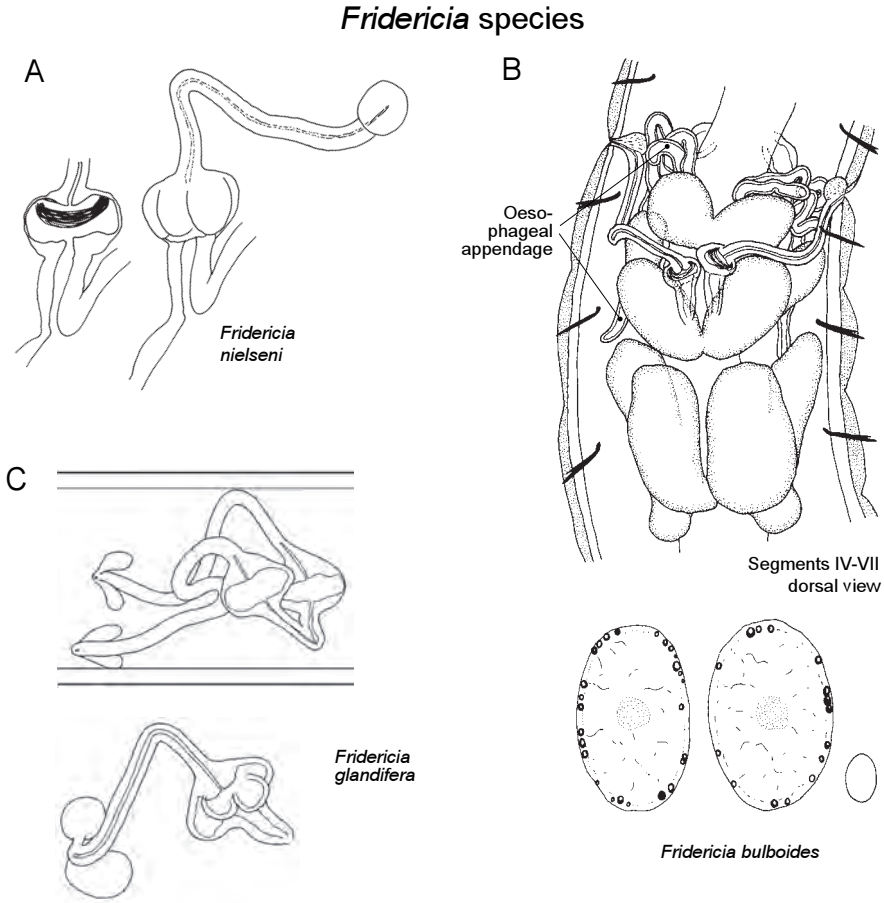

Fig. 53 ***Fridericia*** species, continued. A: ***F. nielseni***, from Schmelz (2003, Fig. 50B). B: ***F. bulboides***, from Schmelz (2003, Fig. 22F,B). C: ***F. glandifera***, from Schmelz (2003, Fig. 34G,H).

5 Clitellum only laterally developed, absent dorsally and ventrally, 1 or no chaeta in many lateral positions; cuticle often thick (1–6 µm); Fig. 52C ....***Fridericia semisetosa*** Dózsa-Farkas, 1970

L 5–7 mm, S 29–34. Chaetae small (length 20–30 µm), formula variable, maximum number ventrally 2, 3, or 4. Oesophageal appendages short, unbranched. Preclitellar nephridia 5 pairs, 6/7 - 10/11. Chylus cells often in preclitellar segments. Seminal vesicle absent, sperm funnel small, bursal slit T-shaped. Subneural glands absent. Spermathecal ectal gland sessile, 2x as wide as ectal duct, ampullae with joint opening into oesophagus. – Widespread; no record from southern Europe.

5* Clitellum present dorsally, no (or only single) bundles with 1 or 0 chaetae; cuticle thin; Fig. 53A .....***Fridericia nielseni*** Möller, 1971

L 5–8 mm, S 37–40. Body wall thin. Oesophageal appendages short, unbranched. Preclitellar nephridia 4 pairs, 6/7 to 9/10. Clitellum absent ventrally. Seminal vesicle large, 1–1.5 segments, sperm funnel large, as long as body diameter. Subneural glands in XIV and XV (not in XIII). Spermathecal ectal gland sessile, 2x as wide as ectal duct, ampulla large, 3x as wide as ectal duct or wider, often with small diverticula-like protrusions; separate openings into oesophagus. – Germany; only known from type locality (Potsdam).

6 Oesophageal appendages very long, coiled in IV, unbranched **7**

6* Oesophageal appendages different.....**8**

7 Ampullar distal part with small knob-like protrusions; coelomo-mucocytes without refractile vesicles; see G7* ....***Fridericia vixdiverticulata*** Sesma & Dózsa-Farkas, 1993

7* Ampullar distal part globular, sperm-containing, without protrusions; coelomo-mucocytes often with refractile vesicles at cell periphery, hyaline when without vesicles; Fig. 53B.....***Fridericia bulboides*** Nielsen & Christensen, 1959

L 5–9 mm, S 29–37. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Coelomo-lenticytes small. Chylus cells sometimes in preclitellar segments. Clitellum girdle-shaped. Seminal vesicle and sperm funnel small, bursal slit longitudinal. Spermathecae with sessile ectal gland (< 2x ectal duct width), ampullae opening separately or jointly into oesophagus. – Widespread and common.

8 One or no chaeta in many lateral bundles; cuticle often thick; see B4 ....***Fridericia semisetosa***

8* More than one chaeta in most lateral bundles; cuticle usually thin **9**

9 Seminal vesicle large (2 segments); subneural glands present in XIII and XIV, distinct, wider than nerve cord; spermathecal ampulla large, diameter equalling that of dorsal pharyngeal gland lobe in V.....**10**

9* Seminal vesicle absent or small (1 segment); subneural glands absent, or, when present, small, hardly wider than nerve cord; spermathecal ampulla small, diameter 1/2 that of dorsal pharyngeal gland lobe or less **11**

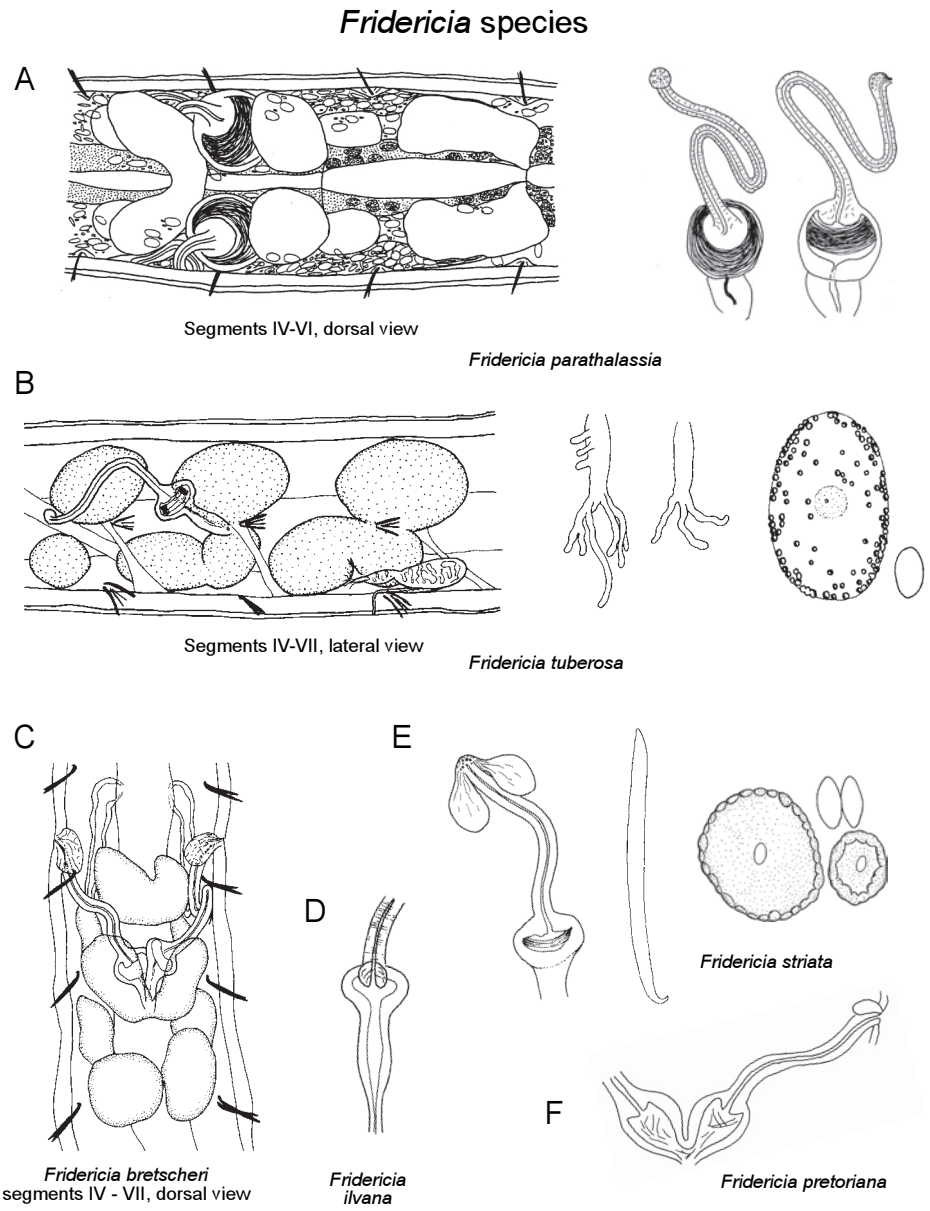

Fig. 54 ***Fridericia*** species, continued. A: ***F. parathalassia***, from Schmelz (2002, Fig. 2G,H,I). B: ***F. tuberosa***, from Schmelz (2003, Fig. 66A,B,K). C: ***F. bretscheri***, from Schmelz (2003, Fig. 21A). D: ***F. ilvana***, from Issel (1905b, Fig. 5). E: ***F. striata***, from Schmelz (2003, Fig. 64C,G,H). F: ***F. pretoriana***, from Dózsa-Farkas (1988a, Fig. 2G, as ***F. caprensis***).

10 Spermathecae fused proximally; ampullar distal part often with diverticula-like protrusions; Fig. 53C ..... ***Fridericia glandifera*** Friend, 1913b

L 5–12 mm, S 25–48. Oesophageal appendages short, unbranched. Preclitellar nephridia 4 pairs, 6/7 – 9/10. Clitellum girdle-shaped, cells in dense/indefinite rows. Sperm funnel ca 2/3 as long as body diameter, twice as long as wide, bursal slit mainly longitudinal. Spermatheca with 2 floppy ectal glands; ampullae joint proximally, distally often with 4–7, unequally large, diverticula-like protrusions. – England, Denmark, Germany, France, few records.

10* Spermathecae attached separately to oesophagus; ampullar distal part globular, without diverticula-like protrusions; Fig. 54A ..... ***Fridericia parathalassia*** Schmelz, 2002

L 10–13 mm, S 42–49. Oesophageal appendages short, unbranched. Preclitellar nephridia 4 pairs, 6/7 – 9/10. Clitellum girdle-shaped, sperm funnel large, as long as body diameter, 2x as long as wide, bursal slit L-shaped. Subneural glands in XIII, XIV (XV), largest in XIII. Spermathecal ectal gland small, sessile. – Common and widespread in soils close to the marine shoreline.

11 Pharyngeal glands with an extra pair of lobes in VII ventrally; coelomo-mucocytes without refractile vesicles; clitellum open dorsally; see E10 ..... ***Fridericia sylvatica*** Healy, 1975

Species with usually two spermathecal diverticula. Specimens with stump-like diverticula may key out here.

11* Pharyngeal glands without extra lobes in VII; coelomo-mucocytes with refractile vesicles; clitellum developed dorsally **12**

12 Refractile vesicles of coelomo-mucocytes numerous, concentrated at cell periphery but also inside, cell aggregations brownish; oesophageal appendages with few branches; small subneural glands in XIII and XIV; Fig. 54B ..... ***Fridericia tuberosa*** Rota, 1995

L 10–11 mm, S 40–45. Preclitellar nephridia 4 pairs, 6/7 – 9/10. Clitellum girdle-shaped, cells mostly in dense to indefinite rows. Seminal vesicle absent, sperm funnel small, length less than 1/2 body diameter, ca 2x as long as wide, bursal slits longitudinal or staple-shaped. Spermathecal ectal gland sessile, up to 2x as wide as ectal duct; ampulla ca 3x as wide as ectal duct, < 1/2 as wide as pharyngeal gland lobes in V. – Moist soils. Widespread.

12* Refractile vesicles of coelomo-mucocytes only at cell periphery, cell aggregations not brownish; oesophageal appendages unbranched; no subneural glands **13**

13 Spermathecal ectal gland small (20–30 µm); 5 pairs of preclitellar nephridia (6/7 – 10/11); male bursal slit transverse; epidermal gland cells pale ..... ***Fridericia schmelzi*** Cech & Dózsa-Farkas, 2005

L 5–8 mm, S 34–37. Oesophageal appendages short, unbranched. Chylus cells in preclitellar segments. Coelomo-lenticytes large, ca 1/3 as long as mucocytes. Clitellum girdle-shaped, cell in dense to separate rows. Sperm funnel very small, length 1/4 body diameter, 2x as long as wide. Spermathecal ectal gland small, sessile, ampulla only little wider than ectal duct, joint opening into oesophagus. – Hungary. Recently also found in Canadian field soils (Schmelz, unpublished).

13* Spermathecal ectal gland large (40–45 µm); 4 pairs of preclitellar nephridia (6/7 – 9/10); male bursal slit longitudinal; epidermal gland cells often yellowish; Fig. 54C .....***Fridericia bretscheri*** Southern, 1907

L ca 8 mm, S 38–42. Oesophageal appendages short, unbranched or with few short distal branches. Chylus cells sometimes in preclitellar segments. Clitellum girdle shaped, cells in indefinite rows. Seminal vesicle absent, sperm funnel length 2/3 body diameter, ca 2x as long as wide. Spermathecae with joint opening into oesophagus, or separate, adjacent. Coelomo-lenticytes small, scarce. – Widespread, few records.

14 Blood coloured, pink-yellow; coelomo-mucocytes 40–60 µm long, without refractile vesicles; worms opaque, milkish-white; body wall thick, inner organs barely distinguishable; Fig. 54D .....***Fridericia ilvana*** Issel, 1905b

L 20–30 mm, S 47–72. Chaetae 4-6 – 5-2 : 4-6 – 6-2. Oesophageal appendages much branched. Clitellar gland cells in reticulate pattern. Seminal vesicle absent, sperm funnel length ca 1/2 body diameter. Spermatheca with one or two ectal glands as wide as ectal duct, ampullae small, separate proximally. – Italy.

14* Blood pale/uncoloured; coelomo-mucocytes with refractile vesicles at cell periphery, mostly < 45 µm long; worms not opaque.....**15**

15 Coelomo-mucocytes with a ring of blurred refractile vesicles at periphery; two large spermathecal ectal glands, ampullae widely separate dorsally; Figs 51A, 54E..... .....***Fridericia striata*** (Levinsen, 1884)

L 12–20 mm, S 45–65. Chaetae often faintly sigmoid, formula 4-6 – 4-2 : (4,5),6,7,(8-10) – (7),6–2. Oesophageal appendages much branched. All pharyngeal glands separate dorsally. Preclitellar nephridia 5 pairs, 6/7 – 10. Vesicles of coelomo-mucocytes often blurred; lenticytes large. Clitellum girdle-shaped. Seminal vesicle absent, sperm funnel small, length < 1/3 body diameter, 2x as long as wide. Bursal slit longitudinal. Spermathecal ectal glands rounded, ampulla 2–3x as wide as ectal duct diameter. – Widespread, common in humic forest litter layer, acidity-tolerant. Parthenogenetic species. Lit.: Christensen et al. (1989).

15* Refractile vesicles of coelomo-mucocytes separate; one or two small spermathecal ectal glands, ampullae proximally joint; Fig. 54F..... .....***Fridericia pretoriana*** Stephenson, 1930 = ***Fridericia caprensis*** Bell, 1947

L 7–20 mm, S 33–51. Chaetal formula variable, maximum number per bundle 6–8. Oesophageal appendages long (2–3 segments), with few branches. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Chylus cells in some specimens in preclitellar segments. Clitellum girdle-shaped. Seminal vesicle small, sperm funnel small, length ca 1/2 body diameter, ca 1.5x as long as wide. Spermathecal ampullae fused proximally. – Common and widespread in circum-mediterranean soils.

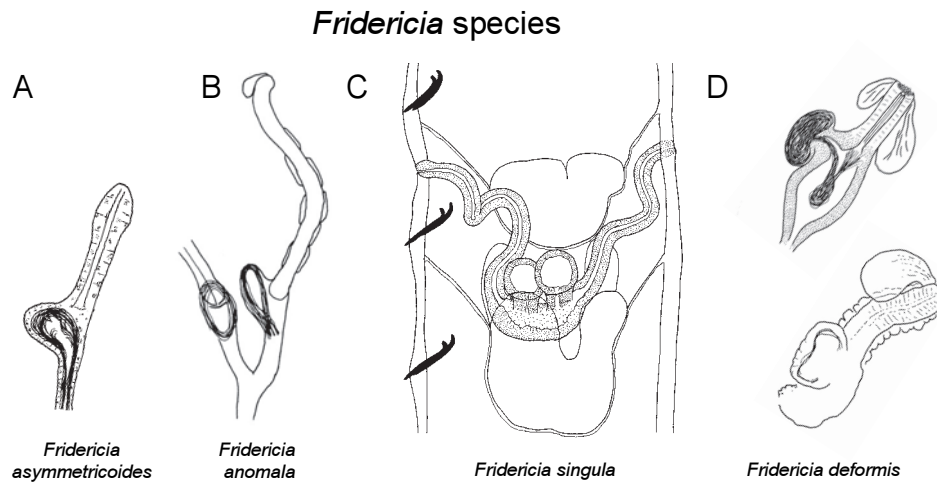

Fig. 55 ***Fridericia*** species, continued. A: ***F. asymmetricoides***, from Kasprzak (1972b, Fig. 1). B: ***F. anomala***, from Košel (1975, Fig. 1). C: ***F. singula***, from Schmelz (2003, Fig. 63A). D: ***F. deformis***, from Schmelz (2003, Fig. 31H), Chalupský (1992, Fig. 11).

C. Spermathecae each with 1 diverticulum

1 A maximum of 2 chaetae per bundle **2**

1* A maximum of 4 chaetae per bundle **3**

2 Spermatheca with large and floppy ectal gland, 1/3 as long as ectal duct; diverticulum elongate, 2/3 as long as ectal duct ..... ***Fridericia monopera*** Cognetti, 1903a

L 8 mm, S 36. Oesophageal appendages short, unbranched. Sperm funnel slightly longer than wide. – Italy. Only known from original description. Insufficiently described.

2* Spermathecal ectal gland and diverticulum much smaller, spermathecae fused proximally; Fig. 55B ..... ***Fridericia anomala*** Košel, 1975

L 6–9 mm, S 33–41. Oesophageal appendages short, unbranched. Sperm funnel 1.5–2x as long as wide. – Slovakia. Only known from original description. Insufficiently described.

3 Spermathecal ectal gland present; Fig. 55D ..... ***Fridericia deformis*** Möller, 1971

L 5–13 mm, S 32–51. Oesophageal appendages short, unbranched. Chylus cells in preclitellar segments. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Clitellum saddle-shaped. Seminal vesicle large, 1–2 segments. Sperm funnel length ca 2/3 body diameter, 2–3x as long as wide, bursal slit longitudinal. One subneural gland, in XIV. Spermathecal ectal gland large, floppy, ectal duct short and stout, diverticulum with narrow connection to ampulla; separate openings into oesophagus. – Northern and Central Europe.

3* Spermathecal ectal gland absent **4**

4 Seminal vesicle large (in 2 segments and more); spermathecae fused proximally; oesophageal appendages unbranched; Fig. 55C ..... ***Fridericia singula*** Nielsen & Christensen, 1961

L 6–8 mm, S 32–44. All pharyngeal glands dorsally united. Preclitellar nephridia 4 pairs, 6/7 – 9/10. Clitellum girdle-shaped. Seminal vesicle large (2–3 segments), sperm funnel length ca 2/3 body diameter, 1–1.7x as long as wide, bursal slit longitudinal. Spermathecal ampullae broadly fused, diverticula spherical, close to each other dorsally. – Widespread; not recorded from South-west Europe. Variants exist with uncertain taxonomic status, comp. Chalupský (1986), Schmelz (2003), Schlaghamerský & Pižl (2009).

4* Seminal vesicle small or absent; spermathecae separate proximally; oesophageal appendages long, branched; Fig. 55A..... ***Fridericia asymmetricoides*** Kasprzak, 1972b

L ca 8 mm, S 28–39. Sperm funnel 2x as long as wide. – Poland. Insufficiently described.

D. Two spermathecal diverticula, a maximum of 2 chaetae per bundle

1 Chaetae absent in anterior lateral bundles. See D9 .. ***Fridericia maculata*** Issel, 1905a

1* Chaetae present in anterior lateral bundles **2**

2 Most lateral postclitellar bundles with less than 2 chaetae; spermathecae usually fused proximally **3**

2* Most bundles (including lateral postclitellar) with 2 chaetae; spermathecae mostly separate proximally **5**

3 Preclitellar ventral chaetae stout, i.e. less than 10x as long as wide; preclitellar septa strongly thickened; chylus cells in clitellar or postclitellar segments; large ***Fridericia*** worms; Fig. 56A ..... ***Fridericia connata*** Bretscher, 1902

L 14–25 mm, S 40–70. Body wall thick, cuticle thick (2–3 µm), septa 5/6 – 10/11 strongly thickened. Oesophageal appendages short, unbranched. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Dorsal vessel from ca XX. Clitellum saddle-or girdle-shaped. Seminal vesicle variable, sperm funnel at least as long as body diameter, 3–4x as long as wide, bursal slit variable. Spermatheca with small sessile ectal gland, ampulla with warty texture, diverticula spherical or semi-spherical, ampullae fused to varying degrees, occasionally separate. – Common and widespread, species complex.

3* Preclitellar ventral chaetae not stout, more than 10x as long as wide; preclitellar septa not strongly thickened; chylus cells in preclitellar segments; small to medium-sized ***Fridericia*** worms **4**

4 Spermathecal ampulla only slightly wider than ectal duct; seminal vesicle small or absent; Fig. 56B..... ***Fridericia monochaeta*** Rota, 1995

L 6.5–11.5 mm, S 32–44. Oesophageal appendages unbranched, not coiled. All pharyngeal glands united dorsally, preclitellar septa not strongly thickened. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Chylus cells in preclitellar segments (X, XI), dorsal vessel from ca XIV. Clitellum saddle-shaped, cells in separate rows. Sperm funnel length ca 1/2 body diameter, 2–3x as long as wide, bursal slit with longitudinal and transverse components. Spermatheca with minute ectal gland, ectal duct longer than body diameter, diverticula spherical. – Italy, Germany, Spain.

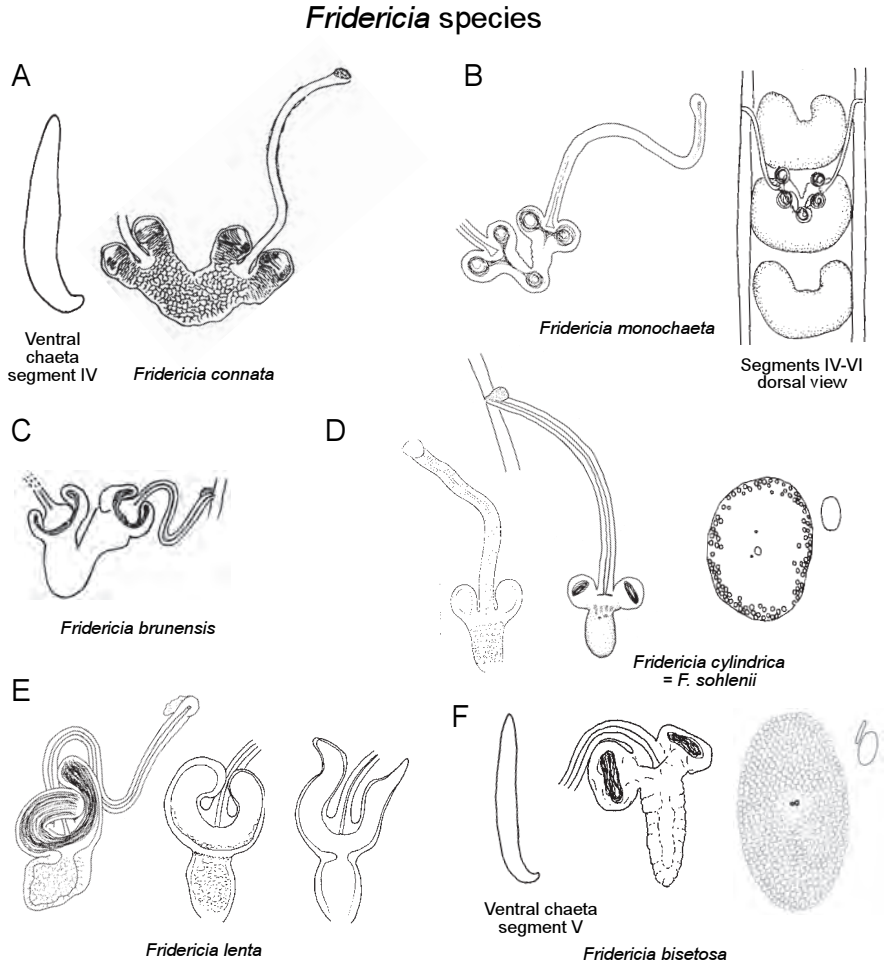

Fig. 56 ***Fridericia*** species, continued. A: ***F. connata***, from Schmelz (2003, Fig. 29K. Chalupský 1986, Fig. 1). B: ***F. monochaeta***, from Schmelz (2003, Fig. 46J,L). C: ***F. brunensis,*** from Schlaghamerský (2007, Fig. 1B). D: ***F. cylindrica***, from Rota et al. (1998, Fig. 2C, as ***F. sohlenii***), Schmelz (2003, Fig. 30F,E). E: ***F. lenta***, from Schmelz (2003, Fig. 41D,E). F: ***F. bisetosa***, from Schmelz (2003, Fig. 19A,I,J).

4* Spermathecal ampulla more than twice as wide as ectal duct; seminal vesicle mostly large; Fig. 56C.....***Fridericia brunensis*** Schlaghamerský, 2007

L 7–15 mm, S 39–51. Oesophageal appendages short, unbranched. All pharyngeal glands united dorsally, preclitellar septa not strongly thickened. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Chylus cells in preclitellar segments. Dorsal vessel from ca XV. Clitellum mostly girdle-shaped. Seminal vesicle mostly large (2–3 segments), spermatozoa conspicuously long (longer than body diameter), sperm funnel longer than body diameter, ca 4x as long as wide, bursal slit with longitudinal and transverse components. Epidermis glandularly thickened ventrally in XIII (comp Fig. 12B). Spermathecal ampullae warty, ectal gland minute, diverticula bean-shaped. – Czech Republic; Northern Germany, Hungary.

5 Coelomo-mucocytes with conspicuous vesicles at cell periphery, opaque in aggregations; Fig. 56D.....***Fridericia cylindrica*** Springett, 1971
= ***Fridericia sohlenii*** Rota et al., 1998

L 10–13 mm, S 40–56. Oesophageal appendages elongate, unbranched or with short distal branches. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Chylus cells often in preclitellar segments. Clitellum girdle-shaped. No seminal vesicle, sperm funnel length 1/2–2/3 body diameter, ca 2x as long as wide, bursal slit T-shaped. Spermathecae with small ectal gland, sessile diverticula, and granulations in ampullar epithelium. – Widespread, moist soils.

5* Coelomo-mucocytes different.....**6**

Fridericia species

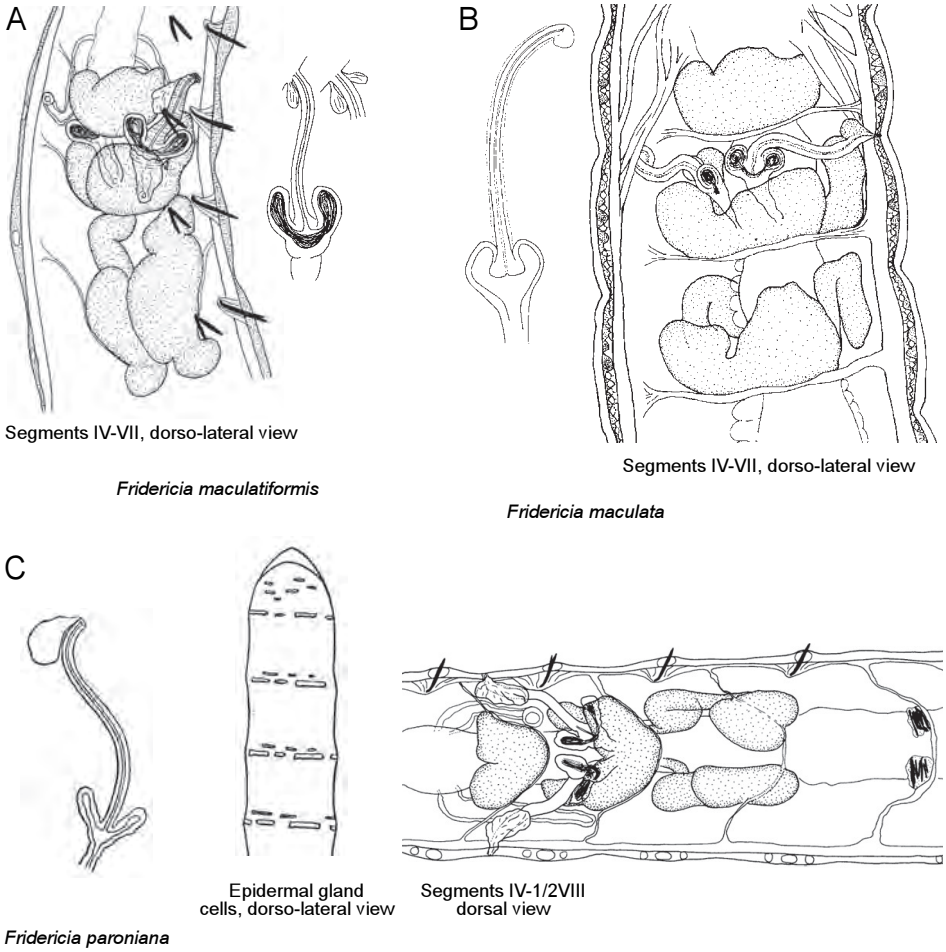

Fig. 57 ***Fridericia*** species, continued. A: ***F. maculatiformis***, from Schmelz (2003, Fig. 45A), Dózsa-Farkas (1972, Fig. 1B,C). B: ***F. maculata***, from Schmelz (2003, Fig. 44A,J). C: ***F. paroniana***, from Issel (1904, Figs 8, 1), Schmelz (2003, Fig. 53M).

6 Subneural glands present; Figs 12C, 57A ..... ***Fridericia maculatiformis*** Dózsa-Farkas, 1972

L 9–10 mm, S 34–46. Oesophageal appendages short, unbranched. Preclitellar nephridia 4 pairs, 6/7 – 9/10. Coelomo-lenticytes large. Clitellum girdle-shaped, cells in dense, regular rows. Seminal vesicle 1–1.5 segments. Sperm funnel length 1/2 body diameter, 2–2.5x as long as wide, bursal slit T-shaped, transverse component short. Subneural gland in XIII, XIV, largest in XIII. Spermathecal gland large, stalked, floppy, diverticula sac-like, longer than wide. – Northern and Central Europe.

6* Subneural glands absent..... **7**

7 More than 48 segments; clitellum not fully developed ventrally; spermathecae conspicuous..... **8**

7* Less than 48 segments; clitellum ventrally fully developed; spermathecae small, inconspicuous..... **9**

8 Spermathecal diverticula much longer than wide, diverticula and ampullar distal part forming one common sperm-filled U-shaped chamber; bursal slit T-shaped with long transverse component; Fig. 56E..... ***Fridericia lenta*** Schmelz, 2003

L 10–12 mm, S 50–68. Epidermal gland cells pale, conspicuous, several rows per segment. Oesophageal appendages short, unbranched. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Clitellum absent mid-ventrally in anterior half. Seminal vesicle large (2–3 segments), sperm funnel as long as body diameter, 2x as long as wide. Spermatheca large, wider than 1/2 body diameter, ectal gland small. – Widespread; not recorded from South-west Europe.

8* Spermathecal diverticula spherical, sperm confined to diverticula; bursal slit longitudinal; Fig. 56F ..... ***Fridericia bisetosa*** (Levinsen, 1884)

L 10–18 mm, S 48–65. Epidermal gland cells in some individuals or local populations distinctly yellowish-brownish. Oesophageal appendages elongate (into VI), mostly with few branches. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Coelomocytes numerous, mucocytes twice as long as wide, filled with distinct pale globular vesicles. Clitellum saddle-shaped, a few rows ventrally continuous behind female pores, gland cells mostly in separate rows. Seminal vesicle 1–2 segments, rarely absent. Sperm funnel 1.5–2x as long as wide, length 1/2–1/3 body diameter, bursal slits staple- or H-shaped. Spermathecal ectal gland sessile, slightly wider than ectal duct, ampulla more than 2x as long as wide, finely granulated, diverticula spherical, sessile. – Species complex. Common and widespread.

9 Spermathecal ectal gland small, sessile; clitellum elevated, cells in reticulate pattern, coelomo-lenticytes minute; cuticle most often thick; epidermal gland cells distinctly yellow-brownish; Fig. 57B..... ***Fridericia maculata*** Issel, 1905a sensu lato
= ***Timmodrilus oligoseta*** Dózsa-Farkas, 1997
= ***Fridericia renatae*** Möller, 1971

L 9–11 mm, S 29–42. Three different chaetal patterns present: (1) four chaetae throughout; (2) two chaetae throughout; (3) 2,1,0 chaetae, most lateral bundles without chaetae, often one chaeta per bundle; the latter form described as ***F. renatae*** (with dorsal pores) and ***Timmodrilus oligoseta*** (without dorsal pores). Oesophageal appendages short, unbranched or with short terminal branches. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Chylus cells often in preclitellar segments. Clitellum ventrally only with granulocytes. Seminal vesicle inconspicuous, sperm funnel small, length < 1/2 body diameter, bursal slit small, mostly T-shaped. – Widespread. Probably a species complex. The two forms with reduced chaetal pattern (No. 3) are only known from northern regions. All four forms may deserve subspecific or specific rank. Lit.: Schmelz et al. (2005).

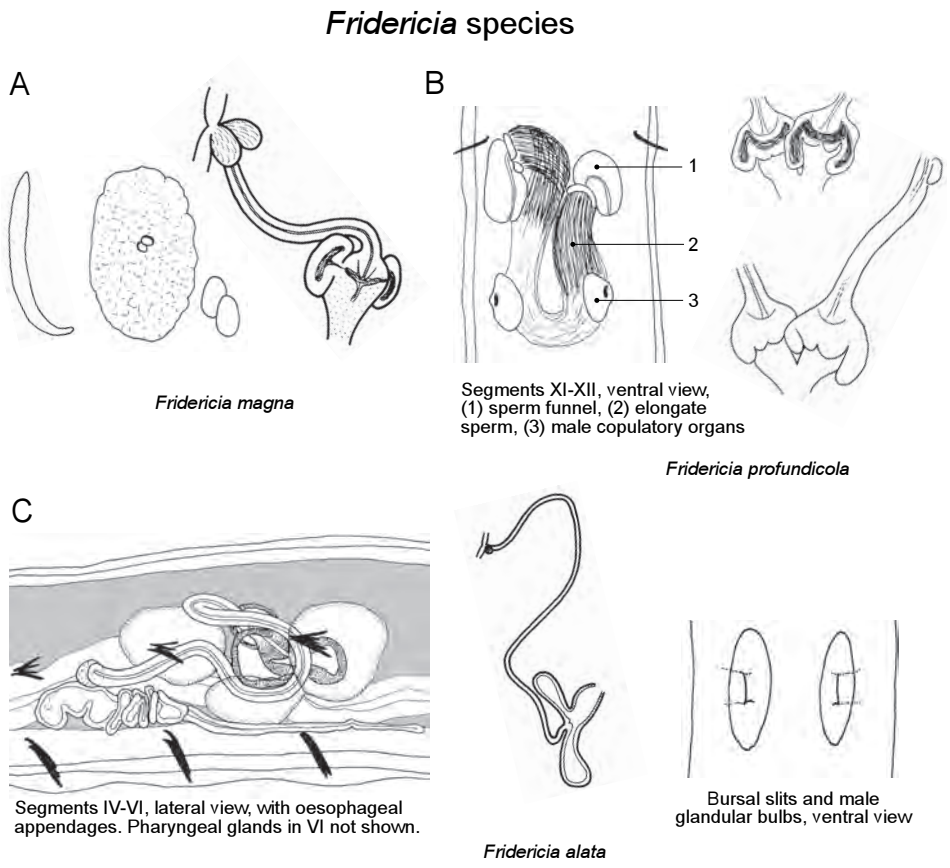

Fig. 58 ***Fridericia*** species, continued. A: ***F. magna***, from Schmelz (2003, Fig. 45F,G), Nielsen & Christensen (1959, Fig. 78). B: ***F. profundicola***, from Schmelz (2003, Fig. 59L), Dózsa-Farkas (1991a, Figs 5, 7). C: ***F. alata***, from Schmelz (2003, Fig. 11A), Nielsen & Christensen (1959, Fig. 80), Schmelz (2003, Fig. 11C).

9* Spermathecal ectal gland large, floppy; clitellum flat, cells in rows; coelomolenticytes large; cuticle always thin; epidermal gland cells pale or only with faint yellowish tinge; Fig. 57C .....***Fridericia paroniana*** Issel, 1904

L 6–12 mm, S 32–48. Oesophageal appendages short, unbranched or with 2 short terminal branches. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Clitellum ventrally with granulocytes and hyalocytes. Sperm funnel 2x as long as wide, length 1/2 body diameter, bursal slit longitudinal. – Species indistinguishable from ***F. benti*** (B4) except for the spermathecal diverticula. Common and widespread.

E. Two spermathecal diverticula, a maximum of 4 (3, 5) chaetae per bundle

1 Up to 3 chaetae per bundle; blood reddish; large specimens, > 30 mm long; Fig. 58A .....***Fridericia magna*** Friend, 1899

L 30–50 mm, S 70–96. Body surface iridescent. Chaetae mostly 2 in lateral bundles, ventrally 3 (anteriorly) or 2 (posteriorly); occasionally 4, 1, or 0. Oesophageal appendages much branched. Preclitellar nephridia 5 pairs. Clitellum girdle-shaped, cells in reticulate pattern. Seminal vesicle absent, sperm funnel ca 3.x as long as wide, length ca 1/2 body diameter, bursal slit longitudinal. Spermatheca with 2 large, often brownish ectal glands, short ectal duct and 2 sessile, sub-spherical diverticula; separate openings into oesophagus. – Widespread, wet sites.

1* Maximum number of chaetae 4 or 5: blood not reddish; specimens smaller **2**

2 Oesophageal appendages long, unbranched, coiled in IV **3**

2* Oesophageal appendages different.....**7**

3 Coelomo-mucocytes almost absent, coelomo-lenticytes very numerous, large; Fig. 58B .....***Fridericia profundicola*** Dózsa-Farkas, 1991a

L 3.5–6 mm, S 27–40. Chaetal formula 2,3,(4) – 2 : 2-4 – 2. Preclitellar nephridia absent at 6/7 (?) and 10/11. Seminal vesicle conspicuous, in XI, spermatozoa about as long as body diameter; sperm funnel 2.5–3x as long as wide, length 1/2–2/3 body diameter; bursal slit longitudinal. Spermatheca with small ectal gland, ampulla with 2 diverticula bent proximad and sometimes further knob-like protrusions; ampullae fused in proximal half. – Hungary. Forest soil, only known from type locality, at depths between 40–125 cm.

3* Coelomo-mucocytes not scarce, instantly recognised **4**

4 Spermathecae separate proximally, seminal vesicle large, occupying 2 segments or more; body length usually > 1 cm, 40 segments or more (***F. vixdiverticulata*** may also key out here, comp. G7*) **5**

4* Spermathecae fused proximally, seminal vesicle small or absent; body length usually below 1 cm, 40 segments or less **6**

5 Spermathecal ectal duct longer than body diameter, thin; male copulatory organ flattened, almost twice as long as wide; Fig. 58C ....***Fridericia alata*** Nielsen & Christensen, 1959

L 12–19 mm, S 40–67. Maximum number of chaetae per bundle 4, 5 or 6; in posteriorly body half mostly 2 chaetae per bundle. Preclitellar nephridia 5 pairs, 6/7 – 10/11, anteseptale 2/5 as long as postseptale. Coelomo-mucocytes large (40–55 µm), with pale vesicles. Clitellum girdle-shaped, cells in dense/indefinite rows. Seminal vesicle large, 2–3 segments; sperm funnel 2–3x as long as wide. Male glandular bulb elongate, large, flat, bursal slit H-shaped. Spermathecae with minute ectal gland, long and thin ectal duct, and 2 thin-walled and hollow diverticula, of same shape as ampulla. – Widespread. Not found in South-west Europe.

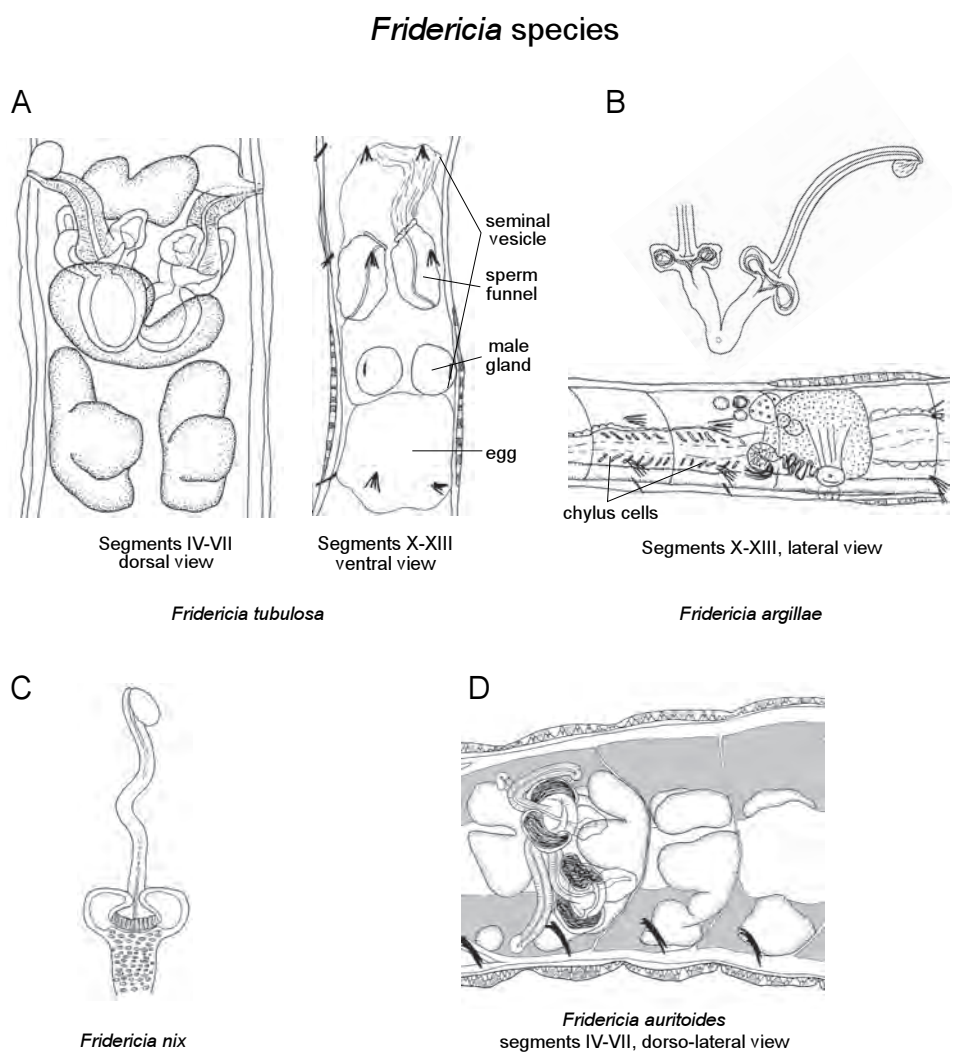

Fig. 59 ***Fridericia*** species, continued. A: ***F. tubulosa***, from Schmelz (2003, Fig. 63G,I). B: ***F. argillae***, from Schmelz (2003, Fig. 12A,C). C: ***F. nix***, from Rota (1995, Fig. 12I). D: ***F. auritoides***, from Schmelz (2003, Fig. 16A).

5* Spermathecal ectal duct shorter than body diameter, stout; male copulatory organ almost spherical, only slightly longer than wide; Fig. 59A..... .....***Fridericia tubulosa*** Dózsa-Farkas, 1972

L 12–18 mm, S 40–57. Up to 4 chaetae per bundle. Preclitellar nephridia at 6/7 – 9/10, probably absent at 10/11. Clitellum girdle-shaped, cells in dense rows. Seminal vesicle large, 3 segments, sperm funnel 3x as long as wide, length equals body diameter. Size of male glandular bulb > 1/3 body diameter; bursal slit longitudinal. Spermathecae large, with two ectal glands, short ectal duct, and 2 sessile diverticula. – Hungary, Poland.

6 Coelomocytes with refractile vesicles at periphery; male copulatory organ small, 1/3 as long as body diameter or smaller; spermathecal ectal duct slightly widened at proximal tip; Fig. 59B .....***Fridericia argillae*** Schmelz, 2003

L 5–9 mm, S 29–37. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Coelomo-lenticytes small, scarce. Chylus cells in preclitellar segments. Clitellum girdle-shaped, cells flat or absent in ventral anterior region. Seminal vesicle and sperm funnel small, bursal slit longitudinal. Spermathecae with sessile ectal gland (< 2x ectal duct width), ampullae opening separately or jointly into oesophagus. – Germany, perhaps Estonia. Indistinguishable from ***F. bulboides*** (B7*) except for the spermathecal diverticula.

6* Coelomocytes with blurred vesicles; male copulatory organ large, up to half as long as body diameter; spermathecal ectal duct canal strongly widening proximad; see G7 .....***Fridericia berninii*** Dózsa-Farkas, 1988a

Species with usually more than 2 spermathecal diverticula.

7 Pharyngeal glands with additional ventral lobes in VII **8**

7* No additional pharyngeal gland lobes in VII.....**11**

8 Coelomo-mucocytes entirely filled with numerous refractile vesicles; body colour speckled white under top light; Fig. 59C.....***Fridericia nix*** Rota, 1995

L 8.5–12 mm, S 36–45. Oesophageal appendages unbranched or with short terminal branches. Preclitellar nephridia 4 pairs, 6/7–9/10. Coelomo-mucocytes distinctly longer than wide, lenticytes almost absent. Seminal vesicle large, 2–3 segments. Sperm funnel 2–4x as long as wide, length equals body diameter. Spermatheca with small ectal gland and large ampulla, separate openings into oesophagus. – Italy, Germany. In the northern population only athecate specimens.

8* Coelomo-mucocytes without refractile vesicles; body colour whitish or yellowish....**9**

9 Segment number > 50; body wall thick; spermathecae (ampulla + diverticula) wider than dorsal pharyngeal gland lobe; Fig. 59D..... .....***Fridericia auritoides*** Schmelz, 2003

L 12–18 mm, S 55–65. Body often yellowish. Chaetal formula 3,4 – 4,3,2 : 3,4,(5) – 4,3,2; chaetae up to 70–80 µm long in caudal segments. Epidermal glands in 3 or more complete segmental rows. Oesophageal appendages elongate, unbranched or with distal branches. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Clitellum girdle-shaped, cells in dense/indefinite rows. Seminal vesicle 1–1.5 segments, spermatozoa long (ca 400 µm), sperm funnel length 1/2–2/3 body diameter, 2–3x as long as wide, shorter than spermatozoa. Bursal slit small, mainly transverse, Y-shaped. A small subneural gland present in XIII. Spermathecal ectal gland small, diverticula sessile, mostly ear–shaped; separate openings into oesophagus. – British Isles, Denmark, Italy, apparently absent in Central and Eastern Europe. Often identified as ***F. aurita*** (see below, E11).

9* Segment number < 50; body wall thin; spermathecae (ampulla + diverticula) narrower than pharyngeal gland lobe **10**

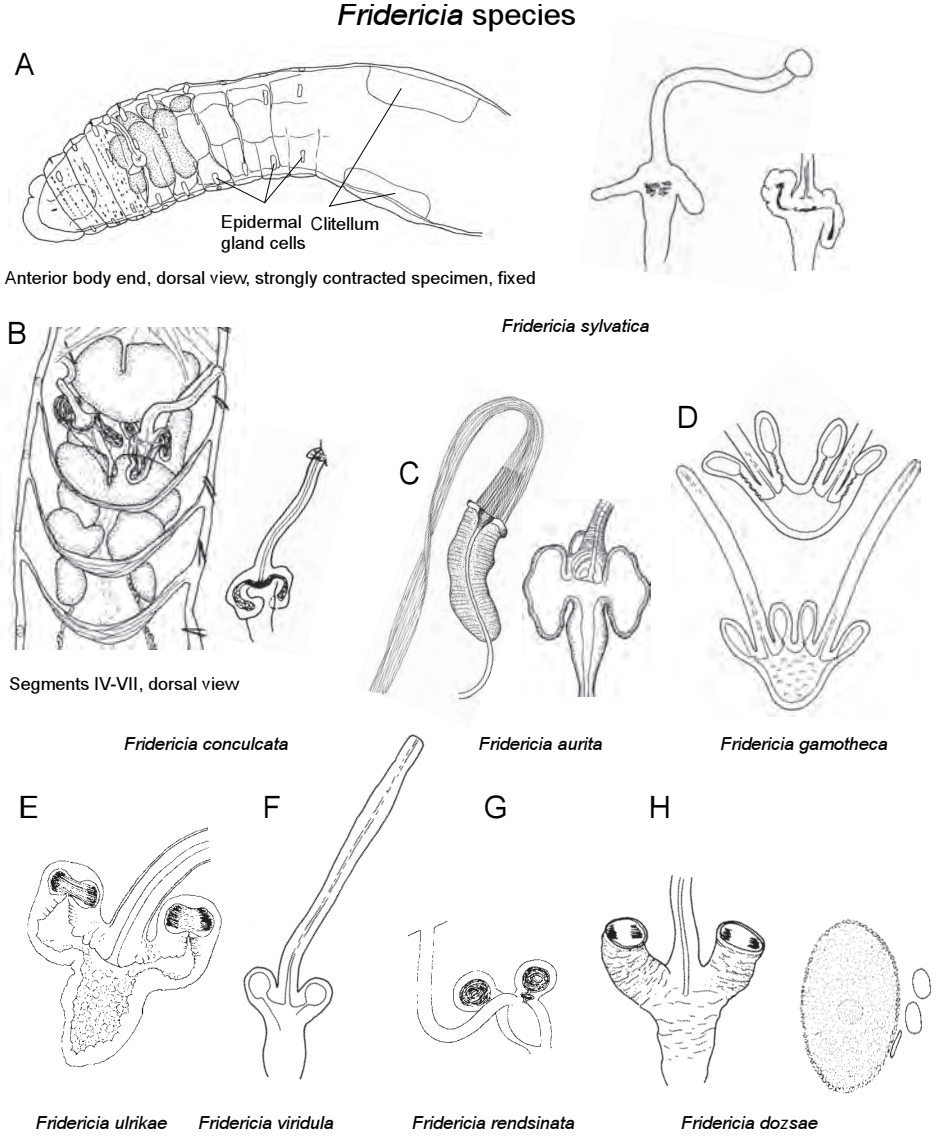

Fig. 60 ***Fridericia*** species, continued. A: ***F. sylvatica***, from Schmelz (2003, Fig. 65B,D), Chalupský (1986, Fig. 26). B: ***F. conculcata***, from Schmelz (2003, Fig. 28A), Dózsa-Farkas (1986, Fig. 1D). C: ***F. aurita***, from Issel (1905a, Pl. 14 Figs 33, 36). D: ***F. gamotheca***, from. Rota (1995, Fig. 10A,C). E: ***F. ulrikae***, from Schmelz (2003, Fig. 58I). F: ***F. viridula***, from Rota (1995, Fig. 10G). G: ***F. rendsinata***, from Dózsa-Farkas (1972, Fig. 3B). H: ***F. dozsae***, from Schmelz (2003, Fig. 32J,M).

10 Lateral chaetae present in most or all postclitellar bundles; subneural glands absent; Fig. 60A .....***Fridericia sylvatica*** Healy, 1979a

L 6–12 mm, S 35–48. Slow movements. Small prostomium. Up to 4 chaetae per bundle. Oesophageal appendages short, unbranched, rarely with short distal bifurcation. Preclitellar septa not strongly thickened. Preclitellar nephridia 4 pairs, 6/7 – 9/10. Clitellum only laterally developed, absent ventrally and dorsally. Seminal vesicle absent or small, sperm funnel small, 1/3–1/2 body diameter, 2.5–3x as long as wide. Spermathecal ectal gland medium-sized, ampulla with a few granulations in distal part, diverticula mostly finger-shaped, occasionally stump-like; separate openings into oesophagus. – Common and widespread.

10* No lateral chaetae in mid-body region; small subneural glands present in XIII and XIV; Fig. 60B.....***Fridericia conculcata*** Dózsa-Farkas, 1986

L 10–20 mm, S 39–45. Chaetal formula 3,4 – 0,2,1 : 2,(3),4 – 2,(1). Oesophageal appendages short, unbranched, rarely with short distal bifurcation. Preclitellar septa 4/5 – 8/9 strongly thickened. Preclitellar nephridia 4 pairs, 6/7 – 9/10. Clitellar gland cells in rows, further details unknown. Seminal vesicle large, 2 segments. Sperm funnel length 1/2 – 2/3 body diameter 1.5–2x as long as wide. Spermathecal diverticula finger-like. – Hungary, Czech Republic, 3 records. Lit.: Schlaghamerský & Pižl (2009).

11 Spermatozoa 1 mm long, i.e. ca twice as long as body diameter in XI; Fig. 60C..... .....***Fridericia aurita*** Issel, 1905a

L 12–18 mm, S 40–65. Four chaetae in anterior bundles, up to 50 µm long. Oesophageal appendages elongate, two distal branches. Seminal vesicle 1–1.5 segments, spermatozoa very long, sperm funnel ca 3x as long as wide, as long as body diameter or longer. Male glandular bulb small. Spermathecae without (?) ectal gland, diverticula sessile, often ear-shaped. – Italian Alps; only known from original description. Subsequent records doubtful (Schmelz 2003), see E9.

11* Spermatozoa shorter.....**12**

12 Spermathecal ectal glands absent **13**

12* Spermathecae ectal glands present **17**

13 Spermathecal ampullae of both sides fused into one common chamber; Fig. 60D..... .....***Fridericia gamotheca*** Issel, 1905c

L 10–15 mm, S 40–50. Maximum number of chaetae 4 or 5, rarely 6. Oesophageal appendages unbranched or with few distal branches. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Clitellum girdle-shaped, cells in dense/indefinite rows. Seminal vesicle small or absent in XI. Sperm funnel 2–3x as long as wide. Bursal slit L-shaped. Spermathecal diverticula oval, stalked. – Italy, Spain.

13* Spermathecal ampullae separate from each other **14**

14 Clitellum saddle-shaped, i.e. not developed ventrally; Fig. 60E..... .....***Fridericia ulrikae*** Rota & Healy, 1999

L 13–18 mm, S 50–55. Maximum number of chaetae 4 per bundle. Oesophageal appendages short, unbranched, or with short distal bifurcation. Preclitellar nephridia 4 pairs, 6/7 – 9/10. Clitellum saddle-shaped, cells in dense/indefinite rows. Seminal vesicle large, 1–2 segments. Sperm funnel ca 3x as long as wide, length at least equalling body diameter. Male glandular bulb large, twice as long as wide, bursal slit longitudinal. Epidermis may be thickened mid-ventrally in XIII–XV (comp. Fig. 12B). Spermathecal ectal gland absent or very small; ampullae with distinct lumen, diverticula stalked, with ciliated subchamber and (hemi-)spherical sperm-containing chamber. – Northern and Central Europe.

14* Clitellum girdle-shaped, i.e. developed ventrally **15**

15 Spermathecae simple and small, diverticula almost sessile, without ciliated subchamber, coelomo-mucocytes with greenish tint; Fig. 60F ..... ***Fridericia viridula*** Issel, 1904

L 15–25 mm, S 49–61. Maximum number of chaetae per bundle 5 or 6. Oesophageal appendages long (IV–VI), with few branches of different length. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Coelomo-mucocytes up to 50 µm long. Seminal vesicle 1 segment, sperm funnel small, 2–3x as long as wide, length 1/2 body diameter or less. Bursal slit staple-shaped. Spermathecal ectal duct often slightly thickened in distal half. – Ireland, The Netherlands, Italy.

15* Spermathecal diverticula distinctly stalked, with spherical sperm-containing chamber and a subchamber, connecting with ampullar lumen; coelomocytes colourless **16**

16 Coelomo-mucocytes with large refractile vesicles; Fig. 60G ..... ***Fridericia rendsinata*** Dózsa-Farkas, 1972

L 10–15 mm, S 49–63. Chaetae 2-4 – 4-2 : 4 – 4-2. Oesophageal appendages with few short distal branches. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Coelomo-mucocytes small (20–30 µm), refractile vesicles concentrated at cell periphery. Clitellum girdle-shaped, cells in dense rows. Seminal vesicle large, 3 segments. Sperm funnel 3–4x as long as wide, slightly shorter than body diameter. Bursal slit H-shaped. Spermathecal diverticula stalked, with ciliated subchamber and (hemi-)spherical sperm-containing chamber. – Hungary, Austria.

16* Coelomo-mucocytes without refractile vesicles; Fig. 60H ..... ***Fridericia dozsae*** Schmelz, 2003

L 16–21 mm, S 59–69. A maximum of 4, 5, or 6 chaetae per bundle. Body wall thick. Oesophageal appendages branched. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Clitellum girdle-shaped, thick (i.e. cells at least 2x as high as wide), cells in reticulate pattern. Seminal vesicle 2 segments, sperm funnel length 2/3 body diameter, 2x as long as wide, collar distinctly smaller than funnel body. Bursal slit mainly longitudinal. Spermathecal ampulla and diverticula with granulation, diverticula stalked, with ciliated subchamber and (hemi-)spherical sperm-containing chamber, stalks often longer than distal chamber. – Ireland, Northern Germany.

17 (12*) Chylus cells in preclitellar segments (IX, X, XI) **18**

17* Chylus cells not in preclitellar segments or indistinguishable **20**

18 Spermathecae separate, diverticula sessile; four or three pairs of preclitellar nephiridia **19**

18* Spermathecae fused, diverticula stalked; five pairs of preclitellar nephridia; Fig. 61B ..... ***Fridericia waldenstroemi*** Rota & Healy, 1999

L 9–15 mm, S 40–54. Up to 4 chaetae per bundle. Oesophageal appendages unbranched, short. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Coelomocytes with several lines of refractile vesicles at periphery. Chylus cells from VIII or IX, 2 segments. Clitellum flat, girdle-shaped in posterior half, saddle-shaped in anterior half, cells in dense rows. Seminal vesicle absent, sperm funnel 2.5–4x as long as wide, almost as long as body diameter. Bursal slit L-shaped. A small subneural gland present in XIV. Spermathecal ectal gland sessile or with short stalk, diverticula oval or spherical, with long stalks; ampullae broadly fused proximally, forming one common globular or U-shaped chamber. – Widespread.

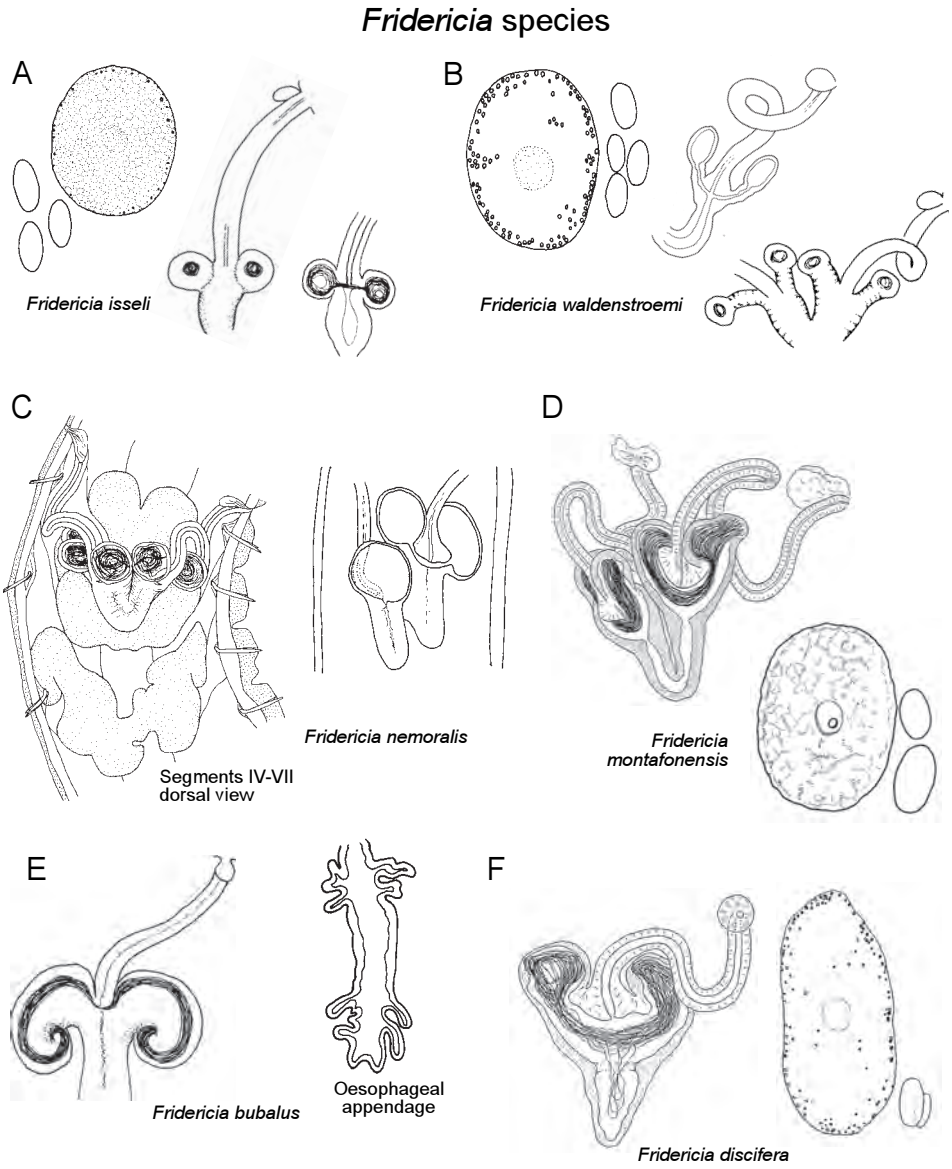

Fig. 61 ***Fridericia*** species, continued. A: ***F. isseli***, from Schmelz (2003, Fig. 39I), Dózsa-Farkas (1989, Fig. 5B), Schmelz (2003, Fig. 39M), B: ***F. waldenstroemi***, from Schmelz (2003, Fig. 68D), Rota & Healy (1999, Fig. 6C), Dózsa-Farkas (1989, Fig. 2G). C: ***F. nemoralis***, from Schmelz (2003, Fig. 48A,F). D: ***F. montafonensis***, from Schmelz (1998, Figs 5, 6). E: ***F. bubalus***, from Sesma & Dózsa-Farkas (1993, Figs 16, 17). F: ***F. discifera***, from Schmelz (1999, Figs 3B, 4C).

19 Four pairs of preclitellar nephridia, 6/7 – 9/10, clitellum saddle-shaped, male copulatory organ tripartite with larger central bulb and small anterior and posterior extra bulb; Fig. 61A .....***Fridericia isseli*** Rota, 1994

L 4–8.5 mm, S 31–37. A maximum of 4 chaetae per bundle (5 in Turkish populations). Oesophageal appendages unbranched, short. Chylus cell canals branched, palmate. Coelomo-mucocytes with one line of small refractile vesicles at periphery, lenticytes small. Clitellum saddle-shaped, cells in separate rows. Seminal vesicle absent, sperm funnel 2–3x as long as wide, length 1/2–2/3x body diameter. Bursal slit longitudinal. Spermathecal ectal gland small, sessile, ampulla little wider than ectal duct, diverticula sessile, spherical, small. – Common and widespread. Originally described from Turkey.

19* Three pairs of preclitellar nephridia, 7/8 to 9/10, clitellum girdle-shaped, male copulatory organ simple, without extra-bulbs ....***Fridericia lacii*** Dózsa-Farkas, 2009

L 4–7 mm (fix), S 30–36. A maximum of 4 chaetae per bundle. Oesophageal appendages unbranched, short. Coelomo-mucocytes pale, without refractile vesicles, lenticytes small. Clitellum in ca 17 dense rows, hyalocytes much larger than granulocytes. Seminal vesicle absent, sperm funnel ca 2x as long as wide, length 1/2–2/3 body diameter, bursal slits longitudinal. Spermathecae as in ***F. isseli***, but ectal gland stalked. – Widespread in Hungary, meadows and oak-hornbeam woods. Only known from original description.

20 Spermathecae proximally fused.....**21**

20* Spermathecae proximally separate, attached separately to oesophagus.....**22**

21 One small subneural gland in XIII; clitellum flat, with cells in separate rows; yellow epidermal gland cells present; Fig. 61C ....***Fridericia nemoralis*** Nurminen, 1970b

L 9–12 mm, S 40–56. Up to 4 chaetae per bundle. Oesophageal appendages exceptionally thin, extending into VII, with few, elongate branches. All pharyngeal glands with dorsal connection. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Clitellum flat, saddle-shaped, with some cells present mid-ventrally, cells in separate rows. Seminal vesicle large, 2–3 segments, sperm funnel almost as long as body diameter, 2.5x–3x as long as wide. Bursal slit T-shaped. Spermathecal ectal glands variable, ectal duct thin, as long as body diameter, ampullae mostly fused, rarely separate, diverticula sessile, globular to kidney-shaped. – Northern and Central Europe.

21* Subneural glands in XIII and XIV, largest in XIV; clitellum elevated, cells in indistinct rows or reticulate; epidermal gland cells pale; Fig. 61D..... .....***Fridericia montafonensis*** Schmelz, 1998

L 10–14 mm, S 49–71. Maximum number of chaetae per bundle 5 or 6, rarely 4. Oesophageal appendage with few short branches. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Clitellum girdle-shaped. Seminal vesicle 1–2 segments. Sperm funnel length 1/2 body diameter, ca 1.5x as long as wide. Bursal slit L-shaped. Spermathecae with large, sessile ectal gland, diverticula of varying shape, forming a common U-shaped sperm-containing chamber together with distal part of ampulla; proximal parts of ampullae fused. – Austria. Only known from original description.

22 Spermathecal diverticula elongate, twisted buffalo-horn-like towards ectal duct; clitellum absent ventrally except between bursal slits; Fig. 61E ..... ***Fridericia bubalus*** Sesma & Dózsa-Farkas, 1993

L 11–19 mm, S 43–60. Maximum number of chaetae 4 per bundle. Oesophageal appendages with wide lumen and many short branches. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Clitellar gland cells in reticulate pattern. Seminal vesicle large, 2 segments. Sperm funnel small, 1.5–2.5x as long as wide, length 1/3 to 1/4 of body diameter. Spermathecal ectal gland not wider than ectal duct diameter. – Spain. Only known from type locality.

22* Spermathecae and pattern of clitellar gland cells different **23**

23 Subneural glands present in XIII **24**

23* Subneural glands absent **26**

24 Subneural gland in XIII only, small, yellow epidermal gland cells present; spermathecae usually fused in this species, see E21 ..... ***Fridericia nemoralis*** Nurminen, 1970b

24* Subneural glands present in XIII and XIV **25**

25 Clitellum absent ventrally; bursal slit longitudinal; coelomo-mucocytes numerous, pale, with blurred vesicles; extremely rare specimens of a usually athecate species, see A2* ..... ***Fridericia christeri*** Rota & Healy, 1999

25* Clitellum present ventrally; bursal slit T- or Y-shaped; coelomo-mucocytes not numerous (i.e. not filling out coelom), with minute refractile granules lining periphery; Fig. 61F ..... ***Fridericia discifera*** Healy, 1975

L 9–13 mm, S 37–46. Maximum number of chaetae 4 per bundle. Oesophageal appendages short, unbranched. Preclitellar nephridia 4 pairs, 6/7 – 9/10. Seminal vesicle large, 2–3 segments, sperm funnel 1.5–2.5x as long as wide, length 1/2–2/3x body diameter. Bursal slit T- or Y-shaped. Spermathecal ectal gland medium-sized, ampulla + diverticula large, wider than 1/2 body diameter. – Ireland, Germany, Austria. Lit.: Schmelz (1999).

26 Clitellum girdle-shaped, i.e. present ventrally **27**

26* Clitellum saddle-shaped, i.e. absent ventrally **29**

27 Epidermal gland cells distinctly yellowish-brownish; clitellar gland cells arranged in reticulate pattern dorsally, ventrally only granulocytes, see D9 ..... ***Fridericia maculata*** Issel, 1905a

27* Epidermal gland cells pale; clitellar gland cells dorsally in rows (rows may be indefinite), not reticulate, ventrally granulocytes and hyalocytes **28**

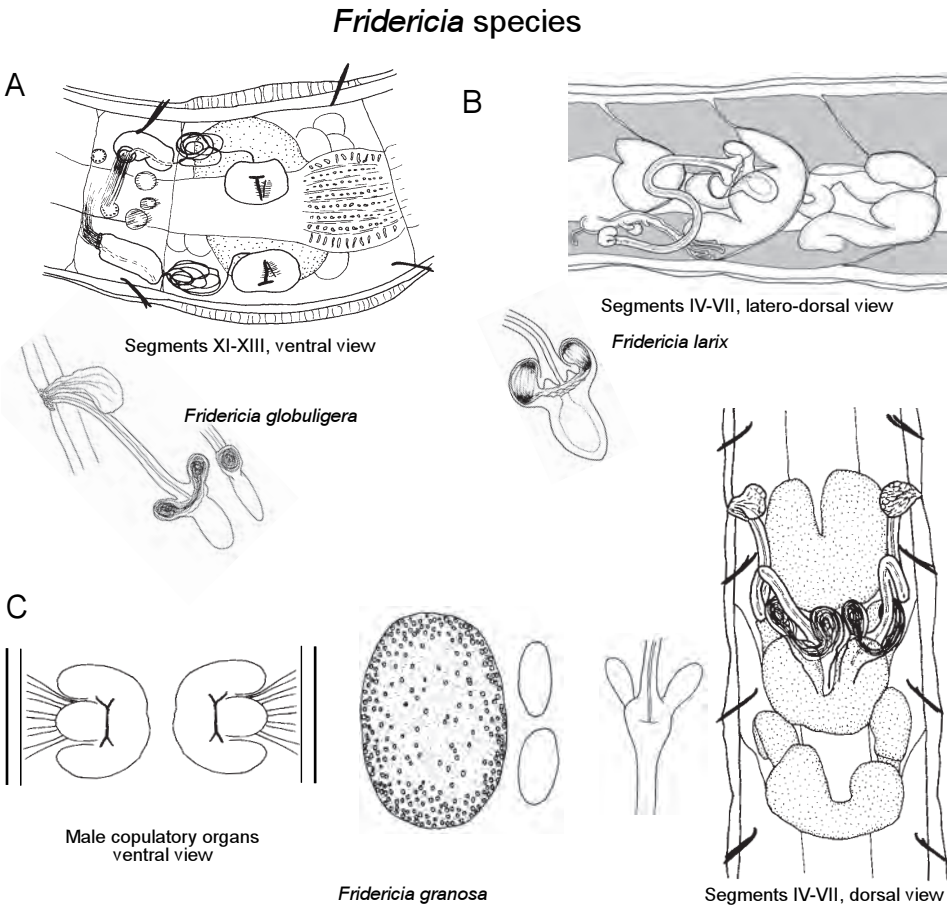

Fig. 62 ***Fridericia*** species, continued. A: ***F. globuligera***, from Schmelz (2003, Fig. 36B,C). B: ***F. larix***, from Schmelz & Collado (2005, Fig. 1C,I). C: ***F. granosa***, from Schmelz (2003, Fig. 37F,B,D,E).

28 Usually 5 or 6 chaetae in some ventral preclitellar bundles; 4 chaetae present in several lateral segments from XIII on; Fig. 62A.....***Fridericia globuligera*** Rota, 1995

L 8–15 mm, S 40–52. Body wall thick. Oesophageal appendages unbranched or with few branches. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Clitellar gland cells in dense rows. Seminal vesicle absent, sperm funnel small, 1/2 as long as body diameter, 2–2.5x as long as wide. Bursal slit T-shaped. Spermathecal ectal gland stalked, floppy, large (up to 60 µm), or two smaller glands present of different size; inner surface of spermathecal ampulla not wavy. – Ireland, Austria, Italy.

28* Never more than 4 chaetae per bundle; 2 chaetae of unequal size present in most lateral segments from XIII on; Figs 50, 62B ..... ***Fridericia larix*** Schmelz & Collado, 2005a

L 12–15 mm, S 43–48. Maximum number of chaetae 4 per bundle. Oesophageal appendages short, with few branches. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Clitellar gland cells in separate/dense rows. Sperm funnel length 1/3–1/2 body diameter, 1.5x as long as wide. Bursal slit mainly transverse. Spermathecal ectal gland sessile, 1.5–2x as wide as ectal duct, inner surface of spermathecal ampulla wavy in distal part. – Ireland, Italy (?). Only known from original description.

29 Coelomocytes with numerous refractile vesicles; spermathecal ectal gland 2x as wide as ectal duct, diverticula without ciliated subchamber; Fig. 62C ..... ***Fridericia granosa*** Schmelz, 2003

L 7–10 mm, S 32–43. Maximum number of chaetae 4 per bundle. Oesophageal appendages short, unbranched. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Refractile vesicles of coelomo-mucocytes concentrating at cell periphery but also present inside. Clitellar gland cells in ca 25 separate rows. Seminal vesicle large, 2–3 segments. Sperm funnel as long as body diameter, ca 4x as long as wide. Bursal slit H- or staple-shaped. Spermathecal ectal duct longer than body diameter; diverticula and ampulla forming a common U-shaped sperm-containing chamber. – Northern Germany, Crete.

29* Coelomocytes without refractile vesicles; spermathecal ectal gland minute, diverticula with ciliated subchamber; see E14 ..... ***Fridericia ulrikae*** Rota & Healy, 1999

F. Two spermathecal diverticula, a maximum of more than 5 chaetae per bundle

1 Spermathecal ectal gland absent **2**

1* Spermathecal ectal gland present **7**

2 Segment number 70 and more; oesophageal appendages short (in V only), unbranched ..... ***Fridericia stephensoni*** Moszyński, 1933

L 17–30 mm or more, S 70–80. Body colour yellow, pygidium with a dark-brown ring; up to 6 chaetae per bundle. Oesophageal appendages short, unbranched. Chylus cells in preclitellar segments. Clitellar gland cells in reticulate pattern (?). Sperm funnel 2x as long as wide. Spermathecae large, diameter of ampulla + diverticula > 1/2 body diameter, diverticula small, sessile; separate openings into oesophagus. – Poland, France (?). Insufficiently known species.

2* Segment number below 70; oesophageal appendages different **3**

3 Subneural glands present; chylus cells in preclitellar segments; spermathecal diverticula sessile ..... ***Fridericia baskini*** Černosvitov, 1937c

L 8–10 mm, S 37–41. Oesophageal appendages branched. Chylus cells in preclitellar and clitellar segments. Clitellum girdle-shaped. Sperm funnel up to 1.5x as long as wide. Male glandular bulb almost spherical. Spermathecal ectal gland absent or very small; ampullae broadly fused. – Ukraine. Only known from original description, insufficiently known species.

3* Subneural glands absent; chylus cells not in preclitellar segments; spermathecal diverticula stalked **4**

4 Spermathecal diverticula oriented towards ampulla (proximad) or perpendicular to spermathecal longitudinal axis (radiad); epidermis glandularly thickened ventrally in XIV (comp. Fig. 12B); male copulatory organ twice as long as wide, often large accessory sexual glands present near spermathecal ectal pore or male bursal slit; species with usually more than 2 diverticula, see H5..... .....***Fridericia galba*** (Hoffmeister, 1843)

4* Spermathecal diverticula oriented towards ectal duct (distad); male copulatory organ shorter; no ventral thickening of epidermis in XIV; no accessory glands near spermathecal ectal pore.....**5**

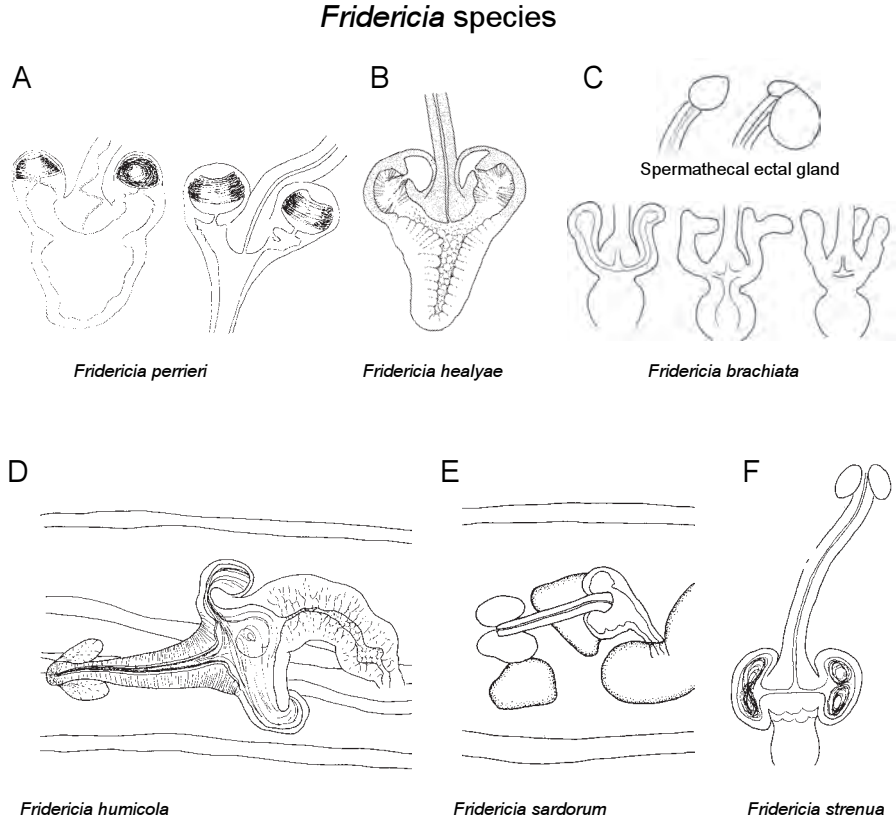

Fig. 63 ***Fridericia*** species, continued. A: ***F. perrieri***, from Schmelz (2003, Fig. 58A,B). B: ***F. healyae***, from Schmelz (2003, Fig. 38A). C: ***F. brachiata***, from Rota (1994, Fig. 4H,N,C,D,G). D: ***F. humicola***, from Schmelz (2003, Fig. 39A). E: ***F. sardorum***, from Schmelz (2003. Fig. 60I). F: ***F. strenua***, from Rota (1995, Fig. 13A).

5 Inner surface of spermathecal ampulla smooth, not granular, not elevated; ampullar lumen well-distinguished, ectal duct canal narrow, often describing spiral course before entering ampulla; active specimens; Fig. 63A ....***Fridericia perrieri*** (Vejdovský, 1878)

L 12–20 mm, diameter 0.3–0.5 mm, S 45–67. Chaetal formula 4-6 – 6-2 : 4-(7,)8 – 6-2. Oesophageal appendages branched or unbranched. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Clitellum girdle-shaped, cells in indefinite rows or in reticulate pattern. Seminal vesicle variable, 1–2 segments. Sperm funnel 2–3x as long as wide, size variable. Bursal slit longitudinal, staple-shaped. Spermathecal ectal duct long and narrow, canal with spiral loops before entering ampulla in some specimens, canal straight as usual in others (comp. Fig. 63A left and right); diverticula stalked, with ciliated subchamber; sperm-containing chamber (hemi-)spherical, small; ampulla usually with distinct and empty lumen. – Widespread, common at wet sites, species complex. Forms intermediate between ***F. perrieri*** and ***F. ulrikae*** occur (comp. E14).

5* Inner surface of spermathecal ampulla granular, uneven or elevated, not smooth; ampullar lumen usually not well-distinguished; ectal duct canal always straight proximally; slow body movements.....**6**

6 Up to 8 chaetae per bundle; spermathecal diverticula with short stalks, always strongly bent towards ectal duct; coelomocytes with large, blurred vesicles; seminal vesicle small or absent; Fig. 63B.....***Fridericia healyae*** Schmelz, 2003

L 15–20 mm, diameter 0.4–0.7 mm, S 51–63. Oesophageal appendages with 4–5 branches in distal half. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Clitellum thick, girdle-shaped, cells in reticulate pattern. Seminal vesicle absent. Sperm funnel as long as body diameter, ca 3x as long as wide. Bursal slit longitudinal. Spermathecal diverticula stalked, with a characteristic double-bend, first outwards, then inwards towards ectal duct; ciliated subchamber present; ampullar inner surface papillate. – Wet sites. Western Europe.

6* Up to 6 chaetae per bundle, spermathecal diverticula with elongate stalk, oriented ectad, more or less parallel to ectal duct; coelomocytes with fine indistinct vesicles, often denser and darker at periphery; seminal vesicle usually present over 2 segments; see E16*. .....***Fridericia dozsae*** Schmelz, 2003

7 (1*) Spermathecal diverticula elongate, 2–3x as long as wide, oriented ectad, 1 or 2 sessile spermathecal ectal glands, together 1.5–3x as wide as ectal duct, spermathecal ampullae separate; Fig. 63C .....***Fridericia brachiata*** Rota, 1994

L 10–22 mm, S 47–63. Chaetal formula 2-4 – 4-2 : 3-6 – 4-2. Oesophageal appendages long, often reaching 6/7, unbranched or with short terminal branches. Clitellar gland cells in rows. Sperm funnel almost 2x as long as wide, tapering at both ends. Two or three spermathecal diverticula. – Turkey. Only known from original description.

7* Character combination different **8**

8 Subneural glands present **9**

8* Subneural glands absent.....**11**

9 Spermathecal ectal duct not longer than ampulla, cone-shaped, much widening proximally, canal also much widened; separate openings into oesophagus; Fig. 63D ..... ***Fridericia humicola*** Bretscher, 1900

L 11–12 mm, S 43–50. Up to 6 or 7 chaetae per bundle. Oesophageal appendages unbranched, not coiled. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Clitellum girdle-shaped, cells in dense/indefinite rows. Seminal vesicle large, 3 segments. Sperm funnel variable. Bursal slit Y-shaped. Subneural glands in XIII–XV, largest in XIII, here more than 2x as wide as nerve cord. Spermathecae with 2–3 ectal glands, separate openings into oesophagus. – Swiss Alps. Only known from type locality.

9* Spermathecal ectal duct longer than ampulla, not cone-shaped, ampullae fused proximally, common openings into oesophagus **10**

10 Chylus cells in postclitellar segments; see E21* ..... ***Fridericia montafonensis*** Schmelz, 1998

10* Chylus cells in clitellar and preclitellar segments; see F3 ..... ***Fridericia baskini*** Černosvitov, 1937c

11 Each spermatheca with two large ectal glands **12**

11* One ectal gland per spermatheca, or two of different sizes, one small **13**

12 Spermathecal ampulla and diverticula forming one large heart-shaped lumen, ampulla thin-walled; epidermal gland cells pale; Fig. 63E ..... ***Fridericia sardorum*** Cognetti, 1901

L 15–25 mm, S 50–65. Maximum number of chaetae 6–9. Oesophageal appendages much branched. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Clitellum girdle-shaped, cells in reticulate pattern. Seminal vesicle small (sperm only dorsally in XI) or absent. Sperm funnel small, length 1/3 body diameter, ca 1.5x as long as wide. Spermathecae with separate openings into oesophagus. – Italy.

12* Lumina of spermathecal ampulla and diverticula separated by a constriction, not forming one large heart-shaped lumen, ampulla thick-walled; yellow epidermal gland cells present; Fig. 63F ..... ***Fridericia strenua*** Rota, 1995

L 16–22 mm, S 55–82. Oesophageal appendages much branched. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Clitellum girdle-shaped, cells in reticulate pattern. Seminal vesicle large, 3 segments. Sperm funnel 2–3.5x as long as wide, length about equalling body diameter. Spermathecal diverticula ear-shaped, separate openings into oesophagus. – Italy. Only known from original description.

13 Seminal vesicle very small or absent, oesophageal appendages branched; see E28 ..... ***Fridericia globuligera*** Rota, 1995

13* Seminal vesicle large, occupying at least 2 segments, oesophageal appendages, long, coiled, unbranched; see E5 ..... ***Fridericia alata*** Nielsen & Christensen, 1959

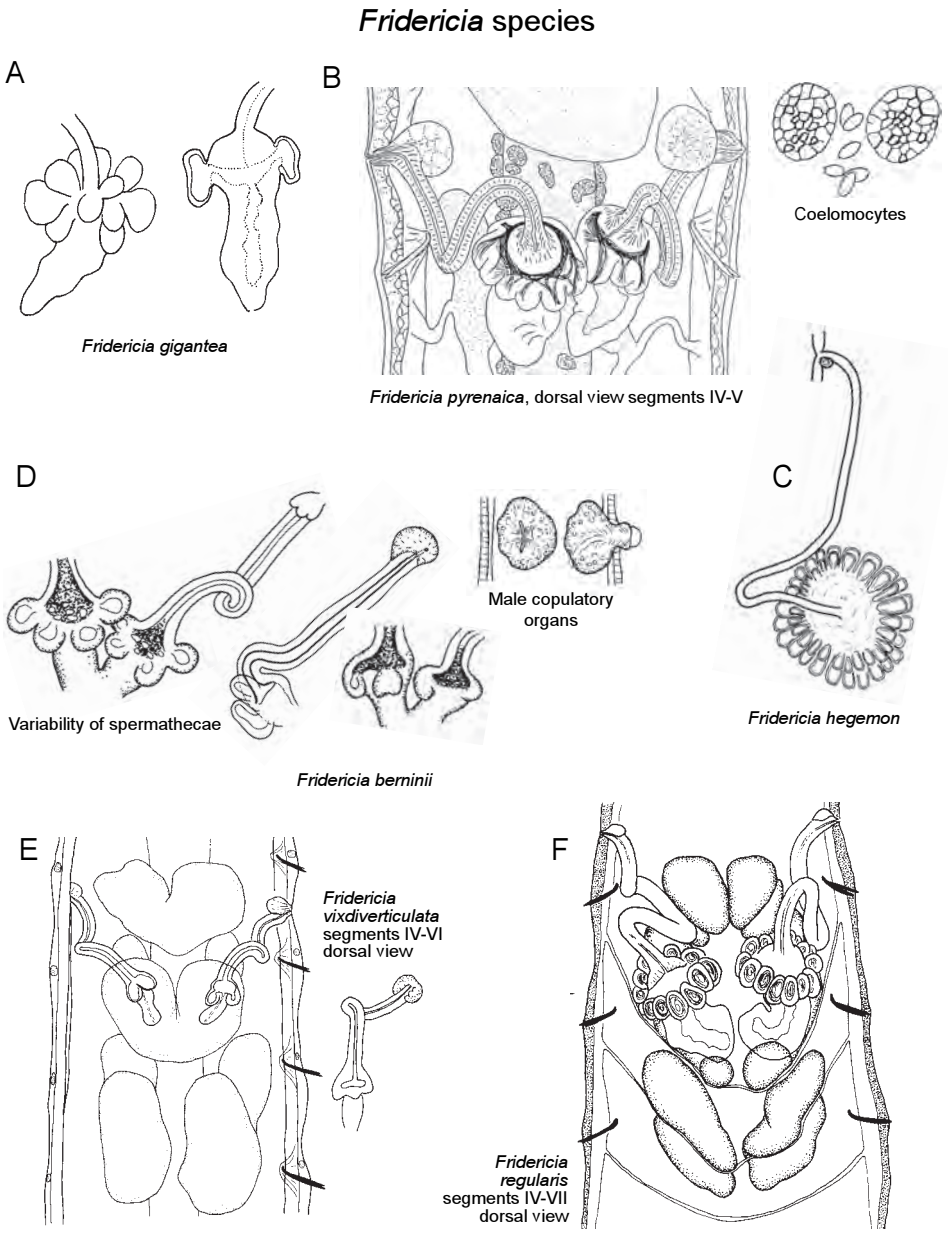

Fig. 64 ***Fridericia*** species, continued. A: ***F. gigantea***, from Dequal (1912, Figs 4, 5). B: ***F. pyrenaica***, from Schmelz et al. (1999a, Fig. 1A,E). C: ***F. hegemon***, from Nielsen & Christensen (1959, Fig. 87). D: ***F. berninii***, from Dózsa-Farkas (1988a, Fig. 1F), Schmelz (2003, Fig. 17J), Dózsa-Farkas (1988a, Fig. 1G,I). E: ***F. vixdiverticulata***, from Schmelz (2003, Fig. 68A), Sesma & Dózsa-Farkas (1993, Fig. 32). F: ***F. regularis***, from Schmelz (2003, Fig. 61A).

G. Spermatheca each with more than 2 diverticula, not more than 5 chaetae per bundle, often less

1 Segment number 90 and more; Fig. 64A .....***Fridericia gigantea*** Dequal, 1912

L 30–45 mm, S 90–95. Chaetae slightly sigmoid,maximum number 5 per bundle. Brain as wide as long, incised posteriorly. Oesophageal appendages with elongate branches. Spermatheca with small ectal gland, ampulla with 6–10 sub-spherical and thin-walled diverticula. – Italy. Only known from original description.

1* Segment number below 90 .....**2**

2 Body colour speckled white, caused by aggregations of numerous strongly refractile coelomo-mucocytes, clitellum absent dorsally; Fig. 64B..... .....***Fridericia pyrenaica*** Giani, 1979

L 11–13 mm, S 38–44. Up to 4 chaetae per bundle. Slow-moving. Thick cuticle. Oesophageal appendages short, unbranched. Preclitellar nephridia 4 pairs, 6/7 – 9/10. Coelomo-mucocytes numerous, refractile by large and coarse granula arranged in mosaic-like fashion. Chylus cells in preclitellar segments, difficult to see in living specimens. Clitellum only laterally developed, one transverse row of cells mid-ventrally near female pores. Seminal vesicle in 1–2 segments, sperm funnel little longer than wide, almost as long as body diameter. Bursal slit L- or H-shaped. Spermatheca with large ectal gland, ampulla with 9–12 small, sessile, spherical diverticula, separate openings into oesophagus. – Only recorded from the French Pyrenees. Lit.: Schmelz et al. (1999a).

2* Animals not intensely white, clitellum present dorsally.....**3**

3 Three to five spermathecal diverticula of varying shape, small, sessile, or larger, longer than wide, oriented ectad; epidermis glandularly thickened mid-ventrally in XIII–XV (comp. Fig. 12B); see H3..... .....***Fridericia terrarossae*** Sesma & Dózsa-Farkas, 1993

Species with usually up to 6 chaetae in ventral bundles.

3* Character combination different **4**

4 Large enchytraeids, ca 35 mm long; spermatheca with 20–50 small diverticula, ectal duct very long and thin, ectal gland present (sometimes minute); Fig. 64C..... .....***Fridericia hegemon*** sensu lato (Vejdovský, 1878)

L ca 35 mm, D 0.5–1 mm, S 50–68. Worms stiff, stout, opaque. Maximum number of chaetae per bundle 4, 5 or 6. Oesophageal appendages much branched. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Clitellum girdle-shaped, cells in reticulate pattern. Seminal vesicle large, ca 3 segments. Sperm funnel about as long as body diameter, 4–6x as long as wide. Bursal slit longitudinal. Spermathecae separate. In specimens from South-east Europe additional pharyngeal glands in VII, 5–6 subneural glands, and no spermathecal ectal gland. – Widespread. Not found in South-west Europe. Lit.: Rota (2001).

4* Character combination different **5**

5 Oesophageal appendages long, coiled, unbranched **6**

5* Oesophageal appendages different.....**9**

6 Less than 40 segments; seminal vesicle absent **7**

6* More than 40 segments; seminal vesicle large **8**

7 Male glandular bulb large, globular; spermathecae fused proximally; Fig. 64D..... .....***Fridericia berninii*** Dózsa-Farkas, 1988a

L 5–9 mm, S 33–39. Up to 4 chaetae per bundle. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Chylus cells in preclitellar segments (IX, X). Clitellum girdle-shaped, cells in dense/indefinite rows. Sperm funnel 2–3x as long as wide, almost as long as body diameter. Bursal slit longitudinal. Spermathecae with large, sessile ectal gland, ampullae proximally fused, each with 2–4 sessile, globular diverticula. – Spain (Mallorca), Greece.

7* Male glandular bulb small, flat; spermathecae separate; Fig. 64E..... .....***Fridericia vixdiverticulata*** Sesma & Dózsa-Farkas, 1993

L 5–7.5 mm, S 31–40. Up to 4 chaetae per bundle. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Coelomolenticytes large. Chylus cells in preclitellar segments. Clitellum girdle-shaped, cells in indefinite rows or in reticulate pattern. Sperm funnel small, bursal slit longitudinal. Spermathecae with sessile ectal gland (2x ectal duct width), ampulla with 3–5 small, stump-like diverticula, often inconspicuous, not more than bulges of ampullar distal wall. – Spain. Only known from type locality.

8 All diverticula globular, epidermis thickened ventrally in XIV (not XIII); Figs 12B, 64F .....***Fridericia regularis*** Nielsen & Christensen, 1959

L 15–20 mm, S 52–68. Up to 4, rarely 6, chaetae per bundle. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Coelomocytes with refractile vesicles at periphery. Clitellum girdle-shaped, cells in dense (often double) rows. Seminal vesicle 3 segments. Sperm funnel 3–5x as long as wide, longer than body diameter. Bursal slit L-shaped. Spermathecal gland absent or minute, ectal duct longer than body diameter, ampullae separate, each with a ring of ca 10–15 sessile, equally large, globular, sperm-filled, diverticula. – Widespread. Not found in Western Europe.

8* Diverticula globular, kidney- or bean-shaped, epidermis thickened ventrally in XIII and/or XIV; Fig. 65A.....***Fridericia minor*** sensu lato Friend, 1913a

L 8–15 mm, S 35–60. Preclitellar nephridia 4 or 5 pairs, 6/7 – 9/10 or 10/11. Coelomocytes with or without refractile vesicles at periphery. Clitellum girdle-shaped, cells in dense/indefinite rows. Seminal vesicle large, 2.5–4 segments, sperm funnel 2–3x as long as wide, almost as long as body diameter. Bursal slit variable. Spermathecal ectal gland small or large, ampullae separate, each with 4–6, globular, kidney- or bean-shaped diverticula. – Species complex. Widespread. Common in soils close to the sea.

9 Spermathecae separate, diverticula longer than wide, with distal sperm-containing chamber; no ectal glands, see H5.....***Fridericia galba*** (Hoffmeister, 1843)

9* Spermathecae fused proximally, diverticula spherical or hemispherical, ectal glands present; see B10.....***Fridericia glandifera*** Friend, 1913

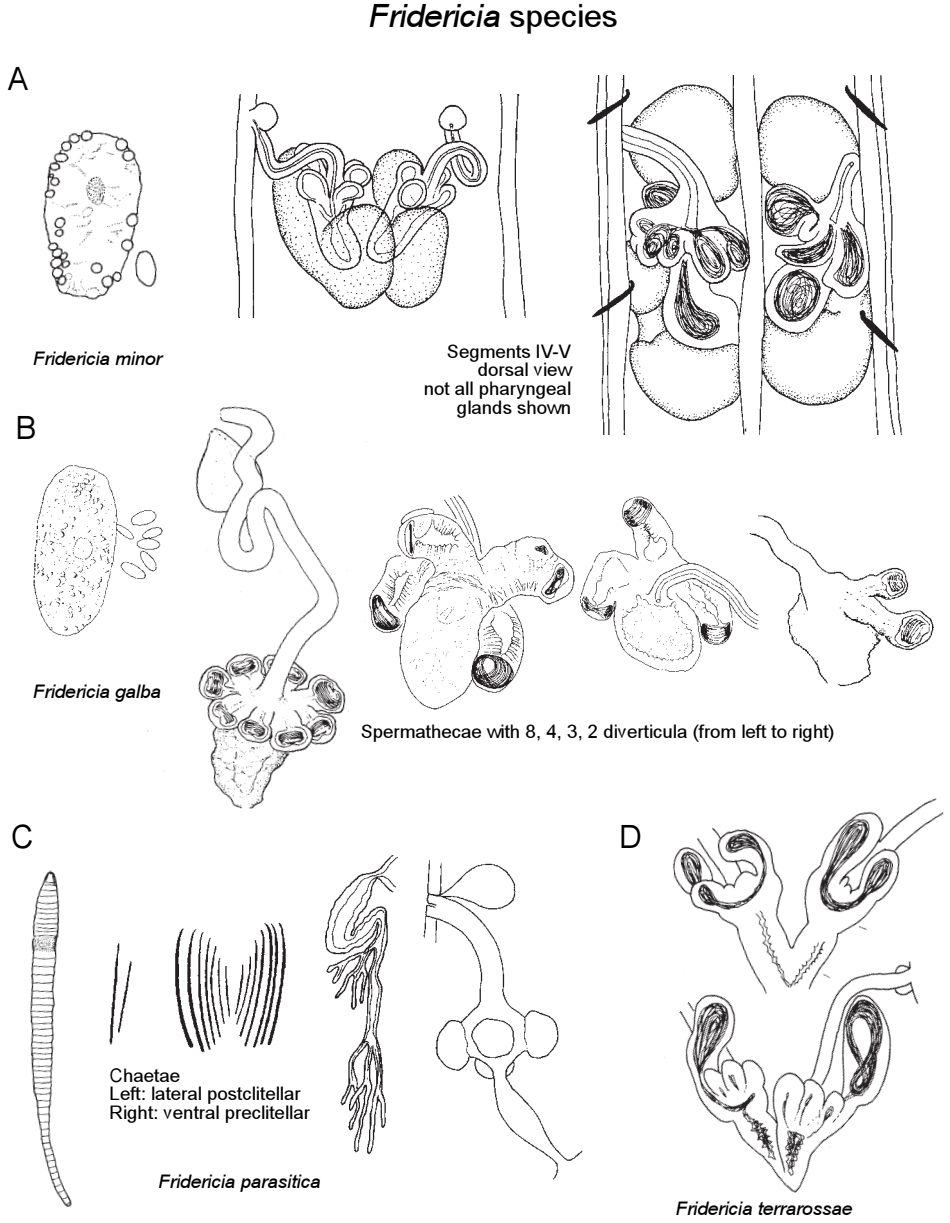

Fig. 65 ***Fridericia*** species, continued. A: ***F. minor***, from Schmelz (2003, Fig. 46B,D,C). B: ***F. galba***, from Schmelz (2003, Fig. 33J), Chalupský (1992, Fig. 12A), Schmelz (2003, Fig. 33M,N), Chalupský (1992, Fig. 12D). C: ***F. parasitica***, from Černosvitov (1928b, Figs 1, 13, 15, 5, 4). D: ***F. terrarossae***, from Sesma & Dózsa-Farkas (1993, Figs 26, 28).

H. Spermathecae each with more than 2 diverticula, a maximum of 6 or more chaetae per bundle

1 More than 10, up to 16 chaetae in ventral preclitellar bundles; first preclitellar nephridia at 8/9; Fig. 65C.....***Fridericia parasitica*** Černosvitov, 1928b

L 6–9.5 mm (fix), S ca 40–52. Ventral chaetae distally bent. Oesophageal appendages much branched, down to VII. Preclitellar nephridia 2 pairs, 8/9 and 9/10. Clitellum girdle-shaped, cells in indefinite rows. Seminal vesicle present. Sperm funnel 2x as long as wide, shorter than body diameter. Bursal slit Y-shaped. Subneural glands in XIV and XV, largest in XV. Ectal gland stalked, > 2x ectal duct diameter. Ampullae separate, each with 4 globular, sessile diverticula. – Serbia. Only known from type locality. Ecto-commensalic (-parasitic?) on large earthworms.

1* Fewer chaetae in ventral preclitellar bundles; first preclitellar nephridia at 6/7 as usual (unknown in ***F. florentina***) **2**

2 Spermatheca with 20–50 small, globular diverticula; see G4 ....***Fridericia hegemon*** (Vejdovský, 1878)

2* Fewer diverticula per spermatheca **3**

3 Spermathecal ectal gland present, some diverticula longer than wide, oriented ectad; epidermis glandularly thickened mid-ventrally in XIII–XV; Fig. 65D ....***Fridericia terrarossae*** Sesma & Dózsa-Farkas, 1993

L 13–19 mm, S 48–65. Body colour yellow due to chloragocytes. Up to 6 chaetae per bundle. Oesophageal appendages slender, with 2–4 terminal branches. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Clitellum girdle-shaped, cells in indistinct rows. Seminal vesicle 1–2 segments. Sperm funnel ca 1.5x as long as wide. Bursal slit longitudinal. Spermathecae with ectal gland about as wide as ectal duct, ampullae fused proximally, each with 3–5 elongate diverticula, often of different size. – Spain. Only known from type locality.

3* Character combination different **4**

4 Diverticula twice as long as wide or longer **5**

4* Diverticula shorter, pear-shaped, globular, or hemispherical **7**

5 Spermathecal ectal glands absent (a large accessory gland in the vicinity of the ectal pore may be present); diverticula subdivided into stalk and sperm chamber; Fig. 65B .....***Fridericia galba*** (Hoffmeister, 1843)

L 15–25 mm, S ca 60–70. Maximum number of chaetae 4–8, most often 6. Oesophageal appendages branched. Clitellum saddle- or girdle-shaped, cells in dense/indefinite rows or in reticulate pattern. Seminal vesicle usually large, 2–3 segments, occasionally absent. Spermathecal diverticula 2-8, stalked, with ciliated sub-chamber; separate openings into oesophagus. – Widespread. Very common in Central Europe. Possibly absent in Southwest Europe. Complex of bisexual species and parthenogenetic lineages (Christensen et al. 1992).

5* Spermathecal ectal glands present; diverticula not subdivided **6**

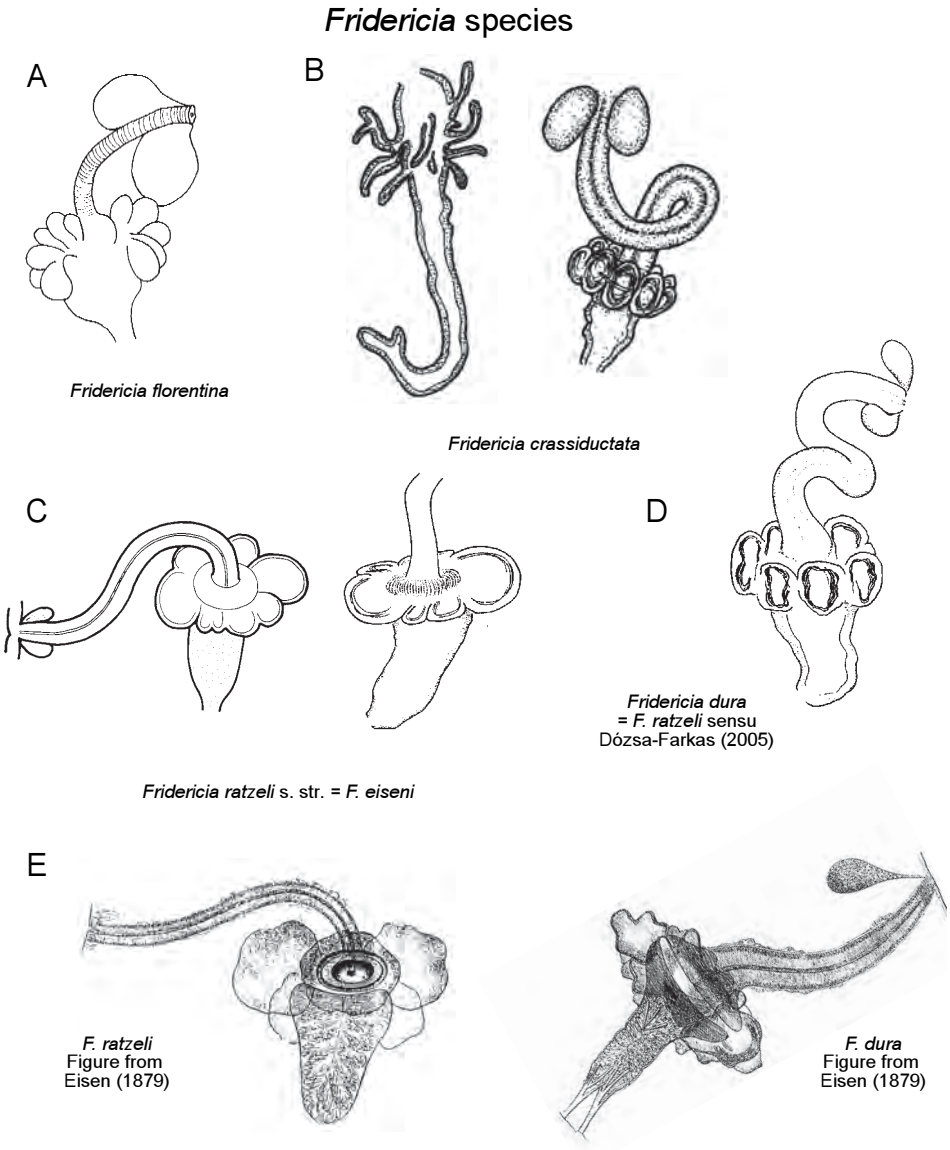

Fig. 66 ***Fridericia*** species, continued. A: ***F. florentina***, from Dequal 1914, Fig. 7. B: ***F. crassiductata***, from Dózsa-Farkas & Cech (2006, Fig. 2A,B). C: ***F. ratzeli*** s. str., from Nielsen & Christensen (1959, Fig. 84), Chalupský (1992, Fig 14B). D: ***F. dura***, from Chalupský (1992, Fig 14A). E: ***F. ratzeli*** s. str., from Eisen (1879, Pl. 12 Fig. 22C); ***F. dura***, from Eisen (1879, Pl. 12 Fig. 23H).

6 Three diverticula, finger-shaped; see F7 .....***Fridericia brachiata*** Rota, 1994

6* More than 3 diverticula, globular, kidney- or finger-shaped, see G8*..... .....***Fridericia minor*** sensu lato Friend, 1913b

7 More than 75 segments; spermathecal diverticula aggregated on two opposite sides of ampullar distal part; Fig. 66A .....***Fridericia florentina*** Dequal, 1914

L 20–25 mm (fix?), S 85–90. Up to 8 chaetae per bundle. Brain as wide as long. Cells of clitellum in reticulate pattern. Sperm funnel 3–4x as long as wide. Spermatheca with 2 very large ectal glands, ampullae separate (?), with a bouquet of ca 10 rounded, sessile diverticula. – Italy. Only known from original description.

7* Fewer segments; spermathecal diverticula in a circle around ampullar distal part.....**8**

8 Oesophageal appendages long, coiled, unbranched; subneural glands absent, epidermis glandularly thickened mid-ventrally in XIII or XIII–XV (comp. Fig. 12B); one spermathecal ectal gland; see G8* .....***Fridericia minor*** sensu lato Friend, 1913

8* Oesophageal appendages branched, subneural glands often present; epidermis not thickened mid-ventrally in XIII–XV; usually two spermathecal ectal glands present, one dorsal, one ventral **9**

9 Coelomocytes with numerous refractile vesicles at cell periphery; spermathecal ectal glands large, 2 (3) in number, brown, sessile, egg-shaped; subneural glands at XIV–XVI; Fig. 66B .....***Fridericia crassiductata*** Dózsa-Farkas & Cech, 2006

S 40–56, L 13–20 mm. Oesophageal appendages variable, with or without numerous small branches proximally, and 2–3 distal branches. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Clitellum girdle-shaped, cells in reticulate pattern. Seminal vesicle large, 3–4 segments. Sperm funnel ca 2.5–3x as long as wide, shorter than body diameter, bursal slit variable, about L- or H-shaped. Spermathecal ectal duct thick (35–48 µm), longer than body diameter; ampullae separate, each with a ring of 9–10 globular sperm-filled diverticula.– Hungary. Only known from original description.

9* Coelomocytes without refractile vesicles at cell periphery; two spermathecal ectal glands (rarely one), small, usually stalked; subneural glands at XIII(–XV) or absent; Fig. 66C,D . . . . . .***Fridericia ratzeli*** (Eisen, 1872) sensu lato **10**

Body stout. L 15–30 mm, D 0.5–1 mm. Maximum number of chaetae 6, 7, or 8. Oesophageal appendages much branched. Preclitellar nephridia 5 pairs, 6/7 – 10/11. Coelomocytes with pale but distinct vesicles, lenticytes small. Clitellum girdle-shaped. Seminal vesicle variable, up to 2 segments; sperm funnel 2–4x as long as wide, about as long as body diameter or shorter. Bursal slit variable. Spermathecal ampullae separate, diverticula globular, sessile, variable: thin-walled, not sperm-containing, differing in size, with the two lateral ones usually being largest; or thick-walled, sperm-containing, all equally large, or intermediates. L 15–25 mm, S ca 50–70. – Species complex. Widespread. Common in Central Europe. Lit.: Nielsen & Christensen (1959), Chalupský (1992), Dózsa-Farkas (2005).

10 L 20–30 mm, D ca 0.8 mm, bursal slit longitudinal; clitellar glands in reticulate pattern; spermathecal diverticula all more or less of same size, mostly thick-walled and filled with sperm, ectal duct stout, canal widening proximally before entering ampulla; only one subneural gland, in XIII, large, or absent (?); seminal vesicle often (always?) filled with cysts of developing sperm but without mature or maturing spermatozoa; Fig. 66C .....***Fridericia dura*** (Eisen, 1879)
= ***Fridericia ratzeli*** (Eisen, 1872) sensu Dózsa-Farkas 2005

10* L 15–20 mm, D ca 0.5 mm, bursal slit T-shaped; clitellar gland cells in dense to indefinite rows; spermathecal diverticula unequally large, the two lateral ones more than twice as wide as the smallest ones, walls very thin, almost devoid of sperm, sperm usually as a ring in ampulla around ectal duct porus, ectal duct slender, canal not widening proximally before entering ampulla; three subneural glands, in XIII, XIV, XV; Fig. 66D .....***Fridericia ratzeli*** (Eisen, 1872) sensu stricto
= ***Fridericia eiseni*** Dózsa-Farkas, 2005

Shortcuts to *Fridericia* species with peculiar characters

(Group codes as above:
A: Spermathecae absent or rudimentary, not differentiated; or spermathecae differentiated but not connected with oesophagus
B: Spermathecae without diverticula, small diverticula-like protrusions may be present
C: Spermathecae each with 1 diverticulum
D:Two spermathecal diverticula, a maximum of 2 chaetae per bundle
E: Two spermathecal diverticula, a maximum of 4 (3, 5) chaetae per bundle
F: Two spermathecal diverticula, a maximum of more than 5 chaetae per bundle
G: Each spermatheca with more than 2 diverticula, not more than 5 chaetae per bundle, often less
H: Spermathecae each with more than 2 diverticula, a maximum of 6 or more chaetae per bundle)

More than 75 segments

E ***F. magna***, ***F. stephensoni*** (partim)
G ***F. gigantea***
H ***F. florentina***

Chaetae slightly sigmoid

B ***F. striata***
G ***F. gigantea***

Chaetal bundles incomplete, often with 1 or 0 chaeta

A ***F. reducata***
B ***F. semisetosa***
D ***F. connata***, ***F. maculata***, ***F. monochaeta, F. brunensis***
E ***F. conculcata***

Epidermal gland cells coloured (yellow-green-orange)

B ***F. bretscheri*** (partim?)
D ***F. maculata***
E ***F. nemoralis***, ***F. tubulosa***
F ***F. strenua***
G ***F. crassiductata***

Oesophageal appendages long, unbranched, coiled in IV/V

B ***F. bulboides***, ***F. vixdiverticulata***
E ***F. alata***, ***F. argillae***, ***F. profundicola***, ***F. tubulosa***
F ***F. alata***
G ***F. berninii***, ***F. minor***, ***F. regularis***, ***F. vixdiverticulata***

Additional pair of pharyngeal gland lobes in VII

A ***F. nix***
E ***F. auritoides***, ***F. conculcata***, ***F. nix***, ***F. sylvatica***
H ***F. hegemon*** (partim)

Coelomo-mucocytes with refractile vesicles

A ***F. nix***
B ***F. bretscheri***, ***F. bulboides***, ***F. glandifera*** (partim), ***F. nielseni***, ***F. pretoriana***, ***F. schmelzi***, ***F. semisetosa***, ***F. striata***, ***F. tuberosa***
D ***F. connata*** (partim), ***F. cylindrica***
E ***F. argillae***, ***F. discifera***, ***F. granosa***, ***F. isseli***, ***F. nix***
G ***F. pyrenaica***
H ***F. crassiductata***, ***F. galba*** (partim), ***F. minor*** (partim)

Nephridia absent at 6/7

E ***F. lacii***, ***F. profundicola***
H ***F. parasitica***

Coelomo-mucocytes sparse, as if absent

E ***F. profundicola***

Coelomo-lenticytes sparse, as if absent

A ***F. nix***
H ***F. minor***

Chylus cells in preclitellar segments

B ***F. benti*** (partim), ***F. bulboides*** (partim), ***F. cusanica***
C ***F. deformis***
D ***F. cylindrica*** (partim), ***F. monochaeta***, ***F. maculata***
E ***F. argillae***, ***F. berninii***, ***F. lacii***, ***F. isseli***, ***F. maculata***, ***F. waldenstroemi***
F ***F. baskini***, ***F. stephensoni***
G ***F. berninii***, ***F. pyrenaica***

Blood coloured (reddish, yellowish)

B ***F. ilvana***
D ***F. magna***
E/F (***F. alata*** sensu Chalupský 1986)

Clitellum open, i.e. not developed dorsally

A ***F. semisetosa***
B ***F. unisetosa***
E ***F. sylvatica***
G ***F. pyrenaica***

Subneural glands in XIII ff.

A ***F. christeri*** (XIII–XV)
B ***F. glandifera*** (XIII, XIV, [XV]), ***F. nielseni*** (XIV, XV), ***F. parathalassia*** (XIII, XIV, [XV]), ***F. tuberosa*** (XIII, XIV)
C ***F. deformis*** (XIV)
D ***F. maculatiformis*** (XIII, XIV)
E/F ***F. auritoides*** (XIII), ***F. baskini*** (?), ***F. conculcata*** (XIII, XIV), ***F. discifera*** (XIII, XIV, [XV]), ***F. humicola*** (XIII–XV), ***F. montafonensis*** (XIII, XIV), ***F. nemoralis*** (XIII), ***F. waldenstroemi*** (XIV)
G/H ***F. parasitica*** (XIV, XV), ***F. ratzeli*** s.l. (XIII or XIII–XV), ***F. crassiductata*** (XIV–XVI), ***F. hegemon*** in Rota (2001)

Glandular thickening of epidermis ventrally in XIII–XV

D ***F. connata*** (partim, in XIII), ***F. brunensis*** (XIII)
E ***F. ulrikae*** (partim, in XIII, XIV)
G ***F. regularis*** (in XIV)
H ***F. galba*** (in XIV), ***F. minor*** (in XIII, or XIII–XIV), ***F. terrarossae*** (XIII–XV)

Spermathecae fused proximally

B ***F. bulboides*** (partim), ***F. bretscheri***, ***F. glandifera***, ***F. losangelensis***, ***F. pretoriana***, ***F. semisetosa***
C ***F. anomala***, ***F. singula***
D ***F. bisetosa*** (rarely), ***F. brunensis, F. connata*** (usually), ***F. monochaeta***
E ***F. argillae***, ***F. berninii***, ***F. bubalus*** (partim), ***F. gamotheca***, ***F. nemoralis*** (partim), ***F. profundicola***, ***F. waldenstroemi*** (partim)
F ***F. baskini***, ***F. montafonensis***
G ***F. berninii***, ***F. terrarossae***

Spermathecal diverticula with ciliated subchamber (+ no ectal gland, no subneural glands)

E ***F. ulrikae***, ***F. rendsinata***
F ***F. dozsae***, ***F. healyae***, ***F. perrieri***
H ***F. galba***

F. cusanica is very similar to ***F. composti*** Schmelz, 2003, described from a compost heap in Vancouver Island, British Columbia, Canada (erroneously transferred to Ontario in Schmelz (2003); the correct coordinates are 132°2'W, 53°6'N). Since both names were published simultaneously, a precedence must be fixed in case of a possible synonymy (ICZN 1999). We fix here ***F. cusanica*** as valid name. A third species in the group is the Californian ***F. berkeleyensis*** Bell, 1936, incompletely described, but with characteristic sac-shaped chylus cell lacunae (one of the traits not included in this key). Recently reinvestigated material of ***F. cusanica*** from Italy (sent by U. Graefe) and a check of live photographs taken from the type specimens before fixation revealed that ***F. cusanica*** has the same type of chylus cells as ***F. berkeleyensis***, which suggests that both may be the same species. However, due to several differences (e.g., no spermathecal ectal glands) and a generally poor description of ***F. berkeleyensis***, new material of ***F. berkeleyensis*** is necessary to see whether a synonymy is justified (see Schmelz 2003). Details of the chylus cell canals in ***F. composti*** must be reinvestigated as well.

F. benti and ***F. paroniana*** are only separable by the absence/presence of two spermathecal diverticula. Different sperm lengths were given in Schmelz (2003) for ***F. benti*** (ca 210 µm, nuclei ca 75 µm) and for ***F. paroniana*** (120 µm, nuclei 35–55 µm), but measurements in new material revealed variations in both species that blur the distinction (Schmelz, pers. obs.). Erséus et al. (2005) also found sperm lengths in Scandinavian specimens of ***F. benti*** to be shorter than originally described. Likewise, ***F. bulboides*** and ***F. argillae*** may be separable only by the absence/presence of two spermathecal diverticula, although the clitellum – absent antero-mid-ventrally in ***F. argillae*** – may serve as a second distinguishing character. A further difference – 2 chaetae in all lateral bundles in ***F. argillae*** and 2–4 in ***F. bulboides*** – is due to an error in the original description of ***F. argillae***; some specimens of ***F. argillae*** have 4 chaetae in lateral bundles as in ***F. bulboides*** (see Schmelz 2003, Fig. 12A).

We believe that each species pair – ***F. benti*** and ***F. paroniana*** on the one hand, ***F. bulboides*** and ***F. argillae*** on the other – represents a genetically heterogeneous group of species, each with more than just two species. Isozyme variations in ***F. benti*** and ***F. bulboides*** support this hypothesis (Schmelz 2003). Furthermore, ***F. paroniana*** and ***F. bulboides*** are variable morphologically; the latter has an unusually wide ecological amplitude. Several other species are very close to the '***bulboides***'-group: ***F. schmelzi***, ***F. semisetosa***, ***F. bretscheri*** (see Cech & Dózsa-Farkas, 2005); together with ***F. bulboides***, they may form a clade within the genus.

The four variants of ***F. maculata*** may deserve species rank, in which case ***F. renatae*** and ***Timmodrilus oligoseta*** would be restored, the latter as ***Fridericia oligoseta***. The bisetose variant would be ***F. maculata***, and the one with four chaetae would need a new name. As to the synonymy of ***Timmodrilus*** with ***Fridericia***, see Schmelz et al. (2005).

F. cylindrica and ***F. sohlenii***. Erséus et al. (2005) question the synonymy of the well-described European ***F. sohlenii*** and the originally poorly described Australian ***F. cylindrica*** The name of ***F. cylindrica*** has priority. The synonymy was proposed in Schmelz (2003), as a result of the reinvestigation of five paratypes of ***F. cylindrica*** and their comparison with collected European material, initially identified as ***F. sohlenii***. Erséus et al. (2005) consider the species comparison in Schmelz (2003) inadequate and the matching of characters incomplete, but we maintain the synonymy here, for three reasons: (1) The alleged inadequacy concerns only one error in Schmelz (2003) – the statement that the body colour of ***F. cylindrica*** is originally described as having a yellowish tint, when in fact it is described

as grey-white. (2) The differences between ***F. cylindrica*** and ***F. sohlenii*** as listed in Erséus et al. (2005) are within the intraspecific variability of the species as documented in Schmelz (2003) (e.g., chylus cell location, extension of oesophageal appendages), or they concern likely fixation artefacts in the types of ***F. cylindrica*** (e.g., shortening of brain and spermathecal ectal duct, sperm in the spermathecal ampullar lumen). In fact, there is not one character that would distinguish ***F. sohlenii*** from ***F. cylindrica***, provided that the paratypes of ***F. cylindrica*** are not originally misidentified. (3) Some characters said to be unknown in ***F. cylindrica*** according to Erséus et al. (2005) are actually described or illustrated in Schmelz (2003) (size of clitellar gland cells, length of chaetae), and they match the description of ***F. sohlenii***. – Several traits known in ***F. sohlenii*** remain unknown in ***F. cylindrica***, namely distribution pattern of preclitellar nephridia, coelomocyte texture, and further details visible only in living specimens; this leaves room for debate. We hope to obtain fresh topotypic material of ***F. cylindrica*** for a more detailed comparison.

F. ratzeli, ***F. dura***, and ***F. eiseni***. ***F. ratzeli*** sensu lato is a complex of sexual species and parthenogenetic lineages, heterogeneous on the morphological, cytological, and molecular level, and with a long list of synonyms (see Schmelz 2003). Two forms are often readily distinguished, named here ***F. ratzeli*** sensu stricto and ***F. dura***, following Chalupský (1992) and Schmelz (2003). Although we doubt that the distinction works for all forms and localities, they are included in the key here to allow a critical check. For specimens that do not fit either of the two species diagnoses, a designation as ***F. ratzeli*** sensu lato remains available. In any case, we recommend a careful record of all key characters. A detailed comparison of both forms and an excellent redescription of ***F. ratzeli*** is given in Dózsa-Farkas (2005); the names, however, are allocated differently in that paper: ***F. ratzeli*** sensu stricto is described as a new species, ***F. eiseni***, and ***F. dura*** is named ***F. ratzeli*** sensu stricto. We believe that our allocation of names is more accurate: a figure in Eisen (1879, see Fig. 66E left) shows a spermatheca of ***F. ratzeli*** with (1) a slender, not widening ectal duct, (2) very thin-walled diverticula, (3) unequal in size, and (4) with sperm in a ring around the ectal duct porus in the ampulla. These traits are among those that according to Dózsa-Farkas (2005) distinguish ***F. eiseni*** from ***F. ratzeli***. On the other hand, the figure of the spermatheca of ***F. dura*** in the same paper (Eisen 1879, see Fig. 66E right) is similar to the spermatheca in ***F. ratzeli*** sensu Dózsa-Farkas (2005). Finally, ***F. eiseni*** is very similar to several other species put into synonymy with ***F. ratzeli*** sensu lato by Schmelz (2003), for example ***F. lobifera*** (Vejdovský, 1878), ***F. sacculata*** Bell, 1936, and ***F. canadensis*** Dash, 1972. If ***F. eiseni*** should be maintained as a species different from ***F. ratzeli***, it would end up as a synonym of one of these mentioned nominal species.

The **valid name** of the genus remains ***Distichopus*** Leidy, 1882, contrary to the opinion in Schmelz (2003: 388); a proposal towards the ICZN is necessary to conserve the name ***Fridericia***.

8. Acknowledgments and permissions to reproduce figures

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State Museum of Upper Austria, Biology Centre (Biologiezentrum/Oberösterreichisches Landesmuseum) Linz: Figure 31C right.

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Wiley-VCH, Weinheim: Figures 25B; 39F; 42H right; 49, 1st to right.

Klára Dózsa-Farkas: Figures 57A right, 60G, 61E, 64E right, 28A, 66B.

Elzbieta Dumnicka: Figures 33F,I; 42I.

Ulfert Graefe: Figures 25C left; 26B; 27B.

Friedrich Möller: Figures 25B; 39F; 42H right; 49, 1st to right.

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Tarmo Timm: Figures 5, 2nd to left; 15A left; 16A left; 30E left; 35A; 44B right.

Wilfried Westheide: Figures 32D, 33D,I.

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