

On the distribution and taxonomic limits of *Lumbricillus pagenstecheri* (Oligochaeta, Enchytraeidae)

Tarmo Timm

Centre for Limnology, Institute of Agricultural and Environmental Sciences, Estonian Agricultural University, 61101 Rannu, Tartumaa, Estonia; <ttimm@zbi.ee>

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Abstract. *Lumbricillus pagenstecheri* (Ratzel, 1869) is the most widely distributed and euryhaline representative of a large, mostly littoral, group of *Lumbricillus* spp. with distinct glandular cover on the ectal spermathecal duct, and a rosette of glands at its ectal end. It is the only species in this group that has been recorded from the shores of both the Atlantic and Pacific oceans and from soil. A freshwater, maybe landlocked, population lives in Lake Kuril'skoe (Far East). It is not identical with *L. kamtschatkanus* Michaelsen (1929), which was previously reported from the same lake. *Lumbricillus pagenstecheri* as currently recognized is morphologically different from the rich assemblage of related species from marine littoral of the North Pacific while no clear differences are found between its own marine and freshwater populations.

Key words: *Lumbricillus*, taxonomy, distribution, freshwater fauna.

INTRODUCTION

Lumbricillus pagenstecheri was first described as *Enchytraeus Pagenstecheri* by Ratzel (1869) from decaying freshwater vegetation in Germany, and later on emended by Vejdovský (1879) and Ude (1892), similarly on inland material. Vejdovský (1879) recorded it from “ammoniakhaltigen Localitäten”, apparently meaning polluted freshwater, and Ude (1892) from wet soil enriched with horse manure. The 20th century records are exclusively for marine littoral habitats, mostly from decaying seaweed.

The worms described as *Pachydrilus Pagenstecheri* by Vejdovský (1879) and Ude (1892), as well as *Lumbricillus pagenstecheri* by Nielsen & Christensen (1959) and subsequent authors, had an ectal spermathecal duct covered with gland cells, and a rosette of larger glands surrounding its ectal end (see, e.g., Erséus 1976). These glands were not mentioned in the short original description by Ratzel

(1869) and the chaetae were almost straight and more numerous (6–10) than reported in later records. Thus the identity of the recent records with the species that was originally described is open to some doubt. There exists no type material (Reynolds & Cook 1976).

Later on, a number of *Lumbricillus* species with spermathecae of the similar type but different in various other characteristics, have been described, mostly from marine littoral. Herewith I give a survey of them, trying to compare them with the *L. pagenstecheri* as presented in the classical monograph by Nielsen & Christensen (1959), and discussing their possible relations with one another.

MATERIAL

My own material originates from Lake Kuril'skoe on the Kamchatka Peninsula, Russian Far East (Fig. 1). About 8860 specimens of *L. pagenstecheri* were collected there in 1994–1998 with routine zoobenthos samples (Timm & Vvedenskaja submitted). Thirteen of them were studied in serial sections, the rest as whole

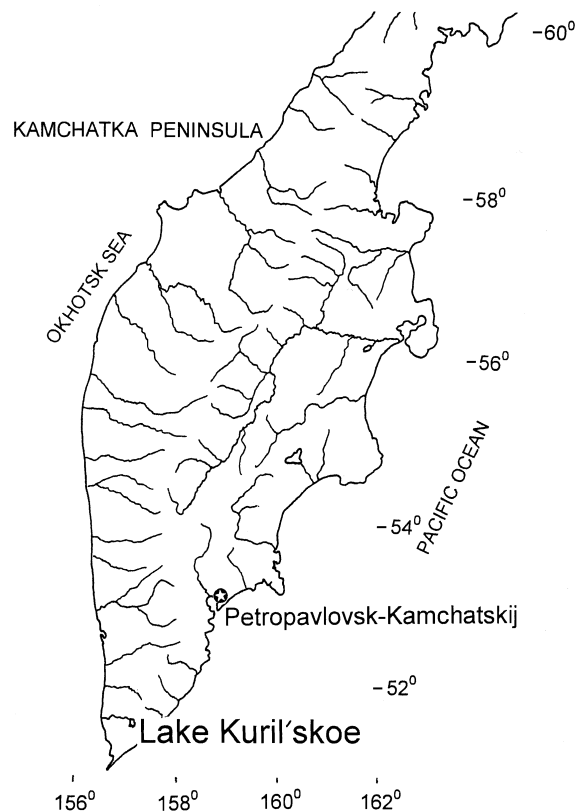


Fig. 1. Geographical location of Lake Kuril'skoe.

mounts. Eleven specimens, mounted on a slide, were later deposited in the Royal Ontario Museum, Toronto, under # ROMIZ 14742. No live material was available for study. Syntypes of *Pachydrilus kamtschatkanus* Michaelsen, 1929 (Zoological Museum of the Hamburg University, # V 8088) were restudied as whole mounts in Canada balsam.

RESULTS

Lake Kuril'skoe is a large (77 km²), 313 m deep, oligotrophic, entirely fresh-water lake. It lies 110 m above sea level, and is of volcanic origin. Enchytraeidae are common in the stony shallow-water zone, and relatively diverse, with at least 13 taxa (Timm 1999, Timm & Vvedenskaja submitted).

Previously only the endemic *Lumbricillus kamtschatkanus* (= *Pachydrilus kamtschatkanus* Michaelsen, 1929) was recorded there dredged in large numbers from depths of 2–5 m in 1909. Michaelsen (1929) thought it was related to *L. pagenstecheri*. However, the ectal rosette of the spermathecae consisted of several small glands while the gland cover on the duct was replaced with a glandular epithelium. Subneural glands (“Kopulationsdrüsen”) were less developed than described in *L. pagenstecheri* by Ude (1892) and (as *L. georgiensis*) Tynen (1969). Differences in the brain and nephridia were also noticed by Michaelsen (1929).

The restudied type series of *P. kamtschatkanus* consists of one clitellate (with ripe eggs) and four maturing or post-reproductive individuals, about 6 mm long and with 41–43 segments. They correspond to Michaelsen's description, including the thick-walled naked spermathecal duct in the clitellate specimen. No ectal rosette was observed. The ampulla was wider than the duct (respectively 55 and 30 µm) but with a similar thick wall and narrow lumen (Fig. 2). Thus, this species is neither identical nor closely related to *L. pagenstecheri*. Neither can it be confused with *L. arenarius* (Michaelsen, 1889), also known from this lake, which is characterized by three almost straight chaetae per bundle, and very large pear-shaped spermathecae with a naked ectal duct and a distinct glandular rosette on the ectal pore.

In the 1990s, *L. pagenstecheri* (= *Lumbricillus* sp. 1 sensu Timm 1999) dominated in the shallowest littoral of Lake Kuril'skoe whereas *L. arenarius* was less numerous and occurred deeper, at 4–13 m. *L. kamtschatkanus* was not observed. “*Lumbricillus* sp. 2” sensu Timm (1999) actually belongs to *Mesenchytraeus* (Timm & Vvedenskaja submitted).

The characteristics of *L. pagenstecheri* from Lake Kuril'skoe are as follows (see also Fig. 3). Mature worms 8–12 mm long when preserved, with 41–51 segments. Chaetae almost straight, 4–5 (2–7) before clitellum, and slightly sigmoid, (2) 3–4 posteriorly, 58–110 µm long (longest on the mid-body) and 5–9 µm thick, without nodulus. Clitellum in XII–XIII, 40–50 µm thick, consisting of irregular small gland cells. Male pores with tubercle; penial bulb sometimes partially everted. Brain wider posteriorly; its posterior edge concave. Subneural glands in XIV–XV. Coelomocytes not seen in preserved material. Pharyngeal glands as three pairs, with dorsal and ventral lobes; dorsal connections in the two anterior pairs.

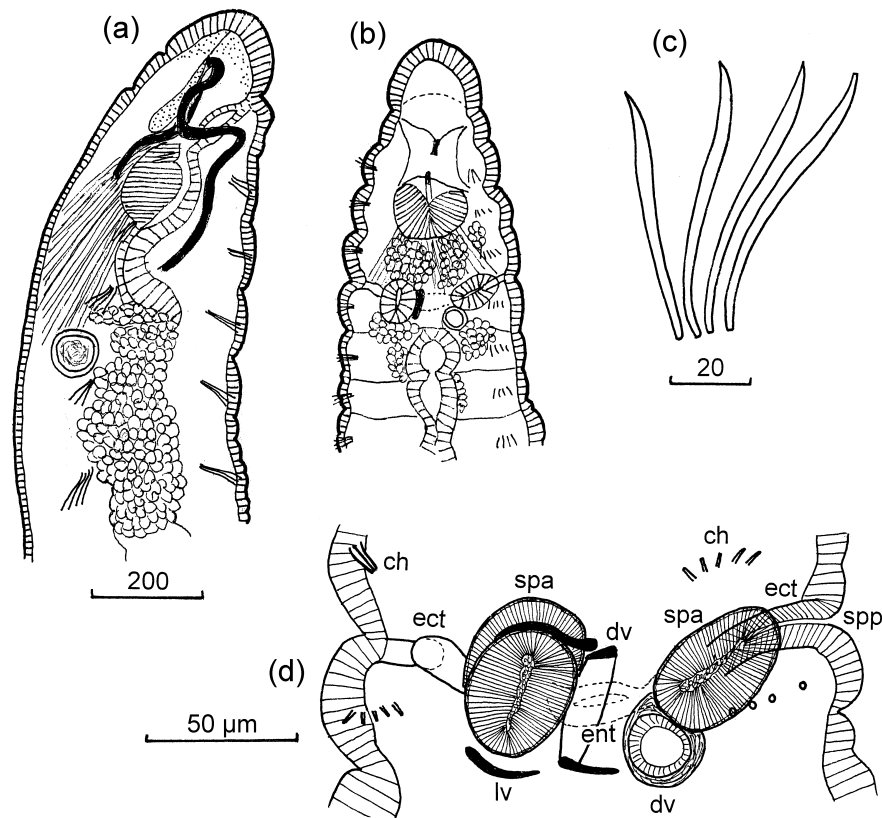


Fig. 2. *Lumbricillus kamtschatkanus* from Lake Kuril'skoe, syntypes. (a) – anterior end of a post-reproductive specimen in side view; (b) – anterior end of a clitellate specimen from above; (c) – chaetal bundle; (d) – spermathecae of the clitellate specimen *in situ*. ch – dorsal chaetae of IV; dv – parts of the dorsal blood vessel; ect – ectal duct of spermatheca; ent – ental ducts of spermathecae; lv – lateral blood vessel; spa – spermathecal ampulla.

Chloragogenous tissue beginning in VI or VII. Intestine gradually dilating in VIII or IX. Dorsal vessel arising in XV or XVI but in some specimens traced from XII only. Postseptals of nephridia tadpole-like in side view, with an approximately 20 µm long duct descending backwards in a bow from the roundish body.

Testes large and bush-like, filling IX–X, often stretching into VIII and XII. Male funnels 2–2.5 times as long as wide (230–350 × 100–170 µm), bent, with 12–14 µm wide lumen. Collar of the same width or slightly narrower (63–140 µm). Vasa deferentia 11–16 µm wide, with lumen 5 µm, tightly coiled into paired ventral plates behind 11/12. Penial bulbs flat oval or partially bilobate (the smaller anterior/lateral lobe can protrude from the male pore), 150–240 µm long, 135–210 µm high, and 115–290 µm wide. Their thin (4 µm) muscular wall surrounds a mixture of muscular and glandular tissue; lumen 35 µm wide.

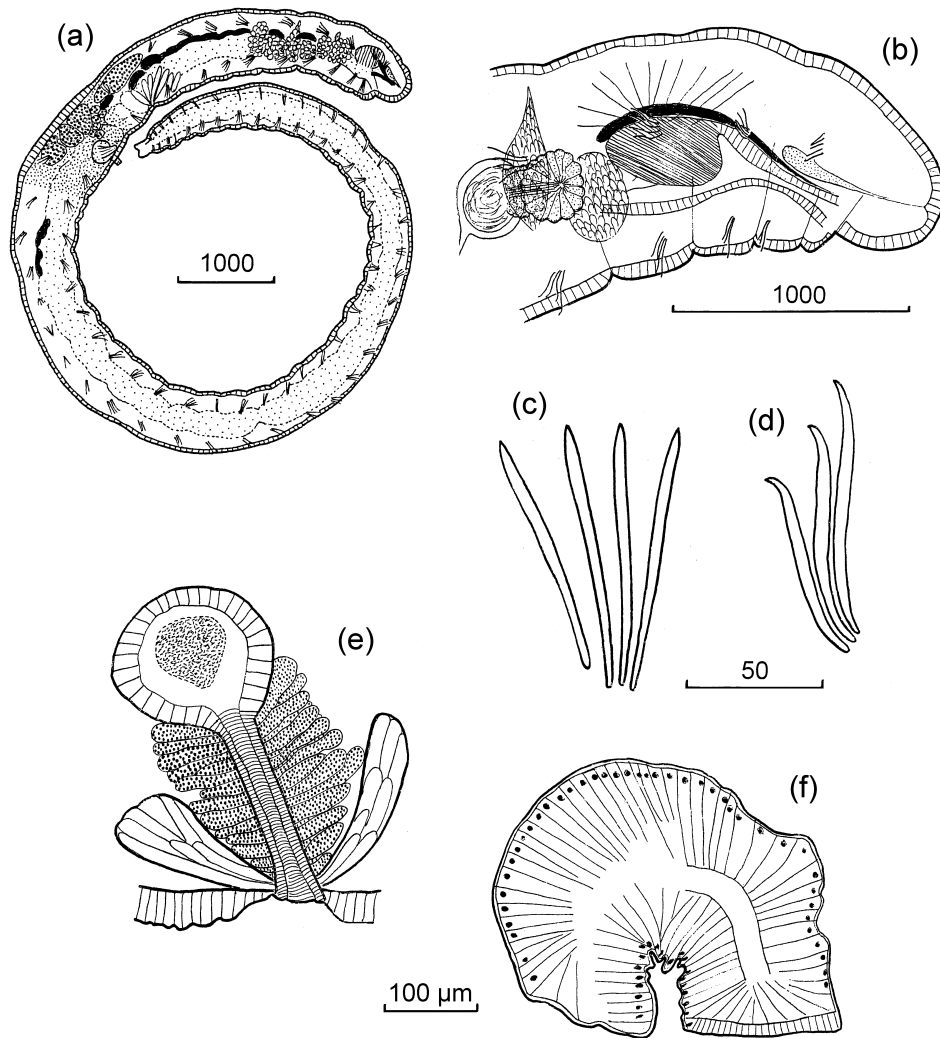


Fig. 3. *Lumbricillus pagenstecheri* from Lake Kuril'skoe. (a) – general view of a whole-mounted specimen; (b) – anterior end; (c) – anterior chaetal bundle from above; (d) – posterior chaetal bundle from side; (e) – spermatheca, reconstructed after sections; (f) – male funnel, from a section.

More than ten eggs in XII. Female funnels either as a thickened part of 12/13 (at least 50 µm long, 24 µm thick), or with two vertical, 60 µm long lips. Egg ducts at 12/13, 30 µm long; female pores either in 12/13 or slightly backwards.

Spermathecae in V with sphaerical, flattened, oval, or pear-shaped ampulla, 85–135 µm wide in separate specimens; its wall smooth, 7–20 µm thick (sometimes thicker distally). Short (80–115 µm) ental duct joining oesophagus in V or at the beginning of VI. Sperm in the ampulla coiled as one or several skeins. Ectal duct

65–145 μm long and 27–30 μm wide, sometimes medially dilated. Its wall consists of epithelial and muscular layers, and is covered with a 45–55 μm thick mass of glands; its total width together with glands 112–125 μm . A rosette of higher glands, 110–200 μm in diameter, surrounds the ectal end.

The above description is in good accordance with *L. pagenstecheri* as defined by Nielsen & Christensen (1959) and Erséus (1976).

DISCUSSION

Other than *L. pagenstecheri*, the species of *Lumbricillus* with spermathecae of generally similar structure live in the marine littoral. Only *L. pagenstecheri* has been recorded, besides seashore, also from the inland habitats: polluted freshwater or rich moist soil in Europe (Ratzel 1869, Vejdovský 1879, Ude 1892), and a clean freshwater lake in Kamchatka (new data). The Kamchatkan population has, on average, a slightly shorter body (8–12 mm, against 14–18 mm) and shorter sperm funnel (length/width ratio 2–3, against 3–4) than those reported by Nielsen & Christensen (1959). There are also some minor differences at the beginning of the dorsal vessel, distribution of subneural glands etc. However, the differences are less than those in *L. ritteri* Eisen, 1904, and *L. georgiensis* Tynen, 1969, synonymized with *L. pagenstecheri* by Coates & Ellis (1981) (see below). The main character of the species, the shape and structure of spermathecae, is persuasively identical with those depicted in Europe by Vejdovský (1879), Nielsen & Christensen (1959), and Erséus (1976).

North Atlantic species

Only three valid *Lumbricillus* species with *pagenstecheri*-like spermathecae occur in the North Atlantic: *L. pagenstecheri* (with several synonyms, see below), *L. semifuscus* (Claparède, 1861), and *L. algensis* Erséus, 1977. *L. henkingi* (Ude, 1901) was synonymized with *L. pagenstecheri* by Nielsen & Christensen (1959); and with *L. aegialites* Stephenson, 1922 and *L. necrophagus* Stephenson, 1922 by Stephenson (1925) and Nurminen (1965). Erséus (1976, 1977) and Coates & Ellis (1981) hesitated to add *L. kalatdlitus* (Nurminen, 1970) from Greenland to the synonymy of *L. pagenstecheri*. However, it does not differ from the latter more than the other synonymous taxa; moreover, Nurminen (1970) did not record nominal *L. pagenstecheri* from the same material.

According to Erséus (1976), *L. semifuscus* differs from *L. pagenstecheri* in many aspects: thin glandular cover on the long ectal duct of spermatheca, small roundish ampulla, weakly divided testes confined to XI, sperm funnel only 1.5 times as long as wide, pharyngeal glands without dorsal connections but with the posterior ventral lobes extending into VII, almost straight chaetae, etc. Stephenson (1911) described it (as *Marionina semifusca*) as having strongly sigmoid chaetae, triangular testes, and a thin-walled spermathecal duct (glandular cover was depicted in the

figure). In *L. algensis*, the spermathecal ampulla is very long, and the glandular cover is extending on its ectal portion. Erséus (1977) did not even compare this species with *L. pagenstecheri*.

Northwestern Pacific species

Thirteen *Lumbricillus* species with “*pagenstecheri*-spermathecae” (gland-covered ectal duct with an ectal rosette) have been recorded in the marine littoral and sublittoral of Russia and Japan by Yamaguchi (1937) and Shurova (1974, 1977, 1978, 1979, 1986): *L. annulatus* Eisen, 1904; *L. nipponicus* (Yamaguchi, 1937); *L. mirabilis* Tynen, 1969; *L. kurilensis* Shurova, 1974; *L. orientalis* Shurova, 1974; *L. rufulus* Shurova, 1974; *L. corallinae* Shurova, 1977; *L. ignotus* Shurova, 1977; *L. pinquis* Shurova, 1977; *L. similis* Shurova, 1977; *L. lentus* Shurova, 1978; *L. taisiae* Shurova, 1978; and *L. sapitus* Shurova, 1979. They differ from each other, as well as from *L. pagenstecheri* sensu Nielsen & Christensen (1959), in having different combinations of various reproductive and somatic characters. Three species – *L. corallinae*, *L. ignotus*, and *L. pinquis* – are most distinct in having paired chaetae; probably they represent a separate clade. *L. similis* may be most closely related to *L. pagenstecheri*, differing only in being smaller (7–8 mm, with 38–45 segments) and with numerous (up to 13) posterior ventral chaetae. *L. pagenstecheri* itself has not been recorded in this region.

Northeastern Pacific species

At least nine valid species of *Lumbricillus* with spermathecae of *pagenstecheri* type were recorded from American side of the Northern Pacific by Eisen (1904), Tynen (1969), Coates (1981), and Coates & Ellis (1981). These are *L. pagenstecheri* (Ratzel, 1869) (syn. *L. ritteri* Eisen, 1904, and *L. georgiensis* Tynen, 1969); *L. merriami* Eisen, 1904 (with var. *elongatus* Eisen, 1904); *L. annulatus* Eisen, 1904 (syn. *L. vancouverensis* Tynen, 1969); *L. franciscanus* Eisen, 1904 (with ssp. *borealis* Eisen, 1904 and *unalaskae* Eisen, 1904); *L. mirabilis* Tynen, 1969; *L. qualicumensis* Tynen, 1969; *L. belli* Tynen, 1969; *L. tsimpseanis* Coates, 1981; and *L. curtus* Coates, 1981.

Coates & Ellis (1981) synonymized *L. ritteri* and *L. georgiensis* with *L. pagenstecheri*, thus considerably expanding the definition of the last. *L. ritteri* is large (up to 25 mm and 60–62 segments), and has very large, lobed subneural glands in XIII–XVII. *L. georgiensis* is 15–20 mm long, with 49–58 segments, and subneural glands in XV–XIX. Its sperm in the spermathecal ampulla was said to be disposed in pyriform packets as in some Northwestern Pacific species described by Shurova (1977, 1978) but not in *L. similis*, which is otherwise close to *L. pagenstecheri*. However, Coates & Ellis (1981) did not find these packets even in syntypes of *L. georgiensis*. Sperm funnels are similar in *L. pagenstecheri*, *L. ritteri*, and *L. georgiensis*.

The synonymies proposed by Coates & Ellis (1981) as well as their new specimens extended the geographic range of *L. pagenstecheri* to the Northeastern Pacific, which thus became a circumholarctic species. The nominal *L. pagenstecheri* has not been recorded from the Russian side of the North Pacific except from a freshwater lake (Kuril'skoe). This lacustrine population is clearly closer to the conspecific European populations than to *L. similis*, its closest known relative in the North-western Pacific.

The total number of valid nominal species in *L. pagenstecheri* group from the North Pacific reaches 20. Only two species (*L. annulatus* and *L. mirabilis*) are without any doubt known from both sides of the Pacific. A potential identity of the Northeastern *L. qualicumensis* with *L. ignotus* from the Russian side, and *L. merriami* with *L. annulatus* or/and *L. nipponicus* was discussed by Coates & Ellis (1981). A clinal infraspecific variability between neighbouring populations (which can be treated as subspecies) is plausible. Thus the taxonomic rank of separate nominal species or subspecies with a limited distribution range can be conditional, particularly in comparison with the Holarctic, variable *L. pagenstecheri*.

Based on the spermathecal form, three series of the *Lumbricillus* species of this group occur along the Pacific.

1. Small ampulla not considerably wider than the ectal duct. The latter is relatively long, with covering gland cells gradually decreasing in length from the ectal rosette towards the ampulla. *L. annulatus*, *L. merriami*, and *L. nipponicus*.
2. Large roundish or pear-shaped ampulla, distinct medium or short ectal duct with dense glandular cover, and a large compact glandular crown near the ectal pore. 15 species, including *L. pagenstecheri* with its possible synonyms.
3. Proportions of ampulla and duct as in the latter group; glands present but poorly developed both on the duct and at the spermathecal pore. *L. tsimpseanis* and *L. lentus*. These species form a transition to the freshwater *L. kamtschatkanus* and several other *Lumbricillus* with bare ectal spermathecal duct.

CONCLUSIONS

There is a large cluster (more than 20) of *Lumbricillus* species sharing with *L. pagenstecheri* a distinct glandular cover on the ectal spermathecal duct, and a rosette at its ectal end. Their largest diversity is concentrated on the coasts of the North Pacific. Terrestrial (wet soil) and freshwater populations are known only for *L. pagenstecheri* itself, in Europe and in the Far Eastern Lake Kuril'skoe. *L. pagenstecheri* is also the most variable and the only circumholarctic species in the group.

Is *Lumbricillus pagenstecheri* sensu Nielsen & Christensen (1959) and Coates & Ellis (1981) the most euryhaline and most easily dispersing member of a large cluster of related species? Or is the currently recognized species an assemblage (superspecies) of different, local species, most of them Pacific? A wide distribution

of *L. pagenstecheri* in the North Atlantic and Northeast Pacific (accepting the presence of a large number of other, related species in the Pacific) is in accordance with the first hypothesis. The second hypothesis may be corroborated by the large variability of *L. pagenstecheri*, as well as by lack of its formal records on the Asian side of the Pacific. However, it may just be undiscovered there, or represented under a different name (e.g., *L. similis*). The actual taxonomic status of many slightly different local forms (e.g., *L. ritteri*) remains obscure.

Presence of *L. pagenstecheri* in Lake Kuril'skoe may mean that it does occur in the marine littoral of the Northwestern Pacific. Maybe this lake was a brackish-water lagoon, becoming fresh after a tectonic rise. Freshwater populations of other seashore enchytraeids occur in this lake – *L. arenarius*, *Marionina klaskisharum* Coates, 1983, and *M. charlottensis* Coates, 1980, according to Timm & Vvedenskaja (submitted).

The diversity of the *L. pagenstecheri* group is much less in the Atlantic than in the Pacific, maybe due to a shorter geological history of the former. Future molecular studies may shed light on the actual relations between these species and infraspecific taxa.

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Liigi *Lumbricillus pagenstecheri* (Oligochaeta, Enchytraeidae) levikust ja taksonoomilisest piiritlemisest

Tarmo Timm

Lumbricillus pagenstecheri (Ratzel, 1869) on levinuim ja eurühaliinseim selle perekonna peamiselt mere litoraalis elavate liikide rühmast, keda iseloomustab näärmekiht seemnehoidla välimisel juhal ja seemnehoidla ava ümbritsev näärmepärg. Ainsa selle rühma liigina on teda leitud ühtaegu nii Atlandi kui Vaikse ookeani randadelt, samuti mullast. Kurilskoje järves Kaug-Idas leiti selle liigi merest isoleeritud mageveeline populatsioon, mis pole identne samast järvest varem teada oleva liigiga *L. kamtschatkanus* Michaelsen (1929).