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The genus *Potamothrix* (Annelida, Oligochaeta, Tubificidae): a literature review

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Abstract. Taxonomy and ecology of all 25 valid species of the genus *Potamothrix* are shortly surveyed. Two main specification centres of *Potamothrix* spp. exist: the Ponto-Caspian basin together with the Balkan Peninsula and the Yunnan Plateau lakes in southern China. Some species of the first group are widely dispersed in Europe and on the other continents, mostly with human aid, and often abundant in lakes, rivers, and estuaries. Freshwater, brackish-water, and euryhaline forms are represented. Different combinations of taxonomic characters do not allow dividing the genus into subgenera.

Key words: Tubificidae, *Potamothrix*, taxonomy, ecology, fresh water, brackish water, invasive species.

INTRODUCTION

The genus *Potamothrix* (Vejdovský et Mrázek, 1903) is a monophyletic, well-defined group of the annelid family Tubificidae, subfamily Tubificinae. These worms are smooth-bodied and relatively fragile in comparison with other tubificids, with short postclitellar segments and conical prostomium when fixed in alcohol (Fig. 1, *1*, *2*). The genus is characterized by long hose-like atria, vestigial vasa deferentia, small or completely lacking prostate glands, and presence (in most species) of simple-pointed and distally grooved, often nib-shaped, spermathecal chaetae (Fig. 1, *3–9*). This groove can be actually a thin-walled tube since spermathecal chaetae are supposed to operate as syringes injecting some stimulating compound into the partner's body during copulation (Cuadrado & Martínez-Ansemil 2001). The sperm in spermathecae is always organized into spermatozeugmata consisting of fertilizing and cortex cells.

Potamothrix spp. are an essential component of zoobenthos in many bodies of fresh and brackish water, being a food item for fish and other predators. They have been aligned to different genera in the past while synonymy has created confusion in treating their ecology and distribution. Several species have been used as indicators of water quality and trophic state of lakes (Milbrink 1978, Lang 1998). Some of them appear to be invasive species on different continents (Milbrink 1977, Brinkhurst 1978). Inconsiderate synonymization of some species,

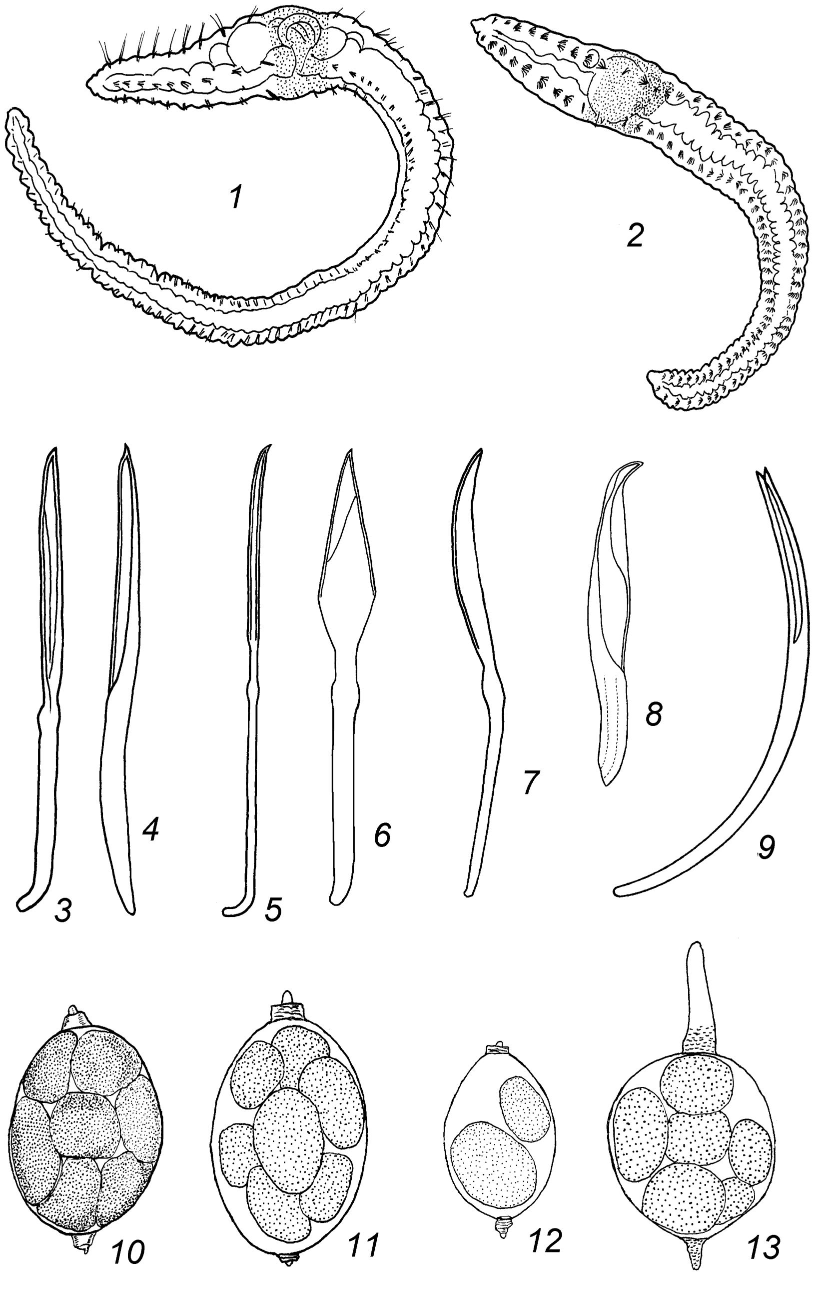

Fig. 1. Whole-mounted specimens: *1 – Potamothrix hammoniensis*, *2 – P. moldaviensis*. Spermathecal chaetae: *3* & *4 – P. hammoniensis* (typical also of several other congeners), *5 – P. heuscheri*, *6 – P. bavaricus*, *7 – P. bedoti*, *8 – P. moldaviensis*, *9 – P. scleropenis*. Egg cocoons: *10 – P. hammoniensis*, *11 – P. vejdovskyi*, *12 – P. bedoti*, *13 – P. moldaviensis* (freed from adhering particles).

e.g., by Brinkhurst (1963, 1971) has caused some confusion with their distribution data. Herewith a short review of taxonomy and ecology of all species of this genus is presented.

Note: in the descriptions of the species, the segment numbers are conventionally denoted with Roman numerals (e.g. X, XI, etc.) and the intersegmental furrows with Arabian numerals (e.g., 10/11).

HISTORY OF THE GENUS

The genus name (meaning 'river thread' in Greek) was coined by Vejdovský & Mrázek (1903) for the species *P. moldaviensis* from the Vltava (Moldau) River; another, the commonest species was described two years earlier from the Elbe River in Hamburg by Michaelsen (1901) as *Ilyodrilus hammoniensis*. Many European species have been described later, particularly by Hrabě (1931, 1941, 1950). These and related species have been erroneously included into the genus *Ilyodrilus* Eisen, 1879 (treated also as a subgenus of the genus *Tubifex* Lamarck, 1816). To separate the group from the original *Ilyodrilus* (sensu stricto), Brinkhurst (1963) introduced the name *Euilyodrilus*, but rejected this later again (Brinkhurst 1971) in favour of the senior synonym *Potamothrix*. Holmquist (1985) revised the genus and used the names *Potamothrix* and *Euilyodrilus* for two subgenera defined by herself (*Euilyodrilus* with a prostate gland on atria, and *Potamothrix* devoid of this gland). Finogenova & Poddubnaja (1990) revised the genus again and, after a closer study, rejected these subgenera as not distinctly delimited from each other. Cui & Wang (2012b) compiled a guide to 26 known species of the genus, erroneously including also *Ilyodrilus svirenkoi* Lastočkin, 1937. The latter was transferred into the genus *Haber*, with some hesitation, already by Holmquist (1979) and, decisively, by Milligan (1986).

Cui & Wang (2005, 2012a) also discovered a separate, apparently monophyletic species group of this genus in ancient lakes of the Yunnan Plateau, southern China (Fig. 2, *3*). In all probability, the common ancestors of the genus *Potamothrix* were connected with the former Tethys Ocean. The Chinese and the western (originally Ponto-Caspian) species groups were separated from each other when the Central Asian mountains arose in the Tertiary and closed the eastern portion of this ocean while the western portion persisted as the Mediterranean and Ponto-Caspian seas. The eastern species group has survived in a few isolated freshwater, mountainous lakes while the western one diversified mainly in the large and versatile Ponto-Caspian water system.

The Ponto-Caspian basin, including the modern Black, Azov, Caspian, and Aral seas together with their estuaries and some now disappeared water bodies (Fig. 2, *1*), has a complicated geological history. Its different parts have been repeatedly transgressed and regressed, connected and isolated, closed and drained, their mineralization fluctuating from fresh to saline water with different rate of the main ions (Great Flood 2012). The region has not been glaciated, thus there has been enough time for evolution. A large number of local euryhaline genera

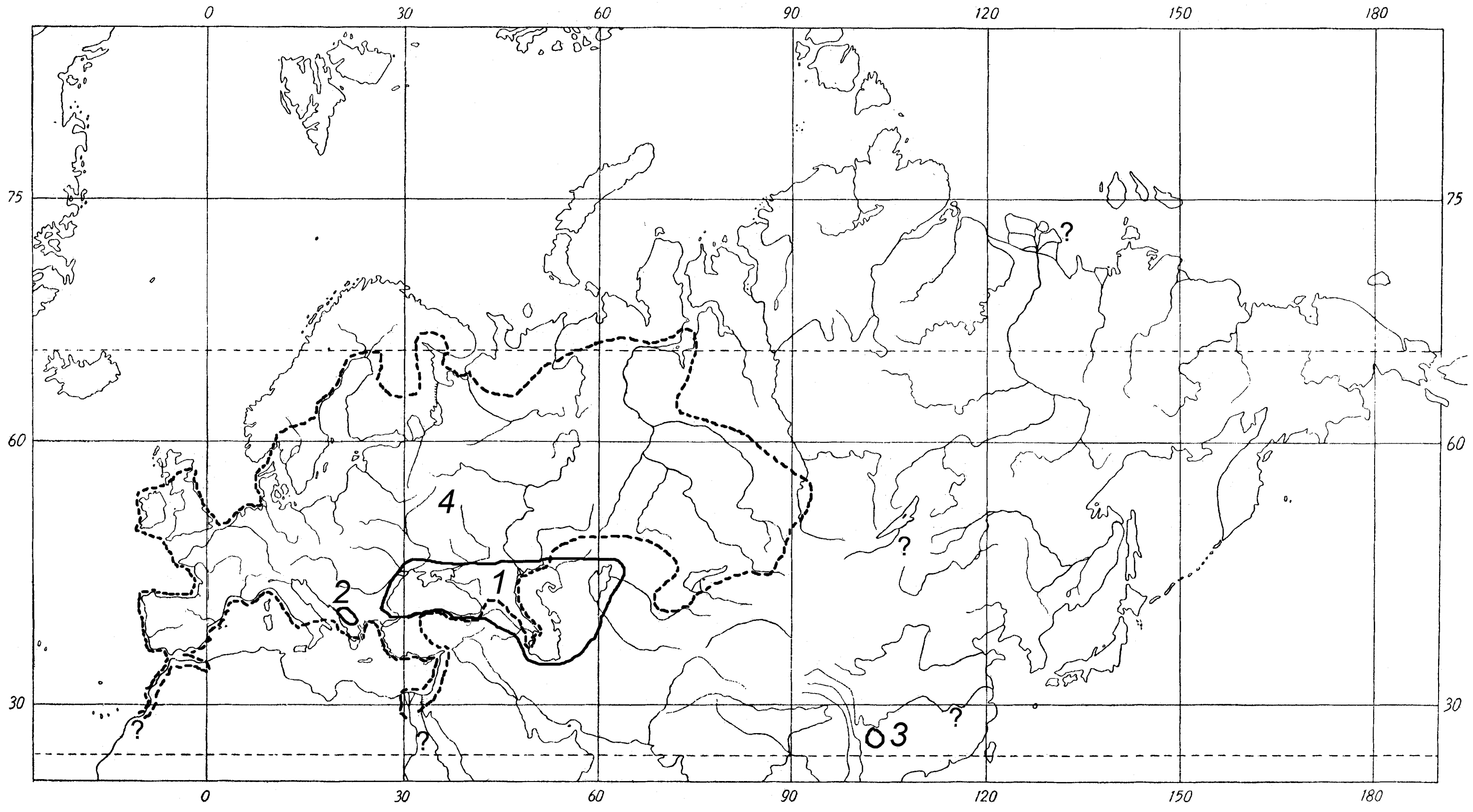

Fig. 2. Distribution area of the genus *Potamothrix* in the Palaearctic. *1* – Ponto-Caspian Basin; *2* – ancient lakes on the western Balkan Peninsula; *3* – ancient lakes on the Yunnan Plateau; *4* (surrounded with dashed line) – distribution area of *P. hammoniensis*; ? – suspicious records of *P. hammoniensis* far from the continuous distribution area.

and species of molluscs, crustaceans, polychaetes, and oligochaetes, thriving in both fresh and brackish water, have arisen in this region. This specific fauna is nowadays well represented in the brackish but relatively carbonate-rich Caspian Sea, inhabited, among others, also by three species of the otherwise strongly freshwater oligochaete family Lumbriculidae (Hrabě 1950, Zinogenova 1975). In the Black Sea, which became saline some millennia ago after connection with the Mediterranean Sea, this specific brackish water fauna has partially survived in the estuaries ('limans') and lower reaches of large rivers such as the Danube, Dniester, Dnieper, and Don. That is why it has been called Ponto-Caspian relict fauna, particularly in the Russian literature (e.g., Morduhai-Boltovskoi 1979, Finogenova 1980a). A few euryhaline representatives of this fauna have dispersed spontaneously in the European freshwater bodies; most others remained endemic. Invasions of some Ponto-Caspian, formerly endemic species, have been accelerated during the last centuries by human activities: shipping along rivers and overseas and construction of navigable canals and water reservoirs on big rivers (Milbrink & Timm 2001). The assemblage of invasive oligochaetes, who originate, in all probability, from the Ponto-Caspian basin, includes several but not all species of the genera *Potamothrix*, *Psammoryctides*, and *Paranais*, as well as the tubificid species *Isochaetides michaelseni* (Lastočkin, 1937) and *Tubifex newaensis* (Michaelsen, 1903). The Ponto-Caspian fauna may be related to the endemic freshwater fauna of the western Balkan Peninsula (Fig. 2, *2*), most diverse in the ancient Lake Ohrid (Hrabě 1931, Šapkarev 1956).

Hereinafter first the 'western' species group and then the Chinese endemic species will be surveyed.

SURVEY OF THE SPECIES

The western species with hair chaetae (mostly accompanied by pectinates) in dorsal bundles

Potamothrix hammoniensis (Michaelsen, 1901), syn. *Tubifex camerani* De Visart, 1901, *Psammoryctes fossor* Ditlevsen, 1904. Hair and pectinate chaetae in the dorsal bundles of fore- and mid-body; ventral chaetae with slightly longer upper tooth anteriorly but with equal tooth in postclitellar segments. Spermathecal chaetae in X single, thicker than locomotory ones, their distal portion furrowed and often slightly contorted around their longitudinal axis (Fig. 1, *3*, *4*). Ordinary but small bifid chaetae at male pores in XI, usually by 1–2. Prostate gland present. Atrium bipartite (consisting of two histologically different portions). Cocoons oval, with smooth, relatively rigid, yellowish shell and two equally short appendages (Fig. 1, *10*). This could be the earliest and most successful invader in the European freshwater bodies already before the transport by humans, although not yet reaching its potential limits in Scandinavia and Siberia (Fig. 2, *4*). Common in both standing and running waters but most important in profundal of many European lakes where it can be the only oligochaete at high eutrophication stage. It is not clear why it is gradually replacing here *Tubifex tubifex* (Müller, 1774), another tubificid tolerant to long oxygen deficiency (T. Timm 1996, 2012). It may prefer somewhat richer organic sediment and higher temperatures than *T. tubifex*. During long periods of oxygen scarcity combined with elevated temperature, *P. hammoniensis* can be replaced by *P. heuscheri* (Erséus et al. 1999). It tolerates a low salinity in the Baltic Sea and in limans but never dominates there. The ecology of *P. hammoniensis* in eutrophic lakes, particularly in those of Denmark and Lithuania, and in the Rybinsk Reservoir in Russia is studied in papers by Jónasson & Thorhauge (1976), Grigelis (1980), and Arkhipova (2010), respectively, and that in the oligotrophic Balkanian lakes by Šapkarev (1959). Competition of *P. hammoniensis* with larvae of *Chironomus* has been observed in Lake Esrom, Denmark (Jónasson & Thorhauge 1976), but not elsewhere. Production of *P. hammoniensis* was studied in Lake Esrom by Jónasson (1975) and in two Estonian lakes by H. Timm (1994). Intraspecific variability described by Hrabě (1958) as expressed in the position of spermathecal pores (named by this author f. *hammoniensis*, f. *subdorsalis*, f. *supralinearis*, and f. s*ublinearis*, respectively) may prove its long dispersal history and indirectly explain its good adaptability to different aquatic conditions. Reduced number of hair chaetae, up to their complete lack in mature individuals, was described in an ecological form from the littoral of Lake Pleshcheevo (Central Russia), named *Ilyodrilus hammoniensis* f. *lacustris* by Lastočkin (1927a). The species is common in the most of Europe, Near East, Central Asia, and the western portion of Siberia but rare in North Africa (maybe introduced into the White Nile, a single record from Algeria, another record by De Henau & Dumont (1976) from the Western Sahara is dubious because it is accompanied by a figure of genitalia of *Tubifex tubifex*). There are also single records from the Yangtze River in China and Lake Titicaca in South America – both possible introductions if not misidentifications. ‘Abnormal’ specimens (with spermathecal chaetae either in IX or IX and X – maybe *P. bedoti*?) were recorded by Brinkhurst (1966a) from the Vaal River, South Africa. For some obscure reasons, *P. hammoniensis* seems to be lacking in the Laurentian Great Lakes of North America (the only record from Green Bay of Lake Michigan by Howmiller & Beeton (1970), with spermathecal chaetae either in VIII or VII and VIII, may be of *P. bedoti*), which otherwise abound with several other, introduced *Potamothrix* spp. Just as remarkable is its absence from the brackish-water Caspian Sea (Finogenova 1975, 1980b). The species is common in lakes, both ancient and young, of the Balkan Peninsula and western Anatolia but lacking in the isolated mountain lakes of Transcaucasia and eastern Anatolia (replaced there by two endemic subspecies of *P. alatus*). It has not conformed to breeding in aquaria with lake mud from Lake Võrtsjärv (Estonia) where several other *Potamothrix* spp. thrived. De Visart (1901) and Ditlevsen (1904) were apparently not yet aware of Michaelsen’s (1901) description when describing *Tubifex camerani* and *Psammoryctes fossor*, respectively.

Potamothrix alatus Finogenova, 1972. Originally described from the Dnieper–Bug Estuary (liman) but later found also in different parts of the Caspian Sea by

Finogenova (1972a, 1975, 1980b). Externally somewhat similar to *P. hammoniensis* but characterized by flattened genital segments X and XI, with wing-like lateral appendages; they can be concave in fixed specimens and separated by each other by a transversal furrow on 10/11, on the ventral surface. Spermathecal chaetae trivial (nib-shaped, distal portion with parallel edges, not twisted). Prostate gland present. Atrium histologically tripartite. *P. paravanicus* Poddubnaja et Pataridze, 1989, endemic in the Transcaucasian lakes, was once treated as a clinal variety of *P. hammoniensis* by Poddubnaja & Semernoy (1989), in the same year described as a separate species and soon transferred into *P. alatus* as a subspecies, *P. alatus paravanicus*, by Finogenova & Poddubnaja (1990) after internal reproductive system although devoid of the external 'wings'. Its ecology and production in the large oligotrophic Lake Sevan (Armenia), where it is dominating in the profundal (like *P. hammoniensis* in many European lakes) and can grow very large and live assumedly up to 20 years, was thoroughly studied by Jenderedjian (1994a, 1994b). Another, still undescribed, subspecies with well-developed 'wings' inhabits the profundal of Lake Hazar in eastern Turkey.

Potamothrix prespaensis (Hrabě, 1931). Hair chaetae only in postclitellar segments, short and only 1–2 per bundle; bifids with equally long teeth; no pectinates; trivial (as in *hammoniensis*?) spermathecal chaetae in X; ventral chaetae of XI unmodified. Prostate gland present. Atrium bipartite (?), widening in its distal portion. Endemic in lakes of the western part of the Balkan Peninsula, dominating oligochaete in Lake Prespa (Šapkarev 1962). Černosvitov (1931) described smaller individuals from Lake Skadar with relatively longer hair chaetae and with slightly thinner and shorter upper tooth in bifids as *P. prespaensis* f. *scutarica*.

Potamothrix ochridanus (Hrabě, 1931). Hair chaetae only in postclitellar segments, short and only 1–2 per bundle; bifids with slightly shorter upper tooth; no pectinates; ventral chaetae of X and XI unmodified. Prostate gland present. Atrium bipartite (?), widening in its distal portion. Endemic in Lake Ohrid (western part of the Balkan Peninsula), one of the dominants in all zones of this deep ancient lake (Šapkarev 1965).

Potamothrix thermalis (Pop, 1968). Similar to *P. hammoniensis* but has only 1–2 particularly long (up to 1200 μm) hair chaetae in some anteclitellar bundles while the spermathecal chaetae are not twisted. Prostate gland present. Histology of atrium unknown. Recorded only from a warm-water stream in Oradea, western Romania, by Pop (1968).

Potamothrix postojnae Karaman, 1974. Hair chaetae only 1–2 per bundle but present up to hind end, pectinates up to midbody; all bifids with longer upper tooth even in the hindbody. Ventral chaetae of X and XI unmodified. Prostate gland present. Atrium homogeneous. Recorded only from the cave of Planinska jama in Slovenia by Karaman (1974).

Potamothrix vejdovskyi (Hrabě, 1941). Externally similar to *P. hammoniensis* except for the different specific shape of dorsal chaetae (short curved hairs and shorter upper tooth in the bifids, no pectinates). Spermathecal chaetae trivial, nib-shaped (of *hammoniensis* type but never twisted). Prostate gland present. Atrium bipartite. Cocoons oval, with light shell and short appendages (Fig. 1, *11*). Occurs generally in fresh water (both in lakes and rivers) but inhabits also the Caspian Sea. An apparently recent invasion of the species in Europe (also in western Anatolia) in the 20th century is partially documented (Milbrink & Timm 2001). Known also from the Great Lakes of North America at least from the 1960s (Brinkhurst 1966b). A single record from Africa (Lake Tana in Ethiopia).

Potamothrix heuscheri (Bretscher, 1900), syn. *Ilyodrilus orientalis* Černosvitov, 1938. A smaller counterpart of *P. hammoniensis* in external morphology but with distinctly different spermathecal chaetae (particularly thin and strict, with parallel edges of the distal grooved portion, and with hooked distal end; Fig. 1, *5*). No prostate gland. Atrium tripartite. Adapted to the Mediterranean climate where oxygen deficiency is coupled with relatively high temperature in lake profundal (replacing *P. hammoniensis*, e.g., in Lake Kinneret, Israel; some small lakes in Spain; Lake Jashan in Turkmenistan; small lakelet of Laduviken in Sweden). Freshwater but also tolerates moderate salinity. Common in South Europe and Near East but lacking in the Caspian Sea. Recorded also from Lake Titicaca in South America (Juget & Lafont 1994), from Lake Sake in Rwanda (Brinkhurst 1970), and Lake Naivasha in Kenya, may be introduced into the latter by migratory birds (Milbrink 1977). No records from North America or Siberia. Described from the profundal of Swiss lakes already at the beginning of the 20th century, first by Bretscher (1900). Dispersion into the Baltic Sea and Scandinavia is documented in the literature (Milbrink 1999). The synonym *Ilyodrilus orientalis*, from the former Lake Huleh in Palestine, was described by Černosvitov (1938) as having only bifid chaetae in dorsal bundles; however, Brinkhurst (1971) found pectinate chaetae in the type material.

Potamothrix bavaricus (Oschmann, 1913). Erroneously treated as senior synonym of *P. bedoti* by Brinkhurst (1963), which caused confusion in distribution data, particularly in North America. Well distinguishable from *P. hammoniensis* and other species when sexually mature after its spear-shaped spermathecal chaetae, with a diagonal groove on them (Fig. 1, *6*). No prostate gland. Atrium tripartite. Cocoons similar to those of *P. hammoniensis*. A brackish-water species tolerating also slightly mineralized fresh water. Its area of distribution includes lakes of Mediterranean and Central Asian arid zones (but not the Caspian Sea!), farther northwards particularly seashore lagoons but also some inland waters (its *terra typica* was in Bavaria). Apparently introduced into brackish waters of North and South America and Australia; recorded from the North American Great Lakes where a confusion with *P. bedoti* is expected due to premature synonymization of the two species by Brinkhurst (1971). Finds at the Baltic Sea and in the Volga River reservoirs can evidence a recent invasion of this species. The author's name (Oschmann 1913) has often been misspelled as Öschmann, following an error in the monograph by Brinkhurst (1971).

Potamothrix bedoti (Piguet, 1913). A small species differing from its congeners in prevailing vegetative reproduction by architomy (fragmentation) followed by a forward shift of reproductive system by two segments. No shift in the individuals developed from eggs (Hrabě 1981). When sexually mature, it can have two pairs of spermathecae and three pairs of uniformly modified genital chaetae of spermathecal type (usually in VII, VIII and IX; Fig. 1, *7*), including one pair at the male pores. However, this set of modified chaetae may often be incomplete. These genital (spermathecal) chaetae are scalpel-shaped, with a groove along the convex edge. No prostata. Atrium tripartite. Sexual maturation occurs mostly at lower temperatures (in wintertime or in cool springs) while in warmer periods when asexual individuals prevail (T. Timm 1972), the latter are hardly different from the young of *P. hammoniensis*. Cocoons with smooth, light shell and short appendages (Fig. 1, *12*). Only in fresh water. Described originally by Piguet (1913) from Switzerland, common in Europe and on the Anatolian Peninsula in Asia; scarce records from Central Asia, Siberia, and China. Apparently introduced into the Northeast of USA including the Great Lakes. Two suspicious records of *P. hammoniensis*, from South Africa and North America, may also belong to *P. bedoti* (Brinkhurst 1966a, Howmiller & Beeton 1970, see above). Dispersion of this species may be easier than that of congeners due to its vegetative reproduction. It may have often remained unidentified in samples when immature.

Potamothrix tudoranceai Šporka, 1994. Hair and pectinate chaetae very numerous (6–11 and 6–12, respectively, in the preclitellar dorsal bundles); the pectinates with very distinct, thick intermediate denticles. Ventral bifids with longer and thinner upper tooth. Spermathecal chaetae in X with curved, scalpel-like distal portion (but the groove is median differently from that in *P. bedoti*). No prostate gland. Atrium histologically homogeneous although widening in three places. Recorded only from Lake Zwai in the Ethiopian Rift Valley by Šporka (1994).

The western species devoid of hair and pectinate chaetae (both dorsal and ventral chaetae bifid)

Potamothrix moldaviensis Vejdovský et Mrázek, 1903, syn. *P. okaensis* Lastochkin, 1927. All locomotory chaetae are bifid with equally long teeth. Spermathecal chaetae short and stout, with shorter proximal shaft, slightly twisted distal portion, and curved tip (Fig. 1, *8*). Single penial chaetae at male pores in XI bifid with considerably longer upper tooth. No prostate gland. Atrium histologically tripartite. The species is mostly rheophilous (oxygen-demanding), preferring sandy sediment, although observed also in larger lakes and in the Caspian Sea. The species seems to belong to the invasive tubificids in Europe (Milbrink & Timm 2001), although recorded from Central Europe already at the beginning of the 20th century, including its *terra typica* in the modern Czech Republic (Vejdovský & Mrázek 1903). Known from the Great Lakes of North America at least from the 1960s (Brinkhurst 1966b). Cocoons firmly stuck to solid substratum if possible and covered with adhering sand or mud particles; one of their two appendages much extended (Fig. 1, *13*). The subspecies *P. moldaviensis mitropolskiji* Hrabě, 1950 is somewhat smaller and with shorter upper tooth of the chaetae; endemic in the Caspian Sea. Even much smaller *P. moldaviensis minimus*, described by Pop (1971) from a cave stream in Switzerland, reveals different shape of spermathecal chaetae (strict, with relatively short furrowed distal portion) and is devoid of modified penial chaetae; its alignment with *P. moldaviensis* is doubtful. *Potamothrix okaensis* from the Oka River in Russia was named by Lastochkin (1927b) without description but with figures of genital chaetae and beginning of male duct similar to those in *P. moldaviensis*.

Potamothrix grimmi (Hrabě, 1950). Anterior chaetae with considerably thicker lower tooth; upper tooth thin and slightly shorter. Spermathecal chaetae in X trivial (of *hammoniensis* type); penial chaetae in XI single, with longer upper tooth like in *P. moldaviensis*. No prostate gland. Atrium bi- or tripartite(?). In brackish and fresh water: Caspian Sea, Danube River. Has been treated as a subspecies of *P. moldaviensis* (see Finogenova & Poddubnaja 1990).

Potamothrix cekanovskajae Finogenova, 1972. Chaetae in the anterior segments with slightly longer and thinner upper tooth; ventral chaetae in X and XI unmodified, by 4–5 and 2, respectively. No prostate gland. Atrium histologically homogeneous but slightly widening distally. Endemic species common in the Caspian Sea (Finogenova 1972b, 1975).

Potamothrix manus Finogenova, 1976. Upper tooth of chaetae slightly longer, equal to or shorter than the lower tooth. Spermathecal chaetae in X trivial; at male pores in XI 1–2 common bifids. No prostata. Atrium bipartite. Endemic species common in the Caspian Sea.

Potamothrix isochaetus (Hrabě, 1931), non Brinkhurst, 1960. Locomotory chaetae as in *P. moldaviensis*; spermathecal chaetae trivial (like in *hammoniensis*?); ventral chaetae in XI unmodified or lacking. Prostate gland present. Atrium bipartite(?), widening in its distal portion. Endemic of the ancient Lake Ohrid, one of dominants in all depth zones (Šapkarev 1965). Brinkhurst (1960) misidentified as *P. isochaetus* the British specimens of *P. moldaviensis*. Repeated records of *P. isochaetus* from the Danube and Tisza rivers, e.g. by Moog et al. (1994) and Atanacković et al. (2011, 2013), may be based on misidentified *P. danubialis* or *P. mrazeki* because those had been treated as synonyms of *P. isochaetus* by Brinkhurst (1971).

Potamothrix mrazeki (Hrabě, 1941). Position of reproductive system variable, with male pores usually in XII but sometimes also in XI, XIII, XIV, or XV, according to Finogenova & Poddubnaja (1990), and spermathecal pores in the respective preceding segment, assumedly in connection with vegetative reproduction by architomy. Chaetae with equally long teeth. Ventral chaetae in the genital segments unmodified, 1–2 per bundle. Prostate gland present. Atrium bipartite. Dissepiments 3/4–10/11 strongly thickened. Described from the middle reach of the Danube River; later found in the Danube and Dnieper–Bug estuaries and in the Caspian Sea.

Potamothrix danubialis (Hrabě, 1941). Chaetae with equally long teeth like in *P. mrazeki*. Originally was supposed to be a non-architomic form of that species but with the reproductive system in normal position. However, it has always spermathecal chaetae in X, with slightly twisted distal, grooved portion. At male pores in XI up to 2 unmodified chaetae or none. Prostate gland present. Atrium bipartite. Dissepiments 3/4–9/10 strongly thickened, that of 10/11 thin. Finogenova

& Poddubnaja (1990) confirmed the status of *P. danubialis* as an independent species. Recorded from the Danube and Tisza rivers as well as from the Dnieper–Bug Estuary.

Potamothrix caspicus (Lastočkin, 1937), syn. *Limnodriloides dnieprobugensis* Jarošenko, 1948. Chaetae in the anterior segments with twice longer upper tooth; ventral chaetae in X and XI unmodified. Prostate gland present. Atrium bipartite. Dissepiments 3/4–10/11 thickened. A brackish-water species common in the Caspian Sea and in the estuaries of the Black Sea from the Don to the Danube River. Hrabě (1967) and Finogenova & Poddubnaja (1990) declared that *L. dnieprobugensis*, well described by Yaroshenko (1948), is a junior synonym of *Ilyodrilus caspicus*. The latter was described by Lastočkin (1937) very shortly but identifiably.

Species of the Yunnan Plateau ancient lakes in China, as surveyed by Cui & Wang (2012b)

Potamothrix scleropenis Cui et Wang, 2005. Dorsal hair chaetae from VI onwards, pilose. Dorsal pectinates mostly with longer upper and branched lower tooth as are the ventral bifids. Spermathecal chaetae in X thin and curved, without nodulus, their distal portion furrowed and the tip finely bifid (Fig. 1, *9*). Ventral chaetae in XI unmodified, by 2–3. No prostate gland. Atrium homogeneous. Penis surrounded with short chitinous thimble-shaped, distally slantwise cut sheath. Known only from the profundal of Lake Fuxian.

Potamothrix aductus Cui et Wang, 2012. Hair chaetae from VII onwards, pilose. In dorsal bundles of II–VI bifid chaetae with slightly longer and thicker upper tooth; from VII onwards pectinates with up to 2 fine intermediate denticles, the upper tooth becoming gradually shorter. Ventral bifids with similarly slightly longer and thicker upper tooth. Spermathecal chaetae straight, with grooved distal portion contorted round the longitudinal axis. No ventral chaetae in XI. Prostate gland present, vas deferens almost lacking. Atrium homogeneous. Penis short and soft. Known only from the profundal of Lake Fuxian.

Potamothrix praeprostatus Cui et Wang, 2012. Hair chaetae from V onwards, pilose. In dorsal bundles of III–V bifid chaetae with longer and thinner upper tooth, the lower tooth occasionally bifurcated; in V–X they become pectinate, with 1–2 intermediate teeth. Ventral chaetae also with longer and thinner upper tooth. Spermathecal chaetae slightly sigmoid. No ventral chaetae at male pores in X. Prostate gland present, attached to atrium at some distance from the beginning of latter. Atrium homogeneous. Known only from the profundal of Lake Fuxian.

Potamothrix rhytipeniatus Cui et Wang, 2012. Hair chaetae smooth, pectinates with slightly longer upper tooth and fine intermediate denticles. Ventral chaetae with conspicuously longer upper tooth. Spermathecal chaetae thin, their ental portion curved but the distal, grooved portion almost straight. No ventral chaetae in XI. Atrium histologically bipartite (differently from the other Chinese congeners). Penis soft but with thin plicated cuticle. No prostate gland. Known only from Lake Xingyun.

Potamothrix paramoldaviensis Cui et Wang, 2012. No hair chaetae; all locomotory chaetae bifid with longer and thinner upper tooth. Spermathecal chaetae with curved ental and almost straight ectal, grooved portion. At male pores in XI 1–2 bifid penial(?) chaetae, shorter than the rest and with equally short teeth. Prostate gland present, attached to atrium at some distance from the beginning of latter. Atrium homogeneous. No penis (differently from other congeners). Known only from the profundal of Lake Fuxian.

Potamothrix parabedoti Cui et Wang, 2012. Hair chaetae from III–V onwards, pilose. Shorter chaetae in the anteriormost dorsal bundles bifid with longer and thicker upper tooth; those accompanying the hair chaetae pectinate with 1–3 intermediate denticles, slightly longer upper tooth and usually bifurcate lower tooth. Ventral locomotory chaetae with longer and thicker upper tooth. Reproductive system shifted 1–2 segments forward. Spermathecal chaetae in VIII or IX, thin with very strongly curved ental end and almost straight ectal, grooved portion. No ventral chaetae at male pores in IX or X. No prostate gland. Atrium homogeneous. Chloragogen tissue on esophagus beginning in IV or V instead of VI common in most other tubificids; this may be another proof of anterior regeneration, possibly as a result of architomic reproduction like in *P. bedoti*. Known only from the profundal of Lake Fuxian.

CONCLUSION

The genus *Potamothrix* includes to date 25 valid species. I agree with Finogenova & Poddubnaja (1990) that division of the European (Ponto-Caspian) species of *Potamothrix* into two subgenera, *Potamothrix* and *Euilyodrilus*, as proposed by Holmquist (1985) and based on presence or absence of a prostate gland on atrium, is not justified. This character occurs in various combinations with other morphological characters (histology of atrium, presence of hair chaetae and modified genital chaetae, etc.) in different species. A similar variation of the same characters occurs among the small, probably monophyletic group of the Chinese species.

In the aspect of the distribution and dispersing ability, four groups can be distinguished. First, *P. hammoniensis*, apparently long ago distributed from its original home (supposedly the Ponto-Caspian water system in southeastern Europe) to a wide area in the Western Palaearctic but, for some obscure reason, not in North America. It has adapted to different habitats in moderate climate and demonstrates certain intraspecific morphological variability. However, its lacking in the Caspian Sea and some high mountain lakes remains an enigma.

Second, the species of Ponto-Caspian origin that have successfully distributed around Europe and some other continents by human aid during the last two centuries. These are *P. moldaviensis*, *P. vejdovskyi*, *P. bavaricus*, and *P. heuscheri*. A similar distribution picture is shown by *P. bedoti*; however, its ability to vegetative reproduction may support also an easier spontaneous distribution in comparison with its congeners.

Third, the taxa still delimited to the Ponto-Caspian Basin. Among them, only *P. caspicus* and *P. mrazeki* have been recorded in all studied parts of this region (the Caspian Sea, the Black Sea estuaries or 'limans', and the Danube River with its tributaries). Here belong also *P. moldaviensis mitropolskiji*, *P. cekanovskajae* (Caspian Sea), *P. a. alatus* (Caspian Sea and limans), *P. grimmi* (Caspian Sea and Danube), and *P. danubialis* (limans and Danube).

Fourth, the species with very limited distribution in ancient lakes or otherwise extremal habitats, such as *P. ochridanus* and *P. prespaensis* in lakes of the western Balkan Peninsula, two subspecies of *P. alatus* in the mountain lakes of Transcaucasia and Anatolia, *P. tudoranceai* in a rift lake in Ethiopia, all the six species described from Lake Fuxian and a neighbouring lake on the Yunnan Plateau, China, *P. thermalis* in a thermal water stream in Romania, *P. postojnae* in a Slovenian cave, and *P. moldaviensis minimus* in a Swiss cave. A special case seems to be *P. isochaetus* recorded both from the ancient Lake Ohrid and the Danube River, but this may be due to misidentifications.

REFERENCES

Arkhipova, N. R. 2010. On the ecology of Oligochaeta of the Rybinsk Reservoir. In *Ékologiya i morfologiya bespozvonochnykh kontinental'nykh vod* (Krylov, A. V. et al., eds), pp. 99–111. Nauka DNC, Makhachkala (in Russian).

Atanacković, A., Jakovčev-Todorović, D., Simić, V., Tubić, B., Vasiljević, B., Gačić, Z. & Paunović, M. 2011. Oligochaeta community of the main Serbian waterways. *Water Research and Management*, **1**(1), 47–54.

Atanacković, A. D., Šporka, F., Csányi, B., Vasiljević, B. M., Tomović, J. M. & Paunović, M. 2013. Oligochaeta of the Danube River – a faunistical review. *Biologia*, **68**(2), 269–277.

Bretscher, K. 1900. Mitteilungen über die Oligochaetenfauna der Schweiz. *Revue Suisse de Zoologie*, **8**(1), 1–44.

Brinkhurst, R. O. 1960. Introductory studies on the British Tubificidae (Oligochaeta). *Archiv für Hydrobiologie*, **56**(4), 395–412.

Brinkhurst, R. O. 1963. Taxonomical studies on the Tubificidae (Annelida, Oligochaeta). *Internationale Revue der gesamten Hydrobiologie, Systematische Beihefte*, **2**, 3–89.

Brinkhurst, R. O. 1966a. A contribution towards a revision of the aquatic Oligochaeta of Africa. *Zoologica Africana*, **2**(2), 131–166.

Brinkhurst, R. O. 1966b. Studies on the North American aquatic Oligochaeta III: Lumbriculidae and additional notes and records of other families. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **118**(1), 1–33.

Brinkhurst, R. O. 1970. A further contribution towards a study of the aquatic Oligochaeta of Africa. *Revue de zoologie et de botanique africaines*, **81**(1–2), 101–108.

Brinkhurst, R. O. 1971. Family Tubificidae. In *Aquatic Oligochaeta of the World* (Brinkhurst, R. O. & Jamieson, B. G. M., eds), pp. 444–625. Oliver & Boyd, Edinburgh.

Brinkhurst, R. O. 1978. Freshwater Oligochaeta in Canada. *Canadian Journal of Zoology*, **56**, 2166–2175.

Černosvitov, L. 1931. Zur Kenntnis der Oligochaeten-Fauna des Balkans, III. Oligochaeten aus Montenegro und Südserbien. *Zoologischer Anzeiger*, **95**(11/12), 312–327.

Černosvitov, L. 1938. The Oligochaeta. In *Report on the Percy Sladen Expedition to Lake Huleh* (Washburn, R. & Jones, R. F., eds). Annals and Magazine of Natural History, **2**(7), 535–550.

Cuadrado, S. & Martínez-Ansemil, E. 2001. External structures used during attachment and sperm transfer in tubificids (Annelida, Oligochaeta). *Hydrobiologia*, **463**, 107–113.

Cui, Y.-D. & Wang, H.-Z. 2005. *Potamothrix scleropenis* sp. nov. (Oligochaeta, Tubificidae) from Fuxian Lake, the deepest lake in Southwest China. *Zoological Science*, **22**(12), 1353–1357.

Cui, Y. & Wang, H. 2012a. Two new species of *Potamothrix* (Oligochaeta: Tubificinae) from plateau lakes of Yunnan Province, southwest China. *Proceedings of the Biological Society of Washington*, **125**(1), 12–17.

Cui, Y. & Wang, H. 2012b. Three new species of *Potamothrix* (Oligochaeta, Naididae, Tubificinae) from Fuxian Lake, the deepest lake of Yunnan Province, Southwest China. *ZooKeys*, **175**, 1–17.

De Henau, A. M. & Dumont, H. J. 1976. A note on some aquatic Oligochaeta from Rio de Oro (North-Western Sahara*). Bulletin de l'Institut fundamental d'Afrique noire*, **38A**(4), 836–840.

De Visart, E. 1901. *Tubifex Camerani*, n. sp. *Bollettino dei Musei di Zoologia ed Anatomia Comparata, Torino*, **16**(387), 1–3.

Ditlevsen, A. 1904. Studien an Oligochäten. *Zeitschrift für wissenschaftliche Zoologie*, **77**(3), 398–480.

Erséus, C., Grimm, R., Healy, B., Lundberg, S., Rota, E. & Timm, T. 1999. Clitellate diversity in Nationalstadsparken, an urban national park in Stockholm, Sweden. *Hydrobiologia*, **406**, 101–110.

Finogenova, N. P. 1972a. New species of Oligochaeta from Dnieper and Bug Firth and Black Sea and revision of some species. *Trudy Zoologicheskogo Instituta*, **52**, 94–116 (in Russian).

Finogenova, N. P. 1972b. New species of Tubificidae (Oligochaeta) from the Caspian Sea. *Zoologicheskij zhurnal*, **51**(12), 1882–1887 (in Russian).

Finogenova, N. P. 1975. Oligochaeta of the Middle and Southern Caspian Sea. In *Gidrobiologicheskie issledovaniya samoochishcheniya vodoemov*, pp. 141–151. Leningrad (in Russian).

Finogenova, N. P. 1980a. Oligochaete fauna of the saline water bodies of the Ponto-Caspian Basin. In *Aquatic Oligochaeta Worms*. All-Union Society of Hydrobiology Trudy, Vol. 37, 71–80. (Translated from the Russian.) Amerind Publishing Co, New Delhi.

Finogenova, N. P. 1980b. Oligochaeta of the northern Caspian Sea. *Gidrobiologicheskij zhurnal*, **16**(5), 52–56 (in Russian).

Finogenova, N. P. & Poddubnaja, T. L. 1990. One more revision of the genus *Potamothrix* Vejdovský et Mrázek, 1902 (Oligochaeta, Tubificidae). *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere*, **117**, 55–83.

Great Flood. 2012. *The late glacial great flood in the Ponto-Caspian Basin.* http://paleogeo.org/flood_en.html (accessed 14.03.2013).

Grigelis, A. 1980. Ecological studies of aquatic oligochaetes in the USSR. In *Aquatic Oligochaete Biology* (Brinkhurst, R. O. & Cook, D. G., eds), pp. 225–240. Plenum Press, New York and London.

Holmquist, C. 1979. Revision of the genus *Peloscolex* (Oligochaeta, Tubificidae). 2. Scrutiny of the species. *Zoologica Scripta*, **8**(1), 37–60.

Holmquist, C. 1985. A revision of the genera *Tubifex* Lamarck, *Ilyodrilus* Eisen, and *Potamothrix* Vejdovský & Mrázek (Oligochaeta, Tubificidae), with extensions to some connected genera. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere*, **112**(3), 311–366.

Howmiller, R. P. & Beeton, A. M. 1970. The Oligochaeta fauna of Green Bay, Lake Michigan. In *Proceedings, Thirteen Conference on Great Lakes Research held at State University College, Buffalo*, pp. 15–46. New York.

Hrabě, S. 1931. Die Oligochaeten aus den Seen Ochrida und Prespa. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere*, **61**(1/2), 1–62.

Hrabě, S. 1941. Zur Kenntnis der Oligochaeten aus der Donau. *Acta Societatis Scientiarum Naturalium Moravicae*, **13**(12), 1–37 (in Czech, with German summary).

Hrabě, S. 1950. Oligochaeta from the Caspian Sea. *Acta Academiae Scientiarum Naturalium Moravo-Silesiacae*, **22**(9), 251–290 (in Czech, with Russian and English summaries).

Hrabě, S. 1958. Die Oligochaeten aus der Seen Dojran and Skadar. *Publicationes Facultatis Scientiarum Universitatis Masarykianae, Brno*, **397**, 337–354.

Hrabě, S. 1967. Two new species of the family Tubificidae from the Black Sea, with remarks about various species of the subfamily Tubificinae. *Publicationes Facultatis Scientiarum Universitatis J. E. Purkyně, Brno*, **485**, 331–356.

Hrabě, S. 1981. Vodní máloštětinatci (Oligochaeta) Československa. *Acta Universitatis Carolinae – Biologica*, **1979**(9), 1–166 (in Czech, with English summary).

Jenderedjian, K. 1994a. Population dynamics of *Potamothrix alatus paravanicus* Poddubnaya & Pataridze (Tubificidae) in different areas of Lake Sevan. *Hydrobiologia*, **278**, 281–286.

Jenderedjian, K. 1994b. Influence of environmental factors on the production of *Potamothrix alatus paravanicus* Poddubnaya & Pataridze (Tubificidae) in different areas of Lake Sevan. *Hydrobiologia*, **278**, 287–290.

Jónasson, P. M. 1975. Population ecology and production of benthic detritivores. *Verhandlungen der Internationalen Vereinigung für Limnologie*, **19**(2), 1066–1072.

Jónasson, P. M. & Thorhauge, F. 1976. Population dynamics of *Potamothrix hammoniensis* in the profundal of Lake Esrom with special reference to environmental and competitive factors. *Oikos*, **27**(2), 193–203.

Juget, J. & Lafont, M. 1994. Distribution of Oligochaeta in some lakes and pools in Bolivia. *Hydrobiologia*, **278**, 125–127.

Karaman, S. 1974. Beitrag zur Kenntnis der Süsswasseroligochaeten Sloweniens. *Biološki vestnik (Ljubljana)*, **22**, 223–228.

Lang, C. 1998. Using oligochaetes to monitor the decrease of eutrophication: the 1982–1996 trend in Lake Geneva. *Archiv für Hydrobiologie*, **141**(4), 447–458.

Lastočkin, D. 1927a. Beiträge zur Oligochaetenfauna Russlands 3. Fauna von Oligochaeta limicola in Gouvernements Iwanowo-Wosnesensk und Wladimir. *Izvestija Ivanovo-Voznesenskogo politekhnicheskogo instituta*, **10**, 65–76 (in Russian, with German summary).

Lastochkin, D. 1927b. Oligochaeta limicola des Oka-Flusses. *Arbeiten der Biologischen Oka-Station (Murom, Russland)*, **5**(1), 5–36 (in Russian, with German summary).

Lastočkin, D. A. 1937. New species of Oligochaeta limicola in the European part of the USSR. *Comptes Rendus (Doklady) de l'Académie des Sciences de l'URSS*, **17**(4), 233–235.

Michaelsen, W. 1901. Neue Tubificiden des Niederelbegebietes. *Verhandlungen des Naturwissenschaftlichen Vereins zu Hamburg*, **8**, 66–70.

Milbrink, G. 1977. On the limnology of two alkaline lakes (Nakuru and Naivasha) in the East Rift Valley System in Kenya. *Internationale Revue der gesamten Hydrobiologie*, **62**(1), 1–17.

Milbrink, G. 1978. Indicator communities of oligochaetes in Scandinavian lakes. *Verhandlungen der Internationalen Vereinigung für Limnologie*, **20**(4), 2406–2411.

Milbrink, G. 1999. Distribution and dispersal capacity of the Ponto-Caspian tubificid oligochaete *Potamothrix heuscheri* (Bretscher, 1900) in Scandinavia. *Hydrobiologia*, **406**, 133–142.

Milbrink, G. & Timm, T. 2001. Distribution and dispersal capacity of the Ponto-Caspian tubificid *Potamothrix moldaviensis* Vejdovský & Mrázek,1903 in the Baltic Sea region. *Hydrobiologia*, **463**, 93–102.

Milligan, M. R. 1986. Separation of *Haber speciosus* (Hrabě) (Oligochaeta: Tubificidae) from its congeners, with a description of a new form from North America. *Proceedings of the Biological Society of Washington*, **99**(3), 406–416.

Moog, O., Konar, M. & Humpesch, U. H. 1994. The macrozoobenthos of the river Danube in Austria. *Lauterbornia*, **15**, 25–51.

Morduhai-Boltovskoi, Ph. D. 1979. Composition and distribution of Caspian fauna in the light of modern data. *Internationale Revue der gesamten Hydrobiologie*, **64**(1), 1–38.

Oschmann, A. 1913. Über eine neue Tubificiden-Art. *Zoologischer Anzeiger*, **42**(12), 559–565.

Piguet, E. 1913. Notes sur les Oligochètes. *Revue Suisse de Zoologie*, **21**(4), 111–146.

Poddubnaja, T. L. & Semernoy, V. P. 1989. Intraspecific variability of *Potamothrix hammoniensis* (Mich.). In *Species in Area. Biology, Ecology and Productivity of Water Invertebrates*, pp. 199–203. Minsk (in Russian).

Pop, V. 1968. *Ilyodrilus thermalis*, eine neue Tubificidenart (Oligochaeta). *Zoologischer Anzeiger*, **181**(1/2), 136–140.

Pop, V. 1971. Oligochètes (Annelida) limicoles des grottes et des eaux interstitielles de Suisse. *Revue Suisse de Zoologie*, **78**(4), 821–827.

Šapkarev, J. 1956. Contribution à la connaissance de la faune des Oligochètes des trois grands lacs Yougoslaves, Prespa, Dojran et Skadar. *Société Serbe de Biologie, Archives des Sciences Biologiques*, **8**(1–2), 135–144.

Šapkarev, J. 1959. *Ilyodrilus hammoniensis* Mich. (Oligochaeta) in the large lakes of Macedonia (Ohrid, Prespa and Dojran*). Section des Sciences naturelles de l'Université de Skopje, Station Hydrobiologique – Ohrid, Recueil des Travaux*, **7**(7)(40), 1–12.

Šapkarev, J. 1962. Distribution and ecology of *Ilyodrilus prespaensis* Hrabě (Oligochaeta) in Lake Prespa. *Prirodno-matematichki fakultet na Univerzitetot – Skopje, biologija*, 29–37 (in Macedonian).

Šapkarev, J. 1965. Fauna of Oligochaeta in Lake Ohrid*. Godishen zbornik na Prirodno-matematichki fakultet na Univerzitetot vo Skopje*, 5–161 (in Macedonian).

Šporka, F. 1994. *Potamothrix tudoranceai* sp. n., a new species of Tubificidae (Oligochaeta) from the Ethiopian Rift Valley Lake Zwai (Africa). *Biologia, Bratislava*, **49**(2), 161–165.

Timm, H. 1994. Production of some oligochaete species in large Estonian lakes. *Hydrobiologia*, **278**, 309–313.

Timm, T. 1972. On the reproduction of *Euilyodrilus bedoti* (Piguet, 1913) (Oligochaeta, Tubificidae). *Eesti NSV Teaduste Akadeemia Toimetised, Bioloogia*, **21**, 235–241.

Timm, T. 1996. *Tubifex tubifex* (Müller, 1774) (Oligochaeta, Tubificidae) in the profundal of Estonian lakes. *Internationale Revue der gesamten Hydrobiologie*, **81**(4), 589–596.

Timm, T. 2012. Profundal oligochaete assemblages in Palaearctic lakes. *Turkish Journal of Zoology*, **36**(1), 121–131.

Vejdovský, F. & Mrázek, A. 1903. Ueber *Potamothrix* (*Clitellio*?) *Moldaviensis* n. g. n. sp. *Sitzungsberichte der königlichen böhmischen Gesellschaft der Wissenschaften*, **1902**(24), 1–7.

Yaroshenko, M. F. 1948. Oligochaeta of the Dnepr–Bug Liman. (Preliminary data). In *Nauchnye zapiski Moldavskoj nauchno-issledovatel'skoj bazy Akademii Nauk SSSR*, Vol. 1, pp. 57–70 (in Russian).