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**TASSERKIDRILUS ACAPILLATUS
(FINOGENOVA, 1972) IN LAKE PEIPSI, WITH A REVISION
OF THE GENUS TASSERKIDRILUS HOLMQUIST, 1985
(OLIGOCHAETA, TUBIFICIDAE)**

Introduction

Lately several mature tubificids were found in Lake Peipsi, belonging to a rare species known here so far only in the juvenile, indeterminable stage. The species proved to be close to *Tubifex kessleri* Hrabě, 1962 described on a single specimen from Lake Onega (Грабье, 1962) but not identical with it. Several subspecies of *T. kessleri* or its relatives are known from Lake Baikal and some other Asian and North American lakes. Peipsi worms seem to be identical to *T. acapillatus* Finogenova, 1972 described from the Caspian Sea and found later also in Lake Baikal.

The so-called *Tubifex kessleri* assemblage is best represented in Baikal where the discrimination of individual species can sometimes be rather difficult (Семерной, 1982; Brinkhurst, 1984). The recent revision of the genus *Tubifex* by Ch. Holmquist (1985) did not include all species of this assemblage but isolated some of them in a new genus, *Tasserkidrilus*. Below I shall try to accomplish, besides the description of the Peipsi worms, also Holmquist's revision with respect to the genus *Tasserkidrilus*.

Acknowledgements

The former postgraduate student Henn Timm (Institute of Zoology and Botany) supplied me with the seasonal samples from Lake Peipsi in 1984—1986. Cand. biol. L. N. Snimschikova (Listvyanka on the Baikal) and cand. biol. V. P. Semernoy (Yaroslavl) donated some specimens of related oligochaete taxa from Lake Baikal, and Prof. R. O. Brinkhurst (Sidney, Canada) a whole mount of *Tubifex kessleri americanus*. Cand. biol. N. P. Finogenova (Leningrad) restudied, together with me, her type material of *T. acapillatus*. She, as well as L. N. Snimschikova and V. P. Semernoy kindly read the preliminary manuscript and helped me with their valuable criticism.

***Tasserkidrilus acapillatus* (Finogenova, 1972)**

Tubifex acapillatus: Финогенова, 1972; Brinkhurst, 1984. *Isochaetides acapillatus*: Hrabě, 1982. *Tasserkidrilus acapillatus*: Тимм, Финогенова, 1987. *Tubifex kessleri variabilis*: Семерной, 1982. *Tubifex kessleri*, forms with bifid setae: Brinkhurst, 1984. *Tubifex superiorensis* (partim, only in Baikal): Brinkhurst, 1984. (?) *Limnodrilus infundibuliferus*: Изосимов, 1972; Izosimov, 1980.

Over 100 specimens (preserved in ethanole) were found in 36 samples collected in 1970—1987 on 5 sampling spots in the sublittoral of Lake Peipsi, on the muddy or clean sand at a depth of 2—7.3 m. Most of them

originate from the seasonal samples of 1984—1986 collected by H. Timm. Six mature specimens were studied on microtome sections, and one was dissected (by L. N. Snimschikova), while 32 juvenile or maturing ones are maintained as whole mounts in Canada balsam. A living mature worm caught on Feb. 5, 1987 was briefly studied under microscope and then placed in a small aquarium together with a juvenile one; they survived at least up to June.

Complete worms are 5—10.5 mm long and consist of up to 65 segments, usually of 26—41. The anterior end of the body is sharp (Fig. 1): prostomium conical (120—175 μm long and 120—190 μm high), the height of the body in slightly compressed whole mounts gradually increases from 0.25 mm (segment I) to 0.5—0.6 mm (VII—IX). Genital region and especially tail are thinner. Body wall is smooth and compact, intersegmental grooves poorly developed. Segments II—V are ventrally double-ringed, the first ring being shorter (Fig. 1). Living worms appear red-coloured.

Bifid crotchets similar on the dorsal and ventral side, 2—6 (usually 3—4) per bundle on anteclytellar segments and 1—3 behind clitellum. Mature specimens miss ventral setae of XI. The length of bifid setae is 45—70 μm on II and 55—110 μm on the following segments, with a maximum usually on V—VII. They are 2.5 μm thick, lower tooth being 3 μm long, and upper, straighter and thinner tooth 5 μm (Fig. 1). No intermediate teeth. Very rarely (so far only in three specimens) some single, small hair setae were observed in dorsal bundles of V, VII, XII, or XVIII segment. They are 170—225 μm long and up to 1 μm thick.

Spermathecal pores on X segment, on lateral line; male pores replace lacking ventral setae of XI. Weakly developed clitellum on XI—XII.

Pharyngeal glands lie over pharynx roof in II—III, in the shape of flat longitudinal lobes, up to 8 of them simultaneously visible on a transversal section. Oesophageal glands amorphous, in IV—V. Chloragogen tissue covers oesophagus starting from VI; intestine begins in VIII.

Transversal vessels form long loops in the body cavity of IV—VII; they are thickened as "hearts" in VIII and, to a smaller extent, in IX. The first pair of nephridia was found in VIII.

Gonads and male ducts are paired. Testes in X, unpaired anterior sperm sac in IX, the posterior one extending backwards by some segments. Cup-shaped sperm funnel is about 100 μm broad when not compressed, its wall being 18 μm thick. Vas deferens is nearly 1 mm long (4.5 times longer than the atrium), ciliated to the full extent. Its first, most distinctly ciliated third is about 20 (15—30) μm thick and bows itself over atrium in the dorsal half of the XI segment. The second part is longer and thicker (35—45 μm , with lumen up to 15 μm wide), forming several loops in the posterior part of the segment. Cilia in this region are short, perpendicular to the wall, sometimes apparently stuck together in a granular layer. Often a third, short and narrow (20 μm) part of vas deferens occurs, regarded as a specific character by both N. P. Finogenova and S. Hrabě. However, the broad part also can immediately discharge in the apical end of atrium (proved to be so even in the holotype).

Atrium is short (220 μm), bent, tubular. Not more than 35 μm broad proximally, it enlarges up to 50 μm (with lumen of 15—20 μm) in its distal part. Its wall consists of large granulated epithelial cells and of a very thin external muscular layer. Granulated secretion partially fills atrial lumen. Bulky, short-stalked prostate gland, substantially embracing atrium, discharges laterally in its middle region. Distal, broader end of atrium clings to penial sac and communicates with penis either immediately or by a very short and fine juncture (Fig. 2).

Penial sac is voluminous, thick-walled, with irregular folds on the

internal side. Separate muscles bind its proximal end with the dorsal part of the body wall. Long, thin conical penis lies loosely in cuticular sheath of very characteristic configuration (funnel-like basis; tubular prolongation with a more or less distinct expansion; narrow, blind beak-shaped endpiece). The sheath is 130—150 μm long, and 60—70 μm broad on its basis. Its expanded part bears a lateral broad, thin-edged opening barely visible even on whole mounts, but usually overlooked on sections (among these on the type material by N. P. Finogenova). This rather gentle penial sheath can be easily deformed during the preparation, as we see on a series of drawings by R. O. Brinkhurst (1984).

Ovaries in XII, female funnels not found, ovisac present.

Both spermathecae lie in X, touching each other above the intestine. Ampulla is mostly bipartite, its single-layer wall being 15—30 μm thick and internally folded when empty, but only about 5 μm thick in full spermathecae. Spermatozeugmata are long, tubular, expanded on their one end. Thick-walled spermathecal duct is about 100 μm long (up to 180 μm) and 40—60 μm thick (Fig. 2).

T. acapillatus lives in Lake Peipsi on the muddy or clean sand of the sublittoral only. Such a distribution is characteristic of oxyphilous species. It breeds in winter or in early spring: fully mature worms with full spermathecae were found in November, February, April and May, maturing specimens also in September and October. In summer only juveniles were observed.

The immature *T. acapillatus* can be confused here with the young of *Potamothrix moldaviensis*, but have a more pointed anterior end, more smooth and compact body, a smaller number of setae per bundle and the longer upper tooth of setae.

The species is known, besides Lake Peipsi, also in the Caspian Sea, from the sandy mud at a depth of 195 m (Финогенова, 1972), and in Lake Baikal near Solzan, from somewhat muddy sand at a depth of 4—60 m (Hrabě, 1982). Worms from all three lakes are identical according to their genital apparatus. In fact, neither N. P. Finogenova nor S. Hrabě have mentioned the ciliation of the vas deferens. However, Fig. 1 in the original description (Финогенова, 1972) shows both the narrow and thick part of the vas deferens ciliated, the cilia of the latter forming a continuous, transparent layer. The total ciliation of the vas deferens distinguishes *T. acapillatus* from the other species of the genus *Tasserkidrilus* (except *T. hrabei*) in which allegedly only the proximal, narrow part of the duct is ciliated. (Perhaps some researchers were confused by the change of the appearance of ciliation?). Both authors note the peculiar tripartition of the vas deferens. Nevertheless, the third, narrow part of the vas deferens is not a constant character. The rare, hardly visible hair setae were not described in this species so far and can be regarded as an atavism.

The variable and abundant assemblage of Baikalian worms described as *Tubifex kessleri variabilis* by V. P. Semernoy (Семерной, 1982) and as "*T. kessleri*, forms with bifid setae" by R. O. Brinkhurst (1984), is morphologically identical to *Tasserkidrilus acapillatus*, as well. Three mature specimens determined as *Tubifex kessleri variabilis* by L. N. Snimshikova and sectioned by me, demonstrated just the same character of ciliation in their vasa deferentia, while the spermathecal ampullae were either single or bipartite (the original description by V. P. Semernoy states that the distal part of vas deferens is unciliated, and the spermatheca has a rounded ampulla). Two of the juveniles in a whole mount obtained from L. N. Snimshikova had even several single hair setae. All the other differences between these taxa are minute and base on rather variable characters.

No real morphological differences are either perceived between *Tasserkidrilus acapillatus* (or *variabilis*), the Baikalian specimens named as *Tubifex superiorenensis* by Brinkhurst (1984), and the inadequately described *Limnodrilus infundibuliferus* Isossimov. However, several important characters are not known for those forms, e.g. the position of spermathecal pores.

Tasserkidrilus acapillatus (together with *Tubifex kessleri variabilis* as its synonym) has a penial sheath and other parts of the reproductive system strikingly similar to *T. kessleri* from Lake Onega and *T. k. baicalensis* Semernoy, 1982 from Lake Baikal (Fig. 1). In fact, they differ mostly in reference to their setal apparatus and could be regarded as the subspecies of one species, as V. P. Semernoy did (Семерной, 1982). Nevertheless, the extensive sympatric coexistence of two of these taxa (*acapillatus* and *baicalensis*) in Baikal demonstrates their genetical isolation as separate species. Therefore I also refrain from a rash connection of *T. acapillatus* with *T. kessleri* as a subspecies, before a thorough re-examination of the Onega population.

Genus *Tasserkidrilus* Holmquist, 1985, emend.

The genus was created by Ch. Holmquist (1985) for the species *Tubifex americanus*, *kessleri* and, with some hesitation, also for *montanus* and *hrabei*. Among the generic characters proposed by her, the peculiar shape of the penial sheath, the short tubular or spindle-shaped atrium with the apical mouth of the vas deferens, lateral spermathecal pores without any modified setae, and the lack of ventral setae in XI seem to be most valuable.

Some other characters should be rejected when we include in this genus also the species *acapillatus* and its probable synonym *variabilis* with their penial sheaths just of the *kessleri* type. These discarded characters are: the obligatory presence of hair and pectinate setae, the restriction of ciliation to the proximal part of the vas deferens, the narrowing of the atrium on its distal end, the different histological structure of different sections of the atrium, circular folds of the penial sac, a very short spermathecal duct and its opening always on the lateral line. Spermathecal pores lie below the lateral line even in the Kamchatka populations of the type species *T. americanus* (Сокольская, 1973, 1983).

Emended diagnosis of the genus *Tasserkidrilus* Holmquist, 1985. Genus of the subfamily *Tubificinae*. Body wall without papillae. Bifurcate chaetae present, sometimes together with pectinate and hair setae. No genital setae; ventral setae of XI lacking in mature specimens. Vas deferens at least two times longer than atrium, consists of 2—3 regions of different thickness, partially or thoroughly ciliated. Atrium tubular or spindle-shaped, vas deferens discharging in it apically, and the bulky, stalked prostate gland in the middle or in the distal part. Ejaculatory duct vestigial or lacking. Penis in a cuticular sheath of a specific shape (funnel-like basis, asymmetrical tubular prolongation, distal opening directed sideways). Voluminous penial sac can have some internal folds. Spermathecal ampulla large, either compact or bipartite; the thick-walled duct opens on the lateral line or somewhat lower. Spermatozeugmata present.

6 known species correspond to this diagnosis.

Type species: *Tasserkidrilus americanus* (Brinkhurst et Cook, 1966). (*Tubifex kessleri americanus*: Brinkhurst, Cook, 1966; Brinkhurst, Jamieson, 1971; Сокольская, 1973, 1983; Морев, 1983. *Tasserkidrilus kessleri americanus*: Brinkhurst, 1986. *Tasserkidrilus americanus*: Holmquist, 1985). Distribution: North America (Great Lakes and several other lakes), Chukotka, Kamchatka.

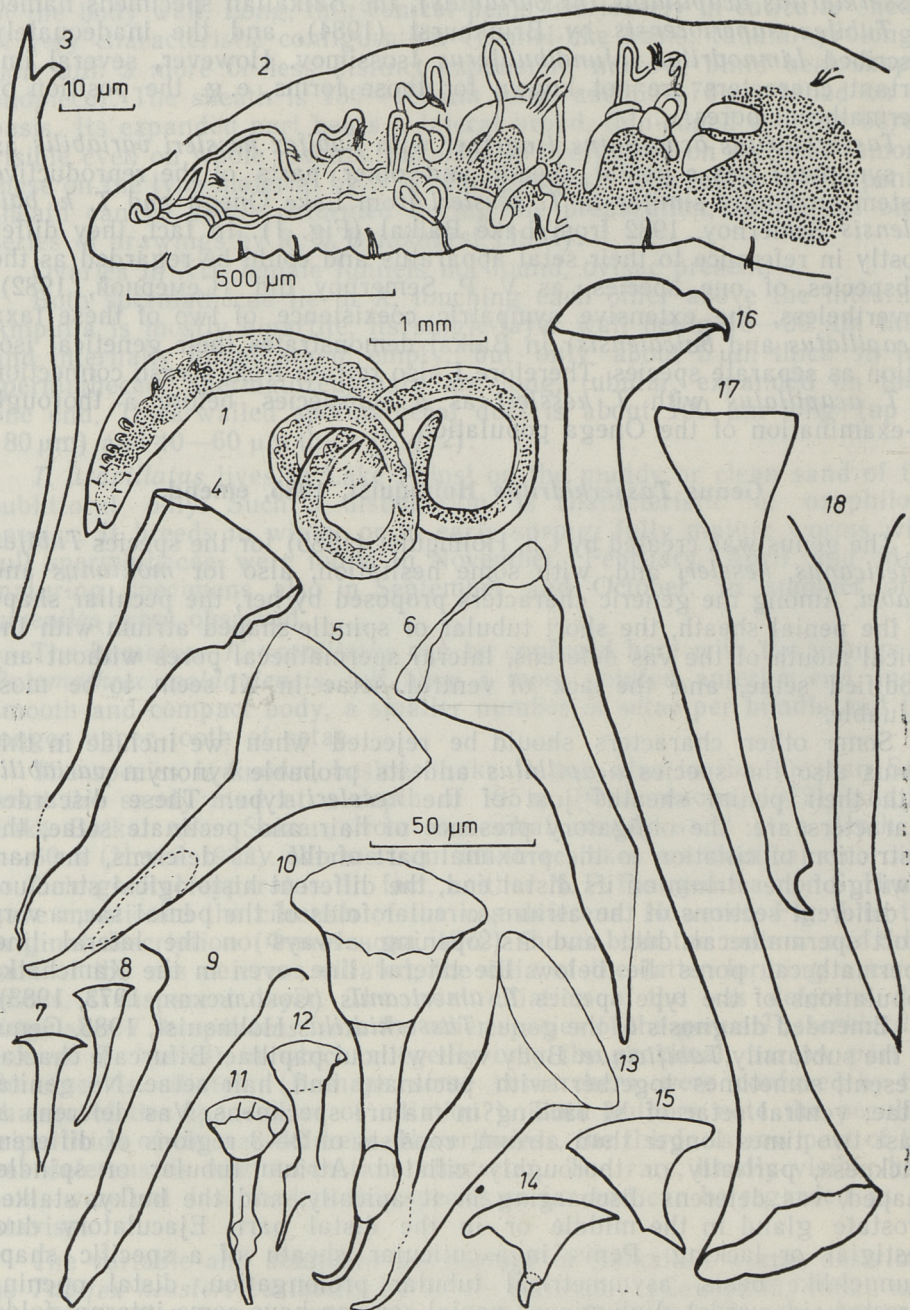


Fig. 1. External characters of *Tasserkidrilus acapillatus* from Lake Peipsi and penial sheaths of different *Tasserkidrilus* species. 1-6: *T. acapillatus* from Lake Peipsi (1 - general appearance; 2 - anterior end of the body in a whole mount; 3 - chaeta; 4-6 - penial sheaths, orig.). 7-18: Penial sheaths of different species (7-8 - *T. acapillatus* from Lake Baikal, after Hrabě, 1982; 9 - *T. acapillatus* from the Caspian Sea, after Финногорова, 1972; 10 - *T. acapillatus* from Lake Baikal, determined as *Tubifex kessleri variabilis*, orig.; 11-12 - *T. kessleri*, after Грабье, 1962; 13 - *T. baicalensis*, orig.; 14-15 - *T. hrabei*, after Сокольская, 1973; 16 - *T. mirandus*, orig.; 17-18 - *T. americanus*, orig.). Scales for the original drawings only.

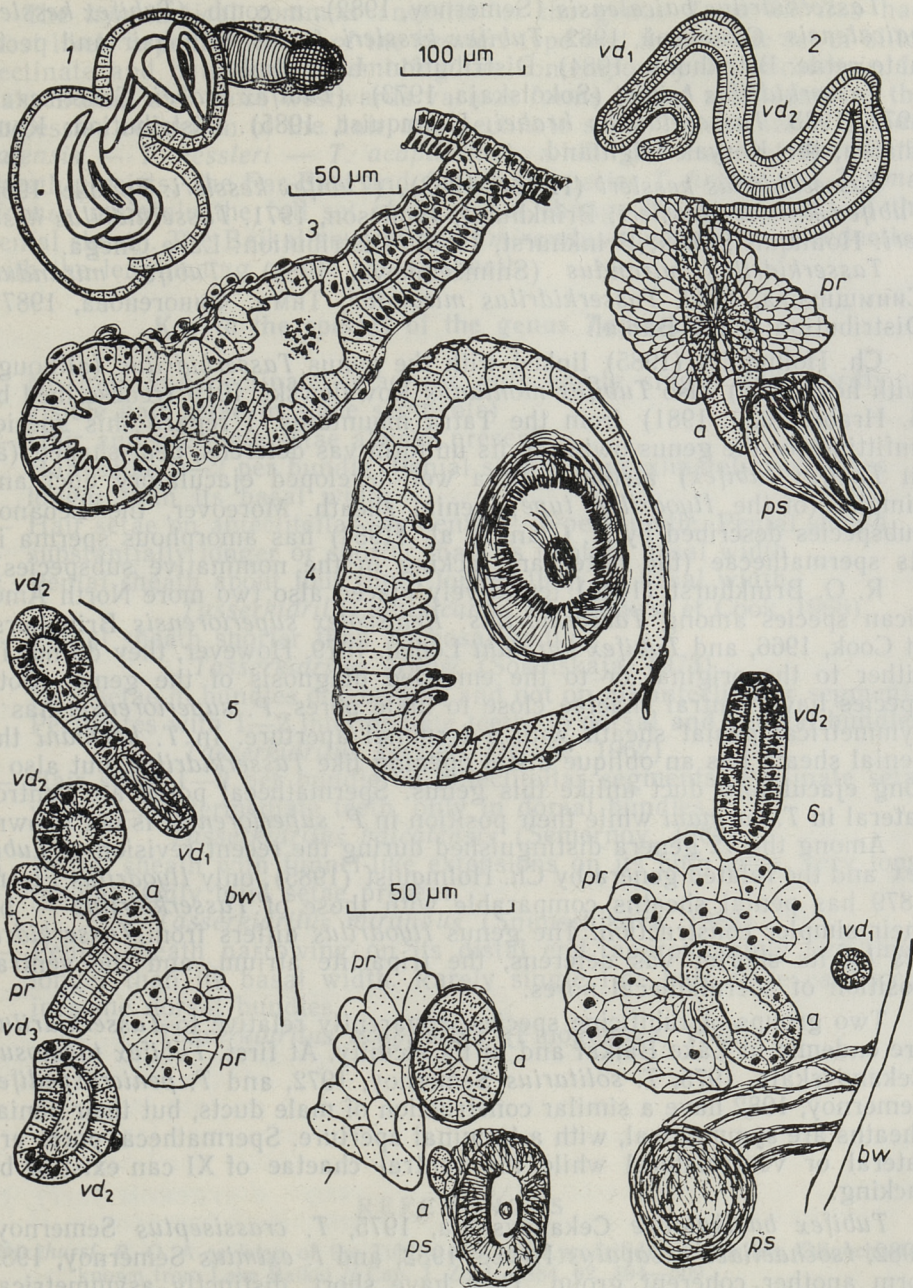


Fig. 2. Details of the genital apparatus of *Tasserkidrilus acapillatus* from Lake Peipsi, on a dissected specimen (1-2) and on microtome sections (3-7). 1 - spermatheca with spermatozeugmata; 2 - male duct (without funnel); 3 - longitudinal section of an empty spermatheca; 4 - cross section of spermathecal ampulla with spermatozeugma; 5 - three different parts of vas deferens and discharge of the third part into atrium; 6 - discharge of prostate gland into atrium; 7 - junction of atrium before its discharge into penis, and a cross section of penial sac. Orig. a - atrium, bw - body wall, pr - prostate gland, ps - penial sac with penis and penial sheath; vd₁, vd₂, vd₃ - successive parts of vas deferens.

Tasserkidrilus acapillatus (Finogenova, 1972). For synonyms see above. Distribution: the Caspian Sea, Lake Baikal together with the Angara River and the Bratsk Reservoir, Lake Peipsi.

Tasserkidrilus baicalensis (Semernoy, 1982), n. comb. (*Tubifex kessleri baicalensis*: Семерной, 1982. *Tubifex kessleri*, forms with hair and pectinate setae: Brinkhurst, 1984). Distribution: Lake Baikal.

Tasserkidrilus hrabei (Sokolskaja, 1973). (*Tubifex hrabei*: Сокольская, 1973, 1983. *Tasserkidrilus hrabei*: Holmquist, 1985). Distribution: Камчатка, the Koryak Highland.

Tasserkidrilus kessleri (Hrabě, 1962). (*Tubifex kessleri*: Грабье, 1962. *Tubifex kessleri kessleri*: Brinkhurst, Jamieson, 1971. *Tasserkidrilus kessleri*: Holmquist, 1985; Brinkhurst, 1986). Distribution: Lake Onega.

Tasserkidrilus mirandus (Snimschikova, 1982). (*Tubifex mirandus*: СНИМЩИКОВА, 1982. *Tasserkidrilus mirandus*: ТИММ, ФИНОГЕНОВА, 1987). Distribution: Lake Baikal.

Ch. Holmquist (1985) linked with the genus *Tasserkidrilus* (although with hesitation) also *Tubifex montanus* Kowalewski, 1919 (redescribed by S. Hrabě, 1939, 1981) from the Tatra mountains. I regard this species unfitting for the genus owing to its uniform vas deferens, pear-shaped (as in *Tubifex tubifex*) atrium with a well-developed ejaculatory duct and simpler (of the *Ilyodrilus* type) penial sheath. Moreover, the Lebanon subspecies described by N. Giani et al. (1984) has amorphous sperma in its spermathecae (the latter are lacking in the nominative subspecies).

R. O. Brinkhurst (1986) tentatively placed also two more North American species among *Tasserkidrilus*: *Peloscolex superiorenensis* Brinkhurst et Cook, 1966, and *Tubifex harmani* Loden, 1979. However, they do not fit either to the original or to the emended diagnosis of the genus. Both species have ventral chaetae close to male pores. *P. superiorenensis* has a symmetrical penial sheath with a terminal aperture. In *T. harmani* the penial sheath has an oblique distal opening like *Tasserkidrilus*, but also a long ejaculatory duct unlike this genus. Spermathecal pores are ventrolateral in *T. harmani* while their position in *P. superiorenensis* is not known.

Among the 12 genera distinguished during the recent revision of *Tubifex* and the related genera by Ch. Holmquist (1985), only *Ilyodrilus* Eisen, 1879 has penial sheaths comparable with those of *Tasserkidrilus* — by their simpler construction. The genus *Ilyodrilus* differs from *Tasserkidrilus* by its shorter vas deferens, the tripartite atrium, and the ventral position of spermathecal pores.

Two groups of tubificine species, apparently relative to *Tasserkidrilus* are endemic in Lake Baikal and in its vicinity. At first, *Tubifex taediosus* Cekanovskaja, 1975, *T. solitarius* Semernoy, 1972, and *T. penicraspedifer* Semernoy, 1982 have a similar construction of male ducts, but their penial sheaths are symmetrical, with a terminal aperture. Spermathecal pores are lateral or ventrolateral while the ventral chaetae of XI can exist or be lacking.

Tubifex bazikalovae Cekanovskaja, 1975, *T. crassiseptus* Semernoy, 1982, *Isochaetides excavatus* Hrabě, 1982, and *I. eximius* Semernoy, 1982 form another coherent group. They have short, distinctly asymmetrical penial sheaths like *Tasserkidrilus hrabei*. Spermathecal pores can be either lateral or ventral while the ventral chaetae are always lacking near the male pores on XI. This group deviates from *Tasserkidrilus* in our sense by having a retort-shaped atrium with a subapical discharge of the vas deferens.

The distribution range of the genus *Tasserkidrilus* comprises many relatively large and cool lakes of the northern hemisphere. The richest in species is Lake Baikal but that does not mean that the genus has originated from here. Probably local endemic forms *T. mirandus*, *T. baicalen-*

sis and various morphs of *T. kessleri variabilis* (= *acapillatus*) mentioned by V. P. Semernoy (Семерной, 1982) should be regarded as the result of the accelerated evolution taking place in this peculiar lake (Лукин, 1986).

The hypothetical common ancestor of the genus *Tasserkidrilus* had most likely a penial sheath of the *kessleri* type and a complete set of bifid, pectinate and hair setae resembling the contemporary *T. baicalensis*. In Lake Baikal and more westwards various forms reveal a tendency of the successive reduction of the hair and pectinate setae (in the series *T. baicalensis* — *T. kessleri* — *T. acapillatus*), while the shape of the penial sheath persists. The Far-East and American species *T. hrabei* and *T. americanus* maintain the full set of setae but change the proportions of the penial sheath. The Baikalian species *T. mirandus* combines setal reduction with the lengthening of the penial sheath.

Key to the species of the genus *Tasserkidrilus*

1. No hair and pectinate setae (or only rarely single fine, hardly visible hair setae in some segments) 5
— Hair and pectinate setae always present 2
2. Hair setae 1—2 per bundle. Penial sheath approximately two times longer than its basal width 4
— Hair setae on antecitellar segments 2—5 per bundle. Penial sheath substantially longer or shorter than its twofold basal width . . . 3
3. Penial sheath about four times longer than its basal width.
Tasserkidrilus americanus (Brinkhurst et Cook, 1966).
— Penial sheath shorter than its basal width.
Tasserkidrilus hrabei (Sokolskaja, 1973).
4. Hair setae in bundles one by one, and not on all antecitellar segments. Pectinates with 1—2 intermediate teeth, in dorsal and ventral bundles.
Tasserkidrilus kessleri (Hrabě, 1962).
— Hair setae 1—2 per bundle on antecitellar segments. Pectinate setae with 2—3 intermediate teeth, only in dorsal bundles.
Tasserkidrilus baicalensis (Semernoy, 1982).
5. Penial sheath with funnel-like extensions on its both ends, very long, tubular. Only bifid setae present.
Tasserkidrilus mirandus (Snimschikova, 1982).
— Penial sheath narrowing on its distal end, approximately two times longer than its basal width. Rarely single fine hair setae can occur in some dorsal bundles.
Tasserkidrilus acapillatus (Finogenova, 1972).

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TASSERKIDRILUS ACAPILLATUS (FINOGENOVA, 1972) PEIPSI JÄRVES NING
PEREKONNA TASSERKIDRILUS HOLMQUIST, 1985 (OLIGOCHAETA,
TUBIFICIDAE) REVISJON

Haruldane, seni vaid Kaspia merest ja Baikalist tuntud väheharjasuss *Tasserkidrilus acapillatus* elab ka Peipsi sublitoraalis, kuid on siin suguküps ja määratav ainult sügise-st kevadeni. Peipsi ja Baikali materjali võrdlev uurimine võimaldas täpsustada liigi ja perekonna kirjeldusi ning sünonüümikat. Uuesti defineeritud ja piiritletud perekonda *Tasserkidrilus* kuulub nüüd 6 liiki.

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TASSERKIDRILUS ACAPILLATUS (FINOGENOVA, 1972) В ЧУДСКОМ ОЗЕРЕ, С
РЕВИЗИЕЙ РОДА TASSERKIDRILUS HOLMQUIST, 1985 (OLIGOCHAETA,
TUBIFICIDAE)

Известный до сих пор только из Каспийского моря и Байкала *Tasserkidrilus acapillatus* обитает и в sublitorали Чудского озера (половозрелым найден только с осени до весны). В результате сравнения особей из Чудского озера и Байкала уточнено описание вида, в том числе установлены сплошная ресничная выстилка семяпровода, непостоянство третьего отдела семяпровода и наличие (изредка) единичных волосных щетинок. Байкальский *Tubifex kessleri variabilis* Sem. считается младшим синонимом *T. acapillatus*. Уточнен диагноз рода *Tasserkidrilus*, недавно выделенного из рода *Tubifex*. Его характерными признаками являются ассимметричный пениальный чехлик; длинный семяпровод, апикально впадающий в трубчатый атрий, лишенный семяизвергательного канала; отсутствие брюшных щетинок XI сегмента. Род *Tasserkidrilus* включает теперь 6 видов: *T. americanus* (Br. et Cook) в качестве типового, *T. acapillatus* (Fin.), *T. baicalensis* (Sem.), *T. hrabei* (Sok.), *T. kessleri* (Hr.), *T. mirandus* (Snim.).