

Life forms in Oligochaeta: a literature review

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Abstract. The main life forms among the Oligochaeta s.l. (= Clitellata) and the related polychaetes are: aquatic (freshwater and marine) sediment-dwellers, inhabitants of the macrovegetation, large and small soil-dwellers, and carnivores. The vegetation-dwellers (Naididae, Pristinidae and Opistocystidae) reproduce mostly in an asexual way; some of them have an ability to swim and possess eyes. A convergent group to the naidid oligochaetes is the aphanoneuran genus *Aeolosoma*. The smaller Enchytraeidae, and the larger “earthworms” (= Megadrili) Crassiclitellata and Moniligastridae, live in the terrestrial soil. Some Enchytraeidae and Crassiclitellata are secondarily aquatic while some (generally aquatic) tubificids can facultatively live in the soil. Carnivory (as parasitism, commensalism or predation) has been developed in separate genera of several families. A large clade, including the Hirudinea, the Acanthobdellidae and the Branchiobdellidae, is highly adapted for carnivory (suckers, jaws, loss of chaetae, etc.). Two evolutionary trends are evident in different clades: reduction in chaetal number from indefinite to two per bundle, or to complete loss of chaetae, and reduction of the upper tooth in the originally bifid sigmoid chaetae. External gills have appeared at least in four independent cases. There exist many convergencies in the mode of life and morphology of separate Oligochaeta and related “oligochaetoid” polychaetes.

Key words. Oligochaeta, Clitellata, Polychaeta, life forms, characters, convergency.

Introduction

The presented brief review deals with survey of the phenotypes and convergencies among the Oligochaeta and some of their phylogenetic relatives. The subclass Oligochaeta is a paraphyletic taxon constituting the bulk of species included in the class Clitellata; in the phylogenetical sense, it is identical with the Clitellata. They are characterized by hermaphroditism, concentration of the reproductive organs in limited number of segments, and by direct development of eggs in a cocoon excreted by the clitellum – as probable adaptations to life in a non-marine environment. The nuchal organs, the paired head appendages and the parapodia characteristic for majority of Polychaeta, are lacking while the dorsal position of the pharyngeal pad, and the shift of the brain from the prostomium into subsequent segments, can represent apomorphies of the Oligochaeta.

Related polychaete taxa

CHRISTOFFERSEN (2012) has included more annelid taxa under the Clitellata s. l. As matter of fact, marine polychaetes of the family Questidae also bear a clitellum and lay their eggs in cocoons like oligochaetes (GIERE & RISER 1981). Thus clitellum-secreted cocoons may have been existed in the hypothetical marine „oligochaetoid polychaete” (a term by GIERE 1997) ancestral for the Clitellata, as preadaptation. By contrast, the “oligochaetoid” annelids

Aphanoneura, Parergodrilidae and *Hrabeiella*, although living in fresh water or in soil, possess no clitellum and lay solitary eggs. Hermaphroditism occurs also in Aphanoneura and *Hrabeiella* while the Questidae and the Parergodrilidae are gonochorists like most polychaetes (STRUCK et al. 2003).

Chaetae

Terrestrial oligochaetes bear short simple-pointed chaetae, usually paired in the larger “earthworms” or megadriles (Crassiclitellata, Alluroidina, Moniligastridae) but with variable numbers in the Enchytraeidae. Among the terrestrial “oligochaetoid” worms, *Parergodrilus* has scarce simple-pointed chaetae while those of *Hrabeiella* are very different, brush-like (ROTA & LUPETTI 1996).

The aquatic Oligochaeta display a big variety of the number and shape of chaetae. Such variety originates from two general chaetal types present also in the polychaetes: the hair chaetae and the short, bifid sigmoid chaetae (Figs 1.1–2). The latter can be modified with intermediate denticles, or with gradual reduction or entire loss of one (mostly upper) tooth (Figs 1.3–11). The function of the hair chaetae is obscure and often not vital as they have disappeared in many genera, species and even intraspecific forms. Bifidity of the sigmoids seems to be another atavistic, non-adaptive character. Presence of hair chaetae only in the dorsal bundles (if not lost) has been regarded as specific to the Oligochaeta, in contrast to the Aphanoneura and many other polychaetes. However, ventral hair chaetae were recently found in the most ancient oligochaete genus, *Capilloventer*, as well as in the tubifcate genus *Parvidrilus*.

Many oligochaetes have exclusively paired chaetae, either with a reduced upper tooth (many Lumbriculidae) or simple-pointed (most Megadrili, many Lumbriculidae, Haplotaxidae). They were treated as the Lumbricomorpha by CHEKANOVSKAYA (1981) setting them in contrast to the Naidomorpha, with an indefinite chaetal number. A trend to having paired chaetae is evident also among many Enchytraeidae. BRINKHURST (1982) speculated that the common ancestor of Oligochaeta had short paired chaetae like the earthworms while other types and numbers of chaetae have been derived. However, the variability of chaetae is strikingly the highest in the aquatic taxa while paired chaetae appear in the Lumbriculidae and in (their sister group?) the soil-dwelling Megadrili (Figs 1.14–17). As a curiosity, some megadriles have developed a perichaetine chaetal arrangement without any bundles (Fig. 1.18). In several other groups, both terrestrial and aquatic, the chaetal number is reduced to one per bundle (*Haplotaxis*; several *Marionina* of Enchytraeidae); dorsal bundles have disappeared from some or all segments (Naididae; many Enchytraeidae), or chaetae are completely lost (*Narapa*; *Achaeta* and some *Marionina* of Enchytraeidae; some *Lamprodrilus* of Lumbriculidae; Hirudinea and Branchiobdellidae).

On the one hand, shorter chaetae are certainly more useful in crawling in burrows or on the substrate, or when attaching to the host than long chaetae. Hair chaetae can have a protective value or enlarge body surface during swimming. However, hair chaetae are also present in many burrowing worms who never swim, and they have convergently disappeared in many taxa. Bifids can bear additional, intermediate denticles (in this case called pectinates), or their upper tooth can be reduced or lost. Ventral chaetae at the genital pores can be modified either as penial, or as spermathecal chaetae (Figs 1.12–13); the latter are syringe-like and may stimulate the copulation partner (CUADRADO & MARTÍNEZ-ANSEMIL 2001).

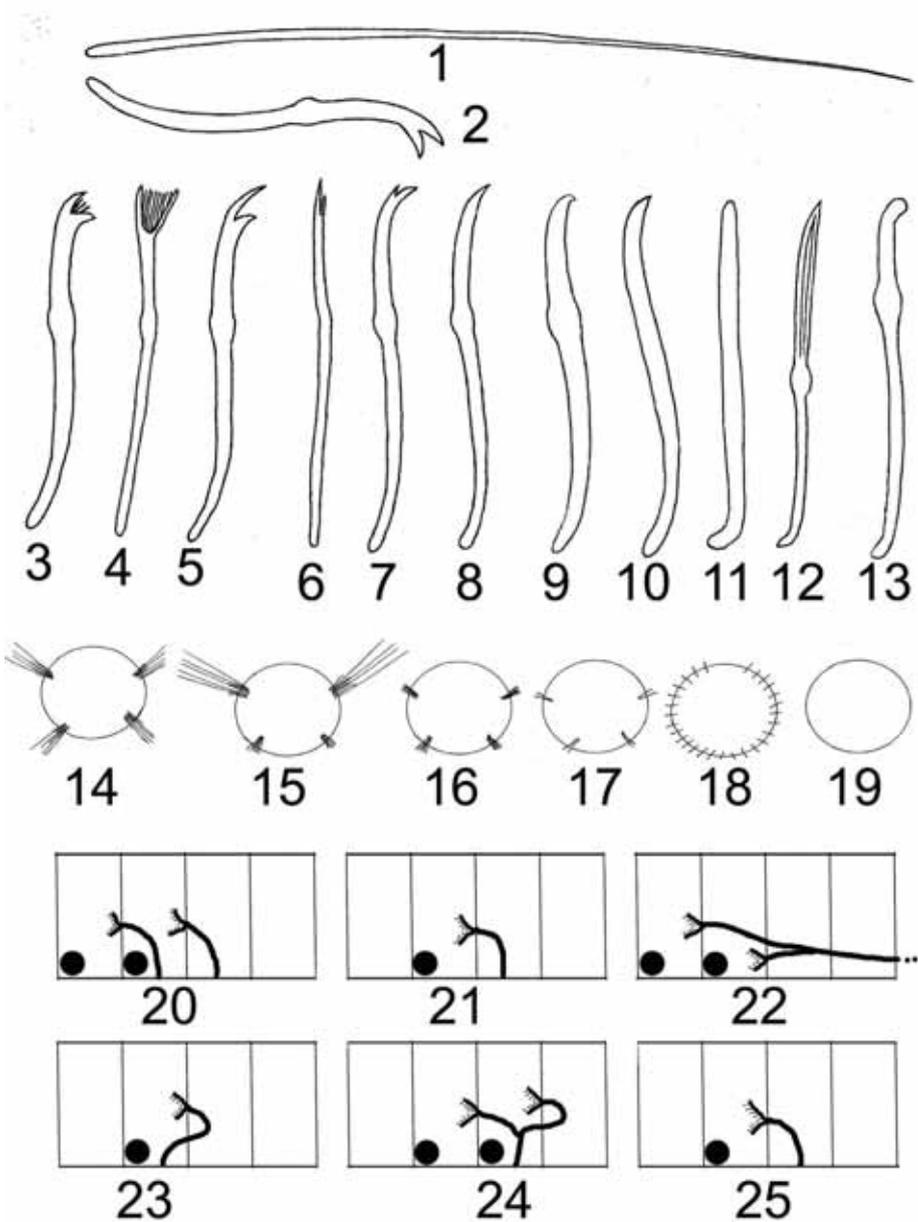


Fig. 1. Some characters of Oligochaeta. Types of chaetae: 1 – hair chaeta; 2 – short bifid chaeta; 3–11 – modifications of short locomotory chaetae; 12 – spermathecal chaeta; 13 – penial chaeta. Chaetal arrangement per segment: 14 – hair chaetae in all bundles; 15 – hair chaetae only in dorsal bundles; 16 – only short chaetae, in indefinite number; 17 – paired short chaetae; 18 – perichaetine arrangement; 19 – without any chaetae. Condition of male ducts in relation to testes: 20 and 21 – primary plesiopore; 22 – opisthopore; 23 – proso-pore; 24 – semiprosopore; 25 – secondary plesiopore (in *Branchiobdella* and *Dorydrilus*).

Aquatic and terrestrial habitat

The division between the aquatic and terrestrial oligochaetes is indistinct. Some „earthworms” are amphibiotic or even aquatic, like *Lutodrilus*, *Criodrilus* and *Biwadrilus*. Several otherwise aquatic tubificids (*Rhyacodrilus falciformis* Bretscher; *Bothrioneurum grandisetosum* Wang, Xie et Liang) and *Pristina* spp. inhabit also soil.

The aquatic oligochaetes have been formerly regarded mainly as freshwater animals, with scarce marine representatives (e.g., *Paranais*, *Tubificoides*, some *Lumbricillus* and *Marionina*) as exceptions. Nowadays, the number of marine tubificids has exceeded the number of freshwater ones; some of their subfamilies are mainly marine. The two supposedly most ancient oligochaete families, Capilloventridae (in part) and Randiellidae, are also marine. Among the otherwise soil-inhabiting Enchytraeidae, there is the marine genus *Grania*, and many marine species of the *Marionina* and *Lumbricillus*. CHRISTENSEN & GLENNER (2010) even suggested colonization of the soil by Enchytraeidae originating from the seashore, as opposed by ERSÉUS et al. (2010). Among the “earthworms” only the genus *Pontodrilus* has become marine.

The original habitat of the ancestral Oligochaeta (= Clitellata) is under discussion. ROUSSET et al. (2008), in an evolutionary study based on DNA sequences, tend to support their freshwater origin.

More than 160 „true” polychaetes (besides the Aphanoneura, *Parergodrilus* and *Hrabeiella*) inhabit continental waters and the soil (GLASBY et al. 2009), without a major reorganization of their anatomy (parapods, paired head appendages, etc.). The ancestral Clitellata lost many “polychaete” characters when settling in fresh water but retained hair and bifid type of chaetae. This seems more probable than descent from a burrowing ancestor with paired simple-pointed chaetae as supposed by BRINKHURST (1982). However, PURSCHKE (1999, 2003) interprets the shift of the brain from the prostomium to subsequent segments, shared by the Clitellata and *Hrabeiella*, as an adaptation to burrowing in the soil. *Hrabeiella* shares also the dorsal pharyngeal pad with the Clitellata.

Leaving the sediment

Most oligochaetes, as well as their “oligochaetoid” counterparts the Questidae, *Parergodrilus*, *Potamodrilus* and *Hrabeiella*, hide inside the soil or aquatic sediment. As an exception, some tubificids of the genus *Baikalodrilus*, protected with mighty papillae, presumably live on sediment surface, and can even be passively rolled by currents (SEMERNOY 2004). Several megadriles in humid tropical forests live on soil surface and even climb on trees (ADIS & RIGHI 1989), or mimic snakes with their colour (MICHAELSEN 1930).

Three tubificate clades (Naididae, Pristinidae and Opistocystidae) have occupied the surface of sediment and aquatic plants. They are relatively small; many of them can swim and even possess pigmented eyespots (e. g., *Stylaria* and *Nais*); some others build temporary slime tubes attached to substratum (e.g., *Dero* and *Ripistes*). They reproduce mainly by paratomy (forming chains of zooids) periodically alternating it with sexual reproduction. Paratomy is prevailing also in the “oligochaetoid” *Aeolosoma*, convergently similar to the naids. Among other oligochaete families, asexual reproduction is rare, being only represented by simple fragmentation, or architomy (e. g., *Lumbriculus*, *Cognettia*, *Bothrioneurum*, *Aulodrilus*). Some facultative vegetation-dwellers among the Lumbriculidae (e. g., *Lumbriculus*) are also able to swim.

External appendages

In several oligochaetes living mostly above sediment surface (*Stylaria*, *Ripistes*, *Arcteonais*, *Pristina*, Opistocystidae, *Rhynchelmis*, *Guestphalinus*), as well as in the interstitial species *Propappus volki* Michaelsen, the prostomium extends into a tactile proboscis. In *Haplotaxis*, the prostomium together with the peristomium forms a tool for grasping prey (BRINKHURST & MCKEY-FENDER 1991).

A few oligochaetes have independently developed finger-like gills located either on the forebody (*Branchiodrilus*), hindbody (*Branchiura sowerbyi* Beddard, *Hesperodrilus branchiatus* Beddard), or surrounding the anus (*Dero*, *Aulophorus*, Opistocystidae). The paludicole “earthworm” genus *Alma* has a pair of claspers-like appendages in the genital region, apparently helpful during copulation.

Feeding on sediment and soil particles

Terrestrial oligochaetes ingest decaying plant remains and fine soil particles. The intestine of the megadriles has a rich microbiota consisting of bacteria, fungi and protists; some of them decompose cellulose with their enzymes, and some of these symbionts or temporal inhabitants will be selectively digested by the worm (DASH et al. 1986; RODRÍGUEZ et al. 1996). At least some megadriles thrive also on pure bacterial cultures (FLACK & HARTENSTEIN 1984). The megadriles have been divided into three ecological classes by BOUCHÉ (1977): the epigeic, the endogeic and the anecic, living and feeding in different soil layers. The mode of life is also reflected in stronger pigmentation of the epigeic earthworms.

The Enchytraeidae are mostly limited to the uppermost, 10-20 cm thick soil layer. As an exclusion, *Fridericia profundicola* Dózsa-Farkas prefers larger depths, 45-125 cm (DÓZSA-FARKAS 1991). Soil fungi are recorded as their preferred food object (DASH & CRAGG 1972, JAFFEE et al. 1997). However, MELLIN (1990) has regarded *Mesenchytraeus glandulosus* (Levinsen) as a facultative primary consumer while BRIONES & INESON (2002) argue that *Cognettia sphagnetorum* (Vejdovský) can thrive on sterile organic matter. *Lumbricillus lineatus* (Müller) feeds mainly on protein-rich biofilm in sewage beds while cellulose can be digested only with aid of bacteria (PALKA & SPAUL 1970).

The aquatic Tubificidae ingest sediment particles, digesting a species-specific selection of bacteria (WAVRE & BRINKHURST 1971), thus mixing the uppermost sediment layer and accelerating the oxydation of organic matter (FISHER et al. 1980). Two marine genera (*Olavius* and *Inanidrilus*) feed on symbiotic bacteria in their body wall while the intestine is reduced (GIERE & LANGHELD 1987).

The phytophile Naididae ingest, besides detritus particles rich in bacteria, also epiphytic algae but digest among them rather diatoms than chlorophytes (STREIT 1978, MCELHONE 1980, BOWKER et al. 1985). As curiosities, *Ripistes parasita* (Schmidt) uses its extra long hair chaetae for food filtration (CORI 1923) while *Uncinaxis uncinata* (Oersted) ingests sand grains, digesting their biofilm.

Carnivory

The large clade of leech-like clitellates (Branchiobdellidae, *Acanthobdella* and Hirudinea) includes specialized carnivores feeding either as parasites, commensals or free-living predators, with all possible transitions. They share several morphological changes (posterior sucker, fixed segment number, reduction of chaetae, muscular pharynx) but display also special

features each. For example, the Hirudinidae have three chitinous jaws while Branchiobdellidae have two; the anteriormost chaetae are preserved in *Acanthobdella*, for anchoring to the host, instead of the anterior sucker in true leeches and branchiobdellids. The Branchiobdellidae are obligatory lodgers on crayfish, either as commensals (micro-predators) or blood-sucking parasites.

There are a few predators present also among the Lumbriculidae, the stem group of the leech-like clade. The North American *Phagodrilus* and the Baikalian *Agriodrilus* ingest smaller oligochaetes with their convergently developed, muscular pharynx (MCKEY-FENDER & FENDER 2001, SEMERNOY 2004). The haplotaxid *Haplotaxis gordioides* has, for the same purpose, a muscular gizzard (BRINKHURST & MCKEY-FENDER 1991). The megadriles can accidentally ingest small soil invertebrates; e.g., *Lampito mauritii* (Kinberg) reduces the abundance of soil nematodes (DASH et al. 1980). The acanthodrilids *Agastrodrilus* spp. feed on other, smaller earthworms (LAVELLE 1983).

The derived naidid genus *Chaetogaster* is convergently similar to the branchiobdellids (strongly cephalized anterior end, terminal mouth, muscular pharynx, partial loss of chaetae). Its larger species ingest small invertebrates, the smaller ones consume mostly diatoms. One species, *C. limnaei* Baer, is living on freshwater molluscs either as an external commensal, or an internal parasite. Another naidid genus, *Allodero*, inhabits the excretory organs of tree frogs. It differs from the free-living *Dero* only in that it lacks the branchial disc.

The enchytraeids *Fridericia parasitica* Černosvitov, *Aspidodrilus kelsalli* Baylis and *Pelmatodrilus planariformis* Moore are ectocommensals on large Megadrili. All three have a convergently flattened body and multiple, modified ventral chaetae for attaching to the host (ČERNOSVITOV 1928, COATES 1990).

The gill chamber of higher crustaceans living in fresh and marine water or on dry land, offers a hiding-place for a rich commensal fauna. Several enchytraeid species have occupied this niche, as *Enchytraeus carcinophilus* Baylis, *E. parasiticus* Baylis, *Lumbricillus catanensis* (Drago), and even the otherwise free-living *L. lineatus*, without essential reorganization of their anatomy (BAYLIS 1915, ČERNOSVITOV 1942). The same is true for three phreodrilid species of the genus *Astacopsidrilus*, and for the "oligochaetoid" aeolosomatid *Hystricosoma chappuisi* Michaelsen (BRINKHURST 1991, KASPRZAK 1976). The leech-like Branchiobdellidae are the only carcinophilous clitellates that have been essentially modified according to this lifestyle.

A polychaete family, the Histriobdellidae, is also highly specialized to life in the gill chambers of the Crustacea but without any suckers or other organs common with the branchiobdellids (STEINER & AMARAL 1999).

Genitalia

Two pairs of testes and two pairs of ovaria (sequentially in segments IX–XII or X–XIII) represent the ancestral set of the oligochaete gonads preserved in some haplotaxids (BRINKHURST 1984). In the presumably most ancient oligochaetes, *Capilloventer* and *Randiella*, the number and position of the gonads vary in different species, being 2–3 pairs, in segments X–XIII (PINDER & BRINKHURST 1997, ERSÉUS 1997). In majority of other groups their number is reduced to two, as in the Tubificidae (segments X, XI), Phreodrilidae, Parvidrilidae, Enchytraeidae (XI, XII) and Propappidae (XI, XIII) (BRINKHURST 1991, MARTINEZ-

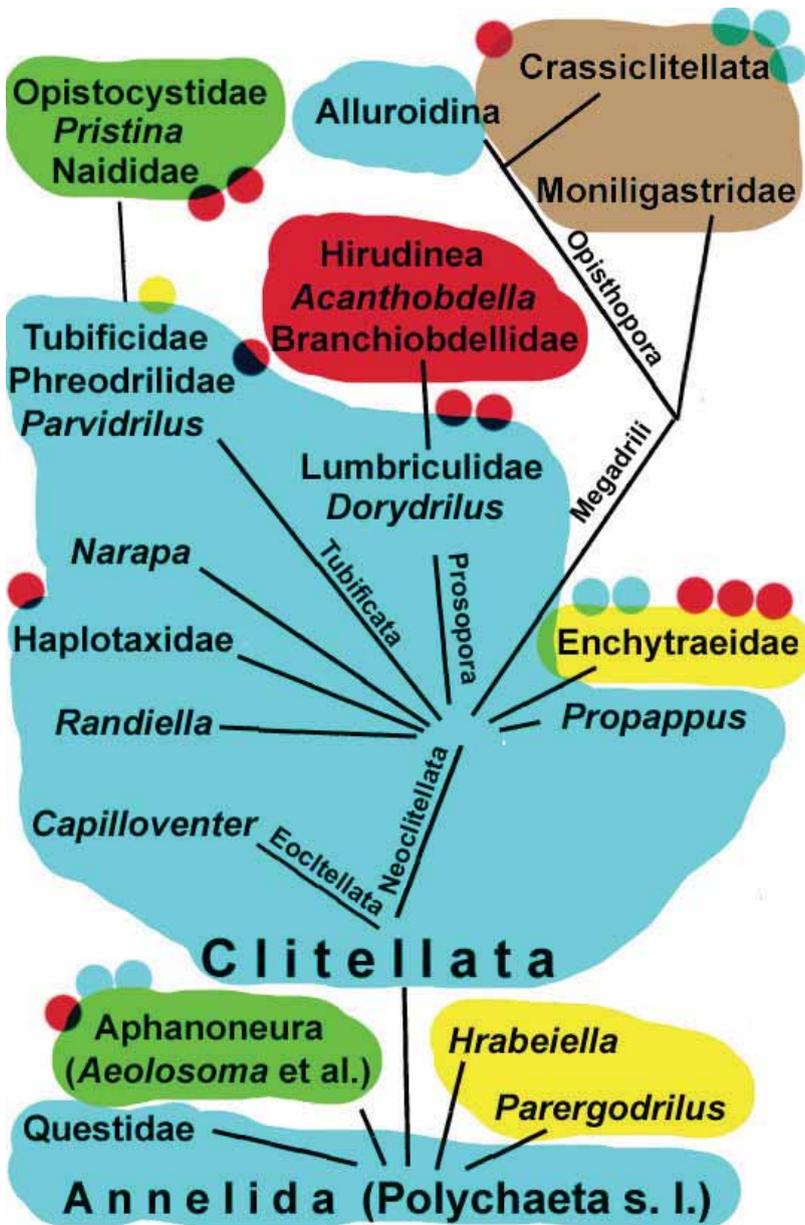


Fig. 2. Distribution of life forms on the simplified evolutionary tree of Oligochaeta and their relatives. Blue: aquatic sediment-dwellers; green: aquatic phytophilous; yellow: small soil-dwellers; brown: large soil-dwellers ("earthworms"); red: carnivores (including commensals and parasites).

ANSEMIL et al. 2002, COATES 1986), or to three pairs, as in the Crassicitellata (X, XI, XIII) and many Branchiobdellidae (X, XI, XII). Secondary polymerization of the testes occurs in some lumbriculids (*Lamprodrilus satyriscus* Michaelsen and its relatives), crassicitellates (*Lutodrilus*), and Hirudinea. The Aphanoneura also reveal (primarily?) multiple testes (2 pairs in *Potamodrilus*, and many in *Aeolosoma*), and a single pair of ovaria.

The paratomic Naididae and Pristinidae display an unusual anterior location of the genital system, with gonads either in segments IV–V, V–VI or VII–VIII. A similar forward shift is peculiar also to some non-paratomic Tubificidae [*Bothrioneurum*, *Aulodrilus*, *Potamothrrix bedoti* (Piguet)], Lumbriculidae (*Lumbriculus*) and Enchytraeidae (*Cognettia*, *Buchholzia*). All these species are capable for architomy (= fragmentation), and the shift occurs only after the regeneration of the anterior end (HRABĚ 1981). The anterior regenerate contains a limited, species-specific number of segments, inaccurately called “larval” segments by IVANOFF (1928) and CHEKANOVSKAYA (1980). The first pair of gonads then always develops in the last regenerated segment. In the paratomic families, preliminary regeneration in a budding zone is genetically fixed, and so is the anterior position of the genitalia. In the third phytophilous family, Opistocystidae, the genital system is often shifted backwards, up to XXI–XXII (HARMAN & LODEN 1978). As they regenerate only 5 anterior segments, the reason for this shift is unclear.

The spermathecae lie in close proximity to the clitellum and the male and female pores in many groups (Tubificidae, Naididae, Phreodrilidae, Haplotaxidae, Moniligastridae, etc.). In several others as the Crassicitellata, Enchytraeidae and *Propappus*, the spermathecal pores are located several segments afore these organs. As the latter pattern occurs also in the “primitive” oligochaete genera *Capilloventer* and *Randiella*, it can be ancestral.

The external spermatophores occur sporadically, together with the spermathecae, in the Lumbriculidae but regularly in the taxa devoid of spermathecae (e.g., *Criodrilus*, the tubificids *Bothrioneurum* and *Paranadrilus*, many Hirudinea). Most oligochaetes have spermathecae like their “oligochetoid” relatives.

MICHAELSEN (1928) has coined three useful terms to describe the types of the male gonoduct: plesiopore (with external pores in the segment following the testicular one), prosopore (with pores in the same segment with the testes), and opisthopore (with the male pore several segments backward) (Figs 1.20–25). The plesiopore type occurs most widely among the oligochaetes and their “oligochaetoid” relatives, definitely as plesiomorphic. The opisthopore male duct is limited to the Alluroididae–Crassicitellata clade, and the prosopore (and semiprosopore) form, to the Lumbriculidae–leech-like clade. Among the latter, the genus *Branchiobdella* demonstrates reversal from the semiprosopore to the secondary plesiopore condition (Figs 1.25). A similar reversal may have happened to *Dorydrilus*, which is very similar to Lumbriculidae except its plesiopore male ducts.

The modified distal portion of the male ducts, the atrium equipped with prostatic cells (not to confuse with the prostates as separate organs in the Crassicitellata!), is remarkably similar to that in the Tubificidae (and several related families) and Lumbriculidae, belonging to two different clades, while it is lacking in many others, e.g., the Haplotaxidae. The atrium can have convergently evolved in different clades, as indicated by the presence of atrium-like structures in some Enchytraeidae. The most “primitive” oligochaetes, *Capilloventer* and *Randiella*, have simple male ducts, without any atria. In the megadriles, the term “prostata” means a separate organ, possibly analogous in the function to the microdrile atrium with the prostate glands.

Conclusions

The Oligochaeta may have derived from an aquatic, sediment-dwelling, polychaete-like ancestor characterized by a possession of variable number and shape of chaetae and by the plesiopore male ducts like present today in many Tubificata (= Naidomorpha sensu CHEKANOVSKAYA 1981). Three separate lines, the Naididae, the Pristinidae and the Opisthocystidae, all nested in the Tubificidae, have adapted to life on sediment surface and aquatic plants, through acquiring several common phenotypic features. A clade with the paired sigmoid chaetae with the reduced or lacking upper tooth (Lumbricomorpha sensu CHEKANOVSKAYA 1981) has separated early from this “tubificate” line. The terrestrial life form with simple-pointed chaetae has arisen twice: as small worms with indefinite chaetal number and plesiopore male ducts (Enchytraeidae), and as larger, megadrile, worms with paired chaetae and either with plesiopore or opisthopore male ducts (Moniligastridae and Alluroididae + Cras-siclitellata, respectively). An aquatic branch of the clade with paired chaetae, the Lumbriculidae, developed their specific, prosopore (or semiprosopore) condition of the male ducts. One of the several evolutionary “attempts” of transition to carnivory among the Lumbriculidae resulted in the leech-like life form (Branchiobdellidae, *Acanthobdella* and Hirudinea) that lost the chaetae but developed the suckers and jaws (Fig. 2).

Several taxa display changes in their preferred environment and mode of feeding. A trend towards loss of hair chaetae and the upper tooth of the bifid sigmoid chaetae, as well a trend towards paired chaetae and a trend towards gradual loss of chaetae can be observed in many separate genera and families. Predatory, commensal and parasitic ways of life have been independently involved in separate taxa of several families, but with profound morphological changes only in the leech-like group. The forward shift of the genital system in paratonic and architonic taxa is connected with the species-specific number of segments regenerating in the anterior end. The reversal of the semiprosopore to the plesiopore male ducts as it occurs in the genera *Branchiobdella* and *Dorydrilus* can confuse their systematic position.

Separate convergent similarities with Clitellata can be found in several “oligochaetoid” polychaetes like the marine Questidae, the freshwater *Aeolosoma* and *Potamodrilus*, the soil-dwelling *Parergodrilus* and *Hrabeiella*, and the commensal *Hystricosoma* (Fig. 2).

Acknowledgements. This study was supported by the target financing of the Estonian Ministry of Education and Research No. 0170006s08. Mrs. Ester JAIGMA has kindly corrected the English text.

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