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Research Article

Profundal oligochaete assemblages in Palaearctic lakes

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Abstract: The profundal oligochaete fauna is mostly formed of species present also in shallower waters. Endemic taxa have developed only in ancient rift lakes like Lake Baikal. “Common” lakes, mostly of glacial or volcanic origin, are too ephemeral for speciation. In the profundal of larger European oligotrophic lakes, there can occur about 10 tubificid and lumbriculid species. With a decline in dissolved oxygen in water, only 1-2 of them will remain, *Tubifex tubifex* often being the last survivor. In eutrophic lakes, *Potamothrix hammoniensis* is the climax species. In the Far East, the profundal is also inhabited by a small assortment of oligochaetes from surrounding waters. In the eutrophic lakes of Honshu (Japan), the widely distributed species *Limnodrilus hoffmeisteri* and *T. tubifex* dominate, while more species occur in the northern oligotrophic lakes. In the eutrophic lakes in China, *L. hoffmeisteri* or *Branchiura sowerbyi* dominates. The zoogeographical origin of the commonest profundal oligochaetes is discussed.

Key words: Lakes, profundal, Oligochaeta, Annelida, Palaearctic, zoogeography

Introduction

The profundal depths of lakes, mostly cool and dark and under high water pressure, have nourished the fantasy of early limnologists. Here the profundal is defined, in accordance with Thienemann (1925), as the deepest, vegetation-free, and muddy zone of the lacustrine benthal. The first data on the profundal oligochaetes originate from Swiss lakes, particularly Lac Léman, from the end of the 19th century (Forel, 1885, 1901; Piguet, 1899); a survey was compiled by Zschokke (1911). The profundal has been suggested as a habitat of relics of the glacial period (Hofsten, 1912; disputed by Zschokke, 1913), or of even more ancient geological periods: Michaelsen (1902) treated Lake Baikal as a palaeontological museum! These hopes were not fulfilled, at least regarding the oligochaetes. Instead, the profundal sediments of most lakes displayed a small variety of oligochaete species mostly originating from shallower waters, sometimes also from groundwater. Oxygen appeared to be limiting this variety, which often reflects the trophic status of a lake (Milbrink, 1978); in the best oxygenated lakes like Baikal, scarcity of nutritious organic material can play some role (Martin et al., 1999). Endemic species living in the profundal of most ancient lakes have arisen on the spot through evolutionary radiation (Semernoy, 2004). The Oligochaeta are usually represented by a limited number of Tubificidae and Lumbriculidae, more seldom also Haplotaxidae or Enchytraeidae. [Author consciously ignores the recent synonymization of the Tubificidae with Naididae, proposed by cladists (Erséus et al., 2008) but hardly acceptable in other branches of zoology – see Schmelz and Timm (2007)].

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Preadaptations of these oligochaetes to profundal life involve living inside sediment, relatively low demand for dissolved oxygen, and sexual reproduction at low temperature. However, some Naididae inhabiting the sediment surface have also been found in the depths of Lake Baikal (Semernoy, 2004), and recent studies of the meiofauna have demonstrated their presence in some large European lakes as well (Särkkä, 1989). The present study provides a short review of relevant literature with some notes on the zoogeography of aquatic Oligochaeta.

Ancient tectonic lakes (Figure 1)

The majority of lakes are geologically ephemeral; their age is measured in thousands or tens of thousands of years. This is a too short period for biological speciation. The ancient rift lakes, existing for millions of years, serve as an exception (Gorthner, 1994; Martin, 1996). The most famous among them is Lake Baikal in Siberia, where speciation can proceed in particularly favorable conditions at least during the last 2 million years (Semernoy, 2004): large size and extraordinary depth; a variety of different, temporarily isolated, and changing habitats; low water temperature; and good oxygen supply at all depths. Even in the deepest parts of the lake, its uppermost sediment layer is oxygenated (Martin et al., 1998). There is no distinct difference between life conditions in the sublittoral and profundal in this lake. Most common Palaearctic oligochaetes are not able to survive in Lake Baikal, either because of specific abiotic conditions or high competition and predation by the local biota, particularly gammarids (Semernoy, 2004). Instead, a few founder taxa, breaking through this ecological barrier, have radiated here into large sympatrical flocks of endemic species of the genera *Lamprodrilus, Styloscolex, Stylodrilus, Rhynchelmis, Baikalodrilus, Rhyacodrilus, Tasserkidrilus, Lamadrilus*, *Isochaetides*, etc. Endemic genera (*Svetlovia, Hrabeus, Lymphachaeta, Burchanidrilus, Wsewolodus*) have also arisen in Lake Baikal but they are not so species-rich. All in all, nearly 200 oligochaete species are known from the Baikal, about 85% of them being endemic in this lake and its outflow (Semernoy, 2004). An accelerated, explosive speciation of Lumbriculidae in Lake Baikal has been confirmed also with molecular methods by Kaygorodova et al. (2007). Several other animal groups like sponges, mollusks, crustaceans, and fishes have also formed a multitude of endemic taxa, even families, here (Kozhova and Izmest'eva, 1998). Therefore, Lake Baikal has been treated as a freshwater zoogeographical region, separate from the Palaearctic (Starobogatov, 1970; Timm, 1980). For some species flocks, their probable Palaearctic founders can be speculated [*Lamprodrilus isoporus* Michaelsen, 1901 for the other Baikalian *Lamprodrilus* spp., and

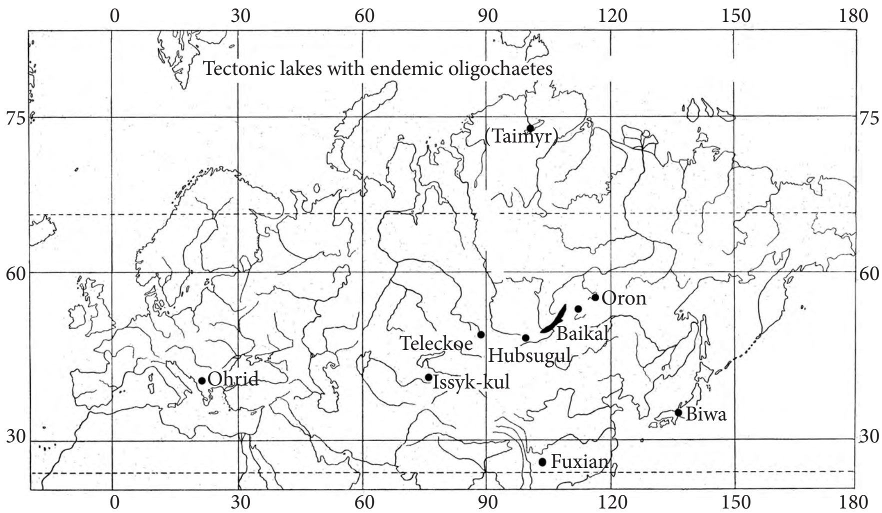

Figure 1. Palaearctic ancient, oligotrophic lakes with endemic oligochaetes in profundal.

the supposedly misidentified Siberian "*Peloscolex velutinus* (Grube, 1879)" for *Baikalodrilus*]. Some other "founder species" may be extinct. Single relatives of some "Baikalian genera" have been discovered later in Europe, e.g., *Pseudorhynchelmis paraolchonensis* Giani et Martinez-Ansemil, 1984. The founders of some Baikalian species flocks can originate from the groundwater fauna that is virtually unexplored in Siberia. In this aspect, the lack of the widely distributed in the European groundwater genus *Trichodrilus* both in Baikal and other Siberian waters is remarkable. The predatory and hence highly modified *Agriodrilus vermivorus* Michaelsen, 1905 (Lumbriculidae) has apparently arisen on the spot, supported by the abundance of small oligochaetes as a food resource. Another supposedly predatory oligochaete, the Holarctic *Haplotaxis gordioides* (Hartmann, 1821), is living in Baikal without any essential morphological changes [but the sympatric and endemic *Haplotaxis ascaridoides* (Michaelsen, 1905) may be a variation of *H. gordioides*]. It has apparently entered Lake Baikal directly from groundwater, a similarly cool and stable environment. Exceptionally high transparency and good oxygen supply in Baikal have enabled many Naididae, mostly connected with the benthic vegetation, to disperse (at least accidentally) to large depths; at least one species, *Nais abissalis* Semernoy, 1984, has been found at a depth of 700 m (Semernoy, 2004).

Many Baikalian endemics are constantly carried by the current into the outflowing Angara River running further as the Enisej River. Some of them have become naturalized in artificial water reservoirs on the Angara, while others have reached the Lower Enisej. The large but shallow Lake Taimyr in northernmost Siberia, which was connected with the Enisej in the geological past, serves as a habitat for several oligochaetes related apparently to the Baikalian fauna: *Lamprodrilus isoporus*, *Tasserkidrilus acapillatus* (Finogenova, 1972), and 3-4 local endemics (*Lamadrilus sorosi* Timm, 1998; *Baikalodrilus alienus* Timm, 1998; *Stylodrilus mollis* Timm, 1998, and an unnamed lumbriculid) (Timm, 1998a, 1998b).

An unintended zoogeographical experiment took place in the southern end of Lake Baikal. A spot of local eutrophication was generated by the wastewater of a large pulp factory. Endemic oligochaetes had become more diverse and abundant there while the Palaearctic species lacking in the "normal" Baikalian conditions had not invaded, except for *Tubifex tubifex* (Müller, 1774) and possibly also *Lumbriculus variegatus* (Müller, 1774) (after Akinšina and Lezinskaja, 1980; some identifications corrected by Semernoy, 2004).

The smaller, Sub-Baikalian rift lakes (Hubsugul, Oron, etc.) reveal several endemic oligochaetes that may be related to the Baikalian species, as belonging to the same genera. They can be treated as members of a bigger faunistic complex of "Great Baikal" but living among the Palaearctic fauna. In the profundal of Lake Hubsugul, southwards and upstream of Baikal, Semernoy and Tomilov (1972) and Semernoy and Akinshina (1980) noted 5 species in the profundal, among them *Limnodrilus profundicola* (Verrill, 1871) (dominant) and 2 endemics, *Isochaetides tomilovi* Semernoy, 1980 and *Enchytraeus platys* Semernoy, 1980. From Lake Oron Kaygorodova and Litvinova (2006) found several undescribed tubificids and lumbriculids, probably related to the Baikalian species. One of the 2 tubificids common in the profundal was the widely distributed *Embolocephalus velutinus* (Grube, 1879) reported earlier also from Lake Baikal but probably confused there with a *Baikalodrilus* sp. "*Isochaetides koshovi*" (Semernoy in litt.), a dominant in the Transbaikalian rift lake of Baunt (Semernoy, 1973), was found in Lake Oron as well.

Other ancient rift lakes studied for oligochaetes in other regions, e.g., Ohrid and Prespa on the Balkan Peninsula (Hrabě, 1931), Issyk-kul' in Kyrgyzstan (Hrabě, 1935), Teleckoe and some others in the Altai Mountains (Michaelsen, 1903, 1935), Fuxian in the Yunnan Province of China (Cui et al., 2008), and Biwa in Japan (Ohtaka and Nishino, 1995) are much smaller than Baikal and hence reveal a smaller number of endemic species each, which are always accompanied with widely distributed species. These endemics are often closely related to the "common" fauna of surrounding water bodies, e.g., the endemic *Potamothrix* spp. in the lakes of Ohrid and Prespa. As an exception, Lake Biwa presents a mysterious, monotypic megadrile genus, *Biwadrilus*, having no close relatives at all. Similarly, no congeners of *Pelodrilus ignatovi* Michaelsen, 1903 from Lake

Teleckoe are known from the whole of Asia.

European younger lakes, mostly of glacial origin (Figure 2)

Large, oligotrophic lakes of glacial origin, with an age of about 10,000 years or slightly more, like Vättern and Vänern in Scandinavia (Ekman, 1915; Milbrink, 1969, 1970), Onega and Ladoga in Karelia (Gerd, 1950; Hrabě, 1962; Popčenko, 1988) or Lac Léman, Luganer See, and Lago Maggiore in the Alps (Zschokke, 1911; Fehlmann, 1912; Nocentini and Bonomi, 1965; Lang and Lang-Dobler, 1980), have shown in their profundal a characteristic assortment of tubificids and lumbricids represented by up to 10 species that all live also in surrounding, smaller water bodies. Some of these species are limited in their distribution either to southern Europe [*Embolocephalus velutinus*, *Stylodrilus lemani* (Grube, 1879), *Bichaeta sanguinea* Bretscher, 1900] or northern and eastern Europe [*Lamprodrilus isoporus*; *Rhynchelmis tetratheca* Michaelsen, 1920; *Alexandrovia ringulata* (Sokolskaja, 1961)]. Some others are common in all regions, like *Spirosperma ferox* Eisen, 1879; *Tubifex tubifex*; *Rhyacodrilus coccineus* (Vejdovský, 1876); *R. falciformis* Bretscher, 1901; *Potamothrix hammoniensis* (Michaelsen, 1901), *Limnodrilus hoffmeisteri* Claparède, 1862, and *Stylodrilus heringianus* Claparède, 1862. Shifts in the qualitative and quantitative content of this profundal assemblage have successfully been used for assessment of the lakes' trophic state by Milbrink (1978, 1983) and Lang and Lang-Dobler (1980). For example, the lumbriculids *Spirosperma ferox* and *Tubifex tubifex* are characteristic of the Scandinavian oligotrophic lakes; *Psammoryctides barbatus* (Grube, 1861), *Limnodrilus profundicola*, *Rhyacodrilus coccineus*, etc. are typical of mesotrophic lakes; *Potamothrix* spp., *Ilyodrilus templetoni* (Southern, 1909), *Aulodrilus pluriseta* (Piguet, 1906), etc. are typical of the eutrophic lakes; and high abundance of *L. hoffmeisteri* and *T. tubifex* is evidence of extremely heavy organic pollution (Milbrink, 1983).

In the Transcaucasian large Lake Sevan and in some neighboring lakes a local, alpine subspecies, *Potamothrix alatus paravanicus* Poddubnaya et Pataridze, 1989, is strongly dominating in the profundal (Jenderedjian, 1994); its sister subspecies lives in brackish-water estuaries of the Black Sea. Other examples of possible speciation in a glacial lake may be *Rhynchelmis granuensis onegensis* Hrabě, 1962 and the unnamed *Lamprodrilus* sp. II, both described by Hrabě (1962) from Lake Onega.

The generally phytophilous family of Naididae has seldom been recorded in the profundal of glacial lakes. As an early exception, Ekman (1915) found *Vejdovskyella intermedia* (Bretscher, 1896), *Stylaria lacustris* (Linnaeus, 1767), and *Chaetogaster diaphanus* (Gruithuisen, 1828) from the great depths of Lake Vättern, Sweden. Recent studies in Lake

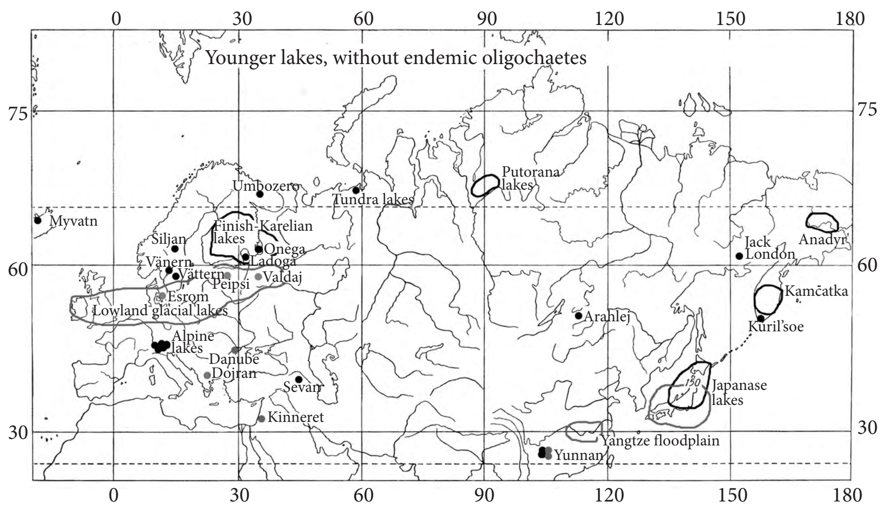

Figure 2. Some younger Palaearctic lakes and lake groups. Blue – oligotrophic, green – eutrophic lakes.

Ladoga and in several Finnish oligotrophic lakes (Särkkä, 1989; Kurashov, 1994) have demonstrated that Naididae (as well as the polychaete Aeolosomatidae) can be diverse and abundant in the profundal when oxygen supply is sufficient. They can be collected most effectively with methods used for collecting meiobenthos. However, no Naididae were observed in the profundal meiobenthos of small stratified eutrophic lakes in Estonia or in adjacent regions (Timm, 2002).

In the subpolar deep, oligotrophic lake of Umbozero on the Kola Peninsula, Russia (of tectonic origin but has been recently glaciated), the profundal is mostly inhabited by *Spirosperma ferox*, *Tubifex tubifex*, and *Stylodrilus heringianus*, accompanied by *Lumbriculus variegatus*, *Rhyacodrilus coccineus* (after Timm and Popčenko, 1978), and the mysterious (endemic?) *R. profundicola* Lastočkin, 1937 that has never been encountered after its brief original description by Lastočkin (1937). In northern Russia (Popčenko, 1988), as well as in central Finland (Särkkä, 1972, 1978), the typical profundal complex in most oligotrophic lakes also consists mainly of *S. ferox*, *T. tubifex*, and *S. heringianus*, sometimes with the addition of *Lamprodrilus isoporus*. Somewhat southwards, in mesotrophic lakes, the lumbriculids will be replaced with *Limnodrilus hoffmeisteri*. In eutrophic lakes, *Potamothrix hammoniensis* and *L. hoffmeisteri* dominate (Popčenko, 1988). A similar succession was observed by me in Sweden, where *S. ferox, T. tubifex, S. heringianus*, and *L. isoporus* occurred in the northern Lake Siljan but *P. hammoniensis*, often accompanied by *L. hoffmeisteri* and some others tubificids, occurred in southern and shallower lakes (unpublished data). The limited number of profundal oligochaete species in smaller lakes can be explained most probably by stronger stratification but sometimes also by their relative isolation.

In the very shallow (4 m!), volcanically fertilized Lake Mývatn, Iceland, only *T. tubifex* and *S. ferox* were found in the profundal (Lindegaard, 1979), just as in some Russian tundra lakes in the northeastern corner of Europe (Baturina, 2007). In some small but deep oligotrophic lakes in northern Germany, Thienemann (1920) found the southern European species *Embolocephalus velutinus* (instead of the similarly papillate *S. ferox*!) dominating in the well-oxygenated profundal. In lakes with oxygen stratification, it was replaced by *T. tubifex*.

In lowland glacial lakes around the Baltic Sea, which are shallower and more eutrophic, most other oligochaete species are gradually disappearing from the profundal until only *Potamothrix hammoniensis* will remain. In the mesotrophic stage of the evolution of lakes, it is still accompanied by *Psammoryctides barbatus* and *Tubifex tubifex*, both gradually dying out after continuing eutrophication. This change was monitored in Lake Esrom, Denmark (Berg, 1938; Jónasson, 1975). A similar succession was noted by Lundbeck (1926), who compared 57 lakes of different limnological types in northern Germany. Wiśniewski and Dusoge (1983) studied 44 mostly eutrophic lakes in northeastern Poland, and found exclusively *P. hammoniensis* in the profundal in all but 2 mesotrophic lakes, where it shared the habitat with *T. tubifex*. Grigelis (1962, 1963, 1974) observed mostly *P. hammoniensis* in the profundal of Lithuanian eutrophic lakes, but sometimes it was accompanied with either *P. barbatus* or *T. tubifex* in the relatively mesotrophic lakes. In Estonia, and in the Valdaj Upland in northwestern Russia too, most eutrophic lakes reveal only *P. hammoniensis* in the profundal. However, in some lakes with features of mesotrophy (including the large Lake Peipsi-Pihkva), a limited population of dwarf, apparently suppressed, individuals of *T. tubifex* exist together with *P. hammoniensis* (Timm, 1996). In some smaller, still oligotrophic but strongly stratified lowland lakes, *Tubifex tubifex* can inhabit the profundal as a single oligochaete. It is also the single, pioneer, species in man-made, gravel-pit lakes in western Germany (Anlauf, 1994) and in Estonia (my unpublished data). In deep, mesotrophic lakes of Valdaj and Užin (NW Russia), an interesting vertical distribution of tubificids was observed, with *T. tubifex* as the single oligochaete in the deepest profundal but accompanied by *P. hammoniensis*, *S. ferox*, and *L. hoffmeisteri* in the shallower zones (my unpublished data). Brinkhurst (1964) noted a successive change from *S. ferox* to *P. hammoniensis*—both being the dominants in different lakes of England—in the conditions of increasing eutrophication. Lakes with extremely soft water, both oligotrophic and dystrophic (humic), seem to be unsuitable for *P.*

hammoniensis. There it can be replaced with either scarce *T. tubifex* or *L. hoffmeisteri* in the profundal, if there are any oligochaetes at all (my observations from Estonia).

The mechanism of the replacement of the otherwise very tolerant, ubiquitous *T. tubifex* with *P. hammoniensis* during the eutrophication of European lakes is not clear. The latter species seems to benefit from eutrophication in relatively warm lakes: Rîşnoveanu and Vădineanu (2001) have observed its clear, increasing dominance over other tubificids, even over *L. hoffmeisteri*, in the shallow floodplain lakes of the Danube Delta. It is dominating also in the profundal of the shallow Lake Dojran on the Macedonian/Greek border (Hrabě, 1958). The species is common, although less abundant, in some other lakes of the Balkan Peninsula, including the tectonic Lake Ohrid (Šapkarev, 1956). In some Mediterranean eutrophic lakes, strongly stratified but with a relatively warm profundal, e.g., (also of tectonic origin) Lake Tiberias or Kinneret in Israel (Gitay, 1968), *Potamothrix hammoniensis* is replaced by a related species, *P. heuscheri* (Bretscher, 1900). Remarkably, the latter has been found also in the central part of the small hypereutrophic, well-warmed lakelet of Laduviken in Stockholm, Sweden (Timm et al., 1997).

Asian glacial and volcanic lakes (Figure 2)

The profundal of the northernmost large lake of Siberia, Lake Taimyr, is exceptional in that it is inhabited by Baikal-related oligochaetes (see above). In contrast, the oligochaete fauna of the tectonic, deep, and oligotrophic but recently glaciated lakes in the Putorana Mountains north of the Polar Circle (Ajan, Agata, Harpicha et al.), studied by V.P. Semernoy (unpublished), has nothing to do with Baikal. Here the main dominant was always *Embolocephalus velutinus* [note: the identity of the non-European *E. velutinus* was questioned by Holmquist (1979)], often accompanied by other species like *Tubifex tubifex, Limnodilus profundicola*, *Rhynchelmis tetratheca*, and *Lamprodrilus* sp.

The Transbaikalian small, lowland lakes of the Ivano-Arahlej group studied by Semernoy (1969) revealed mostly *Tubifex tubifex* in their profundal, on one occasion also *Limnodrilus hoffmeisteri*.

T. tubifex, *L. hoffmeisteri*, and *E. velutinus* had not reached the extreme northeast of Asia (Russia). Instead, the profundal of the thermokarstic lakes in the Anadyr River basin (Morev, 1983) was inhabited by *Rhyacodrilus coccineus*, *Lumbriculus variegates*, and *Styloscolex sokolskajae* Morev, 1978, and the profundal of Lake Jack London in the Magadan region (Morev, 1991) by *Embolocephalus chukotensis* (Morev, 1975) and *Alexandrovia ringulata*.

Caldera lakes of volcanic origin, often deep and oligotrophic but geologically young, are common both on the Kamčatka Peninsula and on the Japan Islands. Their profundal oligochaete assemblages, consisting of species available in local water bodies, do not copy either each other or that of European lakes. However, their structure displays a remarkable parallel. For example, the profundal fauna of Lake Kuril'skoe (Kamčatka, Russia) consists of a tubificid without hair chaetae (*Limnodrilus profundicola*), a smooth-skinned [*Tasserkidrilus americanus* (Brinkhurst et Cook, 1966)] and a papillate [*Embolocephalus kurenkovi* (Sokolskaja, 1961)] tubificid with hair chaetae, and a lumbriculid (*Styloscolex opisthothecus* Sokolskaja, 1969) (Timm and Vvedenskaya, 2006). Only *L. profundicola* occurs in both regions (although marginally in European lakes) while the other species have their morphological counterparts in European deep oligotrophic lakes: *L. hoffmeisteri*; *T. tubifex*, *P. hammoniensis* etc.; *S. ferox* or *E. velutinus*; *S. heringianus, L. isoporus*, and other lumbriculids, respectively. Such similarity may reflect some distribution of resources (?). Sokol'skaja (1983) reports also *Spirosperma apapillatus* (Lastočkin et Sokolskaja, 1953) and *Alexandrovia ringulata*, as well as several otherwise littoral Naididae from the greater depths of some other lakes in Kamčatka.

The profundal of the Japanese caldera and lowland lakes also reveals a variety of tubificids coming from their surrounding waters, as *Rhyacodrilus komarovi* Timm, 1990; *R. hiemalis* Ohtaka, 1995; and *Krenedrilus towadensis* Ohtaka, 2004 (the last of these seems to be endemic in the lake since it has not yet been encountered elsewhere), but is mostly dominated by the widely distributed species *T. tubifex* and *L. hoffmeisteri* (Ohtaka and Kikuchi, 1997; Ohtaka, 2004; Ohtaka and Sato, 2005; Ohtaka et al., 2006; Hirabayashi et al., 2007). All of them are lacking on the Kamčatka Peninsula. Lumbriculids are usually absent from the profundal of Japanese lakes.

Only 4 smaller lakes in the highland part of China, on the Yunnan Plateau, are studied with respect to oligochaetes. *L. hoffmeisteri* is reported to be a dominant in 2 lakes; it is gradually replaced with *Branchiura sowerbyi* Beddard, 1892 in 2 other, apparently warmer and more eutrophic lakes (Cui and Wang, 2008). On the Chinese Lowland, one can find numerous floodplain lakes like Poyang and Dongting, all connected with the Yangtze River. They are shallow and vegetation-rich, without a true profundal zone, and are inhabited by a diverse fauna of Tubificidae and Naididae, usually dominated by *B. sowerbyi* according to Wang and Liang (2001) and Xie et al. (2003).

The origin of some common profundal oligochaetes

There are no specialized profundal oligochaetes in most lakes. Instead, there is a limited range of relatively euryoecious species. Even the endemic species that have arisen in ancient, tectonic lakes are largely not profundal-specific but inhabit shallower zones also. Only in the largest of these lakes, Baikal, are a few of the endemic species like *Lamprodrilus bythius* Michaelsen, 1905 and *L. inflatus* Michaelsen, 1905 definitely adapted to life in the liquid mud at the greatest depths (Semernoy, 2004). An ongoing speciation process along different depth zones has been observed on the example of *Spirosperma stankovici* (Hrabě, 1931) in Lake Ohrid (Šapkarev, 1953).

If we exclude ancient lakes with their endemic fauna, the dominant oligochaete species of the profundal alternate both among lake types and in geographical regions.

The most widely distributed and most tolerant tubificids, *Tubifex tubifex* and *Limnodrilus hoffmeisteri*, are highly anthropochorous. It is difficult to establish their spontaneous distribution range. At least they are still lacking in extreme northeastern Asia, and are certainly alien to Australia. As some genetic forms (possibly cryptic species) of *T. tubifex*, carrying the fish parasite *Myxobolus cerebralis* Hofer, 1903, were discovered in North America only in the 20th century (Beauchamp et al., 2001), the homeland of this species (or species group) may be the western Palaearctic. *T. tubifex* s.l. is highly euryplastic, being characteristic of both ends of the trophic scale in lakes (Milbrink, 1983) but not abundant in moderate conditions, maybe displaced there by competitors. One can speculate that there are different genotypes of *T. tubifex* in oligotrophic and eutrophic water bodies. However, no genetic differences were found between populations in cool springs and “common”, polluted waters of Estonia (unpublished data by R. Marotta). *T. tubifex*, like most other tubificids, needs at least periodically low temperatures for spermatogenesis. It can pass over to parthenogenesis at higher temperatures, as well as in the conditions of absence of a copulation partner. This makes it a successful pioneer species. However, the fecundity decreases after a few parthenogenetic generations (Poddubnaya, 1984). This is the reason why it is lacking in tropical regions (Timm, 1987).

Limnodrilus hoffmeisteri may originate from the Nearctic, known for the highest diversity of the genus *Limnodrilus*. This actually cosmopolitan species inhabits both temperate and tropical waters on several continents, often as a dominant. Its ability for parthenogenetic reproduction is as limited as that of *T. tubifex* (according to Poddubnaya, 1984). Thus, it must have “invented” the ability to reproduce in a sexual way (including spermatogenesis) without “hibernation” in a cool season. Further research must show if this innovation is peculiar to the whole species, or to the single, most widely distributed genotype only. *L. hoffmeisteri* is more cold-sensitive than *T. tubifex*, and is gradually replaced by *L. profundicola* in northern Siberia as well as in northern European and northern American oligotrophic lakes.

Branchiura sowerbyi has definitely become cosmopolitan owing to human activity. Unlike typical tubificids, it is distributed mostly in tropical countries. Its sexual reproduction is promoted by higher temperatures, about +25 °C (Aston, 1968), although maturation takes place in the coolest available season (Casellato, 1984). The homeland of this species is eastern Asia where it occurs in most different ecological conditions, including the cool, winter-freezing Amur River with its floodplain waters, and the profundal of the ancient Lake Biwa. In the latter it occurs as an ecological form devoid of gills, and was even described as a separate taxon, *Kawamuria japonica*, by Stephenson (1917). The gilled *B. sowerbyi* has become common in many parts of Africa and America but is remarkably still lacking in the Amazon basin, although it was originally described from a tank with Amazon plants in London (Beddard, 1892). In Europe it appeared in the wild nature during the 20th century but only in warmer waters and never in the profundal of lakes.

Stylodrilus heringianus and *Spirosperma ferox*, both characteristic of the northern cool, oligotrophic lakes, are undoubtedly of western Palaearctic origin. They are still absent from extreme northeastern Asia, and seem to have been recently introduced to North America. Although *S. heringianus* is now a dominant of the oligotrophic regions of the North American Great Lakes, it was not reported from there by Smith and Verrill (1871).

Potamothrix hammoniensis is a representative of the Ponto-Caspian fauna. The Caspian Sea, morphologically a large lake, is a relic of the large Ponto-Caspian basin with changing contours and alternating salinity during its long geological history. The Caspian Sea and the estuaries of the Black Sea support a variety of brackish- and freshwater oligochaetes, including endemics. Some representatives are dispersing, mostly by human help, in Europe and North America. *P. hammoniensis* belongs to their first wave, starting invasion in the natural way already in the early post-glacial period. Its range is just expanding on the Scandinavian Peninsula (Milbrink and Timm, 2001). *P. hammoniensis* is particularly well adapted to eutrophic freshwaters that are not cool all the year round and will probably be favored by future climate warming.

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