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RÜDIGER M. SCHMELZ & RUT COLLADO

Enchytraeus luxuriosus sp. nov., a new terrestrial oligochaete species (Enchytraeidae, Clitellata, Annelida)

Kurzfassung

Eine neue terrestrische Oligochaetenart aus der Gattung Enchytraeus HENLE, 1837 wird beschrieben, E. luxuriosus sp. nov. Sie gehört zu einer bislang nur ungenügend aufgeklärten Gruppe weit verbreiteter und in Mitteleuropa sehr häufiger Arten, die oft zusammenfassend als E. buchholzi bestimmt werden. E. luxuriosus ist gegenüber allen bekannten Arten der Gattung, inklusive E. buchholzi, durch einen Komplex von acht Merkmalen charakterisiert: (1) Länge ca. 1 cm; (2) Segmentzahl ca. 45; (3) Borstenformel 2 - 2,3 3 - 3, d.h. ventral durchgehend 3 Borsten je Bündel; lateral anteclitellial 2, lateral postclitellial 2 oder 3 Borsten je Bündel; (4) Coelomocyten blass, ohne lichtbrechende Granula; (5) Samentrichter klein, etwa kugelig, mit engem Kragen; (6) Samenblase mittelgroß, mehr als 1/2 Segment lang; (7) männliches Kopulationsorgan (Penialbulbus) klein und kompakt; (8) ektaler Gang der Spermatheke viel kürzer als Ampulle, Wandung zu einem Büschel von Drüsen aufgetrieben, Ampulle 2x so lang wie breit, entaler Gang so lang wie Ampulle. Viele weitere Merkmale dieser Beschreibung, die die korrekte Identifizierung von E. luxuriosus sicherstellen, können zur Artentrennung bislang noch nicht herangezogen werden, da sie in früheren Beschreibungen von Enchytraeus-Arten nur ungenügend berücksichtigt sind.

Abstract

A new terrestrial species of Enchytraeus HENLE, 1837 is described, i. e. E. luxuriosus. It belongs to a hitherto largely unresolved group of species very common in Central Europe and often determined as E. buchholzi. E. luxuriosus is separable from all other species of the genus, including E. buchholzi, by a complex of eight characters: (1) length about 1 cm; (2) segment number around 45; (3) chaetal formula 2 - 2,3 3 - 3, i.e. ventrally 3 chaetae per bundle throughout, laterally 2 chaetae throughout in preclitellar bundles, 3 or 2 chaetae per bundle in postclitellar bundles; (4) coelomocytes pale, i.e. without refractile granula; (5) sperm funnel small, roughly spherical, collar much narrower than funnel body; (6) seminal vesicle mediumsized to large; (7) male copulatory organ (penial bulb) small and compact; (8) spermathecal ectal duct much shorter than ampulla, ampulla twice as long as wide, ental duct as long as ampulla, bouquet of glands around ectal orifice. Many other characters that assure the correct identification are only rarely mentioned in other species descriptions and can therefore not yet be used to separate E. luxuriosus from them.

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Introduction

A new species of Enchytraeus HENLE, 1837 is described, E. luxuriosus. It was found in the top mineral soil of a meadow during a soil fauna survey in the framework of the long-term soil monitoring program in Schleswig-Holstein, Northern Germany. The species, first tentatively named E. minutus or E. buchholzi, was easily cultured on various substrates, and mass populations were obtained within a few months. It now ranks as optional test species recommended for the "Enchytraeid Reproduction Test" (ERT) (RÖMBKE & MOSER 1999), an ecotoxicological risk assessment test for chemicals that has recently been implemented as OECD-standard, and data are available on its susceptibility to carbendazime and 2,4-nitrophenol (COL-LADO et al., in press). Live cultures are maintained in the laboratory of the first author and at ECT Oekotoxikologie GmbH, Flörsheim. They are available for anyone interested in working with that species.

E. luxuriosus belongs to a group of small Enchytraeus species, morphologically close to E. buchholzi VEJDOVSKÝ, 1878 and E. christenseni Dózsa-FARKAS, 1992 (formerly E. minutus NIELSEN & CHRISTENSEN, 1961), which are difficult to identify and to separate from one another (CHALUPSKY 1992, ROTA 1995). A satisfactory taxonomic resolution of the entire species complex requires biochemical data additional to the morphological traits (SCHMELZ et al. 1999). The lightmicroscopical investigation of E. luxuriosus, however, revealed that the species is well-defined on purely morphological terms and that it is clearly separable from all other known species of that group, including cultures of unknown species identity maintained in the laboratory of Systematic Zoology at the University of Osnabrück.

The description is based on live-observation and the study of stained whole mounts. Most of the characters are easily recognized in live specimens. Some characters are rarely mentioned in *Enchytraeus* species descriptions, but they provide, to the authors' opinion, highly useful clues to species identification and separation in *Enchytraeus*. Type material is deposited at the Zoological Museum Hamburg and the State Museum of Natural History Karlsruhe. Other reference material, including live cultures, is in the collection of the first author.

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Material and methods

The new species was obtained from meadow soil samples of a soil monitoring site (Geological Land Office, Schleswig Holstein) in northern Germany and reared and mass-cultured in the laboratories of ECT Oekotoxikologie GmbH, Flörsheim and of Systematic Zoology at the University of Osnabrück. Specimens were examined and photographed alive microscopically in a drop of tap water between slide and cover glass. For microscopical preparation, specimens in water were first anesthetized by adding drops of 30% ethanol until the animals were relaxed, then fixed in hot Bouin's fluid (70°C), stained with Paracarmin, passed through an ethanol-xylol series and mounted whole in Malinol between two cover glasses to make the object examinable from both sides. Examinations of both live and preserved specimens were carried out with a Leitz Diaplan microscope with interference contrast optics. Drawings from whole mounts (Fig. 1) were made with the help of a drawing tube.

Body measurements in the following description refer to sexually mature individuals. Numbers in brackets indicate minimum and maximum dimensions, respectively. Segments are counted using Roman numerals, intersegmental regions (dissepimenta, segment boundaries) are counted using Arabic numerals.

Enchytraeus luxuriosus sp. nov.

Enchytraeus minutus agg. (partim), - GRAEFE et. al. 1998: 345, Tab. 2

Enchytraeus "minutus", – SCHMELZ 1999: 45-46, Figs. 4.7/4.8 Enchytraeus "buchholzi", – COLLADO et al. (in press)

Type locality: Long-term soil monitoring site "BDF 13 Kleihof" of the agency for Nature and Environment of the State Schleswig-Holstein (Boden-Dauerbeobachtungsfläche BDF 13 Kleihof, Landesamt für Natur und Umwelt des Landes Schleswig-Holstein): meadow near Kleihof, St. Peter Ording, Schleswig-Holstein, Germany; coordinates R 3476 H 6020; flat, elevation 1m a.s.l., soil form Knickmarsch of holocene marine clays, (FAO: Fluvi Dystric Gleysol); pH (CaCl₂) 5.3, soil texture silty clay (Tu3).

Material examined: Holotype ZMH OL 14158, one sexually mature specimen, whole mounts stained with Paracarmin. Paratypes ZMH OL 14159, 12 sexually mature specimens, whole mounts stained with Paracarmin. Further paratypes (unlabelled): 10 whole-mounted specimens and 15 specimens fixed in Bouin's fluid and stored in 70% ethanol, in the collection of the State Museum of Natural History Karlsruhe, Germany (Staatliches Museum für Naturkunde Karlsruhe, SMNK). Further 50 specimens fixed and stored in 70% ethanol, 50 more specimens fixed in Bouin's fluid, stored in 70% ethanol. Other examined material: 15 sexually mature Paracarminstained whole mounts, in the first author's collection, ca. 100 more specimens examined alive, not preserved.

Derivatio nominis: *"luxuriosus*" = luxuriant, fertile, rank: referring to the high reproductive potential of the species that builds up mass populations in a short period of time.

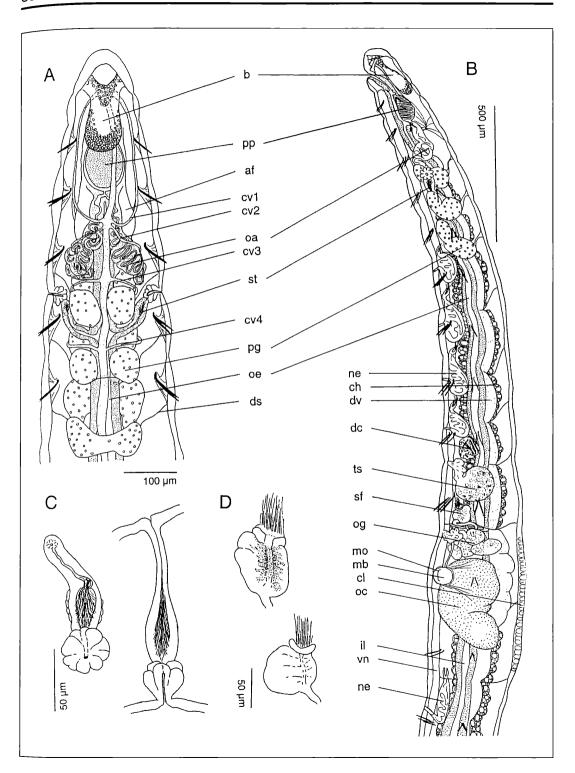
Description

Medium-sized Enchytraeus species, transparent to palish white, clitellum and sperm sac barely visible at low power, but eggs conspicuous. Body dimensions of live specimens: length (8)-11-(13) mm, diameter (unsqueezed) 0.3-0.35 mm in clitellar region, 0.2-0.3 mm in the rest of the body, tapering towards the pygidium. length reduced and diameter increased by fixation Segment number (36)-43-49-(56). Prostomium as Iona as wide, wider than long in fixed specimens, dorsal pore at 0/I. Epidermal gland cells inconspicuous, elongate, roughly rectangular, in one to three transversal rows per segment, adjacent to chaetae, absent middorsally and mid-ventrally. Chaetal formula 2 - 2,3 3 - 3lateral rows: anteclitellarly exclusively 2 per bundle. also in XII; postclitellarly 2, in posterior body half mostly 3, occasionally 2; ventral rows: 3 per bundle in all segments, absent in XII; exceptionally 2, 4, 5 or 6 chaetae in single bundles. Chaetal arrangement fanshaped except in bundles with exceptional numbers. Chaetae large, straight, with pointed distal tip and prominent proximal hook, 47 µm long and 3 µm thick in II, gradually increasing in size; from VIII or IX on down to rear end 60-70 µm long and 4-5 µm thick; maximum size depending on animal size; posteriormost chaetae slightly thicker but not longer than other chaetae; chaetae in lateral bundles posterior to clitellum slightly smaller. Often detached chaetae enclosed in amorphous packages in the coelom (Fig. 1B, dc).

Brain (Fig. 1A,B, b) in O, I and II, longer than wide, length:width ratio 1.5-2 1; 125 μ m long and 85 μ m wide in preserved specimens; posterior margin slightly convex, lateral sides merging anteriad, anterior margin inside prostomium, concave; nuclei concentrated in a U-shaped field posteriorly (as usual) but also anteriorly, extending into prostomial nerves. Postero-laterally a pair of secretory fields. Three pairs of pharyngeal glands (Fig. 1A,B, 2A, pg) in IV, V and VI, dorsally connected in VI, separate in IV and V, dorsal and

Figure 1. E. luxuriosus sp. nov. A, anterior body region, dorsal view. B, anterior body region, lateral view. C, spermatheca, from whole mounted (left) and from living (right) specimen. D, sperm funnel, from living (top) and whole mounted (bottom) specimen. Coelomocytes and various muscles omitted in A and B, chloragocytes omitted in A. af, afferent fascicle of pharyngeal gland; b, brain; ch, chloragocytes; cl, clitellum; cv1-4, commissural blood vessels, 1st to 4th pair; dc, package of detached chaetae in coelomic cavity; ds, dissepiment; dv, dorsal blood vessel; il, intestinal lumen; mb, male glandular bulb (penial bulb); mo, secondary male opening, bursal slit; ne, nephridium; oa, oesophageal appendage (peptonephridium); oc, mature oocyte; og, oogonia; oe, oesophagus; pg, pharyngeal (septal) gland; pp, pharyngeal pad; sf, sperm funnel; st, spermatheca; ts, testis with sperm sac; vn, ventral nerve chord.

SCHMELZ & COLLADO: Enchytraeus luxuriosus sp. nov.



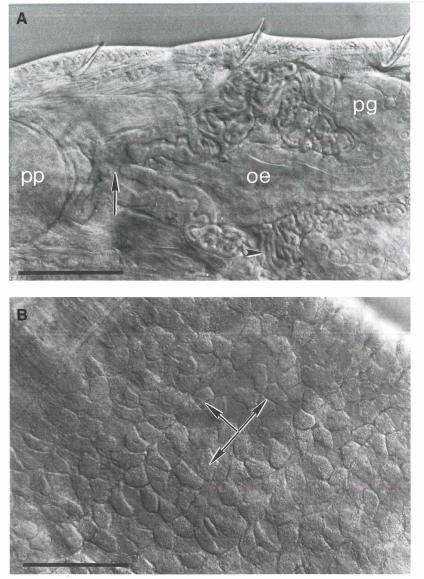


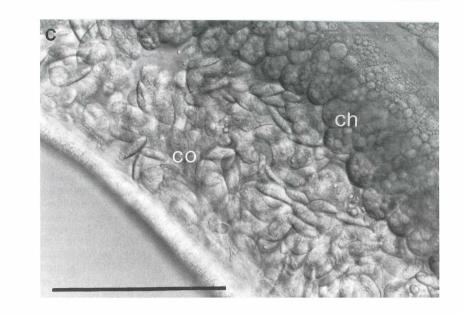
Figure 2. *E. luxuriosus* sp. nov., live photographs.

A, oesophageal appendages (peptonephridia) with anterior common opening (arrow) and enlarged middle third with meandering loops (arrowhead); oe oesophagus; pg, pharyngeal gland; pp, pharyngeal pad.

B, clitellum, anterior margin, dorsal view; simple arrow: longitudinal body axis, pointing towards head region, double arrow: transverse body axis.

C, Posterior body region, with dense packages of chloragocytes (ch) and coelomocytes (co). All bars = 100 µm.

ventral lobes present in all pairs, all roughly spherical to ellipsoid in outline, those in VI largest and with wide dorso-ventral connection. Oesophageal appendages (peptonephridia) (Fig. 1A,B, oa, 2A) paired, in III and IV, attached to and with joint opening into dorsal fold of intestinum between pharyngeal pad (Fig. 1 A,B, 2A, pp) and oesophagus (Fig. 1A,B, 2A, oe), proximal third of tube thick-walled, lumen more or less straight, middle third with loops perpendicular to longitudinal axis (meandering accordion-like), wider than the other parts; distal third much narrower, strongly and irregularly folded; foldings of middle third difficult to see in fixed specimens, but size relations of the three parts (middle third larger than the rest, wider than thick, distal third narrowest) discernible. Chloragocytes (Fig. 1B, 2C, ch) very large in well-fed animals, up to 45 µm high, diameter 20 µm and with refractile globules of differing size; beginning in IV anteriorly to pharyngeal glands with single cells, forming a dense and opaque layer from VII on, obscuring the body anatomy, absent in XII, occupying much of the coelomic space in postclitellar segments. A non-staining elevation of ventral SCHMELZ & COLLADO: Enchytraeus luxuriosus sp. nov.



intestinal epithelial cells detectable in whole mounts in 2-4 segments located ca. 8-10 segments from the rear end. Origin of dorsal blood vessel (Fig. 1A,B, dv) in XIII-XIV, most often at 13/14 or anteriorly in XIV, large and pulsating in clitellar segments, passing anteriad until 0/I, here branching into two circumoral connectives which reunite into ventral blood vessel in IV; four more pairs of commissural vessels (Fig. 1A, cv1-4): the first two pairs branching off the dorsal vessel adjacent to one another at 3/4, passing ventrad and joining circumoral connective vessels widely separately, first pair in III, second pair in IV; third pair branching off dorsal vessel in IV between oesophageal appendages and first pair of dorsal pharyngeal gland lobes, fourth pair in V, between spermathecae and second pair of dorsal pharyngeal gland lobes; third and fourth pair joining ventral blood vessel. Nephridia (Fig. 1B, ne): four pairs in preclitellar segments, from VII to X, large, with shape typical of the genus: anteseptale consisting of funnel only, postseptale as a laterally flattened ovoid body with much coiled canal, efferent duct rising posteroventrally, opening anteriorly of ventral chaetae; terminal vesicle present. Coelomocytes (Fig. 2C, co): flat and elongately ovoid, 25-28 µm long when fully developed, i.e. ca. half the size of the chaetae, filled with spherical, pale, non-refractile bodies; outline of cells ellipsoid or spherical when smaller, contents sometimes partly hyaline.

Clitellum (Fig. 1B, cl, 2B) in XII and XIII, exact extension from dissepiment 11/12 to dissepiment 13/14; welldeveloped, height ca. 20 μ m (live) or ca. 25 μ m (fixed), saddle-shaped, i.e. absent midventrally over its entire length, granulocytes with fine globules, nearly undistinguishable from globulocytes, cell diameter ca. 15-20 µm, both types of same size; gland cells in "disintegrating transverse rows" (Fig. 2B), i.e. in an intermediate state between distinct transverse rows and a clearly reticulate arrangement. Spermatheca (Fig. 1A, B, C) consisting of elongate ampulla without diverticula, short ectal duct surrounded by a bouquet of ca. 10 glands, and long ental duct opening laterally and separately into oesophagus; ectal spermathecal pore in the usual position, on the lateral line slightly ventrally of lateral chaetal rows, at intersegmental groove of 4/5; ectal duct lumen conspicuous, 25 µm long, lined by cuticula, sometimes as if filled with secretory granula; glands surrounding this lumen bush- or bouquet-like; location of secretory surface (i.e. whether around ectal pore or inside ectal duct) not ascertained; no ectal duct epithelium additional to the glands detectable. Spermathecal ampulla thick-walled, much longer than ectal duct, about twice as long (45-70 µm) as broad, sperm embedded with heads in distal ampullar epithel; connection between ampullar and ectal duct lumen very narrow, invisible in live specimens; ampulla gradually merging into ental duct which is as long as ampulla. Testes and sperm sacs (or seminal vesicles) (Fig. 1B, ts) in XI, paired, enclosed by common peritoneum, medium-sized, i.e. occupying more than half (from 2/3 to 3/2) of the segment length, sometimes extending into adjacent segments. No free spermatogonia or spermatozoa in the coelom, except those on top of sperm funnel. Sperm funnel (Fig. 1B,D, sf) of varying shape, roughly spherical, about as long as broad (80 µm), collar distinct but small, diameter 35 µm; only few spermatozoa observed on top of collar, therefore sperm measurements difficult (length roughly 56 µm, nucleus ca. 25 µm). Vas deferens short, ventrally in XII, 11 μ m wide proximally close to sperm funnel, 7 μ m wide distally when entering bursa. Male copulatory organs paired, in XII (as usual); eversible bursa inconspicuous, glandular bulb (Fig. 1B, mb) small and compact, spherical in preserved specimens, diameter 60 μ m, slightly longer (up to 90 μ m) than wide in live specimens, here also with droplike secretory products concentrating around opening of vas deferens into bursa; bursal slit (Fig. 1B, mo) square bracket - shaped with tips oriented laterad. No additional copulatory or subneural glands.

Reproduction

This species is able to reproduce uniparentally, probably by self-fertilization. Freshly hatched and isolated juveniles, devoid of sexual organs, had sperm-filled spermathecae at sexual maturity and they produced eggs, cocoons, and viable offspring. In dense populations maintained over a period of several months, a number of specimens had additional male copulatory organs in XI. They were single or paired and sometimes connected with additional vasa deferentia and even sperm funnels. The genital region in XI was then covered laterally and dorsally with additional clitellar gland cells, separated from the regular clitellum by a transverse interspace. These irregularities, also mentioned in other Enchytraeus species (e.g. E. irregularis NIELSEN & CHRISTENSEN, 1961, E. subitus NURMINEN, 1970), disappeared when the culture substrate was renewed and population density was reduced.

Life cycle data (20-21°C, agar-substrate, abundant food supply): Entire life cycle (from cocoon deposition to cocoon deposition): 19-32 days. Number of eggs per cocoon: 1-8, x=3.6, (n=18). Time from cocoon deposition to hatching [days]: 6-23, x=10.4, (n=16). Time from hatching to sexual maturity [days]: 13-23, x=17.8, (n=11).

Discussion

Comparison with other species

E. luxuriosus is separable from all other known *Enchytraeus* species by the combination of the following characters: (1) length about 1 cm; (2) segments number around 45; (3) the exact chaetal formula, i.e.: ventrally 3 chaetae per bundle throughout, laterally 2 chaetae throughout in preclitellar bundles, 3 or 2 chaetae per bundle in postclitellar bundles; (4) coelomocytes pale, with fine spherical vesicles but without refractile granula; (5) sperm funnel small, roughly spherical, collar much narrower than funnel body; (6) seminal vesicle medium-sized to large; (7) male copulatory organ (penial bulb) small and compact; (8) spermathecal ectal duct much shorter than ampulla, ampulla twice as long as

wide, ental duct as long as ampulla, bouquet $_{\mbox{of}}$ glands around ectal orifice.

E. luxuriosus is morphologically close to a taxonomically most difficult complex of species around F buchholzi VEJDOVSKÝ, 1878 and E. christenseni DÓZSA-FARKAS, 1992 (formerly E. minutus NIELSEN & CHRISTENSEN, 1961) which also comprises unidentified forms (CHALUPSKÝ 1986), sometimes assigned to E buchholzi sensu lato (ROTA 1995 and references therein). The situation is complicated by morphological species conceptions especially of E. buchholzi that differ between authors, by its unknown range of morphological variability, and by the fact that specimens of this species complex are found practically always and everywhere except in marine situations. Most probably, E. luxuriosus has been recorded several times under the name of either E. minutus or E. buchholzi.

Nevertheless, when referring to the original descriptions, the morphological differences between E. luxuriosus and the two mentioned species are clearcut; E. christenseni has (1) only 26-27 segments, (2) the clitellar gland cells are arranged in transverse rows with clear interspaces, (3) and the spermatheca has a long ectal duct with small gland cells at its entire length and a spherical ampulla which is never longer than the ectal duct. E. buchholzi VEJDOVSKÝ 1878 (VEJDOVSKÝ 1879), despite apparent inaccuracies (UDE 1892) and doubtful characters in the original description (SCHMELZ et al. 1999), is also distinct from E. luxuriosus in possessing (1) only 26-28 segments, (2) very large male copulatory organs, (3) a voluminous and much swollen spermathecal ampulla, and (4) a small and simple collar of glands at the spermathecal ectal orifice.

E. buchholzi has been redescribed by NIELSEN & CHRISTENSEN (1959), and the majority of posterior records of the species refer to their morphological diagnosis. Redescription and original description, however, are not identical, e.g. NIELSEN & CHRISTEN-SEN (1959) state the male glandular (penial) bulb to be small, whereas it is large and inflated in VEJDOVSKÝ (1879). The complicated identity of E. buchholzi cannot be treated here, but E. luxuriosus must be compared with E. buchholzi sensu NIELSEN & CHRISTENSEN (1959) all the more as it has spermathecae identical with those of E. luxuriosus. It differs from the new species in possessing (1) coelomocytes with coarse refractile granules, (2) small seminal vesicles, occupying half of segment XI or less, (3) two and three chaetae in ventral bundles, (4) coelomocytes that are only slightly smaller than the preclitellar chaetae. Other differences, such as the higher variability in size and segment number (24-40), the arrangement of clitellar gland cells in transverse rows and the shape of the pharyngeal glands, need reinvestigation. Although the mentioned differences are small, we consider them to be species-specific and speciesseparating. The coelomocyte granulation, for example, is constant in a large number of different *Enchytraeus* cultures, including the cultures of *E. luxuriosus*, reared over a period of three years under varying conditions (SCHMELZ, personal observation).

On further taxonomically useful characters

Some of the above-mentioned eight characters (e.g. coelomocytes, size of seminal vesicle) are only rarely mentioned in other Enchytraeus species descriptions and therefore of limited use for the separation of E. luxuriosus, although they characterize the new species and facilitate its correct identification. This also applies to other easily examinable morphological traits, such as the shape of clitellum, which is saddlelike, i.e. absent midventrally, here, and the number of preclitellar nephridia (four, from 6/7 to 9/10). Other taxonomically possibly useful characters require further studies. The spermatheca in E. luxuriosus, for example, is exactly as NIELSEN & CHRISTENSEN (1959: 93) have stated for E. buchholzi "...the ectal duct is short and all along its length with a dense layer of dand cells but without special glands round the ectal orifice; when the ectal duct is contracted the glands may appear to be arranged in a rosette round the ectal orifice ... " However, they apparently assume that the gland cells form a second epithelial layer that overlies the ectal duct wall epithelium, as they entirely agree with BACKLUNDs description of the spermatheca in E. buchholzi ssp. suecica (1947, Fig. 3), the ectal duct of which is described as consisting of two epithelia, an inner and an outer glandular one. Judging from our observations not only on E. luxuriosus but also on a large number of other species and unclassified forms (SCHMELZ et al. 1999), the spermathecal ectal duct in Enchytraeus has only one epithelial layer, and the ectal glands are nothing but the enlarged and bulged ectal duct wall cells themselves. Further investigations must show whether BACKLUNDS (and NIELSEN & CHRISTENSENS) observations are erroneous or whether they represent a distinct type of spermathecae in Enchytraeus.

Furthermore, the arrangement of clitellar gland cells in *E. luxuriosus* is difficult to specify. It comes close to what BELL (1947) describes as "indefinite transverse rows" for *E. florentinus*. The usual distinction in *Enchytraeus* species descriptions is between "regular", i.e. in transverse rows, and "irregular", i.e. not in rows and in a more reticulate arrangement (NIELSEN & CHRISTENSEN 1959), but MÖLLER (1971) states that the difference is not always obvious and that an arrangement should be named "regular" only when transverse interspaces between the cell rows are visible throughout. Interspaces are absent in *E. luxuriosus*, and the distribution pattern changes between a transverse and a reticulate orientation in

one and the same animal, depending on the observed region, the mode of observation and the state of contraction of the animal. Notwithstanding its vagueness. this intermediate character state is taxonomically useful as it clearly differs from an arrangement in distinct rows as in E. norvegicus ABRAHAMSEN, 1969 and an overall reticulate arrangement as in E. japonensis NAKAMURA, 1993 (SCHMELZ et al. in press). The anterior branching pattern of the blood vessels may also yield taxonomically useful information, but at present it is unknown in most Enchytraeus species. The pattern of *E. luxuriosus* is identical with that in *E.* albidus (MICHAELSEN 1886) but it differs from those in the fragmenting species E. bigeminus NIELSEN & CHRISTENSEN, 1963 (CHRISTENSEN 1964) and E. japonensis NAKAMURA, 1993 (SCHMELZ et al., 2000). VEJDOVSKÝ (1879) discovered only the anterior double pair of small commissural vessels in E. buchholzi. Future studies must elucidate the intrageneric variability of that character. The same applies to the distribution of anterior perikarya in the brain and of enlarged ventral epithelial cells in the posterior intestine, which ROTA (1995) and ROTA et al. (1999) have suggested to be of taxonomic or systematic value.

Acknowledgements

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