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Problem pochodzenia skąposzczetów (Annelida: Oligochaeta) *14

Problem of the origin of oligochaetes (Annelida: Oligochaeta)

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The oligochaetes (Oligochaeta) comprise one of the two classes of the subphylum Clitellata in the phylum Annelida, which occupies a central position among all of the Trochozoa. To this class belong the polymeric Annelida which are characterized by a considerable reduction of the gills and parapodia, from which only a limited number of setae are retained, by the grouping of the reproductive organs in a few segments in the anterior part of the body, by the segmental positioning of the male gonads always anteriorly to the segments with the female

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* The numbers in the right-hand margin indicate the corresponding pages in the original text. (Tr.).

gonads, by the occurrence of the funnels of the gonoducts independently of the nephridial funnels, and by the homogeneous character of the secondary body cavity (coelom), which retains the primitive homonomous metameric structure typical of the hypothetic prototype of the Annelida.

The problem of the origin of the Oligochaeta, which are known in the fossil state from as far back as the Upper Ordovician (Bather, 1920), and the evolution of these forms has for a long time been a focus of interest of all the zoologists who have been concerned with this group of animals. There has never been any doubt in principle concerning the relationship of the Oligochaeta with the primitive Polychaeta, but the views on this subject put forward by various researchers have often been quite erroneous. Eisig (1887) considered representatives of the family Capitellidae (Polychaeta Sedentaria) as being ancestors of the Oligochaeta. In support of his thesis, however, he provided very few convincing data, which have nevertheless been taken into consideration by certain zoologists, as was mentioned by Fedotov (1966). To wit, Eisig (1887) calls attention only to some apparent similarity in the anatomical structure of certain organs (nephridia, coelomoducts) that appears between representatives of the Capitellidae and the families Lumbricidae, Aeolosomatidae and Naididae. Similarly completely unjustified was the derivation of the Oligochaeta from the family Eunicidae (Polychaeta Errantia) (Meyer, 1926, 1929). The latter author called attention to a certain similarity of the nephrostomes appearing between representatives of the genus Tomopteris Eschscholtz (presently family Tomopteridae) and the lumbricids sensu lato. Meyer (1926, 1929) considered this as sufficient evidence for deriving the families Lumbricidae and Megascolecidae, and together with the latter all of the remaining Oligochaeta, from the Polychaeta Errantia. This view was also accepted by Kuźnicki and Urbanek (1967), who considered the Polychaeta Errantia as the central 14 group within the Annelida. In his examination of the problem of oligomerization and polymerization of homologous organs in the Annelida Dogel′ (1954) considered that one may discern within this group the ancestors of not only the Oligochaeta but also of the Polychaeta Sedentaria. It may be that the Archiannelida, whose structure shows many primitive features (eg. the occurrence of homonomous segmentation, the lack of distinct ganglia in the nervous system, the occurrence of a ciliated epithelium and the weak development of the parapodia), should be acknowledged as the most primitive group of the Annelida. There is no lack of views, however, that the structural simplicity of the Archiannelida arose as the result of a secondary simplification of various forms of polyphyletic origin (Gerlach, 1967). It is generally accepted that this is a group which is related to a considerable degree with the Polychaeta, within which it is sometimes considered as a separate subclass (Marinov, 1977). In general, however, the indistinct phylogeny and systematic position of this group within the class is emphasized (Sveshnikov, 1966; Hermans, 1969; Bubko, 1973), mainly on account of the differences occurring in the development of these animals. According to Reisinger (1925) the Archiannelida are related to the Oligochaeta by way of the Aeolosomatidae, manifesting a close relationship to

Parergodrilus heideri Reisinger (Parergodrilidae). On the other hand Stephenson (1930) considered that there was no sense in deriving the Oligochaeta from the Archiannelida, since the latter is a quite artificial group. In spite of the fact that he placed the Oligochaeta close to the Archiannelida, Michaelsen (1919, 1920) left completely open the question of the origin of these animals. In the opinion of Stephenson (1930) the development of the Oligochaeta was initiated under conditions of adaptation to life in desalinated, strongly silted, small and shallow flooded areas and estuaries. Adaptation to life in such an environment led to the development of hermaphroditism and the formation of egg cocoons, protecting the developing embryos in bodies of water that tended to dry up. Basing herself on earlier views put forward by Michaelsen (1929) Chekanovskaya (1962) argues in favour of the concept of a polyphyletic origin of the Oligochaeta. According to this concept some of the primitive Oligochaeta (Aeolosomatidae, Naididae) are derived from forms closely related to some of the contemporary Archiannelida, giving rise to the Enchytraeidae, Tubificidae and Phreodrilidae, while forms related to representatives of the family Haplotaxidae originated from Polychaeta with an elongated body, with reduced parapodia and without natatorial setae. This view was not shared by Shurova (1980), who called attention to the fact that the morphological and anatomical similarities among various groups of the Oligochaeta are much greater than within any group of the Polychaeta.

In drawing up his phylogenetic tree of the Metazoa and subjecting to criticism all of the views concerning this question which existed up till then, Hadži (1963) placed the Oligochaeta on a branch extending from the Myzostomidea and Polychaeta, from which he also derives the Echiuroidea.

The elaboration of a convincing concept of the origin of the Oligochaeta and the tracing of their evolutionary development are undoubtedly made very difficult not only by the scanty knowledge of fossil remains of this group of invertebrates, but also by the occurrence of a serious gap in studies on the development and function of some individual internal organs of these animals. The underestimation or outright disregard by most investigators of the principles of comparative anatomy and of the functional analysis of the role of different organs in the course of development has led in substance to the acknowledgement of a direct origin of the Oligochaeta from the Polychaeta as a binding principle in the systematics of the Annelida. In large measure this principle also results from the generally accepted concept of a marine origin of all of the invertebrates, and hence also of the Oligochaeta, which, on their way to elaborating capacities for morphological and anatomical adaptations, passed through estuaries into fresh waters and then colonized terrestrial habitats. Such an evolutionary trend, which is more or less distinctly evident in various groups of invertebrates (eg. the Mollusca), is not at all so obvious in the case of the Oligochaeta (Brinkhurst, 1971). The considerable differences in the structure of the body occurring between the Polychaeta and the Oligochaeta have been ascribed until now mainly to the development of hermaphroditism in the Oligochaeta. For a long time it was considered that the only type of reproduction of the Oligochaeta is alternating (reciprocal) crossing of hermaphroditic individuals, with a complete lack or only exceptional occurrence of parthenogenesis caused, for example, by the development of parasites (Muldal, 1952). A consequence of the amphimixis of hermaphroditic individuals was the elaboration of a considerable variability in the methods of reproduction within the Oligochaeta (Reynolds, 1974). Parthenogenesis, whose occurrence in the Oligochaeta was first described by Gavrilov (1935, 1939) and Kobayashi (1937), has been found to be a much more frequently encountered phenomenon, especially in terrestrial forms, than was postulated by Muldal (1952), and the sterility of the male gonads may develop in different ways (Gates, 1972). At the present time, however, there are no data concerning the role played by the different types of reproduction in the course of particular trends in the evolution of this group of animals. This was also emphasized by Brinkhurst (1971), who drew attention to the lack of convincing evidence for the existence of an evolutionary value of the adaptive modifications resulting from the hermaphroditism or the separation of the sexes in the Annelida. In his consideration of the problem of the origin of the Oligochaeta the latter author refers to the dynamic theory of the development of the secondary body cavity and of the segmentation presented by Clark (1964), who criticized the enterocoel theory of the Hertwigs (O. Hertwig and R. Hertwig, 1882), according to which the secondary body cavity arose from outpocketings of the gastrovascular cavity of the Coelenterata. Clark (1964) noted that this theory does not define any adaptive advantages resulting from the fact of the appearance of a system of separate secondary body cavities after their separation from the primitive gut. In his opinion, the original significance of this organ depended mainly on the locomotory function, which is of fundamental significance in the development of all of the Bilateralia. 14 The coelom, which is always filled with fluid, gives a definite form to the animal and, cooperating closely with the musculature, to which aspect Livanov (1955) had earlier drawn attention, it allows for locomotion (swimming, crawling, burrowing). Because of the importance of this function and its evolution in different animals, Clark (1964) even considered that, as a result of the influence of the same adaptive factors, the coelom could probably have arisen quite independently in different groups of the Acoelomata with a soft elastic body. According to Clark (1964) the primitive Annelida, or first Coelomata, resembled the Polychaeta with regard to the structure of the reproductive system, but were more closely related to the present Oligochaeta with regard to to the structure of the remaining internal systems. According to Brinkhurst (1971) the progressive evolution of these hypothetical primitive Annelida proceeded in two directions, of which one led to the development of forms which crawled on and penetrated into the substrate, while the other led to swimming forms. The main process of this progressive evolution was the development, through the increase in motility of the individual forms, of new functional differentiations, such as, for example, a strongly muscled dermomuscular sac, parapodia and morphologically differentiated setae, and more highly specialized reproductive organs. One cannot exclude the possibility that among the ancestors of the contemporary Oligochaeta and Polychaeta there occurred a parallel evolution of crawling and swimming forms, which through a gradual stabilization of the new functional adaptations led to the colonization by these animals of the subterranean environment (interstitial and ground waters) and then later of the terrestrial environment. This also made possible the occupation of the freshwater environment by the Polychaeta (contemporary Troglochaetus beranecki (Delachaux), Hypania invalida (Grube) and Manayunkia caspica (Annenkova)), and of the bottom of seas and oceans by the Oligochaeta (Tubificidae: Phallodrilinae). There is no doubt that this evolutionary process was also made possible by the progressive changes in development, which involved in the ancestors of the Clitellata a cessation of the production of small eggs with little yolk, as formed by the primitive Polychaeta, and the development of large eggs with large amounts of yolk, which could develop further with the omission of larval stages. This characteristic preadaptation made it possible for marine animals to colonize freshwater and terrestrial environments (Kuźnicki and Urbanek, 1970). Not until a later stage in the evolution of the Clitellata did the amount of yolk in the eggs decrease and there developed feeding of the embryo on protein contained in the egg cocoon. This phenomenon, which arose independently in the Oligochaeta and the higher Hirudinea, permitted better adaptation for colonization of the terrestrial environment, and is not an evolutionary regression (Ivanova-Kazas, 1977a) but only an improvement in the embryogenesis, as has already been mentioned by Stephenson (1930).

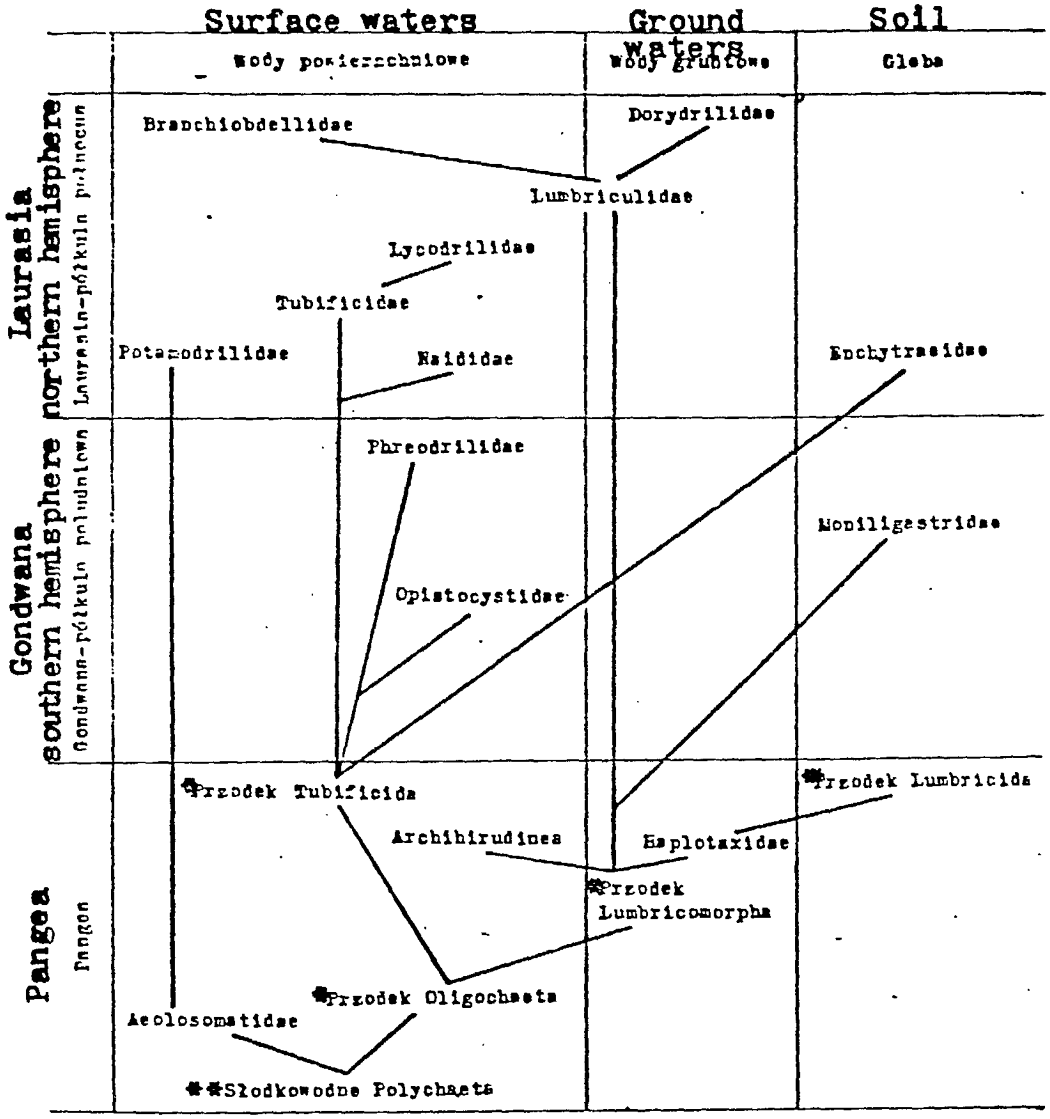
The evolution of the Oligochaeta was considerably influenced in particular by the colonization by these animals of the soil, which in a certain sense is an intermediate environment between bodies of water and terrestrial habitats 14 (Gilyarov, 1949a, 1949b). The colonization of the soil environment permitted the evolution of the Oligochaeta to be directed along new pathways on account of the considerable possibilities of differentiation of the food, which is confirmed, inter alia, by a detailed analysis of the morphology and feeding methods of the contemporary Lumbricidae. The lack of particular generic features in the Lumbricidae is the result of the course of the basic direction of evolution of these animals, which proceeded along the path of a transition from feeding on soil humus to the consumption of plant remains on the surface of the soil. In connection with this, in species representing various genera there are present different adaptive features associated with the way of life and type of food consumed, which have led to the development of the various morphologico-ecological groups of species (Perel, 1979).

Basing himself on Clark's (1964) theory, Brinkhurst (1971) was undoubtedly the first to draw attention to the development of the locomotory functinn of the coelom as a very important factor in the evolution of the Oligochaeta, as in the other Coelomata, permitting these animals to occupy new habitats. At the same time he related this to the mode of origin of the coelom in the phylogenetic process as an especially important problem in the evolutionary morphology of animals. However, reducing the principal and original role of the coelom exclusively to a locomotory function seems debatable, as has also been emphasized by Kuźnicki and Urbanek (1967). Initially the coelom undoubtedly fulfilled various functions, being, for example, a medium which provides precise and constant physiological conditions for the proper functioning of many internal organs. It was not until later that the coelom, or indeed some of its parts, began to become specialized as a locomotory organ. Initially, therefore, the coelom was a polyfunctional organ, which arose from the aggregate of the kinetic activities of the organism (Sveshnikov, 1966), and only its subsequent evolution led to the intensification of one of its several functions. One may therefore acknowledge that all of the other theories of origin of the coelom (Hatschek's (1878) gonocoel theory, Goette's (1884) schizocoel theory, Ziegler's (1898) nephrocoel theory and Livanov's (1955) myocoel theory) are valid to a certain degree and only indicate the complex function of the coelom (Sveshnikov, 1966). It should be remembered, however, that in the Annelida, as in the Mollusca, there is no enterocoelic origin of the coelom, which is formed in a schizocoelic fashion by the moving apart of cells in the mesodermal bands (Beklemishev, 1957).

Closely related with the evolution of the coelom and its kinetic function is the development of the metamerism, i.e. the formation of homologous parts arranged along the long axis of the body (Beklemishev, 1957; Clark, 1964) of all of the Annelida, and hence also of the Oligochaeta (Zenkevich, 1944). The development of metamerism, which Beklemishev (1957) considered as a special type of symmetry (the so-called "progressive symmetry"), indicates a clear relationship of the Oligochaeta and Polychaeta. The external metamerism of the Oligochaeta retains a high degree of homonomy, and hence is as in the primitive Annelida (eg., the Polychaeta Errantia) which appear morphologically as homonomously metameric animals. The Oligochaeta are characterized by a well marked primary heteronomy, which is expressed in the structural dissimilarity of the postlarval and larval segments, discovered in these animals by Ivanov (Ivanoff, 1928; Ivanov, 1944). The larval segments of the Oligochaeta and Polychaeta manifest the same structural features. In these segments, whose primitive number is seven in all of the Oligochaeta, there is no chloragogen tissue, no gonads and no nephridia, and the ganglia of the ventral nerve cord manifest a tendency to fusion. In some forms (eg., in many species of the family Naididae) there are no septa in the larval segments, and the coelom does not display metamerism (Beklemishev, 1957). In comparison with the Polychaeta Sedentaria, however, the secondary heteronomy is considerably more weakly expressed in the Oligochaeta, consisting mainly of the concentration of the reproductive organs in a few segments, the differentiation of the clitellum in the sexually mature forms and the cephalization which is expressed by the lack of setae on segment I and by the fusion of segment I with the prostomium or with several of the anterior segments of the body (segments II-IV) (Branchiobdellidae). A characteristic feature of the Oligochaeta and Polychaeta as polymeric Annelida is their specific method of regeneration, depending on the fact that, regardless of how many segments are cut off, it is always only the larval segments which regenerate. In the case of the Oligochaeta the differences between the larval and postlarval segments are distincly diminished after regeneration (Beklemishev, 1957).

As in the case of the sexual reproduction of the Annelida, there is, in my opinion, no evidence for an evolutionary significance for the widespread occurrence of asexual reproduction in the lower Oligochaeta and the formation of linear colonies, which are formed not by the segments but by multisegmented individuals. The linear colonies of the Oligochaeta, which, as in the Polychaeta, result from the rate of the continuously occurring divisions lagging behind the growth of the individual in length and the rate of formation of the regeneration zones, are short-lived, with a weakly marked colonial individuality and only comparatively rarely lead to the formation of more complex forms (Beklemishev, 1957). Among both the Polychaeta and the Oligochaeta, together with the complex methods of division (eg., paratomy of the "*Stylaria*" type or "*Nais*" type), there are also found more primitive divisions, resembling autotomy. One must suppose that asexual reproduction arose quite independently within different families of the Oligochaeta and Polychaeta and is a secondary phenomenon, whose evolution proceeded along the pattern: autotomy - architomy - paratomy (Ivanova-Kazas, 1977b).

The problem of the precise determination of the time of origin of the Oligochaeta has not been definitively resolved 1
up to the present day. The dating of the beginnings of the evolution of the Oligochaeta and of its most important stages is based on various assumptions. A more credible hypothesis on this subject, in which in many places can be seen the clear influence of earlier studies by Michaelsen (1922, 1928), Černosvitov (1936) and Omodeo (1963), has been presented by Timm (1980, 1981). Presenting a new proposal for the phylogeny of



Schemat przebiegu ewolucji wodnych *Oligochaeta* w różnych środowiskach (według Timma, 1981, zmienione)

* Przodek ... - Ancestor of ...

** Slodkowodne Polychaeta - Freshwater Polychaeta

Scheme of the course of the evolution of the aquatic Oligochaeta in different environments

(according to Timm, 1981, modified)

the Oligochaeta, he considers that the arrangement of the contemporary families associated with the aquatic environment is mainly a reflection of their evolution. In his opinion the Oligochaeta differentiated from the Polychaeta in the second 15 half of the Paleozoic era, probably in the Carboniferous (280-345 million years ago) in the southern hemisphere, where a large number of bogs, colonized by ancestors of the Oligochaeta, were present under the conditions of a warm and wet subtropical climate. During the Permian and Triassic (190-280 million years ago), when the distribution of the primary Oligochaeta had a cosmopolitan character, a division into two evolutionary lines, freshwater and terrestrial, became evident. At the end of the Triassic and during the Jurassic (135-190 million years ago), according to A. L. Wegener's theory of continental drift, Pangea broke up and the continents commenced drifting, which led to the division of the primitive Oligochaeta into various groups. Their evolution in the direction of the formation of the different families began to proceed on new continents under different climatic conditions. In the Paleozoic era, probably during the Permian (225-280 million years ago), in Pangea the ancestors of the contemporary Tubificida originated in the surface waters; the ancestors of the Lumbricomorpha and the family Haplotaxidae originated in the ground waters, and the ancestors of the contemporary Lumbricina originated in the soil environment. After the breakup of Pangea and the climatic changes on the territory of Gondwana the families Opistocystidae and Phreodrilidae came into being in the surface waters, while the family Moniligastridae arose in the soil environment. The remaining families of the aquatic Oligochaeta came into being in Laurasia, mainly in the surface waters under conditions of a moderate and cool climate (Table). The Aelosomatidae became differentiated independently of the ancestors of the Oligochaeta directly from the Polychaeta during the Devonian (345 - 395 million years ago) or Carboniferous, and their evolution towards the differentiation of the Potamodrilidae in the northern hemisphere proceeded in parallel to the evolutionary lines of the Oligochaeta. In his consideration of the geographical distribution of the Megadrili on different continents Omodeo (1963) also considers that the division into the different families, caused by the continental drift, occurred no later than 100 - 200 million years ago. This is corroborated, inter alia, by studies on fossil soils. The formation of soils with a mull-type humus, which results, inter alia, from the activity of earthworms, is generally dated to about 100 - 110 million years ago (Wilcke, 1955, 1960). On the other hand, Černosvitov (1935) and Sims (1980) date the origin of the soil Oligochaeta to the Paleozoic era. The marked similarity in the distribution of the species and genera of the family Enchytraeidae, occurring between the Palearctic and the eastern regions of the Nearctic, can also be explained by continental drift (Nurminen, 1973).

Among all of the Oligochaeta, in Timm's (1981) opinion, only the Aelosomatidae and Tubificidae are paleolimnetic groups as defined by Martinson (1958a, 1958b, 1967) and Starobogatova (1970), characterized by a very wide geographical distribution and occurring in habitats with large temperature fluctuations and varying oxygen content. In contrast, the families Haplotaxidae, Lumbriculidae, Dorydrilidae and Lycodrilidae, which live in cold and well oxygenated waters, are mesolimnetic (= neolimnetic) groups, which colonized freshwaters at the beginning of the mesozoic era. In addition to the transition from the marine environment to inland waters, which led to a concentration of the reproductive organs in a few segments of the body, the evolution of the Oligochaeta was also greatly influenced by the occurrence of cold climatic periods during the Permian, when the first differentiation of the primitive Oligochaeta into groups occurred, and also during the Pleistocene. These periods led to the formation in the Oligochaeta, inter alia, of specific features associated with the biology of sexual reproduction, which generally occurs in the aquatic Oligochaeta during seasons with low temperatures (Timm, 1972). The oligochaete families which are associated with an aquatic environment presently live predominantly in regions with a cool or temperate climate and not in regions with a tropical climate. According to Timm (1981) such a distribution is the result of the evolution and differentiation of the families in conditions of a cool climate. The high temperature of tropical inland waters, where the only endemic family is the Alluroididae, precludes the propagation of many species of Oligochaeta that reproduce sexually. As compared to many other groups of invertebrates, the species diversity of the fauna of aquatic Oligochaeta is distinctly smaller in the tropics (Timm, 1972). The influence of the Pleistocene climatic changes on the evolution and distribution of the Oligochaeta has become fairly well understood only in the case of the family Lumbriculidae, which, according to Izosimov (1960, 1962), is the most primitive family among all the Oligochaeta. In the Tertiary the Lumbriculidae lived mainly in cold waters in the area from the Alps to Japan. Climatic changes during the Pleistocene led to the disruption of its extensive distribution range and to the formation of three separate centers of its subsequent speciation: the European, Baikal and East-Asiatic (Mazepova, 1975). In the Baikal center, where the processes of speciation occurred especially intensively, about 50% of the entire world fauna of Lumbriculidae is presently found.

In summarizing the above-mentioned comments it may be stated that a considerable divergence of opinion exists on the subject of the origin and evolution of the Oligochaeta. This is in large part due to the small amount of direct evidence and the varying interpretation of the postulated hypotheses. Despite considerable persuasive evidence of significance to determining the origin of the Oligochaeta, this problem has still not been adequately elucidated. This applies particularly to the phylogenetic relationships existing between the Polychaeta and the Oligochaeta and also the Archiannelida, which includes groups of obscure systematic affinity within the Annelida. One of the reasons, in addition to the poor knowledge of many groups of primitive Annelida, is the inadequate knowledge of the structure of many organs of these animals and of their organogenesis. This is especially evident in the case of the organs included in the nervous and 1 reproductive systems of various Annelida, associated with the locomotory and reproductive function of the coelom. In the Annelida, as the first Coelomata, there appeared the first specialized central cerebral ganglia, which resulted from the locomotion of most of these animals with the head section anteriorly. The brain of some Polychaeta attains a high degree of differentiation, resembling the development of the brain of some of the Arthropoda and Mollusca. In the more developmentally advanced Polychaeta one may even differentiate a forebrain, midbrain and hindbrain, although these parts are not unequivocally homologous in representatives of different families (Sembrat, 1981). In general, however, many Polychaeta, Oligochaeta and Hirudinea have very simply structured cerebral ganglia. We have only a very superficial knowledge of the structure of the nervous system in most of the species included in the Archiannelida, which are considered by Hermans (1969) as a distinct order within the Polychaeta. Therefore one cannot seek any homology between organs in the nervous system of these animals and the nervous system of larvae of the Polychaeta, other Polychaeta or Platyhelminthes, which search is decidedly premature (Kotikova, 1973). Indispensable for this purpose are further studies, which might lead to new solutions.

I myself consider that the Oligochaeta should be derived together with the contemporary Polychaeta from common ancestors, whose subsequent evolution proceeded in different directions. These animals were characterized by an undifferentiated coelom, a dispersed formation of the reproductive cells and a development without a larval stage. The contemporary Oligochaeta comprise a whole composed of genetically similar but ecologically different elements, whose history, distribution pathways and intensity of speciation were very different. Of decisive significance in the origin of the Oligochaeta and their progressive evolution was the differentiation of organs, depending on a division of functions and a splitting of the whole into different parts. This was manifested by the appearance of many functional adaptations which arose by way of a reconstruction of the differentiated and normally functioning organs in connection with changes in the activity of the whole organism, which led to the appearance of completely new adaptations (Szmalhauzen, 1975). In the case of the Annelida, and inter alia the Oligochaeta, this concerns mainly the evolution of the coelom, and especially the parts of that organ which took on the reproductive functions. Among the many organs of these animals, the reproductive system in particular displays a very diverse degree of differentiation. In the primitive Annelida, in which isolated gonads are absent, there generally occurs a dispersed formation of reproductive cells, which may be formed over the whole course of the ontogeny or a long period of the latter and which are expelled through a rupture of the body. The progressive evolution of the Oligochaeta in this case consisted of the formation of isolated gonads and gonoducts, which Goodrich (1946) has already identified as coelomoducts, and the development of oligomerization processes, as understood 1 by Dogel (1954), associated with the morphological and physiological concentration of the organs and functions. The embryonic development, which is a modification of the spiral method of division occurring in the Polychaeta, was supplemented by the development of large eggs, abundantly supplied with yolk, or by development within the egg cocoon (Anderson, 1971). The change in the type of development exerted a considerable influence on the processes of organogenesis of the Oligochaeta, especially on the change in the initial stages of development of the cephalic organs, which is expressed by a reduction of the cephalic organs at the end of the body in adult individuals (palps and tentacles, eyes, partial reduction of brain). I consider that many of the similarities occurring between different groups of the Annelida result from the derivation of the classes now living from common ancestors, and also from secondary adaptations. Among the contemporary Annelida this concerns particularly the similarities of many anatomical features of the representatives of the family Questidae to the Oligochaeta (Giere and Riser, 1981), and of the Aelosomatidae to the Polychaeta (Brinkhurst, 1971).

Certain problems concerning the phylogenetic relationships between different groups of the Annelida may also be elucidated by studies of the structure and ultrastructure of reproductive cells on the submicroscopic level. This is indicated, for example, by studies on the male reproductive cells of some of the Annelida. The Oligochaeta and Hirudinea have a basically similar structure of the spermatozoa (Garavaglia et al., 1974), while in the primitive Polychaeta (Archiannelida) are found both comparatively simple (Polygordius Schneider) as well as highly modified types of male reproductive cells (Dinophilus Schmidt) (Franzen, 1956, 1975a, 1975b). According to Franzen (1977) the structure of the male reproductive cells of the Archiannelida indicates that this is a very heterogeneous group with a polyphyletic origin and various evolutionary pathways and directions of specialization of the reproductive cells. This undermines Jägersten's (1947) earlier assertion that the Archiannelida comprise a homogeneous group.

It should also be emphasized that any interpretation of the evolution and origin of the different families or groups of the Oligochaeta that is based on zoogeographical data is rendered quite difficult because of the considerable role played by anthropogenic factors in the distribution of these animals and because of the scanty knowledge of the methods of migration along sea-coasts and river shore-lines. Gates (1966) regarded that considerable parts of the range of the European Lumbricidae in North America were the result of the introduction of these animals, carried out by settlers on many occasions over the last 200 - 250 years, and not of the existence of a transatlantic bridge, as Omodeo (1963) believed. Since it is rather improbable that introduced species of the Lumbricidae would have completely displaced the autochthonous earthworm fauna in so short a time, in the opinion of Omodeo (1963) many of the "European" species of Lumbricidae belong to the old fauna of the North American continent. Some European species, however, were spread by settlers more than 200 years ago in 1 isolated regions in Central and South America (Omodeo, 1963). One cannot exclude the possibility that a large role in the distribution of the Lumbricidae was played by the Tertiary connection of the continents in the location of the present Bering Strait, which is very probable in the case of the family Enchytraeidae (Nurminen, 1973). This question, however, has not yet been adequately elucidated, inter alia because of the scanty knowledge of the Lumbricidae and Enchytraeidae fauna of the northern and north-eastern regions of Siberia and Alaska.

Summary

The author presents the development of conceptions concerning the origins and main directions in evolution of *Oligochaeta*. The stress is laid upon the divergences between various hypotheses particulary significant when phylogenetic relations as between *Polychaeta* and *Oligochaeta* — and *Archiannelida* are concerned. Poor knowledge of many groups of primitive *Annelida* as well as insufficiently known structure of many organs of these animals and their organogenesis are main causes of differences in views of researchers. Nervous and reproductive systems of various *Annelida* are of special interest here as being connected with locomotoric and reproductive functions of posterior body cavity.

According to the author's own opinion *Oligochaeta* are to be derived together with modern *Polychaeta* from common ancestors whose further evolution proceeded differently. Undifferentiated posterior body cavity, interspersed formation of reproductive cells, reproduction without larvas are characteristic features of these animals. Modern *Oligochaeta* from a whole composed of genetically similar and ecologically different elements with diverse history, ways of expansion and intensity of speciation. In *Oligochaeta* the origin and progressive evolution, the differentiation of organs consisting in the division of functions between various bod segments is of particular significance. It is evident in the occurrence of sever functional adaptations appearing in result of reconstruction of differentiated and normally functioning organs in connection with the changes in the whole org activity requiring quite new adaptations. In the case of *Annelida*, including *O* *chaeta*, this concerns primarily the evolution of the posterior body cavity — esp cially those parts of this organ that took over the reproductive functions. Th progressive evolution of the reproductive system in *Oligochaeta* consisted in the formation of isolated gonads and gonoducts, in the development of oligomerization processes connected with morphological and physiological concentration of organs and functions as well as in the completion of embryonal development with the formation of big yolky eggs, the development in egg cocoons coincidenty preserving various types of asexual reproduction. This evolutional trend resulted in the appearance of hermaphroditic amphimictic animals with much diversified patterns of reproduction.

The author is the opinion that a number of similarities in various groups of *Annelida* is an effect of the origin of recent groups from common ancestors and secondary adaptations. It seems also possible to elucidate several phylogenetic problems connected with various groups of *Annelida* by means of studies on structure and ultrastructure of repreductive cells on submicroscopic level. More complicated is, however. an interpretation of the evolution and origin of various *Oligochaeta* groups based on zoogeographical data. It is due to the marked share of anthropogenic factors in the expansion of these animals and poorly known migration patterns.

Literatura

1 **Bather**, F. A., 1920: *Protoscolex latus*, a new "worm" from Lower Ludlow Beds. Ann. Mag. nat. Hist., 9: 124–132.

2 **Beklemiszew**, W. N., 1957: Podstawy anatomii porównawczej. Promorfologia. PWN, Warszawa, 1, 491 pp.

3 **Brinkhurst**, R. O., 1971: Phylogeny and classification. Part 1. W: R. O. Brinkhurst, B. G. M. Jamieson (Eds.), Aquatic *Oligochaeta* of the World. Oliver and Boyd, Edinburgh, pp. 165 - 177.

4 **Bubko**, O. B., 1973: O sistematičeskom položenii *Oweniidae* i *Archiannelida* (*Annelida*). Zool. Ž., 52: 1286 - 1296.

5 **Clark**, R. B., 1964: Dynamics in Metazoan Evolution. The Origin of the Coelom and Segments. Clarendon Press, Oxford, 313 pp.

6 **Čekanovskaja**, O. V., 1962: Vodnye maloščetinkovye červi fauny SSSR. Opred. po faune SSSR, 78. Izdat. Akad. Nauk SSSR, Moskva-Leningrad, 411 pp.

7 **Černosvitov**, L., 1935: Monografie československých deštovek. Arch. přir. výzkum Čech, 19: 1 - 86.

8 **Černosvitov**, L., 1936: Notes sur la distribution mondiale de quelques Oligochètes. Mem. Soc. Zool. Tchechosl. 3: 16 - 19.

9 **Dogel**, V. A., 1954: Oligomerizacija gomologičnych organov kak odin iz glavnych putej evolucii životnych. Izdat. Leningrad. Univ. A. Ždanova, Leningrad, 366 pp.

10 **Eisig**, H., 1887: Die Capitelliden. Fauna und Flora d. Golfes v. Neapel, Berlin, 16, 1, I - XXVIII+616 pp.

11 **Fedotov**, D. M., 1966: Evolucija i filogenija bespozvonočnych životnych. Izdat. „Nauka", Moskva, 404 pp.

12 **Franzen**, A., 1956: On spermiogenesis, morphology of the spermatozoon, and biology of fertilization among invertebrates. Zool. Bidr. Uppsala, 31: 355 - 482.

13 **Franzen**, A., 1975a: Sperm ultrastructure in some *Polychaeta*. W: B. Afzelius (Ed.), The Functional Anatomy of the Spermatozoon. Pergamon Press, Oxford, pp. 267 - 278.

14 **Franzen**, A., 1975b: Fine structure of spermiogenesis in *Fabricia sabella* (Ehrenberg), *Polychaeta*, Family *Sabellidae*. Zoon, 3: 1 - 10.

15 **Franzen**, A., 1977: Ultrastructure of Spermatids and Spermatozoa in *Archiannelida* Zoon, 5: 97 - 105.

16 **Garavaglia** C., **Lora Lamia Donin**, C., **Lanzavecchia**, G., 1974: Ultrastructural morphology of spermatozoa of *Hirudinea*. J. Submicr. Cytol., 16: 229 - 244

17 **Gates**, G. E., 1966: Requiem for megadrile utopias. Proc. Biol. Soc. Wash., 79: 239 - [illegible]

18 **Gates**, G. E., 1972: Burmese Earthworms. An introduction to the systematics and biology of megadrile oligochaetes with special references to Southeast Asia. Trans. Amer. Philos. Soc., 62: 1 - 326.

19 **Gavrilov**, K., 1935: Contribution á l'etude de l'autofécondation chez les Oligochètes Acta Zool. Stockholm, 16: 111 - 115.

20 Gavrilov, K., 1939: Sur la reproduction de *Eiseniella tetraedra* (Sav.) forma typica. Acta Zool. Stockholm, 20: 439 - 464.

21 Gerlach, S. A., 1967: *Annelida*, Ringelwürmer. Die Tierwelt Mitteleuropas, 1, 7a: 1 - 8.

22 Giere, O. W., Riser, N. W., 1981: *Questidae* — polychaetes with Oligochaetoid Morphology and Development. Zool. Scripta, 10: 95 - 103.

23 Giljarov, M. S., 1949a: Rol' počvy v filogeneze nazemnych bespozvonočnych. Usp. sovrem. biol., 27: 325 - 341.

24 Giljarov, M. S., 1949b: Osobennosti počvy kak sredy obitanija i jej značenie v evolucii nasekomych. Izdat. Akad. Nauk SSSR, 280 pp.

25 Goette, A., 1884: Abhandlungen zur Entwickelungsgeschichte der Thiere. Hamburg, 2.

26 Goodrich, E. S., 1946: The study of nephridia and genital duct since 1895. Quart. J. Micr. Sci., 86: 113 - 301.

27 Hadži, J., 1963: The Evolution of the *Metazoa*. International Series of Monographs on Pure and Applied Biology, Division: zoology, vol. 16. Pergamon Press, Oxford-London-New York-Paris, 499 pp.

28 Hatschek, B., 1878: Studie über Entwicklungsgeschichte der Anneliden. Ein Beitrag zur Morphologie der Bilaterien. Arb. zool. Inst. Wien, 1: 277 - 404.

29 Hermans, C. O., 1969: The systematic position of *Archiannelida*. Syst. Zool., 18: 85 - 102.

30 Hertwig, O., Hertwig, R., 1882: Die Coelomtheorie. Versuch einer Erklärung des mittleren Keimblattes. Z. Naturw., 15: 1 - 150.

31 Ivanoff, P., 1928: Die Entwicklung der Larvalsegmenten bei den Anneliden. Zeitschr. Morph. u. Oekol. Tiere, 10: 62 - 161.

32 Ivanov, P. P., 1944: Pervičnaja i vtoričnaja metamerija. Ž. Obšč. Biol., 5: 61 - 95.

33 Ivanova-Kazas, O. M., 1977a: Sravnitelnaja embriologija bespozvonočnych životnych. Trochofornye, ščupalčevye, ščetinkočeljustnye, pogonofory. Izdat. „Nauka", Moskva, 312 pp.

34 Ivanova-Kazas, O. M., 1977b: Bespoloe razmnoženie životnych. Izdat. Leningradskogo Univ., Leningrad, 240 pp.

35 Izosimov, V. V., 1960: O proischoždenii fauny ljumbrikulid Bajkala. Tr. Obšč. estestvoispyt. Kazan. Univ., 120: 96 - 111.

36 Izosimov, V. V., 1962: Maloščetinkovye červi sem. *Lumbriculidae*. Tr. Limnol. Inst., 1 (21): 3 - 126.

37 Jägersten, G., 1947: On the structure of the pharynx of the *Archiannelida* with special reference to there — occurring muscle cells of aberrant type. Zool. Bidr. Uppsala, 25: 551 - 570.

38 Kobayashi, S., 1937: On the breeding habit of the earthworms without male pores. I. Isolating experiments in *Pheretima hilgendorfi* (Michaelsen). Sci. Rep. Tohoku Univ., 4, 11: 473 - 485.

39 Kotikova, E. A., 1973: Novye dannye o nervnoj sisteme *Archiannelida*. Zool. Ž., 52: 1611 - 1615.

40 Kuźnicki, L., Urbanek, A., 1967: Zasady nauki o ewolucji. PWN, Warszawa, 1, 617 pp.

41 Kuźnicki, L., Urbanek, A., 1970: Zasady nauki o ewolucji. PWN, Warszawa, 2, 737 pp.

42 Livanov, N. A., 1955: Puti evoljucii životnogo mira. Analiz organizacii glavnejšich tipov mnogokletočnych životnych. Izdat. „Sov. Nauka", Moskva, 400 pp.

43 Marinov, T., 1977: Mnogoščetinesti červei (*Polychaeta*). Izdat. na B'lgar. Akad. Nauk, Sofija. Fauna Bulgarica, 6, 258 pp.

44 **Martinson**, G. G., 1958a: Proischoždenie fauny Bajkala v svete paleontologičeskich issledovanij Dokl. Akad. Nauk SSSR, 120: 1155 - 1158.
45 **Martinson**, G. G., 1958b: Proischoždenie fauny Bajkala. Kraeved. Sb. Burjatsk. fil. geogr. Obšč. SSSR, 3: 37 - 41.
46 **Martinson**, G. G., 1967: Problema proischoždenija fauny Bajkala, Zool. Ž., 46: 1594 - 1598.
47 **Mazepova**, G. F., 1975: O sovremennom sostojanii izučennosti fauny ozera Bajkal. W: G. I. Galazij (Ed.), Novye o faune Bajkala, Čest' 1. Izdat. „Nauka" Sibirskoe Otdel., Novosibirsk. pp. 4 - 31.
48 **Meyer**, A., 1926: Die Segmentalorgane von *Tomopteris*. Zeitschr. wiss. Zool., 127: 297 - 402.
49 **Meyer**, A., 1929: Zur Segmentierungsanalyse und Stammesgeschichte der Oligochaeten. Zool. Anz., 86: 1 - 16.
50 **Michaelsen**, W., 1919: Uber die Beziehungen der Hirudineen zu den Oligochaeten. Mitt. Naturhist. Mus. Hamburg, 36: 131 - 153.
51 **Michaelsen**, W., 1920: Zur Stammesgeschichte und Systematik der Oligochaeten, insbesondere Lumbriciden. Arch. Naturgesch., 86A: 130 - 141.
52 **Michaelsen**, W., 1922: Die Verbreitung der Oligochaeten im Lichte der Wegener'schen Theorie der Kontinental-Verschiebung. Verh. Naturwiss. Ver. Hamburg, 29: 1 - 37.
53 **Michaelsen**, W., 1928: *Oligochaeta*. W: W. Kückenthal, T. Krumbach (Eds.), Handbuch der Zoologie. De Gruyten, Berlin, 2, 8, pp. 1 - 116.
54 **Michaelsen**, W., 1929: *Oligochaeta* der Kamtschatkaexpedition. 1908 - 1909. Ezeg. Zool. Muz. Akad. Nauk SSSR, 30: 315 - 329.
55 **Muldal**, S., 1952: The chromosomes of the earthworms. I. The evolution of polyploidy. Heredity, 6: 55 - 76.
56 **Nurminen**, M., 1973: Distribution of northern Enchytraeids (*Oligochaeta*). Ann. Zool. Fennici, 10: 483 - 486.
57 **Omodeo**, P., 1963: Distribution of terricolous Oligochaetes on the two shores of the Atlantic. W: A. Löve, D. Löve (Eds.), North Atlantic biota and their history. Pergamon Press, Oxford-London-New York-Paris, pp. 127 - 151.
58 **Perel**, T. S., 1979: Rasprostranienie i zakonomernosti raspredelenija doždevych červej fauny SSSR. Izdat. „Nauka", Moskva, 272 pp.
59 **Reisinger**, E., 1925: Ein landbewohnender *Archiannelide*. Z. Morph. Ökol. Tiere, 3: 197 - 254.
60 **Reynolds**, J. W., 1974: Are Oligochaetes Really Hermaphroditic Amphimictic Organisms. The Biologist, 56: 90 - 99.
61 **Sembrat**, K., 1981: Histologia porównawcza zwierząt. PWN, Warszawa, 2, 690 pp.
62 **Shurova**, N. M., 1980: On the taxonomic status of the family *Enchytraeidae* within the class *Oligochaeta*. V International Colloquium on Earthworms, Moscow 6 - 10 X 1980, abstracts, pp. 30 - 31.
63 **Sims**, R. W., 1980: A classification on the distribution of earthworm, suborder *Lumbricina (Haplotaxida: Oligochaeta)* Bull. Brit. Mus. Nat. Hist. (Zool.), 39: 103 - 124.
64 **Starobogatov**, J. I., 1970: Fauna molljuskov i zoogeografičeskoe rajonirovanie kontinentalnych vodoemov zemnego šara. Izdat. „Nauka", Leningrad, 371 pp.
65 **Stephenson**, J., 1930: The *Oligochaeta*. Clarendon Press, Oxford, 978 pp.
66 **Svešnikov**, V. M., 1966: Evoljucija ličinočnogo razvitija archiannelid i polichet. Zool. Ž., 45: 1369 - 1381.
67 **Szmalhauzen**, I. I., 1975: Czynniki ewolucji. Teoria doboru stabilizującego. PWN, Warszawa, 566 pp.

68 Timm, T. E., 1972: Zavisimost' geografičeskogo rasprostranienija vodnych oligochet ot temperatury. W: B. S. Kuzin, B. A. Vajnštejn, T. L. Poddubnaja (Eds.), Vodnye maloščetnonkovye červi. Materialy Vtorogo Vsesojuznogo Simpozjuma, Borok 27 - 30 ijunja 1972. Izdat. Institut Biologii Vnutriennich Vod Akad. Nauk SSSR, Vsesojuznoe Gidrobiologičeskoe Obščestvo, Jaroslavl', pp. 124 - 129.

69 Timm, T., 1980: Distribution of aquatic Oligochaetes. W: R. O. Brinkhurst, D. G. Cook, Aquatic Oligochaete Biology. Plenum Press, New York-London, pp. 55 - 77.

70 Timm, T., 1981: On the Origin and Evolution of Aquatic *Oligochaeta*. Izv. Akad. Nauk EstSSR, 30: 174 - 181.

71 Wilcke. D. E., 1955: Bemerkungen zum Problem des endzeitlichen Alters der Regenwürmer (*Oligochaeta opisthopora*). Zool. Anz., 154: 149 - 156.

72 Wilcke, D. E., 1960: Fossile Lebensspuren von Regenwürmern. Decheniana, 112: 252 - 269.

73 Zenkevič, L. A., 1944: Očerki po evoljucii dvigatel'nogo apparata životnych. Ž. Obšč. Biol., 5: 129 - 171.

74 Ziegler, H. E., 1898: Ueber den derzeitigen Stand der Cölomfrage. Verh. dtsch. zool. Ges., 8: 14 - 78.

REFERENCES

2. Beklemishev V. N. (Beklemiszew W. N.)*, 1957, Fundamentals of comparative anatomy. Promorphology. State Scientific Publishing House, Warsaw, 1, 491 pp.

4. Bubko O. B., 1973, O sistematicheskom polozhenii Oweniidae i Archiannelida (Annelida)**(The systematic position of the Oweniidae and Archiannelida (Annelida)). Zoologicheskii zhurnal, 52: 1286-1296.

6. Chekanovskaya O. V., 1962, Vodnye maloshchetinkovye chervi fauny SSSR. Opredeliteli po faune SSSR, 78 (Aquatic oligochaetes of the fauna of the USSR. Keys to the fauna of the USSR, 78). Publ. Academy of Sciences of the USSR, Moscow - Leningrad, 411 pp.

7. Černosvitov L., 1935, Monograph on Czechoslovakian earthworms. [Archives] Bohemian Archeological Natural Science Research, 19: 1-86.

9. Dogel' V. A., 1954, Oligomerizatsiya gomologichnykh organov kak odin iz glavnykh putei evolutsii zhivotnykh (Oligomerization of homologous organs as one of the main paths of animal evolution). Publ. A. Ždanov Leningrad University, Leningrad, 366 pp.

10. Eisig, H., 1887, The Capitellidae. Fauna and flora of the Gulf of Naples. Berlin, 16, 1, I - XXVIII + 616 pp.

---

* The Polish transliteration of this Russian name is given in parentheses. This reference is to a Polish translation and edition of Beklemishev's book.

** Here and subsequently the Russian references have been retransliterated according to the British-American Standard system.

11. Fedotov D. M., 1966, Évolyutsiya i filogeniya bespozvonochnykh zhivotnykh (The evolution and phylogeny of invertebrate animals). "Nauka" Publ., Moscow, 404 pp.

21. Gerlach S. A., 1967, Annelida. The fauna of Central Europe, 1, 7a: 1 - 8

23. Gilyarov M. S., 1949a, Rol′ pochvy v filogeneze nazemnykh bespozvonochnykh (The role of the soil in the phylogeny of terrestrial invertebrates). Uspekhi sovremennoi biologii (Advances in contemporary biology), 27: 325 - 341.

24. Gilyarov M. S., 1949b, Osobennosti pochvy kak sredy obitaniya i ee znachenie v évolyutsii nasekomykh (Characteristics of the soil as an environment and its significance in the evolution of insects). Publ. Academy of Sciences of the USSR, 280 pp.

25. Goette A., 1884, Treatises on the developmental history of animals. Hamburg, 2.

28. Hatschek B., 1878, Study on the developmental history of the Annelida. A contribution to the morphology of the Bilateria. Arb. zool. Inst. Wien (Vienna), 1: 277 - 404.

30. Hertwig O. and Hertwig R., 1882, The coelom theory. An attempt to explain the mesoderm. Z. Naturw., 15: 1 - 150.

31. Ivanoff P., 1928, The development of the larval segments in the Annelida. Zeitschrift für Morphologie und Ökologie der Tiere, 10: 62 - 161.

32. Ivanov P. P., 1944, Pervichnaya i vtorichnaya metameriya (Primary and secondary metamerism). Zhurnal obshchei biologii (Journal of General Biology), 5: 61 - 95.

33. Ivanova-Kazas O. M., 1977a, Sravnitel′naya émbriologiya bespozvonochnykh zhivotnykh. Trokhofornye, shchupal′cevye, shchetinkochelyustnye, pogonofory (Comparative embryology of invertebrate animals. Trochophora, Sipunculida, Chaetognatha and Pogonophora). "Nauka" Publ., Moscow, 312 pp.

34. Ivanova-Kazas O. M., 1977b, Bespoloe razmnozhenie zhivotnykh (Asexual reproduction of animals). Publ. Leningrad University, Leningrad, 240 pp.

35. Izosimov V. V., 1960, O proiskhozhdenii fauny lyumbrikulid Baikala (The origin of the lumbriculid fauna of the Baikal). Trudy obshchestva estestvoispytatelei pri Kazanskom universitete (Transactions of the Society of Naturalists of Kazan University), 120: 96 - 111.

36. Izosimov V. V., 1962, Maloshchetinkovye chervi sem. Lumbriculidae (Oligochaetes of the family Lumbriculidae). Trudy Limnologicheskogo Instituta (Transactions of the Limnological Institute), 1 (21): 3 - 126.

39. Kotikova E. A., 1973, Novye dannye o nervnoi sisteme Archiannelida (New data on the nervous system of the Archiannelida). Zoologicheskii zhurnal (Zoological Journal), 52: 1611 - 1615.

40. Kuźnicki L. and Urbanek A., 1967, Fundamentals of evolutionary science. State Scientific Publishing House, Warsaw, 1, 617 pp.

41. Kuźnicki L. and Urbanek A., 1970, Fundamentals of evolutionary science. State Scientific Publ., Warsaw, 2, 737 pp.

42. Livanov N. A., 1955, Puti évolyutsii zhivotnogo mira. Analiz organizatsii glavneishykh tipov mnogokletochnykh zhivotnykh (Evolutionary pathways of the animal world. An analysis of the organization of the major types of multicellular animals). "Soviet Science" Publ., Moscow, 400 pp.

43. Marinov T., 1977, Mnogoshchetinesti chervei (Polychaeta. (Polychaete worms (Polychaeta)). Publ. by Bulgarian Academy of Sciences, Sofia. Fauna Bulgarica (The fauna of Bulgaria), 6, 258 pp.

44. Martinson G. G., 1958a, Proiskhozhdenie fauny Baikala v svete paleontologicheskikh issledovanii (The origin of the Baikal fauna in the light of paleontological investigations). Doklady Akademii Nauk SSSR (Reports of the Academy of Sciences of the USSR), 120: 1155 - 1158.

45. Martinson G. G., 1958b, Proiskhozhdenie fauny Baikala. Kraevedcheskii Sbornik Buriatskogo filiala Geograficheskogo Obshchestva SSSR (Origin of the Baikal fauna. Regional studies magazine of the Buryat Branch of the Geographical Society of the USSR), 3: 37 - 41.

46. Martinson G. G., 1967, Problema proiskhozhdeniya fauny Baikala (The problem of the origin of the Baikal fauna). Zoologicheskii zhurnal (Zoological Journal), 46: 1594 - 1598.

47. Mazepova G. F., 1975, O sovremennom sostoyanii izuchennosti fauny ozera Baikal. V: G. I. Galazii (Red.), Novoe o faune Baikala, Chast′ 1. (The contemporary state of knowledge of the fauna of Lake Baikal. In: New information on the fauna of Baikal, Part I. Edited by G. I. Galazii). "Nauka" Publ., Siberian Branch, Novosibirsk, pp 4 - 31.

48. Meyer A., 1926, The segmental organs of Tomopteris. Zeitschrift für wissenschaftliche Zoologie, 127: 297 - 402.

49. Meyer A., 1929, The segmental analysis and phylogeny of the Oligochaeta. Zoologischer Anzeiger, 86: 1 - 16.

50. Michaelsen W., 1919, The relationship between the Hirudinea and the Oligochaeta. Mitteilungen Naturhist. Mus. Hamburg, 36: 131 - 153.

51. Michaelsen W., 1920, The phylogeny and systematics of the Oligochaeta, especially of the Lumbricidae. Archives Naturgesch., 86A: 130 - 141.

52. Michaelsen W., 1922, The distribution of the Oligochaeta in the light of Wegener's theory of continental drift. Verh. Naturwiss. Ver. Hamburg, 29: 1 - 37.

53. Michaelsen W., 1928, Oligochaeta. In: Handbook of Zoology, edited by W. Kückenthal and T. Krumbach. De Gruyten, Berlin, 2, 8, pp. 1 - 116.

54. Michaelsen W., 1929, Oligochaeta of the Kamchatka expedition. 1908 - 1909. Ezhegodnik Zoologicheskogo Muzeya Akademii Nauk SSSR (Annals of the Zoological Museum of the Academy of Sciences of the USSR), 30: 315 - 329.

58. Perel T. S., 1979, Rasprostranenie i zakonomernosti raspredeleniya dozhdevykh chervei fauny SSSR (The spread and patterns of distribution of earthworms of the fauna of the USSR). "Nauka" Publ., Moscow, 272 pp.

59. Reisinger E., 1925, A terrestrial archiannelid. Zeitschrift für Morphologie und Økologie der Tiere, 3: 197 - 254.

61. Sembrat K., 1981, Comparative histology of animals. State Scientific Publishing House, Warsaw, 2, 690 pp.

64. Starobogatov I. I., 1970, Fauna mollyuskov i zoogeograficheskoe raionirovanie kontinentalnykh vodoemov zemnogo shara (The molluscan fauna and zoogeographical regionalization of continental bodies of water in the world). "Nauka" Publ., Leningrad, 371 pp.

66. Sveshnikov V. M., 1966, Évolyutsiya lichinochnogo razvitiya arkhiannelid i polikhet (Evolution of the larval development of the Archiannelida and Polychaeta). Zoologicheskii zhurnal (Zoological Journal), 45: 1369 - 1381.

67. Szmalhauzen I. I., 1975, Factors in evolution. A theory of stabilizing selection. State Scientific Publishing House, Warsaw, 566 pp.

68. Timm T. E., 1972, Zavisimost′ geograficheskogo rasprostraneniya vodnykh oligokhet ot temperatury (The dependence of the geographical distribution of aquatic oligochaetes on the temperature). In: Vodnye maloshchetnokovye chervi. Materialy Vtorogo Vsesoyuznogo Simpozyuma, Borok 27 - 30 iyunya 1972 (Aquatic Oligochaeta. Proceedings of the Second All-Union Symposium, Borok, 27-30 June 1972). Edited by B. S. Kuzin, B. A. Vainshtein and T. L. Poddubnaya. Izdat. Institut Biologii Vnutrennikh Vod Akademii Nauk SSSR, Vsesoyuznoe Gidrobiologicheskoe Obshchestvo, Yaroslavl′ (Publ. Institute of the Biology of Inland Waters of the Academy of Sciences of the USSR, All-Union Hydrobiological Society, Yaroslavl), pp. 124-129.

71. Wilcke D. E., 1955, Comments on the problem of the ......* age of earthworms (Oligochaeta opisthopora). Zoologischer Anzeiger, 154: 149 - 156.

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* The German word here is "endzeitlich", which translates only as "eschatological" and does not seem to have any other meaning. Possible misspelled here? (Tr.).

72. Wilcke D. E., 1960. Fossil traces of earthworms. Decheniana, 112: 252 - 269.

73. Zenkevich L. A., 1944. Ocherki po évolyutsii dvigatel′nogo apparata zhivotnykh (Essays on the evolution of the locomotory apparatus of animals). Zhurnal obshchei biologii (Journal of General Biology), 5: 129 - 171.

74. Ziegler H. E., 1898. The present status of the coelom problem. Verh. dtsch. zool. Ges., 8: 14 - 78.