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Observations on the life cycles of aquatic Oligochaeta in aquaria

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Abstract

Observations on the life cycles of aquatic oligochaetes were made in the period 1962–2017 at the Võrtsjärv Limnological Station (Estonia) using small aquaria with sieved profundal mud covered with unaerated water. The aquaria were mostly inseminated with 10 juvenile worms and checked four times a year, changing the mud and eliminating the progeny, until the natural death of the original worms. Besides, mass cultures were kept in bigger aquaria. Many individuals of *Tubifex tubifex, T. newaensis, Limnodrilus hoffmeisteri, L. udekemianus, Ilyodrilus templetoni, Psammoryctides barbatus, Spirosperma ferox, Potamothrix moldaviensis, P. vejdovskyi, P. bavaricus, Stylodrilus heringianus* and *Rhynchelmis tetratheca* survived for several years, reproduced repeatedly, and died out one by one during the observation period. In some cases, the most longevous individuals reached an age of up to 8 years (*I. templetoni*), 10–12 years (*T. tubifex*), 15–17 years (*L. hoffmeisteri, P. barbatus, S. heringianus*), or even more than 20 years (*L. udekemianus, S. ferox, T. newaensis*). *Criodrilus lacuum* did not reproduce in aquaria, although the oldest individual spent 46 years there. *Potamothrix hammoniensis, Lophochaeta ignota, Lamprodrilus isoporus*, most naidines and some others did not thrive in aquaria and usually died without reproducing. In a cellar, where temperature conditions imitated seasonal fluctuations in lakes, or when the aquaria were maintained at continuously low temperature, the lifetime of worms was often longer than at room temperature. At elevated temperatures (+25° to +35°C) *T. tubifex* and *L. hoffmeisteri* formed cocoons mostly with only 1–2 eggs while their life span was then shorter. Architomic clones of *Potamothrix bedoti, Bothrioneurum vejdovskyanum, Aulodrilus pluriseta* and *A. japonicus* survived and propagated for years. The architomic *Lumbriculus variegatus* was thriving only when fed, e.g., with yeast. Uniparental reproduction by parthenogenesis was observed in *T. tubifex, L. hoffmeisteri* and *S. heringianus* kept or reared single. Two special races(?) were noted both within *T. tubifex* and *L. udekemianus*.

Key words. Aquatic Oligochaeta, aquarial cultures, life cycle, life span, reproduction

Introduction

The life cycles of aquatic oligochaetes, mostly tubificids, have been studied on many occasions, both in the nature and as aquarial cultures. Researchers usually focused on the generation time in sexual reproduction, which was supposed to be mostly one year (e.g., Aston 1968; Bonacina *et al.* 1987), but for *Tubifex tubifex* (Müller, 1774) in aquarial cultures much shorter (e.g., Kosiorek 1974), by default presuming that they would die after forming cocoons with eggs. Sometimes also survival after reproduction, accompanied with the resorption of the reproductive system (e.g., Casellato 1984), or a „resting period“ after reproduction, has been observed (e.g., Block *et al.* 1982).

A two-year reproduction cycle was suggested by Brinkhurst (1964) for *Tubifex costatus* (Claparède, 1864; = *Baltidrilus costatus*) and by Kennedy (1966a) for *Limnodrilus udekemianus* Claparède, 1862. Repeated reproduction in two subsequent years was noted by Jónasson & Thorhauge (1972) for *Potamothrix hammoniensis* (Michaelsen, 1901), and in 2–3 years, by Poddubnaja (1980) for *Limnodrilus newaensis*

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(Michaelsen, 1903; = *Tubifex newaensis*). Two reproduction periods per year were reported by Ladle & Bird (1984) for *Psammoryctides barbatus* (Grube, 1861), and by Lobo & Alves (2011) for *Branchiura sowerbyi* (Beddard, 1892). Kennedy (1966b) found that the reproductive cycle of *Limnodrilus hoffmeisteri* Claparède, 1962 and *Tubifex tubifex* can be longer or shorter depending on environmental conditions. A similar finding was reported by Poddubnaya (1980) who also proposed 2–3 years as the full life span of the two last species. Matsumoto & Yamamoto (1966) established a reproduction frequency of twice per year and an expected life span of 4–6 years for *T. hattai* Nomura, 1926 (= *T. tubifex*). Until now, nobody has attempted to establish the maximum life span of these worms, which can last many years and sometimes exceed their fertile period.

I have been most fortunate to have worked consistenly at the same institution (Centre for Limnology, former Limnological Station, at Lake Võrtsjärv in Estonia) for almost 60 years. In the 1960s, a project was launched on to test local freshwater invertebrates as possible objects for mass cultivation of live food for fish fry. Aquaria with various animals, including oligochaetes, were set up. I continued to keep and supplement them as an „Oligochaete Zoo“ also after the end of this project. These aquarium cultures gave me a chance to follow the individual life span of many oligochaete species, mostly tubificids and lumbriculids, until their natural death. Some individuals became outright my personal acquintances. Some preliminary data of my work were published more than 30 years ago (Timm 1972, 1984, 1987). Here I will undertake a survey of the main results of my recorded observations during a 55-year period, 1962–2017.

Methods and materials

Most observations were made in small cylindrical glass aquaria (crystallizers), diameter 10 cm, height 5.5 cm, volume 300 ml, filled up to ¼–¾ with sieved mud from the profundal of Lake Võrtsjärv, and the remaining space, with artesian well water (Fig. 1).

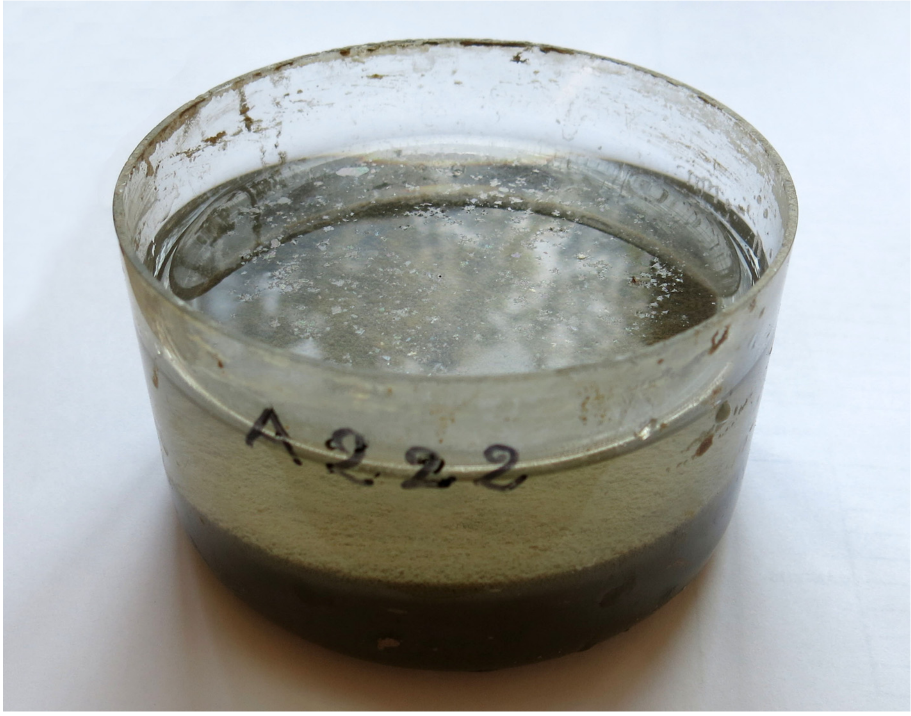

FIGURE 1. A standard aquarium used in long-term observations on aquatic Oligochaeta. Photo by Henn Timm.

The aquaria were maintained either at unregulated, often highly variable, room temperature, or in a cellar with seasonally fluctuating temperatures (about +4°C or less in winter, and about +15°C in summer), seldom also at regulated higher (+20°C, +25°C, +30°C and +35°C) or lower (about +5°) temperatures. The devices for temperature regulation were not reliable on a many-year scale. Usually, a batch of oligochaetes was initiated in each small aquarium with 10 conspecific newborn or young individuals when available, or with adults taken from natural waters, that were expected to produce progeny. The contents of aquaria were usually sieved four times each year, with a few aquaria sieved five or six times per year. Each time the number and the sexual condition of worms was registered, the original (old) individuals were returned to the aquarium with fresh mud and water while young worms and the egg cocoons were either discarded or used for starting a new culture. This procedure was repeated until the natural death of the last individual in the original cohort. Young worms were usually distinguishable from their parents, even when they have reached similar size, owing to the lighter colour of the chloragogen tissue on their intestine. No aeration was used in the aquaria, but a certain amount of water was added considering evaporation. As a rule, the worms subsisted on the muddy substrate only, without any additional food; when tested, small amounts of yeast or fish food pellets accelerated their growth. Besides the small aquaria, bigger ones were used for maintaining mass cultures, and enameled pans or wooden boxes were used for mass cultivation of *Tubifex tubifex*, a topic not discussed further in this paper.

The total number of aquaria and larger containers used during the years 1962 through 2017 was as large as 810, half of them containing *Tubifex tubifex*. In total, 45 species were tested in the above-described conditions but only about 17 tubificids and lumbriculids survived and reproduced during many years. Most species were originally collected from Estonian fresh waters, with the exception of three species: *Criodrilus lacuum*—collected from the Daugava River in Latvia, a strain of *Limnodrilus udekemianus*—collected from irrigation ditches in Kyrgyzstan, and a culture of *Aulodrilus pluriseta*—donated by Dr. N.R. Arhipova (Borok at the Rybinsk Reservoir, Russia). Preliminary results of the above observations were published previously in Timm (1974).

Results

The most common tubificid in Estonian lakes, *Potamothrix hammoniensis* (Michaelsen, 1901) was a disappointment during these studies: although surviving for some years in aquaria and even maturing, it rarely if ever reproduced (Fig. 2). Several other tubificid and lumbriculid species also failed to adapt (e.g., *Lophochaeta ignota* Štolc, 1886 and *Lamprodrilus isoporus* Michaelsen, 1901), as well as the Naididae *s.s.*, Enchytraeidae, *Propappus* and the lumbricid *Eiseniella tetraedra* (Savigny, 1826). The most successful species for cultivation—in both in aquaria and in bigger containers—was the well-known opportunistic pioneer species *Tubifex tubifex* (Müller, 1774). *Limnodrilus hoffmeisteri* Claparède, 1862 may be as suitable; however, its body is 'stickier' and often covered with a slimy mud envelope, making manipulations with it inconvenient.

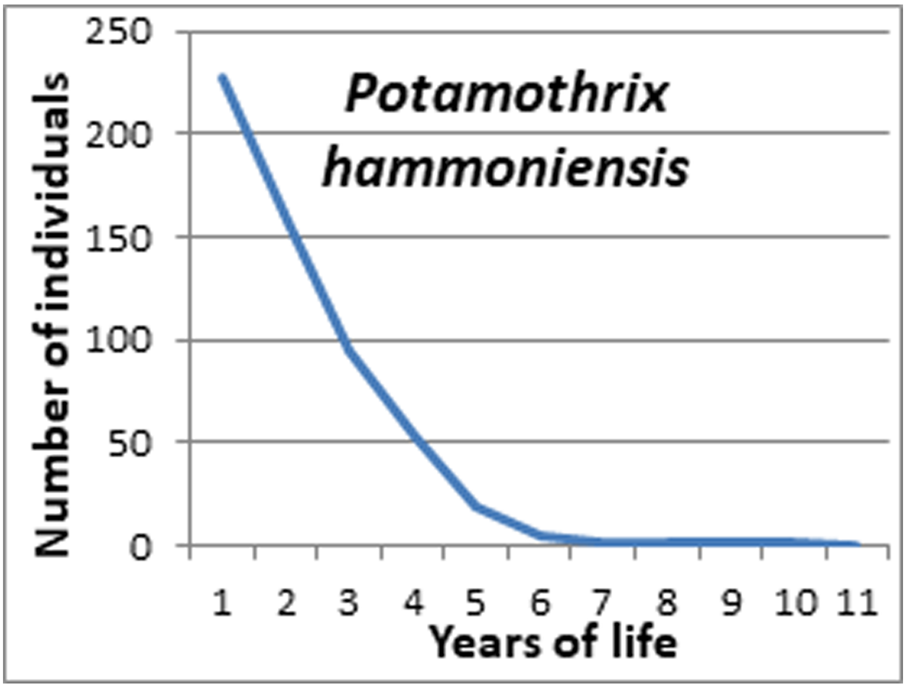

FIGURE 2. Survival of *Potamothrix hammoniensis* in aquaria, at room and seasonally changing temperatures, combined.

Besides *T. tubifex* and *L. hoffmeisteri*, several other tubificids—*L. udekemianus* Claparède, 1862, *Ilyodrilus templetoni* (Southern, 1909), *Psammoryctides barbatus* (Grube, 1861), *Spirosperma ferox* Eisen, 1879, *Potamothrix moldaviensis* Vejdovský et Mrázek, 1903, *P. vejdovskyi* Hrabě, 1941, *P. bavaricus* (Oschmann, 1913), and *Tubifex newaensis* (Michaelsen, 1903), as well as the lumbriculids *Stylodrilus heringianus* Claparède, 1862, and *Rhynchelmis tetratheca* Michaelsen, 1920—survived for years and laid numerous cocoons in the aquaria.

Architomic species—which seldom mature but reproduce well in an asexual way, by fragmentation—were similarly successful in the aquaria: these included the tubificids *Potamothrix bedoti* (Piguet, 1913), *Bothrioneurum vejdovskyanum* (Štolc, 1886), *Aulodrilus pluriseta* (Piguet, 1906), and *Aulodrilus japonicus* Yamaguchi, 1953 (although observations of *A. japonicus* were limited). The lumbriculid, *Lumbriculus variegatus* (Müller, 1774), thrived well only when it was supplied with additional food. Under the paratomic Naididae *s.s.*, only the clones of *Nais communis* Piguet, 1906, and *Nais elinguis* Müller, 1774 managed to survive in the mud for some time (with *N. communis* thriving for up to four years).

Finally, several individuals of the „aquatic earthworm“ *Criodrilus lacuum* Hoffmeister, 1845 lived for many years in the aquaria without reproduction (a single but viable cocoon was laid during the long observation period).

In nature only a few oligochaetes may reach at least the first reproduction period, with the majority of them having perished (mostly consumed as prey?) much earlier. In the conditions of a „Zoo“, in the absence of predation, some individuals also die at a young age (because of diseases?), but most of them perish, one by one, later over the course of several years. They can mature and lay eggs repeatedly, usually once a year (preferably in the spring season), with a „rejuvenation“ [referred to as *ananeosis* by Dózsa-Farkas (1973)]—resorption and renewal of the genital organs (with the exception of the gonads)—after each reproduction period. Many aquatic species can reach an age of up to 10 or even more than 20 years. The most senile worms cease reproducing during their last few years of life, decreasing in size and with their chloragogen tissue turning black.

Figs 3 and 4 demonstrate the gradual decrease of individuals in some comparable micropopulations of *Tubifex tubifex*, at two different temperature regimes.

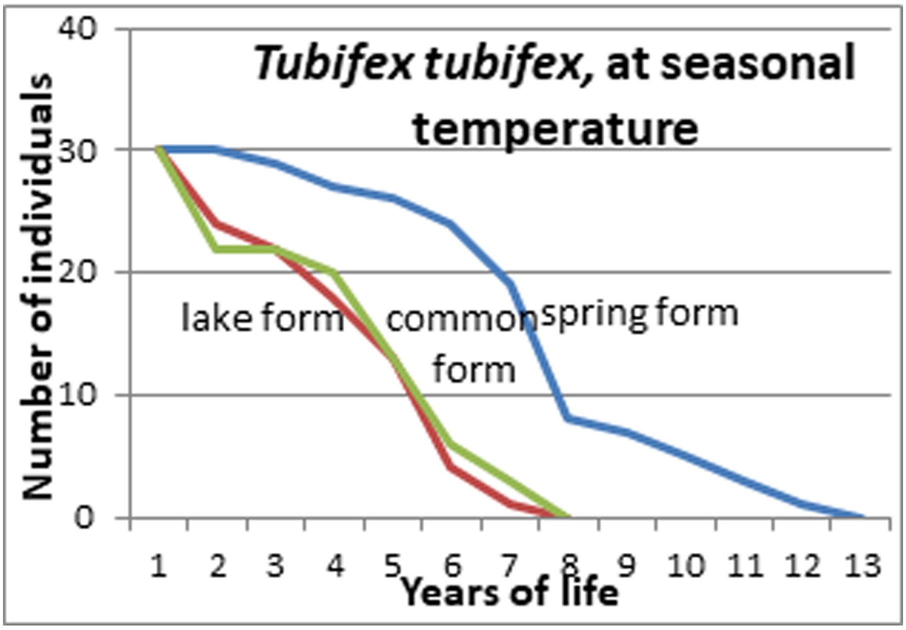

FIGURE 3. Survival of three forms of *Tubifex tubifex* of different origin in aquaria, at seasonally changing temperatures.

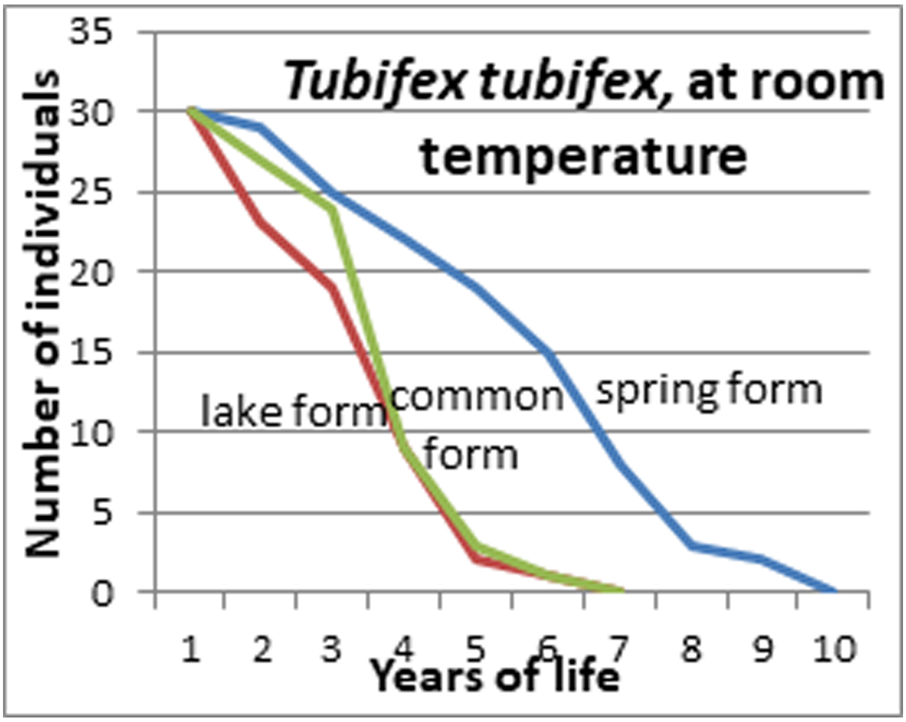

FIGURE 4. Survival of three forms of *Tubifex tubifex* of different origin in aquaria, at room temperature.

Half of the worms survived for 6–8 years in the „spring form" and 3–5 years in two other forms, living in the cellar with cool winters for about two years longer than at those kept room temperature. One individual of the „spring form" reached the maximum age of 12 years, in cellar. The „common form" in the figures represents the widely distributed opportunistic populations. The „lake form" of *T. tubifex* originated from the dwarf individuals living in the profundal of moderately eutrophic lakes together with the dominating *Potamothrix hammoniensis*, and may have been suppressed by it (Timm 1996). Their successors in the aquaria did not differ from the „common form", either in size or in the life cycle. The „spring form" originated from a large and cool (+5°C) karst spring of Roosna-Alliku in Central Estonia. It was always much larger (live weight 6–9 mg instead of 1.5–4 mg) when adult, laid larger cocoons with more eggs, and lived longer both at room and seasonal temperatures (but less at +25°C) compared with the others. It may represent a genetically different form (so far not proved). *T. tubifex* from some other Estonian springs resembled genetically „common" individuals (Marotta *et al.* 2014).

At consistently elevated temperatures (+25°C) the life processes of all three forms of *T. tubifex* accelerated: the worms matured already during a few months and produced several generations a year, without any seasonal resting period. The cocoons were smaller and contained only 1–3 eggs instead of the usual 4–6. The total lifetime decreased nearly by 50%. *Tubifex tubifex* was able to form odd cocoons even at +30°C, while at +35°C the worms died before long. The accelerated reproduction of *T. tubifex* without hibernation at cooler conditions, may have been possible owing to parthenogenesis which excluded the need for lower temperatures for spermatogenesis. Presence of parthenogenesis was confirmed when singly reared *T. tubifex* individuals of all three forms repeatedly produced numerous cocoons with viable eggs. The second generation was also capable of uniparental reproduction and survived for 2–5 years while the third generation left behind no offspring.

Ilyodrilus templetoni, a small tubificid externally similar to *T. tubifex*, also lived and reproduced in various temperature conditions (most effectively at +25°C!), but on an average for only 2–3 years; the oldest individual survived in the cellar for 8 years (Fig. 5). Parthenogenesis can be suspected; unfortunately, no uniparental cultures were founded with this species.

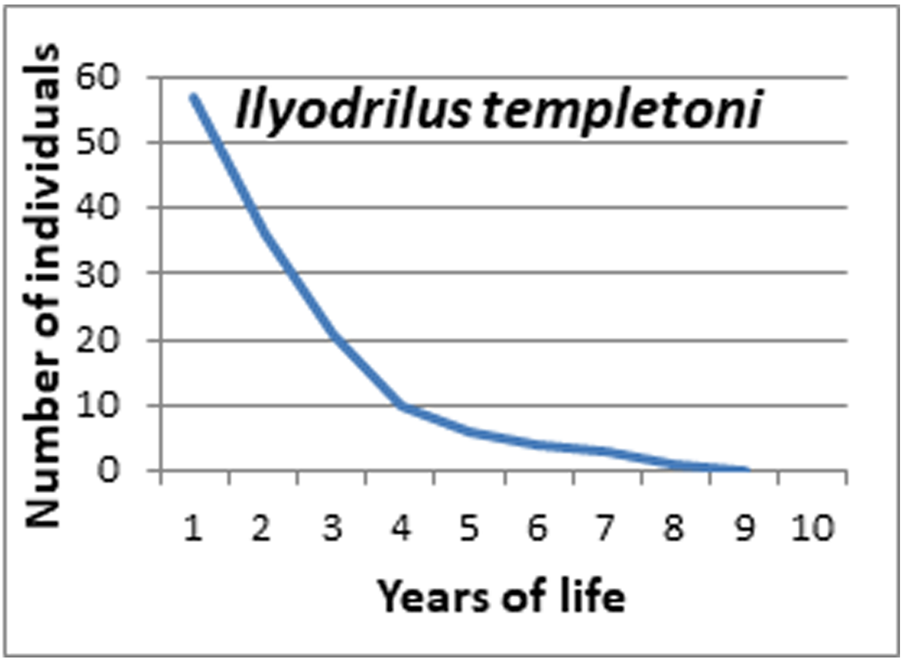

FIGURE 5. Survival of *Ilyodrilus templetoni* in aquaria, at room and seasonally changing temperatures, combined .

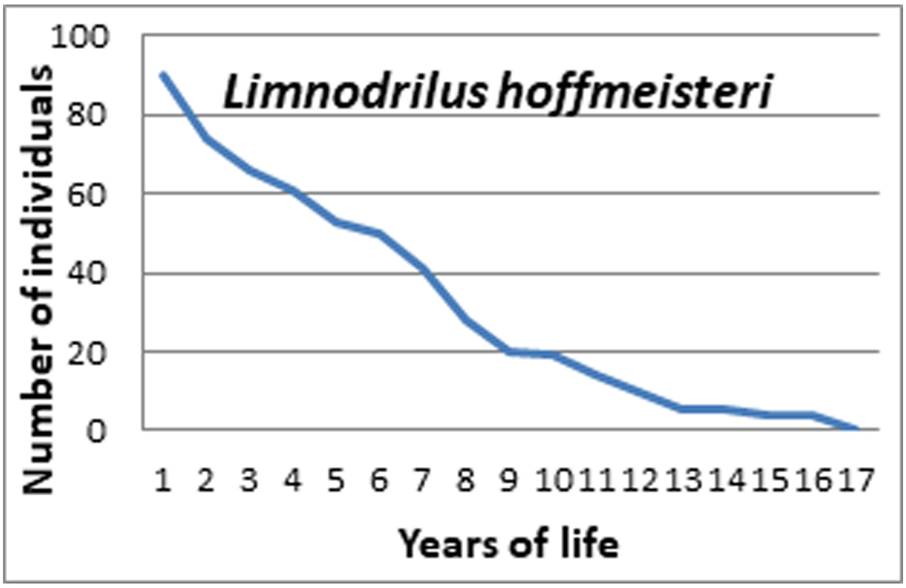

FIGURE 6. Survival of *Limnodrilus hoffmeisteri* in aquaria, at room and seasonally changing temperatures, combined.

Limnodrilus hoffmeisteri survived for an average of 5–6 years, maximum 16–17 years, in the aquaria (Fig. 6). It appeared to be the most heat-resistant tubificid, producing cocoons even at +35°C (then mostly with a single egg) and perishing only at +40°C. At elevated temperatures, several generations per year ocurred, as was the case with *Tubifex tubifex*. In the last case, individuals maturing already in the first summer of life were often relatively small.

Uniparental, probably parthenogenetic, reproduction of single-reared individuals was confirmed, too; however, the second generation was usually infertile in the „Zoo“.

Cultures of *Limnodrilus udekemianus* were represented by two forms of different origins in aquaria (Figs 7 and 8). The worms from Estonian waters were very large, less fertile but long-lived (usually 5–6, maximum 28 years). Those by the parents collected from irrigation ditches of Kyrgyzstan were smaller, more productive, and died at the age of about 2–3 years, maximum 19 years. These cultures from two separate regional areas may represent two different races or cryptic taxa.

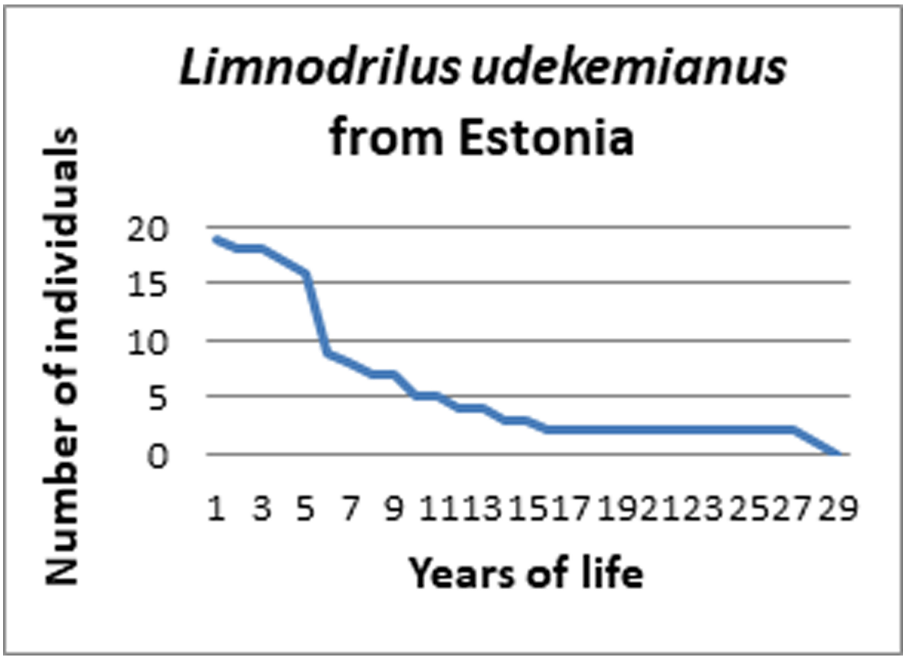

FIGURE 7. Survival of *Limnodrilus udekemianus* from Estonia in aquaria, at room and seasonally changing temperatures, combined.

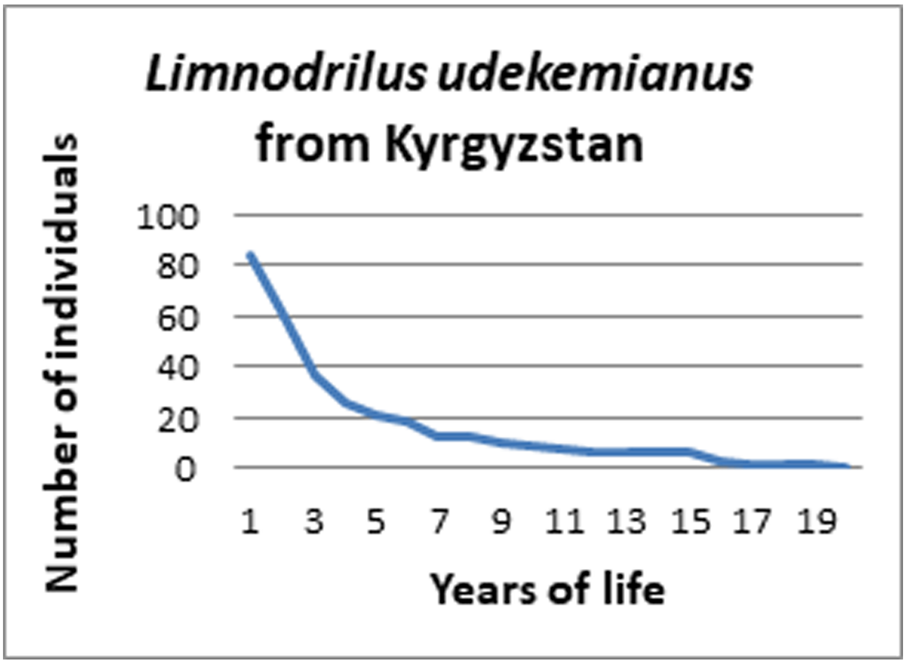

FIGURE 8. Survival of *Limnodrilus udekemianus* from Kyrgyzstan in aquaria, at room and seasonally changing temperatures, combined.

Psammoryctides barbatus survived at room temperature for an average of 3–4 years, maximum 9 years (Fig. 9), forming cocoons once a year. In the case of seasonal temperatures (in the cellar), one individual reached the age of 15 years. Reproduction was suppressed at continuously elevated temperatures (+20°C to +30°C), and the worms soon died when cultures attained temperatures of at +35°C. Uniparentally laid eggs did not develop.

Spirosperma ferox, sluggish in all activities, reproduced for the first time in the aquaria only when approaching the age two years. At unregulated room temperatures, half the individuals survived for about 7 years, the oldest reaching the age of 14 years. At seasonal temperature (in the cellar), the average age reached

15 years while the two oldest individuals, aged 25 years (Fig. 10), perished accidentally after producing a cocoon still at the age of 24 years. Some individuals survived for up to 10 years at +20°C, and for 9 years at +25°C, but with very scarce reproduction.

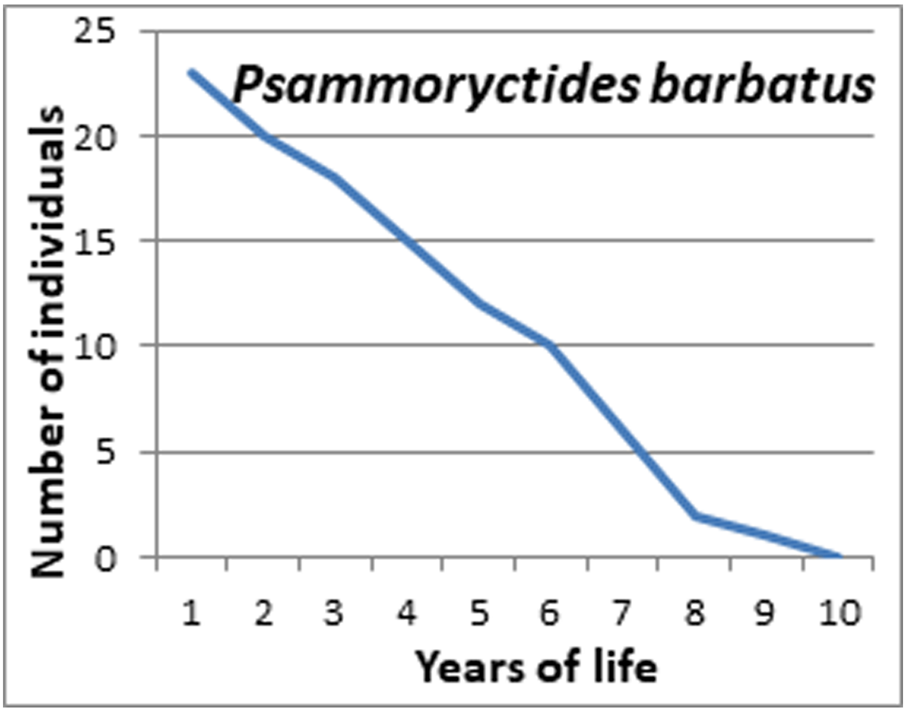

FIGURE 9. Survival of *Psammoryctides barbatus* in aquaria, at room temperature.

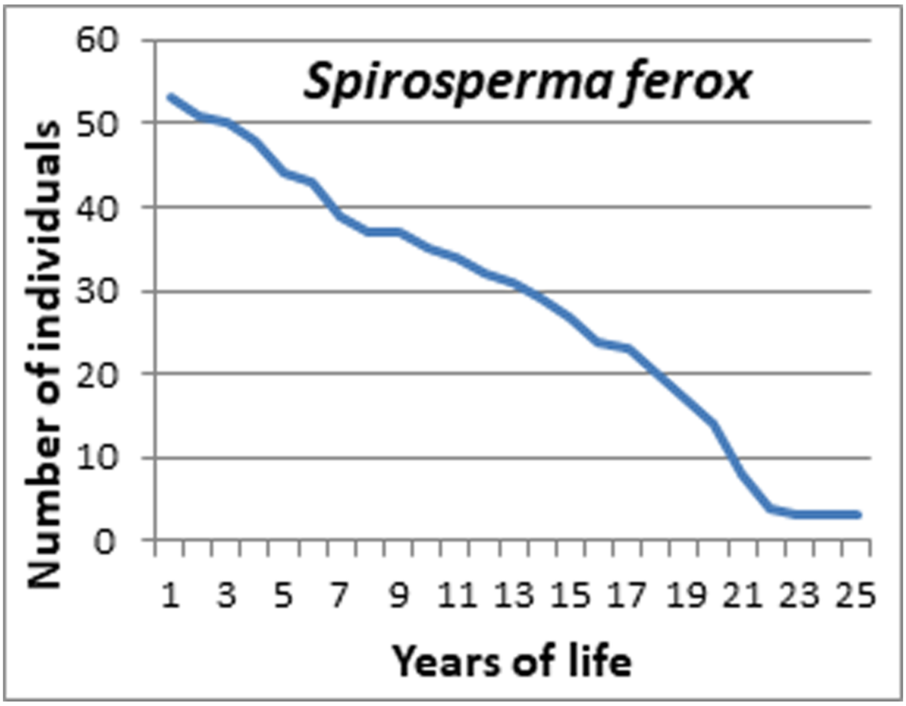

FIGURE 10. Survival of *Spirosperma ferox* in aquaria, at seasonally changing temperature.

Tubifex newaensis, a giant tubificid known mostly from rivers, survived in the standing water of the aquaria at room temperature for up to 8 years and even matured, although without producing any eggs. It also persisted for up to 3 years at +20°C, and for up to 2 years at +25°C. At the seasonally alternating temperature regime (in the cellar, Fig. 11), its average age reached 5–6 years, and maximum age, 22 years. It produced cocoons only at seasonal temperatures, with viable eggs in the first years but with only rotten eggs later on.

Three species of *Potamothrix*: *P. vejdovskyi, P. moldaviensis* and *P. bavaricus* survived in the aquaria for up to 9, 7 and 4 years, respectively (Figs 12–14) and successfully reproduced sexually, unlike their congener *P. hammoniensis*—which did not thrive in aquaria and usually died without reproducing (as noted above).

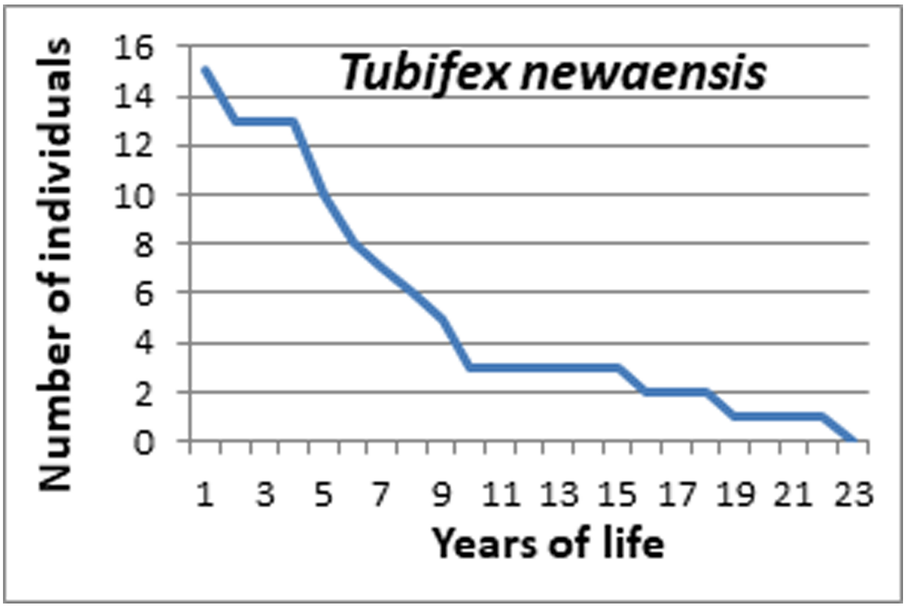

FIGURE 11. Survival of *Tubifex newaensis* in aquaria, at seasonally changing temperature.

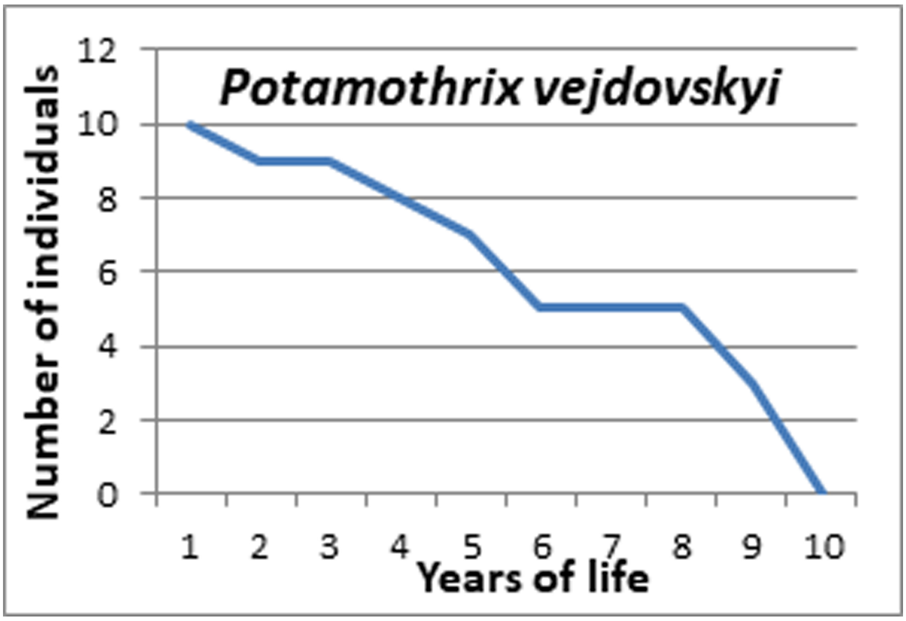

FIGURE 12. Survival of *Potamothrix vejdovskyi* in aquaria, at seasonally changing temperature.

The morphologically tubificid-like lumbriculid *Stylodrilus heringianus*, known as an oxyphilous animal in nature, survived and reproduced in a sexual way both at room and seasonal temperatures surprisingly well, with an average age about 5 years and maximum age of 17 years (Fig. 15). Even at +25°C, some individuals survived for up to 5 years. Single-reared *S. heringianus* reproduced well parthenogenetically, and so did their successors who survived for up to 12 years.

Rhynchelmis tetratheca, another oxyphilous lumbriculid, was also surprisingly well capable to live and reproduce sexually in standing water in the cellar (not tested at room temperature). Half of the individuals survived here for 4 years, with one individual lasting for nearly 13 years (Fig. 16).

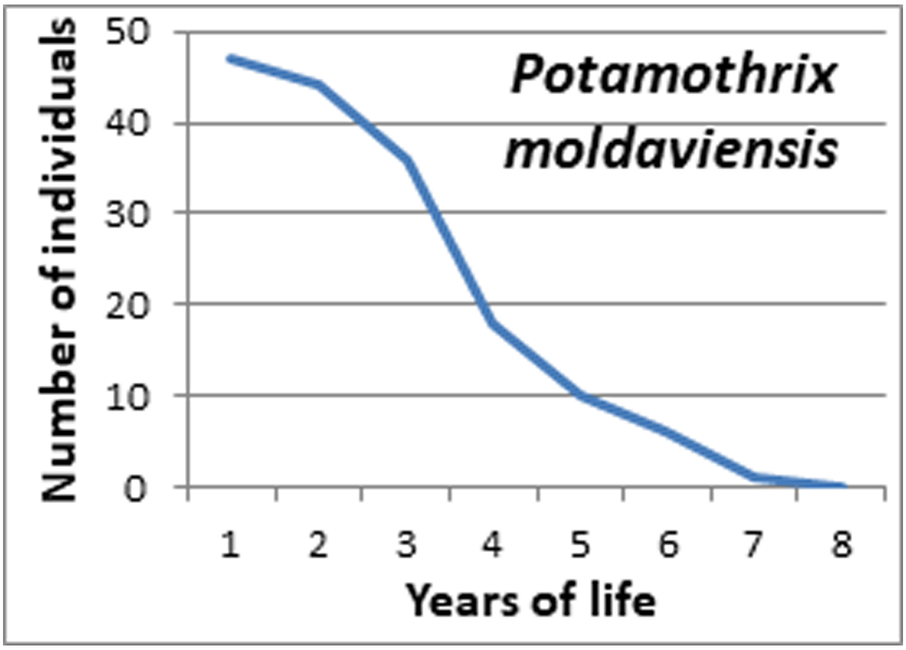

FIGURE 13. Survival of *P. moldaviensis* in aquaria, at room and seasonally changing temperatures, combined.

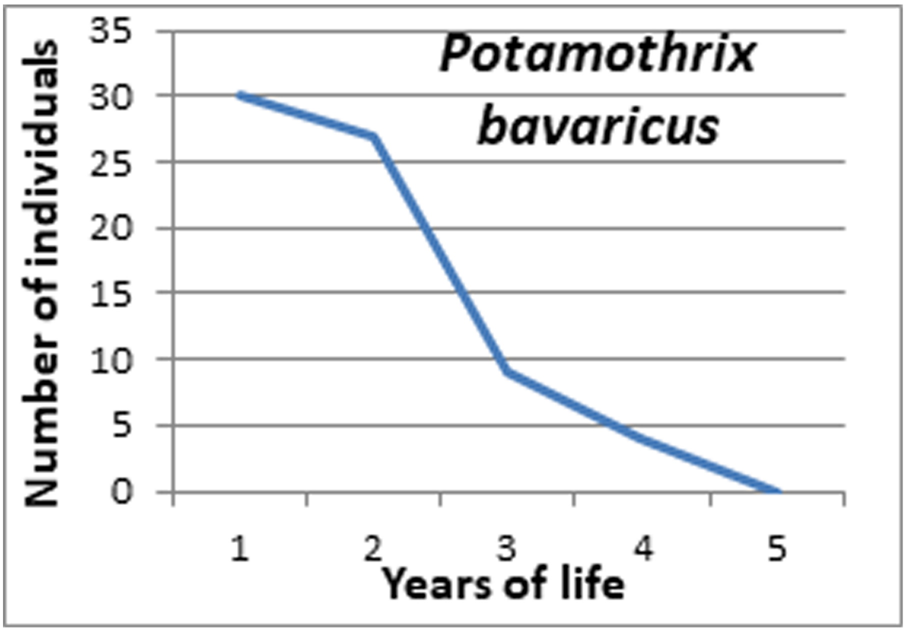

FIGURE 14. Survival of *P. bavaricus* in aquaria, at room and seasonally changing temperatures, combined.

The small architomic (fragmenting) tubificid *Potamothrix bedoti* can survive as a clone for unlimited time. A maximum of 5–10 young per parent were produced asexually during the first three months in the aquarium. When I tried to save only the individuals with darker chloragogen tissue (presumably old ones) at each inspection, the corresponding micropopulations persisted for 4–18 years. One individual, conspicuous because of the presence of a pair of teratological outgrowths in the genital region, was observed during 6 successive years. The clones were able to tolerate, at least temporarily, temperatures reaching +25°C, and some persisted for a short time when temperatures reached +35°C. Although sexually mature individuals of *P. bedoti* forming cocoons and viable eggs were observed mostly at cooler temperatures, a few were even observed when aquaria were maintained at room or seasonal temperatures. At consistently low temperatures, +1°C to +7°C, *P. bedoti* specimens reached considerable length—fragmentation had ceased, and maturing individuals were becoming more common. Of note here: *P. bedoti* in aquaria were repeatedly observed to be infested with plerocercoids of the cestode *Caryophyllaeus laticeps* (Pallas, 1781)—parasites that were close to the same size as their small hosts!

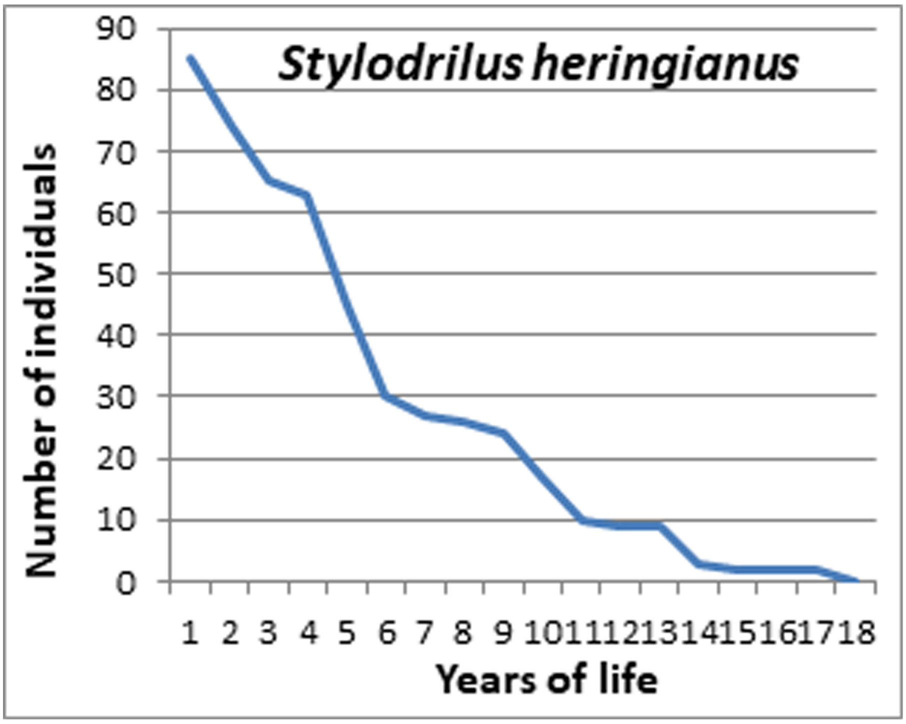

FIGURE 15. Survival of *Stylodrilus heringianus* in aquaria, at room and seasonally changing temperatures, combined.

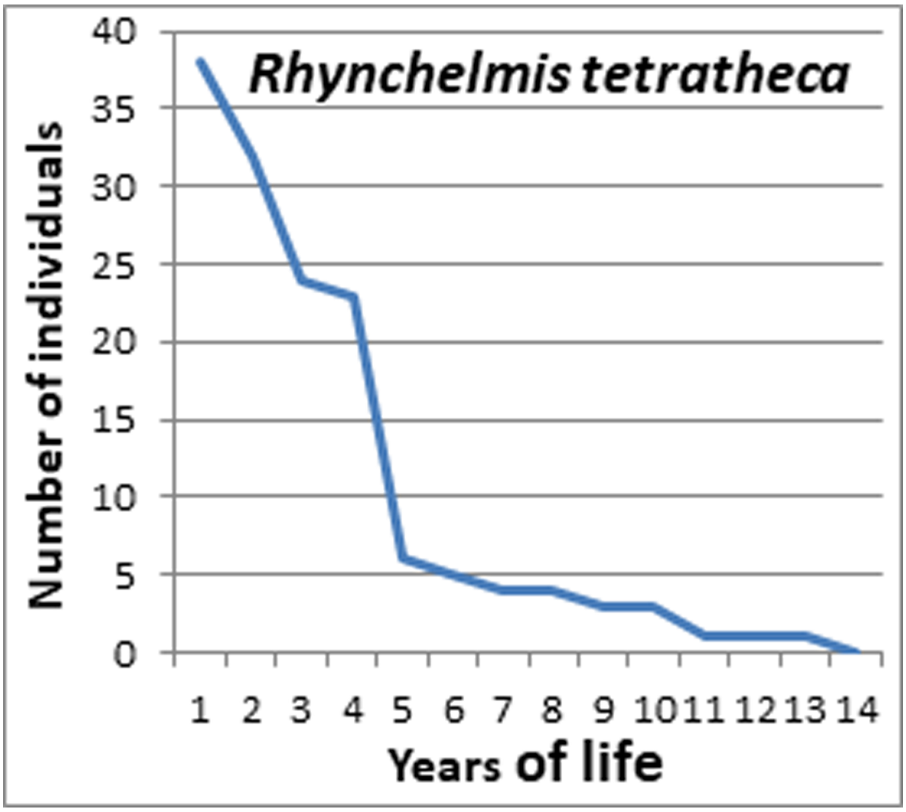

FIGURE 16. Survival of *Rhynchelmis tetratheca* in aquaria, at seasonally changing temperature.

Fragmenting clones of *Aulodrilus pluriseta* survived in the cellar, at room and elevated (+25°C) temperatures for at least 16–18 years and were very productive, usually with 10–30 young produced, per parent, in a three-month period. Some cocoons were occasionally observed in some years, after periods of cooler temperatures. The single micropopulation of *Aulodrilus japonicus* was as productive as that of *A. pluriseta*, but survived for only 5 years. Two mass cultures of *A. japonicus* perished at room temperatures—one culture after one year, and the second after two years—both for unknown reasons.

Populations of *Bothrioneurum vejdovskyanum*—observed to be almost exclusively architomic in Estonian water bodies, expanded the same in aquaria. Several clones lasted for at least 21–30 years, with some perishing as the result of casualties rather than because of senescence. The number of progeny fluctuated between 1–20 per parent during three months. Sexually mature individuals that had copulated (with external spermatophores) were observed, although seldomly. Cocoons occurred in mass cultures but not in the small aquaria.

Lumbriculus variegatus, a widely known architomic laboratory animal and object of mass cultivation, did not grow in the initial sieved mud substrate in aquaria—requiring some additional food (yeast, microalgae, fish food pellets, or presence of live plants like *Elodea*). The number of offspring produced by one *L. variegatus* parent during three months was low, usually 0–2, seldom up to 17. However, some micropopulations survived for 20–30 years. Sexual maturation was never observed.

Criodrilus lacuum, a large aquatic „earthworm“, barely reproduced in the aquaria (only a single cocoon was observed), despite the presence of the external male pores in all full-grown individuals. The numerous individuals taken as adults from the Daugava River in Latvia, usually survived in the aquaria for 5–6 years; some individuals survived for longer than 20 years, with the oldest in captivity observed for 46 years (Fig. 17). They diminished gradually in size and turned black in their last years of life.

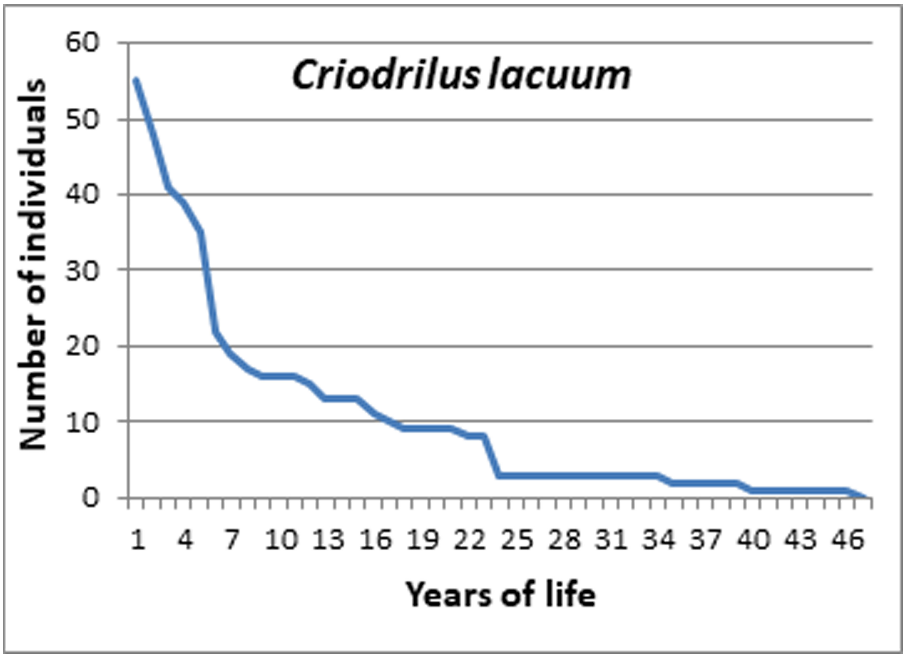

FIGURE 17. Survival of *Criodrilus lacuum* in aquaria, at room and seasonally changing temperatures, combined.

Abnormalities were noted in some individuals of the oligochaetes in aquaria. In the case of sexual maturation in architomic clones of *P. bedoti* and *B. vejdovskyanum*, the entire genital apparatus was always shifted forward, with the male pores in segment IX instead of XI. Individuals with a forked tail (and less often, those with a forked anterior end), were observed in both architomic (e.g., *B. vejdovskyanum*, *P. bedoti*) as well as in sexually reproducing species (e.g., *T. tubifex,* once even with a triple tail; *L. hoffmeisteri, S. ferox,* and *P. hammoniensis*)—persisting sometimes longer than one year. One individual of *P. bedoti* with a forked forebody had developed a reproductive apparatus in each of the two anterior branches. Four short-living „siamese twins“ with a double head and double tail were observed (in two cases) among the newborn *T. tubifex*. An individual of *T. tubifex* regularly produced dumbbell-shaped cocoons, with one shell containing eggs and the other, empty, partially enclosing it. The last inhabitant of the „Zoo" was the posterior half of *L. hoffmeisteri*, with a healed but not regenerated anterior end (Fig. 18). It survived for 2½ years, 2015–2017, mouthless and with an empty intestine, probably assimilating some nutrients osmotically through its body wall.

FIGURE 18. Mouthless individual of *Limnodrilus hoffmeisteri*. Bar = 1 cm. Photo by Henn Timm.

Observations on pure cultures provided opportunities to find and identify cocoons of several tubificid and lumbriculid species. Because descriptions and images of cocoons are scarce in the literature (e.g., Ditlevsen 1904, Penners 1933, Bonacina *et al.* 1986, Arhipova 1983, 1989, Timm 1970, 1972, 2006), a selection of the cocoons found in the aquarium cultures during this study are presented in Figs 19–20 (partially taken from Timm 1970, 1972). One can see that, besides the „traditional", naked and thin-walled, cocoons as in *T. tubifex* and many other species, there can also occur cocoons that are armoured with adhered sand or detritus (e.g., *L. hoffmeisteri, L. isoporus, P. moldaviensis*); their shell can be double (*L. udekemianus*), thickened (*A. pluriseta, B. vejdovskyanum*) or even stone-like and brittle (*Spirosperma ferox*); cocoons can firmly adhere to the substratum either by their unarmoured side (*P. moldaviensis*), or by the terminal stalk (*R. tetratheca*).

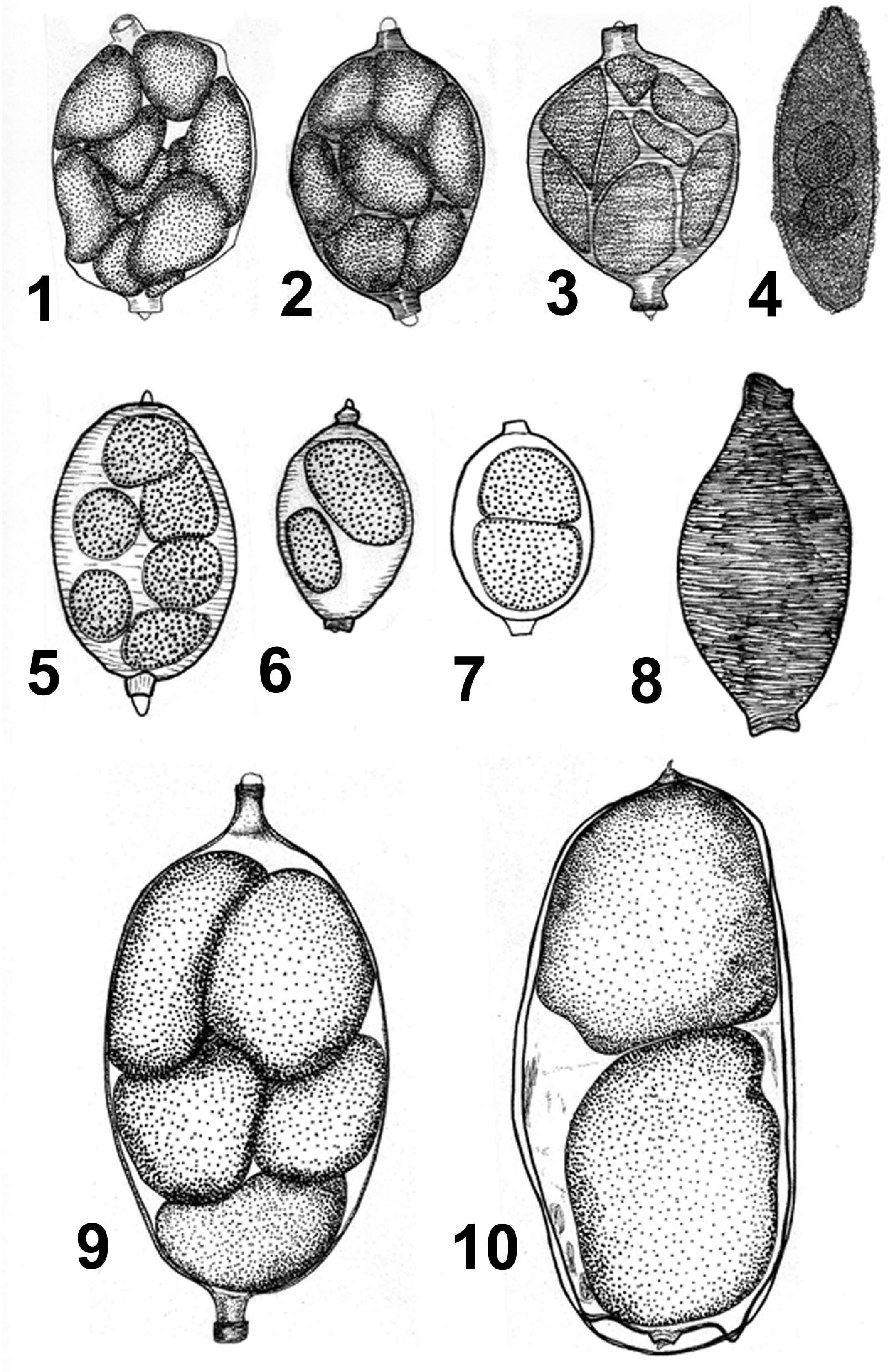

FIGURE 19. Cocoons of some tubificids (drawn without scale). 1—*Tubifex tubifex*; 2—*Potamothrix hammoniensis*; 3—*Psammoryctides barbatus*; 4—*Bothrioneurum vejdovskyanum*; 5—*Potamothrix vejdovskyi*; 6—*Potamothrix bedoti*; 7—*Ilyodrilus templetoni*; 8—*Spirosperma ferox*; 9—*Tubifex newaensis*; 10—*Limnodrilus udekemianus*.

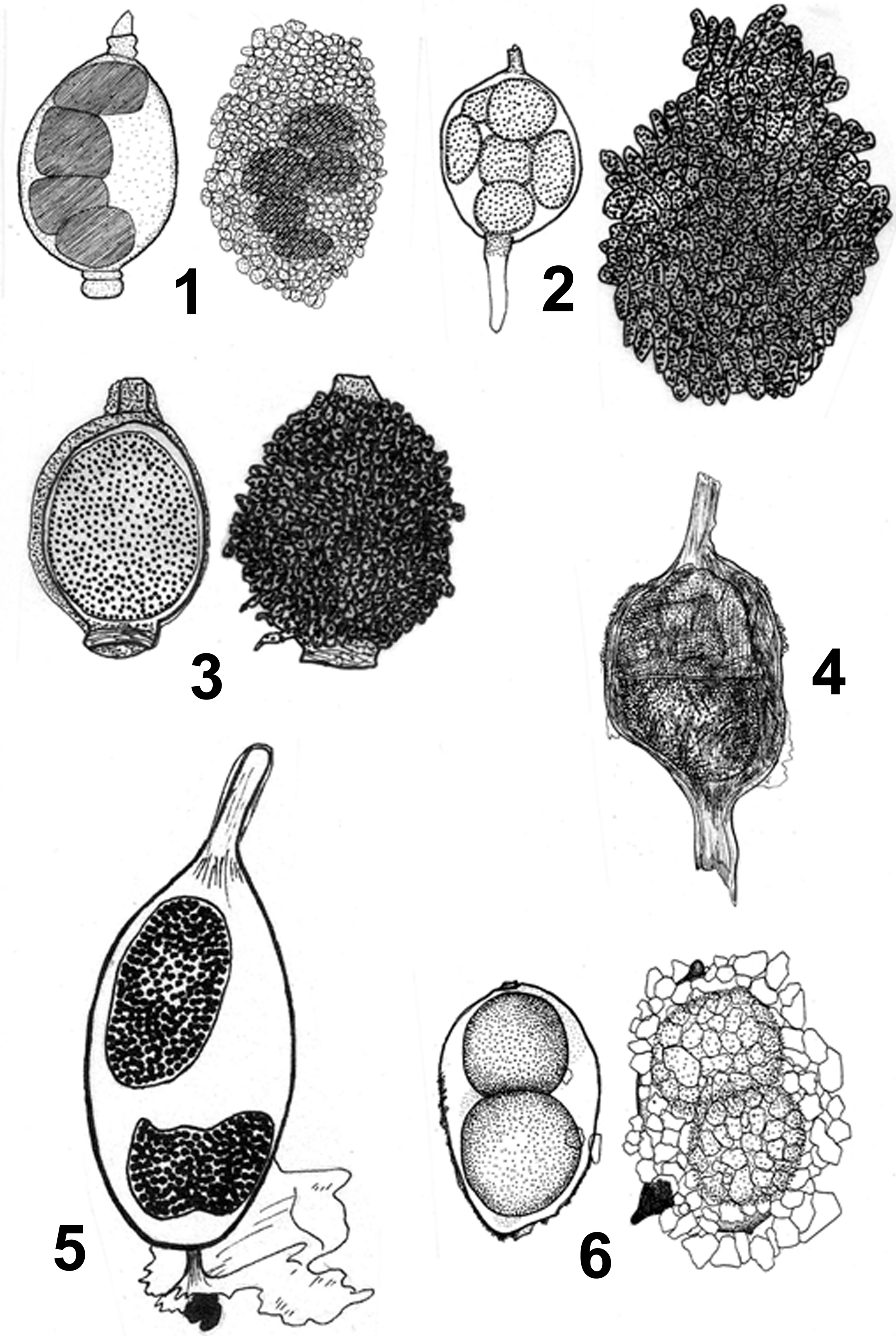

FIGURE 20. Cocoons of some tubificids and lumbriculids (drawn without scale): 1—*Limnodrilus hoffmeisteri*; 2—*Potamothrix moldaviensis*; 3—*Aulodrilus pluriseta*; 4—*Stylodrilus heringianus*; 5—*Rhynchelmis tetratheca*; 6—*Lamprodrilus isoporus* (from sand bottom of Lake Peipsi). Left images in 1–3 and 6 are devoid of ’armour’ of detritus and sand; right images with attached ’armour’ of detritus and sand.

Discussion

The new observations confirmed the experience of several authors (e. g., Block *et al.* 1982; Kaster 1982; Poddubnaya 1971, 1980) that freshwater tubificids and lumbricids resorb their reproductive apparatus (except for the gonads) after oviposition, and restore it in the subsequent reproduction period(s). Observations in the „Zoo" demonstrated an unexpectedly long potential life span in most species, up to 10–20 years, with many annual reproduction periods, but with the number of individuals decreasing gradually every year. Maximum age for an oligochaete (*Criodrilus lacuum*) kept in an aquarium was at least 46 years, for a tubificid *Limnodrilus udekemianus* 28 years, and for *Tubifex tubifex* 12 years. This exceeds considerably the maximum expected life span of 4–6 years suggested by Matsumoto & Yamamoto (1966) for *T. tubifex*. Several authors, e. g. Monti (1986), Arhipova (1976, 1980) and Poddubnaya (1980) had suggested that the lifetime of *T. tubifex, T. newaensis, L. hoffmeisteri, L. claparedianus* and *P. hammoniensis* is likely limited to 1–3 years.

Most aquatic oligochaetes are known to reproduce once a year, usually in spring or early summer, with the first observable reproduction occurring in the year following their hatching. The first reproduction at the age of two years was suggested by Brinkhurst (1964) for *T. costatus* (= *Baltidrilus costatus*), and by Thorhauge (1976) for a deep-water population of *Potamothrix hammoniensis* in Lake Esrom, Denmark. In the „Zoo", the first reproduction at the age of two years was recorded only in *Spirosperma ferox*. Accelerated reproduction in *T. tubifex* and *L. hoffmeisteri*, with several generations per year in suitable temperature conditions, sometimes associated with parthenogenesis (as was the case in the „Zoo"), had been reported previously by several authors (e.g., Arhipova 1976, Poddubnaya 1980, Moroz 1983).

After many years of observing cultures of oligochaetes in the „Zoo", I believe that many past researchers (e. g., Čekanovskaja 1962, Hrabě 1981) may have often misidentified „neotenic" *Limnodrilus hoffmeisteri* individuals—those not yet fully grown during their first summer of life but already sexually mature—as either *L. parvus* Southern, 1909 or *L. hoffmeisteri* f. *parvus*. The latter taxon had also been synonymized with *L. hoffmeisteri* by Brinkhurst (1971).

Phenotypic heterogeneity in the size and reproduction of the nominal species *T. tubifex* and *L. udekemianus* was observed in the aquaria, but was not tested using genetic methods. At the same time, the dwarf *T. tubifex* from the lacustrine profundal (Timm 1996) appeared to be a simple ecological form. In the literature, some phenotypic variability in *T. tubifex* has been described by Bonacina *et al.* (1987), and phenotypically identical cryptic species have been described by Beauchamp *et al.* (2001) and Marotta *et al.* (2014). Matsumoto (1983) described a co-existence of two forms of *T. hattai* (= *T. tubifex*) in cultures—one large and one small, although it is possible that these two forms were in fact representatives of two different age classes.

Uniparental reproduction was first described in *T. tubifex* by Černosvitov (1927) who explained it with possible self-fertilization. Self-fertilization was suggested also by Gavrilov (1935) who obtained offspring from single-reared *L. udekemianus, L. hoffmeisteri* and *L. claparedianus*, although the spermatozeugmata in spermathecae were present only in *L. udekemianus*—where self-fertilization is theoretically possible due to its short penis sheaths in comparison to those of its congeners. Purdy (1945) also associated the uniparental reproduction of *Tubifex* and *Limnodrilus* in aquaria with putative self-fertilization. Gavrilov (1955) later verified parthenogenesis during at least three generations in the tubificid *Paranadrilus descolei* (Gavrilov, 1955). Poddubnaya (1984) explained uniparental reproduction in the tubificids with parthenogenesis. Morev (1983) obtained 3–4 subsequent parthenogenetic generations of putative *L. udekemianus* (which could have been confused with *L. hoffmeisteri* by Morev) and *T. tubifex* reared single at 22–23°C.

Observations in the „Zoo" confirmed that parthenogenesis occurs in several tubificid species as well as in the lumbriculid *S. heringianus*. Parthenogenesis (the laying of viable diploid eggs without fertilization) seems to appear in the case of unavailability of the partner's sperm [due to absence of the spermathecae in some individuals, or running out of spermatozeugmata (see Poddubnaya 1984); lack of copulation partners; and/or elevated temperature—which inhibits spermatogenesis (see Timm, 1987)].

Parthenogenesis can support the colonization of new habitats by single individuals, or reproduction during periods temporarily affected by elevated temperatures. However, parthenogenesis may not be sustainable for longer periods of time, since parthenogenically formed eggs do not develop after a few generations (Poddubnaya 1984, and new data in this study). This can be a plausible explanation for the decline of some mass cultures of *T. tubifex* kept at room temperature, in the „Zoo". Baldo & Ferraguti (2005) were faced with a mysterious situation where sexually mature and copulated *T. tubifex* laid only parthenogenetic eggs. The cause of this can be the relatively high temperature, +21°C, during the experiment. The relative unsustainability of parthenogenesis can indirectly explain the absence of *T. tubifex* in permanently hot tropical regions, e.g., the Tamil Nadu (India) lowlands, although the species inhabits the nearby Ooty Hills with a cool winter (Naveed 2012). The wide circumtropical distribution of *L. hoffmeisteri*, with presumably sexual reproduction, can be explained by the possible adaptation of spermatogenesis of this species [or one of the cryptic forms of this polytypic species separated by Liu *et al.* (2017)] to higher temperatures, avoiding the need for a cooler period.

Architomic clones of some tubificids can survive for many years without any symptoms of degeneration; hovewer, rare maturation and sexual reproduction of some individuals in cooler periods can support their sustainability. Certainly also the posterior fragments are physiologically younger then the most anterior „mother“ fragment. In a situation where only the oldest individuals (with darker chloragogen tissue) were maintained, a micropopulation of *Potamothrix bedoti* in the „Zoo“ tended to cease after some years.

The records of *P. bedoti* mainly from cool springs in Estonia (Timm 1972) are associated with its sexual maturing at relatively low temperatures, as I have confirmed now in aquaria. It is possible that *P. bedoti* is more common in lakes and rivers than has been previously estimated, given that it is often confused with small, immature specimens of *P. hammoniensis*. The results of this study also verify the regular forward shift of the reproductive system in *P. bedoti* and in other architomical oligochaetes occurring after the regeneration of the anterior end—as previously described by Hrabě (1935, 1981) and Sokol'skaja (1968).

The long survival of a mouthless posterior half of *L. hoffmeisteri*, without any possibility to ingest food, seems to support the possibility of osmotic assimilation of dissolved nutrients from surrounding waters by tubificids, as observed by Annabaeva *et al.* (1977), Hipp *et al.* (1985), and Sedlmeier & Hoffman (1989).

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