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ON THE ORIGIN AND EVOLUTION OF AQUATIC *OLIGOCHAETA*

Oligochaetes did not leave any fossil remains. We can decide about their evolution only by the morphology, ecology and distribution of recent groups. Various phylogenetic trees were proposed by several authors, with *Aeolosomatidae*, *Haplotaxidae*, or *Lumbriculidae* in the role of the most primitive family (some examples are shown in Fig. 1). In the most recent monograph on the aquatic oligochaetes, R. Brinkhurst (1971) excludes the *Aeolosomatidae* and *Branchiobdellidae* from the subclass *Oligochaeta* and divides the remaining families into three orders: *Lumbriculida*, *Moniligastrida*, and *Haplotaxida*; the family *Haplotaxidae* is regarded as the probable ancestor of most oligochaetes. His system is consistently based on the structure of genitalia, especially of the male ducts, disregarding the other, the so-called somatic characters. This main principle of the «classical systems» has been sharply criticized in recent years by G. Gates (1974), T. Perel (Перель, 1979), etc. as misleading in the systematics of terrestrial *Oligochaeta*. For the aquatic ones, it also causes confusions: e. g. R. Brinkhurst (1971) derives the *Tubificina*, possessing the ancient polychaete-like setal apparatus, from the *Haplotaxidae* that display specialized lumbricine setae.

The present author, compiling his own scheme of the evolution of the *Oligochaeta*, considered first of all the principle of oligomerization of the homologous organs by V. Dogel (Догель, 1954). Accordingly, the number of setae, gonads, gonoducts, etc. will gradually diminish while their location and functions will be specified in the evolutionary process. Opposite cases (of polymerization) are very rare and never restore the previous situation exactly. Some facts of ecology and palaeogeography were also taken into account.

In Figure 2, an attempt is made to locate the recent families of aquatic oligochaetes, together with some allied groups and hypothetical ancestors, according to their probable places and periods of arising. The vertical columns signify the most probable original habitat of the group (surface waters, soil, and the intermediate zone — phreatic waters). The lower horizontal zone contains the most ancient, Palaeozoic groups, reaching their cosmopolitan distribution range already on the supercontinent Pangaea in the Permian and Triassic. The two upper zones contain younger groups originating in the Mesozoic after the disintegration of Pangaea: in Laurasia, roughly corresponding to the Holarctic region of our times (the uppermost zone), and in Gondwana which later on fell in several continents mostly in the present Southern Hemisphere (the middle zone of Figure 2).

The pedigree of *Oligochaeta*, together with the other *Clitellata*, begins with certain *Polychaeta Errantia* proceeding from the sea to the brackish

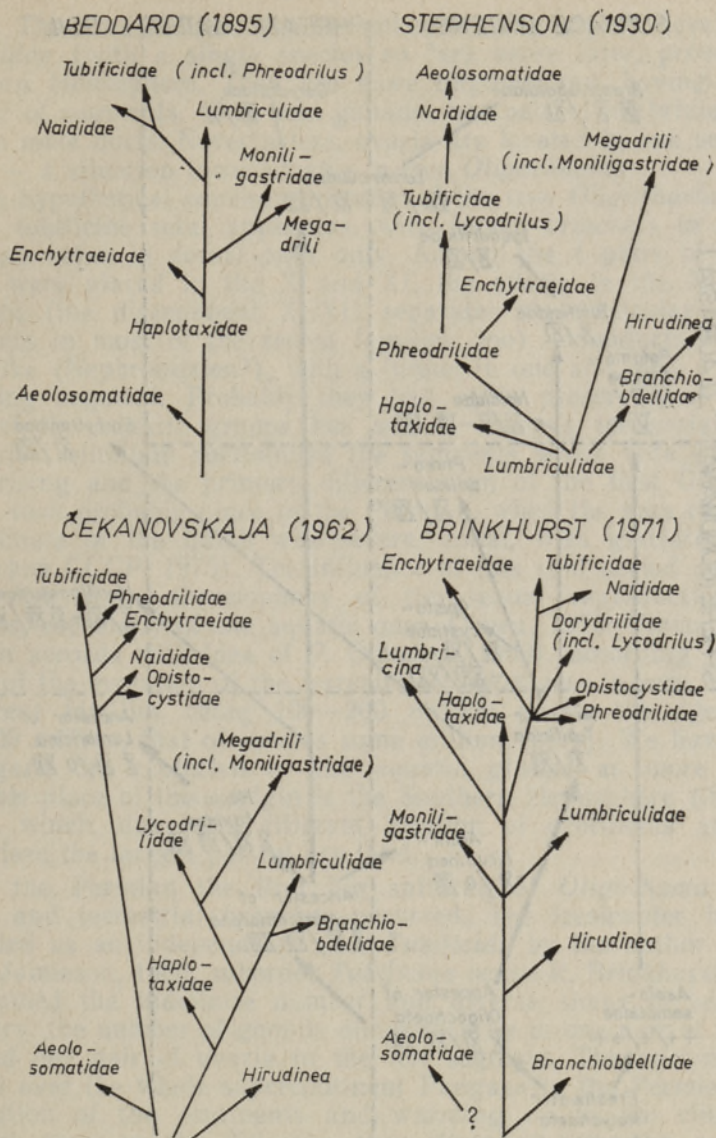


Fig. 1. Phylogenetic trees of aquatic *Oligochaeta* by various authors. Slightly simplified.

and fresh inland waters. This could have happened in the second half of the Palaeozoic, after the formation of the terrestrial vegetation of macrophytes as a source of detritus. In the fresh water those worms lost their pelagic larvae and assumed special cutaneous glands (clitellum) for the secretion of a shell (cocoon) protecting the eggs. It could have occurred convergently in various representatives of *Polychaeta*. In this case, the removal of *Aeolosomatidae* (together with *Potamodrilidae*) from the *Oligochaeta* by R. Brinkhurst (1971), etc. is justified.

These two families are interpreted here as a separate subclass *Aphanoneura*, order *Aeolosomatida*, contrasting in many features with the subclass of *Oligochaeta*. The *Aphanoneura* have hair setae both in

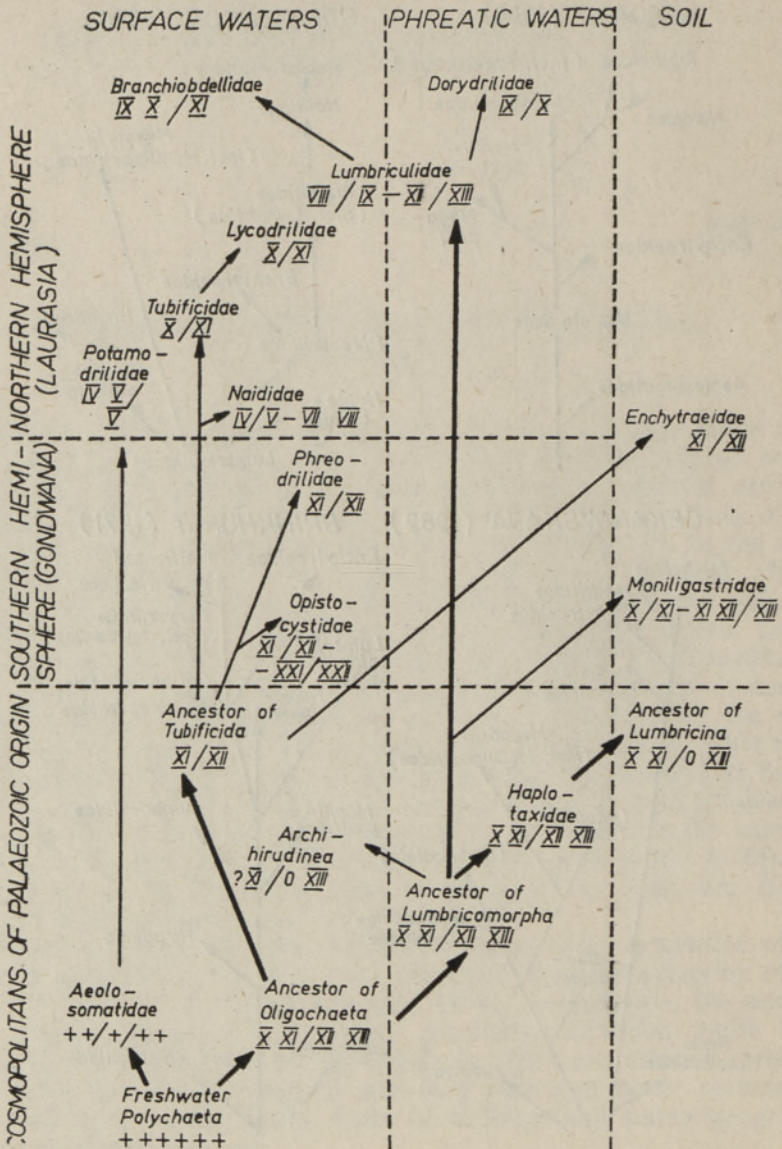


Fig. 2. An improved scheme of the evolution of aquatic *Oligochaeta* and their allies. The Roman numerals mean the testicular and ovarian segments of typical representatives of the groups; +++ — undetermined fertile segments; 0 — sterile segment; / — dissepiment separating the testicular segments from the ovarian ones.

dorsal and ventral bundles. The number of gonads in *Aeolosomatidae* is still indefinite, testes are situated before as well as after the ovaria. Almost unmodified nephridia operate as male ducts, the female pore being unpaired and rather simple, without any duct. The cutaneous glands, analogous to the clitellum, are developed only as a cushion on the female pore. Therefore the eggs will be stuck to the substratum one by one, without forming a true cocoon. *Aeolosomatidae* are a very old group, probably originating already from the Devonian or Carboni-

ferous. The area of their rise is unknown. The higher developed *Potamodrilidae* (with a single species so far) arose later, probably in the Northern Hemisphere. They are more oligomerized, having a constant number of segments, setae and gonads; one pair of nephridia is specialized as male ducts. Nevertheless, ovaria are located in one segment with testes — a situation inconceivable in true *Oligochaeta*.

The hypothetical common ancestor of the true *Oligochaeta* must have had a tubificine setal apparatus, with forked crotchets in all bundles and hair setae in dorsal ones only. Among the 4 pairs of gonads the testes were placed in the X and XI, the ovaria in the XII and XIII segment (the dissepiment XI/XII separates the testicular and ovarian segments in most of the recent families, too). Gonoducts were nephridium-like (Nephromixien?), with a funnel in one and with a duct in the following segment. Probably they had atria, preserved up to now in most of the aquatic groups but lost by various terrestrial ones. The cylindrical clitellum surrounded the segments which bore genital pores. The arising and the primary differentiation of the first *Oligochaeta* in orders took probably place in the Permian, when the seas regressed and the climate of the Earth was severe, zonal, with glaciations (Палеогеография СССР, 1975). The influence of this cold period can be traced up to now in the thermophobia of the sexual reproduction of many families, especially of the aquatic ones (Тимм, 1972; Timm, 1980). This opinion accords with idea of P. Omodeo (1963), according to which the speed of the evolution of the terrestrial *Oligochaeta* is very low (the age of recent families being 100—200 million years, the age of genera 30—100 million, that of species some million years). We have no reason to regard the evolution of the aquatic groups as more rapid. The probable place of their origin is the Southern Hemisphere (its temperate zone), which, due to a different location of continents at that time, comprised the largest part of dry land.

In the Permian the first big splitting of *Oligochaeta* into freshwater and terrestrial branches occurred. The freshwater branch, here regarded as an independent order *Tubificida* by the author (as well as by B. Jamieson, 1980; suborder *Tubificina* sensu R. Brinkhurst, 1971, etc.) maintained the indefinite number and diverse shape of setae. On the contrary, the number of gonads diminished up to one pair of testes in the XI and one pair of ovaria in the XII segment. The ancient *Tubificida* spread over the whole supercontinent Pangaea in the Permian. After the separation of the continents and warming up to the climate of the tropical zone in the Triassic, they diverged into the southern and northern branches.

The southern branch of *Tubificida* on the ancient continent Gondwana maintained the inherited location of gonads. Their spermathecae always lie caudally from the testicular segment. Up to now the family *Phreodrilidae* populates the bottom of the cool fresh water bodies of the southern temperate zone. The other family, *Opistocystidae*, adapted itself to the phytophilous manner of life, assumed the asexual way of reproduction and gills, and, as a result, was able to spread in the torrid Neotropical region. In connection with the asexual reproduction, the reproductive system of *Opistocystidae* tends to shift, though, unlike in various other *Oligochaeta*, not forward, but backward, even up to the XXI—XXII segments.

The northern branch of *Tubificida* on the ancient continent Laurasia is characterized by a certain shift of the reproductive system forward (originally into segments X—XI) as well as by the position of sper-

mathecae in the testicular segment. Like in the southern branch, there occurred here a division into mostly cool-preferring bottom forms (*Tubificidae*) and the phytophilous ones, possessing the asexual mode of reproduction and a more extensive forward shift of the genital organs (*Naididae*). Some genera of the latter family, especially the gilled ones, afterwards successfully colonized the warm tropical waters.

The family *Enchytraeidae*, passing from the fresh water to the soil, is an odd group of *Tubificida*. The shape of setae is simplified convergently with *Lumbricomorpha*, but their number remained indefinite. Gonads are placed in the primary site in segments XI—XII but spermathecae are shifted forward up to the V or IV segment. *Enchytraeidae* are now distributed on all continents, but the most primitive, freshwater representatives (*Propappus*) are known only in North Eurasia.

The above scheme of origin and palaeogeographic distribution of the aquatic *Oligochaeta* in some features coincides with T. Arldt's views (1922). Accordingly, the ancient *Phreodrilidae* (the supposed ancestors of most of the aquatic families except the primitive *Aeolosomatidae* and *Naididae*) arose before the Triassic on the southern continent. However, Arldt's viewpoint about their cosmopolitan distribution already in the Devonian seems rather improbable.

The common ancestor of the terrestrial branch of *Oligochaeta*, *Lumbricomorpha* sensu O. Čekanovskaja (Чекановская, 1962) or *Neoligochaeta* sensu W. Michaelsen (1920), also passed already in the Permian from the surface water bodies into phreatic waters and swamps. Besides, they acquired the lumbricine set of setae, with two simple or weakly forked setae in each bundle. This innovation, primarily of neotenic origin (Michaelsen, 1929), proved to be very successful for the life in soil, and is preserved almost in all of their successors. Gonads remained in their previous place (in X—XIII), but one of two pairs of ovaria is reduced in the most recent *Lumbricomorpha*. Judging by the presence of lumbricine setae and by the location of gonads probably in segments XI and XIII in the recent *Archihirudinea* (Лукин, 1976), leeches may also have been derived from the primitive *Lumbricomorpha*.

The most primitive among the recent *Lumbricomorpha* is the family *Haplotaxidae*, now inhabiting phreatic waters as well as surface waters and soil. Their cosmopolitan distribution is proof of the high age of the family. At the end of the Permian as well as in the Mesozoic their successors, the order *Haplotaxida*, differentiated into separate families analogically to those of *Tubificida*. However, several terrestrial families adapted themselves to the hot climate. The temperate zone is preferred, like by their Permian ancestors, by *Lumbricidae* and some small families in the Northern Hemisphere as well as by many *Acanthodrilidae* in the Southern Hemisphere.

The origin of the terricolous oligochaetes was dated with the Palaeozoic also by L. Černovítov (1935) and R. Sims (1980). However, P. Omodeo (1963) tended to connect it with the formation of soils in the early Mesozoic.

Very early, probably in the Permian, two lateral ramifications (at first connected with each other?) proceeded from the general stem of *Lumbricomorpha*: the *Lumbriculidae* and *Moniligastridae*. Both groups are characterized by an extraordinarily variable, shattered morphology of the genital system. The number and position of gonads vary greatly; in the *Lumbriculidae*, besides an extreme reduction, also cases of a polymerization of testes occur. The position of the male duct in relation to the dissepiment has also changed: among the *Moniligastridae* the

whole duct is shifted forward in the testicular segment, but the typical male duct of the *Lumbriculidae* perforates the posterior dissepiment twice, returning into the testicular segment again.

The *Moniligastridae* are thermophilous and terrestrial, with their native country in the northern, tropical part of Gondwana, on the present Indian Peninsula. On the contrary, the homeland of the thermophobe *Lumbriculidae* undoubtedly lies in Laurasia, probably in its phreatic waters. Unlike the other branches of *Lumbricomorpha*, the *Lumbriculidae* have no terrestrial representatives, but many genera have returned into surface waters.

The small family of *Dorydrilidae* from the phreatic waters is probably a successor of the *Lumbriculidae*. Except the male duct opening on the post-testicular segment as in the *Tubificida* and in the main stem of the *Lumbricomorpha*, they resemble the latter. The author regards this coincidence with *Tubificida* as occasional, as an eventual variant of oligomerization of the reproductive system of the *Lumbriculidae* or their close ancestors (maybe still having the more primitive male duct?). Unfortunately, the *Dorydrilidae* do not suit the order of *Lumbriculida* as defined by R. Brinkhurst (1971). To avoid confusion, one should treat the *Dorydrilidae* as a separate order, or expand the definition of the order of *Lumbriculida*. The author would prefer the latter variant.

The small Baikalian family *Lycodrilidae*, included into the *Lumbricomorpha* by O. Секановская (Чекановская, 1962) and even approximated to the *Dorydrilidae* by D. Cook (1971), is undoubtedly very close to the *Tubificidae*. Perhaps they deserve only a rank of subfamily in the latter. The presence of two setae in every bundle is a character convergent with the *Lumbriculidae*, as it is not yet established in all species. The convergence with the *Lumbriculidae* hints to the possible origin of the *Lycodrilidae* from phreatic waters.

The author supposes that the *Dorydrilidae* and *Lycodrilidae* as well as the aberrant genus *Kurenkovia* of the *Lumbriculidae* are young, beginning families of the cold-preferring oligochaetes. Their differentiation started in the Neogene or Pleistocene, in the conditions of an intensive orogenesis and strong glaciations, resembling the Permian ones.

The *Branchiobdellidae* are considered a separate order or even a subclass by some authors. They are externally leech-like as a result of their parasitic manner of life. However, their internal anatomy, especially of the reproductive system, distinctly resembles that of their probable ancestors, the *Lumbriculidae*. The *Branchiobdellidae* are Laurasian.

The true systematic position of the peculiar marine worm *Lobatocebrebrum*, provisionally placed in the *Oligochaeta* by R. Rieger (1980), is unknown.

As a consequence of the above discussion, the author proposes the following improved classification of the aquatic *Oligochaeta* and their allies:

Class *Clitellata*

Subclass *Aphanoneura*

Order *Aeolosomatida* (families *Aeolosomatidae* and *Potamodrilidae*)

Subclass *Oligochaeta*

Superorder *Naidomorpha*

Order *Tubificida* (families *Tubificidae*, *Lycodrilidae*, *Naididae*, *Phreodrilidae*, *Opistocystidae* and *Enchytraeidae*)

Superorder *Lumbricomorpha*

Order *Haplotaxida* (families *Haplotaxidae*, *Alluroididae*, and many, mainly terrestrial families of «earth-worms»)

Order *Moniligastrida* (family *Moniligastridae*)

Order *Lumbriculida* (families *Lumbriculidae* and *Dorydrilidae*)

Order *Branchiobdellida* (family *Branchiobdellidae*)

Subclass *Hirudinea* (not treated here)

These groups differ from each other mainly by aromorphoses (palinogeneses) in their reproductive system and setal apparatus. The decisive moments in the evolution of the whole assembly were at first transition from the sea into the continental waters (followed by a condensation of genital organs and appearance of the clitellum) and further via phreatic waters into the soil (which led to the appearance of the lumbricine setal apparatus). The main groups of *Oligochaeta* shaped up in the cold Permian period but the differentiation of the recent families took place later, in the conditions of isolation resulting from warming up of the climate and separation of the continents.

Only two orders of the enumerated six — the *Aeolosomatida* and *Tubificida* — are really palaeolimnic in the sense of G. Martinson (Мартинсон, 1967) and J. Starobogatov (Старобогатов, 1970). The representatives of the *Haplotaxidae*, *Lumbriculidae*, *Dorydrilidae* and *Lycodrilidae* inhabit cold, oxygen-rich water bodies, thus resembling the mesolimnic organisms which settled into the fresh waters from the sea only in the Mesozoic. The analogy can be explained by the secondary transition of these oligochaete groups from phreatic waters into the surface ones.

REFERENCES

- Ardt, T. Handbuch der Palaeogeographie. Bd. II. Palaeogeographie. Leipzig, 1922, 681—1647.
- Beddard, F. E. A monograph of the order of *Oligochaeta*. Oxford, 1895.
- Brinkhurst, R. O. Phylogeny and classification. Part 1. — In: *Aquatic Oligochaeta of the world*. Edinburgh, 1971, 165—177.
- Cook, D. G. Family *Dorydrilidae*. — In: *Aquatic Oligochaeta of the world*. Edinburgh, 1971, 647—653.
- Černosvitov, L. Monografie československých děstovek. — Arch. přír. výzkum Čech, 1935, 19, 1—86.
- Gates, G. E. On oligochaete gonads. — *Megadrilologica*, 1974, 1, 1—4.
- Jamieson, B. G. M. Preliminary discussion of an Hennigian analysis of the phylogeny and systematics of opisthoporous oligochaetes. — *Rev. Ecol. Biol. Sol*, 1980, 17, 261—275.
- Michaelsen, W. Zur Stammesgeschichte und Systematik der Oligochäten. — *Arch. Naturgesch.*, 1920, 86A, 130—141.
- Michaelsen, W. Zur Stammesgeschichte der Oligochäten. — *Zeitschr. wiss. Zool.*, 1929, 134, 693—716.
- Omodeo, P. Distribution of the terricolous oligochaetes on the two shores of the Atlantic. — In: *North Atlantic Biota and their History*. Oxford, 1963, 127—151.
- Rieger, R. M. A new group of interstitial worms, *Lobatocerebridae* nov. fam. (*Annelida*) and its significance for metazoan phylogeny. — *Zoomorphologie*, 1980, 95, 41—84.
- Sims, R. W. A classification and the distribution of earthworms, suborder *Lumbricina* (*Haplotaxida*: *Oligochaeta*). — *Bull. Brit. Mus. Nat. Hist. (Zool.)*, 1980, 39, 103—124.
- Stephenson, J. *The Oligochaeta*. Oxford, 1930.
- Timm, T. Distribution of aquatic oligochaetes. — In: *Aquatic oligochaete biology*. New York, 1980, 55—77.
- Догель В. А. Олигомеризация гомологичных органов как один из главных путей эволюции животных. Л., 1954.
- Лукин Е. И. Фауна СССР. № 109. Пиявки, т. I. Л., 1976.

- Мартинсон Г. Г. Проблема происхождения фауны Байкала. — Зоол. ж., 1967, 46, 1594—1598.
- Палеогеография СССР. 2. Девонский, каменноугольный и пермский периоды. М., 1975.
- Перель Т. С. Распространение и закономерности распределения дождевых червей фауны СССР. М., 1979.
- Старобогатов Я. И. Фауна моллюсков и зоогеографическое районирование континентальных водоемов. Л., 1970.
- Тимм Т. Э. Зависимость географического распространения водных олигохет от температуры. — В кн.: Водные малощетинковые черви. Ярославль, 1972, 124—129.
- Чекановская О. В. Водные малощетинковые черви фауны СССР. М.-Л., 1962.

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VEE-VÄHEHARJASUSSIDE TEKKEST JA EVOLUTSIOONIST

Esitatud väheharjasusside (alamklass *Oligochaeta*) fülogeneesi skeem põhineb suguelundkonna ja harjasaparaadi ehitusel, kusjuures on arvestatud ka ökoloogia ja paleogeograafia andmeid. Rühm tekkis külmal permi ajastul magevette asunud hulkharjasussidest ja diferentseerus sugukondadeks ülilandri Pangea lagunemisel. Ainus esmasveeline ja paleolimniline selts on *Tubificida* (ülemselts *Naidomorpha*). Seltsid *Haplotaxida*, *Moniligastrida*, *Lumbriculida* ja *Branchiobdellida* (ülemselts *Lumbricomorpha*) koos alamklassiga *Hirudinea* põlvnevad ühisest esivanemast, kes elas vee ja mulla üleminekubiotoobis — maa-alustes vetes. *Lumbriculida* ja *Moniligastrida* suguelundkonna suur muutlikkus on sekundaarne. Seltsi *Aeolosomatida* käsitletakse väheharjasussidega paralleelselt arenenud alamklassina *Aphanoneura*.

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О ПРОИСХОЖДЕНИИ И ЭВОЛЮЦИИ ВОДНЫХ ОЛИГОХЕТ

Представленная новая схема филогенеза малощетинковых червей (подкласс *Oligochaeta*) основывается на строении полового и щетинкового аппарата их с учетом данных экологии и палеогеографии. Эта группа червей возникла из полихет, переселившихся в пресные воды в холодный пермский период, и дифференцировалась на семейства соответственно с распадом сверхматерика Пангеи. Единственный их первичноводный и палеолимнический отряд — *Tubificida* (надотряд *Naidomorpha*). Отряды *Haplotaxida*, *Moniligastrida*, *Lumbriculida* и *Branchiobdellida* (надотряд *Lumbricomorpha*) вместе с подклассом *Hirudinea* происходят из общего предка, обитавшего в переходном между водой и почвой биотопе — в подземных водах. Большая изменчивость половой системы *Lumbriculida* и *Moniligastrida* — явление вторичное. Отряд *Aeolosomatida* рассматривается в качестве отдельного подкласса *Aphanoneura*, развивавшегося параллельно с *Oligochaeta*.