

Tubificidae (Clitellata, Oligochaeta) from Lake Taimyr, North Siberia, with a description of two new species and *Lamadrilus* gen. nov.

by Tarmo TIMM

Abstract

Seven tubificid species are reported from benthic samples collected in 1943-1944 in the large, but shallow, polar Lake Taimyr. The subarctic *Alexandrovia ringulata* SOKOLSKAJA, 1961 was very abundant on shallows. Among the species limited to the profundal zone, *Baikalodrilus alienus* spec. nov. and *Lamadrilus sorosi* gen. nov. spec. nov. belong to the genera distributed mainly in Lake Baikal. The new genus *Lamadrilus* of the subfamily Tubificinae has a tubular atrium and a short, often asymmetrical penial sheath. Both the vas deferens and prostatic gland enter the atrium subapically, leaving the proximal end free as in the marine genus *Tubificoides* LASTOČKIN, 1937 but without any clear histological separation from the rest of the atrium. Apart from *L. sorosi* gen. nov. spec. nov., four Baikalian species are included in this genus: *Isochaetides excavatus* HRABĚ, 1982 as the type species; *I. eximius* SEMERNOJ, 1982; *Tubifex bazikalovae* ČEKANOVSKAJA, 1975 with several subspecies; and *T. crassiseptus* SEMERNOJ, 1982. *Limnodrilus profundicola* (VERRILL, 1871), *Tasserkidrilus acapillatus* (FINOGENOVA, 1972) and two other taxa represented by immatures only, have also been found.

Key-words: Tubificidae, new taxa, Lake Taimyr, Lake Baikal, fauna, zoogeography.

Résumé

Sept espèces de tubificidés sont signalées à partir d'échantillons benthiques récoltés en 1943-1944 dans le lac polaire Taimyr, système lacustre de grande taille mais peu profond. L'espèce subarctique *Alexandrovia ringulata* SOKOLSKAJA, 1961 est très abondante dans les eaux peu profondes. Parmi les espèces limitées à la zone profonde, *Baikalodrilus alienus* spec. nov. et *Lamadrilus sorosi* gen. nov. spec. nov. appartiennent à des genres essentiellement présents dans le lac Baïkal. Le nouveau genre *Lamadrilus* de la sous-famille des Tubificinae a un atrium tubulaire et une courte gaine pénienne, parfois asymétrique. Le canal déférent et la glande prostatique pénètrent l'un et l'autre subapicalement dans l'atrium, laissant l'extrémité proximale libre, comme dans le genre marin *Tubificoides* LASTOČKIN, 1937, mais sans séparation histologique claire du reste de l'atrium. Outre *L. sorosi* gen. nov. spec. nov., quatre espèces baikaliennes sont incluses dans le genre : *Isochaetides excavatus* HRABĚ, 1982 en tant qu'espèce type; *I. eximius* SEMERNOJ, 1982; *Tubifex bazikalovae* ČEKANOVSKAJA, 1975, comprenant plusieurs sous-espèces; et *T. crassiseptus* SEMERNOJ, 1982. *Limnodrilus profundicola* (VERRILL, 1871), *Tasserkidrilus acapillatus* (FINOGENOVA,

1972) et deux autres taxons, représentés seulement par des formes immatures, ont également été trouvés.

Mots clés : Tubificidae, nouveaux taxons, Lac Taimyr, Lac Baïkal, faune, zoogéographie.

Introduction

Lake Taimyr is the northernmost among the world's large lakes. It is situated on the Taimyr Peninsula in North Siberia, Russia (Fig. 1), between 73°40'-75°20' N and 99-106° E, on average 6 m above sea level, with a surface area of up to 4,650 km² and a maximum depth of 26 m in the summer high water period. It is covered with ice

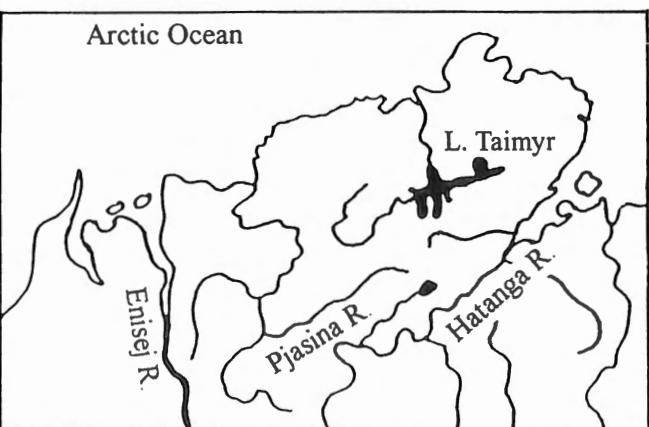


Fig. 1. – Location of Lake Taimyr.

for at least nine months a year. The water level drops by 5.5–6 m during the long winter, leaving 85% of the bottom (corresponding to summer depths of 7–8 m) frozen into ice for several months. There are no macrophytes. The surface water temperature can rise up to 9–12°C in summer. The water is always rich in oxygen in shallower zones, whereas in the deepest part of the muddy profundal, oxygen saturation down to 15% has been measured in winter. Lake Taimyr is a young relict lake that was formed during recent regression of the Arctic Ocean. Its water level decreases continuously by about one metre a century (GRÈZE, 1947a, 1957; summarized also by TIMM, 1996). The average wet biomass of zoobenthos for the whole lake was about 1 g m⁻² in the summer of 1943 and 1944, oligochaetes being the dominant group in all zones, except the shallowest sandy flats (GRÈZE, 1957). Unlike many other extremely northern waterbodies, where oligochaetes are represented mainly by Enchytraeidae and/or Lumbriculidae (see SMITH & WELCH, 1919; NURMINEN, 1973), the Tubificidae formed 76.7% of the oligochaete specimens collected from Lake Taimyr, and half of the oligochaete taxa found (TIMM, 1996). In this paper, revision of all seven tubificid taxa found in Lake Taimyr will follow, including the descriptions of two new species, one of which belongs to a new genus. The probable relations of the local tubificid fauna to the Baikalian fauna will also be discussed.

Material

Lake Taimyr was studied hydrobiologically during one year-long Russian expedition in 1943–1944 (GRÈZE, 1947a, 1957). Seventy-four zoobenthos samples, taken from different places, in different seasons, with a Petersen grab or a dredge, or cut out of the frozen sediment, contained 3612 specimens of Oligochaeta, 2871 of them belonging to Tubificidae. 23 more tubificid specimens were collected from the Gorbita River on the lake's watershed (TIMM, 1996). The worms were preserved in formalin and studied (50 years later!) as whole mounts in glycerine and in Canada balsam. Cross sections five µm thick were made from some mature specimens and stained after MALLORY or according to HAUSER (1969). Type specimens are deposited at the Võrtsjärv Limnological Station (VLS), Tartumaa, Estonia; in the Zoological Institute (ZIN), St.-Petersburg, Russia; in the Swedish Museum of Natural History (SMNH), Stockholm, Sweden; and in the Royal Belgian Institute of Natural Sciences (RBINS), Brussels.

Abbreviations used in figures

<i>a</i>	atrium
<i>ag</i>	accessory gland
<i>ap</i>	aperture for the spermathecal chaeta
<i>ar</i>	armour
<i>b</i>	brain
<i>bw</i>	body wall
<i>c</i>	clitellum

<i>ch</i>	chaeta
<i>chl</i>	chloragogen tissue
<i>cm</i>	circular musculature
<i>cr</i>	crystal-like body in the atrium
<i>cv</i>	circular vessels
<i>d</i>	dissepiments
<i>e</i>	embryos
<i>ed</i>	ejaculatory duct
<i>ep</i>	body wall epithelium
<i>ep1</i>	dark atrial epithelium
<i>ep2</i>	light atrial epithelium
<i>f</i>	chaetal follicle
<i>g</i>	gland of the spermathecal chaeta
<i>h</i>	heart
<i>i</i>	intestine
<i>lm</i>	longitudinal musculature
<i>m</i>	muscle layers
<i>mc</i>	mouth cavity
<i>me</i>	mesothelium
<i>n</i>	nerve cord
<i>oe</i>	oesophagus
<i>p</i>	papillae
<i>pgd</i>	ducts of the prostatic gland cells
<i>pr</i>	prostatic gland
<i>psa</i>	penial sac
<i>psh</i>	penial sheath
<i>se</i>	sensory papillae
<i>spa</i>	spermathecal ampulla
<i>spc</i>	spermathecal chaeta
<i>spd</i>	spermathecal duct
<i>spg</i>	gland of the spermathecal chaeta
<i>spz</i>	spermatozeugmata
<i>ss</i>	sperm sac
<i>vd</i>	vas deferens

Scales in µm

Descriptions

Alexandrovia ringulata (SOKOL'SKAJA, 1961) (Figs 2–15)

Peloscolex ringulatus SOKOL'SKAJA, 1961: 61–64, fig. 5.
Alexandrovia onegensis: HRABĚ, 1962: 291–300, figs 1–11; HOLMQUIST, 1974: 249–268, figs 1–6; TIMM, 1983: 37, figs 3.11–18; POPČENKO, 1988: 192–194, fig. 28.
Telmatodrilus ringulatus: BRINKHURST & JAMIESON, 1971: 534.
Telmatodrilus onegensis: BRINKHURST & JAMIESON, 1971: 534–535, fig. 8.25.
Alexandrovia ringulata: HRABĚ, 1964: 108; SOKOL'SKAJA, 1976: 94–96, fig. 3; 1983a: 74–77, fig. 75; 1983b: 122–123; MOREV, 1992: 128–133.

Material. 8 mature specimens were studied on serial sections, 95 more specimens as permanent whole mounts in Canada balsam, and about 2200 in glycerine only.

DESCRIPTION

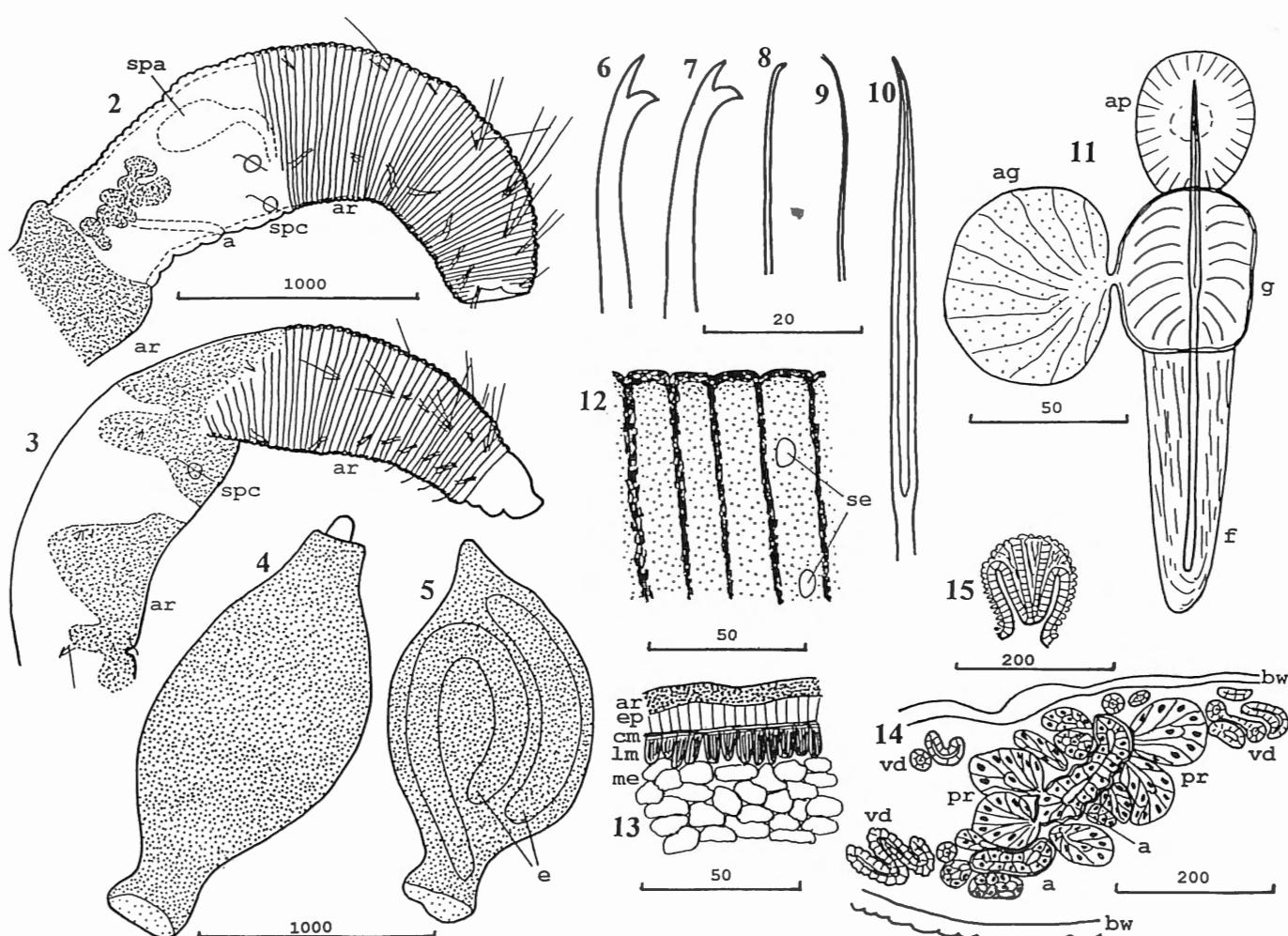
A full description is given because according to the above-listed authors the species has revealed considerable variability.

Length 4.0-18.5 mm, maximum diameter 0.3-1.1 mm under the cover glass, segment number 25-53. Even mature specimens often less than 10 mm long. Prostomium rounded or bluntly conical, often retracted; intersegmental furrows indistinct (Figs 2, 3).

In anteclitellar ventral bundles 1-4 (usually 2-3) bifid chaetae, 100-170 μm long (sometimes shorter in the smallest worms) and 3.5-4 μm thick, with indistinct median or proximal nodulus. Their upper tooth is always longer and thinner; sometimes a tiny intermediate tooth occurs. Postclitellar ventral chaetae one per bundle, more curved and with equal teeth (Figs 6, 7). In sexually mature individuals, usually a pair of modified spermathecal chaetae in X. They are 130-210 μm long and up to 4-8 μm thick, with distal nodulus; the almost straight and sharp distal portion is cleft by a longitudinal, sometimes slightly dilating, furrow while the proximal end can be curved (Figs 10, 11). Large (40-80 μm) roundish glandular sac

covered with 3 μm thick muscle layer surrounds nodulus of spermathecal chaeta. A separate spherical or pear-shaped accessory gland (histologically similar to prostatic gland!), up to 85 μm long and 40-60 μm wide, joins this sac at the anterior or lateral side (Fig. 11). In dorsal bundles 1-6 (usually 4-6) smooth or (seldom) very finely hispid hair chaetae, 200-380 μm long and up to 3.0-3.5 μm thick, sometimes with slightly hooked distal end (Fig. 8). Together with these, 1-6 (usually 2-4) distally tapering, simple (even at 1000x magnification) or very finely bifid needle chaetae, 60-104 μm long and 1-2 μm thick (Fig. 9).

Body wall epidermis 8-22 μm thick (thickest in clitellum embracing X-XII), without any secretory papillae but with numerous circular furrows in every segment. A 2-14 μm thick layer of dark (mostly brown) granular secretion, encrusted with fine (usually <1 μm but seldom up to 30-40 μm) foreign particles, forms armour covering the whole body except I and prostomium which are retractable. As it is



Figs 2-15. – *Alexandrovia ringulata* (SOKOLSKAJA, 1961). - 2-3. Anterior end of two maturing individuals shedding their armour from genital segments. - 2. With the prostomium retracted. - 3. With the prostomium protruded. - 4-5. Cocoons. - 6-10. Distal ends of chaetae. - 6. Anterior ventral chaeta. - 7. Posterior ventral chaeta. - 8. Hair chaeta with a hooked tip. - 9. Needle chaeta. - 10. Spermathecal chaeta. - 11. Spermathecal chaeta *in situ*. - 12. Armoured body surface from the forebody. - 13. Cross section of the body wall from VIII. - 14. Elements of the male duct in a sagittal section. - 15. Penis, from the same sagittal section.

thicker and darker in furrows, the armour gives the worm a transversally striped appearance (Fig. 12). The stripes can join into a continuous dark layer in postclitellar region. Clitellum is smooth and grey, or devoid of armour in mature individuals. Many specimens are in the process of shedding their armour, often beginning from clitellar segments (Figs 2, 3). Others are entirely naked and transparent. Shedding is not distinctly related to maturation or any season, although naked worms are mostly smaller and occur more abundantly in winter. [Shedding of armour was described in *Spirosperma ferox* EISEN, 1879 by BRINKHURST (1964) and TIMM (1974, 1987), as well as in *Tubifcoides benedii* (UDEKEM, 1855) by DUBILIER *et al.* (1995)]. Armour in different body regions often bears sessile ciliates. Two circular rows of sensory papillae per segment are visible as light spots in the dark armour (Fig. 12). Retraction of the anterior end was observed both in armoured and naked individuals. A layer of circular musculature 2-6 µm, a layer of longitudinal musculature 6-12 µm thick. Loose parenchyme-like mesothelium, 2-20 µm thick, lines body cavity, usually beginning from VII but not observed in the foremost and sometimes also in genital segments (Fig. 13).

Prostomium in sectioned specimens often retracted into buccal cavity. Pharynx thick-walled, except for a narrow ventral strip. Contracted muscles, glands, and blood vessels attached to pharynx usually fill body cavity in III-IV. Some loose glands also in V on both sides of oesophagus. Retractor muscles of pharynx attached to body wall up to VI on the dorsal side and V on the ventral side. Oesophagus thin, winding up and down, with wall 15-30 µm thick, internally ciliated. About 15 µm thick layer of chloragogen tissue from VI on. Intestine beginning with a slight dilation in VIII, its wall being 20-40 µm and chloragogen layer 30-40 µm thick.

Nephridia usually observed in VIII, but sometimes in VII-VIII, VI-VIII, or VIII-IX, with pores before ventral chaetae. The nephridia are spindle-shaped, vertical, and consist of 5-20 µm wide tubuli.

Dorsal vessel and transversal vessels free in the foremost segments. From VIII or IX on, dorsal vessel proceeding between intestinal wall and chloragogen layer.

Internal reproductive organs generally paired. Testes in X, variable in their shape even in the same worm; a developing individual had only one testis. Single anterior sperm sac reaches IX, VIII, or even VII, posterior sac XIII, XIV, or sometimes farther. Ovaries in XI beginning as thin strings but thicker and ascending to the dorsal side backwards. Single egg sac reaches XII-XIV, rarely farther.

Male funnels in X mostly as forward-directed bowls, 130-190 µm long and 100-170 µm wide, wall 10-20 µm thick, and cilia 6-20 µm long. Very long ciliated vasa deferentia can be 10-32 µm wide in different portions, without certain regularity (Fig. 14). They are twisting in XI, sometimes reach XII-XIII in egg sacs, and enter atrium apically.

Atria tubular, about 330-500 µm long and 30-70 µm wide (but 120-200 µm with prostatic glands included), straight or bent, their proximal end often entering egg sac. Atrial

wall consisting of variegated glandular epithelium covered with 2-4 µm thick muscle layer (Fig. 14). Atrial lumen 5-15 µm wide.

Prostatic glands abundant (about 20), up to 12-15 of them visible in one single sagittal section, densely covering the whole atrium. They are rounded or pear-shaped, 50-90 µm high and 40-130 µm wide, histologically similar to atrial epithelium but devoid of any muscular cover (Fig. 14). Developing prostatic glands can be colourless (unstained).

Soft conical penis distinctly separated from atrium, 70-110 µm long and 40-70 µm wide, with epithelium 8-15 µm thick (Fig. 15). Basically epithelial penial sac (with muscle layer about 6 µm only), 80-120 µm long and 50-100 µm wide, opening into male pore in XI either immediately, or with duct, 40-80 µm long and 15-22 µm wide, when retracted. Female funnels on 11/12. Usually only upper lip distinguishable, 80-115 µm high and at least 50 µm wide, epithelium up to 25-32 µm in its upper portion, and cilia 4 µm long. In one case, two equal lips were observed, both 80 µm long and 10 µm thick.

Spermathecae opening on the anterior edge of X, before spermathecal chaetae. Duct at least 160 µm long, 40-50 µm wide at either end but sometimes widening up to 90 µm in the middle portion. External muscular layer of duct mostly 3-7 µm thick but thickening to 8-20 µm in distal part. Lumen 2-18 µm wide or invisible in the different parts of duct. Ampulla can be up to 1000 µm long when fully developed, of irregular shape, often bulging into VIII-IX and/or clitellar segments inside sperm sac. Ampullar wall 6-24 µm thick, including 2-5 µm of external muscle layer. The inner surface can be either smooth, rough, or even bearing 5-7 µm high papillae with nuclei. Long vermiform spermatozeugmata, twisted in the form of 8, can fill ampullae. However, most of the ampullae studied contained only some slimy matter, or dark-coloured remains of resorbed spermatozeugmata.

FEEDING AND INTESTINAL PARASITES

Intestine was empty in specimens caught in October-December but filled with fine detritus and mineral particles in those collected in July. One specimen, collected in November, has a dense bunch of vermiform parasites (ciliates?) in XI-XII. They are attached to the gut wall by their thinner end; cell membrane transversally striped (with basal bodies of cilia?), nucleus almond-shaped.

REPRODUCTIVE BIOLOGY

Immature, maturing, and post-reproductive specimens were found in all seasons, even frozen into the ice in winter, while those with well-developed clitellum occurred in July-August, and only two individuals with spermatozeugmata in August. Forty-two cocoons and empty cocoon shells were studied, collected in September and November together with specimens of *Alexandrovia ringulata*, and probably belonging to this species. They

were 1.3-2.0 mm long and 0.8-1.2 mm wide, lemon-shaped, with short tubular appendages either equal or one of them being wider (Figs 4, 5). The shell is fragile, encrusted with very fine foreign particles as in the cocoons of *Spirosperma ferox* described by TIMM (1974). A cocoon can contain up to 3 embryos. Thus, *A. ringulata* is a summer-breeder. The scarcity of breeding individuals (with spermatozeugmata in spermathecae) may be evidence of a very short oviposition period. HRABĚ (1962) found breeding individuals in July only. Maturity occurring mostly in June-July has also been described from Karelia by POPČENKO (1988), in June-August from the Čukči Peninsula by SOKOL'SKAJA (1983b), and in May-September from Kamčatka by SOKOL'SKAJA (1983a).

DISTRIBUTION AND HABITAT

Very abundant, dominating (and often the only) oligochaete species on the shallows of Lake Taimyr where it freezes into ice in wintertime. Found mostly on muddy bottom, but also on sand. Its abundance was from several hundreds to 2000-3000 ind. m⁻² in this zone; a maximum of 6420 ind. m⁻² was found in a sample of frozen mud taken in May. Only some single individuals occurred in the more species-rich profundal. One specimen originates also from the Gorbita River in the lake catchment area.

Otherwise, known in many scattered localities in the Northern Palaearctic and Alaska (SOKOL'SKAJA, 1961, 1976, 1983a, 1983b; HRABĚ, 1962; HOLMQUIST, 1974; ZALOZNYJ, 1976, 1979a, 1979b, 1984; TIMM, 1983; POPČENKO, 1978, 1988; POPČENKO & ALEKSANDROV, 1983; MOREV, 1983, 1986, 1992; MOREV *et al.* 1985).

TAXONOMICAL REMARKS

The species was originally described from Kamčatka as *Peloscolex ringulatus* by SOKOL'SKAJA (1961) who misinterpreted the mass of small prostate glands as a single large one. The mistake was corrected by HRABĚ (1964), who transferred the species into the genus *Alexandrovia* HRABĚ, 1961, and then by SOKOL'SKAJA (1976) herself. Later on, *A. onegensis* HRABĚ, 1962 from Karelia was considered a junior synonym by SOKOL'SKAJA (1983a). *A. onegensis* was described also from lakes in Alaska (HOLMQUIST 1974), Karelia and North Russia (TIMM, 1983; POPČENKO, 1988). These descriptions reveal some local (or subjective?) differences. The terminal portion of the male duct was named pseudopenis (denoting a protrusible but unmodified ectal end of the atrial duct) in the Karelian material, although depicted as lying in a special sac (HRABĚ, 1962). A distinct penis with a penial sac was described in Asian and Alaskan material (HOLMQUIST, 1974; SOKOL'SKAJA, 1983a; MOREV, 1992; and Lake Taimyr worms). Prostate glands are sparser in the figure by SOKOL'SKAJA (1983a) than elsewhere, hair chaetae are reported to be distinctly hispid (either hispid or smooth, according to MOREV, 1992), and needles to

have 2 µm long parallel teeth in the material of the Far East (SOKOL'SKAJA, 1983a, 1983b). The Karelian and Lake Taimyr worms have smooth hair chaetae, while the teeth of needles are hardly visible. Different curvatures of the distal or proximal end of the spermathecal chaetae, as well as their occasionally doubled number noted by SOKOL'SKAJA (1983a, 1983b) are probably individual variations. Accessory glands on the nerve cord are described by HRABĚ (1962) and HOLMQUIST (1974) only. The thick layer of the parenchyme-like mesothelium common with *Baikalodrilus alienus* and some other tubificids of Lake Taimyr was not described in *A. ringulata* from other localities. Thus, it is difficult to qualify these differences as specific without a scrutiny of all original materials. Perhaps some local populations of *A. ringulata* will be qualified as subspecies after a thorough revision.

Lumping the genera *Alexandrovia* and *Telmatodrilus* EISEN, 1879, as proposed by BRINKHURST (1966), was convincingly rejected by HOLMQUIST (1974).

ZOOGEOGRAPHICAL REMARKS

With the new finding in Lake Taimyr, *A. ringulata* reveals a more continuous range of distribution along the northern edge of the Eurasian continent. So far, it was known from the northeastern Europe and West Siberia, as well as from northeastern Asia, with some populations on the western tip of North America. The ability to withstand regular freezing seems to support its abundance in shallow tundra lakes and streams. However, two more southern subranges are known in the taiga zone: Kamčatka, where it lives in various waterbodies, and Karelia, where it inhabits a few lakes only. The range is distinctly limited both in the West where the species is lacking on the Scandinavian and Kola Peninsulae (TIMM, 1987), and in the East where it is not found in the greater part of Alaska (HOLMQUIST, 1974).

Baikalodrilus alienus spec. nov. (Figs 16-44)

Baikalodrilus sp.: TIMM, 1996

Holotype. VLS, No. 23-1: cross sections of a breeding mature specimen on two slides, collected 17 April 1944 at a depth of 11.5 m.

Type locality. Profundal of Lake Taimyr, muddy bottom.

Paratypes. VLS, No. 23-2: whole mount with three specimens (a mature, a juvenile and a posterior fragment), together with a small postclitellar fragment of the holotype, and an empty cocoon shell, from type locality. ZIN, No. 48168: cross sections of a post-reproductive specimen on three slides, and a posterior fragment of the same specimen together with two cocoons containing embryos, mounted on the fourth slide, depth 11.7 m, 11 May 1944. ZIN, 48169: whole mount of three specimens (one half-mature

and two juveniles) on one slide, depth 5.2 m, 29 August 1943.

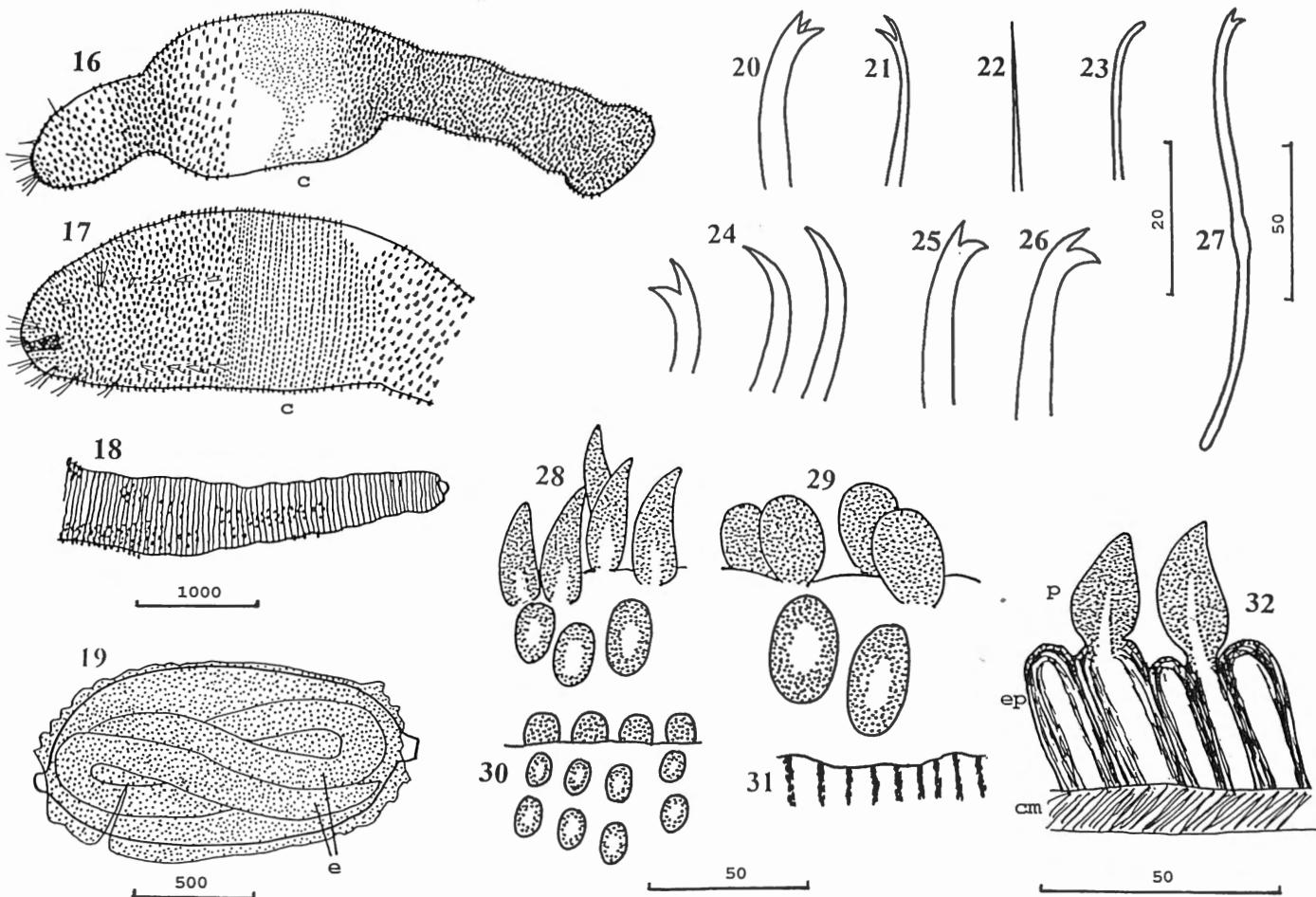
Etymology. The species name means "strange" or "foreign" in Latin.

DIAGNOSIS

Medium-sized species (between 10 and 20 mm) of *Baikalodrilus*. Most of body densely covered with large but separate secretory papillae. 4-5 simple-pointed and bifid chaetae in ventral bundles of II, the latter ones with equal teeth. In anteriormost dorsal bundles, about 4 smooth hair chaetae with slightly hooked tip, and 3-4 thin sigmoid pectinates with very fine intermediate teeth. In the following segments the number of chaetae of all kinds decreases gradually; only single bifid chaetae remain in ventral bundles of postclitellar region, while dorsal pectinates are replaced by simple-pointed needles.

DESCRIPTION

Length 13-19 mm, width on cross sections 0.5-0.6 mm in anterior and 0.2-0.3 mm in posterior segments but 1.2 mm in the slightly flattened genital region of fully mature individuals. Segment number unknown. Prostomium tiny and usually retracted together with several anterior segments. Intersegmental furrows indistinct in fixed material (Figs 16-18). Most of body densely covered with brown hollow leaf-shaped secretory papillae (SNIMSKHOVA & TIMM, 1992: 56) up to 50-100 µm high, 50x30 µm in diameter on mid-body (Figs 29, 32). Papillae gradually smaller (20-30 µm), scarcer and sharp-tipped near the anterior end (Fig. 28), almost disappearing in I-II. On the posterior third of body, papillae are dense and about 30 µm high. The posteriomost segments can be either smooth and transparent, or armoured with low glandular pads in the transverse furrows (Figs 18, 31). Developing clitellum (in XI, with indistinct extensions to



Figs 16-32. - *Baikalodrilus alienus* spec. nov., external characters. - 16. Post-reproductive specimen, not compressed. - 17. Anterior end of a specimen with developing clitellum, compressed under cover glass. - 18. Posterior end. - 19. Cocoon. - 20-22. Succession of dorsal anteclitellar chaetae from pectinate to needle. - 23. Distal end of an anteclitellar hair chaeta. - 24. Ventral chaetal bundle of III, ectal tips. - 25. Ventral chaeta of VIII. - 26. Postclitellar ventral chaeta. - 27. Ventral chaeta of VIII. - 28. Papillae of the forebody. - 29. Papillae of the last anteclitellar segments. - 30. Clitellar papillae. - 31. Non-papillate armour of the tail. - 32. Connection of papillae with epithelial cells, after cross sections.

X and XII) with small roundish papillae (Figs 17, 30); full-developed clitellum smooth, covered with up to 10 µm thick layer of secretion mixed with fine foreign particles (Fig. 16). The surface of papillae also encrusted with fine particles.

Chaetae in II-III usually retracted together with the head end, in the mid-body hidden between papillae, on the tail portion more protruded. Ventral chaetae in II 4-5 per bundle, in II-IV 3-4, and in V-VI 2-3, 100-170 µm long and up to 5 µm thick, with proximal nodulus; in II-IV both simple and bifid chaetae in the same bundle, tapering distally, bifids with equal teeth (Fig. 24); in V-VI either both kinds of chaetae or bifids only. In VII-VIII 1-2 bifid chaetae per bundle (Figs 25, 27), in X-XI one bifid in juveniles. A rudimentary ventral chaeta was observed near both spermathecal pores in X on the sections of holotype but none in XI in mature worms. No modified genital chaetae. Posteriorly, single ventral chaetae with a strongly bent distal end, with short teeth of equal length protruding about 50 µm; 4 µm but distally only 3 µm thick (Fig. 26). Anteriormost dorsal bundles in II-IV, usually with 4 (3-5) smooth hair chaetae with a slightly hooked tip (Fig. 23), 180-280 µm long and 4-6 µm thick, accompanied by 3-4 sigmoid bifid chaetae. The latter are 80-110 µm long and 2-3 µm thick, with indistinct intermediate teeth (seen at 1000x only, Fig. 20). Dorsal chaetae in the following segments gradually decrease to 1-2 of either kind. Bifid chaetae become shorter (about 60 µm), their distal end and teeth thin (Fig. 21) until they are replaced by straight, apparently simple needles (Fig. 22). Postclitellar dorsal bundles with 2-3 hair and 1-2 fine needle chaetae; on the very tail one single fine (3 µm) and flexible hair chaeta per bundle, stretching 80-140 µm over body surface. Body wall consisting of four layers of tissue: external epithelium (12-24 µm thick without papillae), circular musculature (6-12 µm), longitudinal musculature (18-32 µm), and internal mesothelium, from about VI onward hypertrophied into a 20-50 µm thick irregular mass of weakly stained cells (Fig. 34). In the genital region of fully mature worms, body wall is thinner (epithelium 8-12, circular musculature 2-4, and longitudinal musculature 12-25 µm thick), while mesothelium is lacking like external papillae. On the contrary, in their degenerating postclitellar segments longitudinal musculature can increase to 40 µm, while mesothelium fills the whole coelomic cavity (Fig. 35).

Mouth opens into secondary cavity formed by retracted foremost segments like in many other armoured tubificids when preserved. Proper mouth cavity, thick-roofed pharynx, surrounding muscles, dissepiments, glands and blood vessels are all strongly contracted in preserved specimens (Fig. 33). Oesophagus thick-walled and ciliate, transition into wider and thin-walled midgut was observed in IX of holotype. In the other, post-reproductive (maybe degenerating) specimen sectioned, intestine forms some blind lobes in the genital region. After genital segments, intestine transforms into a sole thin disrupted string of tissue disappearing caudad in both sectioned specimens (Fig. 35). Intestine was totally empty in both of them.

Dorsal vessel lies freely in the body cavity of anteclitellar segments but is attached to intestine beginning from the genital region. Nephridia not observed. Nerve cord 80 µm broad in VIII but tapering down to 45 µm in genital segments, and 40 µm afterwards.

Internal reproductive organs generally paired. They are in good condition in the holotype but in a stage of post-reproductive resorption in the other individual sectioned. Testes in X, ovaries in XI, with single sperm and egg sacs extending into the following segment, respectively. Sperm mass observed in sperm sacs only. Eggs present in the egg sac of the holotype, while the only large egg of the other specimen lies in XI.

Sperm funnels on 10/11 are 180x130 µm wide in the holotype and bear tufts of long spermatozoa. Vasa deferentia long, winding in XI near atrium and entering its proximal end (Figs 42-44). They are gradually widening from 10 to 40 µm, their lumen being about 5 µm, sparsely ciliated in its proximal portion only.

Atrial ampullae in XI spindle-shaped, one longer and bent (length not measurable, Figs 42-44) but the other shorter (320 µm, Fig. 40) in the holotype, with a diameter of 65-160 µm in different parts, and lumen 0-40 µm wide. Atrial wall consists mostly of differently staining glandular epithelium, external muscular layer being about 5 µm thick. Both atria contain a short "crystal", a 40 µm thick rod-shaped body with sharp ends, uniformly staining with Orange G like the blood in large vessels (Figs 41, 43). Large prostatic gland enters directly the anterior side (convex side when atrium is bent) of the middle portion of both atria (Fig. 43). It is up to 180 µm high and 315x125 µm wide, consisting of a tissue similar to atrial epithelium. The distal end of ampullae in the holotype is stretched by a dorsoventral retractor muscle, thus producing an "ejaculatory duct" up to 380 µm long (on one side) and 20-30 µm wide, with epithelial wall covered with a thin layer of longitudinal muscle fibres, and with lumen being up to 6 µm wide (Figs 41, 42). Male pore in the place of lacking ventral chaetae, without any distinguishable penis (Fig. 42). In the other, post-reproductive specimen only spindle-shaped rudiments of atria occur, up to 60 µm in diameter, with external muscle layer 4-5 µm thick. They are attached at an acute angle to putative male pores in the place of lacking ventral chaetae of XI. Neither egg funnels nor female pores were seen.

Spermathecae of the holotype in X, partially extending into XI. Oval ampulla up to 240-250 µm wide in its middle portion. Its wall consists of 4 µm thick external muscle layer (in places covered with another 4 µm of mesothelium), and 6-32 µm thick internal epithelium either smooth, rough, or bearing unicellular papillae (Figs 39, 40). Several veriform, about 20 µm wide spermathegmata together with an irregular lump of sperm mass fill partly the lumen of ampulla (Fig. 40). Well-distinguished spermathecal duct spindle-shaped, proximally 75-85 µm wide, then expanding up to 115 µm (with lumen up to 40 µm wide, papillate internal epithelium 20-30 µm thick, and both muscular and mesothelium layers 2-3 µm thick; Figs 37-39). In its distal portion,

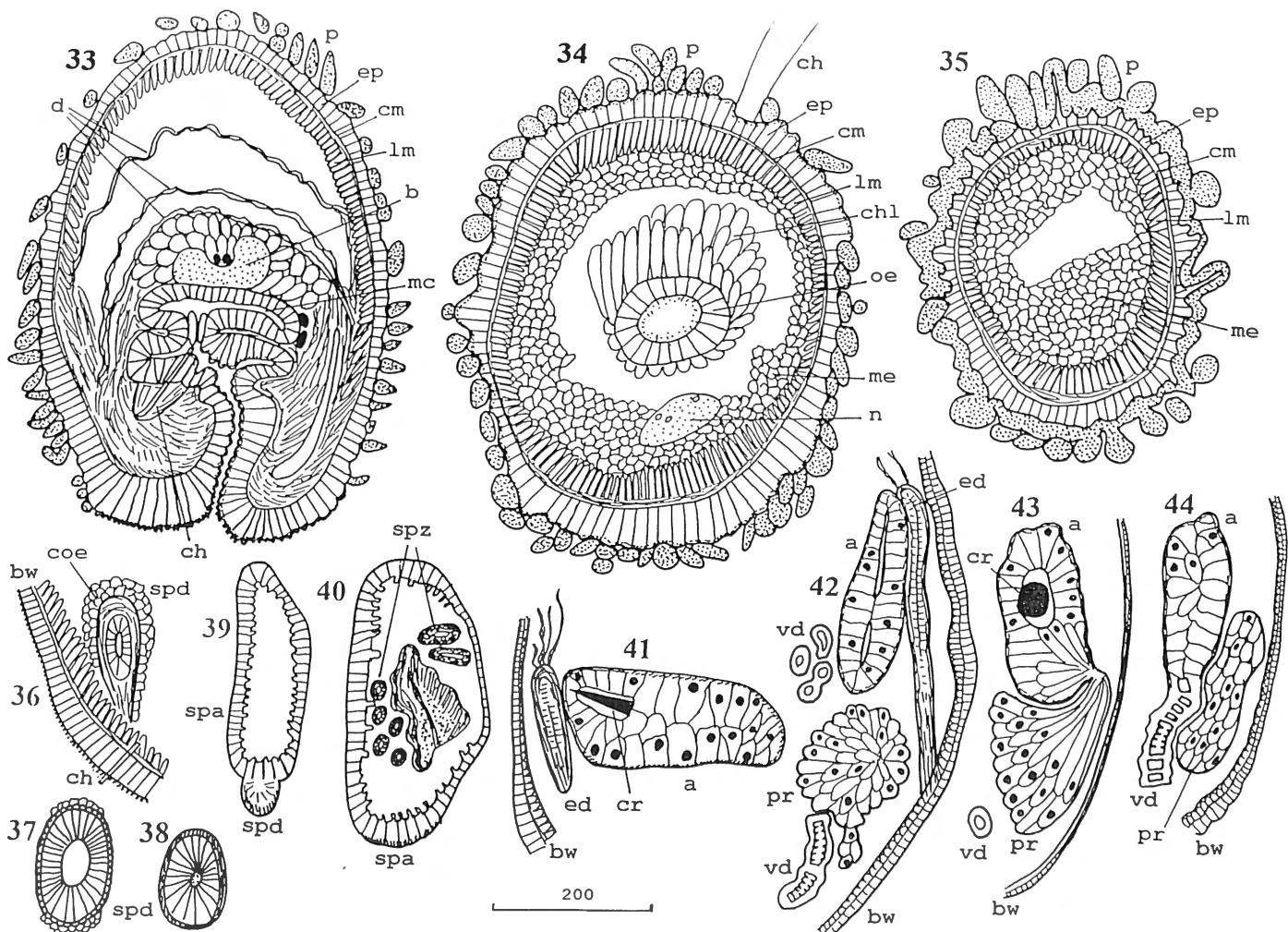
spermathecal duct tapers gradually down to 20 µm, with a thickening of both muscle and mesothelial layers, and opens near single rudimentary ventral chaetae of X (Fig. 36). The other, post-reproductive individual has no spermathecae in X, but a separate spermathecal ampulla in the stage of resorption in sperm sac, forming a 130x70 µm wide isolated bag with 5 µm thick muscular wall and containing a solid lump of epithelial tissue.

REPRODUCTIVE BIOLOGY

On 11 May 1944, two cocoons were collected together with a post-reproductive individual of *B. alienus*, probably belonging to this species. They are 1.28 and 1.51 mm long, 0.78 and 0.70 mm broad, respectively; cylindrical, with rounded ends bearing short (0.06-0.08 mm) tubular appendages. The shell is covered with a thin armour

encrusted with granules 1-10 µm in diameter like the clitellum of mature *B. alienus*. 2-3 vermiform embryos occur in either cocoon (Fig. 19). On 17 April 1944, an empty shrunken cocoon shell was collected in the same spot together with three specimens of *B. alienus* at different stages of maturity. It measures 1.2x0.9 mm, has an oval shape, short tubular appendages of different diameter (0.012 and 0.008 mm), and is encrusted like the former ones.

Judging by the presence of cocoons, reproduction occurs in late winter (March-April) under the ice. The finding of individuals with a developing clitellum in both August and April demonstrates that the beginning of maturation is not simultaneous. Both the breeding and post-reproductive individuals sectioned had stopped feeding. Their tail portion was in process of decay, the genital region reminding of a slack bag. Probably, these individuals were dying after laying cocoons.



Figs 33-44. *Baikalodrilus alienus* spec. nov., internal characters (after cross sections, mainly of the holotype). - 33. Section of the retracted anterior end. - 34. Section of VIII. - 35. Section of the degenerating tail portion of a post-reproductive specimen (paratype). - 36-40. Sections of a spermatheca, backward from the distal end of the duct to the ampulla. - 41. Section of the distal end of the left atrium with the beginning of the efferent duct. - 42-44. Sections of the right male duct, backward from the male pore to the connection of the vas deferens with the atrium.

DISTRIBUTION AND HABITAT

Known from the profundal of Lake Taimyr only. Found on mud at depths of 5.2, 11.5 and 11.7 m, together with several other, more numerous species of Tubificidae and Lumbriculidae (TIMM, 1996). Lacking on shallows where sediments are subjected to seasonal freezing.

TAXONOMICAL REMARKS

The genus *Baikalodrilus* was established by HOLMQUIST (1978) for several papillate tubificids in Lake Baikal, formerly attributed to *Peloscolex* LEIDY, 1850. Later, all armoured tubificids known from this lake were lumped in *Baikalodrilus* by SNIMSKHOVA & TIMM (1992). The genus appeared to be highly endemic, with at least 22 exclusively Baikalian species-level taxa (SNIMSKHOVA & AKINSHINA, 1994). BRINKHURST (1991) accepted it as a separate clade of armoured Tubificinae. Internal reproductive organs are quite uniformous here, while ventral chaetae are always absent near the male pores. The presence of unique crystal-like bodies of organic matter in the atrium is a distinct synapomorphy of the genus. The new species belongs undoubtedly to *Baikalodrilus*. The apparent lack of a penis (present in all other species) in the holotype may be a specific feature, though the above-described "ejaculatory duct" can well represent a strongly extended penial sac.

According to the identification key by SNIMSKHOVA & TIMM (1992: 74–75), the new species lies close to the weakly specialized species *B. paradoxus* (SNIMSKHOVA, 1984), *B. bifidus* SNIMSKHOVA, 1989, *B. medianus* SNIMSKHOVA, 1991 and *B. crassus* SNIMSKHOVA, 1989 by its chaetae and armour, differing from each of them by some characters. Thus, in *B. paradoxus* papillae are fused in a continuous layer while hair chaetae are plumose; *B. bifidus*, *B. medianus* and *B. crassus* have folded armour covered with lower papillae in transverse rows while the hair chaetae are plumose; the last species is also much larger and bears more chaetae in its anterior bundles. The papillae of *B. discolor acinacifer* SNIMSKHOVA, 1989 are comparable with those of *B. alienus* by their shape and size; however, this species is devoid of any bifid ventral chaetae. The hooked end of hair chaetae, weakly expressed in *B. alienus*, is very characteristic of *B. phreodriloides* (MICHAELSEN, 1905). Thus, *B. alienus* reveals a combination of characters typical of different congeners. The peculiar thick layer of the mesothelium has so far not been registered in the genus but occurs in several other tubificids in Lake Taimyr (see below). Nor have any chaetae been observed on spermathecal pores in X, but they can sometimes be overlooked when they are covered with the armour.

The new species may in the past have been identified as *Peloscolex velutinus* (GRUBE, 1879) in the broad sense by some researchers of the Siberian fauna who used ČEKANOVSKAJA's key (1962; translated as CHEKANOVSKAYA,

1981), since this key does not provide any better alternative. The real *Embocephalus velutinus* (GRUBE, 1879) s. s. as revised by HOLMQUIST (1979) has sensory papillae, only two ventral chaetae in the anterior ventral bundles, and spermathecal chaetae. The poorly described *P. oregonensis* BRINKHURST, 1965 sensu TIMM & MEDVED'EV (1972) could also be confused with *B. alienus*. Having no ventral chaetae in X and XI, it could also belong to *Baikalodrilus*. It has been found in West Siberia, but the internal reproductive system was resorbed in those specimens. The bigger and less numerous chaetae, facultative plumosity of hair chaetae, and the presence of distinct intermediate teeth in the needles of the Siberian *P. oregonensis* are features that clearly distinguish it from *B. alienus*.

ZOOGEOGRAPHICAL REMARKS

Baikalodrilus alienus spec. nov. can easily be treated as an immigrant from Lake Baikal, carried downstream first by the outflowing Angara River and then by the Enisej River. The latter probably had a connection with Lake Taimyr via the lowland rivers of Pjasina and Taimyra (Fig. 1) in the recent past (GRÈZE, 1947a, 1957). However, its broader distribution cannot be excluded. "*Peloscolex velutinus*" has many times been recorded not only from Lake Baikal (according to SNIMSKHOVA & TIMM, 1992, there are various species of *Baikalodrilus* there), but also from other Siberian waterbodies by different researchers using ČEKANOVSKAJA's key (1962) only, e.g. VERŠININ (1976), AKINŠINA & TOMILOV (1976), TOMILOV *et al.* (1978), ZINOV'EV (1981), but has never been properly described here. Nor is there any good description of the reproductive system of *P. oregonensis* reported from different parts of West Siberia by TIMM & MEDVED'EV (1972) and ZALOZNYJ (1976, 1979a, 1984). The latter author also presents *P. inflatus* (MICHAELSEN, 1901) in his faunal lists (ZALOZNYJ, 1976, 1984), which is a badly defined member of the genus *Baikalodrilus* in a modern sense (SNIMSKHOVA & TIMM, 1992). Thus, *B. alienus* spec. nov. can be one of several non-Baikalian members of the genus *Baikalodrilus* that are probably living in various waterbodies of Siberia.

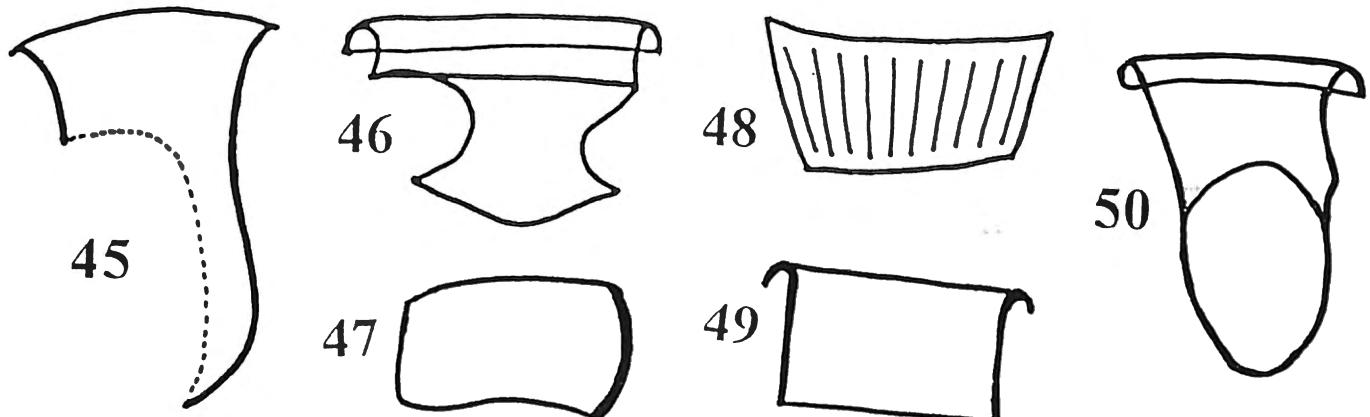
Lamadrilus gen. n.

Isochaetides HRABĚ, 1966 (partim); *Tubifex* LAMARCK, 1816 (partim).

Type species: *Isochaetides excavatus* HRABĚ, 1982.

Other (sub-)species: *Tubifex bazikalovae* ČEKANOVSKAJA, 1975; *Tubifex bazikalovae aliquantulus* SNIMŠČIKOVA, 1985; *Tubifex bazikalovae grandis* SNIMŠČIKOVA, 1985; *Tubifex crassiseptus* SEMERNOJ, 1982; *Isochaetides eximius* SEMERNOJ, 1982; *Lamadrilus sorosi* spec. nov. (in this paper).

Etymology. Derived from Lama, the name of Lake Baikal in the Evenk language, and δριλος, "worm" in Greek. Gender masculine.



Figs 45-50. – Penial sheaths of five species attributed to *Lamadrilus* gen. nov. – 45-49. Free-hand drawings after illustrations in original descriptions. – 45. *L. excavatus* (HRABĚ, 1982). – 46. *L. sorosi* spec. nov. – 47. *L. eximius* (SEMERNOJ, 1982). – 48. *L. bazikalovae* (ČEKANOVSKAJA, 1975). – 49. *L. crassiseptus* (SEMERNOJ, 1982). – 50. Penial sheath of *L. bazikalovae* after unpublished drawing by V.P. SEMERNOJ.

DIAGNOSIS

Freshwater Tubificinae with paired reproductive organs placed as typical of the subfamily. Atrium tubular, with slightly expanded and bent, blunt blind proximal end which is histologically similar to the remaining portion of atrium. Vas deferens at least twice as long as atrium, entering subapically, single stalked prostate gland also subapical, entering the opposite side of atrium. Penis in penial sac, with short, mostly asymmetrical penial sheath (Figs 45-50). Sperm in spermathecae arranged in spermatozeugmata. Body surface smooth. Chaetae usually bifid, but hair, pectinate and spermathecal chaetae can occur in some species. No modified penial chaetae. No large coelomocytes.

REMARKS

Lamadrilus belongs to the subfamily Tubificinae in every respect. It shares the blind proximal end with the genera *Tubificoides* LASTOČKIN, 1937 and (probably synonymous) *Telliclio* TIMM, 1978, whereas in all other genera either the vas deferens or the prostate gland enters the atrium apically. A short, often asymmetrical penial sheath is also characteristic of *Tubificoides*. However, the blind proximal end is longer and histologically well separated from the rest of the atrium in *Tubificoides* and *Telliclio*. In *Lamadrilus*, there exists no clear separation. The atrial epithelium is specialized in the proximal portion of the atrium in *L. sorosi*, indeed, but this kind of epithelium extends also into its narrower distal portion. Moreover, the prostate gland enters the atrium just on the site where this special epithelium is the thickest (see below). There exist no data on this character in the other congeners; however, the external shape of their atrium is remarkably similar. *Tubificoides* is a monophyletic marine/brackish-water group mostly armoured with papillae or detritus like the freshwater “*Peloscolex*” clade of Tubificinae. All known species of *Lamadrilus* are externally smooth and

live in fresh water only, four of them in Lake Baikal, and the fifth in Lake Taimyr.

Among the species belonging to *Lamadrilus*, *L. bazikalovae* with the subspecies *aliquantulus* and *grandis* represent different rates of reduction in hair and pectinate chaetae, while in the remaining four species only bifid locomotory chaetae occur. The penial sheath is originally described and depicted as a truncated cone in *L. bazikalovae* (Fig. 48; but having an asymmetrical appendage after the unpublished drawing by V. SEMERNOJ, Fig. 50); as an obliquely cut ring in *L. crassiseptus* (Fig. 49); as a short ring thickened on one side in *L. eximius* (Fig. 47); as bearing a shovel-shaped or flat appendage in *L. excavatus* and *L. sorosi* (Figs 45, 46). The distinct spermathecal duct opens almost ventrally in *L. bazikalovae* but laterally in three other species. No genital chaetae are described in *L. bazikalovae*, *L. crassiseptus*, *L. eximius*, and *L. excavatus*, while ordinary bifid ventral chaetae can be present or absent near genital pores in X and/or XI. *Lamadrilus excavatus*, the type species, has no ventral chaetae in XI, whereas they are present in *L. sorosi* spec. nov. Modified spermathecal chaetae with a grooved distal portion are observed in X in some individuals of *L. sorosi* spec. nov. only.

Several other Baikalian tubificids have a short penial sheath, e. g. *Tubifex penicraspedifer* SEMERNOJ, 1982 and *Isochaetides adenodicystis* SEMERNOJ, 1982. The latter also has a spermathecal chaeta what is similar to that of *L. sorosi* but equipped with two separate accessory glands. Somewhat longer asymmetrical penial sheaths with a distal appendage are characteristic of the genus *Tasserkidrilus* HOLMQUIST, 1985 which is also represented in both Lake Baikal and Lake Taimyr (see below). However, vas deferens always joins the atrium apically in these two species. This is also the case with the genus *Isochaetides* HRABĚ, 1966, to which, due to external similarity, specimens of *L. sorosi* were originally ascribed (TIMM, 1996). The proper systematic position of *T. penicraspedifer* and *I. adenodicystis* needs further revision.

Lamadrilus sorosi gen. spec. nov.
(Figs 51-67)

Isochaetides sp.: TIMM, 1996.

Holotype. VLS, No. 22-1: sagittal sections on two slides, collected on 3 June 1944.

Type locality. Lake Taimyr, the deeper region at a depth of 11.7 m where bottom sediment never freezes into ice.

Paratypes. VLS, No. 22-2: cross sections, 6 January 1944, 2.7 m. VLS, No. 22-3: cross sections on two slides, 3 June 1944, 11.7 m. VLS, No. 22-4: cross sections, 27 August 1943, 5 m. VLS, No. 22-5: sagittal sections, 27 August 1943, 5 m. VLS, No. 22-6: dissected specimen, 3 June 1944, 11.7 m. VLS, No. 22-7: seven whole-mounted specimens on one slide, 3 June 1944, 11.7 m. ZIN, No. 48166: sagittal sections, 27 August 1943, 5 m. ZIN, No. 48167: six whole-mounted specimens on one slide, 11 May 1944, 11.7 m. SMNH, No. 4780: sagittal sections, 29 August 1943, 5.2 m. SMNH, No. 4781: two whole-mounted specimens on one slide, 4 June 1944, depth unknown. RBINSc, No. I.G. 28619a,b: cross sections on two slides, 27 August 1943, 5 m. RBINSc, No. I.G. 28619c: five whole-mounted specimens on one slide, 3 June 1944, 11.7 m.

Other material. 79 specimens at different stages of maturity, as whole mounts in Canada balsam on 23 slides,

including one with dissected reproductive organs. Serial sections of 15 mature specimens on 19 slides, stained either according to MALLORY or HAUSER. About 300 more specimens studied as whole mounts in glycerin only. The exact number is not established since in some cases the immatures are hardly distinguishable from the sympatric *Limnodrilus profundicola* (VERRILL, 1871).

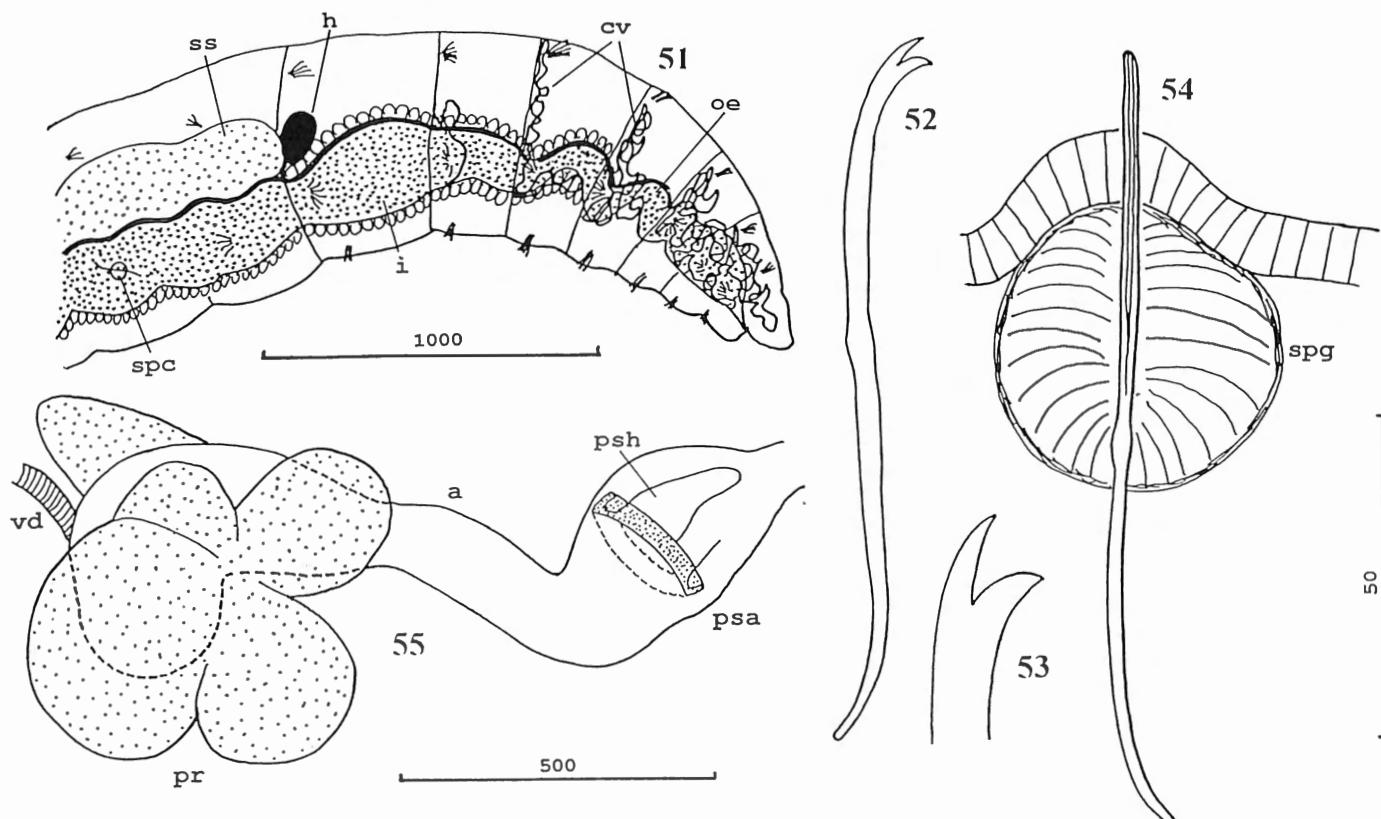
Etymology. Named after Mr. GEORGE SOROS who generously supported the study of Lake Taimyr oligochaetes through the International Science Foundation.

DIAGNOSIS

Lamadrilus without any hair or pectinate chaetae. Either modified spermathecal chaetae or ordinary chaetal bundles present, or no chaetae ventrally in X of mature individuals. Ventral bundles present in XI near the male pores. Short penial sheaths with a spade-shaped distal appendage.

DESCRIPTION

Length of intact mature or maturing specimens measured 10-28 mm, segment number 23-99, width of segment VIII 0.50-0.85 mm when compressed under the cover glass. Body cylindrical with weakly expressed intersegmental



Figs 51-55. - *Lamadrilus sorosi* gen. spec. nov. - 51. General appearance of the anterior end, whole mount in Canada balsam. - 52. Somatic chaeta. - 53. Distal end of somatic chaeta (free-hand drawing). - 54. Spermathecal chaeta *in situ*, from the whole mount. - 55. Male duct of a dissected specimen, mounted in glycerin.

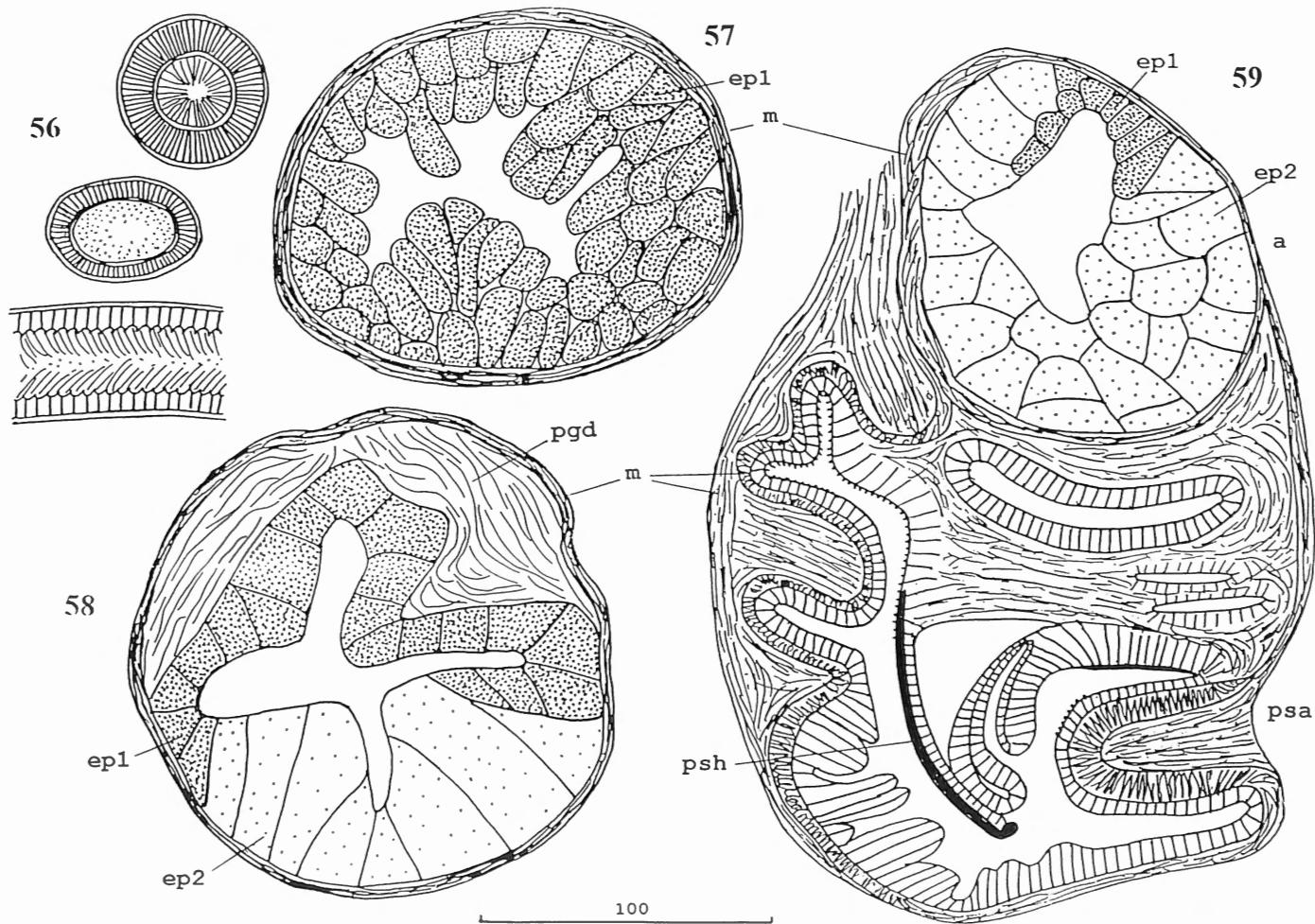
furrows, anteclitellar segments slightly wider than tail, anteriormost segments tapering. Body surface smooth. Prostomium distinct, shortly conical, never retracted (Fig. 51).

Somatic chaetae bifid, with distal nodulus, their upper tooth slightly thinner and longer or of the same length as the lower one (Figs 52, 53). 3-10 chaetae per bundle in anteclitellar and 2-4 in postclitellar segments. Their length varies within 50-70 µm in anteclitellar segments of the smallest worms and within 80-130 µm in those of the largest worms, while postclitellar chaetae are somewhat shorter. The chaetae are about 3 µm thick. In XI, near the male pores usually 2 short bifid chaetae. In X often ordinary ventral bundles of 3-4 chaetae occur, these are sometimes either lacking or replaced by a single modified spermathecal chaeta. The latter is 58-130 µm long, thin, with a hooked proximal end and a straight, narrow, grooved distal portion. Its middle part is surrounded by a large round thick-walled gland, 32-68 µm in diameter (Figs 51, 54).

Clitellum always weakly developed, in XI-XII. Male pores in XI, as well as ventrolateral spermathecal pores in X, often elevated on conical papillae along with the accompanying chaetae.

Body wall epithelium 6-21 µm thick, only slightly thicker (10-36 µm) in clitellum; circular muscle layer 2-3 µm, longitudinal musculature 7-50 µm thick. Body cavity lined with sparse weakly stained mesothelium up to 20 µm thick in some anteclitellar segments. Dissepiments 4/5-8/9 thickened, sometimes up to 25 µm in 6/7 and 7/8. Pharynx in III, ciliated, its thick roof forming a posterior appendage covered with a thin layer of glandular tissue. Narrow, winding oesophagus in IV-VII, surrounded with sparse glandular tissue in IV or IV-V, and covered with chloragogen cells from VI on. Intestinal dilation in VIII or (seldom) IX (Fig. 51).

Very long transverse blood vessels freely winding in body cavity in prostomium and I-III but resting on posterior dissepiment in IV-VII. Short dorsal "hearts" in VIII (Fig. 51).



Figs 56-59. *Lamadrilus sorosi* gen. spec. nov., different parts of male duct, from cross sections. - 56. Vas deferens. - 57. Proximal end of atrium. - 58. Proximal part of atrium after the entrance of prostatic gland. - 59. Distal part of atrium and penial sac.

Nephridia rarely observed, as loose bundles of 14-16 µm wide tubuli on 11/12, 12/13 or 13/14 but never anterior to the clitellar segments.

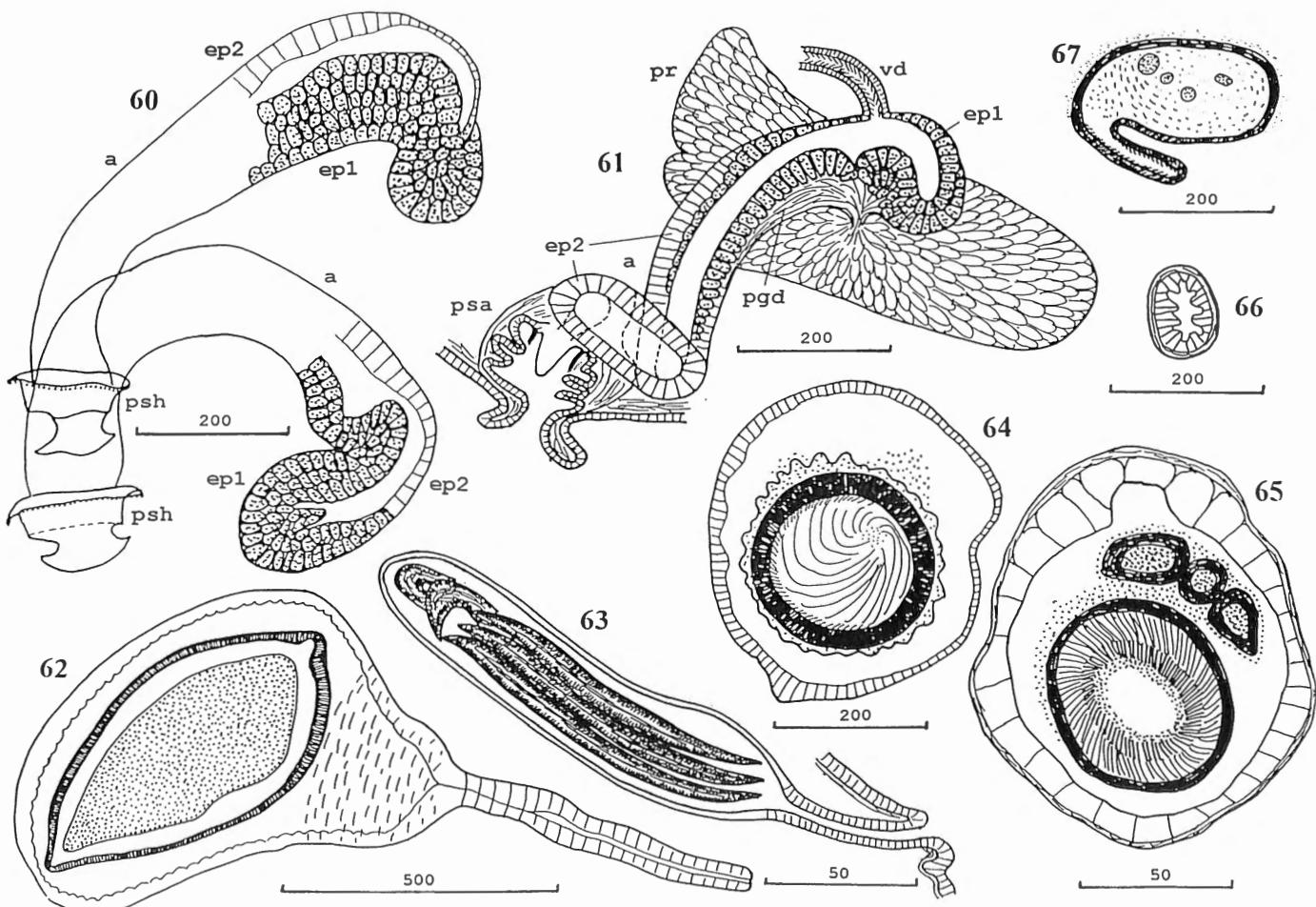
Testes in X, ovaries in XI. A single anterior sperm sac in IX or even reaching VIII (Fig. 51); posterior single or paired sperm sac (sometimes two sacs of different length) together with egg sacs can reach backwards up to XVI or farther. Ripe eggs not abundant.

Male ducts paired. Male funnel usually (in specimens caught in June-August) as a large irregular ciliated sac at 10/11, up to 400 µm high in the largest individuals, its wall up to 20 µm thick (but 8-10 µm in smaller worms). However, a single mature specimen caught in January had functioning bowl-shaped male funnels only 40-50 µm wide.

Vas deferens several times longer than atrium, its loops winding in XI but also inside egg sac, often reaching XV. (A dense coil of vas deferens, restricted to XI only, occurred in the January specimen). Its width varies irregularly along the length, within 40-50 µm in the biggest

worms but only 20-30 µm in the smallest ones, its wall being 5-14 or 6-9 µm thick, respectively. The lumen is densely ciliated all over (Fig. 56).

Atrium in XI-XII tubular, with its slightly dilated blunt proximal end directed caudad and bent downwards within egg sac (Figs 55, 60, 61). Atrium is about 900 µm long in the largest specimens and about 500 µm in the smallest ones. The width of its proximal end reaches 170-180 µm in the largest specimens but only 50-80 µm in the smallest ones; the middle and distal portions can be 30-160 µm wide in different individuals. External muscular layer 2-8 µm thick. Atrial epithelium has highly variable thickness (6-60 µm) and occurs in two kinds. The proximal part of atrium is lined with dark, dense epithelium arranged in longitudinal folds (Figs 57, 60, 61). This epithelium is the thickest on the concave side but extremely thin on the convex side. Some stripes of this dark epithelium proceed into the distal portion of atrium (Figs 58, 59, 61). The lining of the distal portion of atrium consists mainly of light epithelium of uniform



Figs 60-67. *Lamadrilus sorosi* gen. spec. nov. - 60. Both atria with penial sheaths *in situ*, from a strongly compressed whole mount in Canada balsam. - 61. Reconstruction of male duct after sagittal sections. - 62. Spermatheca of a dissected specimen, with single large lemon-shaped spermatozeugma, mounted in glycerin. - 63. Spermatheca with several vermiciform spermatozeugmata, reconstruction after sagittal sections. - 64. Cross section of spermathecal ampulla with a single large lemon-shaped spermatozeugma. - 65. Cross section of spermathecal ampulla with four spermatozeugmata of different size. - 66. Cross section of spermathecal duct. - 67. Tangential section of large spermatozeugma having a vermiciform appendage and containing several parasites.

thickness, staining weakly with both MALLORY and HAUSER (Figs 58-61).

Large irregular prostatic gland enters the concave side of atrium subapically with a short stalk (Figs 55, 61); extensions of prostatic cells run inside atrial wall between its muscular layer and dark epithelium towards atrium's distal end (Fig. 58). Vas deferens enters, also subapically, the opposite side of atrium where epithelium is the thinnest (Figs 55, 61). Thus, the proximal portion of atrium has a strongly eccentric lumen. In several specimens, some lobes of prostatic gland can reach XIV in egg sac.

Penial sac well-developed, 100-360 µm long and 40-280 µm wide in different individuals, mostly pear- or mushroom-shaped (when compressed by the distal end of atrium), heavily folded on its inner side (Figs 59, 61). It can partially protrude beyond the body surface as a conical appendage, but may also be deeply retracted inside the body. Soft conical or cylindrical penis is 100-170 µm long and 34-80 µm wide, consisting of muscular and non-glandular epithelial tissue distinctly different from atrial epithelium.

Short asymmetrical penial sheath as a fold of cuticle surrounding the middle portion of penis. Its main, thickest (1-5 µm) portion represents a short ring, 30-80 µm long and 80-140 µm wide in specimens of different size. Proximal edge turns to the inner wall of penial sac like a finely granulate collar reaching a width of 120-180 µm. The distal end of sheath usually forms a unilateral spade-like appendage (Figs 46, 55, 59-61). The total length of sheath including the appendage varies within 80-130 µm. Soft penis is partially retracted into sheath (Figs 59, 61). Female funnels, usually indistinct, were seen only in sections of one worm as a 25 µm wide lip of epithelial tissue resting on body wall at 11/12.

Spermathecae opening more or less laterally of ventral chaetae of X, usually on conical appendages including also the chaetae (the latter sometimes modified as genital chaetae). Spermathecal duct distinct, shorter than ampulla, its length attaining 530 µm in the largest specimens but only 70-180 µm in the smallest ones, the width being 25-125 µm in different individuals (Figs 62, 63). Muscular layer 3-18 µm thick, inner epithelial lining 2-25 µm thick and often arranged in longitudinal folds (Fig. 66). In some cases a 80-180 µm wide dilation, resembling a small ampulla, was observed in the middle of duct. Proper ampulla sacciform, up to 735 µm long and 100-630 µm wide in different specimens (Figs 62, 63), and can be located in X or reach IX, XI, or even XII inside sperm sacs. The wall is 3-40 µm thick depending on the degree of extension; this includes 2-7 µm of external muscular layer. The internal surface of epithelium is rough when relaxed.

Spermatozeugmata in spermathecal ampullae variable. There can be 2-5 or more vermicular spermatozeugmata per ampulla, about 300 µm long and 20-50 µm wide, sometimes expanding to 50-90 µm at one end (Fig. 63). They consist of a 3-7 µm thick envelope of modified sperm cells, externally covered with an indistinct light layer of flagella, and of a core of longitudinally arranged

regular spermatozoa. Sometimes, only dark strings of decaying spermatozeugmata were observed in ampullae but once also in spermathecal duct. Some other ampullae can contain one single large lemon-shaped spermatozeugma up to 620 µm long and 170-420 µm wide (Figs 62, 64). It has extremely dense 12-40 µm thick dark envelope covered with an uneven layer of small flagella and sometimes also with an additional thin, shrunk external case. The sperm inside can be spirally arranged. Lemon-shaped and vermicular spermatozeugmata can coexist in the same ampulla (Fig. 65), or a lemon-shaped spermatozeugma can have a vermicular appendage on one end (Fig. 67). Once (in the specimen caught in January), a small, 45 µm long and 7 µm wide spermatozeugma (?) was observed in the external "duct" of retracted penial sac. Its position and shape resembled those of atrial "crystals" characteristic of the genus *Baikalodrilus* HOLMQUIST, 1978 (SNIMSKHOVÁ & TIMM, 1992).

FEEDING AND PARASITES

The intestine contained sand and debris regularly in August but seldom in other months. In the intestine of one sectioned individual caught in August, dense bundles of vermicular gregarines 18-28 µm thick occurred in VIII-IX. A developing spermatheca of another specimen caught in April included a similar gregarine 23 µm in diameter. In one case (in June), globular cysts of a unicellular parasite, 10-24 µm in diameter, were observed in sperm sac among spermatids. In two cases (July-August), similar cysts were found in spermatozeugmata (Fig. 67). They were spherical or rod-shaped, usually 7-17 µm in diameter, in two cases about 50 µm. One of them contained about 10 smaller globules 15 µm in diameter.

REPRODUCTIVE BIOLOGY

Lamadrilus sorosi spec. nov. is evidently a summer-breeding species since mature individuals with spermatozeugmata and ripe eggs were found in June-August, with one exception in January; however, the latter specimen was peculiar in several aspects (see above). Several cohorts seem to participate simultaneously in reproduction as is evidenced by the highly different size of breeding individuals (and their genitals). Full-grown immatures occurred in all seasons. Only developing reproductive organs were found in mature worms in April. Some individuals with sperm sacs and half-developed spermathecae were devoid of vasa deferentia or whole male ducts. It was in these specimens that typical spermathecal chaetae were often found, but not in breeding (copulated) worms. One breeding individual with spermatozeugmata (in July) was also devoid of any male ducts, thus clearly representing an aberrant, female individual. Most breeding individuals were hermaphroditic. No cocoons attributed to this species were collected.

DISTRIBUTION AND HABITAT

Known only from Lake Taimyr. The species was collected from 12 different stations, at depths of 2.2-18.5 m. It was most frequent and abundant on mud in the deepest part of the lake, scarce on muddy pebbles, but never found on the sandy shallows or as frozen into ice.

TAXONOMICAL REMARKS

L. sorosi spec. nov. reveals remarkable individual variability in several characters such as the number of chaetae per bundle, presence or absence of spermathecal chaetae, different types of spermatozeugmata, development of the penial sheath, and even the presence or absence of some elements of the reproductive apparatus (male ducts or spermathecae) in some specimens, as well as the highly different size of breeding worms. Having only two or three different specimens, one can easily treat them as belonging to separate taxa. However, a large collection of specimens reveals irregular combinations of variable characters. Typical structure of the atrium is common to all specimens studied. Some other characters (long transversal vessels concentrated to the back wall in IV-VII, tapering forebody with a small but distinct prostomium, presence of ventral chaetae in XI etc.) were also characteristic of most individuals.

When compared with its Baikalian congeners (see above), confusion with *L. excavatus* (HRABĚ, 1982) is possible in case modified spermathecal chaetae are missing, since their penial sheaths are almost similar (Figs 45, 46). However, the ventral chaetae of XI are usually present in *L. sorosi* spec. nov. but always missing in *L. excavatus* when mature. The latter species urgently needs a more thorough anatomical study.

Some immature specimens of *Lamadrilus sorosi* with extremely scarce chaetae and invisible transverse vessels can easily be confused with *Limnodrilus profundicola* (VERRILL, 1871), and vice versa (see below). *Lamadrilus*

sorosi spec. nov. has usually more chaetae per bundle, while these are also thinner than in *Limnodrilus profundicola*; the anterior end of its body is tapering in a characteristic way, and the transverse vessels form dense plates on the anterior surface of several dissepiments in the forebody.

ZOOGEOGRAPHICAL REMARKS

Lamadrilus sorosi can be treated as a possible immigrant from Lake Baikal like *Baikalodrilus alienus* (see above). However, it can also belong to the aboriginal stock of the Siberian fauna like the former species.

***Limnodrilus profundicola* (VERRILL, 1871)**
(Figs 68-69)

Tubifex profundicola: SMITH & VERRILL, 1871: 451.

Limnodrilus helveticus: ČEKANOVSKAJA, 1962: 252-253, fig. 153A; CHEKANOVSKAYA, 1981: 316-317, fig. 153A.

Limnodrilus profundicola: BRINKHURST & JAMIESON, 1971: 470, figs 8.4.D,E.

Material studied. One single, incomplete mature individual. About 70 juvenile and maturing individuals in different samples from Lake Taimyr and the Gorbita River, all devoid of penial sheath, can also be tentatively attributed to this species.

DESCRIPTION

Length up to 22 mm and width 0.3-0.5 mm when compressed under the cover glass. Up to 70 segments. 2-5 uniform bifid chaetae in anterior bundles, 47-114 µm long (usually 70-90 µm) and 4 µm thick, with teeth of equal length but the upper tooth thinner (Fig. 68). No ventral chaetae in XI of maturing individuals. Chloragogen tissue on the oesophagus begins with VI. "Hearts" are observed in VIII. Transversal blood vessels, when visible, are loosely distributed. Penial sheaths of the mature specimen had a mushroom-shaped distal end characteristic of this species, and they were 3.3-3.6 times longer than wide (Fig. 69).

***Tasserkidrilus acapillatus* (FINOGENOVA, 1972)**
(Figs 70-76)

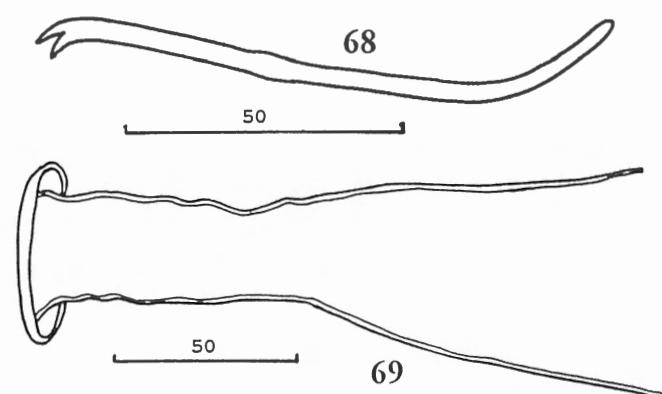
Tubifex acapillatus FINOGENOVA, 1972: 1883, figs 1-2; BRINKHURST, 1984: 498.

Isochaetides acapillatus: HRABĚ, 1982: 177-178, figs 5-12.

Tasserkidrilus acapillatus: TIMM & FINOGENOVA, 1987: 6; TIMM, 1989: 52-55, figs 1-2.

Tubifex kessleri variabilis: SEMERNOJ, 1982: 68-70, fig. 7.

?*Limnodrilus infundibuliferus*: IZOSIMOV, 1972: 33-34, fig. 1; 1980: 35-37, fig. 1.



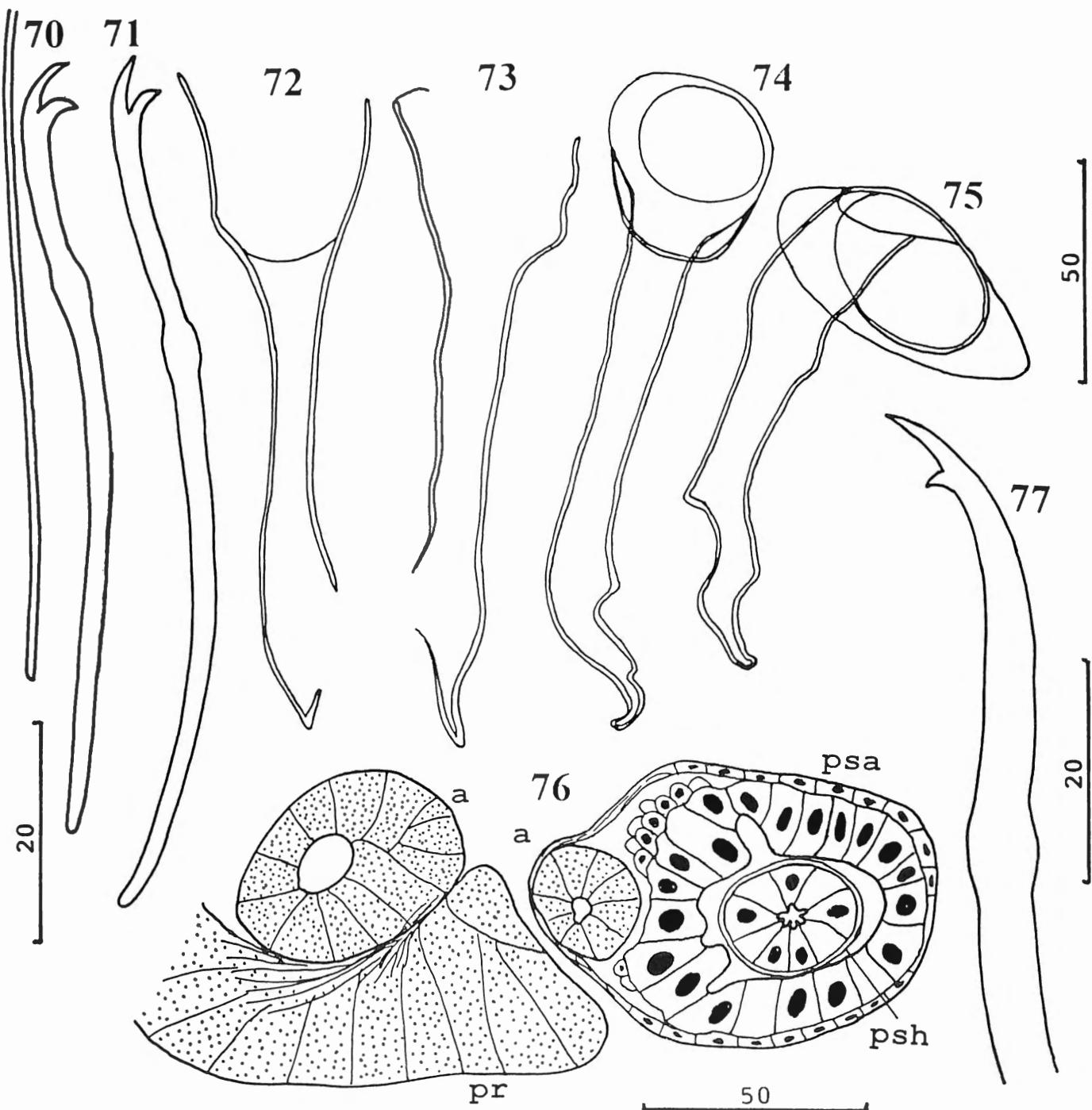
Figs 68-69. - *Limnodrilus profundicola* (VERRILL, 1871) from Lake Taimyr. 68. Chaeta. - 69. Penial sheath.

?*Tubifex superiorensis* (partim, only those in Baikal): BRINKHURST, 1984: 498, fig. 3.

Material studied. 21 specimens in 10 samples, one of them from the Gorbita River, the rest from Lake Taimyr, depth 2.3-18.5 m. Three individuals were mature or maturing. One specimen was studied on serial sections, the others as whole mounts in Canada balsam or glycerine.

DESCRIPTION

The only intact specimen was a small juvenile, 7.5 mm long and up to 0.4 mm wide in VIII when compressed under the cover glass, segment number 40. Several anterior ends belonged to somewhat bigger individuals. Prostomium bluntly conical, intersegmental furrows weak, body surface smooth.



Figs 70-76. *Tasserkidrilus acapillatus* (FINOGENOV, 1972) from Lake Taimyr. 70. Dorsal chaetae. - 71. Ventral chaeta. - 72-75. Penial sheaths of two specimens in the whole mounts. - 76. Cross section of two portions of the atrium and of the penial sac. Fig. 77. *Tubificidae* gen. sp. No. 1. Chaeta.

2-6 bifid chaetae both in dorsal and ventral anterior bundles, 63-93 µm long, their upper tooth slightly longer and straighter (Figs 70, 71). Dorsal bifids may have a very tiny intermediate tooth. Hair chaetae either lacking, or present as single short (117-210 µm) and thin (<1 µm) smooth hairs in some bundles of III-VIII (Fig. 70). No ventral chaetae in XI. No modified genital chaetae. Only bifids in posterior bundles.

Pharynx thick-walled, with dorsal glands in II-III. Chloragogen tissue covers oesophagus beginning from VI. Intestinal dilation in VIII. Transverse blood vessels in forebody short, in VIII dilated as "hearts".

All reproductive organs paired. Testes in X, ovaries in XI, sperm and egg sac can reach up to XV. Clitellum not yet developed in the worms studied.

Male funnels in X like forward-directed bowls, 120-186 µm high, their epithelium about 12 µm thick. Thread-like spermatozoa on funnels visible. Vasa deferentia considerably longer than atria, 14-40 µm wide, internally ciliated along their whole length. Their proximal portion is comparatively narrow and straight, whereas the distal portion forms several loops near atrium.

Atria in XI, unevenly tubular, at least 200 µm long and 18-56 µm wide. Their wall consists of glandular epithelium only, no muscular layer was observed. The longer, proximal portion of atrium descends vertically. After a sharp bend, the distal portion ascends again but clinging closely to penial sac (Fig. 76). A narrow neck connects atrium with penis.

Prostatic gland compact, up to 193 µm broad, tightly embracing the middle portion of atrium (Fig. 76) and bound to it with a short, broad stalk.

Penial sacs in XI, measured 185 µm long and 47-80 µm wide, containing distinct penial sheath. The latter is 128-140 µm long, up to 60 µm wide in its funnel-shaped proximal end but only 9-19 µm in the tubular middle portion, the wall being less than 1 µm thick. Distally, sheath terminates with thin, closed appendage, while distal pore always lies subapically (Figs 72-75). A fold of epithelial tissue (penis proper) fills the inside of sheath (Fig. 76).

Spermathecae in X, with distinct duct and ampulla. Duct 32-50 µm wide, including external muscular layer up to 5 µm thick. Ampulla bipartite, about 90 µm wide when empty; epithelial wall 5-14 µm thick, sometimes internally folded or papillate. When filled with spermatozeugmata, ampullae occupy the whole cavity of X and can bulge into XI. Spermatozeugmata vermiform, winding, up to 35 µm broad.

REPRODUCTIVE BIOLOGY

A few individuals with reproductive organs were caught in June and August.

DISTRIBUTION AND HABITAT

Found in small numbers in different zones of Lake Taimyr, once also in the Gorbita River. Known from some other

Eurasian large lakes, as the Caspian Sea (FINOGENOVA, 1972), Baikal (HRABĚ, 1982, etc.) and Peipsi (TIMM, 1989).

TAXONOMICAL REMARKS

The hair (and also pectinate) chaetae are lacking or are very rare in a typical *T. acapillatus* as redescribed and discussed by TIMM (1989). In Lake Taimyr specimens, they often occur in several segments like in *Tasserkidrilus kessleri* (HRABĚ, 1962) described as *Tubifex kessleri* on the basis of a single specimen from Lake Onega. However, *T. kessleri* has simple spermathecal ampullae, a non-ciliated distal portion of the vasa deferentia and pear-shaped glands associated with ventral chaetal bundles. These differences are large enough to reject the possible subspecific status in relation to or even synonymization of *T. acapillatus* with *T. kessleri*, as suggested by BRINKHURST (1984). For a conclusive solution of the problem, a redescription of the Lake Onega population on new material is needed.

Tasserkidrilus baicalensis (SEMERNOJ, 1982), originally described as a subspecies of *T. kessleri* by SEMERNOJ (1982), has several well-developed hair and pectinate chaetae in all anterior dorsal bundles. The other Baikalian species of *Tasserkidrilus*, described by SNIMŠČIKOVA (1982) and SNIMŠČIKOVA & AKINŠINA (1993), differ from the above mentioned taxa both by their chaetal apparatus and the shape of the penial sheath.

Tubificidae gen. sp. No. 1 (Fig. 77)

Two damaged juveniles, about 0.3 mm thick, were caught at a depth of 3.4 and 11.7 m. All chaetae bifid, two per bundle, 105-123 µm long in anterior bundles of the larger specimen but only 56-70 µm in the smaller one. In anterior chaetae, upper tooth long and thin, with rudimentary lower tooth attached to it at a right angle (Fig. 77). In the caudal direction, the teeth gradually becoming equal. Mature specimens would be needed to determine the specific status of this form.

Tubificidae gen. sp. No. 2

Two small, damaged juveniles, 0.3-0.5 mm thick, one of them 8 mm long, were caught at a depth of 2.2 and 2.5 m, respectively. Anterior dorsal bundles mostly with 2 hair and 2 pectinate chaetae, and the ventral ones with 3-4 bifid crotchets. Posteriorly, only 2 bifids remaining in all bundles, with lower tooth slightly thicker like in *Tubifex tubifex* (MÜLLER, 1774) and many other tubificids. This setal pattern is insufficient for species identification.

Discussion

The dominance of tubificid oligochaetes in zoobenthos is not common in the extremely severe conditions of Arctic lakes (e. g. SMITH & WELCH, 1919; NURMINEN, 1973). In the case of Lake Taimyr, this may be due to its high productivity. A large amount of allochthonous detritus and dissolved nutrients is carried into the lake from the (although pristine) watershed by tributaries, since the whole water mass seems to be replaced about once a year. GRÈZE (1957) even wrote about the "arctic eutrophy" of this lake.

Two different habitats are distinguishable in the benthal of Lake Taimyr (GRÈZE 1957; TIMM 1996). Sandy or silted sandy bottoms, up to 7-8 m deep in summertime, which freeze solid for a larger part of the year when the water level decreases, cover about 85% of the lake area. Frozen bottom animals can be subjected to temperatures down to -20°C here in mid-winter (GRÈZE, 1947b). Therefore, this zone resembles shallow tundra ponds. Only *Alexandrovia ringulata*, a species highly tolerant to freezing, can thrive here, seldomly accompanied by accidental single individuals of other tubificids.

The deeper, mud-covered zone reveals an environment similar to the profundal of temperate oligotrophic lakes, with a stable low temperature and high oxygen concentration. All other tubificid species, apart from *A. ringulata*, inhabited mainly this truly lacustrine zone, sharing the environment with Lumbriculidae. *Lamadrilus sorosi* gen. spec. nov. was the most abundant species here, while *Baikalodrilus alienus* spec. nov., *Tasserkidrilus acapillatus*, *Limnodrilus profundicula* and the two unnamed taxa occurred in low numbers.

The number of tubificid taxa found in Lake Taimyr is low, when compared with that recorded for other large lakes, e.g. Peipsi (22, after TIMM, 1979) or Baikal (70 valid species and subspecies, with at least 22 more nondescribed taxa according to SNIMSKHOVA & AKINSHINA, 1994). This can be explained by the low geological age of the lake as well as by severe conditions (short summer, freezing of the bottom) here and in the surrounding waterbodies. *Alexandrovia ringulata* is the only abundant widely distributed species here. Some other species which are common at lower latitudes in Middle Siberia according to ZINOV'EV (1981), AKINSHINA & TOMILOV (1976), VERŠININ (1976) etc., such as *Limnodrilus profundicola* and maybe *Tubifex tubifex* (in case Tubificidae No. 2 proves to be identical with the latter) are scarce in Lake Taimyr. *Baikalodrilus alienus* spec. nov., *Lamadrilus sorosi* gen. spec. nov. (and perhaps also Tubificidae No. 1) have so far not been found anywhere else, while *Tasserkidrilus acapillatus* is confined to some large lakes, including Baikal.

The representatives of both "Baikalian" genera, *Baikalodrilus* and *Lamadrilus* (maybe also *Tasserkidrilus acapillatus*), in Lake Taimyr can be easily treated as immigrants from Lake Baikal, carried downstream by the rivers of Angara and Enisej. The latter probably had a connection with Lake Taimyr via the modern rivers of Pjasina and Taimyra in the recent past (Fig. 1). GRÈZE

(1947a, 1957) has explained in the same way the presence of some other basically Baikalian Bryozoa, Polychaeta, and Gammaridae in Lake Taimyr. Several tubificids of apparently Baikalian origin, e. g. *Rhyacodrilus korotneffi* (MICHAELSEN, 1905), *Lycodrilus dybowskii* GRUBE, 1873, and *L. schizophaetus* MICHAELSEN, 1901 were found in the Angara and Enisej Rivers (ČEKANOVSKAJA, 1956; AKINŠINA & TOMILOV, 1976; TOMILOV *et al.*, 1978), the first species is even found in the Krasnojarsk Reservoir on the Upper Enisej (VERŠININ & SEMERNOJ 1977).

The principal difference between Lake Baikal and the smaller lakes of northern Siberia is the persistence of this huge rift lake over a long time, which has resulted in the establishment of species-rich communities usually not mixing with the original Palaearctic fauna. Accelerated speciation of aquatic animals together with the conservation of numerous newly formed taxa in Lake Baikal has proceeded due to the diverse but stable environment (SNIMSKHOVA & TIMM, 1992). Owing to its rich endemic fauna, Lake Baikal is regarded as a separate zoogeographical region (STAROBOGATOV, 1970; TIMM, 1980). The smaller, more temporary lakes of Siberia, inhabited mostly by widely distributed Palaearctic species, can be quite suitable for the survival of Baikalian animals in case those would invade them. However, the short lifetime of these waterbodies does not allow significant evolutionary radiation. The cold and oxygen-rich waters of the deep central part of Lake Taimyr can indeed provide shelter for invaders from Baikal.

However, an alternative explanation would be possible. The founder taxa of large species clusters in Lake Baikal once arose elsewhere, and this may be the case with *Baikalodrilus* and *Lamadrilus*. Close relatives of these ancestral taxa may have survived in various poorly studied waterbodies of Siberia. Some records of the possible members of the genus *Baikalodrilus* in West and Middle Siberia were already discussed above in connection with *B. alienus*. The finding of a species of some basically Baikalian genus in another lake does not necessarily mean that it is an invader from Baikal. Thus, *B. alienus* and *L. sorosi* could be regarded as non-Baikalian members of their genera. Their existence in some other Siberian waterbodies cannot be excluded.

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