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Review of the genus *Baikalodrilus* HOLMQUIST, 1978 (Oligochaeta, Tubificidae)

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Abstract

Baikalodrilus is a genus of armoured tubificids, endemic to Lake Baikal. The existence of organic crystals in their atria is regarded as a common characteristic apparently correlated with the abscence of genital setae. Illustrated descriptions of all 22 known species and subspecies are given and discussed in this contribution, together with an emended diagnosis of the genus and an identification key. The evolution of the genus is discussed, in connection with the unique geological history of Lake Baikal.
Baikalodrilus paradoxus (SNIMSCHIKOVA, 1984) is probably most similar to the common ancestor of the genus. The alleged occurrence of *Embolocephalus velutinus* (GRUBE, 1879) in Lake Baikal must be disputed, while *Baikalodrilus inflatus* (MICHAELSEN, 1901) is shown to belong to the genus *Baikalodrilus* as a *species inquirenda*.
Key-words : Tubificidae, Baikal, ecological radiation, palaeolimnology.

Résumé

Baikalodrilus est un genre de tubificides cuirassés endémique du lac Baikal. L'existence de cristaux organiques dans les atria est considérée comme un caractère commun, apparemment corrélée avec l'absence de soies génitales modifiées. Des descriptions illustrées de l'ensemble des 22 espèces et sous-espèces connues sont données et comparées dans l'article, associées à une diagnose corrigée du genre, et avec une clé d'identification pour l'espèce. L'évolution du genre est discutée en relation avec la longue et unique histoire du lac Baikal.
Baikalodrilus paradoxus (SNIMSCHIKOVA, 1984) est probablement le plus semblable à l'ancêtre du genre. L'existence présumée de *Embolocephalus velutinus* (GRUBE, 1879) dans le lac Baikal doit être discutée, alors que *Baikalodrilus inflatus* (MICHAELSEN, 1901) appartient au genre *Baikalodrilus* en tant que *species inquirenda*.
Mots-clés : Tubificidae, Baikal, radiation écologique, paléolimnologie.

Introduction

The ancient rift Lake Baikal has been characterized by many researchers as a great centre of speciation, where a peculiarly rich, endemic fauna arose and evolved, based on a small number of relict species living in different geological periods. About 1600 animal species have, so far, been registered in Lake Baikal, 60 % of which are endemic. The most diverse group of Baikalian animals, the Gammaridae, with 255 endemic species, may have originated from 4-5 ancestral species (BAZIKALOVA, 1945); while 34 mollusc species of the family Baicaliidae probably had 1-2 ancestors (KOZHOV, 1962, 1963), and 23 species of Baikalian Cottidae had 2-3 ancestors (TALIYEV, 1955). Numerous oligochaetes and turbellarians have also evolved from a small number of ancestral forms (IZOSSIMOV, 1962; PORFIRYEVA, 1977). Due to the peculiarity of ecological processes in Lake Baikal, divergence has had an explosive character, resulting in many series of related species. Because of this high degree of endemicity, Lake Baikal has been treated as a separate zoogeographic region of inland waters (STAROBOGATOV, 1970; TIMM, 1980).
A similar phenomenon occurs in many other large ancient rift lakes of the world. Most of the animal species inhabiting them can be regarded as successors of a few ancestral invaders (KOZHOV, 1962, 1963). The "thalassoid" gastropod fauna of Lake Tanganyika (BROOKS, 1950; HUBENDICK, 1952), the fish fauna of African rift lakes (WORTHINGTON, 1954) and Lake Lanao on the Philippines (HERRE, 1933), as well as the fauna of Lake Ohrid on the Balkan Peninsula (STANKOVIĆ, 1960) serve as prime examples.
The present review discusses the species diversity in the endemic tubificid genus *Baikalodrilus*, with a discussion of evolutionary trends, possible phylogenetic relationships and ecological speciation factors. All taxa of *Baikalodrilus* described so far in different (mainly Russian) works are compared, and a key to assist researchers in the further study of this group is compiled.
The richness of the tubificid fauna of Lake Baikal was discovered quite recently. Only 10 species of this family were known in the lake up to 1975, while the Lumbriculidae were regarded as the dominant family among the local oligochaetes (IZOSSIMOV, 1962).
During the last 17 years the number of tubificid species found in Baikal has exceeded 80, with 20 genera being represented (CHEKANOVSKAYA, 1975; HOLMQUIST, 1978, 1979; SEMERNOY, 1982; HRABĚ, 1982; BRINKHURST, 1984; SNIMSCHIKOVA, 1982, 1984, 1985, 1986, 1987, etc.). Among these, the armoured species (papillate or covered with adhering particles) are of special interest.

Prior to 1978, 6 species of armoured tubificids were known in Lake Baikal, all belonging to the genus *Peloscolex* LEIDY, 1850 : *P. ferox* (EISEN, 1879); *P. velutinus* (GRUBE, 1879); *P. inflatus* (MICHAELSEN, 1901); *P. werestschagini* MICHAELSEN, 1933; *P. kozovi* HRABĚ, 1969; *P. malevici* CHEKANOVSKAYA, 1975.

HOLMQUIST (1978, 1979) revised *Peloscolex* and divided it into eight smaller genera. Thus, *P. ferox* was transferred to *Spirosperma* EISEN, 1879, *P. velutinus* to *Embolocephalus* RANDOLPH, 1892, and *P. kozovi* to the new genus *Baikalodrilus* HOLMQUIST, 1978, together with a new species *B. digitatus* HOLMQUIST, 1979. The position of two species, *P. inflatus* and *P. werestschagini,* remained obscure, while *P. malevici* was not discussed.

BRINKHURST (1981a, 1981b) criticized HOLMQUIST's revision and merged three of her genera again. Furthermore, he declared the type species of the genus *Peloscolex* as dubious, thus discarding the generic name. HRABĚ (1982), as well as SEMERNOY & SHIDLOVSKAYA (1983) suggested maintaining the previously large genus *Peloscolex* for most freshwater representatives. TIMM & FINOGENOVA (1987) listed all 12 known species of *Baikalodrilus* as a subgenus within the genus *Spirosperma,* which was a compromise, aimed at alleviating problems created by decisions reached by HOLMQUIST.

In this contribution we provide evidence for the generic separation of *Baikalodrilus*. Below, new evidence of its independence is given and its relationship to some related genera is discussed.

HOLMQUIST (1978, 1979) created the genus *Baikalodrilus* for two rather similar species, *Peloscolex kozovi* and *Baikalodrilus digitatus,* limiting the generic diagnosis to these species. BRINKHURST (1981a) added two more species with similar male ducts, *P. werestschagini* and *P. inflatus* to the genus. SNIMSCHIKOVA (1982, 1984, 1991b) completed the descriptions of *P. malevici* and *P. werestschagini,* and redescribed *Lycodrilus phreodriloides* MICHAELSEN, 1905, which all appear to be members of *Baikalodrilus*. She also described 14 new species and 2 subspecies of *Baikalodrilus,* although some as species of *Peloscolex* (SNIMSCHIKOVA, 1982, 1984, 1989a, 1989b, 1991a). SNIMSCHIKOVA, TIMM & PARELE (1987) united all endemic armoured Baikalian tubificids into the single genus *Baikalodrilus*.

The very characteristic atrial crystal was first described as a "Gallertstab" by MICHAELSEN (1933, 1935) in his *Peloscolex werestschagini*. Owing to this character, the group was defined as *Peloscolex* (*Crystallifer*) by SNIMSCHIKOVA (1984, 1987). However, according to SNIMSCHIKOVA, TIMM & PARELE (1987) the latter name must be rejected as a junior synonym of *Baikalodrilus*.

In the present contribution we regard *Baikalodrilus* as a separate, highly endemic genus with 22 species and subspecies. However, several additional species still remain undescribed (personal communication by V. SEMERNOY).

Material and methods

The material for this contribution, as well as for the preceding papers of the first author on the topic (SNIMSCHIKOVA, 1982, 1984, 1985, 1987, 1989a, 1989b, 1991a,b), originates from different benthic surveys made between 1961 and 1984 by the Limnological Institute of the Siberian Branch of the Academy of Sciences of the USSR on Lake Baikal, mostly in the Northern part of the lake and in the shallows in front of the delta of the Selenga River (Fig. 1). Collecting was carried out with a Petersen grab, a trawl, or *in situ* by SCUBA divers. The animals were preserved, either in formalin or ethanol. Altogether approximately 300 benthic samples from depths between 0 and 500 m were used. About 9500 of the 48000 oligochaete specimens found, belong to the genus *Baikalodrilus*.

The worms were studied as whole mounts in glycerine or in Canada balsam, mature specimens were dissected and their genitalia were mounted separately. Series of paraffin sections, stained with Mallory, 4-6 μm thick, were made for some specimens. Drawings were made with the aid of a camera lucida RA-6 on a light microscope.

The remaining specimens of the type series of *Tubifex inflatus* MICHAELSEN, 1901 from the collection of WAGNER in the Zoological Institute in Leningrad (presently St. Petersburg) were re-examined by the first author, as well as a series of sections made by HOLMQUIST from a specimen identified by her as *Peloscolex inflatus* in the same museum. Unfortunately, another possible source of type material of Baikalian oligochaetes, the collection of KOROTNEW in Kiev, has perished during the Second World War.

Abbreviations used in the figures

at	atrium
c	crystal(s)
c^1	crystal(s) of the other atrium
DS	dorsal seta(e)
f	male funnel
FC	furrows of the cuticle
GV	general view
GVA	general view of the anterior end
MD	male duct
MDD	distal part of the male duct
p	penis
post	posterior part of the body
pr	prostate gland
PS	papilla(e) in side view
PT	papilla(e) in top view
SP	spermatheca
SPZ	spermatozeugma(ta)
ST	setal tubercle(s)
vd	vas deferens
VS	ventral seta(e)

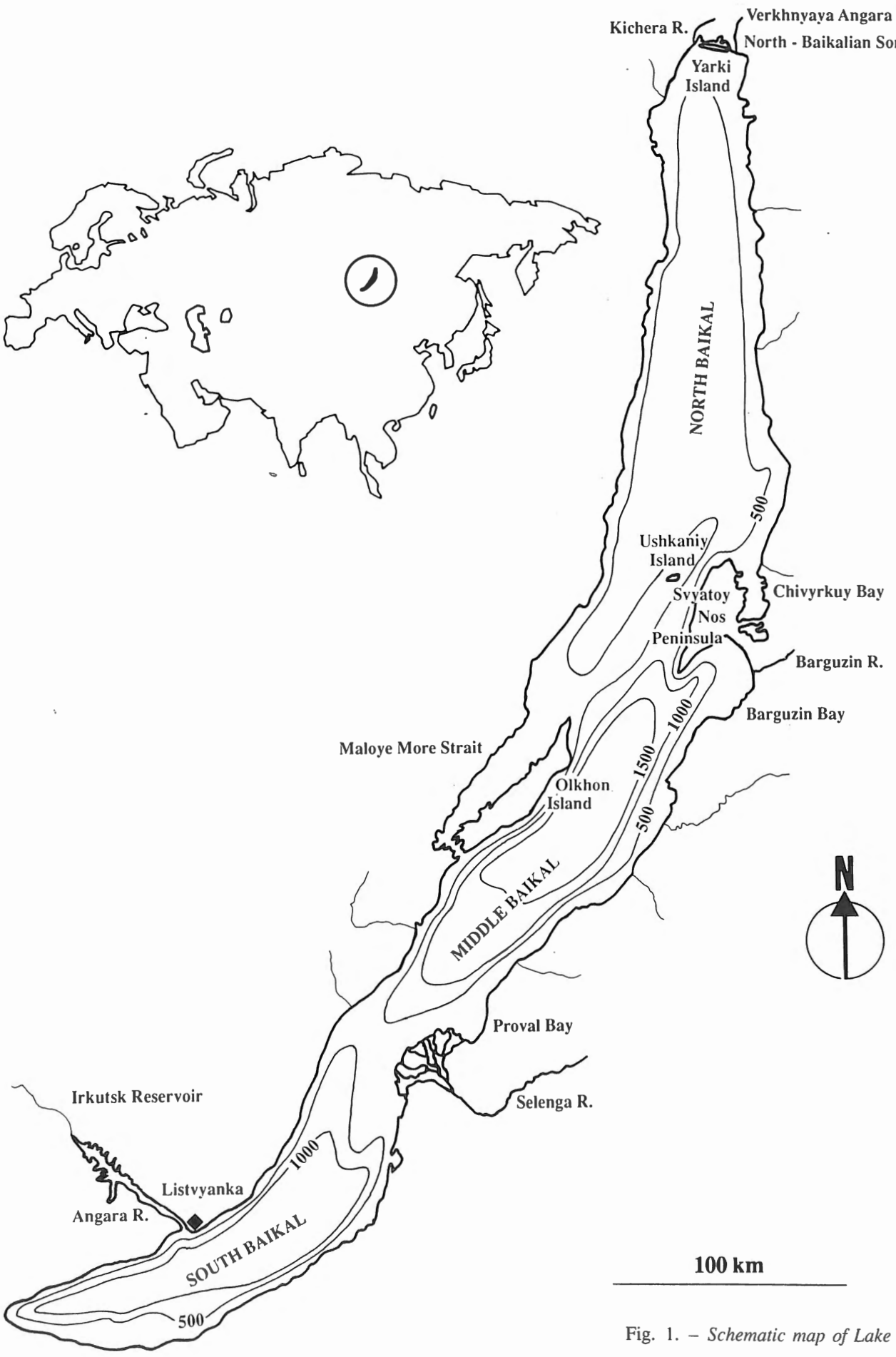

Fig. 1. – *Schematic map of Lake Baikal.*

Roman numerals indicate segment numbers. Length of the scale bars is given in micrometers.

Systematic account

Genus **Baikalodrilus** HOLMQUIST, 1978

Syn. : *Crystallifer* SNIMSCHIKOVA, 1978

DIAGNOSIS

Length 1.2-30 mm. Body surface covered with armour, formed by thickened cuticle. The armour consists of transversal ridges, which are sometimes very dense or in a continuous, hard coating; bearing sensory and secretory papillae. The latter can be of a different size, from hardly visible tubercles to large, finger-shaped appendages. Secretory papillae surrounding epidermal glands, their secretion discharging from the pores on the tips of the papillae and thickening the armour, also adhering small sediment particles. Sensory papillae are usually of smaller size and without any cuticular cover.
Prostomium and segments I-II (up to first setae) retractable. Clitellum usually lighter, with thinner cuticle and papillae smaller and sparser than on the rest of body.
Dorsal bundles with some bifid, pectinate or simple needle setae in addition to hair setae. Ventral bundles with bifid or simple (sabre-shaped or hooked) crotchets; teeth of bifids can be reduced to a varying extent. Simple and bifid crotchets can alternate in the same bundle, then usually the most lateral seta of every bundle bifid, followed by a simple one, and so on. As a rule, only single setae are present in postclitellar bundles. Ventral setae absent from XI. No modified genital setae.
Reproductive organs paired, typically positioned for Tubificidae. Male funnel of varying size. Vas deferens considerably longer than atrium, usually widening distally, discharging into atrium apically. Atrium of medium size, cylindrical, straight or curved, with thick internal epithelium. One or several oblong crystals lying along atrial lumen. They are named thus for convenience, as their structure is not exactly known. Crystals soft and flexible, probably secreted by the prostate gland. Rarely crystals are extruded from the atrium , or lie near the atrium in the body cavity (Fig. 11, 20). Ejaculatory duct short or absent. Penis in penial sac, without any sheath or thickened cuticle. Prostate gland compact, discharging into the medial or into proximal half of atrium. Spermatheca with round or sacculate ampulla, and with distinct external duct. Long, thin spermatozeugmata in ampulla.

DISTRIBUTION

Lake Baikal and reservoirs on the Angara River, the outflow of the lake.

TYPE SPECIES

Peloscolex kozovi HRABĚ, 1969.

REMARKS

Among the armoured Tubificidae, the genus *Embolocephalus* RANDOLPH, 1892 seems to be the closest relative of *Baikalodrilus*. Both genera have long coiled vasa deferentia, almost twice as wide distally; cylindrical atria of medium length; short ejaculatory ducts (lacking in several species of *Baikalodrilus*); and short, soft naked penes. Unlike *Embolocephalus, Baikalodrilus* has organic crystals inside or nearby the atria, and no spermathecal setae. The nodulus of the ventral crotchets is ental in *Baikalodrilus,* but median in *Embolocephalus.*
In the genus *Quistadrilus* BRINKHURST, 1981, no spermathecal setae, penial sheaths or ejaculatory ducts occur. *Quistadrilus* differs from *Baikalodrilus* in the presence of coiled tubular atria, with a ciliated lining in their ental part (the atrial lining being smooth in *Baikalodrilus*). The vas deferens discharges apically in the atrium in *Baikalodrilus,* but subapically in *Quistadrilus,* the prostate gland is situated more or less in the medial part of the atrium in *Baikalodrilus,* but proximally in *Quistadrilus.* The armour, although of varying consistency, is always continuous in *Baikalodrilus,* but thin and mottle in *Quistadrilus.*
Differences between *Baikalodrilus* and the genus *Spirosperma* EISEN, 1879 are even more pronounced. The latter genus is characterized by a rather short crescent-shaped atrium; a long and coiled ejaculatory duct, ciliated in its ental part; and a large penis with thick chitinous sheath. *Spirosperma* is similar to *Baikalodrilus* and *Quistadrilus* in having no spermathecal setae, a feature present in *Embolocephalus.*
Relying on the above comparison, we reject the incorporation of *Embolocephalus* as a subgenus in the genus *Spirosperma* by BRINKHURST (1981a). We regard *Embolocephalus* as a separate genus.
It was also held separate from *Spirosperma* within the monophyletic clade (possible tribe) of freshwater armoured tubificids, recently discriminated by BRINKHURST (1991). The rank of tribe for the former genus *Peloscolex sensu lato* (including the marine representatives) was also proposed by SEMERNOY & SHIDLOVSKAYA (1983).

Baikalodrilus paradoxus (SNIMSCHIKOVA, 1984) (Fig. 2)

Peloscolex paradoxus SNIMSCHIKOVA, 1984 : 9-12, fig. 3.

DESCRIPTION

Length 20-24 mm, maximal diameter 2 mm, 67-72 segments. Colour brown, usually brighter on anterior seg-

ments. Dense papillae fused into a regular layer. Fine detritus stuck in grooves of this armour, forming several dark rings on each segment. II biannulate, III and IV triannulate; starting from V, the number of annuli reaching 10-12 per segment. Large round, bright setal tubercles rising distinctly over the dark armour, forming four longitudinal rows.

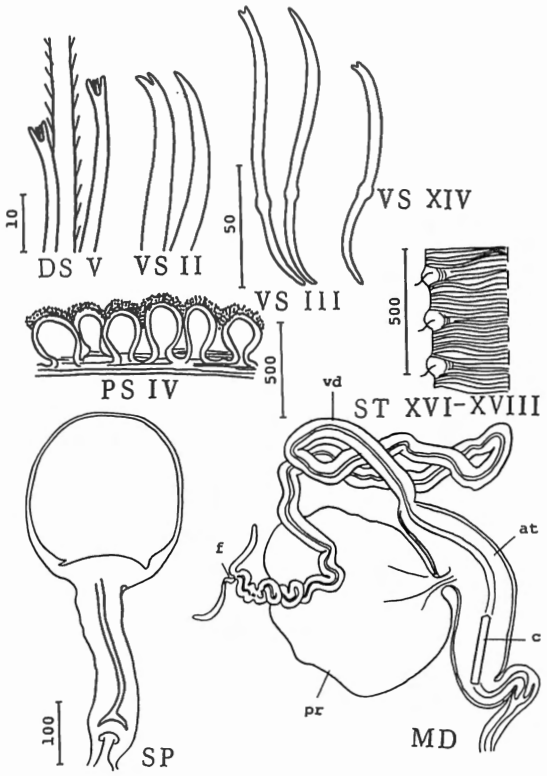

Fig. 2. – Baikalodrilus paradoxus.

2-3 plumose hair setae in anteclitellar dorsal bundles, and 2-3 pectinates with equal lateral teeth and several very fine intermediate teeth. Hair setae 350-420 μm long, pectinates 80-120 μm. Postclitellar dorsal bundles with a single plumose hair seta, 170-180 μm long, and very fine needle seta, 70 μm long. Ventral bundles of II consisting of one simple and two bifid crotchets, those of III and further backwards, with one simple and one bifid crotchet, the simple one always lying on the ventral side of the bundle. Bifids either with equal teeth, or with a rudimentary distal tooth. Anteclitellar ventral setae measuring 180-210 μm. Postclitellar ventral bundles consisting of a single, strongly curved bifid crotchet, 140 μm long, with short proximal and rudimentary distal teeth.

Clitellum bright, circular, on X-XII. Spermathecal and male pores situated on one line with ventral setae. Vas deferens about 2150 μm long, proximally narrow and curled, gradually widening from 30 to 42 μm. Large massive prostate gland joining the middle part of the atrium. Atrium elongated, tapering on both ends, with two sharp distal bends, terminating with a soft penis in the penial sac. In the atrial lumen a single longitudinal, rectangular crystal is present, 150 μm long and 17 μm thick.

Spermatheca consisting of a globular ampulla, 350 μm long and 320 μm wide, and a well-differentiated efferent duct, 460 μm long and 85 μm wide. Spermatozeugmata not observed.

DISTRIBUTION AND HABITAT

In North and Middle Baikal, common in large shallow areas near the mouth of big inflows (Kichera, Verkhnyaya Angara, Selenga), between 5 and 250 m deep (more often at 10-50 m), on mud and muddy sand. Densities up to 2000 individuals per square metre. A large number of specimens studied. Mature specimens very rare, only found in August and September.

REMARKS

Amongst the armoured tubificids, *Baikalodrilus paradoxus* is most similar to the type species of the genus *Embolocephalus, E. velutinus* (Grube, 1879), according to its setal apparatus and male duct. However, *E. velutinus* bears only 2-3 transversal rows of papillae per segment, while in *B. paradoxus* papillae are numerous and fused. *E. velutinus* lacks the prominent setal tubercles, characteristic of *B. paradoxus*. Pectinates are 2-3 times smaller in *E. velutinus,* the ventral setal nodulus is situated almost medially in this species and entally in *B. paradoxus*. Spermathecal setae are present in *E. velutinus,* but not in *B. paradoxus*. The spermathecal duct is considerably longer in *E. velutinus*. Finally, *E. velutinus* lacks the atrial crystals.

Embolocephalus velutinus is allegedly distributed in Siberia, perhaps also in the littoral-sor zone of Lake Baikal ("Sor" is the local term for shallow, half-isolated bays of Lake Baikal). However, it was not found during our studies. Holmquist (1979) did not rely on any non-European records of this species. Researchers observing it in Baikal (e.g. Michaelsen & Verescagin, 1930; Chekanovskaya, 1975; Akinshina & Lezinskaya, 1978; Semernoy & Shidlovskaya, 1983) probably confused *E. velutinus* with several species of *Baikalodrilus,* particularly *B. paradoxus*. In the material at our disposal a large variability in the setal apparatus was noticed. Snimschikova (1984, 1987) doubted the distribution of *E. velutinus* in the open part of Lake Baikal. To date, its presence in the lake still remains doubtful.

Baikalodrilus scaphoideus Snimschikova, 1989
(Fig. 3)

Baikalodrilus scaphoideus Snimschikova, 1989b: 23-25, fig. 1.

DESCRIPTION

Length 14-16 mm, maximal diameter 1.3-1.4 mm. Prostomium retracted. Cuticular cover translucent, without any papillae, but with a striped appearance, due to fine transversal furrows in which small sediment particles accumulate. Setal tubercles small, almost not protruding from the body surface.

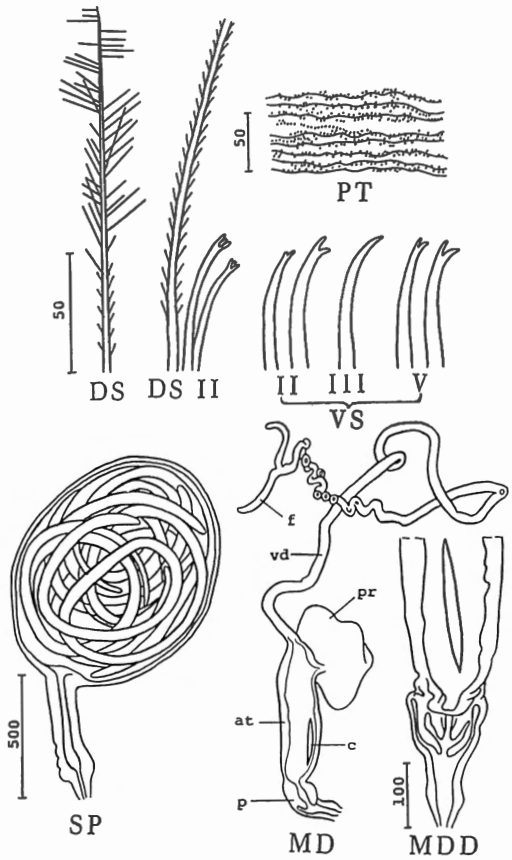

Fig. 3. – Baikalodrilus scaphoideus.

Dorsal bundles containing 2-3 plumose hair setae, 180-220 μm long, and 2-3 pectinates, 70-80 μm long, with two intermediate teeth. Beginning from V, pectinates with shorter outer teeth than in anterior segments. Ventral bundles of II-VI consisting of two crotchets, 120-130 μm long. One of these crotchets always bifid with equal teeth, the other in VI simple; in II-IV with hardly distinguishable distal tooth, and in V with fine teeth (the distal one being finer and a little shorter); beginning from VII or VIII only one crotchet per bundle.

Bright circular clitellum occupying X-XII. Spermathecal and male pores situated on one line with ventral bundles. Vas deferens 2600-2700 μm long, proximal part coiled and narrow, middle and distal parts straighter and wider. Atrium cylindrical, straight, tapering equally at both ends, 500-510 μm long and 154-156 μm wide. Atrial wall only 30-34 μm thick, formed mainly by muscle layer. Distal part of voluminous atrial lumen with a pointed boat-shaped crystal, 180-182 μm long. Penial sac about 170 μm long. Prostate gland medium-sized, shorter than atrium, connected with the proximal half of the latter by a distinct narrow stem. Spermathecal ampulla oval, 950 μm long and 760 μm wide, full of coiled, long and thin spermatozeugmata. Spermathecal duct well-defined, 470 μm long, equipped with a small sphincter near the body wall.

DISTRIBUTION

Middle Baikal, Selenga Delta Region, found at 18 m depth on mud mixed with sand and detritus. Eight specimens studied, 3 of them mature.

REMARKS

Baikalodrilus scaphoideus is most similar to *B. paradoxus*. They both have an almost identical setal apparatus (but with somewhat longer teeth in the crotchets of *B. scaphoideus*), and miss any projecting papillae on their armour. *B. scaphoideus* differs from *B. paradoxus* in being only half the size of the former, in having a thin translucent armour, small non-protruding setal tubercles, a longer vas deferens, a straight thin-walled atrium, a boat-shaped crystal, and a more proximal opening of the prostate gland.

Baikalodrilus undatus SNIMSCHIKOVA, 1989
(Fig. 4)

Baikalodrilus undatus SNIMSCHIKOVA, 1989b : 25-26, fig. 2.

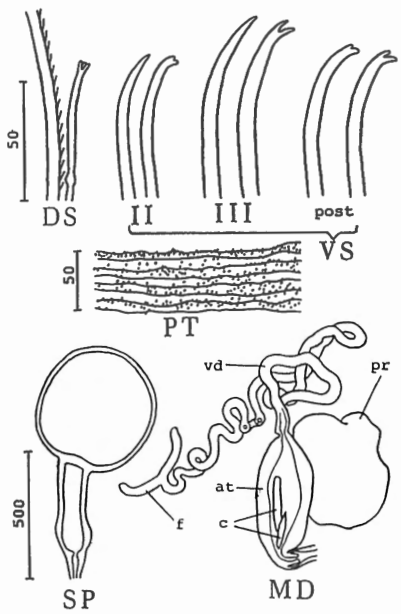

Fig. 4. – Baikalodrilus undatus.

DESCRIPTION

Only a single fragment studied, 6.5 mm long and up to 2 mm wide, with 25 anterior segments. Prostomium retracted. Anterior 4-5 segments biannulate, with the first ring broader. Colour light brown or yellow. Armour thin and translucent, finely undulate due to numerous transversal folds. No projecting papillae. Setal tubercles small, faintly prominent, almost invisible.

In each dorsal bundle, 2 (rarely 1) hair setae and just as many pectinates. Hair setae finely serrate, 157-300 μm long. Pectinate setae 60-140 μm long, with short outer teeth and a single stout intermediate one. Ventral crotchets simple or bifid, slightly curved, with ental nodulus. In anteclitellar bundles one simple (more ventrally placed) and one bifid crotchet, both 130-175 μm long. Bifid crotchets of II with rudimentary teeth, those of the following segments with normal teeth, equal or proximal tooth being longer. In postclitellar ventral bundles single bifid crotchets, 60-140 μm long, more curved, with rudimentary teeth.
Circular clitellum in X-XII. Male funnel medium-sized. Vas deferens more than 2000 μm long, about 30 μm wide all through its length, coiled. Atrium resembling a short thick-walled cylinder tapering at both ends, 400 μm long and 190 μm wide.
Medium-sized prostate gland almost as long as atrium, compact, roundish, discharging into atriums proximal half. Two crystals occurring in the voluminous atrial lumen, the bigger one (210 μm long) pointed at its distal end, the smaller (130 μm) and more ectal one pointed at both ends. Spermathecal ampulla almost spherical, 374 μm long and 340 μm wide; duct well-defined, 400 μm long, with a small sphincter near its distal end.

DISTRIBUTION AND HABITAT

Only one single mature specimen found in Middle Baikal, Selenga Delta Region near Possolsk, on muddy sand at 8 m depth.

REMARKS

Externally, *B. undatus* is rather similar to *B. scaphoideus* in the lack of papillae, as well as in the shape and number of ventral setae. Both species differ in the structure of hair setae (serrate in *B. undatus*, but plumose in *B. scaphoideus*), also to some extent by the smaller number of setae in dorsal bundles of *B. undatus*. More significant differences are found in their reproductive organs. *B. undatus* has a shorter and coiled vas deferens; shorter and wider thick-walled atrium; smaller penial sac; two atrial crystals of a different shape, instead of a single crystal in *B. scaphoideus*; and smaller spermatheca of another form of the ampulla. *B. undatus* is also somewhat larger than *B. scaphoideus*.

Compared to *B. paradoxus*, *B. undatus* has very small and inconspicuous setal tubercles; fewer dorsal setae; serrate instead of plumose hair setae; smaller ventral crotchets; a straight, short atrium and two atrial crystals of a different shape.

Baikalodrilus bifidus Snimschikova, 1989
(Fig. 5)

Baikalodrilus bifidus Snimschikova, 1989b : 26-28, fig. 3.

DESCRIPTION

Length 8-8.5 mm, maximum diameter approximately 1 mm; 50-60 segments. Prostomium retracted. Thick cuticule plicated in front of clitellum, with 7-9 folds per segment. Roundish or ellipsoid, flat papillae (7-9 μm high) arranged in transverse rows on the ridges of folds, forming dark brown stripes on a light background. In furrows between these folds many annular pores (of sensory organs ?) are visible. Folds behind clitellum weaker or even absent, papillae increasing in size (up to 17 μm high), placed sparsely and irregulary in stretched and swollen segments XIV-XX, more densely on the posterior, shorter segments. Setal tubercles small, low, hardly distinguishable between papillae.

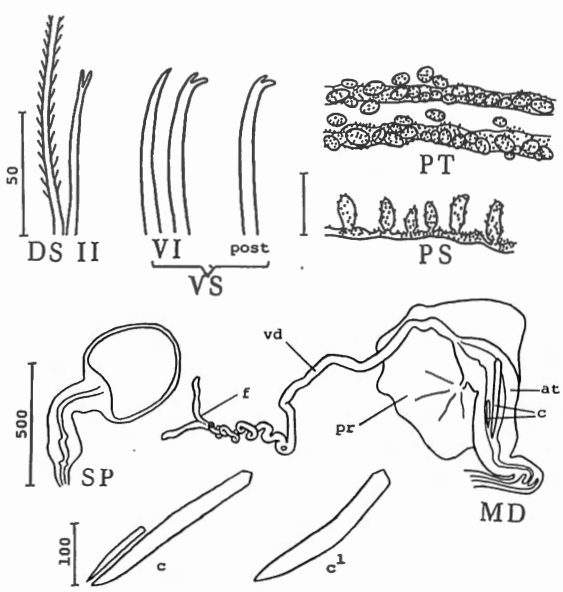

Fig. 5. – Baikalodrilus bifidus.

Anteclitellar dorsal bundles with 2-3 plumose hair setae (250-300 μm long) and 4 bifid setae (70-90 μm) with long equal teeth diverging at an acute angle. Only one hair seta observed in dorsal bundles behind clitellum. Simple and bifid crotchets side by side in ventral bundles, very slightly curved, with ental nodulus. In bifid crotchets proximal tooth longer than distal one. In II, 4 crotchets per bundle, simple and bifid ones alternately;

in II-V 3 crotchets (2 simple and 1 bifid), in VI-X 2 (1+1); most ventral crotchet in bundle always simple. Postclitellar ventral bundles containing a single bifid crotchet with longer and thicker proximal tooth. Crotchets 140-165 μm long before clitellum, 122-125 μm after clitellum.

Light, circular clitellum occupying X-XII. Spermathecal and male pores on the ventral setal line. Male funnel small. Vas deferens more than 1300 μm long, in proximal part narrow (27 μm) and coiled, in middle and distal parts wider (34 μm) and straighter. Atrium cylindrical, 476 μm long and 136 μm wide, its proximal part slightly wider and curved, tapering towards mouth of vas deferens; distal end curved at a right angle, somewhat narrowing. Prostate gland large, lobate, opening into atriums proximal half. Lumen of one atrium with two parallel crystals, 292 and 115 μm long respectively, with sharp ends. Partner atrium of the same worm containing a single crystal. Atrium terminating with short penis in penial sac, the latter being 340 μm long. Spermathecal ampulla oval, 340-370 μm long and 260-290 μm wide; duct well-distinguished, 340 μm long and 95 μm wide near the ampulla, with a small sphincter near the distal end. Spermatozeugmata not observed.

DISTRIBUTION AND HABITAT

Found in Middle Baikal only, Selenga Delta, Srednyaya Arm, on muddy sand at 18 m depth. Forty-eight specimens studied, 20 of them being mature.

REMARKS

B. bifidus resembles *B. paradoxus, B. scaphoideus,* and *B. undatus* in its setal and genital apparatus. However, some significant differences enable one to regard it as a separate species. *B. bifidus* has prominent papillae lacking in the other three species. It has more crotchets in the ventral bundles, while the dorsal bundles contain bifid setae of a characteristic shape, not pectinates. The wider proximal half of the atrium is typical of *B. bifidus,* as well as the asymmetry in a number of crystals (1 and 2). *B. bifidus* is also considerably smaller than the three other species. It was found together with *B. paradoxus* in one sample.

Baikalodrilus medianus SNIMSCHIKOVA, 1991 (Fig. 6)

Baikalodrilus medianus SNIMSCHIKOVA, 1991a : 136-137, fig. Ž-N.

DESCRIPTION

Length of the single specimen 14 mm, diameter 1.3 mm, 50 segments. Prostomium retracted. Armour with up to

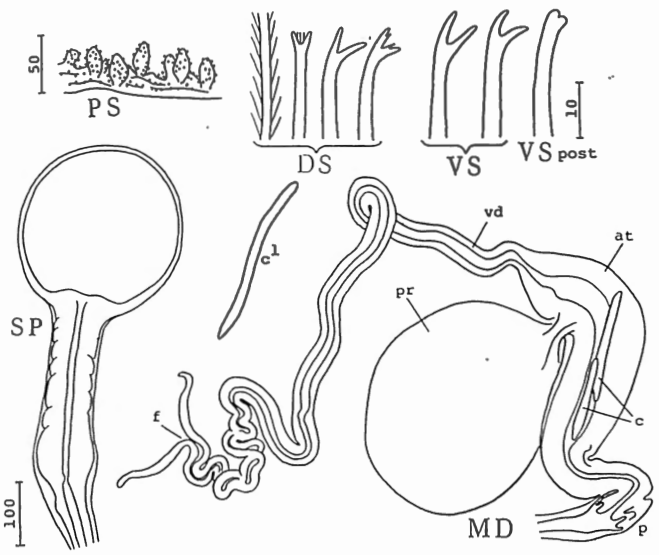

Fig. 6. – Baikalodrilus medianus.

12 folds per segment. Roundish or ovoid papillae, 20 μm high, in transverse rows on the ridges of folds in anterior segments, sparse in the postclitellar ones. Setal tubercles small, hardly visible.

Hair, bifid, and pectinate setae in dorsal bundles. Pectinates either straight with short lateral and three small intermediate teeth, or distally curved with long lateral teeth and a single intermediate one. Bifid and pectinate setae 60-78 μm long in the anteclitellar dorsal bundles. Hair setae 210 μm long, plumose. Dorsal bundles of II consisting of 3 hair setae and 2 bifid setae, in III 3-4 hair setae and 3 bifid ones, in IV alternately 2-3 hair, 2 bifid and 2 pectinate setae, in V-VIII 1-2 hair setae and 2 pectinates. One hair seta and one very small (48 μm long) pectinate seta in postclitellar dorsal bundles. Simple and bifid crotchets in anteclitellar ventral bundles, 96-100 μm long, with ental nodulus. In II two simple crotchets and one, laterally placed, bifid crotchet with short teeth, the distal tooth twice as long as the proximal one. Other anteclitellar segments with one simple and one bifid crotchet (with equal teeth) per bundle. In postclitellar ventral bundles 1-2 setae, 148-150 μm long, either simple and blunt or bifid with short teeth. Light circular clitellum occupying X-XII. Male funnel large, not deep. Vas deferens 1360 μm long, in proximal part 20 μm in diameter and very coiled, in middle and distal parts widening up to 34 μm and straightening out. Atrium cylindrical, tapering more at proximal than at distal end, curved in a right angle in proximal part of the prostate gland and again (in the opposite direction) on its distal end. Short penis in a rather long penial sac. In atrial lumen either one long or two unequal crystals with sharp ends. Prostate gland large, rounded, as long as atrium, discharging in proximal part of the latter with a distinct broad stem. Atrium 370-380 μm long and 108-115 μm wide, penial sac 204 μm long and 54 μm wide, crystals 115-238 μm long. Spermathecal ampulla

spherical, 204 μm in diameter; well-defined duct 340 μm long and 68 μm wide; spermatozeugmata not observed.

DISTRIBUTION AND HABITAT

One single mature specimen, found in Middle Baikal, Selenga Delta Region, on muddy sand at 18 m depth.

REMARKS

B. medianus resembles *B. bifidus* in the structure of the armour, spermatheca and male duct. However, it is almost twice as large, its armour is more finely folded, the papillae are higher, the spermatheca and atrium are smaller than those in *B. bifidus*. Two types of pectinate setae are present in *B. medianus* but none in *B. bifidus*. The anteclitellar ventral bifids have long equal teeth in *B. medianus*, while in *B. bifidus* they are furnished with longer and thicker proximal tooth. The postclitellar crotchets are simple and blunt, or with rudimentary teeth in *B. medianus*; but with bigger proximal tooth in *B. bifidus*. Finally, the atrial crystals are also of a different shape.

Baikalodrilus crassus Snimschikova, 1989 (Fig. 7)

Baikalodrilus crassus Snimschikova, 1989b : 28-29, fig. 4.

DESCRIPTION

Length 32-35 mm, diameter 3.5-3.8 mm, 70-72 segments. Body comparatively short and stout, covered with finely folded papillate armour. Papillae lying on folds in regular transverse rows, 9-12 rows in every anteclitellar segment. In anterior segments papillae rather sparse and small, 17-28 μm high, rounded or ellipsoid. On clitellum, papillae light-coloured, very sparse and irregular, only 10 μm high. Behind the clitellum papillae longer (up to 35 μm high) and narrower, placed in dense rows on the ridges of armour, causing the more vivid colour of the hind part. Sensory papillae translucent, uncovered, twice as high as secretory ones. Setal tubercles small, looking like short gaps between secretory papillae.

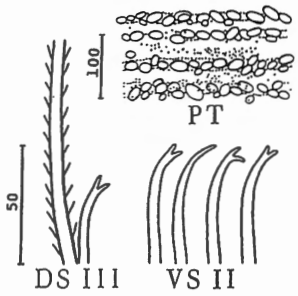

Fig. 7. – Baikalodrilus crassus.

Dorsal bundles containing both plumose hair setae (220-240 μm long) and pectinates (70 μm long), with a hardly distinguishable (even under immersion) delicate membrane between the teeth. 4-5 hairs and 4 pectinates per bundle in II-IV, 2-3 hairs and 3 pectinates in V-XII; 1 hair and 1 pectinate seta in postclitellar bundles. Ventral crotchets simple and bifid, slightly curved, with median nodulus. Their length decreasing from 140-170 μm in anteclitellar bundles to 80-90 μm in middle segments and 35-40 μm on tail. Length of teeth varying to a high degree in bifid crotchets, proximal tooth either equal or longer. In II 6-7 crotchets per bundle, simple crotchets alternating with bifids, or bifids with longer and shorter teeth in every bundle. Beginning from III, 3-5 crotchets per bundle, behind clitellum only a single crotchet with rudimentary distal tooth per bundle.
Light circular clitellum occupying 1/2X-XII. Internal reproductive organs totally resorbed in specimens studied.

DISTRIBUTION AND HABITAT

Middle Baikal, near Cape Tolsty on the east shore, on muddy sand at 13 m depth. North Baikal, underwater canyon near Cape Kurly, sand and clay at 50 m depth. Four specimens studied.

REMARKS

B. crassus is characterized by its very stout, swollen body. It is 1.5 times longer and about 2 times wider than *B. paradoxus*. It also differs from *B. paradoxus* by its finely folded armour with higher papillae, small oblong setal tubercles, and a larger number of setae. *B. crassus* is remarkable in having the most numerous setae in the whole genus (up to 7 in ventral bundles).
Common features in both *B. crassus* and *B. bifidus* are found in the structure of the armour and, to a lesser extent, in the setal tubercles. The size and number of setae are different in both species.
B. crassus is probably closest to the problematic species *Tubifex inflatus* Michaelsen, 1901 in having a similarly inflated, swollen body. However, the original description of *T. inflatus* reveals a longer and two times narrower body than in *B. crassus*, only bifid crotchets in ventral bundles, and a smaller number of setae of all types.

Baikalodrilus discolor discolor (Snimschikova, 1984) (Fig. 8)

Peloscolex discolor Snimschikova, 1984 : 3-6, fig. 1 ; 1987 : 51-54, fig. 15.

DESCRIPTION

Length 28-30 mm, maximal diameter 2.5-3 mm; 60-62

segments. Prostomium usually oblong. Intricately coloured when mature. Anteclitellar segments dark brown, intensity of colour gradually increasing backwards from the anterior end. Dense, dark, pea-shaped papillae, not fused; more sparse in II-III and on the ventral side of the following segments, and absent around clear, elongate, transversally oriented setal tubercles. Clitellum beige, papillate; papillae fused in a thick armour on its dorsal side, diminishing on the ventral side and absent around the male pores. The first postclitellar segments (XIII-XVII), especially their dorsal sides, are bright orange due to large rounded quadrangular lumps of some secretion densely covering the papillae. Due to this secretion layer, postclitellar segments considerably broader than clitellum. Caudal region with alternating beige, brown and orange rings. Immature specimens uniformly brown, only slightly darker on their dorsal side, with finer papillae ventrally and on the anterior end.

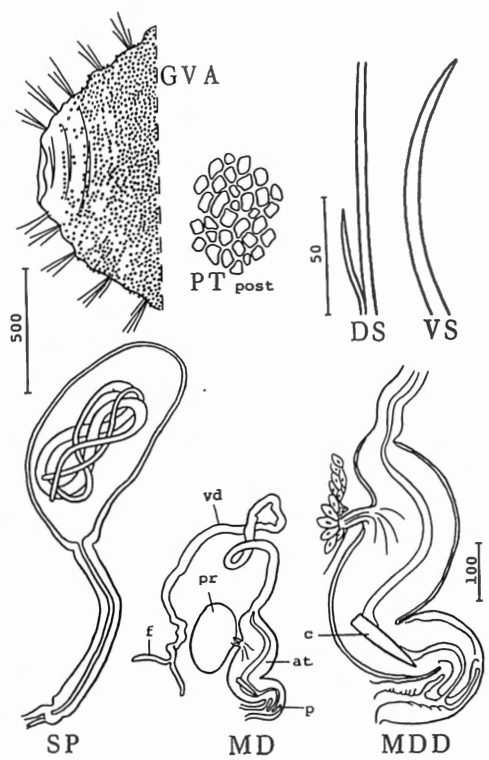

Fig. 8. – Baikalodrilus discolor discolor.

Dorsal bundles consisting most often of 3 hair setae (sometimes 2 in II-III, and up to 5 in VI-VII) and 2 needle setae (sometimes only 1 in II). Hair setae smooth, 380 μm long in II and up to 400 μm in the following segments. Needle setae very fine, only 35 μm long in II and up to 50 μm rearwards. Postclitellar segments bearing 2 hair setae in every dorsal bundle, up to 350 μm long, and 2 needles,up to 40 μm long. Three ventral crotchets in II (sometimes also in III) and 2 in III-X, simple sabre-shaped, with ental nodulus, 120 μm long. Ventral bundles of postclitellar segments consisting of a single thicker crotchet, up to 200 μm long.

Circular clitellum from the posterior half of X to XII. Spermathecal and male pores on one line with ventral setae. Vas deferens about 2500 μm long, forming a number of loops in XI, gradually widening from 36 μm to 50 μm. Bulky prostate gland laterally discharging into expanded proximal half of atrium. Tapering distal part of atrium forming two very sharp curves and terminating in a soft penis in a well-developed penial sac. Ectal part of atrial lumen with a distally pointed crystal, 176 μm long and 35 μm thick. Atrium 710 μm long, 156 wide near the prostate and 140 μm around the crystal. Penial sac 200 μm long and 58 μm wide. Spermatheca very large, its egg-shaped ampulla being 1200 μm long and up to 660 μm wide, the duct 1400 μm long. Spermatozeugmata, two per ampulla, very long and thin, twisted threefold in an 8-shape.

DISTRIBUTION AND HABITAT

North Baikal, Sosnovskaya Bank, on dark brown mud at 5-360 m depth. Twenty specimens studied, 6 of them being mature.

REMARKS

The bright three-coloured appearance of mature worms is very characteristic of this subspecies. *B. d. discolor* is rather similar to *B. paradoxus* in several features of its reproductive system : distinct long spermathecal duct, gradually widening vas deferens, and the structure of the atrium with a crystal in its distal part. They differ in their dimensions, structure of armour, lack of bifid crotchets and pectinates in *B. d. discolor,* discharge of the prostate gland, and in the shape of spermathecal ampulla and crystal.

Baikalodrilus discolor acinacifer SNIMSCHIKOVA, 1989 (Fig. 9)

Baikalodrilus discolor acinacifer SNIMSCHIKOVA, 1989b : 30-32, fig. 5.

DESCRIPTION

Length more than 20 mm, maximum diameter 2 mm; more than 80 segments (all mature specimens studied were broken). Prostomium retracted. II-V double-ringed. Colour dark brown. Dense ovoid papillae, 28-42 μm high, forming a non-transparent, finely furrowed armour on the anteclitellar segments, on which small non-protruding setal tubercles, looking like short transversal light strips, are present. Behind clitellum, papillae fusing into a continuous dark layer, setal tubercles not visible.

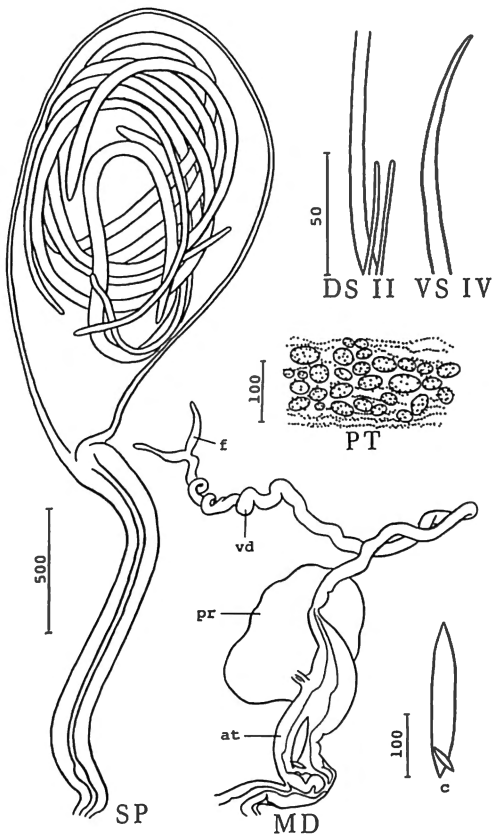

Fig. 9. – Baikalodrilus discolor acinacifer.

Dorsal bundles consisting of 2-3 smooth hair setae, 380-420 μm long, and 2 obtuse needles, 70-80 μm long. Ventral setae simple, sabre-shaped crotchets, 100-120 μm long, with ental nodulus. Before clitellum 2-3 per bundle, behind it only 1 seta present.

Brightly coloured clitellum with a thickened cuticle embracing X-XI . Male funnels medium-sized, deep. Vas deferens 34 μm broad and coiled proximally, up to 54 μm broad and more straight in middle and distal parts. Atrium cylindrical, S-shaped, considerably tapering towards its proximal end, a little broader from its middle to distal end, terminating with a short penis in penial sac, the latter being curved in the opposite direction to the atrium. Two boat-shaped crystals of different size (200 and 50 μm long) in every atrium; smaller crystal lying near the distal end of the larger one at some angle to it. Atrium 680-715 μm long and up to 180-184 μm wide, penial sac 280-300 μm long. Prostate gland shorter than atrium, lobate, discharging with a rather long stem into the proximal half of the atrium near its middle. Spermatheca with a very large, 1620-1710 μm long and up to 950-1040 μm wide bag-like ampulla and a 1225-1240 μm long ectal duct. Several long, thin, spirally twisted spermatozeugmata in every ampulla.

DISTRIBUTION AND HABITAT

Middle Baikal, Selenga Delta Region at Cape Krestovy, on mud at a depth of 300 m. Forty-one specimens studied, among them 7 mature ones.

REMARKS

This subspecies considerably resembles *B. d. discolor* in the structure of its armour, setae and reproductive system. The main differences are its less vivid colour, twice as large needle setae with obtuse tips, a less curved atrium with two crystals instead of one, somewhat bigger spermathecal ampulla of a different shape, and shorter spermathecal duct. These differences are large enough to distinguish this taxon from the nominative subspecies. Both subspecies also inhabit different regions of Lake Baikal.

Baikalodrilus discolor brevipectinatus
SNIMSCHIKOVA, 1989
(Fig. 10)

Baikalodrilus discolor brevipectinatus SNIMSCHIKOVA, 1989b : 32-33, fig. 6.

DESCRIPTION

Length of the single specimen studied 24 mm, diameter 3 mm; 68 segments. Prostomium retracted. II-IV biannulate. Colour dark brown. Armour finely folded, with 3-5 folds on every anteclitellar segment and with 16-18 on postclitellar ones. Papillae ovoid, irregularly and not densely distributed. Setal tubercles low, appearing as narrow transverse slits in the dark armour.

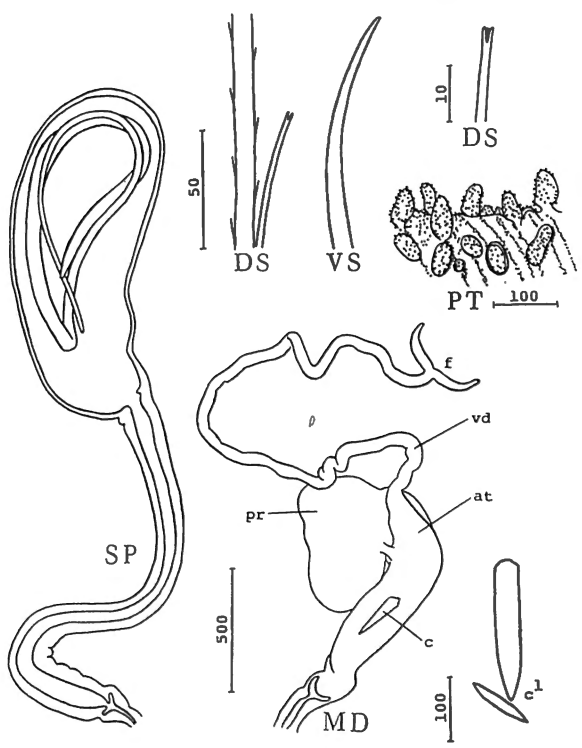

Fig. 10. – Baikalodrilus discolor brevipectinatus.

Two to five distally plumose, 500-560 μm long hair setae and 3-6 pectinate setae in anteclitellar bundles. The latter measuring 70-100 μm and with short, as if broken, external teeth; several very fine intermediate teeth hardly visible, even with oil immersion. Ventral crotchets simple, sabre-shaped, with ental nodulus, 200-270 μm long; 2 (seldom 3) in anteclitellar bundles, simple crotchets posterior of clitellum.
Short, circular clitellum occupying 1/2X-XI, rising over the body surface due to rich secretion of glands. Spermathecal and male pores on line of ventral setae. Male funnel small. Long (2700-2800 μm) vas deferens coiled near the funnel, then straightened, starting from its middle part. Atrium cylindrical, its proximal part tapering and curved at a right angle, distal part only slightly curved, terminating with a short penis in a long penial sac. One of the studied atria contained a single large cuneiform crystal, the other atrium with an additional small boat-shaped crystal, lying at an angle near the distal point of the large crystal. Large crystals measuring 170 and 175 μm, smaller ones 80 μm. Atrium itself 680-740 μm long and 150 μm wide, penial sac being 340 μm long. A large, lobate prostate gland discharging into the proximal half of atrium. Spermatheca with bean- or bag-shaped ampulla (1230 or 1250 μm long, 513 or 627 μm broad) and a well-distinguished ectal duct, 1700 μm long. One long and thin coiled spermatozeugma in every ampulla.

DISTRIBUTION AND HABITAT

Only one single mature specimen, found in Middle Baikal, Selenga Delta Region near the Kharauz Creek, on mud at a depth of 43 m.

REMARKS

B. discolor brevipectinatus differs somewhat more from the nominative subspecies than from *B. d. acinacifer*, in having numerous plumose hair setae and pectinates in dorsal bundles; atria are only curved strongly in their proximal part and contain a variable number of crystals. The shape of the spermathecal ampullae is the same as in the nominative subspecies, but the duct is longer. The apparently sympatric distribution of *B. d. acinacifer* and *B. d. brevipectinatus* could cast some doubt as to their subspecific status.

Baikalodrilus solitarius (SNIMSCHIKOVA, 1982)
(Fig. 11)

Peloscolex solitarius SNIMSCHIKOVA, 1982 : 96-98, fig. 7; 1987 : 50-51, fig. 14.

DESCRIPTION

The only fragment studied consisted of 14 anterior segments, 11.5 mm long, and 3.6 mm wide. Prostomium broad and blunt. Body surface scattered with small, light brown elliptic papillae.
Dorsal bundles with 2 plumose hair setae and 3 very fine needle setae. The former measuring 435 μm in II, longer in the following segments, up to 800 μm in VII; needles about 80 μm long. In ventral bundles 2 sabre-shaped simple crotchets, 230 μm long, with ental nodulus.
Clitellum embracing X-XI as a distinct bright ring. Vas deferens long and coiled, widening in its second half. Atrium cylindrical, 580 μm long and 206 μm wide, curved at a right angle in its distal part, terminating with a soft penis in a penial sac. Along the curve, a group of small crystals adhered to the external surface of atrium, these have probably the same origin as the crystals within the atria of other *Baikalodrilus* species. Bulky prostate gland discharging into proximal half of atrium. Spermatheca exceptionally large, with a bag-like ampulla (1230 μm long, up to 554 μm wide) and long (856 μm) efferent duct. Long thin spermatozeugmata in the ampulla.

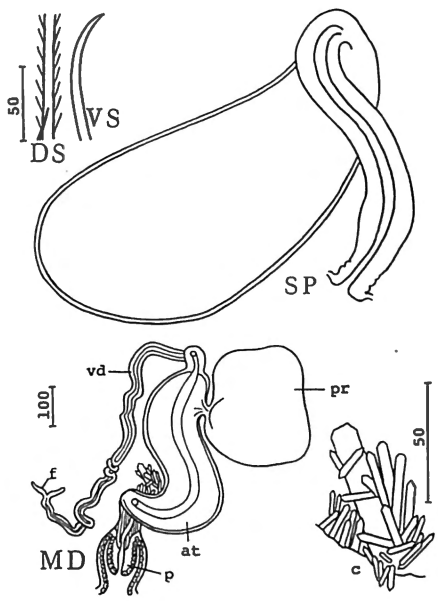

Fig. 11. – Baikalodrilus solitarius.

DISTRIBUTION AND HABITAT

Only one single mature specimen, found in North Baikal near the mouth of Kichera River, on muddy sand at a depth of 10 m.

REMARKS

B. solitarius is most similar to *B. d. discolor* in its setal and genital apparatus. It differs from the latter by having plumose hair setae, a differently shaped spermathecal

ampulla and distal part of the atrium. It also differs from all other known species of *Baikalodrilus* by having crystals outside the atrium, however, these could easily be an artefact or individual aberration.

Baikalodrilus multicrystallifer SNIMSCHIKOVA, 1989 (Fig. 12)

Baikalodrilus multicrystallifer SNIMSCHIKOVA, 1989a : 300-302, fig. A-I.

DESCRIPTION

Length 14-18 mm, maximal diameter 1.2-1.4 mm; 47-62 segments. Body slender; the anterior part gradually widening from head to clitellum, without any swollen segments. Colour light brown, body wall translucent. Papillae ellipsoid or rounded, in I-III smaller (up to 20 μm high) and sparse, posteriorly higher (35 μm) and denser, arranged in 8-10 transverse rows per segment; largest and densest papillae occurring on the tail part. Setal tubercles not prominent (up to 50 μm), resembling small bright vesicles. Clitellum colour dark grey, caused by a dense, finely granulated layer of secretion, without papillae, not elevated above the neighbouring segments.

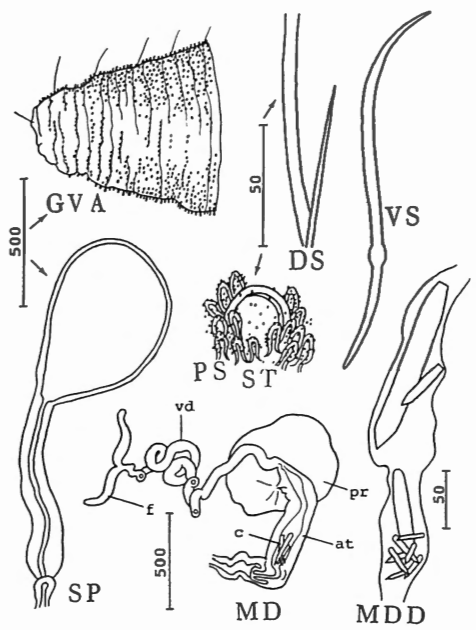

Fig. 12. – Baikalodrilus multicrystallifer.

Anteclitellar dorsal bundles consisting of 2-4 hair setae, 480-680 μm long, slightly plumose in their distal part, and 2 straight needle setae, 87-110 μm long. Postclitellar dorsal bundles with one hair seta, 110-240 μm long, and a needle seta, 100 μm long. Ventral crotchets simple, sabre-shaped, with ental nodulus, 160 μm long in II and up to 260 μm starting from V. These usually occur per 2 in bundles in anteclitellar segments, but sometimes up to 4 in III-V; behind clitellum ventral setae single, up to 220 μm long.

Circular clitellum occupying 1/2X-XII. Spermathecal and male pores on one line with ventral setae. Male funnel large. Vas deferens more than 1500 μm long, narrower (24 μm) and coiled in its proximal part, gradually widening up to 45 μm in the distal part. Prostate gland bulky and compact, covering the atriums' proximal end like a cap, discharging into its proximal half. Atrium itself cylindrical, proximally tapering more than distally, its proximal part slightly curved. Atrium terminating with a short penis; penial sac at a right angle to atrium. Distal half of atrial lumen containing a group (8-10 or even more) of longitudinal crystals of different size, the largest one being 150 μm long, the others 17-35 μm. Atrium 350-476 μm long and 136-150 μm wide in different specimens; penial sac 150-170 μm long. Spermathecal ampulla bladder-like, up to 580 μm long and 450 μm wide; spermathecal duct 700 μm long, diameter 80 μm near ampulla and 140 μm near the orifice. Spermatozeugmata in groups of 2 in every ampulla, long and thin, spirally coiled.

DISTRIBUTION AND HABITAT

Middle Baikal, Selenga Delta Region near the mouth of Severnaya Creek and Possolskaya Bank, on mud at depths of 50-65 m. North Baikal, near Cape Ireksokon, coarse sand at a depth of 60-70 m. Six specimens studied, among them 5 mature ones.

REMARKS

This species resembles *B. d. discolor* and *B. solitarius* in its setal apparatus and male duct. It differs from *B. d. discolor* in being half the size, by having plumose hair setae, a different colour, differently shaped spermatheca and atrium, and the presence of several crystals in the atrium instead of a single one. It differs from *B. solitarius* in size, differently shaped spermatheca and atrium, the atrium is not sigmoid and without a narrower efferent part, and the location of a group of crystals inside the atrial lumen (outside in *B. solitarius*).

Baikalodrilus malevici (CHEKANOVSKAYA, 1975) (Fig. 13)

Peloscolex malevici CHEKANOVSKAYA, 1975 : 128-129, fig. 7; BRINKHURST, 1984 : 499; SNIMSCHIKOVA, 1982 : 92-93, fig. 4; 1987 : 43-45, fig. 9.

DESCRIPTION

Length 12-25 mm, maximal diameter 1.6-1.8 mm; 41-57 segments. Prostomium retracted. Anterior part of body swollen. Colour light brown. Armour thin, with

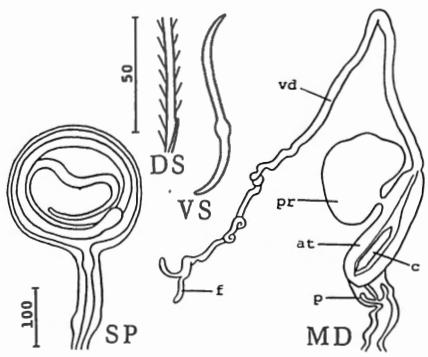

Fig. 13. – Baikalodrilus malevici.

small round secretory papillae. Sensory papillae bigger than secretory ones, oval translucent.
Anteclitellar dorsal bundles with 5-6 plumose hair setae, 230 μm long, and 3-4 fine, slightly curved simple needles, 65 μm long. Ventral setae as simple S-shaped crotchets with ental nodulus, 2 per bundle up to V and 1 posteriorly. Length about 100 μm anteriorly of the clitellum and up to 150 μm behind clitellum.
Bright circular clitellum occupying X-XI. Vas deferens proximally with many coils, thin and ciliated; halfway the walls start to become thicker and more muscular. Atrium cylindrical, 260 μm long and 92 μm wide, terminates with a soft penis. Distal part of atrial lumen with a cylindrical crystal, 127 μm long. Large prostate gland discharging into the proximal half of atrium. Spermatheca consisting of sphaerical ampulla, 174 μm in diameter, and ectal duct, 260 μm long and 58 μm wide. Long thin spermatozeugmata in the ampulla.

DISTRIBUTION AND HABITAT

All regions of Lake Baikal, at all depths. Prefers mud with detritus, more seldom occcurring on stones, muddy sand with detritus, etc. Abundance, usually 20-80 individuals per square metre , sometimes up to 680 per square metre. A large number of specimens studied.

REMARKS

B. malevici resembles *B. d. discolor, B. solitarius* and *B. multicrystallifer* in its setal apparatus, all species having simple ventral crotchets with ental nodulus. It differs from them in its smaller dimensions, larger number of setae, shape of spermathecal ampulla, which is spherical in *B. malevici* but oblong or sacculate in the related species, and in the crystal, which is single and rectangular in *B. malevici,* distally pointed in *B. d. discolor,* and numerous in *B. solitarius* and *B. multicrystallifer.*

Baikalodrilus falcatus (SNIMSCHIKOVA, 1982) (Fig. 14)

Peloscolex falcatus SNIMSCHIKOVA, 1982 : 98-99, fig. 8; 1987 : 47-48, fig. 12.

DESCRIPTION

Length of the immature specimens studied 7.5 mm, maximal diameter (in III) 0.4 mm; 28 segments. Length of prostomium equal to its basal width. I-III can be retracted. Armour strewn with secretory papillae, up to 17.5 μm high. Two smooth hair setae, 320 μm long, in dorsal bundles, together with 2 bifid needle setae, 145 μm long, with very short teeth distinguishable only under immersion. Ventral bundles with single large, simple crotchets, 300 μm long, sickle-shaped, with ental nodulus.
Reproductive system not observed.

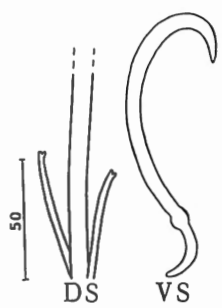

Fig. 14. – Baikalodrilus falcatus.

DISTRIBUTION AND HABITAT

Found in North Baikal near Yarki Island, on sandy mud at a depth of 18 m, two immature specimens studied.

REMARKS

In spite of our lack of knowledge of the reproductive system, *B. falcatus* differs from all other known armoured tubificids by its ventral setae. The structure of the armour is somewhat similar to *B. bifidus,* while the dorsal setae resemble those of *B. scaphoideus.*

Baikalodrilus bekmanae (SNIMSCHIKOVA, 1984) (Fig. 15)

Peloscolex bekmani SNIMSCHIKOVA, 1984 : 6-9, fig. 2; 1987 : 48-50, fig. 13.

DESCRIPTION

Length 8-10 mm, maximal diameter 1.2 mm; 58-62 segments. Anterior body region usually swollen. Colour from light to dark brown. Cuticle thin and translucid,

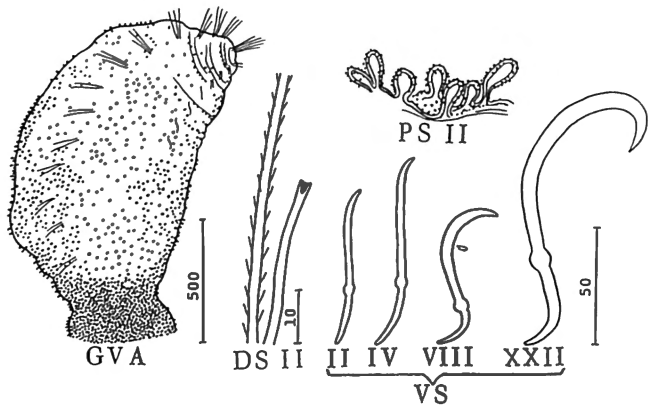

Fig. 15. – Baikalodrilus bekmanae.

with 8-10 fine furrows per segment, ridges bearing papillae. The latter larger and more dense in postclitellar segments than in anterior and tail regions, as a result of which the latter segments appear brighter.

Dorsal bundles in II-IV consisting of 4-5 plumose hair setae, up to 200 μm long, and 4-5 pectinates, up to 70 μm, in V-VI number of setae diminishing to 3 hairs and 3 pectinates per bundle, from VII onwards only 2 hairs and 2 pectinates. Hair setae up to 300 μm long in V-VIII, and up to 170 μm in postclitellar segments; pectinates respectively 100 and 30 μm long. Pectinates having equally large lateral teeth and very small intermediate teeth, the latter hardly visible even in immersion. Ventral bundles of II-IV (or V) containing 2 crotchets, those of II sometimes 3; starting from V or VI only 1 seta per bundle; from IX onwards ventral setae entirely lacking in 10-15 segments, appearing again in XX-XXV. All ventral setae simple, with ental nodulus. Those of anterior bundles thin, not much curved, 100-110 μm long. They gradually become thicker and more curved from V onwards, and large (160 μm long), sickle-shaped after the gap, from XX-XXV onwards.

No mature worms were found. Only in one dissected specimen a spermatheca occurred, all the other genital organs were reduced. Egg-shaped ampulla 280 μm long and 140 μm wide, well-defined duct only 50 μm long. Two long and thin spermatozeugmata in the ampulla, coiled in an 8-shape.

DISTRIBUTION AND HABITAT

North Baikal, near Yarki Island and Cape Ireksokon, on more or less muddy sand and gravel at depths of 10-20 m. Thirty-two specimens studied.

REMARKS

The lack of ventral setae in more than ten middle body segments is characteristic of *B. bekmanae*. The shape and number of the anterior ventral setae is rather similar in both *B. bekmanae* and *B. malevici*. Posteriorly enlarged sickle-shaped crotchets are identical in *B. bekmanae* and *B. falcatus*, the latter species having them in all ventral bundles. All three species differ from each other in the shape of their dorsal setae, which are simple needles in *B. malevici*, bifids with short teeth in *B. falcatus*, and fine pectinates in *B. bekmanae*.

Baikalodrilus exilis (Snimschikova, 1982)
(Fig. 16)

Peloscolex exilis Snimschikova, 1982 : 93-95, fig. 5; 1987 : 45-46, fig. 10.

DESCRIPTION

Very small worms, 2.1-2.3 mm long, and 0.2 mm wide in clitellar region; with 17-20 segments. Anterior region slightly swollen, prostomium retracted. Colour dark brown, due to scattered sticky secretory papillae with adhering sediment particles.

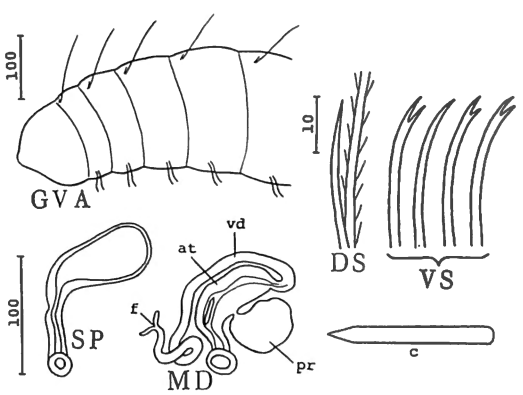

Fig. 16. – Baikalodrilus exilis.

Dorsal bundles of II consisting of a single, fine needle seta, 25 μm long. Following bundles with a plumose hair seta, 174 μm long, and a needle seta, length of the latter up to 75 μm in VIII. In anteclitellar ventral bundles 2 sabre-shaped crotchets with ental nodulus : one simple, the other, laterally situated, bifid with distal tooth longer. Length of crotchets from 62 μm in II-V up to 120 μm in XVIII.

Clitellum indistinct. Vas deferens 320 μm long, its proximal part narrower than distal part. Atrium cylindrical, slightly curved, 86 μm long and 34 μm wide, with a crystal in its lumen. Distinct bulky prostate gland discharging in the middle of atrium. Penial sac 30 μm long. Spermathecal ampulla bag-like, 100 μm long and 43 μm wide, gradually merging into a 57 μm long duct. Long thin spermatozeugmata present.

DISTRIBUTION AND HABITAT

The whole of Lake Baikal, mostly on detritus-rich mud, less frequent on clean or muddy sand. At depths of 5-500 m, most frequently over 100 m. A large number of specimens studied.

REMARKS

B. exilis is remarkable in its minute size, being about ten times smaller than *B. paradoxus* or *B. malevici*. Other peculiarities include a thin translucid armour with small papillae and a minimal number of setae. *B. exilis* resembles *B. malevici* in the shape of its needle setae. It shares with the *B. paradoxus*-group (especially *B. undatus*) the presence of two types of crotchets and their regular disposition in ventral bundles. However, crotchets are more thin and slender, with long naidid-like teeth in *B. exilis*.

Baikalodrilus intermedius SNIMSCHIKOVA, 1991 (Fig. 17, 20)

Baikalodrilus intermedius SNIMSCHIKOVA, 1991a : 134-136, fig. A-E.

DESCRIPTION

Length 2.5-4 mm, diameter of the clitellum 0.22-0.35 mm, 20-27 segments. Anterior end usually retracted to the middle of II. External segmentation distinct. Colour yellowish brown. Armour thin and translucent, with a layer of small adhering particles on its folds, without any secretory papillae. Sparse, indistinct sensory papillae up to 8 μm high, not covered with armour. Setal tubercles small and weakly developed.

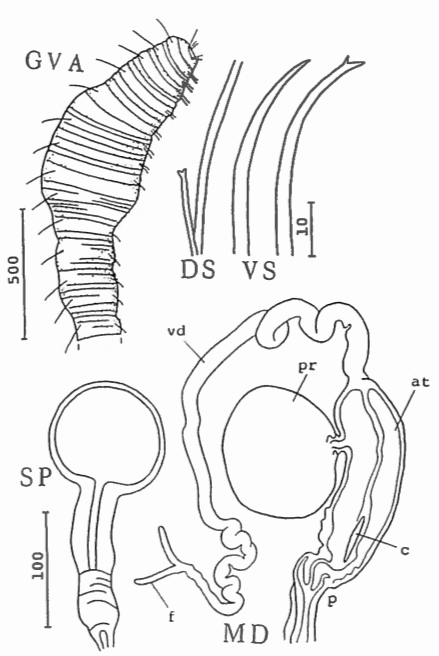

Fig. 17. – Baikalodrilus intermedius.

Dorsal bundles consisting of one hair seta (120-160 μm long, probably plumose, but not distinct under immersion), and one thin bifid seta with short equal teeth (40-50 μm long), hardly visible under the armour, sometimes replaced with a simple needle. Ventral crotchets simple or with rudimentary distal tooth, sabre-shaped, with ental nodulus, 2 per bundle and 70-90 μm long in anteclitellar segments; single and 105-110 μm long posteriorly.
Bright and high circular clitellum occupying X-XII. Vas deferens 450 μm long, 9 μm wide in its proximal part, 16 μm wide in middle and distal parts. Atrium cylindrical, very slightly curved towards prostate gland, tapering at both ends, muscular, with narrow efferent part, normally containing a fine crystal. Short penis in a long penial sac. Atrium 150 μm long and up to 45 μm wide, penial sac about 100 μm long, crystal 50 μm long. Prostate gland roundish, its diameter being about 2/3 the length of atrium; it discharges into the proximal half of atrium with a well-developed stem. Spermatheca with spherical ampulla (56-77 μm in diameter), and distinct thick-walled duct (120 μm long) ending with a weakly developed sphincter. Spermatozeugmata not observed.

DISTRIBUTION AND HABITAT

Found in Middle Baikal, Selenga Delta Region, on mud at a depth of 240 m. Seven specimens studied, 3 of them being mature.

REMARKS

B. intermedius is closest to *B. exilis,* sharing with it the small size and number of segments, structure of armour, shape of dorsal setae, number of setae in ventral and dorsal bundles, and the single crystal in the efferent part of the atrium. However, *B. intermedius* is about one and a half times larger than *B. exilis,* has only simple crotchets in ventral bundles (*B. exilis* having two kinds of crotchets), shorter postclitellar crotchets, spermatheca with spherical ampulla and distinct duct, vas deferens longer, atrium bigger, penial sac longer than in *B. exilis*; prostate gland discharging into proximal half of atrium in *B. intermedius,* but into distal half in *B. exilis*.
Some characters of *B. intermedius* are similar to those in *B. malevici,* such as the shape and number of ventral setae, shape of spermatheca and of male duct. *B. intermedius* differs from *B. malevici* in being almost ten times smaller, in number of dorsal setae, shape of needle setae, and shape and size of the crystal. According to these characters, *B. intermedius* occupies an intermediate position between *B. exilis* and *B. malevici*.

Baikalodrilus cristatus (SNIMSCHIKOVA, 1982)
(Fig. 18)

Peloscolex cristatus SNIMSCHIKOVA, 1982 : 95-96, fig. 6; 1987 : 46-47, fig. 11.

DESCRIPTION

Length 3-3.5 mm, diameter in clitellar region 0.4-0.5 mm; 23-25 segments. Prostomium retracted. Body surface covered with large epidermal secretory papillae, increasing in size from ventral to dorsal side; a row of long, finger-shaped papillae forms a ridge along dorsum. Clitellum lacking papillae and looking like a distinct bright ring.

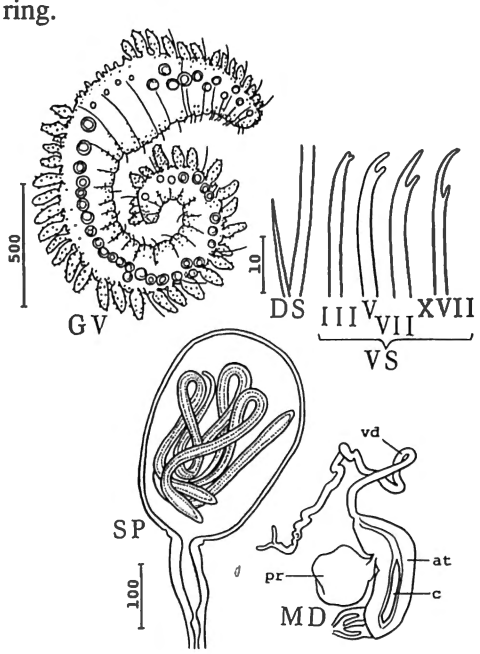

Fig. 18. – Baikalodrilus cristatus.

Dorsal bundles with one smooth hair seta (up to 280 μm long) and one very fine needle seta (up to 31 μm). Anteclitellar ventral bundles containing 2 setae : a simple ventral and a bifid lateral crotchet. Teeth of bifid crotchets subequal in II-IV, in the following segments distal tooth growing considerably longer and thicker than the proximal one . Postclitellar ventral bundles with a single bifid crotchet, with a large distal and rudimentary proximal tooth. Crotchets about 90 μm long in anterior segments, 184-186 μm in XII-XV.
Clitellum in X-XI. Vas deferens narrower in its proximal part, widening gradually in distal direction, 740 μm long. Atrium cylindrical, 320 μm long and 127 μm wide, terminating with a short penis in penial sac. Distinct bulky prostate gland opening almost in the middle of atrium. Large crystal, pointed at both ends, occupying the distal half of atrial lumen; measuring 123 μm long and 11 μm thick. Spermatheca with egg-shaped ampulla (220 μm long, 174 μm wide) and distinct duct (203 μm long). Long thin spermatozeugmata in the ampulla.

DISTRIBUTION AND HABITAT

In the whole North Baikal, at depths between 5 and 500 m. Most abundant (up to 180 individuals per square metre) on muddy sediments at depths greater than 50 m. Occurs also on clean and muddy sand. A large number of specimens studied.

REMARKS

The small size combined with the long finger-like papillae forming a dorsal ridge is typical of *B. cristatus*. It has some similarities with *B. exilis* in setal apparatus and male duct, but differs from it in having smooth hair setae, differently shaped ventral setae, spermatheca and crystal, as well as in general appearance.
The closest relationship seems to be between the species *B. cristatus* and *B. digitatus, B. werestschagini* also being a close relative (see below).

Baikalodrilus digitatus HOLMQUIST, 1979
(Fig. 19, 20)

Baikalodrilus digitatus HOLMQUIST, 1979 : 50-51, fig. 16B-D, 17.

DESCRIPTION

Length 3-3.5 mm, maximal diameter 0.75-0.8 mm; about 20 segments. Prostomium retracted. Colour brown or dark grey, depending on the colour of sediment particles mingled with cutaneous secretion, adhering to armour as a dense layer.

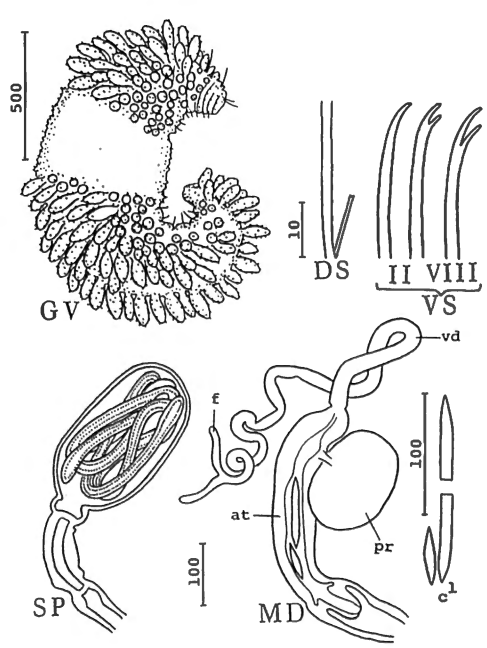

Fig. 19. – Baikalodrilus digitatus.

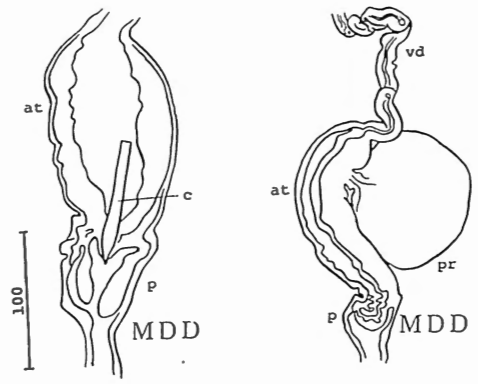

Fig. 20. – *Probable stages of the extrusion of atrial crystals. Left : a crystal entering the penis (in* Baikalodrilus digitatus*); right : an empty atrium (in* B. intermedius*).*

Body densely set with finger-like secretory papillae built up of epidermal tissue, up to 175-210 μm long dorsally, gradually becoming shorter ventrally. Circular bright clitellum without large papillae and adhering particles. Dorsal bundles consisting of one smooth hair seta (60-100 μm long), and a very fine bifid seta (20-24 μm) with almost reduced teeth. In ventral bundles two fine, slender crotchets with ental nodulus, 90-110 μm long : a simple ventral and a bifid lateral one, teeth of the latter caudally becoming gradually longer.

Clitellum on X-1/2XII. Spermathecal and male pores on ventral setal lines. Male funnel large, broad. Vas deferens 420-490 μm long, up to 14 μm wide and curved proximally; widening to 21 μm, becoming straighter in its middle part, and making 2-3 loops. Atrium cylindrical, bow-shaped, tapering proximally; its distal end continuing with an oblong penis in penial sac. Atrium 255-262 μm long and 60-70 μm wide, penial sac 157-175 μm long. Prostate gland compact and rounded, laterally emptying into the proximal part of atrium. Atrial lumen containing 2-3 crystals of different size, 60-90 μm, with sharp ends. In one case, extrusion of the crystal from the atrium was observed. Spermatheca with oval ampulla (340 μm long and 204 μm wide) and well-defined duct (272 μm long). One to two spermatozeugmata in every ampulla, coiled in an 8-shape.

DISTRIBUTION AND HABITAT

The whole of Lake Baikal, on different kinds of soft sediment at depths of 5-200 m. Densities up to 640 individuals per square metre. A large number of specimens studied.

REMARKS

The short, stout body with numerous high, erected papillae gives *B. digitatus* a rather curious, hedgehog-like appearance. It is quite similar to *B. cristatus* in its minute size, and in the structure of armour, setae and genital organs. The significant differences, allowing us to regard these taxa as separate species, are a shorter and more stout body in *B. digitatus*; a gradual increase in the length of papillae on the dorsal side without any distinct mid-dorsal ridge; shorter dorsal setae, with bifid needles; distal tooth in anteclitellar bifid crotchets almost twice as long as the proximal one; vas deferens shorter; atrium less curved and containing more than one crystal; spermathecal ampulla more oblong. For the relationship to *B. werestschagini,* see below.

Baikalodrilus werestschagini (MICHAELSEN, 1933) (Fig. 21)

Peloscolex wereschtschagini MICHAELSEN, 1933 : 326-333, fig. 1-3.

Peloscolex werestschagini, MICHAELSEN, 1935 : 15-21, fig. 1-3; CHEKANOVSKAYA, 1962 : 284-285; 1981 : 356; BRINKHURST & JAMIESON, 1971 : 519; SNIMSCHIKOVA, 1984 : 12-14, fig. 4; 1987 : 57-59, fig.17.

Baikalodrilus werestschagini, BRINKHURST, 1981a : 1061-1062; 1984 : 498-499.

DESCRIPTION

Length 3.1-3.5 mm, maximal diameter 0.5 mm, 26-29 segments. Prostomium retracted. Body bluntly quadrangular in cross section, broader in the middle part. Body surface covered with thick bright armour consisting of fused epidermal secretory papillae. Two kinds of epidermal glands within these papillae : larger ones (up to 60 μm high), often filled with secreted particles, and smaller (33 μm high) flask-shaped, empty glands. Four longitudinal rows of large apertures in the armour on setal lines, causing a squarish body form. From these aper-

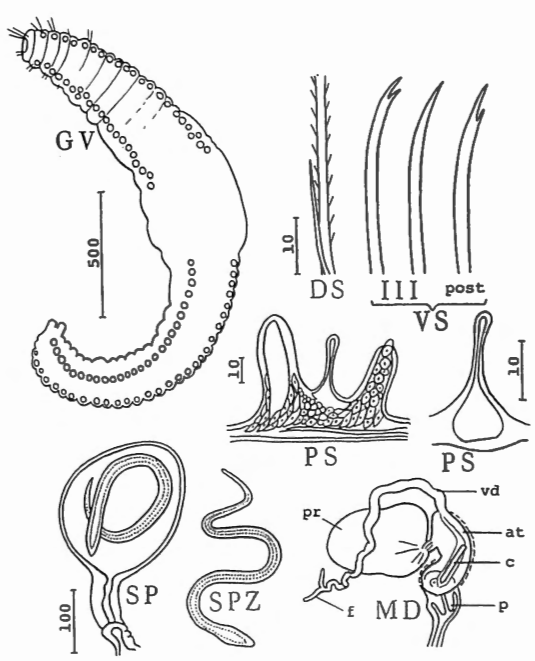

Fig. 21. – Baikalodrilus werestschagini.

tures, four rows of large glandular setal tubercles protrude, regarded as sensory papillae ("Sinneshügel") by MICHAELSEN (1933, 1935). Clitellum covered with comparatively thin armour, without large glands.
Dorsal bundles consisting of a single (rarely 2) plumose hair seta, 250 μm long, and a very thin and short (50 μm) needle seta, the latter being visible only after removing armour. Anteclitellar ventral bundles containing 2 crotchets, a ventral simple and a lateral bifid one, the latter with distal tooth twice as long as proximal tooth; nodulus ental. Crotchets 83 μm in II-III, about 100 in IV-VIII. Behind clitellum, only one crotchet occurring in ventral bundles, about 150 μm long, with rudimentary proximal tooth.
Circular clitellum from (partially) X to XII. Spermathecal and male pores on one line with ventral setae. Vas deferens about 520 μm long, diameter gradually growing from 17 to 28 μm. Compact rounded prostate gland laterally discharging into the atriums proximal half. Atrium cylindrical, curved almost at a right angle in its middle part; distal end curving in the opposite direction. Soft penis in penial sac. A pencil-shaped crystal, 105 μm long, lying in atrial lumen. Atrium 190 μm long and 70 μm wide, penial sac 60 μm long. Spermathecal ampulla egg-shaped, 284 μm long and 230 μm wide; distinct spermathecal duct 210 μm long. Comparatively short, coiled spermatozeugmata with swollen heads, 2 per ampulla.

DISTRIBUTION AND HABITAT

Middle and South Baikal, Olkhon Strait, Mukhor Bay. On muddy sand or mud mixed with sand and detritus, at depths of 3-1410 m. A large number of specimens studied.

REMARKS

B. werestschagini has a very peculiar appearance with its squarish semilunar body embedded in an extremely thick and compact bright armour, exposing only four longitudinal rows of prominent glands. It is most similar to *B. cristatus* and *B. digitatus* in its small size, general body form, and setal and genital apparatus. However, the species differ considerably, above all by the structure of their armour, *B. cristatus* and *B. digitatus* have long separate papillae instead of a thick continuous layer perforated by glands in *B. werestschagini*. *B. werestschagini* has plumose hair setae, while these are smooth in *B. cristatus* and *B. digitatus*.
B. werestschagini is very similar to *B. exilis* in setal apparatus. However, *B. exilis* is smaller, has a thin armour and different spermatheca.
The set of ventral crotchets in *B. werestschagini* resembles somewhat the one in *B. paradoxus*, while the latter one also has four similar longitudinal rows of big glands on setal tubercles.

B. werestschagini was originally described by MICHAELSEN (1933, 1935) on a single, not well preserved specimen; its description remained incomplete, especially in regards of the setae. On the other hand, it should be noted that MICHAELSEN was the first to discover the atrial crystal, characteristic of the whole genus *Baikalodrilus*. He described it as "einen eigentümlichen in Hämatoxylin-Eosin tief rot gefärbten dünnen (ca 5 μm dicken) glatten, der Krümmung des Atriums entsprechend gekrümmten Stab, der wie ein Gallertstab aussieht" and postulated that this little peg could be connected to the formation of spermatozeugmata. This structure was later omitted by authors of guides and textbooks. SNIMSCHIKOVA (1984) emended the description when studying the setal apparatus and epidermal glands after the armour was removed.

Baikalodrilus phreodriloides (MICHAELSEN, 1905)
(Fig. 22)

Lycodrilus phreodriloides MICHAELSEN, 1905 : 16.
Lycodrilus phreodriloides, CHEKANOVSKAYA, 1962 : 386-387; 1981 : 482-483; BRINKHURST & JAMIESON, 1971 : 652; BRINKHURST, 1984 : 506 - *species incertae sedis*.
Baikalodrilus phreodriloides, SNIMSCHIKOVA, 1991b : 221-223.

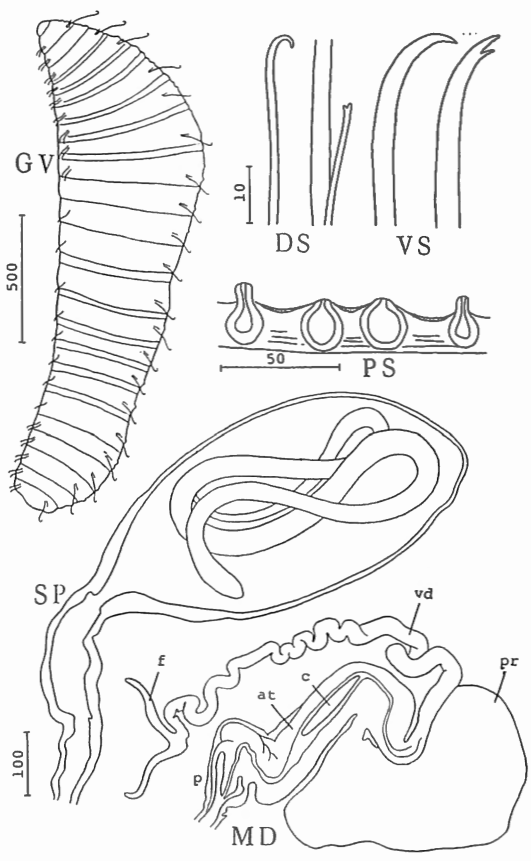

Fig. 22. – Baikalodrilus phreodriloides.

DESCRIPTION

Length 3-4.4 mm, maximal diameter 0.6-0.9 mm; 24-25 segments. External segmentation distinct. Armour translucent, with few sediment particles between the folds. Secretory papillae sparse, shaped like indistinct low tubercles, bladder-like in cross section. Sensory papillae small and translucent, flask-shaped, 7-10 μm high, in two transverse rows per segment, one row per annulus. The small prolobic prostomium can be retracted together with the first segments, up to setae of II. Body unpigmented, light grey or yellow when preserved.
Dorsal bundles consisting of one hair and one needle seta. Hair setae 170-250 μm long, longest in XII, smooth; slightly curved proximally, the very thin distal end equipped with a fine hook. Needle setae 50-60 μm long in anteclitellar segments and up to 100 μm long on the tail, slightly sigmoid, simple or with short rudimentary teeth, sometimes with a small knob on the end. Ventral setae in anteclitellar bundles 100 μm long, usually by 2 (sometimes by 4 in II), the ventral one being simple and the lateral one with rudimentary proximal tooth. Postclitellar ventral bundles containing a single simple seta, up to 180 μm long on the tail.
Circular clitellum, with high glandular cells, occupying 1/2X-XII. Spermathecal pores situated a little higher than the ventral setae in X, male pores replacing the absent ventral setae in XI. Male funnel large and deep. Vas deferens about 1400 μm long, strongly wound, 18 μm wide in its proximal part and gradually widening to 28 μm in distal part. Atrium cylindrical, thick-walled, suddenly tapering and curved in a right angle at its proximal end; similarly curved, but in opposite direction at the distal end. A boat-shaped crystal in the middle part of atrial lumen. No efferent part in the atrium. Penial sac wide and short, penis conical. Atrium 400-420 μm long and 100-120 μm wide, penial sac 100-140 μm long and 100 μm wide, crystal 140-200 μm long. Prostate gland bulky and irregular, of the same length as atrium, discharging into atriums proximal curve by a short thick stem. Spermatheca with elliptical or ovoid, thin-walled ampulla, 600-900 μm long and 300-470 μm wide, and with a weakly defined, 340-400 μm long duct. Two long spermatozeugmata in every ampulla coiled in an 8-shape. Spermatheca can reach XII inside the sperm sac.

DISTRIBUTION AND HABITAT

Middle Baikal, near Cape Ukhan of the Olkhon Island, on sand and stones at a depth of 3 m. North Baikal, near Cape Kurly, on stones and gravel at a depth of 2 m. Six specimens studied, 4 of them being mature.

REMARKS

Baikalodrilus phreodriloides is most closely related to *B. werestschagini* in its short body with few segments, and in the basical structure of the setal and genital apparatus. They are nevertheless well distinguishable. In *B. phreodriloides* the body is shorter and round, not quadrangular as in *B. werestschagini*; hair setae are smooth and hooked, ventral bifids with thinner and shorter proximal tooth, vas deferens is much longer, atrium longer and more curved, spermatheca with longer ampulla and duct, and all internal organs are bigger than in *B. werestschagini*.
MICHAELSEN (1905), when first describing the species, did not describe the armour and, hidden in it, the very fine needle setae. Nor did he discover the atrial crystal, he did however describe a short and narrow efferent part of the atrium, which in reality is not present. The species was recently redescribed and transferred to the genus *Baikalodrilus* by SNIMSCHIKOVA (1991b).

Baikalodrilus kozovi (HRABĚ, 1969)
(Fig. 23)

Peloscolex kozovi HRABĚ, 1969 : 269-272, fig.1-6.
Baikalodrilus kozovi, HOLMQUIST, 1978 : 206, fig. 3B, 10E; 1979 : 49-50, fig. 16A.

DESCRIPTION

Body short, almost oviform, 1.2 mm long and 0.78 mm wide; 16 segments. Anterior segments retracted. Epidermis covered with a continuous thin layer of solid secretion, imbedded with sediment particles, surface seemingly undulating on longitudinal sections.

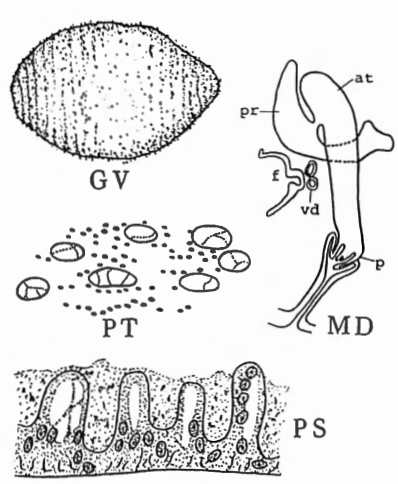

Fig. 23. – Baikalodrilus kozovi *(after HRABĚ, 1969)*.

Numerous cylindrical secretory papillae, each containing one large vacuola being disposed in each segment in several transverse lines. Secretion layer missing on dorsal side of clitellum. Clitellar epidermis smooth, low and consisting of cubic glandular cells with granular secretion. Dorsal bundles containing one short hair and one bifid seta, anteclitellar ventral bundles consisting of two bifid setae, postclitellar ones with a single bifid

seta. Clitellum occupying X-XI. Spermathecal and male pores on one line with ventral setae. Male funnels large, covered with a layer of long spermatozoa. Thin-walled vas deferens at least as long as atrium, with equal diameter over the entire length (25 μm). Atrium long, nearly cylindrical, 85 μm wide at the proximal end and 65 μm in the middle and before the penial part. Large stalked prostate gland opening in proximal, dilated portion of atrium. High glandular epithelium covering the inner wall of atrium. Conical penis without cuticular sheath is formed by a thin-walled fold of epithelium lying in 230 μm long penial sac. Spermatheca with large pear-shaped ampulla and short duct. Ampulla containing about 200-230 μm long spermatozeugmata rolled up in a spiral.

DISTRIBUTION AND HABITAT

South Baikal, near Bolshiye Koty on sand, at a depth of 3.4-6 m, and in several other places.

REMARKS

The species was never seen by us, so the present redescription relies on the one given by HRABĚ (1969).
B. kozovi resembles *B. cristatus, B. digitatus* and *B. werestschagini* in several external and internal characters : short body, papillate armour, minimal number of dorsal setae (one hair and bifid seta per bundle), two crotchets in anteclitellar ventral bundles (HRABĚ does not mention their shape, but there may be a simple and a bifid crotchet in every bundle), and a single bifid in postclitellar ones. The construction of the male duct is generally similar in these species, therefore the presence of a crystal in the atrium of *B. kozovi* (not described by HRABĚ) can also be supposed.
B. kozovi differs from the other species in its short, egg-shaped body of size and also the presence of a pear-shaped spermathecal ampulla with a short duct, short vas deferens (not widening in its distal part ?) and almost straight atrium.
SEMERNOY & SHIDLOVSKAYA (1983) claim that some specimens of *B. kozovi* have atria of more swollen shape, twice as wide as given by HRABĚ (1969).

Baikalodrilus inflatus (MICHAELSEN, 1901) (Fig. 24)

Tubifex inflatus MICHAELSEN, 1901 : 141-145, Table I, fig. 8-10; BRINKHURST, 1981b : 8-9.
Tubifex (Peloscolex) inflatus, MICHAELSEN, 1905 : 23-24 (partim).
Peloscolex inflatus, CHEKANOVSKAYA, 1962 : 284; 1981 : 355; BRINKHURST & JAMIESON, 1971 : 517 (partim); *non* HOLMQUIST, 1978 : 190, 195, 199, fig. 4B, 7E, 10D; 1979 : 57; *non* HRABĚ, 1982 : 178-179.
Baikalodrilus inflatus, BRINKHURST, 1984 : 499.

DESCRIPTION

Length 40 mm, maximal diameter on clitellum 1.6-2.5 mm, in middle part 1-1.3 mm; 120-140 segments. Anterior part of body swollen (not caused by preservation). Prostomium rounded, retractable together with I, length slightly larger than width. Colour brownish or greenish grey, in posterior part rusty brown. Numerous small papillae in 15-18 irregular, dense rows on every segment except prostomium, I and clitellum. Papillae of ovoid, stretched shape, slightly tapering at their base. Their glands with granulose, olive coloured content responsible for the colour of the worm. On posterior part of body, papillae become broader and are fused into transverse ferruginous rings. Clitellum circular, not elevated above body surface, glossy silvery grey, without papillae, covered with a thin layer of sediment particles. Setal tubercles small, whitish, with thickened hypodermis.

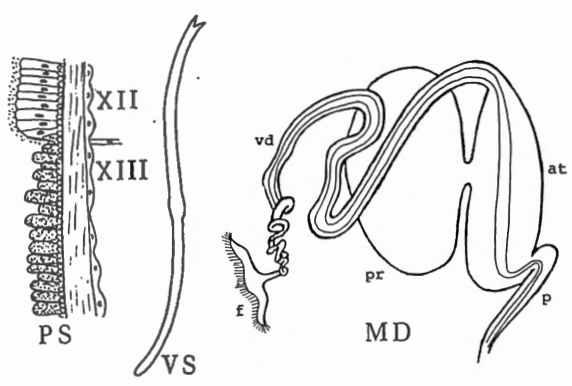

Fig. 24. – Baikalodrilus inflatus *(after MICHAELSEN, 1901).*

Dorsal bundles with 2-4 hair setae, 200-400 μm long, and 2-4 pectinates in anteclitellar segments. Pectinates about 240 μm long, slightly sigmoid, with equal delicate teeth diverging in an acute angle and bound together with a folded or ribbed membrane. In ventral bundles bifid crotchets only, about 200 μm long anteriorly and a little shorter behind clitellum, 6 μm thick, with slightly longer proximal tooth. Distal end of crotchets similar at least in II-XVIII. Number of crotchets in II-III(IV) 3-4, caudally almost always two.
Clitellum on 1/2X-XII. Spermathecal pores positioned laterally to the ventral setae of X, male pores replacing the ventral setae in XI. Male funnel broad and flat. Vas deferens long, its proximal third narrow and coiled, middle and distal parts broader and irregularly wound. Atrium resembles an oblong chamber with sharper proximal end; bulky, smooth egg- or bean-shaped prostate gland with short thin stem discharging in its proximal half. Atrial ampulla merging, with a curve, in a short ejaculatory duct; the latter terminating after another curve with thin penis without any sheath, in a long thin penial sac. Spermathecal ampulla sacculate, same length as distinct duct. Spermatozeugmata in ampulla numerous, thin brooch- or query-shaped.

DISTRIBUTION AND HABITAT

The type material was collected in Lake Baikal on the muddy sediments at depths 60-272 m.

REMARKS

The papillate species described by MICHAELSEN (1901) as *Tubifex inflatus,* and transferred by BRINKHURST (1981a) into *Baikalodrilus,* differs from all other known species of the genus in having only bifid crotchets in the ventral bundles. In another contribution, MICHAELSEN (1905) added to the species diagnosis the presence of simple crotchets in ventral bundles together with the bifids, and also stressed the high abundance of the species in different depth zones of the lake. HOLMQUIST (1978, 1979) found no papillae, only a folded armour in the scanty material (5 specimens in the Moscow and Leningrad zoological museums) of *Peloscolex inflatus* studied by her; in regards to the internal anatomy several important differences were apparent in comparison with the original description. HRABĚ (1982) described, as *Peloscolex inflatus,* some new material from Lake Baikal, the worms papillated like the original specimens, but with alternating simple and bifid (with shorter distal tooth) crotchets in ventral bundles. BRINKHURST (1981b, 1984) found in the, probably immature, syntypes in Hamburg, as well as in the new material specimens with a different degree of papillation, whilst the setae were mostly broken.

The first author of the present contribution examined the remains of the collection of WAGNER in the Zoological Institute of Leningrad. 15 tails and immature specimens were found, identified as *Tubifex inflatus* by MICHAELSEN. 11 of them correspond to *Baikalodrilus paradoxus* and 2 to *B. d. discolor* according to their armour and setae. Two more specimens, very similar to the original description of *Tubifex inflatus,* still have 2 bifid and 2 simple crotchets in the anterior ventral bundles, as *B. paradoxus,* but their continuous dark armour with broad folds and weak setal tubercles is different. This form can be regarded as a species or subspecies related to *B. paradoxus.* Furthermore, a series of sections made by HOLMQUIST (in the Zoological Institute, Leningrad) was studied, and is regarded as being identical to *B. paradoxus.* It has a thick cuticle, smooth or wavy in the anterior segments, but already distinctly folded in IV; a crystal is clearly visible in the atrium.

Thus, various researchers describing *Tubifex inflatus* (or *Peloscolex inflatus* or *Baikalodrilus inflatus*), or indicating it in their benthic fauna lists of Lake Baikal and the reservoirs on the Angara River, flowing out from this lake, evidently dealt with different large species of the genus *Baikalodrilus* or even with a mixture of species. It is not possible to establish whether MICHAELSEN (1901) really had specimens with bifid crotchets only in their ventral bundles when compiling the original description, or whether simple crotchets were omitted by him (perhaps broken). One can not deny the possibility that a specimen, identical to the first description will be discovered in Lake Baikal again. So far, we failed in discovering it. Therefore we prefer to regard *B. inflatus* as a *species inquirenda,* limiting it to the definition by MICHAELSEN (1901), without any subsequent additions.

The inclusion of *Tubifex inflatus* in the species list of the Petrograd Government by IVANOV (1922) must be due to a misinterpretation of MICHAELSEN (1905), where *T. (P.) ferox* is treated immediately after *T. inflatus,* listing the above mentioned problematic data.

Key to the species of *Baikalodrilus*

1.	Hair setae with finely hooked tips. Armour translucent, with sparse small papillae. Body 3-4.4 mm long	*B. phreodriloides*
—	Hair setae not hooked	2
2(1).	Body always shorter than 4 mm	3
—	Adult body longer than 4 mm	8
3(2).	Body about 1.2 mm long, egg-shaped, covered with transverse rows of low papillae	*B. kozovi*
—	Body 2-3.5 mm long, slender and curved	4
4(3).	Secretory papillae very high, finger-shaped	5
—	No finger-shaped papillae	6
5(4).	The highest papillae forming a dorsal longitudinal ridge. Only one crystal, with parallel margins and bluntly sharpened tips, in each atrium. Spermathecal ampulla oviform	*B. cristatus*
—	Papillae gradually diminishing from dorsal to ventral side, not forming any distinct longitudinal ridges. 2-3 acute crystals in each atrium. Spermathecal ampulla spherical	*B. digitatus*
6(5).	Papillae fused, forming a thick armour, with 4 rows of large setal tubercles on edges of the square body	*B. werestschagini*
—	Armour thin and translucent	7
7(6).	Armour with scattered papillae. Spermatheca with sac-like ampulla gradually transforming into duct. Body 2.3-2.5 mm long	*B. exilis*
—	Armour without any secretory papillae, only with a layer of small adhering particles. Spermatheca with spherical ampulla and distinct duct. Body 2.5-4 mm long	*B. intermedius*
8(2).	Both simple and bifid crotchets in ventral bundles	9
—	Only crotchets of one kind in ventral bundles	14

9(8). More than 2 crotchets in ventral bundles of II. Armour with papillae : 10
— Only one simple and one bifid crotchet in the foremost ventral bundles. Armour without papillae, with transverse stripes of adhering particles only in cuticle furrows : 13
10(9). 6-7 crotchets in ventral bundles of II. 4-5 hair setae and 4 pectinates with a delicate membrane between lateral teeth in anterior dorsal bundles. Maximal body diameter up to 3 mm : . . . . . *B. crassus*
— 3-4 crotchets in ventral bundles of II. 2-3 hair setae, besides bifid or pectinate setae, in anterior dorsal bundles. Maximal body diameter 1-2 mm : 11
11(10). One simple and two bifid crotchets in ventral bundles of II, and a single bifid beginning with III. 2-3 pectinate setae in anterior dorsal bundles. Papillae fused in a continous layer in most segments. Setal tubercles large, prominent, light. One rectangular crystal in each atrium : . . . . . *B. paradoxus*
— Two simple crotchets besides 1-2 bifids in ventral bundles of II. Papillae not fused. Setal tubercles small, indistinct. 1-2 crystals in each atrium : 12
12(11). Two simple and two bifid crotchets (with proximal tooth longer) in ventral bundles of II, and 2-3 crotchets in II-X. 4 bifid setae without any intermediate teeth in anteclitellar dorsal bundles : . . . *B. bifidus*
— Two simple and one bifid crotchet (with longer distal teeth) in ventral bundles of II, and two different crotchets in III-X. 2-4 bifid and/or pectinate setae of different shape in anterior dorsal bundles : . . . . . *B. medianus*
13(9). 2-3 plumose hair setae and 2-3 pectinate setae with two intermediate teeth in anteclitellar dorsal bundles. One single crystal in each atrium. Spermathecal duct shorter than ampulla : . . . . . *B. scaphoideus*
— 2 serrate hair setae and 2 pectinate setae with one intermediate tooth in anteclitellar dorsal bundles. Two crystals in each atrium. Spermathecal duct longer than the ampulla : . . . . . *B. undatus*
14(8). Ventral crotchets bifid. 2-4 hair setae and 2-4 pectinates in anteclitellar dorsal bundles : . . . . *B. inflatus, s.s., sp. inquir.*
— Ventral crotchets simple : 15
15(14). Ventral crotchets at last behind the clitellum sickle-shaped : 16
— Ventral crotchets in all bundles sabre-shaped : 17
16(15). Ventral crotchets straight to sigmoid in II-IX, lacking in X-XX, sickle-shaped in posterior segments. 4-5 plumose hair setae and 4-5 pectinates in anterior dorsal bundles : . . . . . *B. bekmanae*
— Single sickle-shaped crotchets in all ventral bundles. 2 smooth hair setae and 2 bifids with short teeth in anterior dorsal bundles : . . . . . *B. falcatus*
17(15). 1 or 2 crystals in each atrium : 18
— Many crystals in (or near) each atrium : 21
18(17). 5-6 plumose hair setae together with 3-4 simple sharp needle setae in anteclitellar dorsal bundles. Only 2 crotchets in anterior ventral bundles. Atrial crystals single, with parallel margins and sharp tips : . . . . . *B. malevici*
— Hair setae either smooth, usually less than 5 in dorsal bundles, or hair setae plumose and then accompanied by pectinate setae : 19
19(18). Hair setae plumose, accompanied by 3-6 pectinates with short lateral teeth and very fine intermediate teeth. A large cuneiform crystal in atrium can be associated with a smaller boat-shaped one : . . . . . *B. discolor brevipectinatus*
— Hair setae smooth : 20
20(19). Dorsal needle setae up to 50 μm long, sharp. Armour vividly coloured in brown, orange and beige tones in mature worms, uniformly brown in juveniles. A single cuneiform crystal in each atrium : . . . . . *B. discolor discolor*
— Dorsal needle setae 70-80 μm long, obtuse. Armour dark brown. Two boat-shaped crystals of different size in each atrium : . . . . . *B. discolor acinacifer*
21(17). A cluster of crystals in atrial lumen. 2-4 hair setae and 2 needles in anterior dorsal bundles, up to 4 crotchets in anterior ventral bundles. Body slender, up to 1.4 mm wide : . . . . . *B. multicrystallifer*
— A cluster of crystals outside atrium, 2 hair setae and 3 needles in anterior dorsal bundles, up to 2 crotchets in ventral bundles. Body stout, 3.6 mm wide : . . . . . *B. solitarius*

Reproductive biology

All known *Baikalodrilus* species seem to propagate sexually, like most other known Tubificidae. The presence of elongate organic crystals in the atria is characteristic of the genus. These crystals could have some stimulating or spermatozeugma-forming function in

copulation, perhaps compensating for the lack of modified genital setae and penial sheaths. The location of the crystals outside the atrium described in one species (*B. solitarius)* is problematic and may be an artefact.

Cocoons of *Baikalodrilus* were first erroneously described as foraminiferans by LUKINA (1967). They were found in Chivyrkuy Bay at 5 m depth as spherical chambers of 1-1.4 mm diameter, their wall incrusted with fine sand, and furnished with two round, slightly excentric pores lying on small tubercles. Later on, KOZHOV & OKUNEVA (1969) attributed them to "*Peloscolex inflatus*". They found two sympatric forms of this "species" in Baikal, the first one with high papillae, depositing cocoons from January to mid-April, the second one being smooth, depositing cocoons from March to June. Clitellate worms were observed from December to June. Cocoons described and depicted by these authors were light-coloured, incrusted with sand and diatoms, roundish lemon-shaped, with slightly excentric pores of variable diameter, situated on short tubercles and closed by fibrous plugs. Cocoons were 0.8-1.6 mm in diameter, seldom up to 2 mm. There were 2-35 eggs or embryos in cocoons laid in aquaria, and 5-25 (rarely up to 50) in those found in the lake. The incubation period was 2-2.5 months in aquaria at 8-10°C, and young worms hatched when 2.4-3.5 mm long.

Discussion

The genus *Baikalodrilus* incorporates a coherent group of species diverging in Lake Baikal. Although all species exhibit a similar reproductive system, a large variation is present in external characters, so that without any knowledge of internal anatomy one can hardly lodge them in the same genus. Large worms, such as *B. crassus* (32-35 mm long) and *B. d. discolor* (28-30 mm), but also dwarfs like *B. kozovi* (1.2 mm) and *B. cristatus* (3-3.5 mm) exist. The armour consists of a thickened cuticle, as in other armoured tubificids, but shows a different structure in different species. The cuticle can form folds or papillae, the latter can fuse into a continuous hard, thick coat. For example *B. bifidus* and *B. medianus* have round or egg-shaped papillae of medium size, projecting from the cuticle surface, while *B. scaphoideus* and *B. undatus,* morphologically adjacent to the former two species, lack any protruding papillae, but have small inconspicuous glands hidden between cuticle folds. In *B. digitatus* and *B. cristatus* the papillae are very high, especially on the dorsal side. In *B. exilis* small papillae are sparsely distributed over the thin and translucent cuticle. In *B. werestschagini* the papillate folds of the cuticle are fused into a continuous thick horn-like coat.

Three obvious trends are discernable in the amount of variation in armour among the species of *Baikalodrilus*. The first trend is expressed by the gradual thickening of cuticle folds and their tendency to fuse (*B. paradoxus, B. undatus, B. scaphoideus, B. kozovi, B. werestschagini*), the second by the gradual enlargement of papillae (*B. medianus, B. digitatus, B. cristatus*), while the third is characterized by a gradually thinner armour with papillae becoming even smaller and sparser (*B. malevici, B. intermedius, B. exilis, B. phreodriloides*). The setal apparatus of *Baikalodrilus* reveals a tendency of gradual simplification, from pectinates (*B. paradoxus*) to simple needles in dorsal bundles (*B. malevici*), and from bidentate crotchets (*B. crassus*) to simple sabre-shaped (*B. d. discolor*) or sickle-shaped ones in ventral bundles (*B. falcatus*), as well as a decrease of setal number from 6-7 per bundle (*B. crassus*) to 2 in anterior and 1 in postclitellar segments (*B. solitarius*), or even to the complete loss of ventral setae in several mid-body segments (*B. bekmanae*). Several changes occur also in the structure of the internal reproductive organs, such as a shortening of the vas deferens, the shift of the opening of the prostate gland from the middle to the proximal part of the atrium, the multiplication of the atrium crystals from one single crystal to up to 10-12, variations in the shape of spermatheca and the length of spermatozeugmata, etc.

In our opinion, the variability in the different characters of *Baikalodrilus* is due to the complicated history of the lacustrine environment wherein the genus has evolved. Earlier we regarded the Palaearctic *Embolocephalus velutinus* or some of its close relatives, possibly distributed in Siberia during the Tertiary, as the likely ancestor of the assemblage of Baikalian armoured tubificids (SNIMSCHIKOVA, TIMM & PARELE, 1987). Yet the genus *Baikalodrilus* seems to have an earlier origin. Probably, the genera *Embolocephalus* and *Baikalodrilus* evolved from a common ancestor (see also BRINKHURST, 1991) and developed independently of each other over a long period of time.

The hypothetical ancestor of *Baikalodrilus* was probably covered with medium-sized papillae of an ovoid or leaf-like shape, which are rather common among the armoured tubificids. It had numerous ventral setae (probably bifids, 5 or more per bundle), hair and pectinate setae in dorsal bundles, no spermathecal setae, an elongate atrium without any ejaculatory duct, and a long vas deferens. The distribution range of this ancestor, probably Eurasian, cannot be established at present, the species probably became extinct in the distant geological past. Its successors survived and diverged in several large lakes which existed on the site of contemporary Lake Baikal in the Oligocene and Miocene.

Recent palaeolimnological investigations (POPOVA *et al.*, 1989) have reconstructed the history of the lakes of the Baikalian Rift in connection with tectonic and climatic factors. Numerous data accumulated as a result of interdisciplinary research support the opinion of the majority of investigators that Lake Baikal together with its biota has had a very long (tens of millions of years) and

unique history (amongst others : BERG, 1948, 1949; VERESCHAGIN, 1930, 1940; BAZIKALOVA, 1945; SHMALHAUSEN, 1946, 1983; KOZHOV, 1962, 1963, 1972; MARTINSON, 1967, 1989; OBRUCHEV, 1953; FLORENSOV, 1978; LUT, 1978; MAZEPOVA, 1987, 1990; PORFIRYEVA, 1977; SIDELEVA, 1982; SEMERNOY, 1987). A second hypothesis accepts that both Lake Baikal and its fauna are rather young, of postglacial age (DOROGOSTAYSKIY, 1923; TALIYEV, 1948; GOLDYREV, 1972, 1982; LUKIN, 1986). This viewpoint has been disputed by KOZHOV (1962, 1963, 1972), MAZEPOVA (1990), and others.

MATS, VOROBYEVA & SHIMARAYEVA (1989) proposed the following scheme of geological events forming the Baikal lake basin. During the Late Cretaceous and Eocene, extensive flat depressions were occupied by shallow lakes. During the Oligocene, Miocene and Early Pliocene several large and quick sinkings of the earth crust occurred, resulting in the formation of South and Middle Baikal basins, nearly within their present-day boundaries. In these basins, under the conditions of the warm subtropical climate of alternating humidity, existed large and deep lakes. In the second half of the Pliocene, the climate became cooler and vertical tectonic processes stronger. In the Eopleistocene (1.8-1 million years ago) several cold periods occurred repeatedly, while during the Middle Pleistocene (0.4-0.2 million years ago) the region was glaciated. The actual contours of Lake Baikal were established during the Pliocene and Eopleistocene while the development of the bottom relief and the increase of depth continued during the Pleistocene and Holocene (LUT, 1978; FLORENSOV, 1978). Tectonic activity has not ceased in the basin up to now. Lakes of different depth and surface area were formed during the whole of the Cenozoic on the territory

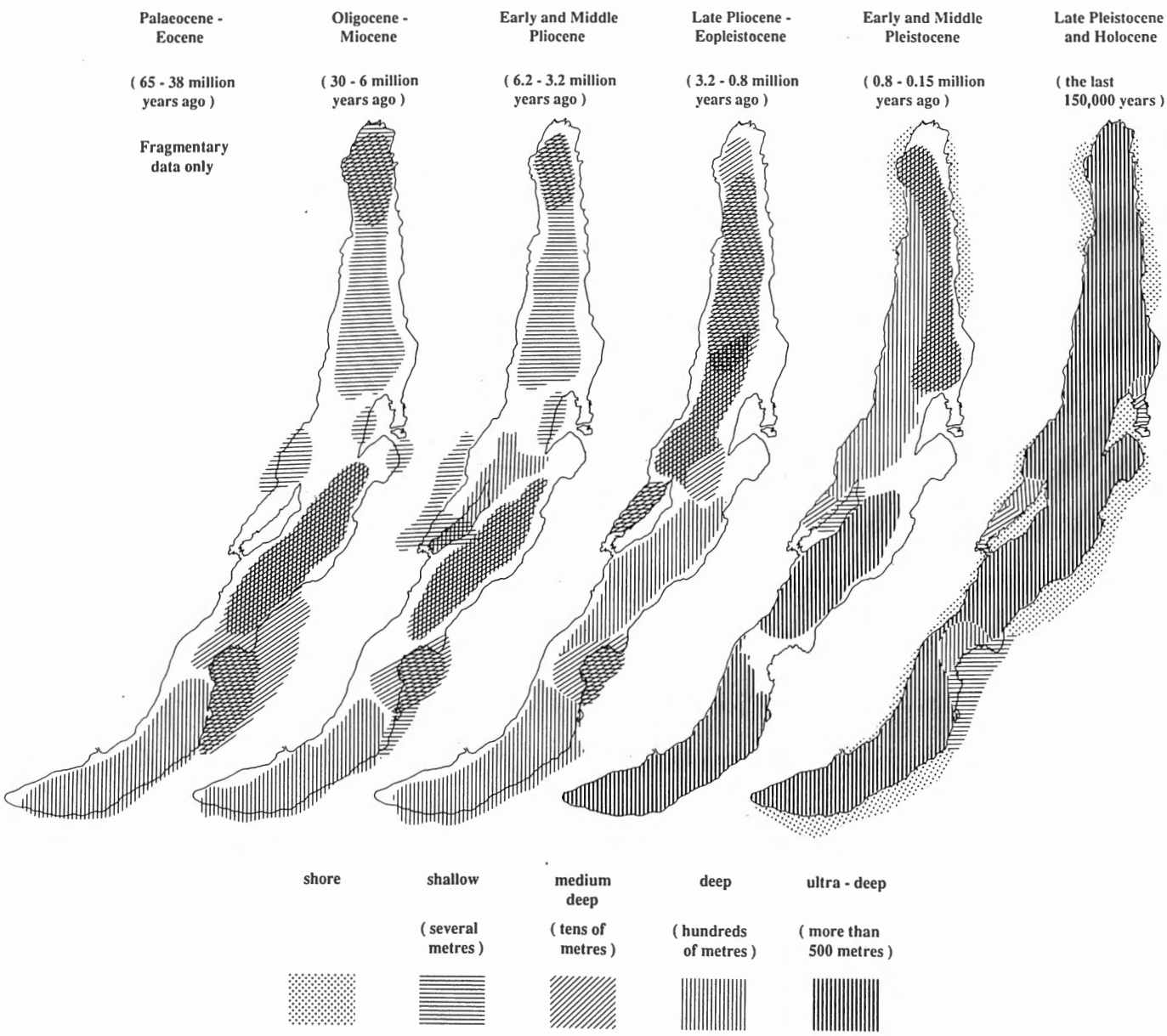

Fig. 25. – *Development of the Pre-Baikalian rift lakes in Cenozoic (after* POPOVA et al., *1989).*

of the present Lake Baikal (Fig. 25). These were inhabited by different organisms. The continuous presence of large depths for millions of years allowed the accumulation and the existence of various groups of animals, these being the ancestors of the endemic fauna of the modern Lake Baikal (POPOVA *et al.*, 1989). However, such ancient deep lakes as Baikal were not only simple collectors of fauna but also a place for accelerated evolution, since climatic changes and active geological processes caused considerable perturbations of the biota (RUBTSOV, 1945). The lakes became increasingly deeper, their water level and physico-chemical properties changed. However, the basic conditions of the aquatic environment in Lake Baikal and its predecessors remained stable due to their large depth and size. LAMAKIN (1952) stated that Lake Baikal never became shallow, never warmed up like its sors, was never frozen all the way to the bottom, never lost its oxygen richness, and it was never of a small size. Long-term duration and diversity of favourable life conditions are regarded as the main factors in the formation of the extraordinary rich Baikalian biota (MAZEPOVA, 1990).

POPOVA *et al.* (1989), referring to some earlier papers (MAYR, 1947; KOZHOV, 1962), expressed the opinion that the existence of several more or less isolated large pre-Baikalian lakes in the Oligocene and Miocene promoted allopatric speciation. Sympatric speciation could have prevailed later, the last 3.2 million years, beginning from the Eopleistocene, while both modes were characteristic of the intermediate Pliocene period.

Supposedly, the most primitive representatives of the genus, namely *Baikalodrilus crassus, B. bifidus, B. paradoxus, B. undatus,* and *B. scaphoideus* can date their origin from Oligocene pre-Baikalian lakes, already several hundreds of metres deep. Their hypothetical ancestor which had come from shallower and warmer lakes was able to settle in the littoral of large pre-Baikalian lakes. Its immediate descendants had to adapt their physiology to new environmental conditions, while their morphological characters probably changed only to a slight extent. The long existence of several large lakes (about 25 million years) favoured the diversification of these ancestral forms.

During the Early and Middle Pliocene, apart from the two large lakes in the South and Middle Baikal depressions, the southern part of the North Baikal depression also began to sink, forming the third deep pre-Baikalian lake. The warming and aridization of the climate in the first half of the Pliocene (POPOVA *et al.*, 1989) consolidated the ecological isolation of the deep lakes. Probably, at that time the deep-water populations of *Baikalodrilus,* the progenitors of the subsequent species, *B. malevici* and *B. medianus,* were formed, differing more from the hypothetical ancestor than the shallow-water species.

A consensus exists amongst researchers that the glacial period (Late Pliocene and Pleistocene) had a crucial importance for the biological evolution in Lake Baikal, although specialists disagree as to the duration and the extent of glaciation. Several authors postulate a long full glaciation (DUMITRASHKO, 1952, 1956; BELOVA, 1975; LAMAKIN, 1953), others mention the periodical existence of valley glaciers only on lake shores (POPOVA *et al.*, 1989). According to SEMERNOY (1987), this problem is important when one treats the possible mass extinction of hydrobionts and the degree of post-glacial rearrangement of faunistic complexes.

The climatic cooling in the Late Pliocene and Eopleistocene (3.2-0.8 million years ago) took place with a large scale orogeny in the whole East Siberia. During this period, the area of large lakes decreased while many smaller lakes became shallower or disappeared. Intense flushing of rock material from the surrounding mountain ranges filled several lake depressions. Thus, lakes in the Tunkin Valley, the southern extension of the Baikalian Rift, gradually disappeared.

During the same period, the South and Middle Baikal hollows were intensely deepened, while rocky sediments accumulated on the shores. In the Eopleistocene the North Baikal hollow, occupied at first by several lakes of medium depth, also acquired its contemporary configuration. That period was characterized by an especially high water level in the lakes of the whole rift zone (MATS, 1987). The lake biota responded to the rapid cooling of climate by the elimination of more thermophilous species, at first those inhabiting shallow lakes or the bays and littoral of larger lakes. The inhabitants of deep-water biotopes were cold-resistant, since they live at a constant +4°C, even in subtropical climates (POPOVA *et al.*, 1989).

SEMERNOY (1987) expresses the opinion that in the Pliocene and Eopleistocene the mass extinction, not only of thermophilous shallow-water forms, but also of open-lake fauna occurred as a result of the catastrophic consequences of changes in climate, relief and hydrochemical conditions (especially resulting from volcanic eruptions), water level fluctuations, sediment shifts and their burial under fresh rocky material. LUKIN (1986) sketches the full destruction of the Baikalian fauna during the ice age.

Apparently, such ideas about the cataclysmic character of the events are very overestimated. However, a few mass extinctions of near-shore organisms of pre-Baikalian lakes undeniably took place. In all probability, many littoral populations of *Baikalodrilus* vanished. The survivors extended their distribution range to deeper zones, due to the freezing of the littoral, abrasion of shores, or exuberance of terrigenous sediments. Many modern species of *Baikalodrilus,* abundant in shallow places, occur also at considerable depths (*B. paradoxus* at 5-250 m, *B. malevici* at 2-1450 m, *B. exilis* at 5-500 m, *B. digitatus* at 7-200 m, *B. cristatus* at 5-500 m).

Various benthic organisms may also have invaded greater depths in a passive way, for example together with the abrupt sinking of parts of the lake bottom. The

populations finding themselves at larger depths, started an adaptive radiation (very characteristic of the genus *Baikalodrilus*) under the influence of a changing environment. Most likely, the formation of the deep-water groups of *B. discolor* and *B. exilis* began in this period. At the same time, large areas near the shore offered new biotopes, e.g. gravel, boulders and rocks. Settling in these regions was connected to adjusting to a harsh temperature regime with strong diurnal and seasonal fluctuations, followed by the differentiation of new taxa. One of the possible adaptations was dwarf size, which enabled species to live within coarse sediments. The predecessors of *Baikalodrilus phreodriloides* and *B. kozovi* may have evolved under such circumstances.

In the Early and Middle Pleistocene (0.8-0.15 million years ago), South and Middle Baikal became very deep (over 500 m), while North Baikal also deepened; later on all three parts became united. Drastic climatic fluctuations were characteristic of this period, severe glaciations repeatedly alternated with interglacial times, similar to the present one with respect to annual temperature. Maximum glaciation occurred during the second half of the Pleistocene (Osadchiy, 1989), when glaciers reached Lake Baikal waters twice (Mats, 1987).

As a result of the gradually cooling climate, a great deal of the common Siberian hydrofauna was extinguished. Many species only survived as relicts in deep lakes. In Lake Baikal, which has been very deep since the Middle Pleistocene, representatives of the Siberian fauna survived glaciations because they became adapted to the deep-water environment, side by side with numerous autochtonous species. Due to increasing depth and active orogeny, perturbations of biocoenoses often occurred. These were accompanied by the appearance of new ecological niches and adaptive zones. Oxygen saturation, low mineralization and positive temperatures at all water depths favoured the colonization of new biotopes. All these processes resulted in the accelerated evolution of organisms and a quick adaptive radiation of many animal groups.

In the Pleistocene several species of the genus *Baikalodrilus* (*B. malevici, B. werestschagini, B. exilis, B. cristatus, B. discolor acinacifer*) colonised the biotopes at depths of 500 m or more. Some other species (*B. multicrystallifer, B. intermedius, B. digitatus, B. d. discolor, B. paradoxus*) thrived at depths of 100-500 m. Most of these are eurybathic species, widely distributed in Lake Baikal. Genuine deep-water forms, such as *B. intermedius* (found only at 240 m depth) and *B. discolor acinacifer* (100-500 m) are quite rare, and few in number. The latter two species, together with some inhabitants of the middle and large depth zones, such as *B. multicrystallifer* (50-120 m), *B. d. discolor* (5-360 m), *B. d. brevipectinatus* (43 m), and *B. crassus* (13-50 m), already show a considerable deviation from the hypothetical ancestor. They exhibit several of the different specializations, peculiar to Baikalian deep-water oligochaetes, e. g. gigantism, nanism, improvements in integument structure,elongated and thin ventral crotchets, general simplification of the setal apparatus. Some deep-water taxa seem to be rather young, their morphological differences being insufficient for a species designation (e.g. subspecies of *B. discolor*). Many other species are well-defined and were probably established a long time ago.

In the Late Pleistocene and Holocene (the last 150,000 years) Baikal consisted of a single very deep lake. The climate gradually warmed up, with a maximum 8000-4000 years ago. The melting of glaciers and the rise of the water level facilited, as in warm interglacial periods, the dispersion of animals over the whole lake, the colonization of the shallows, and perhaps also speciation by means of hybridization.

When discussing the autochtonous speciation process in Lake Baikal Kozhov (1962) emphasized that the majority of endemic species and genera do not occur in near-shore shallow areas, but at depths of 8-200 m. Apparently, this zone is the original center for most Baikalian endemics, including the contemporary shallow-water fauna. Most of the *Baikalodrilus* species dwell within the above mentioned depth range (Table 1). Even those species found considerably deeper, are most abundant between 5-10 and 100 m of depth. The near-shore zone of the open lake is inhabited either by the most eurybiont species, or by a few highly specialized shallow-water forms.

The littoral (0-20m deep) and the sublittoral (20-70 m) exhibit a large variety of bottom sediments. The littoral of the open lake is mostly paved with rocks and stones, alternating with coarse sand. Near the mouth of large effluents or in shallow bays, the stony bottom is interrupted by large scale sandy and muddy areas, extending from the shore up to maximum depths. *Baikalodrilus paradoxus* is widely distributed near river-mouths at depths of 5-250 m. In large shallows at the mouth of the Selenga River, at 8-50 m depth, besides *B. paradoxus,* also *B. undatus, B. scaphoideus, B. bifidus,* and *B. crassus* occur.

B. paradoxus and its close relatives are sluggish, like many other armoured tubificids. Possibly, they spend some time on the surface of the substrate, as individuals with a regenerating anterior end are often encountered, probably bitten off by some predator. Usually tubificid predators only attack the tail when it is stretched out above the sediment (Poddubnaya, 1962; Wiśniewski, 1978). An asexual mode of reproduction by means of fragmentation is another possible explanation for the anterior regenerating segments. Mature individuals in the abundant species, *B. paradoxus,* are rare. This seems to support the latter hypothesis, however, no direct evidence exists.

In the sandy littoral zone of North Baikal, washed by waves and underwater currents, large sickle-shaped ventral crotchets evolved in *Baikalodrilus falcatus* and

Table 1.
Depth range and sediment types inhabited by different species and subspecies of the genus *Baikalodrilus*.

Group	Taxon	Depth, m	Sediments
Littoral	*B. kozovi*	3.4-6	s
	B. phreodriloides	2-18	r, s, ms
	B. undatus	8	ms
	B. solitarius	10	ms
	B. bifidus	18	ms
	B. scaphoideus	18	msd
	B. medianus	18	ms
	B. falcatus	18	ms
	B. bekmanae	5-20	s, ms
Sublittoral	*B. crassus*	13-50	s, ms
	B. discolor brevipectinatus	43	m
Eurybathic and eurybiont	*B. inflatus*	1-300	r, s, ms
	B. paradoxus	5-250	s, ms, m, md
	B. digitatus	5-200	s, ms, md
	B. cristatus	5-500	s, ms
	B. exilis	5-500	s, ms, m, msd
	B. werestschagini	3-1410	ms, m
	B. malevici	2-1450	r, s, ms, m, md
	B. discolor discolor	5-360	m, md
Deep-water	*B. multicrystallifer*	50-120	s, m
	B. discolor acinacifer	100-500	ms, m
	B. intermedius	240	m

Abbreviations of sediment types : m - mud; md - mud with detritus; ms - muddy sand; msd - muddy sand with detritus; r - rocks and stones; s - sand.

B. bekmanae, probably for attachment to the bottom. This adaptive process correlates with a general simplification in the setal apparatus : the number of ventral setae has decreased up to the loss of several mid-body bundles in *B. bekmanae*, while pectinates have become sparse and small in *B. falcatus*.

Baikalodrilus kozovi represents another form shaped by incessant wave action on coarse and medium littoral sands in South Baikal. This worm is similar in size and shape to a sand grain; when rolling together with moving sand, it always remains on the surface of the bottom due to its smaller specific weight. The armour protects it from friction from the sand grains.

Baikalodrilus phreodriloides has adapted to life among algal periphyton on the rocks of South Baikal. It is a little larger and more slender than *B. kozovi*, while its armour is thin and flexible, enabling the worm to move within algal mats. Its peculiar hooked hair setae may have some function in the fixation of the crawling animal to algae.

Deep-water life gave rise to several physiological changes in animals such as slow growth, late maturation, a different life cycle, followed by different new morphological characters. Two trends can be distinguished in the evolution of *Baikalodrilus* in deep-water biotopes. The first branch is formed by species equipped with simple needle setae in dorsal bundles, and simple sabre-shaped ventral crotchets. This branch consists of *B. malevici*, *B. multicrystallifer*, *B. solitarius*, and *B. discolor*. The body size of this species group increases with increasing depth of the biotope and the degree of specialization.

The second branch is formed by small worms with a short body and delicate ventral setae of two kinds, simple and bifid, the latter with the proximal tooth gradually disappearing caudad. This branch consists of *B. intermedius*, *B. exilis*, *B. cristatus*, *B. digitatus*, *B. werestschagini*, *B. kozovi*, and *B. phreodriloides*. The two latter species are littoral, but probably evolved from deep-water ancestors, who returned to shallow water. This group evolved towards a diminishing of body dimensions. Small size facilitated sheltering within coarse sediment. This was important in escaping from abundant predators, as the armour alone (especially when becoming thinner at large depths) was not sufficient to protect

individuals. For example, *B. exilis* living at depths of 5-500 m is ten times smaller than *B. paradoxus*, with a thin and flexible armour, suitable for easy crawling in sediment.

Baikalodrilus cristatus and *B. digitatus* were collected from dense sediments tightened by currents, sediments in which small worms would find it difficult or impossible to burrow. Their bulky secretory papillae give additional weight, preventing the worms from being carried away by currents, and maybe also from falling prey to smaller predators. The strong protective armour of *B. werestschagini* (0.2-0.25 mm thick, possibly the thickest among Oligochaeta) consists of moderatly high but fused secretory papillae. A detailed morphological study of the closely related species of *Baikalodrilus* which replace each other at different depths, confirms the statement of KOZHOV (1962) that Lake Baikal was colonized by different animal groups starting from the littoral, while the main species radiation occurred in the deeper zones.

Evolutionary changes in the morphology of the species of *Baikalodrilus* are in accordance with the principle of DOGEL (1954) on the oligomerization of homologous organs. The number of segments, setae, etc. tends to decrease, while their place and function become more exactly established (Table 2).

Table 2.
Some tendencies of oligomerization in the genus *Baikalodrilus*.

Taxon	Number of segments	Shape and number of setae in : dorsal bundles	ventral bundles
B. inflatus	120-140	hair 2-4 + pect. many	bifid 3-4
B. crassus	70-72	plumose hair 4-5 + pect. 4	simple + bifid or short teeth 6-7 + long teeth
B. bifidus	56-60	plumose hair 2-3 + equal bifid 4	simple + bifid 2 1 (2)
B. paradoxus	67-72	plumose hair 2-3 + pect. 2-3	simple + bifid 1 2 (1)
B. scaphoideus	?	plumose hair 2-3 + pect. 2-3	simple + bifid or both bifid 1 1
B. undatus	?	plumose hair 2 (1) + pect. 2 (1)	simple + bifid 1 1
B. medianus	50	plumose hair 3-4 + pect. and bifid 3-4	simple + bifid 2 (1) 1
B. malevici	41-45	plumose hair 5-6 + needle 3-4	simple 2
B. solitarius	?	plumose hair 2 + needle 3	simple 2
B. multicrystallifer	47-62	slightly plumose hair 2-4 + needle 2	simple 2 (4)

Table 2.
Some tendencies of oligomerization in the genus *Baikalodrilus*.

Taxon	Number of segments	Shape and number of setae in : dorsal bundles		ventral bundles
B. discolor brevipectinatus	68	slightly plumose hair 2-5	+ pect. 3-6	simple 2-3
B. discolor acinacifer	> 80	smooth hair 2-3	+ blunt needle 2	simple 2-3
B. discolor discolor	60-62	smooth hair 2-3	+ needle 2	simple 2-3
B. bekmanae	58-62	plumose hair 4-5	+ pect. 4-5	simple or sickle 0-2
B. falcatus	28	smooth hair 2	+ reduced bifid 2	sickle 1
B. intermedius	20-27	slightly plumose hair 1	+ bifid or needle 1	simple or reduced bifid 2
B. exilis	17-20	slightly plumose hair 1	+ needle 1	simple + bifid 1 1
B. cristatus	23-25	smooth hair 1	+ needle 1	simple + bifid 1 1
B. cristatus	23-25	smooth hair 1	+ needle 1	simple + bifid 1 1
B. digitatus	20	smooth hair 1	+ reduced bifid 1	simple + bifid 1 1
B. werestschagini	26-29	plumose hair 1 (2)	+ needle 1	simple + bifid 1 1
B. phreodriloides	24-25	hooked smooth hair 1	needle or reduced + bifid 1	simple + bifid 1 (2) 1 (2)
B. kozovi	16	hair 1	+ bifid 1	? 2

The most primitive littoral and sublittoral species of *Baikalodrilus* have a large number of segments (56-72, in *B. inflatus* even 120-140), pectinate (except *B. undatus*) and plumose hair setae, while the ventral bundles contain both simple and bifid crotchets. Some individuals of *B. crassus* and *B. scaphoideus* have only bifids in separate ventral bundles, while *B. inflatus* is said to have only bifid ventral crotchets (MICHAELSEN, 1901). Bifid crotchets appear to be a primitive character in the genus, *B. inflatus* being closest to the common ancestor of the genus. Further oligomerization in the segment number and setae seems to have progressed in the following order : *B. crassus, B. bifidus, B. paradoxus, B. scaphoideus, B. undatus, B. medianus.*

In the more advanced, large species of probable deep-water origin (*B. malevici, B. discolor, B. solitarius, B. multicrystallifer*), the dorsal pectinate setae gradually turn into simple needles, while only simple crotchets remain in the ventral bundles. In the specialized shallow-water forms, *B. bekmanae* and *B. falcatus,* these crotchets undergo a further change to become sickle-shaped. The dwarf species, *B. intermedius, B. exilis, B. cristatus, B. digitatus, B. werestschagini, B. phreodriloides,* and *B. kozovi,* exhibit a minimal segment number (16-29), and usually only two setae of different types per bundle. No pectinates have been found in these species. The ventral bundles contain usually one simple and one bifid crotchet, the latter often with a longer distal tooth.

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