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From morphology to phylogeny (on the example of study of the fish leeches of Palearctic)

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The article considers the methodology of cognition of the fauna of the fish leeches (Hirudinea, Piscicolidae) of Palearctic – from description of their appearance to description of the structure of the major organs systems, and more – to construction of a classification of the family at the levels of subfamilies and tribes, to understanding their zoogeography and to working out phylogenetic hypotheses.

Key words: *methodology, fish leeches, reproductive system, classification, phylogeny.*

От морфологии к филогении (на примере изучения рыбьих пиявок Палеарктики)

В.М.Эпштейн

В статье рассматривается методология познания фауны рыбьих пиявок (Hirudinea, Piscicolidae) Палеарктики – от описания их внешнего облика к описанию строения основных систем органов, и далее – к построению классификации семейства на уровнях подсемейств и триб, уяснению их зоогеографии и разработке филогенетических гипотез.

Ключевые слова: *методология, рыбьи пиявки, половая система, классификация, филогения.*

Від морфології до філогенії (на прикладі вивчення риб'ячих п'явок Палеарктики)

В.М.Епштейн

У статті розглядається методологія пізнання фауни риб'ячих п'явок (Hirudinea, Piscicolidae) Палеарктики – від опису їхнього зовнішнього вигляду до опису будови основних систем органів і далі – до побудови класифікації родини на рівнях підродин і триб, з'ясування їх зоогеографії та розробки філогенетичних гіпотез.

Ключові слова: *методологія, риб'ячі п'явки, статева система, класифікація, філогенія.*

History of research

Morphology of leeches of the family Piscicolidae. The modern stage in the study of the fish leeches family began from publication of the article of Swedish zoologist L.Johansson (Johansson, 1896) about necessity of studying the anatomy of the fish leeches to construct their classification. Then Johansson (1898) published the descriptions of many marine fish leeches species of Sweden that included a brief description of the structure of their internal organs, especially lacunar system. Soon the French zoologist E.Brumpt (1900) identified the main types of the structure of reproductive system of the fish leeches. Fundamental monograph of Russian zoologist V.D.Zelensky "Investigations on the morphology and systematics of the Hirudinea. 1. Organization of Ichthyobdellidae" was published in 1915, in which the major organs systems – nervous, lacunar, digestive, excretory and reproductive – were subjected to a detailed analysis on the examples of many freshwater and marine species.

The first characteristic of the fish leeches of Palearctic was presented in the key to leeches by L.Johansson with additions of E.A.Vasilyev (1935). This work gives a brief appearance characteristics of the 5 species of fish leeches: *Piscicola geometra* (Linnaeus, 1761), *Piscicola fasciata* Kollar, 1842, *Piscicola respirans* Troschel, 1850, *Cystobranchus mammillatus* (Malm, 1863), *Limnotrachellobdella turkestanica* Stschegolev, 1912 (here and below modern genera of Piscicolidae are indicated). The first review of the fish leeches of Palearctic was presented in "Key to parasites of freshwater fishes" (Epshtein, 1962). This review has been compiled only by external characteristics of species, since the internal structure of most species at that time was unstudied. Anatomical information about the most important organs systems was given in the

descriptions of only 3 species – *P. respirans*, *Limnotrachelobdella sinensis*, Blanchard, 1896, *L. turkestanica*. Information about the anatomy of other species lacked (*Piscicola fasciata* Kollar, 1842; *Baicalobdella torquata*, 1871; *Baicalobdella cottidarum* Dogiel, 1957; *Codonobdella truncata* Grube, 1873; *Acipenserobdella volgensis* (Zykoff, 1903), or the information was fragmented (*Caspiobdella caspica* Selensky, 1915). Later, the author described 4 new species (*Limnotrachelobdella taimeni* Epstein, 1957; *Caspiobdella fadejewi* Epstein, 1961; *Taimenobdella amurensis* Epstein, 1964; *Caspiobdella tuberculata* Epstein, 1966). These species were established on the basis of anatomic researches. During the research, the standard of species description, which included 50 systematic features, was developed. Accordingly to this standard, species descriptions (text and iconography) of the fish leeches of Palearctic were published (Epshtein, 1987). Later, on the basis of this standard dissertations of A.Yu.Utevsky (1994) and S.Yu.Utevsky (1996) and a monograph on the fish leeches of Poland by A.Bielecky (Bielecky, 1997) were made.

Classification of the leeches of the family Piscicolidae. New addressing problems of classification of the family of the fish leeches began in the second half of the last century, when the Hungarian zoologist A.Soos (Soos, 1965) expounded the system of the class of leeches as a whole. In it all genera of the family of the fish leeches were arranged in the alphabetical order. During these years, we did a series of works devoted to ***audit of genera on the anatomical grounds.*** As a result, new diagnoses of all genera of the fish leeches of Palearctic were formulated. New genera *Caspiobdella* Epstein, 1966 and *Limnotrachelobdella* Epstein, 1968 were defined, genus *Baicalobdella* Dogiel, 1957 was substantiated, the genera *Piscicola* and *Cystobranchus* were separated.

The results of investigations were presented in the PhD dissertation of the author titled "Fish leeches (Hirudinea, Piscicolidae) of fresh waters and seas of the USSR" and the series of publications, which are represented in the work of bibliographers of Kharkov State University M.G.Shvalb and S.V.Glibitskaya "Bibliography of scientific papers of V.M.Epshtein" (1999) and in the third volume of the monograph by T.R.Sawyer (Sawyer, 1986) on the class of leeches. The latter contains a list of 30 publications of the author on the taxonomy of the fish leeches with reports of the translation the most important ones into English in various institutions of the USA and Canada.

Revision of the family at the genera level led to its division into ***subfamilies*** (Epshtein, 1970b; Epshtein, et al., 1994). Classification at the subfamilies level was based on complexes of morphological features, of which the weightiest were structure types of lacunar system established by L.Johansson and V.D.Zelensky. The classification became generally accepted. It is commonly referred to as "traditional", without mentioning the author or with references to other authors who used it. Attempts of some experts to reduce it to the structure types of lacunar system, allocated by V.D.Zelensky, lacks sufficient grounds. Classification of structure types of lacunar system is the basis for the species classification, but no more. Thus, in the subfamilies Piscicolinae Johnston, 1865 and Pontobdellinae Llewellyn, 1966 lacunar system consists of 4 lacunar channels (ventral, dorsal and lateral lacunae) and transverse communications, which are associated with lateral bladders. Species of the first subfamily have one pair of outer bladders in somites of midbody, species of the second subfamily – two pairs of small hypodermic bladders. However, the third subfamily – Platybdellinae Epstein, 1970, unites the various structure types of this system. Some species have only single lacuna (abdominal), while others have all four lacunar channels (ventral, dorsal and lateral) without lateral bladders; third species also have four lacunae, but they show a tendency to form primitive lateral bladders, one pair for somite. *Structure of lacunar system as a taxonomic trait that has the most significance at two subfamilies level is elected, because this trait most correlates with the rest complex of the traits. In the third subfamily the most important is the general similarity of traits.*

For 15 years passed from the publication of Soos to constructing author`s classification, other attempts to construct family classification were absent. Subfamilies characteristics and features of their geographical distribution were first introduced in the author's papers (Epshtein, 1970a), then in his doctoral dissertation (Epshtein, 1989) and, finally, in the collective work (Epshtein et al., 1994).

The similar situation arose in the division of subfamilies into the **tribes**. Types of reproductive system structure, allocated by E.Brumpt (1900), served as its basis. This fundamental work as well as the monograph of V.D. Zelensky, was in the field of evolutionary morphology, although Brumpt suggested that the types of reproductive system structure of the fish leeches can be used in order to classify them. Ideas of Brumpt partially were used in the works of many researchers, but only were realized in the form of classification of the fish leeches family at the tribes level in the above mentioned papers.

The fundamental difference between the researches in evolutionary morphology and taxonomy was first discovered by S.V.Meighen and Y.A.Schrader (1976). They separated the area of system descriptions (=

meronomy) from the area of classifications (= taxonomy). Meronomy corresponds to the first two sublevels of empirical scientific knowledge (Stepin, 1992). It includes recognition of species – the first level of empirical scientific knowledge and their holistic description – the second sublevel. Taxonomy and its interpretation in time – reconstruction of phylogeny (= filonomy) – correspond to the third, the highest level of empirical scientific knowledge. The last review of fish leeches of Palearctic is represented in "Atlas. Part One" (Epshtein, 2013).

Revision of the fish leeches of Palearctic, their geographical distribution and phylogeny

Relation between classification and zoogeography of the fish leeches at subfamilies level. Let's turn to the value of separation of the fish leeches family into subfamilies to analyze their geographical distribution. We try to consider some of the events of its phylogeny with the reference to the geological time scale (under appropriate reservations: lack of paleontological data, preliminary character of generalizations, rejection of classification by molecular taxonomists etc.).

Subfamily Piscicolinae (perfect lacunar system, one pair of lateral bladders in full somites, lateral bladders mostly bicameral). The species of this subfamily, having the most perfect lacunar system, assimilated the continental water bodies of the northern continents that were part of the supercontinent Laurasia. In the Palearctic this subfamily includes the most of species.

Subfamily Pontobdellinae is represented by only marine species. Continental water bodies lack any species. The most of the species live in tropical areas of the littoral zone, many species – in the Antarctic region. Two species inhabit the North Atlantic. In the North Pacific they are not found.

Subfamily Platybdellinae in the littoral ocean zone is distributed bipolarly. Some species are invasive in continental water bodies. The continents that used to be parts of the supercontinent Gondwana lack the fish leeches, except for one species – *Phyllobdella maculata* Moore (Platybdellinae) from the Tanganyika lake. Thus, each subfamily, allocated on the basis of the structure of the lacunar system possesses its zoogeographical aspect.

Types of reproductive system structure and areas of tribes, genera and species. At the taxonomic levels lower than subfamily (tribes and genera) special taxonomic significance belongs to the structure of the reproductive system. Let's consider the relationship between the structure of the reproductive system of the fish leeches, their combination into genera and tribes and geographical distribution. To designate the types of reproductive system structure we use the name of typical genera.

1) "***Type Piscicola***" **(Fig. 1).** This type of reproductive organs was allocated by E.Brumpt. Type is characterized by the following traits: the presence of the accessory glands on the atrium, long copulatory pouch; the presence of array and bundles of conducting tissue; ovisacs round the conducting tissue array on the sides and combined into the vagina in front of it. On the ventral side of the fascia copulatory area situated, which consistently has 3 holes: male gonopore, female gonopore and spermatheca.

Prior to our audit two of three Palearctic species of the genus in our interpretation – *P. fasciata* and *P. respirans* belonged to the genus *Cystobranchus*. At this species distribution, the genus *Cystobranchus*, from the standpoint of zoogeographer, is characterized by an eclectic mix of different areas. Zoogeography of the genus in the proposed interpretation is: genus *Piscicola* – holarctic genus, *P. geometra* – holarctic species, *P. fasciata* – species, representing the Caspian type fauna, *P. respirans* – species, widespread to the west from the former USSR in Eastern and Western Europe (about genus *Cystobranchus* see below). Fauna of Piscicolinae of North America is much poorer than fauna of Eurasia and from many paleolimnic species includes only three species of the genus *Piscicola*: *P. geometra*, *Piscicola milneri* Verril (Verril, 1871) and unstudied anatomically species *Piscicola punctata* (Verril, 1871). *P. milneri* (unpublished data) by the structure of the reproductive system is almost identical to *P. geometra*. Information about the distribution of *P. geometra* and *Acanthobdella peledina* in the northern regions of Eurasia and North America corresponds to the ideas about the exchange of faunas of the northern parts of continents through the "bridges" that repeatedly emerged between them in Antropogene (3.5 million years ago – present time).

2) "***Type Caspiobdella***". This type of reproductive system structure is allocated by the author (Epshtein, 1961b). It is typical for the genera *Caspiobdella*, *Acipenserobdella*, *Italobdella* and *Pawlowskiella* (subtribe Caspiobdellina). It is similar to the previous one, but oviducts enter into the middle or back part of conducting tissue array or go around behind it. Depending on this fact, in the copulatory zone on the ventral side of the fascia there are 2 holes – male gonopore and hole of spermatheca, in which the vagina is opened, or 3 holes – male gonopore, spermatheca and female gonopore behind the hole of spermatheca.

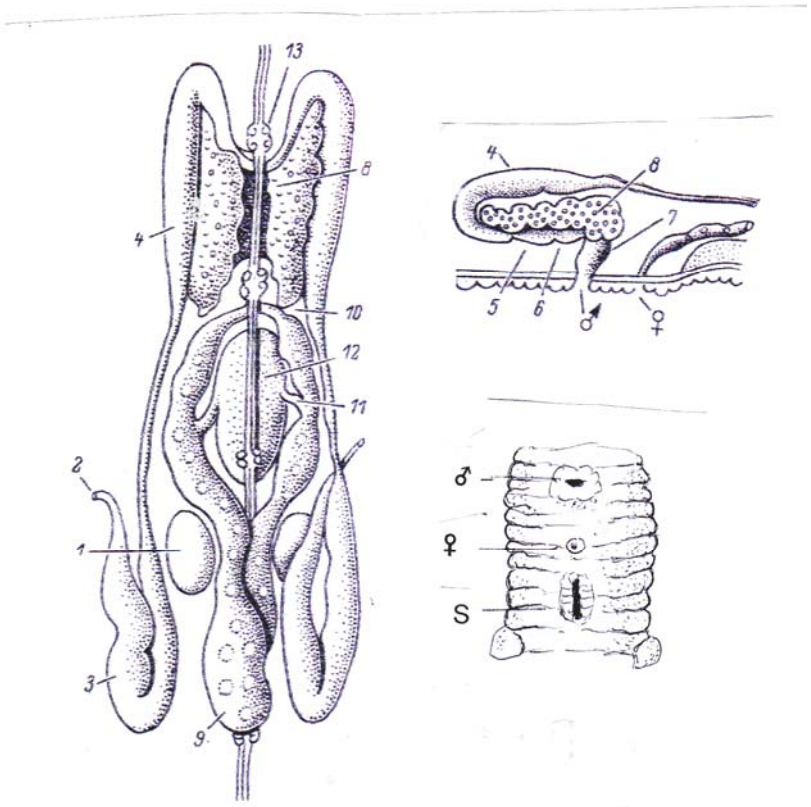

Fig. 1. Reproductive system of *Piscicola geometra*

Notes: 1 – spermatic pouch first pair; 2 – spermaduct; 3 – spermatic reservoir; 4 – ejaculatory duct; 5 – end section of the atrium; 6 – general department of the atrium; 7 – copulatory pouch; 8 – accessory glands; 9 – ovisacs; 10 – oviducts; 11 – bundles of conducting tissue; 12 – conducting tissue array; S – spermatheca.

The first version is typical for two genera – *Caspiobdella* Epstein, 1966 and *Acipenserobdella* Epstein, 1969. Their differences from the genus *Piscicola* on these grounds allowed the author to define the mentioned genera and to transfer 2 species from the genus *Piscicola* to the genus *Caspiobdella* – *P. caspica* Selensky, 1915 and *P. fadejewi* Epstein, 1961. Species of this genus – *C. caspica* and *C. tuberculata* are distributed in the Caspian Sea, while *C. fadejewi* – in the basins of the rivers falling into the Black and Azov seas, as well as in the Volga basin, where this species penetrated after the construction of the Volga-Don Canal. In addition, it continues its expansion in Eastern Europe. *A. volgensis* is distributed from the Baikal region at the middle latitudes to Eastern Europe inclusive. The similarity of this species to studied in detail *Caspiobdella fadejewi* (Epshtein, 1961b, 1987; Bielecky, 1997) indicates the origin of the fauna of the Caspian type of leeches in continental water bodies of Eurasia. Findings of species of the pharyngeal leeches of genus *Dina* (Arhynchobdellea, Erpobdellidae) in the lake Baikal, similar to other species of this genus, inhabiting the southern part of the European continent, and *Archaeobella esmonti* Grimm 1876, widespread in the Caspian Sea, confirm these assumptions.

Location of oviducts and vagina behind the conducting tissue array is typical for species of the two genera – *Italobdella* – *I. ciosi*, *I. epshteini*, – and *Pawlowskiella* – *P. stenosa* Bielecky, 1997. The first species is found in Italy, the second and the third – in water bodies in Eastern Europe. Species of the genera *Caspiobdella*, *Acipenserobdella*, and *Italobdella* form a complex of Eurasian species having no analogue in Neoarctic area. The area of this group of Palearctic genera indicates that the archetypes of the Caspian type fauna formed later than archetypes of genus *Piscicola*, in Eurasia. We can assume the evolution of this group of genera took place in the later derivatives of Tethys. Species of the genus *Piscicola* and species of the Caspian type genera, which never had connection with the sea, after G.G.Martinson (1958), we name paleolimnic.

Since N.A.Livanov (1955) and many other researchers believe that the leeches were formed as ectoparasites of fishes, one should compare their appearance with the information about the evolution of fish. Cartilaginous fishes appeared on the border of Silurian and Devonian (about 420 million years ago) and flourished in the Carboniferous. Bony fishes appeared in the Devonian. It can be assumed that the appearance of leeches relates with Devonian. In this case, also it is possible to assume that in the Devonian period there was a transition of part of species of the fish leeches with their hosts from freshwaters to the sea. Orders and families of the class Leeches except the setigerous and the fish leeches are spread on all continents except Antarctica. It can be argued that their ancestors spread across Pangaea during its existence (Permian – end of Triassic). About the time of origin of the fish leeches it is currently impossible to say anything definite. Either they were formed in the Devonian, but in Permian were able to overcome obstacles, that prevented their penetration into the southern part of Pangaea, or have occurred after its collapse (200–210 million years ago) in the territory of Laurasia. Anyway, freshwater and marine fish leeches evolved independently and convergently.

3) "***Type Limnotrachelobdella***". This type of reproductive system structure was allocated by the author (Epshtein, 1987). It is typical for the genus *Limnotrachelobdella* (tribe Limnotrachelobdellini) and characterized by the following traits: absence of accessory glands on the atrium, long copulatory pouch, lack conducting tissue. In copulatory zone consistently there are arranged 2 holes – male and female gonopores. Spermatheca is absent. We separate the genus *Limnotrachelobdella* Epstein, 1968 from the genus *Trachelobdella* Diesing, 1850 on the basis of differences in the structure of the reproductive system. The anatomy of four species was studied. Species of these genera present a chain of areas, which begins at the Pacific coast (west coast of Japan, Peter the Great Bay, the Amur Bay) and ends at the south-eastern Transcaucasia. The first link in this chain is *Limnotrachelobdella okae* – the species found in the fresh waters of Japan and Tokyo Bay. We found this species (Epshtein, 1964) in the Amur basin and the Gulf of Peter the Great. The area of *L. okae* extends all the way to the Amur sources. Areas of the other species: *L. taimeni* – Amur basin; *L. sinensis* – Amur basin, lake Hanka, lake Hovsgol (Mongolia); *L. turkestanica*: Chu and Ili rivers, lake Balhash, the Syr Darya and Amu Darya rivers, the Aral Sea, water bodies of Lankaran. According to the structure of the reproductive system the genus is the closest to the genus *Branchellion*, widespread in tropical and temperate regions of the World Ocean. Thus *Limnotrachelobdella* species are among the neolimnic species.

4) "***Type Cystobranchus*" *(Cystobranchini tribe).*** This type of reproductive system structure was allocated by E.Brumpt. It is typical for species *Cystobranchus mammillatus* (Malm, 1863) ***(tribe Cystobranchini)*** and characterized by the following traits: lack of accessory glands on the atrium, long copulatory pouch, absence of conducting tissue array. Bundles of conducting tissue connect ovisacs with copulatory pouch. Copulatory zone on the fascia is absent. Two holes are on the ventral side of the fascia – male gonopore, also performing the function of spermatheca, and female gonopore. The ventral side of fascia has 2 holes – male and female gonopores. *C. mammillatus* is distributed in the northern regions of Eurasia and North America. This species is similar to the species of the marine genus *Calliobdella* van Beneden et Hesse, 1863. It is the neolimnic species which settled the continental water bodies of both continents during the quaternary transgression of the Arctic Ocean.

5) "***Type Dagarabdella*" *(Mysidobdellini tribe).*** This type of structure is typical for the Baikal species *Dagarabdella selenskii* Finogenova et Snimschikova, 1991. This species was originally in detail described by the authors (Finogenova, Snimschikova, 1991), and quite rightly attributed to a new genus *Dagarabdella*. However, the next year N.P.Finogenova (Finogenova, 1992) published a new article in which she transferred this species to the genus *Codonobdella*. Traits of the structure of the reproductive system of *D. selenskii* are: lack of accessory glands on the atrium, long copulatory pouch. Bundles of conducting tissue connect ovisacs with conducting tissue array. Oviducts are combined into a long vagina, which is opened by female gonopore in front of conducting tissue array. Reproductive system of *D. selenskii* differs from the "Type Piscicola" important taxonomic trait – lack of accessory glands on the atrium. Therefore, for the transfer of this species into the genus *Codonobdella* there is no reason. The origin of this species discussed below.

3. About the origin of the fauna of leeches of Lake Baikal

The origin of Palearctic fauna is inextricably linked with the problem of the origin and formation of the Baikal fauna. First of all, it should be noted that in fauna of open Baikal there are no higher leeches. In Lake Baikal leeches are presented only by the families of Proboscidian leeches (Rhynchobdellidae) – Glossiphonidae and Piscicolidae.

Baikal glossifonids were studied by A.E.Grube (Grube, 1871,1873), R.Blanshard (Blanchard, 1893, 1894), G.G.Schegolev (1922), E.I.Lukin and the author of this article (Lukin, Epshtein, 1960a, b). We published the results of the audit of Baikal glossifonids, based on the study of new extensive collections. In two reports about Baikal Glossiphonidae previously known species were redescribed – *Clepsine echinulata* Grube, 1871 and *Torix baicalensis* Stschegolev, 1922; new species of glossifonids were described and 2 new genera were defined - *Baicaloclepsis* (Lukin, Epshtein, 1960a) and *Paratorix* (Lukin, Epshtein, 1960b). The first genus includes *C. echinulata* and the new species – *Baicaloclepsis grubei* Lukin et Epstein, 1960, the second genus – *T. baicalensis*. Thus the modern names of these three species are *Baicaloclepsis echinulata*, *Baicaloclepsis grubei*, *Paratorix baicalensis*. These two genera along with some other genera, species of which are distributed in the lake Hanka, water bodies of Ussuri region, Shikotan island, Japan, Korea, Canada, were allocated in a new subfamily Toricinae Lukin et Epstein, 1960. It is suggested that this faunistic group was formed in warm climates of the Miocene (25–5 million years ago). At this time, the "bridges" repeatedly were formed between North America and Eurasia. In the late Miocene, the exchange of their faunas occurred that is likely to explain the wide distribution of Toricinae nowadays.

Researches of the fish leeches (Epshtein, 1959, 1961a) led to a different result. Reproductive system of Baikal fish leeches – *Baicalobdella torquata* Grube, 1871, *B. cottidarum* Dogiel, 1957, *Codonobdella truncata* Grube, 1873 corresponds to the "Type Piscicola". However, the species *Baicalobdella* have distinct primitive three annulated somites that distinguishes them from the species of the genus *Piscicola*. Annulation of *Codonobdella truncata* varies from 3 to 14 rings (like *P. respirans*). However, this leech is very different from the species *Piscicola* by coloring, numerous papillae on the body surface and the absence of the esophagus diverticula – important systematic trait. Therefore, the view that the similarity in the structure of the reproductive system of *Piscicola* species on the one hand, and *Baicalobdella* and *Codonobdella* – on the other hand, is explained by convergence, is preferably. The hypothesis remains valid about their marine origin. *D. selenskii* lacks an outer side bladder – the feature of the subfamily Platybdellinae. By the structure of the reproductive system this species belongs to the tribe Mysidobdellini. This fact suggests that the fauna leeches of Lake Baikal originated from different sources – older – Cretaceous relicts associated with fauna of Tethys derivatives (the fish leeches), and later – relicts of the Neogene (the glossifonids).

So, the neolimnic elements of Palearctic fauna include 9 species of 5 genera: 4 species of *Limnotrachelobdella*, 1 species of *Taimenobdella*, 2 species of *Baicalobdella*, 1 species of *Codonobdella*, 1 species of *Dagarabdella*. Thus, Palearctic leeches fauna includes paleolimnic species whose ancestors probably inhabited the territory of Pangaea (Permian – Triassic); neolimnic species of Pacific origin (Cretaceous), paleolimnic warm-water species (Neogene); neolimnic species of Arctic marine origin (anthropogenic).

The proposed article captures attention to the traditional methodology of research in evolutionary systematics. The path to cognition of Palearctic fauna begins with the separation of morphological criteria of similarity and difference of species; passes through the construction of classification and determination of zoogeographical status of allocated taxa and ends by the reconstruction of phylogeny. Perhaps it is a fragment of ordinary intuitively perceived path that cyclically repeats at each new stage of scientific development, improving our scientific knowledge.

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