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The previous and contemporary conceptions on phylogeny and systematic classifications of *Oligochaeta* (Annelida)¹

[With 1 Table]

Abstract. The author presents various phylogenetic opinions concerning the origin and evolution of oligochaetes, especially aquatic. In the contemporary classifications of the aquatic and terrestrial oligochaetes very important significance have conceptions presented by O. V. ČEKANOVSKAJA, R. O. BRINKHURST, B. G. M. JAMIESON, T. TIMM and N. M. SHUROVA. The author supposes that the families *Aeolosomatidae* and *Potamodrilidae* should be considered a separate class of *Aphanoneura* (order *Aeolosomatida*) of the subtype *Clitellata*. Also the family *Branchiobdellidae* is considered a separate class of the subtype *Clitellata*. The family *Enchytraeidae* is considered a separate superorder (order *Enchytraeida*) of the class *Oligochaeta*.

The problem of the origin of the *Oligochaeta* and their evolution, has for a long time, been the centre of interest of all zoologists investigating this group of animals. Generally speaking, the relation between the *Oligochaeta* and the primitive *Polychaeta* has never aroused any doubt; however, various scientists expressed different views on the matter. Undoubtedly, a great difficulty in working out a convincing concept of the origin of the *Oligochaeta* and establishing the line of their evolutionary development is due not only to the fact that little is known about their fossil remains but also to a tremendous gap in studies

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of the development and functions of all internal organs of these animals (KASPRZAK 1982a). Since the majority of scientists tended to underestimate or ignore principles of comparative anatomy as well as the importance of functional analysis of the role and development of various organs, the direct origin of the *Oligochaeta* from the *Polychaeta* was considered an obligatory principle in the systematics of the *Annelida*. The principle is also, to a large extent, due to the fact that all invertebrates are generally assumed to have originated in the sea. This applies also to the *Oligochaeta* which, through the development of morphological and anatomical adaptation abilities, went through estuaries to freshwater and, next, to land environments. This line of evolution, marked in various groups of invertebrates with varying intensity, is not so obvious in the case of the *Oligochaeta* (BRINKHURST 1971). Considerable differences in the body structure of the *Polychaeta* and the *Oligochaeta* have so far been ascribed to the development of hermaphroditism in the *Oligochaeta*. For a long time it was claimed that the only type of reproduction in the *Oligochaeta* is the alternate crossbreeding of hermaphroditic individuals. Parthenogenesis was considered nonexistent or exceptional, and caused, for example, by parasites (MULDAL 1952). Amphimictic reproduction of hermaphroditic animals led to a remarkable diversity of types of reproduction among the *Oligochaeta* (REYNOLDS 1974). Parthenogenesis, first described in *Oligochaeta* by GAVRILOV (1935, 1939) and KOBAYASHI (1937), turned out to occur much more frequently than it was assumed by MULDAL (1952), and the sterility of testes can develop in different ways (GATES 1972). For example, the variability of reproductive systems in earthworms of family *Lumbricidae* is due to the existence of two modes of insemination, to parthenogenesis and to the possibility of alternation of parthenogenetic and amphimictic reproduction (PEREL 1982a). In many species both modes of insemination coexist. The emergence, in the course of evolution, of the ability to produce spermatophores made it possible for the two partners to exchange sperm during copulation when the mutual exchange of sperm into the spermathecae is impossible or when the difference in the size of the two is too pronounced (PEREL 1980). The loss, by some *Lumbricidae*, of the spermathecal exchange of sperm, and their transition to the exchange of sperm through spermatophores, connected, most probably, with the occurrence of these animals under negative environmental conditions, is considered proof of the evolutionary regress of this group of the *Oligochaeta* (PEREL 1980). The sperm exchange through spermatophores is considered more primitive than the spermathecal exchange. It emerged in various groups of invertebrates when they were transferred from the water to the land environment (GILJAROV 1958). Polyploidy is generally connected with parthenogenesis and is very common in *Lumbricidae*. Several species in which the polyploidy is known reproduce parthenogenetically. Parthenogenesis and amphimictic reproduction can alternate in some species (PEREL 1982a). Polyploid forms of *Lumbricidae* can disperse significantly wider than diploid forms of the same species. The regions with climatic conditions

unfavourable for the *Lumbricidae*, e. g. taiga, tundra and steppe, are populated by parthenogenetic or secondarily amphimictic polyploid forms of *Lumbricidae*. The polyploid forms occur in the mountains as well where the conditions, in case they are diverse enough, favour the evolution of parthenogenetic and secondarily amphimictic polyploid forms of *Lumbricidae*. The polyploid arising in *Lumbricidae* on the basis of parthenogenesis not only contributes to the assimilation of new territories, but also provides for a possibility of more complete utilization of the environment by means of increase of the set of life-forms (PEREL 1982b). However, so far no data have been available on the participation of specific types of reproduction in the development of distinct evolutionary trends in the *Oligochaeta*. This was emphasized also by BRINKHURST (1971) who stressed lack of convincing proofs of the evolutionary value of adaptative modifications caused by hermaphroditism or sex separation in the *Annelida*. The main process in the progressive evolution of the *Oligochaeta*, as suggested by BRINKHURST (1971) who referred to CLARK'S (1964) dynamic theory of the coelom and segmentation, was the development of new functional diversities through an increase in the mobility of crawling and burrowing forms. To the most important traits developed belong a strong body-wall musculature and parapodia, morphologically diversified setae and developed specialised reproductive organs. We can assume that the period which followed the shaping of the coelom was of paramount importance, since it was then that the adaptive radiation of new structural and functional types could be started. According to CLARK (1964), the primary *Coelomata* were most probably sedentary animals. Their effective locomotive faculty required considerable changes in the shape of the body, which was very difficult or entirely impossible in the case of the coelom undivided into segments. Consequently, the coelom had to be divided into segments as a locomotoric adaptation at a later stage. CLARK'S (1964) theory, emphasizing the functional aspects of occurrence is, in this respect, in agreement with the schizocoelic theory. The coelom was shaped in the course of the many years generic development independently and in many ways. CLARK (1964) ascribes to the coelom a particular role as the hydraulic skeleton. In his opinion, it was this function of the coelom that caused coelomatic animals to be the most successful ones in the development of the animal world. The evolutionary development of swimming and crawling forms, which enabled them to inhabit the underground and land environment, was possible also due to changes in the development when ancestors of the *Clitellata* ceased to produce small eggs with little yolk, characteristic of the primitive *Polychaeta*, and replaced them with large eggs with a substantial amount of yolk; the development of those eggs could continue without larval stages. It was in a later phase of the evolution of the *Clitellata*, after they inhabited the fresh water and land environments, that the amount of yolk in eggs was reduced, and the mechanism of embryo feeding on the protein in the egg cocoon was formed. This phenomenon developed independently in the *Oligochaeta* and the higher *Hirudinea*, which facili-

tated adaptation to the land environment. This indicates not regress in evolution but the improvement of embryogenesis (IVANOVA-KAZAS 1977), as was previously mentioned by STEPHENSON (1930). It should be also noted that the evolution of the *Oligochaeta* was strongly affected by their transfer to the soil which, in a way, is an intermediate habitat between the water and land environment (GILJAROV 1949a, 1949b). This was conducive to new lines of evolution of the *Oligochaeta*, due to feeding differentiation which was confirmed, among others, by a detailed analysis of morphology and modes of feeding of the contemporary earthworms family *Lumbricidae*.

Basing on CLARK's (1964) theory, BRINKHURST (1971) was undoubtedly the first scientist who emphasized a very important factor in the evolution of the *Oligochaeta*, i. e. the development of the locomotoric function of the coelom, which made it possible for these animals to inhabit new environments. However, considering the main and primary role of the coelom exclusively in terms of the locomotoric functions seems to be a debatable point. At first, the coelom performed many functions, i.e. that of an environment ensuring constant physiological conditions necessary for the correct functioning of many internal organs. It was later that the coelom or, to be more exact, only some of its parts, became the locomotoric organ. At second, the coelom was thus a polyfunctional organ whose development was stimulated by a group of kinetic tasks of the body (ŠVEŠNIKOV 1966). What caused the intensification of one of many functions was further evolution.

Besides, the development of metamery, i.e. of homological parts along the longitudinal axis of the body (BEKLEMISZEW 1957, CLARK 1964), in all the *Annelida* is also closely connected with the evolution of the coelom and its kinetic function. The development of metamery, regarded by BEKLEMISZEW (1957) as a special kind of symmetry (the following symmetry), indicates a distinct relationship between the *Oligochaeta* and the *Polychaeta*. In the external metamery of the *Oligochaeta* a high degree of homonomy is preserved, which is also the case with the primitive *Annelida* whose morphology is that of homonomic-metameric animals. In the *Annelida* the coelom metamery is of a primary nature, while the musculature is not divided into segments. The *Oligochaeta* are characterized by pronounced primary heteronomy, the characteristic trait of which is, as in the *Polychaeta*, the occurrence of differences in the structure of post-larval and larval segments. Secondary heteronomy is much less marked in the *Oligochaeta* than in the *Polychaeta*; in the former it appears mainly as the concentration of reproductive organs in several segments, the development of the clitellum, and cephalisation.

Just as in the case of sexual reproduction of the *Annelida*, there are also no proofs evolutionary importance with regard to asexual reproduction and linear colonies of polysegmental individuals in many aquatic *Oligochaeta*. Linear colonies of the *Oligochaeta* last for a very short time, showing little colonial individuality. Besides, colonies seldom lead to the development of more complex

forms. Asexual reproduction, developing individually in various *Oligochaeta* and *Polychaeta* is a secondary phenomenon, the development of which took place as follows autotomy-architomy-paratomy (IVANOVA-KAZAS 1977).

Despite many convincing proofs, significant for the determination of the origin of the *Oligochaeta*, the final explanation of this problem has not yet been found. This applies mostly to the phylogenetic relations between the *Polychaeta* and the *Oligochaeta* as well as the *Archannelida*, consisting of groups whose systematic position within the *Annelida* is unclear. One of the reasons for such a state of affairs is the fact that little is known not only about many groups of the primitive *Annelida*, but also about the structure of many organs of these animals and about their organogenesis. This is particularly obvious in the case of organs of the nervous and reproductive systems in various *Annelida*, connected with the locomotoric and reproductive functions of the coelom. In the *Annelida*, i.e. the first *Coelomata*, specialised brain ganglia appeared, which was due to the fact that most of these animals walked with the head part forward. Very little is also known about the structure of nervous system in the majority of *Archannelida* species, considered a separate order within the *Polychaeta* (HERMANS 1969). This is why it would be wrong to look for homology between organs of the nervous system of these animals, and the nervous system of the *Polychaeta* larvae and other *Polychaeta* or *Plathelminthes*, such a conclusion is definitely premature (KOTIKOVA 1973). It is necessary, therefore, to conduct further studies which may suggest new solutions.

In my opinion the *Oligochaeta* should, together with contemporary *Polychaeta*, be derived from common ancestors whose further evolution went along different direction. These animals were characterized by the non-differentiated coelom, the dispersed development of reproductive cells and the non-larval development. Contemporary *Oligochaeta* are a whole consisting of elements similar from the point of view of genetics and different from the point of view of ecology. In addition, there were many differences between the history, modes of expansion and speciation intensity of these elements. The differentiation of organs, involving the distribution of functions and the division of a whole into different parts was of paramount importance for the origin of the *Oligochaeta* and their progressive evolution. This differentiation manifested itself as a number of functional adaptations emerging through the restructuring of differentiation organs with normal functions, due to transformations of body activity as a whole. This, in turn, results in entirely new adaptations (SZMALHAUZEN 1975). In the case of the *Annelida*, among others the *Oligochaeta*, this tendency applies to the evolution of the coelom, especially these part of the organ which specialised in reproductive functions. Out of many organs of these animals, it is the reproductive system that is unevenly differentiated. In the primitive *Annelida*, apart from lack of isolated gonads, we observe the dispersed development of reproductive cells which can be formed throughout the whole year or over a long period of ontogenesis, and are led out through the crack of body.

In this case, progressive evolution of the *Oligochaeta* involved, apart from the formation of isolated gonads and gonoducts, already identified by GOODRICH (1946) as coelomoducts, the development of oligomerous processes (as understood by DOGEL (1954)) connected with the morphological and physiological concentration of organs and function. In addition to the embryo development, which is a modification of the spiral pattern of cleavage occurring in the *Polychaeta*, the development of large eggs with abundant yolk or the development in the egg cocoon appeared (ANDERSON 1971). The transformation of the type of development affected the organogenesis in the *Oligochaeta* to a large extent. This was particularly evident in the change of the initial stages of the development of head organs, manifesting itself as the reduction of head organs of the body in adult individuals (palps and tentacles, eyes, partial reduction of cerebral ganglion). In my opinion, the development of similarities between various groups of the *Annelida* is due to the derivation of contemporary classes of *Annelida* from common ancestors, and to secondary adaptations. Among the contemporary *Annelida* this applies mostly to numerous similarities of anatomical features of the family *Questidae* and the *Oligochaeta* (GIERE, RIESER 1981) as well as *Aeolosomatidae* and *Polychaeta* (BRINKHURST 1971).

Some problems of phylogenetic relations between various groups of the *Annelida* can also be explained on the basis of research on the structure and ultrastructure of reproductive cells at the submicroscopic level (JAMIESON 1981). This is indicated, for example, by investigations of spermatozoa in some *Annelida*. The ultrastructure of acrosome of some aquatic *Oligochaeta* (*Tubificidae*) is similar to earthworms (*Lumbricidae*, *Megascolecidae*) (JAMIESON et al. 1978). Basically, the structure of sperm in the *Oligochaeta* and the *Hirudinea* is similar (GARAVAGLIA et al. 1974), while in the primitive *Polychaeta* (*Archiannelida*) both simple (*Polygordius* SCHNEIDER) and highly modified types of spermatozoa occur (*Dinophilus* SCHMIDT) (FRANZEN 1956, 1975a, 1976b). According to FRANZEN (1977), the structure of spermatozoa in the *Archiannelida* indicates that the animals are a non-homogenous group of polyphyletic origin, with different lines of spermatozoa evolution and specialization. This finding is not in agreement with JÄGERSTEN's (1947) earlier opinion that the *Archiannelida* are a homogeneous group.

While the classification of *Oligochaeta* species within specific familiae has not, except for a few instances, aroused any doubt, phylogenesis of specific familiae and their grouping into higher taxonomical categories have always been a controversial issue. First attempts at classification of the *Oligochaeta* were made late in the XIXth century, thus coinciding with the considerable development of taxonomical studies of these animals. Within a period of over 125 years it was possible to work out more and more improved systems of classification giving a clear picture of kinship. This was due to continuous progress in studies of systematic and phylogenesis of the *Oligochaeta*, which has been continued to the present day (KASPRZAK 1982b). BRINKHURST and JAMIESON

(1971), JAMIESON (1978, 1980) and ČEKANOVSKAJA (1962) studies were the most significant contribution to investigations of the *Oligochaeta*. Their classifications was, to some extent, supplemented and developed further by TIMM (1981). In my opinion, of paramount importance in these classifications [especially of BRINKHURST and JAMIESON (1971) classification], is analysis of distribution of component parts of the reproductive apparatus, particularly gonads, and of its evolution. Another significant issue is stressing the role of the oligomerisation of homological organs as one of the modes of body integration. Despite considerable progress on the anatomy, morphology and taxonomy of the *Oligochaeta* within the last decade, the final differentiation of the first *Oligochaeta* from their hypothetical ancestors, and the taxonomical position of the *Aeolosomatidae* and *Potamodrilidae* still belong to the most controversial problems. In my opinion, the most primitive family of the *Oligochaeta*, from which, however, only land forms of animals can be derived, are the *Haplotaxidae*, which, due to their structure of the reproductive apparatus (4 pairs of gonads, 1-4 pairs of spermathecae) are the least oligomeric forms of all the *Oligochaeta* [as was particularly emphasized by DOGEL (1954)], and the *Lumbriculidae* which developed independently and whose phylogenesis is probably shorter. This stand was previously presented by TIMM (1981) who drew our attention to a certain discrepancy within BRINKHURST's (1971) system. The latter maintains that the *Tubificidae* characterized by the primitive setal apparatus with hair setae come from *Haplotaxidae* possessing specialised setae, characteristic of all the contemporary land *Oligochaeta*. Both the *Tubificida* and the *Haplotaxida* and *Lumbriculida* come from the hypothetical ancestors of all *Oligochaeta*, in which setal apparatus of "Tubificidae" type, 2 pairs of male gonads in segments X-XI, 2 pairs female gonads in segment XII and gonoducts similar to nephridia occurred. However, the *Aeolosomatidae* defy classification within the *Archannelida*. If we considered this a possibility, than also the *Potamodrilidae*, distinguished by BUNKE (1967), should be classified within the *Archannelida* — an entirely artificial group. Such a classification is impossible due to structural differences between the *Aeolosomatidae* and the *Potamodrilidae*, above all more complex reproductive organs in the latter. Both the *Aeolosomatidae* and the *Potamodrilidae* have no distinct gonads; however, unlike the *Aeolosomatidae*, the *Potamodrilidae* posses a pair of male gonoducts with funnels. Despite their undoubtedly primitive structure, the *Aeolosomatidae*, living in various water environments, are a homogeneous group from the point of view of morphology and anatomy. This applies to all genera of this family, including the *Hystriocosoma* MICH. whose external and internal structure as well as locomotion are very much like those of the genera *Aeolosoma* EHREN. and *Rheomorpha* RUTTNER-KOLISKO (POP 1975, KASPRZAK 1976, 1981). This is why I support TIMM (1981) who classified the *Aeolosomatidae* and the *Potamodrilidae* as a separate subclass of *Clitellata*. However, TIMM's (1981) classification does not, in my opinion, indicate the proper systematic position of the family *Enchytraeidae* characteri-

ized by a specific structure of many organs, which was emphasized earlier by BEDDARD (1895), VAILLANT (1889) and MICHAELSEN (1930). The *Enchytraeidae* seem to be linked with both the families *Naididae* and the *Tubificidae*; basing on this assumption ČEKANOVSKAJA (1962) considered them a side branch of the *Naidomorpha* leading the *Naididae* to the *Tubificidae*. The relationship of the *Enchytraeidae* and the *Tubificidae* is indicated, for example, by the structure of nephridia, similar in both *Rhyacodrilinae* and the *Enchytraeidae*. Besides, in the *Enchytraeidae* spermathecae are frequently connected with the oesophagus, which occurs also in some *Rhyacodrilinae*. This arrangement seems, to some extent, be analogous to the communicatio genito-intestinalis occurring in a number of forms from various orders of the *Turbellaria* and *Monogenea* (*Plathelminthes*), whose function is to carry excessive sperm and yolky cells to the intestine (BEKLEMISZEW 1958). The relationship of the *Enchytraeidae* and the *Haplotaenidae*, in turn, is indicated by setae morphology, their distribution and number in young individuals, and the occurrence of setal glands, oesophageal appendages, septal glands and structure of male gonoducts. Considering these data I fully agree with SHUROVA (1980), who in order to emphasize the unique structure of the *Enchytraeidae* among all the *Oligochaeta*, as well as their relationship with representatives of the orders *Naidomorpha* and *Lumbricomorpha* as classified by ČEKANOVSKAJA (1962), separated the family *Enchytraeidae* as a specific superorder *Enchytromorpha*.

Opinions concerning the place of the family *Branchiobdellidae* in systematics have been differed for a long time. KENNEL (1893), PIERANTONI (1912), GODNIGHT (1940) and HOFFMAN (1963) classified the *Branchiobdellidae* as belonging as a family to *Oligochaeta*. HENNIG (1959) and earlier LEIDY (1851), VERRIL (1873) and ODIER (1823) maintained that the *Branchiobdellidae* belong to the class *Hirudinea*, and the former divided it into three groups: *Branchiobdellae*, *Acanthobdellae*, *Autobdellae* (= *Achaetobdellae*), without specifying their systematic rank. Also HOLT (1963) questioned the status of the *Branchiobdellidae* within the *Oligochaeta* and suggested that they should be treated as a separate taxon of a higher rank within the *Annelida*. Taking under consideration a number of morpho-anatomical and behavioral features distinguishing the *Branchiobdellidae* from the *Oligochaeta* and the *Polychaeta*, HOLT (1965) considered them to be a separate class within the *Clitellata* divided into the *Oligochaeta*, *Branchiobdellida*, *Acanthobdellida* and *Hirudinea*. Thus he resigned from his previous statment that the *Branchiobdellidae* are an *Oligochaeta* family (HOLT 1953). HOLT's (1965) stand was also adopted by KARAMAN (1967). For reasons difficult to explain VAN DER LAND (1978), without taking into account hitherto data on the status of the *Branchiobdellidae* among the *Clitellata*, does not express his opinion and considers the *Branchiobdellidae* as *Annelida* incertae sedis. LIVANOV (1931, 1940) and STEPHENSON (1930) regarded the *Branchiobdellidae* as a transitional link between the *Lumbricidae* and the primitive *Hirudinea* from the genus *Acanthobdella* GRUBE (*Archihirudinea*) — forms closely related

to the ancestors of the *Hirudinea*, possessing some traits characteristic of the *Oligochaeta*. There are, however, many differences between the *Branchiobdellidae* and the *Hirudinea*, classified previously as one group — the *Discophora*, and existing similarities should be regarded as the result of convergence (ČEKANOVSKAJA 1962). One of the basic differences between the *Branchiobdellidae* and the *Hirudinea* — a group younger from the point of view of phylogeny — as a different structure of the coelom in the two. With regard to the structure of this organ, the *Oligochaeta* are a very homogenous group; partial reduction occurs very rarely (*Naididae*: *Chaetogaster* BAER, *Branchiobdellidae*). The total reduction of the coelom occurs only in the front segments of *Agriodrilus vermivorus* MICH. (*Lumbriculidae*). The reduction of the coelom in the *Hirudinea* is of a different origin; it leads to the transformations of this organ into a system of channels (BEKLEMISZEW 1958). Further differences between the *Branchiobdellidae* and the *Hirudinea* concern mostly the structure of the back acetabulum, the reproductive organs, and — to a lesser degree — the jaws. In the *Branchiobdellidae* the acetabulum is the result of transformation of the last body segment, while in the *Hirudinea* the acetabulum resulted from the fusion of seven or four (*Acanthobdella* GRUBE) segments of body; this is also confirmed by the fusion of the back nervous ganglia into one big mass of ganglia. In the *Hirudinea*, the axis of the acetabulum and of the longitudinal axis of body are more or less square to each other, while in the *Branchiobdellidae* the axis of the acetabulum is an extension of the longitudinal axis of the body (PAWŁOWSKI 1936). The structure of the reproductive organs in the *Branchiobdellidae* is remarkably different than in the *Hirudinea*. Although unpaired number of male reproductive orifices appear in both, a tendency of the distal parts of the gonoducts to fuse is observed frequently in the *Oligochaeta*, and occurs independently in various families. Similarly, the jaws of the *Branchiobdellidae* developed independently of the jaw apparatus in the *Gnathobdellidae*. This may apply also to other organs, e.g. the musculature of the *Branchiobdellidae* resembles that of the *Hirudinea* (FRANZEN 1963).

In many classifications considerable importance is ascribed to the structure of the reproductive apparatus whose organs have been regarded as most conservative from the phylogenetic point of view within the entire class *Oligochaeta*. It should be pointed out here, however, that both the structure and the placement of specific parts of reproductive organs change in the *Oligochaeta* which was emphasized earlier by GATES (1974a), one of the critics of the classifications suggested by MICHAELSEN (1930) and STEPHENSON (1930). This applies also to the placement of gonads; their occurring in various segments, thus distinguishing *Oligochaeta* families. For example, in the family *Naididae* the gonads are placed in segments IV and V, while in the family *Opistocystidae* they developed as far as in segments XXI and XXII. Relatively often, a manifold increase in some parts occurs in the *Oligochaeta*, which is frequently considered anomalous. This applies, for example, to male gonads [7 pairs in *Pheretima anomala* MICH.

(*Megascolecidae*), 9 pairs in *Agastrodrilus multivesiculatus* OMOD. et VAIL. (*Octochaetidae*), female gonads (up to 7 pairs in some *Lumbricidae*), atria [3-4 pairs in *Lumbriculus multiatriatus* YAMAG. (*Lumbriculidae*), 2 pairs in *Nais elinguis* O. F. MÜLL. (*Naididae*) and *Stylodrilus heringianus* CLAP. (*Lumbriculidae*)], as well as to spermathecae [2 pairs in *Fridericia bisetosa* (LEV.) and *Enchytraeus polonicus* DUM. (*Enchytraeidae*)] (GATES 1974a, 1974b, DUMNICKA, KASPRZAK 1979). Particularly often, changes in the structure and placement of parts of the reproductive apparatus (gonads, reproductive orifices) occur in parthenogenetic polyploidal forms of *Lumbricidae* (OMODEO 1951, POOL 1937, ZAJONC 1980). This phenomenon may also occur on other *Oligochaeta* families. Referring, to a degree to the classification of *Lumbricidae*, presented by OMODEO (1956), GATES (1976) stressed the systematic importance of traits linked with the morphology of female gonads, and the development of oocytes.

In my opinion a computer analysis, based on HENNIG's principles of classification, of all hitherto taxonomic traits and zoogeographical data, used successfully by SIMS (1980, 1982) with regard to the systematics of *Lumbricina*, will be a new approach to the classification of the *Oligochaeta*; other necessary procedures are studies of the systematic status of other families of the *Clitellata*, unexplained so far, e.g. of the family *Lobatocerebridae*, classified temporary as *Oligochaeta* by RIEGER (1980).

As the result of this study and the work of JAMIESON (1977, 1978), BRINKHURST (1971, 1982) and TIMM (1981) I now propose the new classification (Table 1).

Table 1. The proposed classification of oligochaetous *Clitellata*

Class	Superorder	Order	Characteristic
1	2	3	4
<i>Aphanoneura</i>			Nerve cord double, developing in body wall. Coelom very well developed. Number of segments small, a few variable or constant. Fusion of segments in separate parts of body absent. Generally setae present.
		<i>Aeolosomatida</i>	Testes in front of and behind ovaries. Segmentation and dissepimentes reduced. Hair setae in dorsal and ventral bundles, or setae absent. Two families: <i>Aeolosomatidae</i> and <i>Potamodrilidae</i> .
<i>Oligochaeta</i>	<i>Naidomorpha</i>		Nerve cord single, separate from body wall. Coelom, segmentation and dissepimentes generally very well developed. Number of segments great, very variable. Fusion of segments in separate parts of body absent. Generally setae present.
		<i>Tubificida</i>	Male ducts usually with atria, and with or without prostates. Muscular stomach absent. Number of setae in a bundle varies; even if present in only a few segments, almost always more than two. Shape of setae highly variable, usually bifid, very rarely of lumbricine type; hair setae often present in dorsal bundles. Spermathecae one pair.
		<i>Dorydrilida</i>	Plesioporous microdriles with gonads in variable position from IV-V to XXI-XXII. Atria present usually with prostates. Spermathecae in second, third or fourth gonadal segments. Setae usually numerous, hair setae may be present dorsally. Four families: <i>Naididae</i> , <i>Tubificidae</i> , <i>Opisthocystidae</i> and <i>Phreodrilidae</i> .
		<i>Dorydrilida</i>	Plesioporous microdriles with testes in IX, and ovaries in X. Atria present without prostates. Spermathecae in X or XI or both. Setae of lumbricine type. One family: <i>Dorydrilidae</i> .

Table 1. (Continuation)

1	2	3	4
	<i>Enchytromorpha</i>	<i>Enchytraeida</i>	<p>Male ducts without atria and prostates. Muscular stomach absent. Setae of lumbricine type or slightly more abundant, usually simple pointed, very rarely bifid; hair setae always absent, rarely setae absent. Spermathecae one pair, very rarely two pairs.</p> <p>Plesioporous microdriles usually with testes in XI, and ovaries in XII (exceptionally testes extend forwards into VII, and ovaries into VIII). Spermathecae always in V, rarely in V and VI. Penial bulbs glandular.</p> <p>One family: <i>Enchytraeidae</i>.</p>
	<i>Lumbricomorpha</i>	<i>Haplotaxida</i>	<p>Male ducts with or without atria and prostates. Muscular stomach oesophageal or intestinal usually present. Number of setae in a bundle not more than two. Setae of lumbricine type, rarely perichaetine; if setae bidentate then distal denticle tends to be rudimentary; hair setae always absent; rarely setae absent. Spermathecae one, two or more pairs.</p> <p>Plesioporous microdriles. Octogonadal or gonads missing in third, fourth, or first and fourth gonadal segments. Atria and prostates absent. Setae normally developed or reduced.</p> <p>One family: <i>Haplotaxidae</i>.</p>
		<i>Lumbriculida</i>	<p>Prosopore microdriles. Octogonadal or gonads missing in fourth, and also sometimes in first or second gonadal segments. Atria and prostates present. Setae sometimes bidentate.</p> <p>One family: <i>Lumbriculidae</i>.</p>
		<i>Lumbricida</i>	<p>Opisthopore megadriles usually (<i>Lumbricina</i>), and opisthopore microdriles (<i>Alluroidina</i>) or plesiopore-opisthopore microdriles (<i>Moniligastrina</i>). Gonads usually missing in third very rarely in first of second gonadal segments. Atria with prostates or separate prostates present (<i>Alluroidina</i>, <i>Moniligastrina</i>) or atria absent, and prostates present or absent (<i>Lumbricina</i>). Spermathecae one pair in VI or IX (<i>Alluroidina</i>), and one or two pairs in VIII or IX or both (<i>Moniligastrina</i>), or number and distribution of spermathecae</p>

		<p>variable (<i>Lumbricina</i>). Clitellum one cell thick (<i>Alluroidina</i>, <i>Moniligastrina</i>) or clitellum multilayered (<i>Lumbricina</i>).</p> <p>Twenty one families: <i>Alluroididae</i>, <i>Syngenorilidae</i> (<i>Alluroidina</i>), <i>Moniligastridae</i> (<i>Moniligastrina</i>), <i>Lumbricidae</i>, <i>Komarekionidae</i>, <i>Diporochaetidae</i>, <i>Ailoscolecidae</i>, <i>Glossoscolecidae</i>, <i>Sparganophilidae</i>, <i>Criodrilidae</i>, <i>Microchaetidae</i>, <i>Hormogastridae</i>, <i>Megascolecidae</i>, <i>Acanthodrilidae</i>, <i>Ocnerodrilidae</i>, <i>Octochaetidae</i>, <i>Eudrilidae</i>, <i>Biwadrilidae</i>, <i>Alimidae</i>, <i>Lutodrilidae</i> and <i>Kynotidae</i> (<i>Lumbricina</i>).</p>
<i>Branchiobdellae</i>	<i>Branchiobdellida</i>	<p>Nerve cord single, separated from body wall. Body very short, number of segments constant, fusion of segments in particular parts of body present: head (four segments), trunk (ten segments), and acetabulum (one segment). Coelom well developed in trunk part of body only, in head part and acetabulum coelom reduced. Setae always absent.</p> <p>Quadrangonal or sextagonal; one pair of testes in XI or two pairs in IX and X, one pair of ovaries in XI. Twin vas deferens connected in unpaired male duct with atrium. Male reproductive orifice unpaired in X, female orifices paired in XII. Unpaired spermatheca in IX. Segmentation very weakly, dissepiments well developed. In mouth cavity one pair of jaws present. One family: <i>Branchiobdellidae</i>.</p>

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STRESZCZENIE

[Tytuł: Dawne i współczesne koncepcje filogeneii i systematycznych klasyfikacji skąposzczetów (*Oligochaeta*)]

W syntezie dotychczasowych poglądów na temat filogenezy i klasyfikacji *Oligochaeta* przedstawiono uwagi na temat stosunków pokrewieństwa, przebiegu ewolucji i stanowiska systematycznego różnych rodzin. Szczególnie duży wkład w poznanie przebiegu ewolucji oraz systematyki *Oligochaeta* wniosły badania R. O. BRINKHURSTA, dalej rozwinięte przez B. G. M. JAMIESONA i T. TIMMA, który nawiązał do dynamicznej teorii rozwoju wtórnej jamy ciała i segmentacji przedstawionej przez R. B. CLARKA. Głównym procesem progresywnej ewolucji *Oligochaeta* było powstanie poprzez zwiększenie się ruchliwości form pełzających i penetrujących podłoże nowych różnicowań funkcjonalnych, jak wytworzenie się silnie umięśnionego wora skórno-mięśniowego, rozwoju parapodiów, różnicowanych morfologicznie szczecin, powstanie bardziej wyspecjalizowanych narządów rozrodczych oraz zmian w rozwoju embrionalnym. Duży wpływ na ewolucję *Oligochaeta* miało także zajęcie przez te zwierzęta gleby, co umożliwiło skierowanie ich ewolucji na nowe tory ze względu na duże możliwości różnicowania pokarmu. W przypadku *Lumbricidae*, a także innych rodzin *Oligochaeta*,

duże znaczenie dla opanowania różnych środowisk lądowych miało powstanie rozmnażania partenogenetycznego i rozwój populacji poliploidalnych.

Dyskusyjne wydaje się sprowadzanie głównej i pierwotnej roli wtórnej jamy ciała, której R. B. CLARK przypisuje szczególną rolę jako szkieletowi hydraulicznemu, wyłącznie do funkcji lokomotorycznej. Pierwotnie wtórna jama ciała była organem polifunkcyjnym powstałym na bazie zespołu kinetycznych zadań organizmu, a dopiero dalsza jej ewolucja doprowadziła do intensyfikacji jednej z kilku funkcji. W ścisłym związku z ewolucją wtórnej jamy ciała i jej funkcją kinetyczną stoi także rozwój metamerii wszystkich *Annelida*. Należy sądzić, że podobnie jak w przypadku rozmnażania płciowego *Annelida*, nie ma także żadnych dowodów dla ewolucyjnej wartości powszechnie występującego u wielu wodnych *Oligochaeta* rozmnażania bezpłciowego i wytwarzania kolonii liniowych, utworzonych przez wielosegmentowe osobniki.

Podkreślono, że mimo wielu przekonujących dowodów mających znaczenie dla określenia pochodzenia *Oligochaeta*, problem ten nadal nie jest ostatecznie wyjaśniony. Dotyczy to zwłaszcza stosunków filogenetycznych występujących między *Polychaeta* i *Oligochaeta* oraz *Archiannelida*, w których skład wchodzi grupy o niejasnej pozycji systematycznej w obrębie *Annelida*. Jednym z powodów jest nie tylko słaba znajomość wielu grup prymitywnych *Annelida*, ale także niedostatecznie poznana budowa wielu narządów tych zwierząt i ich organogeneza. *Oligochaeta* należy wyprowadzać razem ze współczesnymi *Polychaeta* od wspólnych przodków, których dalsza ewolucja przebiegała w różnych kierunkach. Zwierzęta te charakteryzowały się nieodróżnioną wtórna jamą ciała, rozproszonym tworzeniem się komórek rozrodczych i rozwojem bezlarwalnym. Współczesne *Oligochaeta* są całością złożoną z podobnych genetycznie i różnych pod względem ekologicznym elementów, których historia, drogi rozprzestrzeniania się oraz intensywność specjacji były bardzo różne. Podkreślono, że w powstawaniu *Oligochaeta* i ich progresywnej ewolucji decydujące znaczenie miało różnicowanie się narządów polegające na podziale funkcji i rozłożeniu całości na części. Szereg podobieństw występujących między różnymi grupami *Annelida* jest właśnie wynikiem pochodzenia wspólnie żyjących gromad od wspólnych przodków oraz wtórnych adaptacji.

We współczesnych klasyfikacjach *Oligochaeta* szczególnie istotne jest wykorzystanie analizy rozmieszczenia poszczególnych części aparatu rozrodczego i jego ewolucji oraz zwrócenie uwagi na oligomeryzację organów homologicznych jako jednego ze sposobów integracji organizmu. Zarówno budowa, jak i rozmieszczenie poszczególnych części narządów rozrodczych wykazują jednak w obrębie *Oligochaeta* dużą zmienność. Dotyczy to nawet usytuowania gonad, których rozmieszczenie w określonych segmentach jest cechą różniącą szereg rodzin *Oligochaeta* między sobą. Najbardziej prymitywną rodziną *Oligochaeta*, od której wyprowadzać można jednak tylko lądowe formy tych zwierząt, są *Haplotaxidae*, będące ze względu na budowę aparatu rozrodczego najbardziej

oligomerycznymi formami spośród wszystkich *Oligochaeta* oraz rozwijające się niezależnie i najprawdopodobniej młodsze filogenetycznie *Lumbriculidae*.

Przedstawiając nową propozycję klasyfikacji *Oligochaeta* podtrzymano wcześniejszą propozycję T. TIMMA wydzielenia *Aeolosomatidae* i *Potamodrylidae* w osobną gromadę *Clitellata*. Podkreślając unikalność budowy *Enchytraeidae* wśród wszystkich *Oligochaeta* oraz występowanie wielu podobieństw z przedstawicielami różnych rzędów *Naidomorpha* i *Lumbricomorpha* wydzielono *Enchytraeidae* w osobny rząd *Enchytraeida* (nadrząd *Enchytromorpha*). Zakwestionowano także status *Branchiobdellidae* w obrębie gromady *Oligochaeta* i zaproponowano, podobnie jak uczynili to wcześniej niektórzy autorzy, przyjęcie ich jako osobnej gromady *Branchiobdellae* w obrębie *Clitellata*.

РЕЗЮМЕ

[Заглавие: Прежние и современные концепции по филогенезу и систематическим классификациям малощетинковых червей (*Oligochaeta*)]

Автор представил различные концепции относительно происхождения, эволюции и систематики *Oligochaeta*, в основном водяных. Автор предполагает, что семейства *Aeolosomatidae* и *Potamodrylidae* следует объединить в самостоятельный подкласс *Aphanoneura* (отряд *Aeolosomatida*) подтипа *Clitellata*. Семейство *Branchiobdellidae* принадлежит, по мнению автора, к отдельному классу подтипа *Clitellata*, а семейство *Enchytraeidae* составляет отдельный надотряд и отряд (*Enchytraeida*) класса *Oligochaeta*. Предложенная классификация представлена в Таблице I.