Research paper

# *Paralumbricillus* gen. nov. and other new marine enchytraeids from the North Atlantic

Mårten J. Klinth[1,3], Emilia Rota[2], Svante Martinsson[3], Christer Erséus[3]

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*Lumbricillus* is one of the largest enchytraeid genera and its species can mainly be found on the coasts of temperate and polar regions around the world. However, the monophyly of the genus has been questioned by recent molecular studies. In this paper we further examine the phylogenetic relationships of *Lumbricillus* species and their close relatives by estimating a phylogeny of 62 species, many collected along the Norwegian coastline, with seven genetic markers. We confirm *Lumbricillus* to be non-monophyletic and resolve this issue by establishing the new genus *Paralumbricillus*, into which ten of the known species are transferred: *Paralumbricillus arenarius*, *Paralumbricillus cervisiae*, *Paralumbricillus christenseni*, *Paralumbricillus crymodes*, *Paralumbricillus dubius*, *Paralumbricillus eltoni*, *Paralumbricillus eudioptus*, *Paralumbricillus muscicolus*, *Paralumbricillus nielseni*, *Paralumbricillus westheidei*, all comb. nov. In this paper we also describe eight new species: *Lumbricillus bibulbus*, *L. boreas*, *L. elisae*, *Paralumbricillus bicornis, P. bilobatus, P. lofotensis*, *P. sanguineus*, and *Claparedrilus torquatus*.

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*1. Station Linné, Ölands Skogsby 161, SE-386 93 Färjestaden, Sweden*
*2. Department of Physics, Earth and Environmental Sciences, University of Siena, Via P.A. Mattioli 4, IT-53100 Siena, Italy*
*3. Department of Biological and Environmental Sciences, University of Gothenburg, Box 463, SE-405 30 Göteborg, Sweden*

*Corresponding author:* Mårten Klinth
*E-mail:* marten@stationlinne.se

## INTRODUCTION

With regard to clitellate annelid worms, marine beaches of the North Atlantic Ocean are dominated by enchytraeids, and three genera in particular: *Marionina* sensu lato Michaelsen, 1890 (in Pfeffer (1890)), *Enchytraeus* Henle, 1837 (specifically the *E. albidus* complex, see Erséus *et al*. (2019)), and *Lumbricillus* Ørsted, 1844. *Lumbricillus*, with its about 80 species, is found throughout the littoral zone, with larger species generally living under rocks and among stranded algae and beach detritus, and smaller species interstitially in finer sediments. Previous molecular studies have questioned the monophyly of *Lumbricillus* because a number of species, referred to as the *arenarius* group (Klinth *et al*. 2017b), have been found to be more closely related to *Marionina* sensu stricto and *Grania* Southern, 1913 (Erséus *et al*. 2010; Klinth *et al*. 2017a; Klinth *et al*. 2022). In this study, we attempt to resolve the true phylogenetic relationship between these *Lumbricillus*-like taxa by including more species from both the *arenarius* group and the rest of *Lumbricillus* sensu lato.

## MATERIAL AND METHODS

Worms were mainly collected between 2014–2018 from the Norwegian coastline, but also Denmark, Greenland, Spain, Svalbard, and Sweden, by sieving through the intertidal substrate, or by hand picking larger worms, and preserving them all in 80 % ethanol. The specimens were sorted in the lab after fixation and had their posterior ends cut off for

molecular studies. The anterior ends were stained in paracarmine, dehydrated in ethanol and xylene, and mounted in Canada balsam on microscope slides, following Erséus (1994), to be used for the morphological studies. The specimens were illustrated using a camera lucida and the figures were edited using the software Gimp v.2.8.10. Some specimens were borrowed from the Natural History Museum, London (BMNH) for comparisons to our specimens, and in some cases to be illustrated. The new vouchers are deposited in the Swedish Museum of Natural History (SMNH; Stöhr 2023), the Zoological Museum, University of Bergen (ZMBN) or the Norwegian University of Science and Technology, NTNU University Museum in Trondheim (NTNU-VM; Bakken *et al*. 2023). Supplementary Table 1 contains more specific data on collecting sites and sequence data (with GenBank accession numbers) of the studied specimens.

The posterior ends were lysed in QuickExtract and the extracted DNA was used to amplify seven genetic markers (COI, 12S and 16S from the mitochondrion, 18S, 28S and ITS2 from the nuclear ribosomal genome, and Histone 3 (H3)), using the primers and PCR protocols in Klinth *et al*. (2022). All sequencing was performed by Eurofins and the resulting sequences edited in Geneious v.6.1.8 (created by Biomatters; available from http://www.geneious.com). All specimens were sequenced for COI, the commonly used DNA barcode for animal species, and this marker was used to initially cluster the specimens into hypothetical species. A subsample of specimens was then sequenced for 16S and the independently evolving nuclear ITS2 and H3, to be used for species delimitation. A further subsample of specimens was sequenced for 12S, 18S and 28S to be used in estimating the phylogeny (Table S1).

Gene trees for COI, 16S, H3 and ITS2 were estimated in MrBayes v.3.2.6 (Ronquist *et al*. 2012), by combining our newly generated data with the dataset used to estimate the species tree in Klinth *et al*. (2022), see Table S1. The sequences of each genetic marker were aligned using MAFFT (Katoh *et al*. 2002) and the alignment for ITS2 was further refined using MUSCLE (Edgar 2004), resulting in 120 specimens for COI (658bp); 113 specimens for 16S (499bp); 104 specimens for H3 (328bp); and 108 specimens for ITS2 (556bp). In the ITS2 dataset, for one heterozygous specimen the two alleles were separated using the PHASE algorithm (Stephens & Donnelly 2003, Stephens *et al*. 2001), as implemented in DNAsp v.5.10 (Librado & Rozas 2009) resulting in 109 sequences. The four gene trees were estimated using nst = mixed (to allow the program to estimate the substitution models), rates = invgamma, and brlenspr = unconstrained:Exp(100). COI and H3 were partitioned according to codon position, each partition unlinked to allow for different base frequencies, shape of the gamma distribution, proportion of invariable sites and substitution rates. The mcmc was set to run for 10 million generations with two chains sampled every 10 000 generations, and consensus trees were summarized after discarding the initial 25 % as burn-in. To ensure proper convergence, the p-files were evaluated in Tracer v.1.7 (Rambaut *et al*. 2018).

A species tree was estimated in *BEAST (Heled & Drummond 2010) by again combining the species tree dataset from Klinth *et al*. (2022) with a subset of our new data for all seven genetic markers. In total, 77 specimens were included, grouped into 62 species, where *Bryodrilus diverticulatus* Černosvitov, 1929 and *Globulidrilus riparius* (Bretscher, 1899) were included as additional outgroups. Four specimens with sequences generated for this study were lacking one of the seven markers and were included by replacing the missing marker with a sequence entirely made up of N's (see Table S1). Due to their linked inheritance, COI, 12S and 16S as well as 18S, 28S and ITS2 were, respectively, given linked tree models. Each genetic marker was set as unlinked for site and clock models, using HKY+G+I as the substitution model, with empirical base frequencies. The model was selected as a compromise between the number of parameters that needed to be estimated (thereby reducing computation time) and the fit to the data. The clocks were set as lognormal relaxed uncorrelated with the evolutionary rate for COI set as 1 and all other rates estimated in relation to that. The tree priors used the Yule process with piecewise linear and constant root for population sizes. The Yule process was used as it is computationally less intensive compared to more complex models like the Birth-Death process, as it does only assume speciation and no extinction. The ploidy size of the mitochondrial markers was manually doubled in the XML-file to account for the fact that the worms are hermaphrodites. The clock priors (which were arranged in relation to the fixed value of 1 for COI) were set as uniform ranging from 0 to 2 with an initial value of 1 for 12S, 16S and ITS2, and 0 to 1 with an initial value of 0.5 for 18S, 28S and H3, based on previous knowledge on the relative substitution rates of the genes (Klinth *et al*. 2022). The species.popMean and species.yule.birthRate priors were given lognormal priors with default values. The species tree was run for 500 million generations in BEAST v1.8 (Drummond *et al*. 2012) with sampling every 50 000 generations. The result was evaluated in Tracer v.1.7, TreeAnnotator v.1.8 was used to remove the first 10 % as burn-in, and a maximum clade credibility tree was generated using median node heights. The gene trees and the species tree were illustrated using FigTree 1.4.2 (Rambaut 2014) and further edited in Adobe Illustrator.

# RESULTS

## Molecular analyses

The COI gene tree (Figure 1) revealed 12 distinct clusters from the newly sampled specimens, all more than 10% genetically distant from the other included specimens and with less than 2% variation within (uncorrected p-distances) the clusters. Virtually all the same clusters were also found in the 16S, ITS2 and H3 gene trees (Figs. S1-3), supporting them as corresponding to separate species (further supported by differences in morphology, see below). The only exception was *L. elisae* sp. nov. which was found together with *L. lineatus* (Müller, 1774) in the H3 gene tree (Figure S3), but H3 is known to evolve slowly and we still consider *L. elisae* sp. nov. a separate species supported by the other gene trees and by its unique morphology.

The species tree (Figure 2) largely follows the topology of the one in Klinth *et al*. (2022) (the data of which were included in the dataset that we used for the new tree). We confirm the superclade containing *Lumbricillus* s. str., *Marionina* s. str. (i.e., three species from the Southern Hemisphere), *Grania* and the previously coined "*arenarius* group", the latter described herein as *Paralumbricillus* gen. nov., all with high support (PP>0.98). The superclade also includes the ambiguous species "*Lumbricillus*" cf. *macquariensis*, the taxonomic status of which has not yet been properly determined, although it is clearly not affiliated with any of the previously recognized genera in the superclade, neither genetically nor morphologically (Klinth *et al*. 2022). Three of the species described herein as new were found within *Lumbricillus* s. str.: *L. boreas* sp. nov. and *L. elisae* sp. nov. are nested with *L. scoticus* Elmhirst & Stephenson, 1926 within the *lineatus* group (Klinth *et al*. 2017a), and *L. bibulbus* sp. nov. is sister to the *lineatus* group, while the undetermined *L.* sp. "Greenland" is sister to the *pagenstecheri* group (Klinth *et al*. 2017a). Another four of the new species were found within *Paralumbricillus* gen. nov. [*P. bicornis* sp. nov., *P. bilobatus* sp. nov., *P. lofotensis* sp. nov., and *P.*

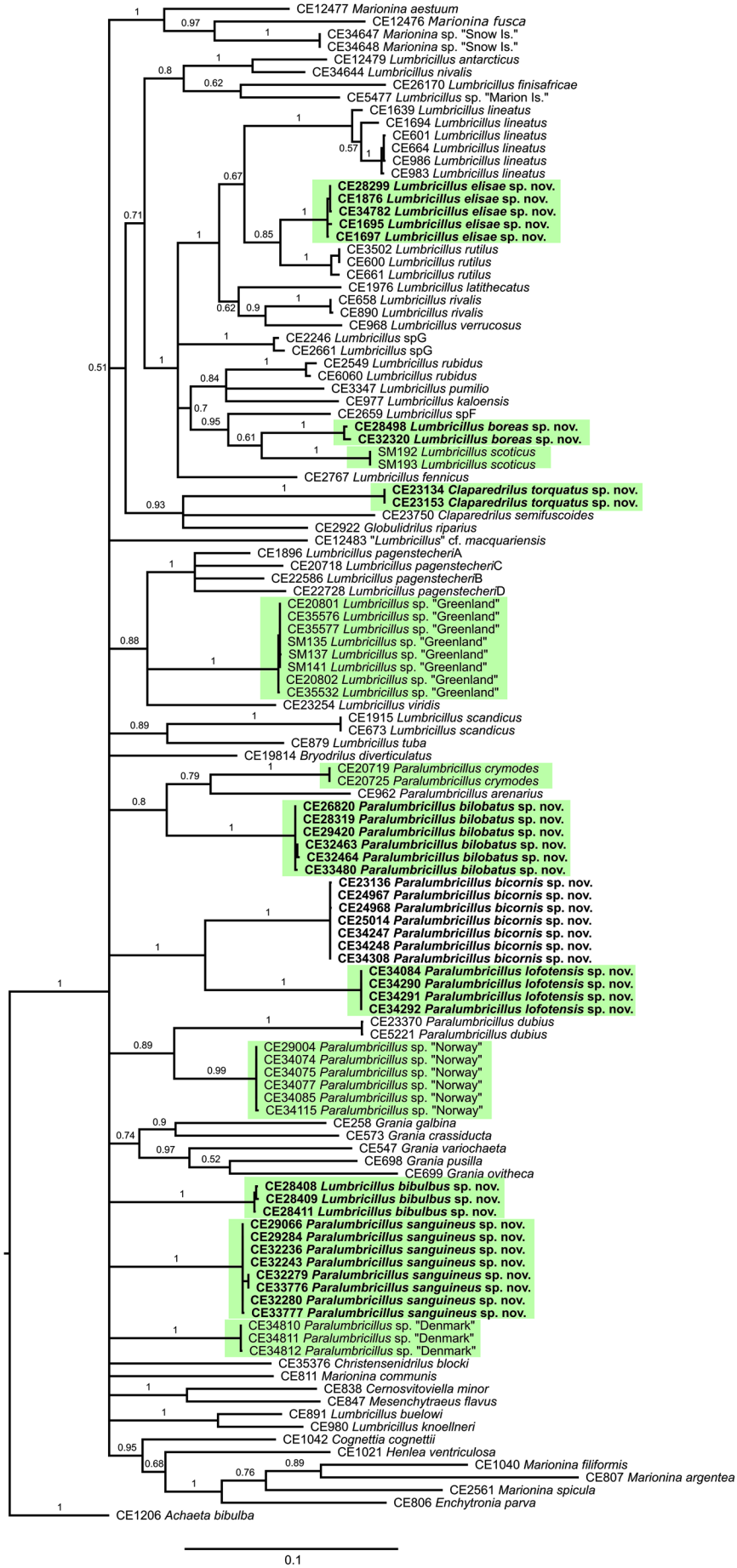



Figure 1. Majority-rule consensus tree for COI estimated with Bayesian inference. Specimens marked in green are new to this study. Support values are posterior probabilities. Scale bar represents the estimated number of substitutions per site.

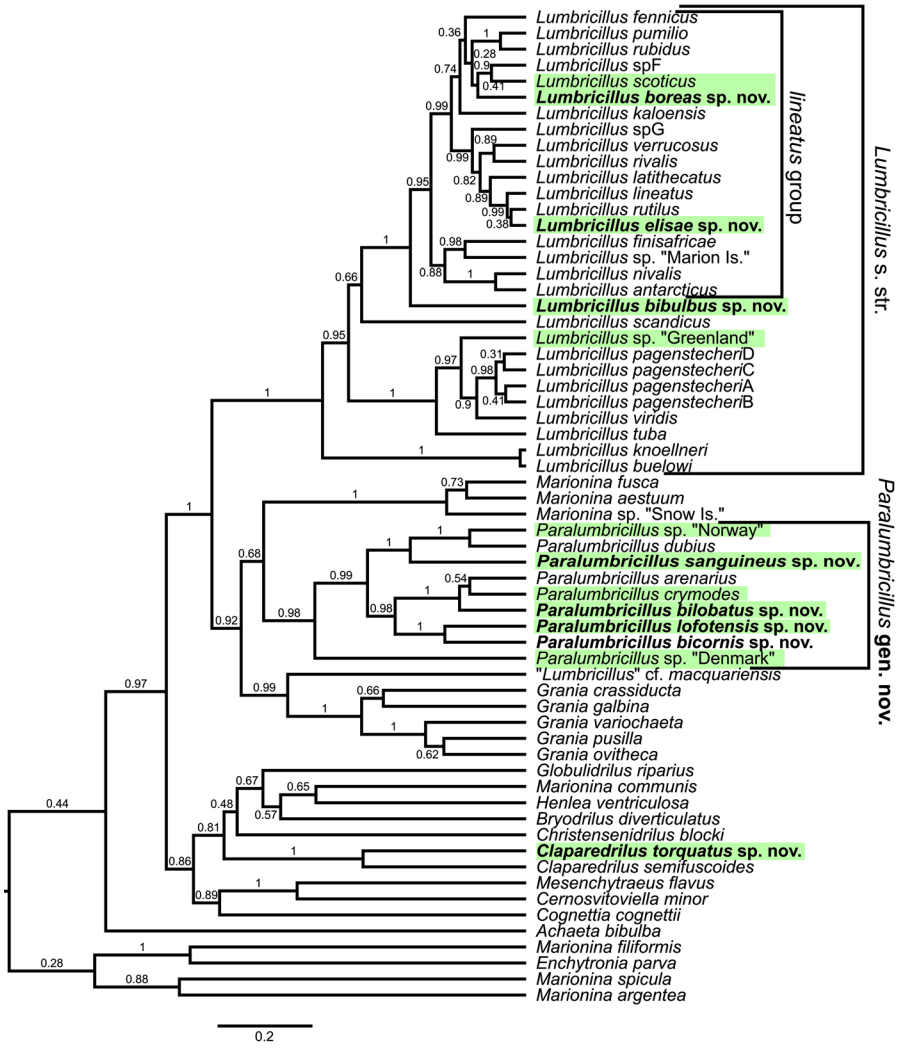



Figure 2. Species tree estimated using the multispecies coalescent model in *BEAST. Species marked in green are new to this study. Species new to science are highlighted in bold. Support values are posterior probabilities. Scale bar shows the expected number of changes per site scaled in accordance with the substitution rate of COI.

*sanguineus* sp. nov.], along with *P. crymodes* (Stephenson, 1922) and the undetermined *P.* sp. "Denmark". However, *P.* sp. "Denmark" is positioned as sister to the remaining species of this new genus with quite some genetic distance, and since none of the studied specimens was fully mature we have yet to decide whether to consider it as a member of this genus. Finally, the last of the new species [*C. torquatus* sp. nov.] was found as sister to *Claparedrilus semifuscoides* Klinth, Rota & Erséus, 2017b, and is supported as a member of the same genus also by morphology (see below).

## Taxonomy

### On the penial bulbs of *Lumbricillus* and its close relatives

In this study many species with intricate morphology of the penial bulbs were found, mainly in *Paralumbricillus* gen. nov. but also some in *Lumbricillus* s. str. This made us want to re-examine the species treated in previous works more carefully. Indeed, we found that the penial bulbs of *Lumbricillus* s. str. and some species now transferred to *Paralumbricillus* gen. nov. were not as round and compact as initially thought. Instead, the general shape of the bulbs seems to be slightly bilobed, with a main lobe extending dorsolaterally from the pore and a smaller lobe that extends ventromedially (Figure 3A). The smaller lobe is hard to make out in a whole-mounted worm, which is often viewed from the lateral side. The vas deferens enters through the larger lobe. We will continue to refer to these penial bulbs as compact and only use "bilobed" to describe penial bulbs where there is a distinct division between these two lobes and where the smaller lobe is of considerable size, close to that of the larger lobe (Figures 3B–C).

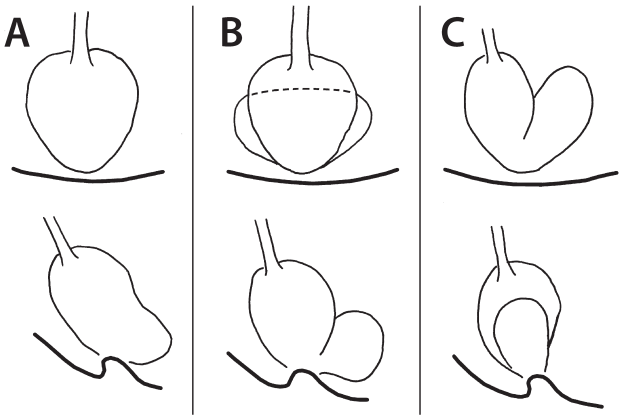



Figure 3. General organisation of the penial bulbs of *Lumbricillus* and *Paralumbricillus* gen. nov. in lateral view (top) and cross section (bottom), thick line representing body wall. **A** Compact bulb. **B** Bilobed bulb with dorsolateral and ventromedial lobes. **C** Bilobed bulb with anterior and posterior lobes.

Table 1. The morphological groups of *Lumbricillus*, updated from Klinth *et al.* (2017b), the "*tuba*" group is not monophyletic.

| | Testis sacs | Spermathecal shape | Penial bulb shape | Spermfunnels | Chaetae per bundle |
|---|---|---|---|---|---|
| *lineatus* group | Regularly lobed, fan-shaped | Spindle-shaped, indistinct ampulla | Compact or bilobed | 1-5 times longer than wide | 3-6 or more |
| *pagenstecheri* group | Regularly lobed, fan-shaped | Club-shaped, distinct ampulla, glands along duct | Compact | About twice as long as wide | 3-6 or more |
| "*tuba*" group | Regularly lobed, fan-shaped | Club-shaped, distinct ampulla | Compact | About as long as wide | 3-6 |
| *buelowi* group | A single compact mass | Club-shaped, distinct ampulla | Compact | About as long as wide | 2-3 |
| *lineatus* group | *L. alaricus* Shurova, 1974<br>*L. antarcticus* Stephenson, 1932b<br>*L. americanus* (Ude, 1896)<br>*L. borea*s sp. nov.<br>*L. elisae* sp. nov.<br>*L. enteromorphae* von Bülow, 1957<br>*L. fennicus* Nurminen, 1964<br>*L. finisafricae* Klinth, Rota & Erséus, 2022<br>*L. healyae* Rodriguez & Rico, 2008<br>*L. incisus* Wang & Liang, 1997<br>*L. insularis* (Ude, 1896)<br>*L. immoderatus* Finogenova, 1988<br>*L. kaloensis* Nielsen & Christensen, 1959<br>*L. latithecatus* Klinth, Rota & Erséus, 2017b<br>*L. lineatus* (Müller, 1774)<br>*L. maximus* (Michaelsen, 1888)<br>*L. minimus* (Černosvitov, 1929) | | | *L. minutus* (Müller, 1776) sensu Michaelsen, 1911<br>*L. murmanicus* Finogenova & Streltsov, 1978<br>*L. nivalis* Klinth, Rota & Erséus, 2022<br>*L. parabolus* Shurova, 1978<br>*L. parvus* (Ude, 1896)<br>*L. pseudominutus* Timm, 1988<br>*L. pumilio* Stephenson, 1932a<br>*L. pygmaeus (*Michaelsen, 1935)<br>*L. rivalis* Levinsen, 1884<br>*L. rubidus* Finogenova & Streltsov, 1978<br>*L. rupertensis* Coates, 1981<br>*L. rutilus* Welch, 1914<br>*L. sadovskyi* Marcus, 1965<br>*L. santaeclarae* Eisen, 1904<br>*L. scoticus* Elmhirst & Stephenson, 1926<br>*L. sejongensis* Lee, Klinth & Jung, 2019<br>*L. verrucosus* (Claparède, 1861) | |
| *pagenstecheri* group | *L. annulatus* Eisen, 1904<br>*L. belli* Tynen, 1969<br>*L. corallinae* Shurova, 1977<br>*L. curtus* Coates, 1981<br>*L. franciscanus* Eisen, 1904<br>*L. ignotus* Shurova, 1977<br>*L. kalatdlitus* Nurminen, 1970<br>*L. kamtschatkanus* (Michaelsen, 1929)<br>*L. kurilensis* Shurova, 1974<br>*L. maritimus* (Ude, 1896)<br>*L. merriami* Eisen, 1904<br>*L. mirabilis* Tynen, 1969 | | | *L. orientalis* Shurova, 1974<br>*L. pagenstecheri* (Ratzel, 1868)<br>*L. pinquis* Shurova, 1977<br>*L. qualicumensis* Tynen, 1969<br>*L. reynoldsoni* Backlund, 1948<br>*L. rufulus* Shurova, 1974<br>*L. taisiae* Shurova, 1978<br>*L. tenuis* (Ude, 1896)<br>*L. tsimpseanis* Coates, 1981<br>*L. sapitus* Shurova, 1979<br>*L. similis* Shurova, 1977<br>*L. viridis* Stephenson, 1911 | |
| "*tuba*" group | *L. balticus* von Bülow, 1957<br>*L. bibulbus* sp. nov.<br>*L. charae* (Tynen, 1970)<br>*L. helgolandicus* (Michaelsen, 1927)<br>*L. imakus* Nurminen, 1970<br>*L. lentus* Shurova, 1978 | | | *L. macrothecatus* Erséus, 1976<br>*L. niger* Southern, 1909<br>*L. ochotensis* Shurova, 1979<br>*L. scandicus* Klinth, Rota & Erséus, 2017b<br>*L. tuba* Stephenson, 1911 | |
| *buelowi* group | *L. buelowi* Nielsen & Christensen, 1959<br>*L. knoellneri* Nielsen & Christensen, 1959 | | | *L. mangeri* (Michaelsen, 1914) | |
| *Uncertain placement* | *L. algensis* Erséus, 1977 (seminal vesicles irregularly lobed but otherwise *lineatus*-like) possibly a member of *Paralumbricillus*<br>*L. brunoi* Martinez-Ansemil, 1982 (seminal vesicles irregularly lobed but otherwise *lineatus*-like) possibly a member of *Paralumbricillus* | | | *L. horridus* Finogenova, 1988 (intricate penial apparatus unlike that of other *Lumbricillus*)<br>*L. intricatus* Finogenova, 1977 (spermathecae with ventral openings, nodulate chaetae, but otherwise *lineatus*-like)<br>*L. macquariensis* Benham, 1905 | |

### On the position of the chaetae of *Lumbricillus* and its close relatives

The three genera with species descriptions treated herein (*Lumbricillus*, *Paralumbricillus* gen. nov. and *Claparedrilus* Klinth, Rota & Erséus, 2017b) all have the upper chaetal bundles that are positioned high above the lateral line, and we therefore refer to them as dorsolateral bundles. Rota (2001), in the redescription of *Lumbricillus maximus* (Michaelsen, 1888), describes the position of the upper bundles in relation to the lower bundles in this way: "interval between the two dorsolateral bundles (DD) as great as that between two homolateral bundles (DV) and twice the distance between the two ventral bundles (VV), (DD = DV = 2VV)", which is also true for the species treated in this study.

*Abbreviations in the figures*

as=anteseptale, b=brain, dg=duct glands, ds=developing sperm, e=mature or maturing egg, ed=ectal duct of spermatheca, eg=ectal gland, en=ental duct of spermatheca, mu=musculature, nd=nephridial duct, oe=oesophagus, oo=oocytes, ov=ovary, pb=penial bulb, pg=pharyngeal glands, ph=pharynx, ppb=postpharyngeal bulb, pr=prostate gland, ps=postseptale, sa=spermathecal ampulla, sf=sperm funnel, sm=sperm mass, sp=spermathecal pore, t=testis, ts=testis sac, vd=vas deferens.

## ***Lumbricillus*** Ørsted, 1844

**Type species.** *Lumbricus lineatus* Müller, 1774.
**Included species.** See Table 1.

## ***Lumbricillus elisae*** Klinth & Rota sp. nov.

Figure 4

urn:lsid:zoobank.org:act:89F72C45-268A-4258-9019-C21F1B4EAE3E

**Holotype.** SMNH Type Coll. 9896 (CE34782), Figures 4B, C, E, an amputated mature specimen stained in paracarmine and mounted on a slide. COI barcode: BOLD NVENC1608-22.

**Type locality.** Vilsund, Erslev, Nordjylland, Denmark. Upper-intertidal, in shelly sand and decaying algae. Coll. M. Klinth & Elise Eriksson, 16 May 2018.

**Paratypes.** SMNH Type Coll. 9897 (CE1695) & SMNH Type Coll. 9898 (CE1697) two mature specimens from Spain. For details on collection site and GenBank accession numbers see Table S1.

**Other material examined.** SMNH 212150 (CE1876) an immature specimen from Sweden, and ZMBN 128876 (CE28299) an immature specimen from Norway. For details on collection site and GenBank accession numbers see Table S1.

**Etymology.** Named after the first author's sister who collected the specimen we designate as the holotype.

**Diagnosis.** This species is distinguished from most other *Lumbricillus* species by a distinctly bilobed penial bulb. *Lumbricillus sadovskyi* Marcus, 1965, and *L. finisafricae* Klinth, Rota & Erséus, 2022 have bilobed penial bulbs but with anterior and posterior lobes as opposed to the lateral and ventral lobes in *L. elisae* sp. nov. *Lumbricillus bibulbus* sp. nov. (see below) has similarly lobed penial bulbs but has spermathecae with glands along the ectal duct which *L. elisae* sp. nov. is lacking.

**Description.** Pinkish-orange worms. Length of first 11–36 segments 1.3–4.9 mm (fixed, amputated specimens); first 15 segments 2.1–3.1 mm long; width at clitellum 0.49–0.68 mm. Chaetae sigmoid. Dorsolateral bundles with 3–6 chaetae anterior to clitellum, 3–5 chaetae in postclitellar segments. Ventral bundles with 4–7 chaetae anterior to clitellum, 4–6 chaetae posteriorly. Each worm's longest measured chaetae 55–90 µm long, about 5 µm wide. Clitellum extending over XII–XIII, difficult to discern proportion of coverage of XIII. Head pore at 0/1.

Coelomocytes numerous, 15–20 µm long, round or oval, granulated with distinct nucleus. Paired pharyngeal glands present in IV, V and VI; all pairs converging dorsally (Figure 4A). Dorsal vessel originating in XIII or XIV. Nephridia observed in 7/8–8/9, about 95–110 µm long. Anteseptale small, consisting of funnel only. Postseptale oval, tapering into posteroventral efferent duct (Figure 4B). Brain with posterior incision.

Male genitalia paired (Figure 4C). Testes originating in XI, with testis sacs forming regular club-shaped lobes extending forwards into X or IX. Sperm funnels in XI, more than 285–420 µm long, 150–180 µm wide, making them at least 2–3 times longer than wide, funnels tapering towards vasa deferentia. Large parts of vasa irregularly coiled around ovaries in XII, vasa 15–20 µm wide. Penial bulbs bilobed with larger dorsolateral lobe 110–125 µm in diameter and smaller ventromedial lobe 90–100 µm in diameter (Figures 4C–D), vas entering dorsolateral lobe. No mature eggs observed.

Spermathecae (Figures 4E–F) in V, spindle-shaped, with short ectal duct rapidly widening into ampulla, the latter tapering into ental duct connected to oesophagus. Sperm filling lumen of ampulla. Spermathecae 190–265 µm long, 40–50 µm wide at the ectal duct, 80–95 µm wide at widest part of ampulla. Ectal pore at lateral line surrounded by gland cells forming compact, somewhat lobed mass, glandular body up to 135–180 µm wide. Three midventral subneural glands in XIII–XV, 65–100 µm, 80–100 µm and 45 µm long, respectively; gland in XV not observed in all specimens.

**Geographical distribution including BOLD data.** We find it quite remarkable that our five specimens of this seemingly rare species were found in four different countries, even though three are Scandinavian. Furthermore, there is a 99 % match on BOLD with a specimen collected in Shandong, China (private sequence, not yet published), where it has probably been introduced through shipping. This suggests that this species has a great capability for dispersal.

**Remarks.** In the phylogeny, this species is firmly nested within the *lineatus* group, closest to *L. rutilus* Welch, 1914 and *L. lineatus*. The spermathecae are reminiscent of many species within the *lineatus* group, but the distinctly bilobed penial bulbs distinguish this species from most others. As mentioned as an introductory remark under Taxonomy above, closer studies have shown that the penial bulbs of *Lumbricillus* are not perfectly round and that many species have a tendency for a larger dorsal and a smaller median lobe. However, in most cases said "lobes" are mere protrusions from a single compact bulb, whereas in this species they are clearly divided and only connected at the base, close to the male pore. The known species of *Lumbricillus* with clearly bilobed penial bulbs are *Lumbricillus sadovskyi*, *L. finisafricae*, *L. bibulbus* sp. nov. and possibly *L. scoticus* (see below). The two former species have anterior and posterior lobes, and the rest, including *L. elisae* sp. nov., have dorsolateral and ventromedial lobes. The male apparatus of *L. scoticus* is further complicated with an additional lobe/prostate gland and is discussed in more detail below. The penial bulbs of *L. elisae* sp. nov. are most similar to those of *L. bibulbus* sp. nov., but these two species can easily be differentiated by the morphology of their spermathecae, where *L. bibulbus* sp. nov. has glands along the ectal duct.

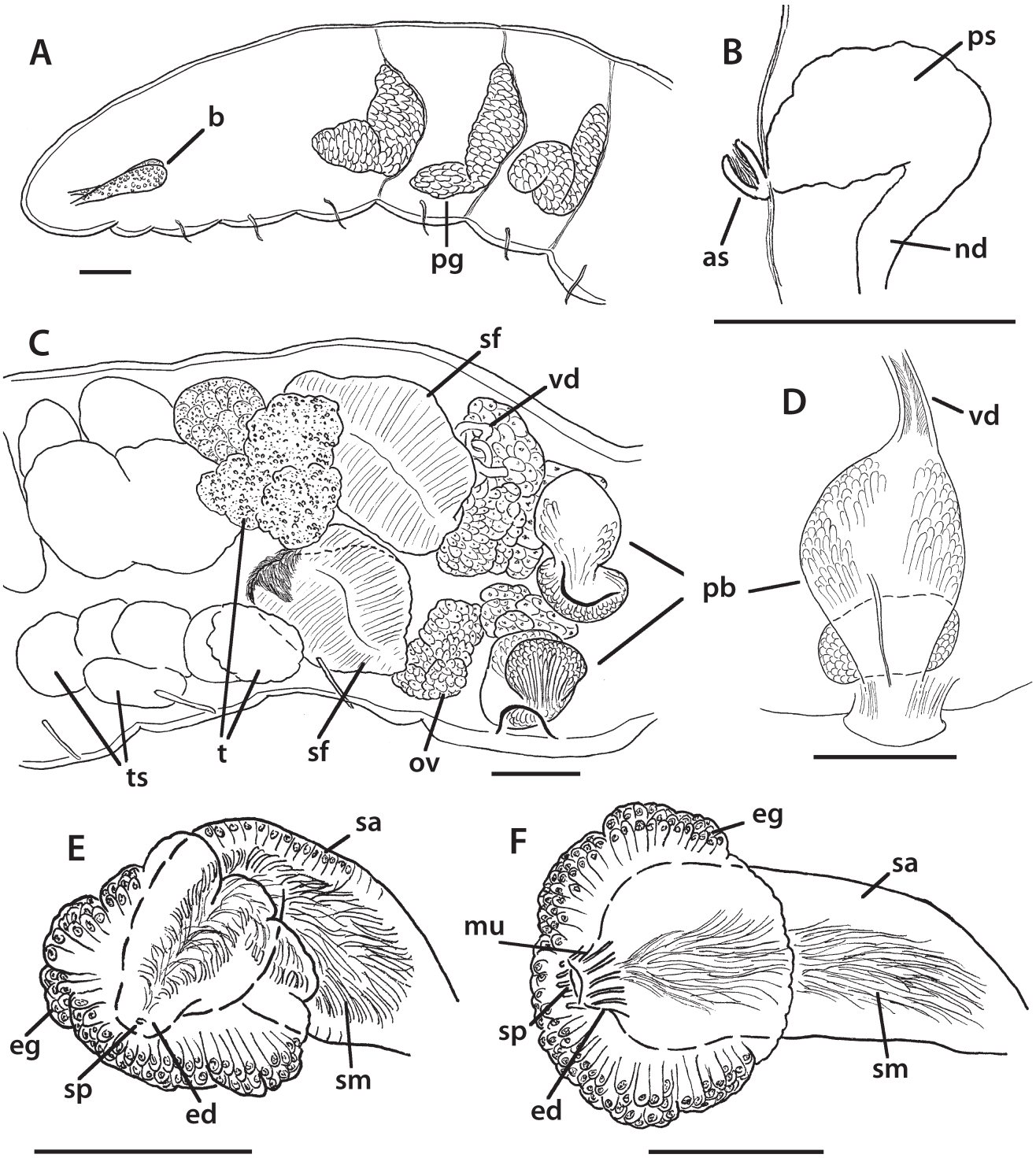



Figure 4. *Lumbricillus elisae* sp. nov. B, C, E=Holotype. **A** Anterior body (SMNH Type Coll. 9897). **B** Nephridium at septum 7/8 (SMNH Type Coll. 9896). **C** Genitalia (Type Coll. 9896). **D** Bilobed penial bulb (SMNH Type Coll. 9897). **E-F** Spermathecae (SMNH Type Coll. 9896 and SMNH Type Coll. 9897). Abbreviations under general notes. Scale bars: 100 µm.

## ***Lumbricillus boreas*** Klinth & Rota sp. nov.

Figure 5

urn:lsid:zoobank.org:act:555A23DD-6F3D-446A-B837-CCB938A9504E

**Holotype.** ZMBN 129201 (CE32320), Figure 5, an amputated mature specimen stained in paracarmine and mounted on a slide. COI barcode: BOLD NOENC415-18.

**Type locality.** Atlanterhavsveien Road, W side of Geitøya Island, Averøy, Møre og Romsdal, Norway. Mid-intertidal, in coarse sand. Coll. C. Erséus & M. Klinth, 31 May 2017.

**Other material examined.** ZMBN 128903 (CE28498) an immature specimen from Norway. For details on collection site and GenBank accession numbers see Table S1.

**Etymology.** Noun in apposition, from the Greek god of the North Wind.

**Diagnosis.** This species is a member of the *lineatus* group (see Table 1). In the spermathecae it resembles above all *L. rivalis* Levinsen, 1884 and *L. rutilus*, but can be separated from both by having shorter sperm funnels, i.e. about as long as wide as opposed to at least twice as long as wide.

**Description.** Length of first 19–20 segments 2.5 and 3.4 mm (two fixed, amputated specimens, respectively); first 15 segments 1.8 and 2.4 mm long; width at clitellum 0.35 mm. Chaetae sigmoid. Dorsolateral bundles with 3–7 chaetae anterior to clitellum, 4–7 chaetae in postclitellar segments. Ventral bundles with 3–7 chaetae anterior to clitellum, 4–7 chaetae posteriorly. Each worm's longest measured chaetae 35–55 µm long, about 3 µm wide. Clitellum extending over 1/2XI–1/2XIII. Head pore not observed.

Coelomocytes numerous, 10–15 µm long, round or oval in shape, granulated with distinct nucleus. Paired pharyngeal glands present in IV, V and VI; all pairs converging dorsally (Figure 5A). Dorsal vessel originating in XI–XIII. Nephridia observed in 7/8–8/9 and from 14/15 rearwards, about 55–70 µm long. Anteseptale small, consisting of funnel only. Postseptale oval, tapering into posteroventral efferent duct (Figure 5B). Brain with posterior incision.

Male genitalia paired (Figure 5C). Testes originating in XI, with testis sacs forming regular club-shaped lobes extending forwards into IX. Sperm funnels in XI, 125 µm long, 115 µm wide, making them about as long as wide, funnels tapering towards vasa deferentia. Large parts of vasa irregularly coiled around ovaries in XII, vasa 15 µm wide. Penial bulbs compact and round, 75 µm in diameter. One mature egg observed.

Spermathecae (Figure 5D) in V, spindle-shaped, with short ectal duct clad in musculature and rapidly widening into ampulla. Ampulla with midway bend, dividing it into two parts, entally connected to oesophagus via tapering ental duct. Sperm in lumen of ampulla and more aggregated in ental part than in ectal part. Spermathecae 185–210 µm long, 20 µm wide at the ectal duct, 50–55 µm wide at widest part of ampulla. Ectal pore at lateral line surrounded by gland cells forming compact mass, glandular body up to 90–95 µm wide. One midventral subneural gland in XIV, 100 µm long.

**Geographical distribution including BOLD data.** Only known

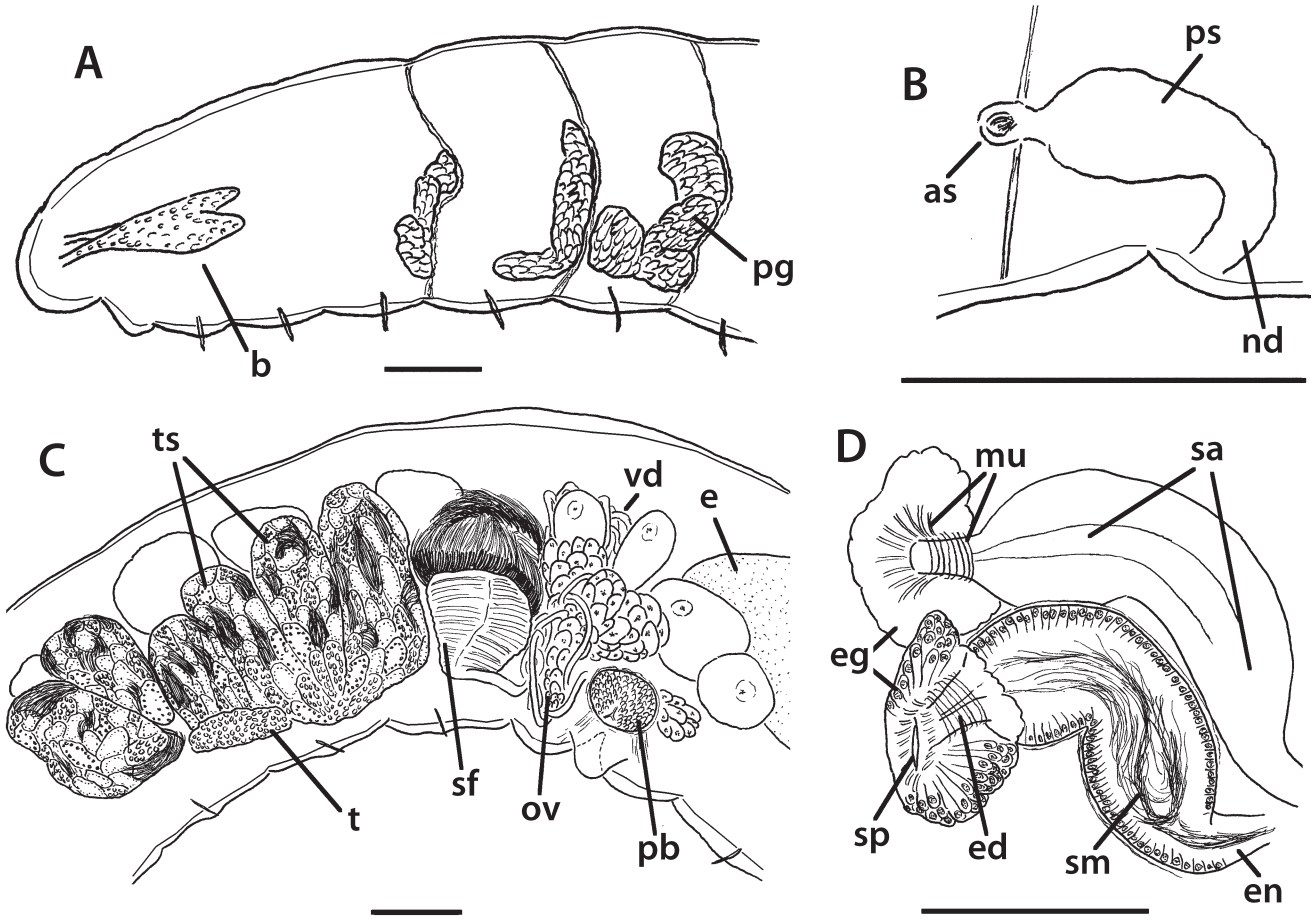



Figure 5. *Lumbricillus boreas* sp. nov. Holotype (ZMBN 129201). **A** Anterior body. **B** Nephridium at septum 8/9. **C** Genitalia. **D** Spermathecae. Abbreviations under general notes. Scale bars: 100 µm.

from Møre og Romsdal and Sogn og Fjordane in Norway.

**Remarks.** Despite only having one mature specimen we have decided to describe this new species based on its clear genetic delimitation and the good quality of the holotype slide. *Lumbricillus boreas* sp. nov. is clearly a member of the *lineatus* group and has a compact penial bulb, as do most other species in this assemblage. Its spermathecae are spindle-shaped and thus at least superficially similar to those of the other members of the group. Most similar are *L. rivalis* and *L. rutilus* and perhaps also the yet unidentified species F and G (Klinth *et al*. 2017b), although the spermathecae of the two latter are only vaguely described due to poor slide mounts. All these four mentioned species do however have sperm funnels that are longer in relation to their width, at least 2 times longer than wide, whereas *L. boreas* sp. nov. has sperm funnels only about as long as wide. This character is known to vary with the contractions of the musculature and organs, when the worms are put in ethanol, and therefore, additional fully mature specimens of this species are required to determine how well this character distinguishes it from its close relatives.

## ***Lumbricillus scoticus*** Elmhirst & Stephenson, 1926

Figure 6

*Lumbricillus scoticus* Elmhirst & Stephenson, 1926: 469-473, figs. 1-3.

*Lumbricillus scoticus*; Christensen 1962: 8; Nurminen 1970: 206; Tynen 1972: 28.

Non *Lumbricillus scoticus*; Erséus 1976: 9.

**Material examined.** SMNH 212160 (SM192) & SMNH 212161 (SM193) two mature specimens from Greenland. For information on collection localities and GenBank accession numbers for COI barcodes see Table S1.

**Description.** Length of first 23–25 segments 4.5 and 5.1 mm (two fixed, amputated specimens, respectively); first 15 segments 3.2 and 3.3 mm long; width at clitellum 0.68 and 0.82 mm. Chaetae sigmoid. Dorsolateral bundles with 6–10 chaetae anterior to clitellum, 8–10 chaetae in postclitellar segments. Ventral bundles with 10–14 chaetae anterior to clitellum, 9–13 chaetae posteriorly. Each worm's longest measured chaetae 135–140 µm long, about 8–10 µm wide. Clitellum extending over XII–3/4XIII. Head pore at 0/1.

Coelomocytes numerous, 20–25 µm long, round, oval or spindle-shaped, granulated with distinct nucleus, in one specimen deeply stained. Paired pharyngeal glands present in IV, V and VI; first two pairs converging dorsally (Figure 6A). Dorsal vessel originating in XI. Nephridia observed in 7/8 and from 14/15 rearwards, about 115–170 µm long. Anteseptale small, consisting of funnel only. Postseptale oval, tapering into posteroventral efferent duct (Figure 6B). Brain with posterior incision.

Male genitalia paired (Figure 6C). Testes originating in XI, with testis sacs forming club-shaped lobes extending forwards into X, lobes not arranged in a typical fan shape. Sperm funnels in XI, slightly lobed and not entirely cylindrical, at least 500–525 µm long, 240–260 µm wide, making them at least twice as long as wide, but probably closer to 3 or 4 times longer than wide in living specimens, funnels tapering towards vasa deferentia. Large parts of vasa irregularly coiled around ovaries in XII, vasa 25–30 µm wide. Male apparatus divided into distinct parts, from male pore a round muscular structure extends dorsolaterally through which the vas deferens connects with the pore. Into the muscular structure two glandular organs connect, one large round bulb positioned dorsomedially, and one smaller pear-shaped bulb anterior to the muscular structure. The diameter of the muscular structure 205–230 µm; large bulb 180–260 µm, and small bulb 85–120 µm. Five to six maturing eggs observed.

Spermathecae (Figure 6D) in V, spindle-shaped, with ectal duct gradually widening into ampulla. Ampulla bent, entally sac-like, connection to oesophagus not distinguishable. Sperm in lumen of duct and ampulla, with heads aggregated in wall of ental part of ampulla. Spermathecae 340–400 µm long, 60–105 µm wide at the ectal duct, 135–150 µm wide at widest part of ampulla. Ectal pore at lateral line surrounded by gland cells forming deeply lobed mass, glandular body up to 265–285 µm wide. No midventral subneural glands observed.

**Geographical distribution including BOLD data.** Reported from Great Britain (Scotland and Wales), Iceland and Greenland.

**Remarks.** Our two specimens from Greenland greatly resemble the original description of *L. scoticus* from Scotland. The size, high number of chaetae and most notably the shape of the penial bulbs suggest that our specimens belong to the same species. The penial bulbs have a unique morphology, not known from any other *Lumbricillus* species, and are described in great detail, although not depicted, in the original description. Elmhirst & Stephenson distinguish in the bulbs six rough parts (a-f), where we could clearly make out (a) where the vas deferens passes through the penial body, (c) the mass of cells that we call the dorsomedial bulb, (d) a pear-shaped gland on the anterior of the penial body, (e) the muscular capsule, and (f) the scattered cells and musculature in between the other parts. Elmhirst & Stephenson also describe (b) a tubular cavity from which (c), the main glandular mass, expands. We could not clearly make this out in our whole mounts but we can assume that the secretions produced in this main bulb are transported through an internal cavity towards the vas deferens and the pore, and that this structure only becomes apparent in sectioned material. Furthermore, the muscular capsule (e) is said to surround "the greater part of the mass" but not the pear-shaped gland (d), whereas we interpret it as being separate from not only the pear-shaped gland but also the larger dorsomedial bulb and mainly surrounding the vas deferens. That said, we did observe other musculature connecting all the different parts of the penial apparatus and still consider our specimens as belonging to *L. scoticus*.

*Lumbricillus scoticus* was originally described from the shores of Great Cumbrae Island in Scotland, and later from other parts of Great Britain (Tynen 1972). Christensen (1962) and Erséus (1976) reported it from Iceland, but subsequently, having studied type material, Erséus concluded his findings to belong to another species (Erséus 1977). Nurminen (1970) reported it from the west coast of Greenland close to where we got our samples.

## ***Lumbricillus bibulbus*** Klinth & Rota sp. nov.

Figure 7

urn:lsid:zoobank.org:act:6F4AE903-82D8-4C98-954D-99DA4D457023

**Holotype.** ZMBN 153439 (CE28409), Figures 7A & E, an amputated mature specimen stained in paracarmine and mounted on a slide. COI barcode: BOLD NOENC411-18.

**Type locality.** Sulesund, Sula, Møre og Romsdal, Norway. Mid-intertidal, in sand and gravel under stones on boulder beach. Coll. C. Erséus, 29 July 2016.

**Paratypes.** ZMBN 128888 (CE28408), ZMBN 153277 (CE28410) & ZMBN 153278 (CE28411) three mature specimens from the type locality. For details on collection site and GenBank accession numbers see Table S1.

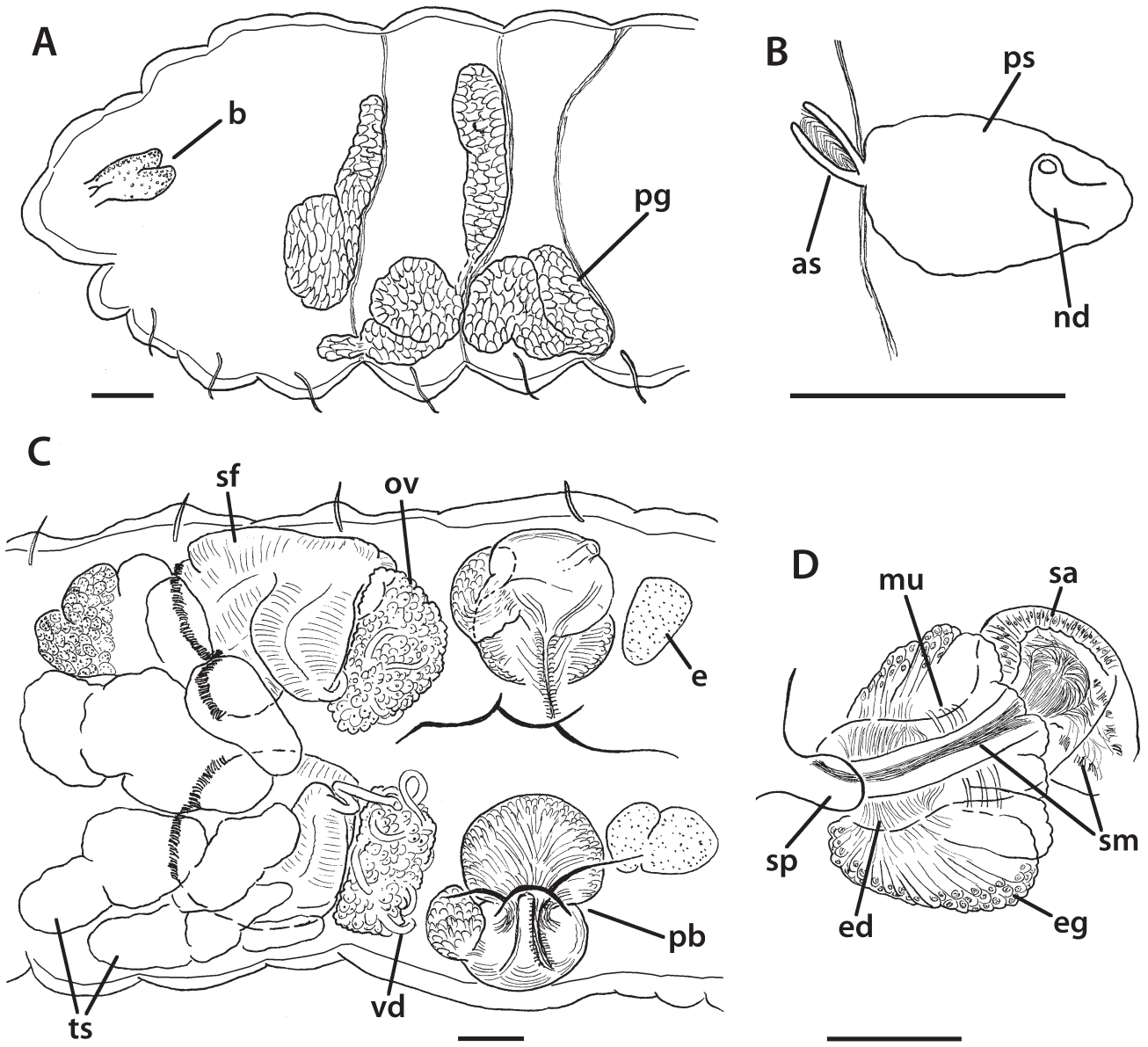



Figure 6. *Lumbricillus scoticus*. **A** Anterior body (SMNH 212160). **B** Nephridium at septum 15/16 (SMNH 212161). **C** Genitalia (note that the eggs are not fully mature) (SMNH 212161). **D** Spermathecae (SMNH 212161). Abbreviations under general notes. Scale bars: 100 µm.

**Etymology.** The name is Latin for two bulbs, referring to the bilobed penial bulbs of this species.

**Diagnosis.** This species can be distinguished from other *Lumbricillus* species by a combination of bilobed penial bulbs and spermathecae with both an ectal gland and glands along the ectal duct.

**Description.** Yellowish worms. Length of first 17–30 segments 2.5–4.3 mm (fixed, amputated specimens); first 15 segments 1.7–2.2 mm long; width at clitellum 0.33–0.39 mm. Chaetae sigmoid. Dorsolateral bundles with (2)3–4 chaetae anterior to clitellum, 2–5 chaetae in postclitellar segments. Ventral bundles with 3–6 chaetae anterior to clitellum, 3–5 chaetae posteriorly. Each worm's longest measured chaetae 55–60 µm long, about 5 µm wide. Clitellum extending over XII–1/2XIII. Head pore at 0/1.

Coelomocytes numerous, 15–20 µm long, round or oval, granulated with distinct nucleus. Paired pharyngeal glands present in IV, V and VI; first and second pairs converging dorsally (Figure 7A). Dorsal vessel originating in XVII. Nephridia observed in 7/8–9/10 and from 13/14 rearwards, about 75–130 µm long. Anteseptale small, consisting of funnel only. Postseptale oval, tapering into posteroventral efferent duct (Figure 7B). Brain with posterior incision.

Male genitalia paired (Figure 7C). Testes originating in XI, with testis sacs forming regular club-shaped lobes extending forwards into IX. Sperm funnels in XI, 135–180 µm long, 65–90 µm wide, making them about 1.5 or 3 times longer than wide, funnels tapering towards vasa deferentia. Large parts of vasa irregularly coiled around ovaries in XII, vasa 10 µm wide. Penial bulbs bilobed with dorsolateral lobe and ventromedial lobe (Figure 7C), both lobes 75–130 µm in diameter, vas entering dorsolateral lobe. One to two mature eggs present at a time.

Spermathecae (Figure 7D) in V, spindle-shaped, with short ectal duct rapidly widening into round ampulla, followed by tapering ental duct connected to oesophagus. Ball of sperm in lumen of ampulla. Spermathecae 80–120 µm long, 20–35 µm wide at the ectal duct, 50–85 µm wide at widest part of ampulla. Ectal pore at lateral line surrounded by gland cells forming compact mass, glandular body up to 80–95 µm wide; glands also along the ectal duct. Two midventral subneural glands in XIV–XV, 55–65 µm and 65 µm long, respectively; not observed in all specimens.

**Geographical distribution including BOLD data.** Only known from the type locality in Møre og Romsdal, Norway.

**Remarks.** At a first glance this new species of *Lumbricillus* is reminiscent of *L. pagenstecheri* (Ratzel, 1868) and the many species that resemble it morphologically. This similarity comes mainly from the spermatheca, which not only has an ectal gland but also glands along the ectal duct, a character shared by the more than 20 species that make up the *pagenstecheri* group. However, unlike *L. pagenstecheri* s. lat., the spermatheca of *L. bibulbus* sp. nov. has a distinct ectal duct and quite large ental duct. The caliber and length of the ectal duct of *L. pagenstecheri* s. lat. can hardly be made out, usually only the thin lumen of the duct is visible among the dense glands along the duct. More importantly, *L. bibulbus* sp. nov. has a bilobed penial bulb, neither seen in the *pagenstecheri* group nor in most *Lumbricillus* species. Backlund (1947) did describe a *Pachydrilus lineatus* with a bilobed penial bulb, but its spermathecae seem more reminiscent of *L. latithecatus* Klinth, Rota & Erséus, 2017b and completely different from those of *L. bibulbus* sp. nov. Also, *Lumbricillus sadovskyi* from South America, and *L. finisafricae* from South Africa have bilobed penial bulbs, but similarly to *L. latithecatus* they have spermathecae that lack glands along the ectal duct and do not have an ampulla as clearly set off from the duct as in *L. bibulbus* sp. nov. Genetically, this new species is not found as sister to the other species in the *pagenstecheri* group but rather as sister to the *lineatus* group (Figure 2).

## *Lumbricillus* sp. "Greenland"

Figure 8

**Material examined.** SMNH 212157 (SM135), SMNH 212158 (SM137) & SMNH 212159 (SM141) three immature or partially mature specimens from Greenland, ZMBN 153287 (CE35532), ZMBN 153288 (CE35576) & ZMBN 153289 (CE35577) three immature or partially mature specimens from Svalbard. For details on collection site and GenBank accession numbers see Table S1.

**Description.** Length of first 16–32 segments 1.4–5.4 mm (fixed, amputated specimens); first 15 segments 1.3–2.7 mm long; width at clitellum 0.26–0.37 mm. Chaetae with ental bend, ectally straight. Dorsolateral bundles with 2–4 chaetae anterior to clitellum, 2–3 chaetae in postclitellar segments. Ventral bundles with 2–4(5) chaetae anterior to clitellum, 2–3 chaetae posteriorly. Each worm's longest measured chaetae 55–95 µm long, about 5 µm wide. Clitellum not developed. Head pore not observed.

Coelomocytes numerous, about 10–25 µm long, round, oval or spindle-shaped, granulated with distinct nucleus. Paired pharyngeal glands present in IV, V and VI; first two, and possibly also the third pair connected dorsally (Figure 8A). Dorsal vessel originating in X–XII. Nephridia observed in 7/8–9/10, and postclitellar segments, about (60)105–165 µm long. Anteseptale small, consisting of funnel only. Postseptale oval, tapering into posteroventral efferent duct (Figure 8B). Brain with posterior incision.

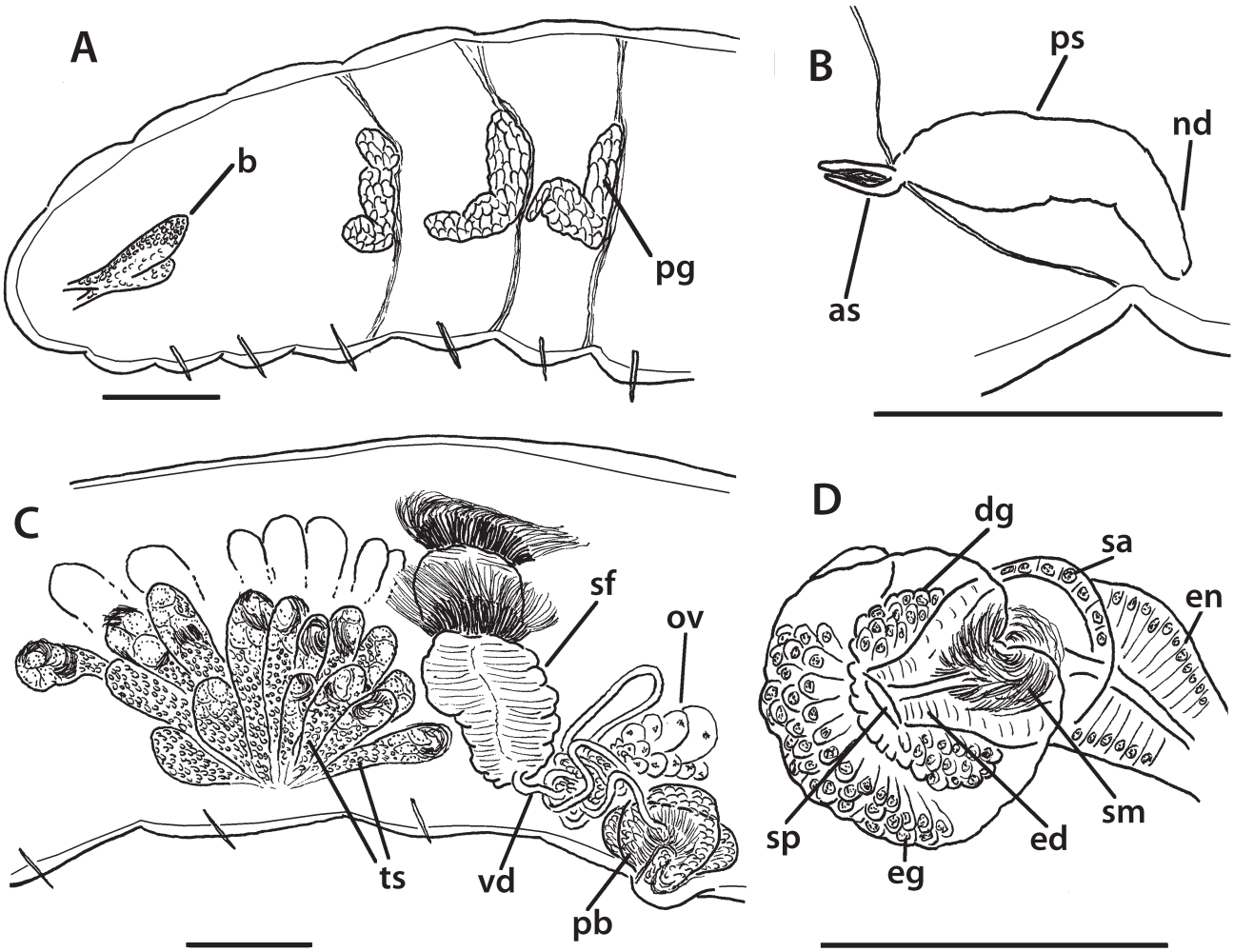



Figure 7. *Lumbricillus bibulbus* sp. nov. A, D=Holotype. **A** Anterior body (ZMBN 153439). **B** Nephridium at septum 7/8 (ZMBN 153278). **C** Genitalia (ZMBN 153277). **D** Spermathecae (ZMBN 153439). Abbreviations under general notes. Scale bars: 100 µm.

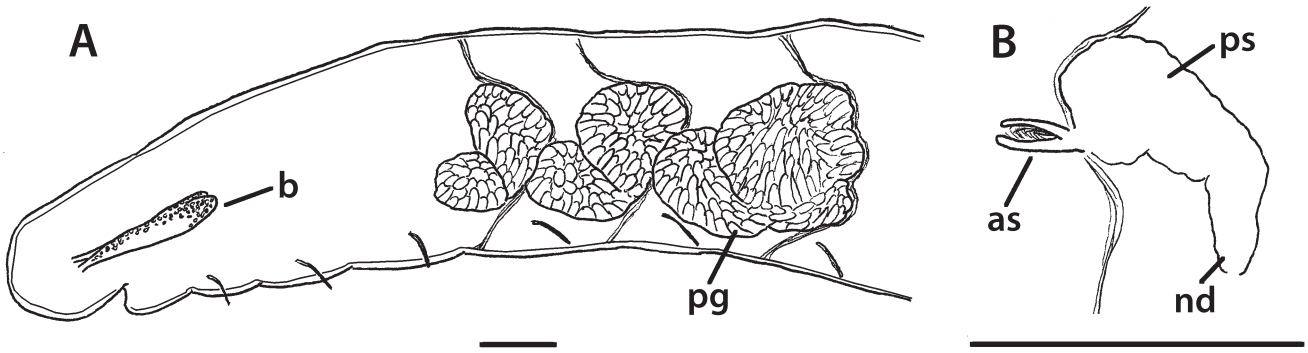



Figure 8. *Lumbricillus* sp. "Greenland". **A** Anterior body (ZMBN 153289). **B** Nephridium at septum 7/8 (ZMBN 153288). Abbreviations under general notes. Scale bars: 100 µm.

Male genitalia only partially developed. Testes in XI, lobed, ovaries and penial bulbs in XII. Spermathecae developing in V, with pore at lateral line. No midventral subneural glands observed.

**Geographical distribution including BOLD data.** Only known from Greenland and Svalbard.

**Remarks.** Unfortunately, we found no fully mature specimens of this species, but the species tree (Figure 2) suggests it to be related to, but not necessarily to be regarded as a member of, the *pagenstecheri* group.

## ***Paralumbricillus*** Klinth & Rota gen. nov.

urn:lsid:zoobank.org:act:201A2FB8-DF30-447B-A186-42157549D4B4

*Lumbricillus* Ørsted, 1844 partim
*Pachydrilus* Claparède, 1861 partim
**Type species.** *Enchytraeus arenarius* Michaelsen, 1889: pp. 12–14, figs 5a–d.
**Included species:**
*Paralumbricillus arenarius* (Michaelsen, 1889) comb. nov.
*Paralumbricillus bicornis* sp. nov.
*Paralumbricillus bilobatus* sp. nov.
*Paralumbricillus cervisiae* (Kossmagk-Stephan, 1983) comb. nov.
*Paralumbricillus christenseni* (Tynen, 1966) comb. nov.
*Paralumbricillus crymodes* (Stephenson, 1922) comb. nov.
*Paralumbricillus dubius* (Stephenson, 1911) comb. nov.
*Paralumbricillus eltoni* (Stephenson, 1924) comb. nov.
*Paralumbricillus eudioptus* (von Bülow, 1955) comb. nov.
*Paralumbricillus lofotensis* sp. nov.
*Paralumbricillus muscicolus* (Stephenson, 1924) comb. nov.
*Paralumbricillus nielseni* (Nurminen, 1965) comb. nov.
*Paralumbricillus sanguineus* sp. nov.
*Paralumbricillus westheidei* (Kossmagk-Stephan, 1983) comb. nov.

**Etymology.** The prefix *para*, Greek for "next to", refers to the close phylogenetic relationship to *Lumbricillus*, in which most species have at some point been placed historically.

**Genus description/diagnosis.** White to yellow worms, about 5 to 20 mm in length. Prostomium hemispherical. Head pore at 0/1. Epidermis with transverse rows of gland cells. Chaetae straight or slightly sigmoid, without nodulus, usually 2 or 3 per bundle, rarely 4, upper bundles dorsolateral. Oesophageal appendages absent. Pharyngeal glands in three pairs, located in IV–VI, usually converging dorsally, sometimes connected dorsally, usually with ventral lobes, but secondary glands absent. Only nucleated coelomocytes present.

Dorsal vessel originating in XII–XIV. Nephridia with anteseptale made up of funnel only. Clitellum covering XII-XIII. Testis sacs, forming irregular lobes, sometimes budding off into free floating cysts. Penial bulbs compact or lobed. Midventral subneural glands usually present in XIII–XV, sometimes further back. Spermathecae in V, club- or pear-shaped, attached to and usually communicating with lumen of oesophagus; glands surrounding ectal pore. Mainly marine littoral but some species also found in limnic habitats.

## ***Paralumbricillus bilobatus*** Klinth & Rota sp. nov.

Figure 9

urn:lsid:zoobank.org:act:1F64EADD-27E0-4DF5-B8DA-9AE0AAED5386

**Holotype.** NTNU-VM 74104 (CE29420), Figs 9D–E, an amputated mature specimen stained in paracarmine and mounted on a slide. COI barcode: BOLD NOENC414-18.

**Type locality.** Beach west of road to Stavøya Island, Slettvik, Orkland, Trøndelag, Norway. Upper intertidal, sand and gravel near freshwater stream on beach. Coll. C. Erséus, 9 September 2016.

**Other material examined.** ZMBN 111482 (CE26820), ZMBN 153276 (CE28319), ZMBN 129228 (CE32463), ZMBN 153282 (CE32464) and ZMBN 129338 (CE33480) two mature, two partially mature and one immature specimen from Norway. For details on collection site and GenBank accession numbers see Table S1.

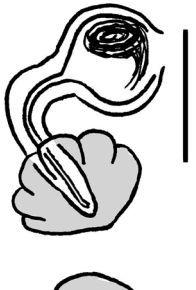
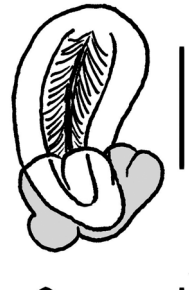
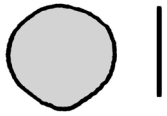
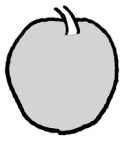
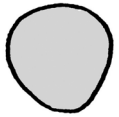
**Etymology.** Referring to the bilobed structure of the penial bulbs.

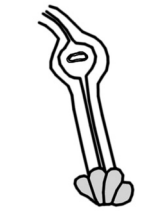
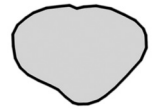
**Diagnosis.** This species has a bilobed penial bulb, but unlike other *Paralumbricillus* species with bilobed bulbs, where one lobe is anterior and the other posterior, *P. bilobatus* sp. nov. has a dorsolateral and a ventromedial lobe. It is also one of the few *Paralumbricillus* species that regularly have ventral preclitellar bundles with up to 4 chaetae.

**Description.** Length of first 19–37 segments 2.9–5.9 mm (fixed, amputated specimens); first 15 segments (2.2)2.4–3.5 mm long; width at clitellum (0.24)0.39–0.46 mm. Chaetae straight or slightly sigmoid. Dorsolateral bundles with (1)2–3 chaetae anterior to clitellum, and 2 chaetae in postclitellar segments. Ventral bundles with 2–4 chaetae anterior to clitellum, and 2 chaetae in postclitellar segments. Each worm's longest measured chaetae 55–95 µm long, about 5–10 µm wide. Clitellum extending over XII–XIII. Head pore not observed.

Coelomocytes, about 20–40 µm long, oval or spindle-shaped, granulated with distinct nucleus. Paired pharyngeal glands present in IV, V and VI, third pair sometimes extending into VII; each

Table 2. Comparison of key morphological characters of *Paralumbricillus* **gen. nov.** species. Chaetal formula indicates preclitellar–postclitellar dorsolateral bundles: preclitellar–postclitellar ventral bundles. Sperm funnel (SF) ratio is meant as length/width. Scale bars: 100 µm (missing for *P. eudioptus*). *Paralumbricillus eudioptus* redrawn from von Bülow, 1955: fig 8; *P. muscicolus* spermatheca illustrated from Stephenson's specimen 1933.2.23.317, penial bulb from 1933.2.23.320; *P. cervisiae* and *P. westheidei* redrawn from Kossmagk-Stephan, 1983: table 1; *P. christenseni* spermatheca and penial bulb illustrated from Tynen's syntype specimens 1965.12.1-22.

| Species | *P. arenarius* | *P. bicornis* | *P. bilabatus* | *P. cervisiae* | *P. christenseni* | *P. crymodes* | *P. dubius* |
|---|---|---|---|---|---|---|---|
| Chaetal formula | 2,3-2(3):<br>2,3(4)-2,3 | 2,3-2:<br>2,3-2 | 2,3-2:<br>2,3,4-2 | 2-2:<br>2-2 | 2-2:<br>2-2 | 2,3,4-2,3:<br>3,4-2 | 2-2:<br>2-2 |
| SF ratio | 6-13:1 | 7-12:1 | 9-15:1 | 3-4:1 | 7-8:1 | 6-9:1 | 2.5-4:1 |
| Spermatheca |  |  |  |  |  |  |  |
| Penial bulb |  |  |  |  |  |  |  |

| Species | *P. eltoni* | *P. eudioptus* | *P. lofotensis* | *P. muscicolus* | *P. nielseni* | *P. sanguineus* | *P. westheidei* |
|---|---|---|---|---|---|---|---|
| Chaetal formula | 2,3-2:<br>2,3-2 | 2,3-2,3:<br>2,3-2,3 | 2,3-2<br>2,3-2 | 2,3-2:<br>3-2 | 2-2:<br>2,3(4)-2,3(4) | (2)3(4)-2(3):<br>(2)3-2(3) | 2-2:<br>2-2 |
| SF ratio | 1-1.5:1 | "Average size" | 3.5:1 | 1.5-2:1 | 2-3:1 | 1.5-2.5:1 | 10:1 |
| Spermatheca | Club-shaped<br>62 µm wide<br>at ampulla |  |  |  | Club shaped,<br>ampulla<br>"onion-shaped" |  |  |
| Penial bulb | Tuft-like*<br>115-125 µm | "Particularly<br>stout" |  |  | "Medium-sized,<br>compact" |  |  |

*described as less compact and ovoid than in *Lumbricillus* but more so than in *Enchytraeus*.

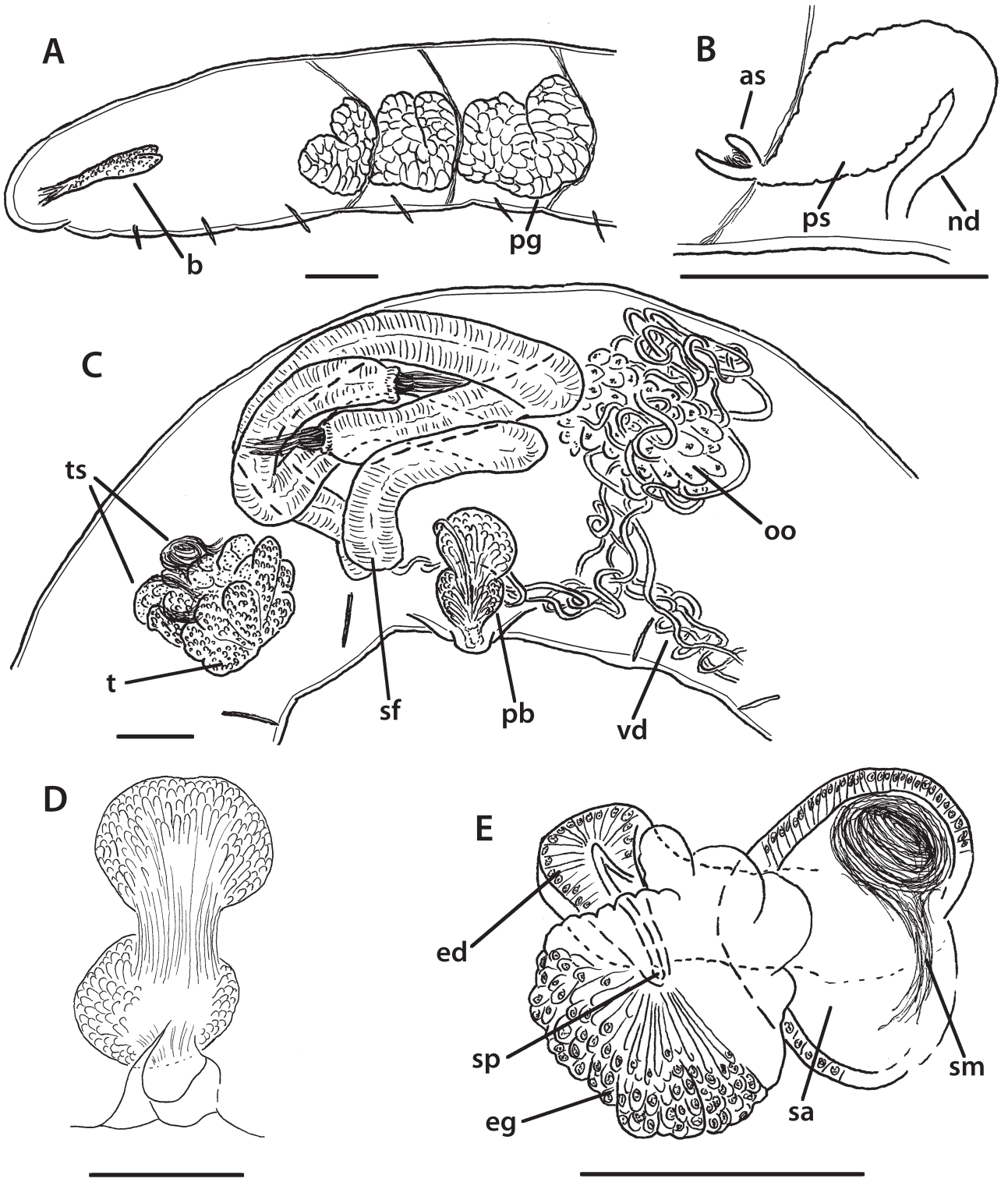



Figure 9. *Paralumbricillus bilobatus* sp. nov. D-E=Holotype. **A** Anterior body (ZMBN 129338). **B** Nephridium at septum 9/10 (ZMBN 129338). **C** Genitalia (ZMBN 153282). **D** Bilobed penial bulb (NTNU-VM 74104). **E** Spermatheca (NTNU-VM 74104). Abbreviations under general notes. Scale bars: 100 µm.

pair converging dorsally (Figure 9A). Dorsal vessel originating in XIII. Nephridia observed in 7/8–9/10 and from 13/14 rearwards, about 90–165 µm long. Anteseptale small, consisting of funnel only. Postseptale oval, tapering into thin posteroventral efferent duct (Figure 9B). Brain with posterior incision.

Male genitalia paired (Figure 9C). Testes originating in XI, with developing sperm seemingly held together by testis sacs, forming irregular lobes. Sperm funnels in XI, sometimes extending back into XII, at least 540–990 µm long, 65–120 µm wide, making them about (5)9–15 times longer than wide (leaning towards the higher ratio due to the difficulties in measuring the total length in the mounted material), funnels tapering towards vasa deferentia. Large parts of vasa irregularly coiled around ovaries in XII, sometimes also extending backwards into XIII–XIV, vasa 10–15 µm wide. Penial bulbs bilobed with dorsolateral lobe 100–105 µm in diameter, and ventromedial lobe about 110 µm in diameter (Figure 9D), vas entering dorsolateral lobe. One to two mature eggs observed.

Spermathecae (Figure 9E; Table 2) in V, club-shaped, with a long

ectal duct suddenly widening into ampulla. Ampulla oval, with sperm arranged in a tight ball. Ampulla entally connected to oesophagus. Spermathecae more than 195–210 µm long, 30–50 µm wide at the ectal duct, 105 µm wide at widest part of ampulla. Ectal pore at lateral line, surrounded by gland cells forming a somewhat lobed compact mass, glandular body up to 105 µm wide. One specimen with midventral subneural glands in XIII–XVIII, 50 µm, 50 µm, 55 µm, 55 µm, 65 µm and 55 µm long respectively.

**Geographical distribution including BOLD data.** Only known from the middle of Norway (Hordaland, Møre og Romsdal, Trøndelag and Nordland).

**Remarks.** According to the species tree (Figure 2), this species is genetically close to *P. arenarius* and *P. crymodes* with which it shares the particularly long sperm funnels. However, the spermathecae of *P. bilobatus* sp. nov. have a long ectal duct, abruptly widening into the ampulla, whereas *P. arenarius* and *P. crymodes* have pear-shaped spermathecae with ducts gradually widening into the ampulla. Furthermore, the bilobed penial bulbs of *P. bilobatus* sp. nov. with dorsolateral and ventromedial lobes distinguish it from all other *Paralumbricillus* species.

## ***Paralumbricillus crymodes*** (Stephenson, 1922) comb. nov.

Figure 10

*Enchytraeus crymodes* Stephenson, 1922: pp. 1133–1135, figure 6
*Enchytraeus crymodes*; Stephenson, 1925: p. 1317.
*Marionina crymodes*; Nielsen & Christensen, 1959: p. 109.
*Lumbricillus crymodes*; Coates, 1989: p. 31.

**Type locality.** Svalbard, Spitsbergen, Bruce City, from among mosses on banks of freshwater pond and near salt marsh, August 2021.

**Material examined.** ZMBN 110573 (CE20719) a mature specimen from Svalbard, Spitsbergen, Nordfjorden, Tschermark Stream. Coll. K. Hårsaker, 27 July 2013. BMNH 1933.5.25.1271–1274, 1279–1282, 1284, 1287, sectioned material on slides from Stephenson's collection, it is unclear if any of these specimens are part of the type series or if they are from Liefde Bay, another locality on Spitsbergen (Stephenson 1925). For details on collection site and GenBank accession numbers see Table S1.

**Description of new specimen.** Length of first 26 segments 6.4 mm (fixed, amputated specimen); first 15 segments 4.0 mm long; width at clitellum 0.30 mm. Chaetae straight or slightly sigmoid. Dorsolateral bundles with 2–3 chaetae anterior to clitellum, 2–3 chaetae in postclitellar segments. Ventral bundles with 3–4 chaetae anterior to clitellum, 2 chaetae posteriorly. The worm's longest measured chaetae 60 µm long, about 3–5 µm wide. Clitellum extending over XII–1/2XIII. Head pore not observed.

Coelomocytes, about 25 µm long, round or oval, granulated with distinct nucleus. Paired pharyngeal glands present in IV, V and VI; each pair converging dorsally. Dorsal vessel originating in XIII. Nephridia observed in 7/8–8/9, about 175 µm long. Anteseptale small, consisting of funnel only. Postseptale oval, tapering into posteroventral efferent duct (Figure 10B). Brain with posterior incision.

Male genitalia paired (Figure 10A). Testes originating in XI, with developing sperm seemingly held together by testis sacs, forming irregular lobes extending forwards into X. Sperm funnels in XI, extending forward into X, 655 µm long, 70 µm wide, making them about 9 times longer than wide, funnels tapering towards vasa deferentia. Large parts of vasa irregularly coiled around ovaries in XII, vasa 10–15 µm wide. Penial bulbs compact, 110 µm in diameter. Two mature eggs observed.

Spermathecae (Figure 10C; Table 2) in V, pear-shaped, with ectal duct, and lumen of ectal duct, gradually widening into ampulla. Ampulla round, filled with sperm arranged in tightly packed balls. Ampulla entally connected to oesophagus. Epithelium of duct with cylindrical cells, ampulla with cells not as tall, but more or less cubical. Spermathecae 245 µm long, 25 µm wide at the ectal duct, 115 µm wide at widest part of ampulla. Ectal pore at lateral line, surrounded by rosette of separate glands, together forming a glandular body up to 70 µm wide. Midventral subneural glands observed in XIII–XVI, 70 µm, 50 µm, 60 µm and 65 µm long, respectively.

**Geographical distribution including BOLD data.** Known from Spitsbergen and Nunavut in Northern Canada. Charlotte Holmquist reported the species from Alaska, USA (Stöhr 2023), but we have not been able to verify these records.

**Remarks.** Our single specimen could readily be identified as *P. crymodes*, a species originally described from a freshwater pond and a salt marsh on Spitsbergen. The only difference we noted is that our specimen has 2–3 chaetae in postclitellar dorsolateral bundles, compared to only 2 in the original description. Our examination of the museum vouchers from Stephenson's collection confirmed the similarity to our specimen in the shape of the spermathecae, long sperm funnels and thin vasa deferentia. *Paralumbricillus crymodes* is similar to *P. arenarius*, which also has long sperm funnels, unlobed penial bulbs and spermathecae with a gradually widening lumen of the ectal duct, and the two species were found close together in our species tree (Figure 2). Both have been found on Spitsbergen but *P. arenarius* is more widespread and reported from most of the North East Atlantic, whereas *P. crymodes* seems to have a more Arctic distribution.

## ***Paralumbricillus lofotensis*** Klinth & Rota sp. nov.

Figure 11

urn:lsid:zoobank.org:act:89DC1C3D-5E33-4271-9720-E4AE2ADCE90C

**Holotype.** ZMBN 153285 (CE34291), Figs 11A, D, an amputated mature specimen stained in paracarmine and mounted on a slide. COI barcode: BOLD NVENC1605-22.

**Type locality.** Rolvsfjorden, Vestvågøy, Lofoten, Nordland, Norway. In coarse sediment in a tidal stream. Coll. C. Erséus & M. Klinth, 8 September 2017.

**Paratypes.** ZMBN 129448 (CE34290) & ZMBN 153286 (CE34292) one mature and one partially mature specimen from the type locality. For details on collection site and GenBank accession numbers see Table S1.

**Etymology.** Named after the archipelago Lofoten in Norway.

**Diagnosis.** Preclitellar bundles regularly with 3 chaetae, sperm funnels about 3.5 times longer than wide, compact penial bulbs, and club-shaped spermathecae with separate bud-like glands surrounding the ectal pore (Table 2).

**Description.** Whitish transparent worms. Length of first 26–37 segments 4.6–9.5 mm (fixed, amputated specimens); first 15 segments (2.9)4.0–4.2 mm long; width at clitellum (0.37)0.51–0.52 mm. Chaetae straight or slightly sigmoid. Dorsolateral and ventral bundles with 2–3 chaetae anterior to clitellum, and 2 chaetae in postclitellar segments. Each worm's longest measured chaetae 85–100 µm long, about 6 µm wide. Clitellum extending over XII–1/2XIII. Head pore at 0/1.

Coelomocytes numerous, about 20–35 µm long, oval or spindle-

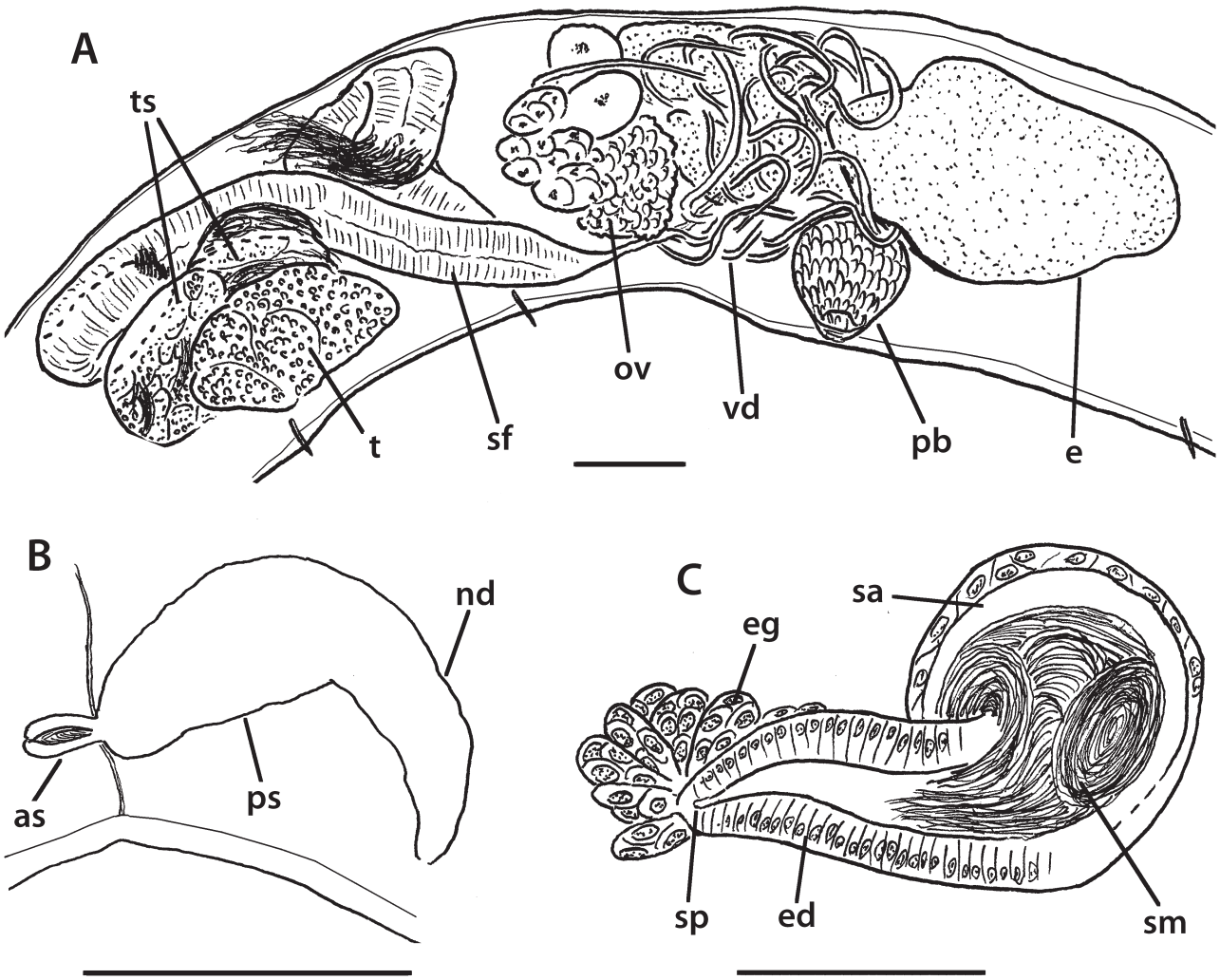



Figure 10. *Paralumbricillus crymodes* (ZMBN 110573). **A** Genitalia. **B** Nephridium at septum 8/9. **C** Spermatheca. Abbreviations under general notes. Scale bars: 100 µm.

shaped, granulated with distinct nucleus. Paired pharyngeal glands present in IV, V and VI; each pair converging dorsally (Figure 11A). Dorsal vessel originating in XIV. Nephridia observed in 7/8–8/9, about 150–180 µm long. Anteseptale small, consisting of funnel only. Postseptale oval, tapering into thin posteroventral efferent duct (Figure 11B). Brain with posterior incision.

Male genitalia paired (Figure 11C). Testes originating in XI, with some developing sperm seemingly held together by testis sacs, forming irregular lobes, other cysts of developing sperm floating free in XI. Sperm funnels in XI, 195–215 µm long, 60–65 µm wide, making them about 3–3.5 times longer than wide, funnels tapering towards vasa deferentia. Large parts of vasa irregularly coiled around ovaries in XII, vasa 6 µm wide. Penial bulbs compact, 85–95 µm in diameter. Two mature eggs observed.

Spermathecae (Figure 11D) in V, club-shaped, with ectal duct suddenly widening into ampulla. Ampulla round, with sperm arranged in a circle perpendicular to the duct. Ampulla connected to oesophagus via ental duct. Epithelium of duct with cylindrical cells, ampulla with cubical cells. Spermathecae 150–160 µm long, 30–35 µm wide at the ectal duct, 75–90 µm wide at widest part of ampulla. Ectal pore at lateral line, surrounded by rosette of separate bud-like glands, entire arrangement of these glands about 65 µm wide. No midventral subneural glands observed.

**Geographical distribution including BOLD data.** Only known from the type locality in Nordland, Northern Norway.

**Remarks.** This species can be distinguished from most other members of *Paralumbricillus* by the combination of compact penial bulbs and several preclitellar bundles with more than two chaetae. Among the species of *Paralumbricillus* that share these characters, *P. eltoni* (Stephenson, 1924) and *P. muscicolus* (Stephenson, 1924) have shorter sperm funnels than *P. lofotensis* sp. nov. The two species that most resemble *P. lofotensis* sp. nov. are *P. eudioptus* (von Bülow, 1955) and *P. nielseni* (Nurminen, 1965). Unfortunately, the original description of *P. nielseni* is brief and without illustrations, but it seems that this species can be separated from *P. lofotensis* sp. nov. for never having more than 2 chaetae in preclitellar dorsolateral bundles. *Paralumbricillus eudioptus* can be distinguished from *P. lofotensis* sp. nov. by having postclitellar bundles with more than 2 chaetae and by the shape of its spermathecae, which have a strange internal structure (Table 2).

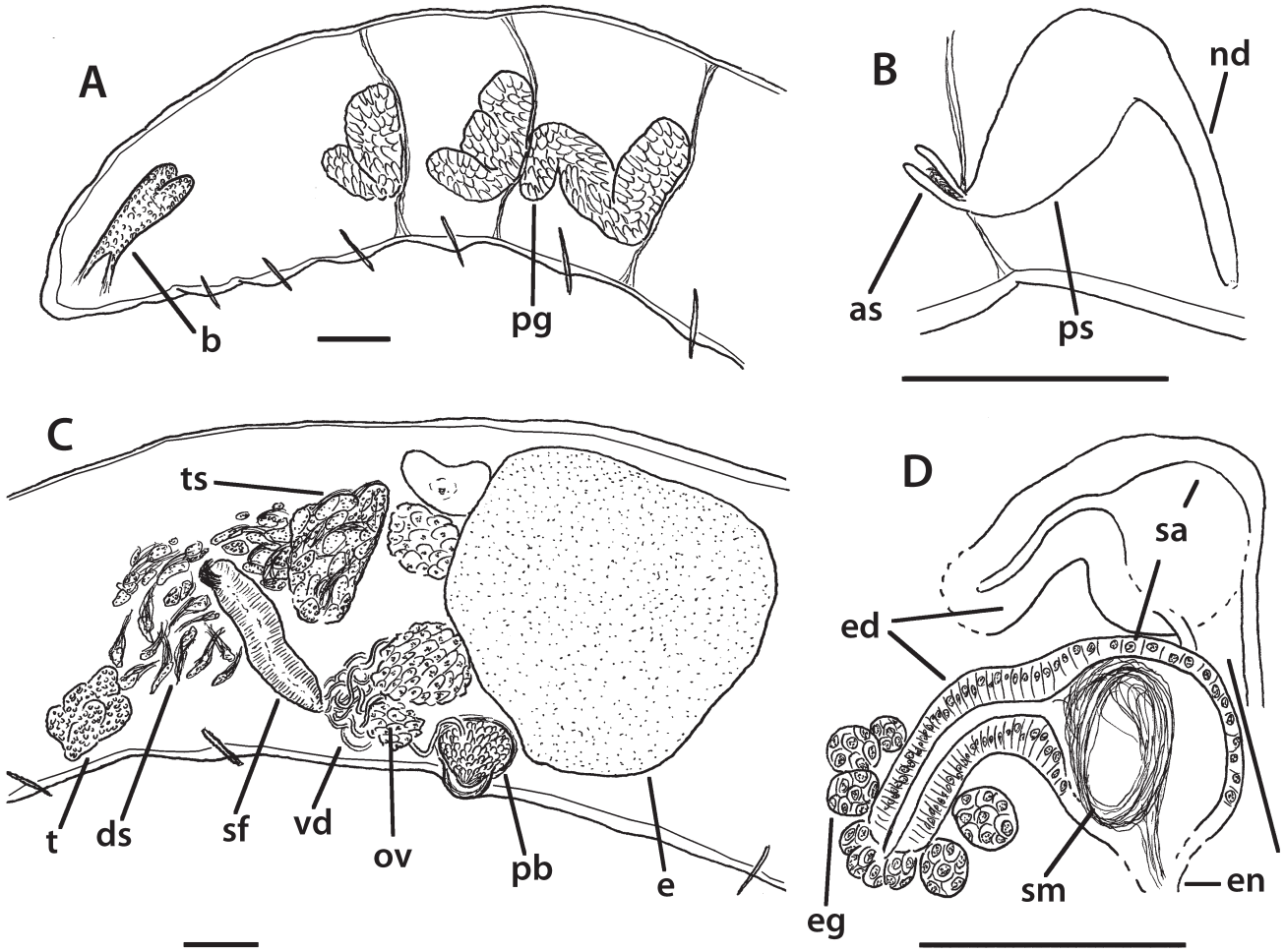



Figure 11. *Paralumbricillus lofotensis* sp. nov. A,D=Holotype. **A** Anterior body (ZMBN 153285). **B** Nephridium at septum 7/8 (ZMBN 129448). **C** Genitalia (ZMBN 129448). **D** Spermathecae (ZMBN 153285). Abbreviations under general notes. Scale bars: 100 µm.

## ***Paralumbricillus bicornis*** Klinth & Rota sp. nov.

Figure 12

urn:lsid:zoobank.org:act:B0F118D1-C246-4677-AAEA-9C7C09AB7FEF

*Lumbricillus* sp. H; Klinth *et al*. 2017a; Klinth *et al*. 2017b, figure 22.

**Holotype.** ZMBN 153402 (CE25014), Figs 12A–C, an amputated mature specimen stained in paracarmine and mounted on a slide. COI barcode: BOLD NOENC410-18.

**Type locality.** Holmsundsfjorden Bay, 2 km south of Kjellingbrua Bridge, Kjøpstad, Gildeskål, Nordland, Norway. Upper intertidal, rock pool, gravel and grey sand. Coll. C. Erséus & E. Willassen, 11 September 2014.

**Paratypes.** ZMBN 107947 (CE24967) & ZMBN 107948 (CE24968) two partially mature specimens from the type locality. For details on collection site and GenBank accession numbers see Table S1.

**Other material examined.** ZMBN 107945 (CE23136), ZMBN 129442 (CE34247), ZMBN 153284 (CE34248), ZMBN 129452 (CE34308) four partially mature specimens from Norway. For details on collection site and GenBank accession numbers see Table S1.

**Etymology.** Latin, from *bi-*, two, and *cornu* for horn, describing the horns extending from the penial bulb.

**Diagnosis.** The tripartite penial bulbs, with a central round bulb and two horns or lobes extending one anteriorly and one posteriorly, distinguishes this species from other *Paralumbricillus* species.

**Description.** Length of first 29–33 segments 4.1–7.9 mm (fixed, amputated specimens); first 15 segments 2.1–3.0 mm long; width at clitellum 0.38–0.56 mm. Chaetae straight or slightly sigmoid. Dorsolateral and ventral bundles with 2–3 chaetae anterior to clitellum, and 2 chaetae in postclitellar segments. Each worm's longest measured chaetae 70–95 µm long, about 5 µm wide. Clitellum extending over XII–1/2XIII. Head pore at 0/1.

Coelomocytes numerous, about 15–20 µm long, round, oval or spindle-shaped granulated with distinct nucleus. Paired pharyngeal glands present in IV, V and VI, third pair sometimes extending back into VII; each pair converging dorsally. Dorsal vessel originating in XIII. Nephridia observed in 7/8–8/9, and from 12/13 rearwards, about 100–145 µm long. Anteseptale small, consisting of funnel only. Postseptale oval, tapering into thin posteroventral efferent duct (Figure 12A). Brain with posterior incision.

Male genitalia paired (Figure 12C). Testes originating in XI, with some developing sperm seemingly held together by testis sacs, forming irregular lobes, other cysts of developing sperm floating free in X–XI, sometimes XII. Sperm funnels in XI, 465–505 µm long, 40–65 µm wide, making them about 7–12 times longer than wide, funnels tapering towards vasa deferentia. Large parts of vasa irregularly coiled around ovaries in XII, vasa 10–20 µm wide. Penial bulbs tri-partite with round central mass, 65–105 µm in diameter, from which two smaller lobes extend, one anterior and one posterior, both lobes more ventromedial than the central lobe, vas entering

central lobe (Figure 12D). No fully mature eggs observed.

Spermathecae (Figure 12B) in V, club-shaped, with long ectal duct suddenly widening into ampulla. Ampulla oval, entally connected to oesophagus. No sperm observed in it. Spermathecae 180–190 µm long, 25–35 µm wide at the ectal duct, 55–60 µm wide at widest part of ampulla. Ectal pore at lateral line, surrounded by rosette of separate glands, glandular rosette up to 50–55 µm wide. Two midventral subneural glands in XV–XVI, 45–100 µm and 50–95 µm long, respectively.

**Geographical distribution including BOLD data.** Only known from Nordland and Troms, Norway.

**Remarks.** The partially mature penial bulb observed by Klinth *et al*. (2017b, figure 22E) appeared bilobed, but with additional material the fully mature bulbs turned out to be actually tripartite, with a central round bulb and two horn-like lobes. This makes this new species less similar to *P. westheidei* (Kossmagk-Stephan, 1983), which was previously suggested as a possible candidate for our specimens (Klinth *et al*. 2017b). *Paralumbricillus dubius* (Stephenson, 1911) also has penial bulbs with two horn-like lobes, but unlike *P. bicornis* sp. nov. where the horns extend from a central bulb, the bulbs in *P. dubius* are divided in two lobes and each lobe extends into a horn. Our species tree (Figure 2) shows *P. bicornis* sp. nov. as genetically closest to *P. lofotensis* sp. nov., which has a similar chaetal pattern and spermathecal morphology, but the latter species has much shorter sperm funnels (only 3-3.5 times longer than wide) and compact penial bulbs (lacking horns).

## *Paralumbricillus sanguineus* Klinth & Rota sp. nov.

Figure 13

urn:lsid:zoobank.org:act:BAFB0A34-FC7D-4AD7-AFA3-84486770406D

**Holotype.** ZMBN 129381 (CE33777), Fig 13C, an amputated mature specimen stained in paracarmine and mounted on a slide. COI barcode: BOLD NOENC418-18.

**Type locality.** Damsgård, Andenes, Andøya, Nordland, Norway. Mid-intertidal pebbles, sand and shells. Coll. C. Erséus & M. Klinth, 6 September 2017.

**Paratype.** ZMBN 129380 (CE33776) a partially mature specimen from the type locality. For details on collection site and GenBank accession numbers see Table S1.

**Other material examined.** NTNU-VM 74055 (CE29066), NTNU-VM 74080 (CE29284), ZMBN 129189 (CE32243), ZMBN 153279 (CE32236), ZMBN 153280 (CE32279) & ZMBN 153281 (CE32280) two partially mature and four immature specimens from Norway. For details on collection site and GenBank accession numbers see Table S1.

**Etymology.** From *sanguis*, Latin for blood, referring to the conspicuous dorsal and ventral blood vessels observed in this species.

**Diagnosis.** This species can be separated from other members of the genus by the combination of bilobed penial bulbs (with anterior and posterior lobes) and club-shaped spermathecae with very narrow

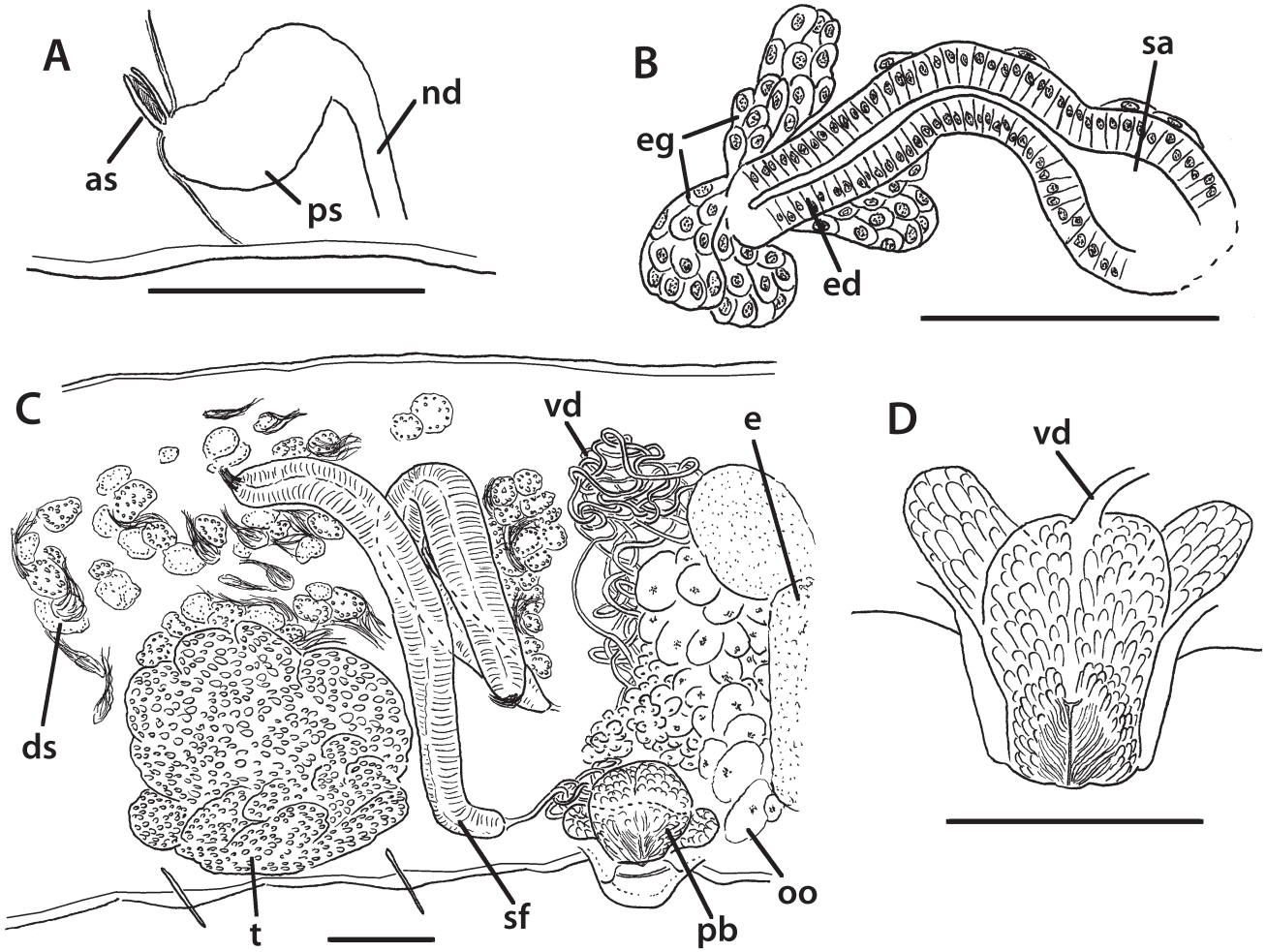



Figure 12. *Paralumbricillus bicornis* sp. nov. A–C=Holotype. **A** Nephridium at septum 8/9 (ZMBN 153402). **B** Spermatheca (ZMBN 153402). **C** Genitalia (ZMBN 153402). **D** Penial bulb (ZMBN 129442). Abbreviations under general notes. Scale bars: 100 µm.

ectal ducts. The conspicuous blood vessels may also help in the identification, but they are more apparent in immature specimens than in mature specimens. This is also one of the longest and most slender species in *Paralumbricillus*, with some specimens reaching more than 70 segments.

**Description.** Length of first 27–69 segments 5.1–16.7 mm (fixed, amputated specimens); first 15 segments 2.5–3.1 mm long; width at clitellum 0.24–0.29 mm. Chaetae straight or slightly sigmoid. Dorsolateral bundles with (2)3(4) chaetae anterior to clitellum, and 2(3) chaetae in postclitellar segments. Ventral bundles with (2)3 chaetae anterior to clitellum, and 2(3) chaetae in postclitellar segments. Each worm's longest measured chaetae 65–75 µm long, about 5 µm wide. Clitellum extending over XII–1/2XIII. Head pore at 0/1.

Coelomocytes numerous, about 10–20 µm long, round or oval, granulated with distinct nucleus. Paired pharyngeal glands present in IV, V and VI; each pair converging dorsally (Figure 13A). Dorsal and ventral vessels conspicuous throughout, stained yellow in paracarmine; origin of dorsal vessel uncertain but seems posterior to XIV. Nephridia observed in 7/8–9/10 and in postclitellar segments, about 120–165 µm long. Anteseptale small, consisting of funnel only. Postseptale oval, tapering into thick posteroventral efferent duct (Figure 13B). Brain with posterior incision.

Male genitalia paired (Figure 13C). Testes originating in XI, with developing sperm seemingly held together by testis sacs, forming large compact mass extending forwards into IX and backwards into XII, some cysts of developing sperm free floating in XI. Sperm funnels in XI, 110–155 µm long, 45–95 µm wide, making them about 1.5–2.5 times longer than wide, funnels tapering towards vasa deferentia. Large parts of vasa irregularly coiled around ovaries in XII, vasa 10 µm wide. Penial bulbs bilobed with anterior and posterior lobes, vasa entering where lobes fuse ventrally, each lobe about same width, their combined length about 65–80 µm. No mature eggs observed.

Spermathecae (Figure 13D) in V, club-shaped, with very thin ectal duct suddenly widening into round ampulla, reminiscent of some *Fridericia* Michaelsen, 1889 or *Marionina* species. Ampulla connected to oesophagus via ental duct. No sperm observed in it. Spermathecae 100–165 µm long, 10–15 µm wide at the ectal duct, 60 µm wide at widest part of ampulla. Ectal pore at lateral line, surrounded by rosette of separate glands, rosette up to 35–60 µm wide. Two midventral subneural glands in XIII–XIV, 75 µm and 60 µm long, respectively.

**Geographical distribution including BOLD data.** Only known from the middle of Norway (Møre og Romsdal, Trøndelag and Nordland).

**Remarks.** This species is unusually long and slender compared to other species of *Paralumbricillus* or most *Lumbricillus*, and is in this way more alike the species of *Grania* and *Randidrilus* Coates & Erséus, 1985. Another striking feature are the conspicuous blood vessels, but the bilobed penial bulbs and thin spermathecal ducts also stand out. The lack of sperm in the spermathecae does suggest that the specimens were not fully mature and that the shape of the spermathecae was not fully developed but the well-developed male genitalia and clitellum contradict this. The bilobed penial bulbs are somewhat similar to those of *P. westheidei*, but that species can be separated by having much longer sperm funnels. In our species tree (Figure 2), *P. sanguineus* sp. nov. was found in a clade together with *P. dubius* and *P.* sp. "Norway" with maximum support, but with large genetic distance between the species.

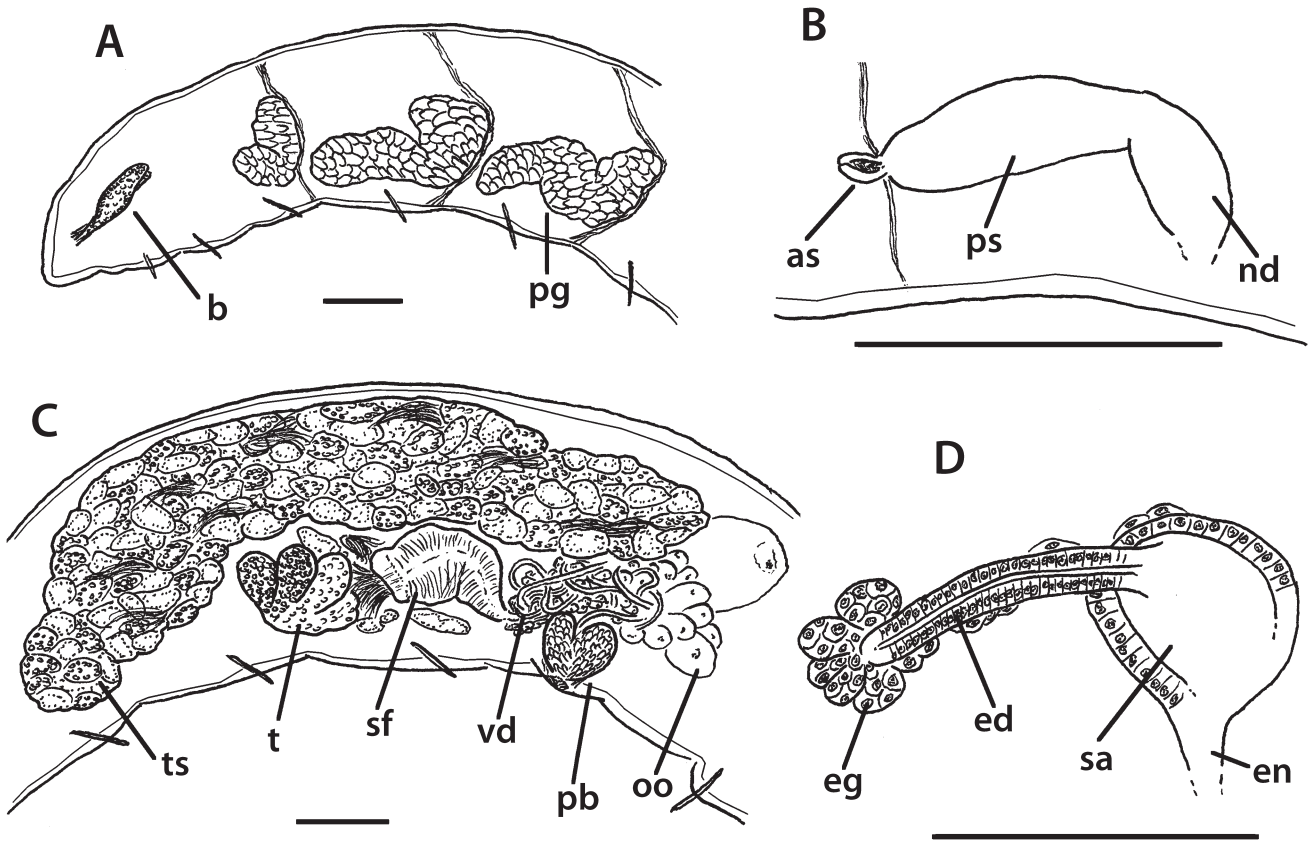



Figure 13. *Paralumbricillus sanguineus* sp. nov. C=Holotype. **A** Anterior body (ZMBN 153281). **B** Nephridium at septum 8/9 (ZMBN 153281). **C** Genitalia (ZMBN 129381). **D** Spermatheca (NTNU-VM 74080). Abbreviations under general notes. Scale bars: 100 µm.

## *Paralumbricillus* sp. "Norway"

Figure 14

**Material examined.** ZMBN 129412 (CE34074), ZMBN 129413 (CE34075), ZMBN 157976 (CE34077), ZMBN 153283 (CE34085) & ZMBN 129422 (CE34115) five immature or partially mature specimens from Reinefjorden, Reine, Moskenes, Lofoten, Nordland, Norway. In lower intertidal. Coll. C. Erséus & M. Klinth, 7 September 2017. For details on collection site and GenBank accession numbers see Table S1.

**Description.** White worms. Length of first 25–44 segments 3.1–6.0 mm (fixed, amputated specimens); first 15 segments 1.6–1.9 mm long; width at clitellum 0.29–0.34 mm. Chaetae straight or slightly sigmoid, usually with an expanded ental hook similar to that of the chaeta in many *Grania* species. Dorsolateral and ventral bundles with 2 chaetae anterior and posterior to clitellum. Each worm's longest measured chaetae 65–75 µm long, about 5 µm wide. Clitellum not developed. Head pore at 0/1.

Coelomocytes numerous, about 10–20 µm long, round or oval, granulated with distinct nucleus. Paired pharyngeal glands present in IV, V and VI; each pair converging dorsally (Figure 14A). Dorsal vessel originating in XII–XV. Nephridia observed in 7/8–9/10, and from 13/14 rearwards, about 45–105 µm long. Anteseptale small, consisting of funnel only. Postseptale oval, tapering into posteroventral efferent duct (Figure 14B). Brain with posterior incision.

Male genitalia only partially developed. Testes and sperm funnels in XI, ovaries and penial bulbs in XII. Spermathecae developing in V, with pores at lateral line. No midventral subneural glands observed.

**Geographical distribution including BOLD data.** Only known from two localities in Norway, Reinefjorden (Nordland) and Orkland (Trøndelag).

**Remarks.** Unfortunately, we found no fully mature specimens of this species, which evidently can be regarded as a part of the new genus *Paralumbricillus*, according to the molecular data (Figure 2). All five examined specimens had only two chaetae per bundle, a character shared with *P. dubius* (which genetically is a separate species but supported as sister to this species), *P. cervisiae* (Kossmagk-Stephan, 1983), *P. christenseni* (Tynen, 1966) and *P. westheidei*, all of which could be identical to our species but none of which have been reported from Norway.

## *Paralumbricillus* sp. "Denmark"

Figure 15

**Material examined.** SMNH 212154 (CE34810), SMNH 212155 (CE34811) & SMNH 212156 (CE34812) three immature or partially mature specimens from Griseta Udde Peninsula, Oddesund, Struer, Jutland, Denmark. In upper intertidal. Coll. M. Klinth & E. Eriksson, 16 May 2018. For details on collection site and GenBank accession numbers see Table S1.

**Description.** Length of first 25–37 segments 2.4–3.2 mm (fixed, amputated specimens); first 15 segments 1.2–1.4 mm long; width at clitellum 0.18–0.19 mm. Chaetae straight with ental hook. Dorsolateral and ventral bundles with 2 chaetae anterior and posterior to clitellum. Each worm's longest measured chaetae 40–50 µm long, about 5 µm wide. Clitellum not developed. Head pore at 0/1.

Coelomocytes numerous, about 10–20 µm long, round or oval, granulated with distinct nucleus. Paired pharyngeal glands present in IV, V and VI; each pair converging dorsally (Figure 15A); third pair sometimes extending into VII. Dorsal vessel originating in XII–XIII. Nephridia observed in 7/8–9/10, and postclitellar segments, about 70–75 µm long. Anteseptale small, consisting of funnel only. Postseptale oval, tapering into posteroventral efferent duct (Figure 15B). Brain with posterior incision.

Male genitalia only partially developed. Testes in XI, ovaries and penial bulbs in XII. Spermathecae developing in V, with pores at lateral line. No midventral subneural glands observed.

**Geographical distribution including BOLD data.** Only known from one locality in Jutland, Denmark.

**Remarks.** Unfortunately, we found no fully mature specimens of this species. It is genetically supported as sister to the remaining *Paralumbricillus* in our taxon sample, but with rather large genetic distance (Figure 2). Having only 2 chaetae per bundle supports its inclusion into *Paralumbricillus* and suggests that it could be, e.g., *P. cervisiae*, *P. christenseni* or *P. westheidei*, but mature specimens are required to resolve this.

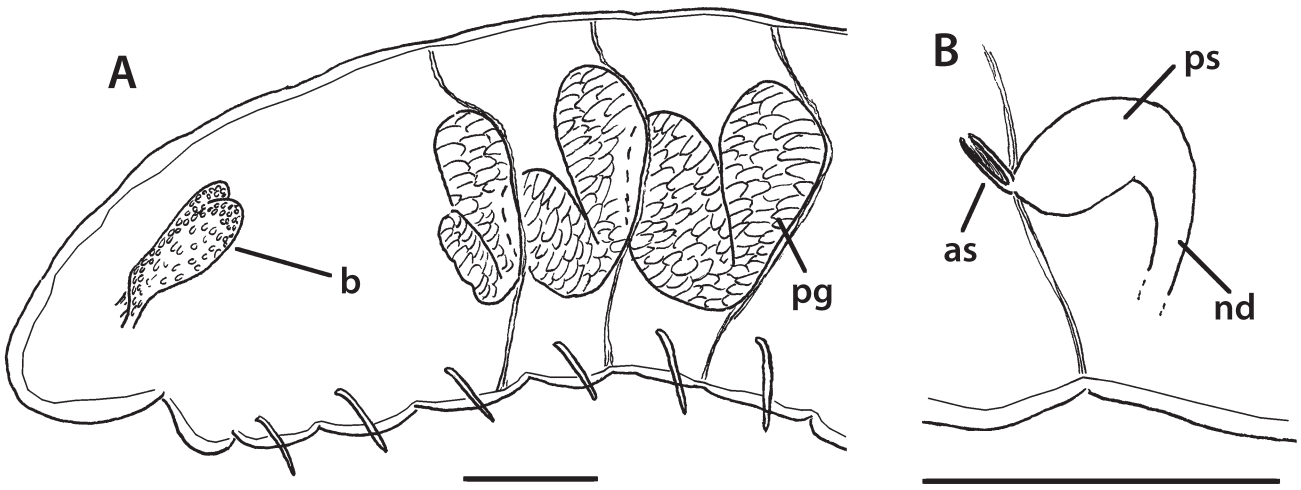



Figure 14. *Paralumbricillus* sp. "Norway". (ZMBN 153283). **A** Anterior body. **B** Nephridium at septum 8/9. Abbreviations under general notes. Scale bars: 100 µm.

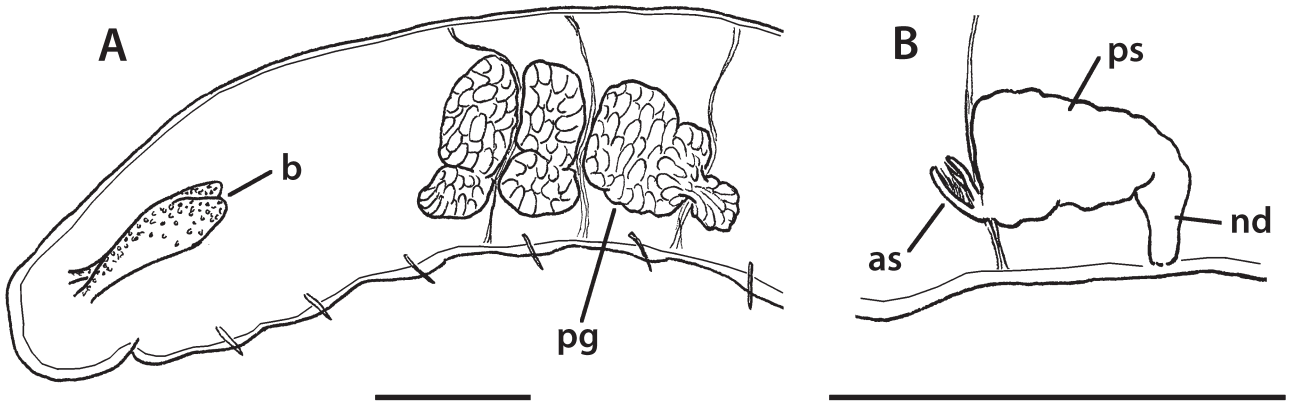



Figure 15. *Paralumbricillus* sp. "Denmark". (SMNH 212156). **A** Anterior body. **B** Nephridium at septum 9/10. Abbreviations under general notes. Scale bars: 100 µm.

## *Claparedrilus* Klinth, Rota & Erséus, 2017b

**Type species.** *Claparedrilus semifuscoides* Klinth, Rota & Erséus, 2017b.

**Other species.** *Claparedrilus semifuscus* (Claparède, 1861).

## *Claparedrilus torquatus* Klinth & Rota sp. nov.

Figure 16

urn:lsid:zoobank.org:act:F346D5D2-E051-43FE-B089-A7D26FC7AE82

**Holotype.** ZMBN 110970 (CE23134), Figs 16A,C–E, an amputated mature specimen stained in paracarmine and mounted on a slide. COI barcode: BOLD NOENC418-18.

**Type locality.** Rotsundselv, Nordreisa, Troms, Norway. In sand at the upper intertidal. Coll. C. Erséus, 14 August 2014.

**Paratype.** ZMBN 110972 (CE23153) one immature specimen from the type locality. For details on collection site and GenBank accession numbers see Table S1.

**Etymology.** The name refers to the large ectal glands forming a collar at the ectal end of the spermathecae (Latin *torquatus*, meaning collar-bearing).

**Diagnosis.** This new species can be distinguished from *C. semifuscus* (Claparède, 1861) which has huge penial bulbs, much larger than the sperm funnels, whereas the penial bulbs of *C. torquatus* **sp. nov.** are about as large as the sperm funnels. It can be distinguished from *C. semifuscoides* by having an ectal spermathecal gland mass that is larger than the spermathecal ampulla, whereas *C. semifuscoides* has a gland mass that is about the same size or smaller than the ampulla.

**Description.** Length of first 30–35 segments 4.0–5.0 mm (fixed, amputated specimens); first 15 segments 2.0–2.2 mm long; width at clitellum 0.44–0.54 mm. Chaetae sigmoid. Dorsolateral bundles with 3–5 chaetae anterior to clitellum, and 3–6 chaetae in postclitellar segments. Ventral bundles with 4–6 chaetae anterior to clitellum, and 4–7 chaetae in postclitellar segments. Each worm's longest measured chaetae 75–80 µm long, about 5 µm wide. Clitellum extending over XII–1/2XIII. Head pore at 0/1.

Coelomocytes numerous, about 15–20 µm long, round or oval, granulated with distinct nucleus. Paired pharyngeal glands present in IV, V, VI and VII; dorsal connection uncertain (Figure 16A). Dorsal vessel originating in XIII. Nephridia observed in 7/8–8/9 and postclitellar segments, about 135 µm long in segment VIII. Anteseptale small, consisting of funnel and a thin neck. Postseptale oval, tapering into thin posteroventral efferent duct (Figure 16B). Brain with posterior incision.

Male genitalia paired (Figure 16C). Testes originating in XI, with some developing sperm seemingly held together by testis sacs, forming irregular lobes in IX–XI, other cysts of developing sperm floating free in VIII–XI. Sperm funnels in XI, 145 µm long, 90 µm wide, making them about 1.5 times longer than wide, funnels tapering towards vasa deferentia. Large parts of vasa irregularly coiled around ovaries in XII, vasa 10 µm wide. Penial bulbs compact, 140 µm in diameter. No fully mature eggs observed.

Spermathecae (Figures 16D–E) in V, club-shaped, with ectal duct suddenly widening into ampulla. Ectal duct lined by layer of musculature. Ampulla round, connected to oesophagus via tapering ental duct. Sperm filling lumen of ectal duct and ampulla. Spermathecae 120 µm long, 35 µm wide at the ectal duct, 55 µm wide at widest part of ampulla. Ectal pore at lateral line, surrounded by gland cells forming a large collar-like, somewhat lobed compact mass, up to 115 µm wide. No midventral subneural glands observed.

**Geographical distribution including BOLD data.** Only known from the type locality in Northern Norway (Troms).

**Remarks.** This species is supported as a member of *Claparedrilus* both genetically (Figure 2) and morphologically by the following characters: four pairs of pharyngeal glands, irregularly lobed testis sacs, and a thin anteseptale neck on the nephridium. It is similar to both *C. semifuscus* and *C. semifuscoides* in chaetal pattern and size, but has smaller penial bulbs than the former and larger spermathecal ectal glands than the latter. The quality of the original description of *C. semifuscus* was questioned by Klinth *et al.* (2017b) and its relationship to both *C. semifuscoides* and *C. torquatus* sp. nov. may be revaluated after future sampling.

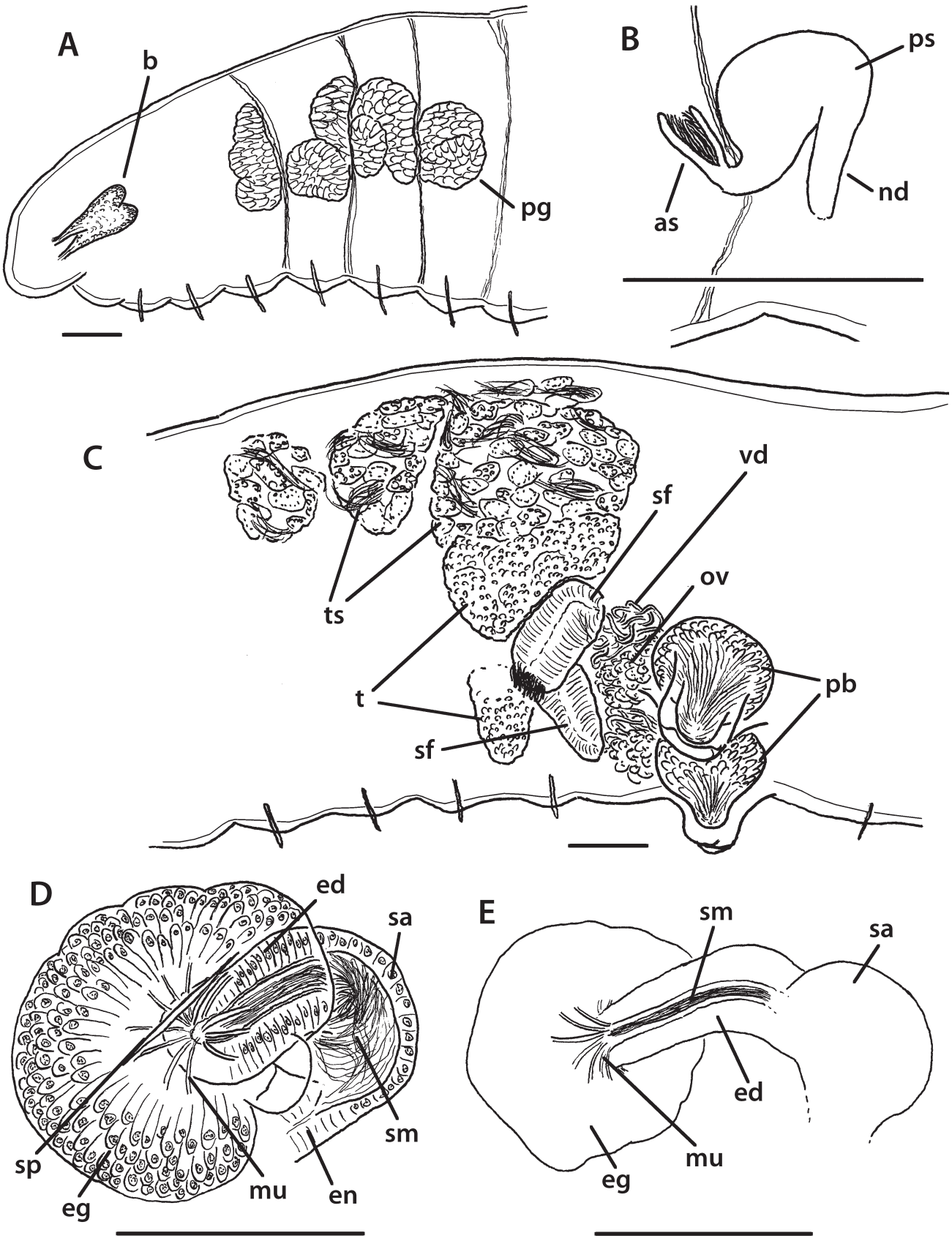



Figure 16. *Claparedrilus torquatus* sp. nov. A, C–E=Holotype. **A** Anterior body (ZMBN 110970). **B** Nephridium at septum 7/8 (ZMBN 110972). **C** Genitalia (ZMBN 110970). **D-E** Spermathecae (ZMBN 110970). Abbreviations under general notes. Scale bars: 100 µm.

## DISCUSSION

This paper is the culmination of work started in 2017 (Klinth *et al*. 2017a; 2017b) that became the basis for a revision of *Lumbricillus*, with a focus on the North East Atlantic species. The addition of specimens from the Southern Hemisphere, which also included material of what we consider to be *Marionina* s. str., provided another important piece of the puzzle (Klinth *et al*. 2022). Now, with the establishment of *Paralumbricillus* gen. nov., we can finally exclude the *arenarius* group from *Lumbricillus*. This has led to a more clearly defined *Lumbricillus* in which most species have the characteristic lobed testis sacs arranged in a fan shape. Exceptions remain in the *buelowi* group, which constitutes the sister clade to the remaining *Lumbricillus* species, where the included species have testes with only a single lobe. The members of the *buelowi* group resemble those of *Paralumbricillus* gen. nov. in having only 2 or 3 chaetae per bundle and club-shaped spermathecae but have short sperm funnels (unlike most *Paralumbricillus* gen. nov.) and the testis sac is not irregularly lobed or budding off into free floating cysts. There remains some dubious species in *Lumbricillus* with irregularly lobed testis sacs that should most probably be transferred to another genus, perhaps even *Paralumbricillus* gen. nov. (Table 1), but we believe that better descriptions in combination with genetic information are needed before making such changes. Another future aspect concerning *Lumbricillus* is the re-evaluation of the numerous species still with incomplete descriptions, including the unnamed ones treated in this study and in Klinth *et al*. (2017b). Of course, there are most likely a high number of unknown species yet to be discovered around the world. So far we have focused mainly on the Scandinavian coasts and even here not all species have been identified.

In previous papers (Klinth *et al*. 2017b; 2022), the *arenarius* group was discussed in relation to *Enchytraeoides* Roule, 1888 (see Rota *et al*. 2008). In short, the type species *Pachydrilus enchytraeoides* Saint-Loup, 1885 (possibly the same as *Enchytraeoides marioni* Roule, 1888) resembles most members of the *arenarius* group in having almost straight chaetae, irregularly lobed testis sacs, long sperm funnels and pear-shaped spermathecae. However, it was described as having up to 8 chaetae per bundle, a much higher number than any member of the *arenarius* group. There are further strange details in the description of *E. enchytraeoides* and new material must be examined to redefine this genus. As this has not yet been possible to do, we herein decided to erect the new genus *Paralumbricillus* gen. nov. to encompass the members of the rather homogeneous assemblage that we earlier recognized as the *arenarius* group, and which is strongly supported as monophyletic by molecular data.

Besides *Enchytraeoides*, there are some other groups of interest that could belong to the superclade with *Lumbricillus*, *Marionina* s. str. and *Grania*. *Randidrilus* is morphologically similar to *Grania* and probably belongs to the same superclade, if not even as a part of *Grania*. There is also the ambiguous species "*Lumbricillus*" cf. *macquariensis* which our molecular data supported as a member of the mentioned superclade, but it seems to require its own genus, despite being superficially similar to *Lumbricillus*. All members of the superclade contain littoral species mostly found in marine environments.

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## SUPPLEMENTARY INFORMATION

**Figure S1.** Majority-rule consensus tree for 16S estimated with Bayesian inference. Specimens marked in green are new to this study. Support values are posterior probabilities. Scale bar represents the estimated number of substitutions per site.

**Figure S2.** Majority-rule consensus tree for ITS2 estimated with Bayesian inference. Specimens marked in green are new to this study. Support values are posterior probabilities. Scale bar represents the estimated number of substitutions per site.

**Figure S3.** Majority-rule consensus tree for H3 estimated with Bayesian inference. Specimens marked in green are new to this study. Support values are posterior probabilities. Scale bar represents the estimated number of substitutions per site.

**Table S1.** List of specimens used in this study, with specimen identification number, collection data, GPS coordinates (in decimal degrees, WGS84), GenBank accession numbers for seven different markers (bold numbers are new sequences generated in this study) and voucher numbers. Letters for *Lumbricillus pagenstecheri* refer to barcoding clusters (see Klinth *et al*. 2017a). Country codes: AU=Australia, DK= Denmark, ES=Spain, FR=France, GL=Greenland, NL=Netherlands, NO=Norway, SE=Sweden and UK=United Kingdom. * Unsuccessfully sequenced marker.

## REFERENCES

Backlund HO. 1947. Swedish Enchytraeida II. Lunds Universitets Årsskrift N.F. Avd. 2 43: 1–30.

Backlund HO. 1948. *Lumbricillus reynoldsoni* n. sp., an enchytraeid from the beaches of North Wales. Journal of the marine biological Association of the United Kingdom 27: 710–717. doi: https://doi.org/10.1017/S0025315400056083

Bakken T, Hårsaker K, Daverdin M. 2023. Marine invertebrate collection NTNU University Museum. Version 1.1633. Norwegian University of Science and Technology. Occurrence dataset accessed via GBIF.org on 2023-11-13. doi: https://doi.org/10.15468/ddbs14

Benham WB. 1905. On the Oligochaeta from the Southern Islands of the New Zealand Region. Transactions and Proceedings of the New Zealand Institute 37: 285–297.

Bretscher K. 1899. Beitrag zur Kenntnis der Oligochaeten-Fauna der Schweiz. Revue Suisse de Zoologie 3: 369–426. doi: https://doi.org/10.5962/bhl.part.82518.

von Bülow T. 1955. Oligochaeten aus den Endgebieten der Schlei. Kieler Meeresforschungen 11: 253–264.

von Bülow T. 1957. Systematisch-autökologische Studien an eulitoralen Oligochaeten der Kimbrischen Halbinsel. Kieler Meeresforschungen 13: 69–116.

Černosvitov L. 1929. Communication préliminaire sur les Oligochètes récoltés par M. P. Remy pendant la croisière arctique effectuée par le "Pourquoi-Pas?" en 1926 sous la direction du Dr. J.-B. Charcot. Bulletin du Muséum National d'Histoire Naturelle. Paris, 2(1): 144–149.

Christensen B. 1962. Oligochaeta 3. Enchytraeidae. The Zoology of Iceland 2, Part 20c: 1–11.

Claparède E. 1861. Études anatomiques sur les Annélides, Turbellariés, Opalines et Grégarines observés dans les Hébrides. Mémoires de la Société de Physique et d'Histoire Naturelle de Genève 16: 71–164. doi: https://doi.org/10.5962/bhl.title.14795.

Coates KA. 1981. New species of *Lumbricillus* (Oligochaeta, Enchytraeidae) from littoral habitats of British Columbia. Canadian Journal of Zoology 59(7): 1302–1311. doi: https://doi.org/10.1139/z81-182

Coates KA. 1989. Phylogeny and origins of Enchytraeidae. Hydrobiologia 180(1): 17–33. doi: https://doi.org/10.1007/BF00027534

Coates KA, Erséus C. 1985. Marine enchytraeids (Oligochaeta) of the coastal northwest Atlantic (northern and mid USA). Zoologica Scripta 14(2): 103–116. doi: https://doi.org/10.1111/j.1463-6409.1985.tb00181.x

Drummond AJ, Suchard MA, Xie D, Rambaut A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. Molecular Biology and Evolution 29(8): 1969–1973. doi: https://doi.org/10.1093/molbev/mss075 .

Edgar RC. 2004. MUSCLE: a multiple sequence alignment method with reduced time and space complexity. BMC bioinformatics 5(1): 1–19. doi: https://doi.org/10.1186/1471-2105-5-113

Elmhirst R, Stephenson J. 1926. On *Lumbricillus scoticus* n. sp. Journal of the marine biological Association of the United Kingdom 14: 469–473. doi: https://doi.org/10.1017/S0025315400007943

Eisen G. 1904. Enchytraeidae of the west coast of North America. In Harriman Alaska Expedition series. Vol. XII. Annelids. Smithsonian Institution, New York, 1–166. doi: https://doi.org/10.5962/bhl.title.11673

Erséus C. 1976. Littoral Oligochaeta (Annelida) from Eyjafjörður, North Coast of Iceland. Zoologica Scripta 5: 5–11. doi: https://doi.org/10.1111/j.1463-6409.1976.tb00677.x

Erséus C. 1977. Marine Oligochaeta from the Koster Area, west coast of Sweden, with descriptions of two new enchytraeid species. Zoologica Scripta 6: 293–298. doi: https://doi.org/10.1111/j.1463-6409.1978.tb00781.x

Erséus C. 1994. The Oligochaeta. In J. A. Blake & B. Hilbig (eds). Taxonomic Atlas of the Bentic Fauna of the Santa Maria Basin and Western Santa Barbara Channel Volume 4 Oligochaeta to Polychaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae). Santa Barbara, California: Santa Barbara Museum of Natural History. pp 5–38.

Erséus C, Rota E, Matamoros L, De Wit P. 2010. Molecular phylogeny of Enchytraeidae (Annelida, Clitellata). Molecular Phylogenetics and Evolution 57(2): 849–858. doi: https://doi.org/10.1016/j.ympev.2010.07.005

Erséus C, Klinth MJ, Rota E, De Wit P, Gustafsson DR, Martinsson S. 2019. The popular model annelid *Enchytraeus albidus* is only one species in a complex of seashore white worms (Clitellata, Enchytraeidae). Organisms Diversity & Evolution 19(2): 105–133. doi: https://doi.org/10.1007/s13127-019-00402-6

Finogenova NP. 1977. The oligochaetes of Tyup River and Tyup Bay on Lake Issyk-kul' Hydrobiological studies of the Tyup River and of Tyup Bay on Lake Issyk-Kul'. Collection of scientific papers; USSR Academy of Sciences, Zoological Institute 115–123.

Finogenova NP, Streltsov VE. 1978. Two new species of oligochaetes of the genus *Lumbricillus* from the east Murman littoral. Biologiya Morya 1: 17–23.

Finogenova NP, Timm T. 1988. Enchytraeids (Oligochaeta, Enchytraeidae) of the littoral of the White Sea. Benthic ecosystems of the south-eastern part of the Kandalaksha Bay and adjacent waters of the White Sea. Explorations of the fauna of the seas 38(46): 91–108.

Heled J, Drummond AJ. 2010. Bayesian inference of species trees from multilocus data. Molecular biology and evolution 27(3): 570–580. doi: https://doi.org/10.1093/molbev/msp274

Henle FGJ. 1837. Ueber *Enchytraeus*, eine neue Anneliden-Gattung. Müllers Archiv für Anatomie, Physiologie und Wissenschaftliche Medizin, Berlin 1837: 74–90.

Katoh K, Misawa K, Kuma K, Miyata T. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic acids research 30(14): 3059–3066. doi: https://doi.org/10.1093/nar/gkf436

Klinth MJ, Martinsson S, Erséus C. 2017a. Phylogeny and species delimitation of North European *Lumbricillus* (Clitellata, Enchytraeidae). Zoologica Scripta 46(1): 96–110. doi: https://doi.org/10.1111/zsc.12187

Klinth MJ, Rota E, Erséus C. 2017b. Taxonomy of North European *Lumbricillus* (Clitellata, Enchytraeidae). Zookeys 703: 15–96. doi: https://doi.org/10.3897/zookeys.703.13385

Klinth MJ, Rota E, Martinsson S, Prantoni AL, Erséus C. 2022. New insights into the systematics of *Lumbricillus* and *Marionina* (Clitellata: Enchytraeidae) inferred from Southern Hemisphere samples, including three new species. Zoological Journal of the Linnean Society 194(4): 1103–1133. doi: https://doi.org/10.1093/zoolinnean/zlab073

Kossmagk-Stephan KJ. 1983. Marine Oligochaeta from a sandy beach of the island of Sylt (North Sea) with description of four new enchytraeid species. Mikrofauna des Meeresbodens 89: 1–28.

Lee J, Klinth MJ, Jung J. 2019. Two species of *Lumbricillus* (Enchytraeidae, Annelida) new to Antarctica. Polar Research 38: 3325. doi: https://doi.org/10.33265/polar.v38.3325

Levinsen GMR. 1884. Systematisk-geografisk Oversigt over de nordiske Annulata, Gephyrea, Chaetognathi og Balanoglossi. II. Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjøbenhavn for Aaret 1883: 92–350. doi: https://doi.org/10.5962/bhl.title.16117

Librado P, Rozas J. 2009. DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. Bioinformatics 25(11), 1451–1452. doi: https://doi.org/10.1093/bioinformatics/btp187

Marcus E. 1965. Naidomorpha aus brasilianischem Brackwasser. Studies on Neotropical Fauna and Environment 4: 61–83. doi: https://doi.org/10.1080/01650526509360380

Martínez-Ansemil E. 1982. Les Oligochètes aquatiques de la peninsule Ibérique (2e note) avec la description de *Lumbricillus brunoi* n. sp. (Enchytraeidae). Bulletin de la Société d'Histoire Naturelle, Toulouse 118: 145–151.

Michaelsen W. 1888. Die Oligochaeten von Süd-Georgien nach der Ausbeute der Deutschen Station von 1882–1883. Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten 5: 53–73.

Michaelsen W. 1889. Oligochaeten des Naturhistorischen Museums in Hamburg. Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten 6: 1–17.

Michaelsen W. 1911. Littorale Oligochäten von der Nordküste Russlands. Travaux de la Société Impériale des Naturalistes de St. Pétersbourg 42: 106–110.

Michaelsen W. 1914. Oligochaeta. In: Beiträge zur Kenntnis der Land- und Süßwasserfauna Deutsch- Südwestafrikas. Ergebnisse der Hamburger deutsch-südwestafrikanischen Studienreise 1911: 137–182. doi: https://doi.org/10.5962/bhl.title.7352

Michaelsen W. 1927. Oligochaeta. In: Grimpe G, Wagler E (eds). Die Tierwelt der Nordund Ostsee VIc. Leipzig. pp 1–44.

Michaelsen W. 1935. Meeresstrand-Enchyträiden des südlichen Atlantischen Ozeans. Scientific Results of the Norwegian Antarctic Expeditions 1927-1928 et sqq., instituted and financed by consul Lars Christensen 14: 2–7.

Müller OF. 1774. Vermium terrestrium et fluviatilum, seu animalium infusoriorum, helminthicorum, et testaceorum, non marinorum, succincta historia. Vol. 1, Part 2. Copenhagen and Leipzig: Heineck and Faber. 72 p. doi: https://doi.org/10.5962/bhl.title.12733

Müller OF. 1776. Zoologiae Danicae Prodromus. Copenhagen. 282 p.

Nielsen CO, Christensen B. 1959. The Enchytraeidae: Critical revision and taxonomy of European species. Natura Jutlandica 8-9: 1–160.

Nurminen M. 1964. *Lumbricillus fennicus* sp.n. and some other Enchytraeids (Oligochaeta) from Finland. Annales Zoologici Fennici 1: 48–51.

Nurminen M. 1965. Enchytraeid and lumbricid records (Oligochaeta) from Spitsbergen. Annales Zoologici Fennici 2(1): 1–10.

Nurminen M. 1970. Records of Enchytraeidae (Oligochaeta) from the west coast of Greenland. Annales Zoologici Fennici 7: 199–209.

Ørsted AS. 1844. De regionibus marinis. Copenhagen: J. C. Scharling. 89 p.

Pfeffer GJ. 1890. Die niedere Thierwelt des antarktischen Ufergebietes. In Neumayer G (ed). Die internationale Polarforschung 1882–1883. Die Deutschen Expeditionen und ihre Ergebnisse. Band II. Beschreibende Naturwissenschaften in einzelnen Abhandlungen Hamburg. pp 455–574.

Rambaut A. (Producer). 2014. Figtree, a graphical viewer of phylogenetic trees. Available from: http://tree.bio.ed.ac.uk/software/figtree.

Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA. (Producer). 2018. Tracer v1.7, Available from http://beast.community/tracer.

Ratzel F. 1868. Beiträge zur anatomischen und systematischen Kenntniss der Oligochaeten. Zeitschrift für wissenschaftliche Zoologie 18(4): 563–591.

Rodriguez P, Rico E. 2008. A new freshwater oligochaete species (Clitellata: Enchytraeidae) from Livingston Island, Antarctica. Polar Biology, 31(10): 1267–1279. doi: https://doi.org/10.1007/s00300-008-0465-5

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Hohna S, Huelsenbeck JP. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology, 61(3): 539–542. doi: https://doi.org/10.1093/sysbio/sys029

Rota E. 2001. Oversized enchytraeids (Annelida, Clitellata): a comparative study, with a revised description of *Lumbricillus maximus* (Michaelsen). Organisms Diversity & Evolution, 1(3): 225–238. doi: https://doi.org/10.1078/1439-6092-00019

Rota E, Matamoros L, Erséus C. 2008. In search of *Marionina* (Clitellata, Enchytraeidae): A taxonomic history of the genus and redescription of the type species *Pachydrilus georgianus* Michaelsen, 1888. Italian Journal of Zoology 75(4): 417–436. doi: https://doi.org/10.1080/11250000801930433

Roule L. 1888. Sur la structure histologique d'un oligochaete marin appartenant à un genre nouveau. Comptes rendus hebdomadaires des Séances de l'Académie des Sciences 116: 308–310.

Saint-Loup R. 1885. Sur l'organisation du *Pachydrilus enchytraeoides*. Comptes rendus hebdomadaires des Séances de l'Académie des Sciences 101: 482–485.

Schmelz RM, Collado R. 2010. A guide to European terrestrial and freshwater species of Enchytraeidae (Oligochaeta). Soil organisms, 82(1): 1–176.

Shurova NM. 1974. Enchytraeidae of the genus *Lumbricillus* (Oligochaeta) from the intertidal zone of the Kurile Islands. In: The plant and animal world of the littoral of the Kurile Islands. Far-Eastern Scientific Centre, Novosibirsk: 128–136.

Shurova NM. 1977. New littoral species of the genus *Lumbricillus* (Oligochaeta). Biologiya Morya 1: 57–62.

Shurova NM. 1978. The intertidal oligochaetes from the eastern coast of Kamchatka. In: Kusakin OG. (ed.). Litoral Beringova morya i yugovostochnoj Kamchatki (Littoral of the Bering Sea and the southeastern Kamchatka). Nauka, Moscow. pp 98–105.

Shurova NM. 1979. Enchytraeids (Oligochaeta) of the far-east seas of the USSR. In: Studies on the pelagic and ground inhabiting organisms of the Far East seas. Vladivostok. pp 75–89.

Southern R. 1909. Contributions towards a monograph of the British and Irish Oligochaeta. Proceedings of the Royal Irish Academy 27 (Section B): 119–182.

Southern R. 1913. Clare Island survey part 48: Oligochaeta. Proceedings of the Royal Irish Academy 31: 1–48.

Stephens M, Donnelly P. 2003. A comparison of bayesian methods for haplotype reconstruction from population genotype data. The American Journal of Human Genetics, 73(5): 1162–1169. doi: https://doi.org/10.1086/379378

Stephens M, Smith NJ, Donnelly P. 2001. A new statistical method for haplotype reconstruction from population data. The American Journal of Human Genetics 68(4): 978–989. doi: https://doi.org/10.1086/319501

Stephenson J. 1911. On some littoral Oligochaeta of the Clyde. Transactions of the Royal Society of Edinburgh 48: 31–65. doi: https://doi.org/10.1017/S0080456800018755

Stephenson J. 1922. The Oligochaeta of the Oxford University Spitsbergen Expedition. Proceedings of the Zoological Society of London 92(4): 1109–1138. doi: https://doi.org/10.1111/j.1469-7998.1922.tb07096.x

Stephenson J. 1924. On some Oligochaete worms from Spitsbergen. Results of the Merton College expedition to Spitsbergen. Annals and Magazine of Natural History. London 13: 210–216. doi: https://doi.org/10.1080/00222932408633029

Stephenson J. 1925. The Oligochæta of Spitsbergen and Bear Island; some additions and a summary. Proceedings of the Zoological Society of London 95(4): 1293–1322. doi: https://doi.org/10.1111/j.1469-7998.1925.tb07438.x

Stephenson J. 1932a. Oligochaeta from Australia, North Carolina, and other parts of the world. Proceedings of the Zoological Society of London 1932: 899–941. doi: https://doi.org/10.1111/j.1096-3642.1932.tb01571.x

Stephenson J. 1932b. Oligochaeta. Part. I. Microdrili. Discovery Reports 4: 233–264. doi: https://doi.org/10.5962/bhl.part.17059

Stöhr S. 2023. Invertebrates Collection of the Swedish Museum of Natural History. Swedish Museum of Natural History. Occurrence dataset accessed via GBIF.org on 2023-11-13. doi: https://doi.org/10.15468/eyda6l

Tynen MJ. 1966. A new species of *Lumbricillus*, with a revised checklist of the British Enchytraeidae [Oligochaeta]. Journal of the Marine Biological Association of the United Kingdom, 46(1): 89–96. doi: https://doi.org/10.1017/S0025315400017562

Tynen MJ. 1969. New Enchytraeidae (Oligochaeta) from the east coast of Vancouver Island. Canadian Journal of Zoology 47(3): 387–393. doi: https://doi.org/10.1139/z69-072

Tynen MJ. 1970. *Marionina charae*, a new species of enchytraeid (Oligochaeta) from the Canadian arctic. Canadian Journal of Zoology 48: 1359–1361. doi: https://doi.org/10.1139/z70-232

Tynen MJ. 1972. The littoral Enchytraeidae (Oligochaeta) of Anglesey and the Menai Strait with notes on habitats. Journal of Natural History 6(1): 21–29. doi: https://doi.org/10.1080/00222937200770031

Ude H. 1896. Enchytraeiden. Hamburger Magalhaensische Sammelreise III (5). Hamburg: L. Friedrichsen & Co. 43 p.

Wang H, Liang Y. 1997. Two new species of Oligochaeta (Annelida) from King George Island, Antarctica. Oceanologia et Limnologia Sinica 28: 177–184.

Welch PS. 1914. Studies on the Enchytraeidae of North America. Bulletin of the Illinois State Laboratory of Natural History, Urbana 10: 123–211. doi: https://doi.org/10.21900/j.inhs.v10.373

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