Lauterbornia 52: 181-193, D-86424 Dinkelscherben, 2004-12-30

On the origin of the Hirudinea fauna, especially Piscicolidae, in ancient lakes

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With 6 figures

Keywords: Piscicolidae, Hirudinea, world, ancient lakes, taxonomy, systematics, morphology, anatomy, distribution, phylogenetics
Schlagwörter: Piscicolidae, Hirudinea, Welt, alte Seen, Taxonomie, Systematik, Morphologie, Anatomie, Verbreitung, Phylogenese

In this contribution the leech fauna of ancient lakes in Asia, Europe, and Africa is described with special reference to members of the family Piscicolidae. Based on the analysis of the distribution of leeches in ancient lakes, a hypothesis is expressed about rise and forming of two types of Palearctic leech fauna from their marine roots: the eastern type, comprising Far East, Baikal, Middle Asia, Eastern Trans-Caucasia, and the western (Caspian) type, reaching from the Caspian Sea to the Appenines peninsula.

1 Introduction

"Ancient lakes"as Lake Baikal and some others arised in Tertiary or earlier. They harbour an unique fauna of endemic species (up to 80 %), closely allied to ancestors extinct elsewhere in the world. The leech fauna of ancient lakes comprises species of interest for understanding origin and evolution of the families they belong to. This contribution focuses on the family Piscicolidae against the background of the whole leech fauna in Lake Baikal, Lake Khubsugul, Aral Sea, Caspian Sea and the lakes Tanganyika, Chilka and Biwa.

2 Taxonomic problems of the family Piscicolidae

This family was divided by the author into three subfamilies: Platybdellinae Epstein, 1970, Pontobdellinae Llewellyn, 1966 and Piscicolinae Johnston, 1865. This was mainly based on the character of their coelomic system, agreed by other taxonomists. In 1983 the author divided the subfamilies into tribes using mainly basic variants of the reproductive system. The new more refined and supplemented version of the classification of the family consists of 3 subfamilies, 18 tribes, 52 genera, 122 species (Epshtein et al. 1994). A probablistic system of the family (Fig.1) was elaborated and some of prognosticated tribes were discovered later (Epshtein 2002).

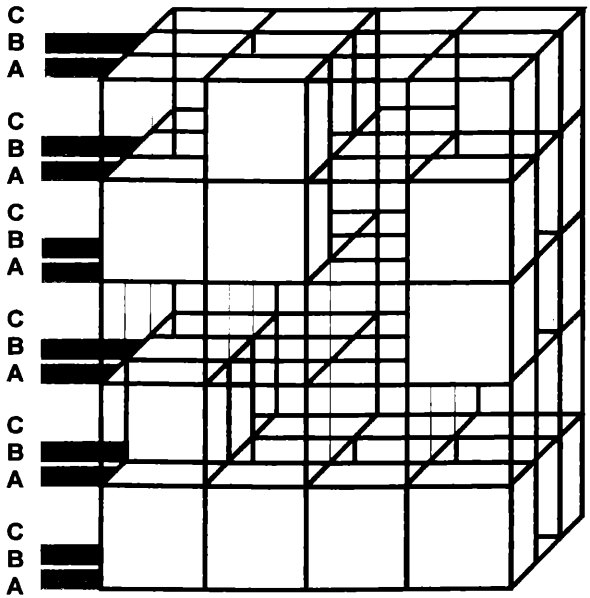

Fig. 1: Probabilistic classification of leeches of the family Piscicolidae. Level of the subfamilies and tribes: A = Platybdellinae, B = Pontobdellinae, C = Piscicolinae. The covered cells of the matrix correspond with existing tribes, the empty cells with hypothetical tribes (from Epshtein 2002)

Platybdellinae are the most primitive and variable subfamily, characterizised by absence of external pulsatile vesicles. Platybdellinae are parasiting mostly on Osteichthyes and are distributed bipolar in coastal waters in the World Ocean. Some of the species penetrated into freshwater (Harding & Moore 1927, Sawyer et al. 1975).

The Subfamily Pontobdellinae is more complicated and least of all variable. Its diversity reaches a maximum in tropical waters of the oceans, some genera inhabit Antarctic seas, North Atlantic and adjacent waters. They are absent in North Pacific and in freshwater and are parasites of Chondrichthyes.

The Subfamily Piscicolinae is the most complex one; it is characterized by stability of the lacunary system which is the most complex and provided by external pulsatile vesicles. This subfamily is very variable in other relations. Piscicolinae are distributed in all coastal waters of the ocean and inhabit freshwater of North continents. Piscicolinae in North America and Eurasia are different but there are some closely related species and one common taxon *Piscicola geometra* (Linnaeus). Piscicolinae are parasites on Osteichtyes mainly, but some species are parasiting on Chondrichthyes and Crustacea.

The leech fauna of southern continents is known entirely and it is assumed that Piscicolidae are absent there with the exception of some species in lake Chilka and Lake Tanganyika. Glossiphonidae and higher leeches (Arhynchobdellae) inhabit freshwater of South America, Africa and Australia.

3 Lake Baikal

Baikal is the oldest - at least 25 million years - and the deepest lake of the world. The general Siberian species of leeches are absent here, the lake has several peculiar species belonging to Glossiphonidae and Piscicolidae. The highest leeches (order Arhynchobdellae) are absent.

The family Glossiphonidae is represented by 3 species: *Paratorix baicalensis* (Stschegolev, 1922), *Baicaloclepsis echinulata* (Grube, 1871), and *B. grube*i Lukin & Epshtein, 1959 (Fig. 2). All of them belong to the subfamily Toricinae Lukin & Epshtein, 1959 and are closely related and probably evolved in Baikal from a common progenitor. Endemic Baikalian Toricinae evidently are connected by their origin with the genera *Torix* (China), *Oligobdella* (Japan, Korea, Amur basin, North America) and *Oligoclepsis* (Japan, South Kuril Islands).

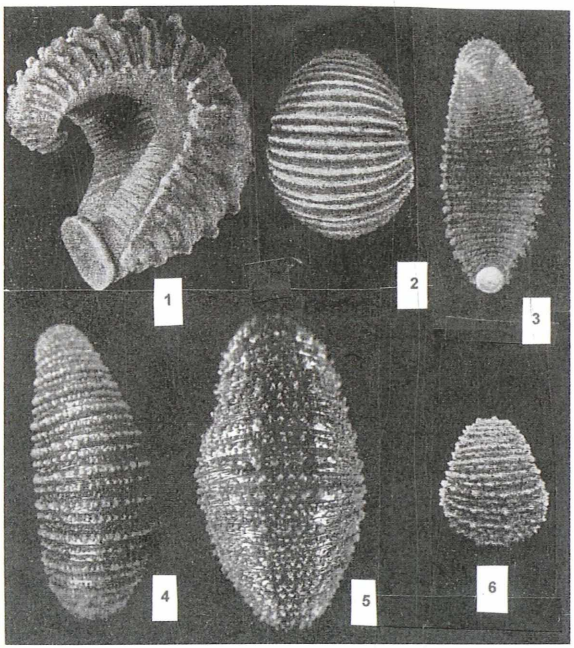

Fig. 2: Baikalian Toricinae. 1 = *Baicaloclepsis grubei*, 2-3 = *Paratorix baicalensis*, dorsal view and ventral view (from Lukin & Epshtein 1960), 4-6 = *Baicaloclepsis echinulata*, dorsal view (from Kozhov 1963 and Lukin & Epshtein 1960)

The family Piscicolidae is represented by four species: *Baicalobdella torquata* (Grube, 1871), *B. cottidarum* Dogiel, 1957, *Codonobdella truncata* Grube, 1872 (Fig. 3), and *Dagarabdella zelenskiji* Finogenova & Snimschikova, 1991 (Fig. 5).

B. torquata, D. cottidarum and *C. truncata* belong to the tribe Piscicolini Johnston, 1865 which includes the holarctic genus *Piscicola* and the palaearctic genera *Caspiobdella, Acipenserobdella* and *Italobdella*. It is supposed that the si-

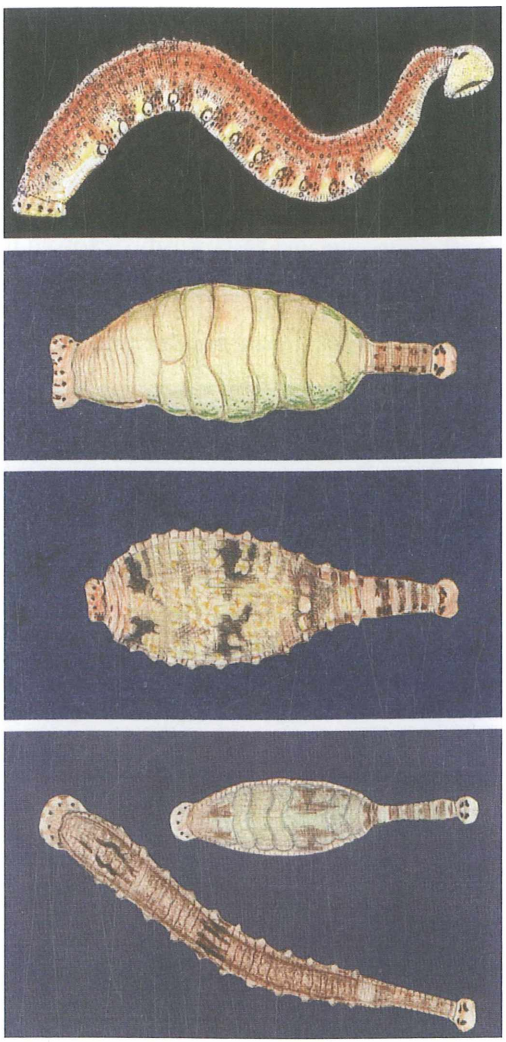

Fig. 3: Baikalian Piscicolinae. 1 = *Codonobdella truncata*, 2 = *Baicalobdella torquata*, 3-4 = *Baicalobdella cottidarum* (original)

milarity of the Baikalian Piscicolinae to genus *Piscicola* is a result of convergence in the evolution of the reproductive organs and that there is a common origin of Baikalian Piscicolinae with species of the genus *Limnotrachelobdella* not ocurring in Baikal.

The areal of the genus *Limnotrachelobdella* extends from the mouth of Amur and coastal waters of Japan to waters in Azerbaijan, it outlines the fauna of the eastern part of Tethys from which Baikal derives.The genus includes five species: *L. elegans* (Blanchard, 1896), *L. turkestanica* (Stschegolew, 1912) (Fig. 4), *L. okae* (Moore, 1924), and *L. taimeni* (Epshtein, 1964). *L. okae* is unique to inhabit the marine and fresh waters. The distribution of *Limnotrachelobdella* species is related to the distribution of the neolimnic fauna in accordance with Martinson (1958). He calls the freshwater fauna which could have developed from marine progenitors in Mesozoic and Tertiary time "neolimnic" as distinct from the "palaeolimnic" fauna, which was formed in most remote times. According to Martinson, the Baikalian fauna (Baicaliidae, Lubomirskiidae etc.) is to be referred to the neolimnic complex. All species of *Limnotrachelobdella* have the flattened body, large pulsatile vesicles and simple reproductive system. One of them, *L. turkestanica*, has the primitive typical somit (3 annuli) and very primitive crop caeca (separated for their entire length). *Baicalobdella torquata* and *B. cottidarum* have 3 annuli, *Codonobdella truncata* may have 3-14 annuli in the typical somit, but their caeca are fused excluding 5 orifices on the level of ganglia. It is possible to reconstruct the prototype of *Limnotrachelobdella* and Baikalian Piscicolidae: probably it had a flattened body, smaller respiratory vesicles, 3 annuli per somit, separated caeca, a reproductive system without prostate glands, conductive tissue and a copulatory area. The genus *Limnotrachelobdella* is related to the marine genus *Trachelobdella* Diesing, 1850, which is characterized by a flattened body and well developed pulsatile vesicles. This genus is widely distributed in tropical and subtropical regions of the World Ocean. The progenitor described above is more primitive than *Trachelobdella* and it is possible to reconstruct the ways of phylogeny of all mentioned genera and species now. The Cretaceous period is probably the beginning of the evolution of Piscicolidae, in the Tertiary the invasion into the continental waters took place, and in the Quaternary the ancestors of the Baikalian Piscicolidae evolved. This hypothesis is closely related to the ideas of G. Y. Vereshchagin and G. G. Martinson.

The D. N. Taliyev's idea that the progenitor of the Baikalian Cottidae reached Lake Baikal along the Amur system from the far-eastern seas in Quaternary and post-Quaternary is of significance for leech study because many species of Pacific Piscicolidae are parasiting on Cottidae. But as it was mentioned above that the leeches reached the Baikal region probably in the Terti-

ary period. Baikalian Glossiphonidae are progenies of tertiary thermophilic freshwater leeches.

From Baikal and Angara there are described many more species. *Piscicola conspersa* Grube, 1871 is probably identical with *Acipenserobdella volgensis* (Zykoff, 1903). The latter is found as parasite on Acipenseridae in rivers from Volga to Jenisej. *P. multistriata* Grube, 1871 was mentioned by Dogiel and Bogolepova (1957). The presence of this leech in Baikal may be a sensation: it was regarded by leech specialists as identical with the marine *Heptacyclus virgatus* (Oka, 1910), widely distributed in North Pacific as parasite on Cottidae. This leech has not been found in Lake Baikal later. May be this record was the result of a confusion of the labels. The leech mentioned by Dogiel & Bogolepova (1957) is identical with *Baicalobdella torquata* (Epshtein, 1987).

A very interesting event is the description of a new species, *Dagarabdella zelenskiji* Finogenova & Snimschikova, 1991, probably belonging to the subfamily Platybdellinae. The absence of pulsatile vesicles is a character of this subfamily. As stated above, Platybdellinae include marine species and some freshwater species which take the root from the sea. *Dagarabdella* can be the peculiar representative of this marine subfamily in Lake Baikal. Later, Finogenova has published the paper on the status of *Dagarabdella* (Finogenova, 1992). Comparing young specimens of *Codonobdella truncata* and *D. zelenskiji,* she found that they are more related to *D. zelenskiji* than the adults are, but she confirmed that this leech has no pulsatile vesicles. Finogenova place *D. zelenskiji* species into the genus *Codonobdella* and mentioned its similarity to *Cystobranchus mammillatus*. But both of them belong to the subfamily Piscicolinae. The external characters of *Dagarabdella* (the absence of warts, eyes and eye-like spots) and the details of reproductive system (short ovaries, long vagina, absence of isolated prostate glands) are a convincing proof that *Dagarabdella* should be regarded as a separate genus.

4 Lake Khubsugul and Aral Sea

Lake Khubsugul is situated ca. 200 km west of the southern end of Lake Baikal in Northern Mongolia, age about 1.6 million years. In this lake two species of Piscicolidae were found, *Piscicola geometra* and *Limnotrachelobdella sinensis*.

The Aral Sea inhabits *P. geometra* and *L. turkestanica*. From author's point of view these both ancient lakes differ from Baikal by the presence of the common palaearctic species *P. geometra* because these lakes do not have such geological properties as Lake Baikal has.

5 Caspian Sea

The Caspian Sea (age approx. 3 million years) as well as Lake Baikal has an endemic fauna of leeches, separated from the palaearctic fauna.

The Caspian Sea is a refuge for an unique fauna of Piscicolidae. Some of them, which originated in freshwater, can live in saline waters. From the coastal waters of the Pacific Ocean and the Amur bassin to the Aral Sea and the South Caucasus the leech fauna is characterized by the presence of a series of peculiar species of *Limnotrachelobdella*. Azerbaijan is the western range of their areal. From the Caspian Sea and the Danube bassin to the Apennines stretches the region of the Caspian fauna. The species of this type belong to the subfamily Piscicolinae, tribe Piscicolinae (like Baikalian Piscicolidae), but include genera which differ from the holarctic Piscicolidae and the Baikalian Piscicolidae in the structure of the female reproductive organs. These genera are *Caspiobdella* Epshtein, 1966, *Italobdella* Bielecki, 1993, and *Pawlowskiella* Bielecki, 1997 with a total of 6 species: *Caspiobdella caspica* (Selensky, 1915) (Fig. 4), *C. fadejewi* (Epshtein, 1961) (Fig. 4), *C. tuberculata Epstein*, 1966, *Italobdella ciosi* Bielecky, 1993, *I. epshteini* Bielecki, 1997, and *Pawlowskiella stenosa* Bielecki, 1997. This group of species sharply differs from *Limnotrachelobdella* by complex morphological and anatomical features.

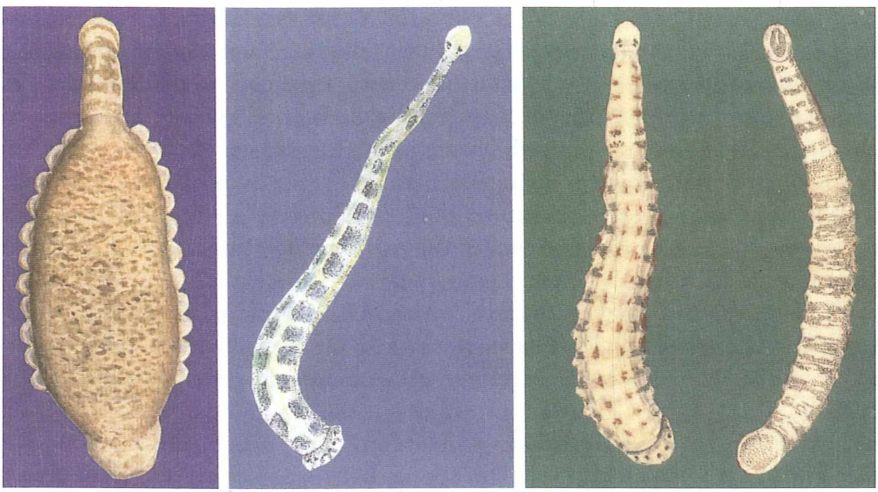

Fig. 4: *Limnotrachelobdella turkestanica* (1), representative of the "East-type" fauna; *Caspiobdellla caspica* and *Caspiobdella fadejewi*, representatives of the "West-type" fauna

In coastal waters of the southern Caspian Sea *Piscicola geometra* occurs, whereas the greater part of Northern Caspian is inhabited by *Caspiobdella caspica*; *P. geometra* is absent here. From the middle part of Caspian Sea only one Piscicolidae species, *Caspiobdella tuberculata,* was described.

Caspiobdella fadejewi was found in the rivers of the Black Sea bassin and the Asow Sea bassin (Donets, Dnieper, Dniester, the mouth of Danube) (Epshtein, 1987). In the River Volga this leech was absent. After building the Volga-Don canal, *C. fadejewi* penetrated in the area of Volga-Don and Volga, and in course of time it arrived upstream the Rybinsk reservoir, where this leech is a very numerous parasite of fish (Epshtein, 1987). Bielecki (1997) has reported the distribution of *C. fadejewi* in the rivers San and Biebrza in Poland, and Nesemann (1997) noted dates of its arrival in the Danube and its tributaries. It can be seen, that this species outcompetes *Piscicola geometra* everywhere.

The genus *Italobbdella* Bielecki, 1993 includes two species, *I. ciosi* Bielecki, 1993 and *I. epshteini* Bielecki, 1997 The first was found in the Adda River (Rivolta) near Milan (North Italy); the second in the Zegrzynski reservoir (North-East Poland). Nesemann (1997) added that *Italobdella* is present in the Danube region of Germany, Austria and Hungary. The occurence of *I. ciosi* in North Italy has some significance for the understanding of the origin of Caspian Piscicolidae. Its occurrence demonstrates the west boundary of the Caspian fauna. It can be supposed that it is a relict of waters deriving from the Tethys Sea and it inhabits bassins of rivers that fall into these: Mediterranean Sea, Black Sea and Asow Sea. Freshwater Piscicolidae are absent in the Mediterranean Sea due to its high salinity (it is populated by marine species), and they are absent in Black Sea and Asow Sea because of the salinity which is high for Caspian species but low for marine species. To this group of species belongs *Acipenserobdella volgensis* which resembles *Caspiobdella*, *Pawlowskiella* and *Italobdella* concerning the structure of the reproductive system; it is distributed from Angara to Poland.

Thus we can recognize in Eurasia two neolimnical groups of the family Piscicolidae: The eastern which is characterized by *Limnotrachelobdella* and genera related to Baikalian leeches and the western including the genera of the Caspian type.

Furthermore, *Archaeobdella esmonti* Grimm (Arhynchobdellea, Erpobdellidae; Fig. 5) has to be mentioned. This species lives in the mouths of some rivers which fall into Black Sea and Asow Sea and in coastal waters in the eastern part of Asow Sea; it inhabits the open sea with significant salinity only in the Caspian Sea.

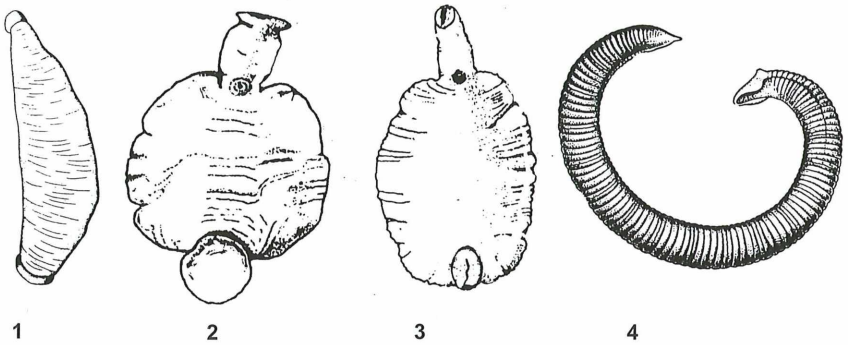

Fig. 5: Relict species of leeches. 1 = *Dagarabdella zelenskyi* (Baikal - from Finogenova & Snimschikova 1991), 2 = *Phyllobdela maculata* (Tanganyika - from Moore 1939), 3 = *Phyllobdellina kazatschenkoi* (depth of Nord Pacific - from Epshtein & Utevski 1993), 4 = *Archaeobdella esmonti* (Caspian Sea - from Grimm 1876)

6 Lake Ohrid

This ancient, 4-10 million year old deep lake in Macedonia is characterized by an endemic fauna, many elements of which bring it together with the fauna of Baikal and Caspian Sea. The leech fauna "Ohrid Lake Region" is described in a number of Sket's articles (1981, 1985, 1992 and others) and in Sket & Sapkarev (1992). They show that in Ohrid and its bassin 11 endemic and 9 non-endemic leech species occur. The majority of non-endemic species inhabit an eutrophic zone, except *Erpobdella octoculata*, which inhabits the *Chara* zone and the non-polluted littoral. A characteristic feature of Ohrid is the dominance of Erpobdellidae over Glossiphonidae. It should be taken in notice that all species of endemic leeches in this lake belong to the usual Palearctic genera *Glossiphonia* and *Dina*. Endemic *Glossiphonia* and *Dina* have been discovered at a depth of 200 m and more. Fish leeches are represented by two species, *Piscicola geometra* (doubtful) and *Piscicola* (*Cystobranchus*) *pavlovskii* (Sket, 1968). There are doubts about the independence of these two species. Bielecki (1997), considers them as good species but much more widely-distributed than Sket supposes. Thus, information about fish leeches of Ohrid is not fully reliable. It is emphasized that *Piscicola hadzii* Sket, 1985 from Herzegovina is a typical representative of the genus *Caspiobdella* (Bielecki 1997).

7 Lake Tanganyika and Lake Chilka

Tanganyika - 2 million years old - is the biggest lake in the Rift Valley; Lake Chilka is situated in India. As stated above, the distribution of the subfamily Platybdellinae is bipolar and species belonging to this family are absent in

tropical regions of the World Ocean. But this subfamily (tribe Austrobdellini) is represented by two species in the lakes Chilka and Tanganyika: *Pterobdella amara* Kaburaki, 1921 in Chilka and *Phylobdella maculata* Moore, 1939 (Fig. 5) in Tanganyika. These species have many common features. They have a foliaceous body and primitive structure of the female reproductive organs but the male reproductive organs are well developed. *P. amara* has no posterior crop caeca; *P. maculata* has separate caeca such as Glossiphonidae. Thus they are relicts of an ancient tropical fauna which is extinct in the sea but survive in freshwater. Some years ago in the North Pacific near Paramushir Island specimens of a new species were found, *Phylobdellina kazatshenkoi* Ephstein & Utevsky, 1993 (Fig. 5), on the fish *Clidoderma asperrimum*, trawled from a depth of 705 m. This species is related to *Phylobdella maculata*, having a foliaceous body but a more primitive structure of the alimentary tract and the reproductive organs. For that reason, *P. maculata* belongs to the tribe Austrobdellini and *Phylobdellina kasatschenkoi* to the tribe Platybdellini. The latter is related (excluding body form) to the progenitor of Platybdellinae. It is possible to reconstruct a prototype of Platybdellini with flattened body, which is similar to the common prototype of *Trachelobdella*, *Limnotrachelobdella* and *Baicaliobdella* in structure of alimentary and reproductive systems, but having primitive structure of lacunary system which was developed further. Both groups developed parallel from similar progenitors by the way of elaboration of reproductive organs; *Phylobdella maculata* can be one of the steps on this direction. The next step is the tribe Pterobdellinini (subfamily Platybdellinae), which has complicated reproductive organs. The last step, the tribe Hemibdellini, has the most complicated reproductive systems and lacunary vessels, but no pulsatory vesicles.

8 Lake Biwa

Lake Biwa is situated near Kyoto, Japan; the age is 4 million years. The interesting species of this lake is *Ancyrobdella biwae* Oka, 1917 (Glossiphonidae). The excellent description was given by a famous researcher but there are no further records in the literature. Nesemann (1997) includes the leech *Glossiphonia smaragdina* Oka, 1910 in the genus *Ancyrobdella*, which includes two species ocurring in Japan. These species have no specifical features which have Baikalian Glossiphonidae. "The investigated specimens are surprisingly similar to the European *Glossiphonia paludosa* in their habitus, colour and shape, but they all belong to the genus *Ancyrobdella*. There is no possibility to distinguish undoubtedly the two genera *Glossiphonia* and *Ancyrobdella* based on their external morphology" (Nesemann, 1997: 10).

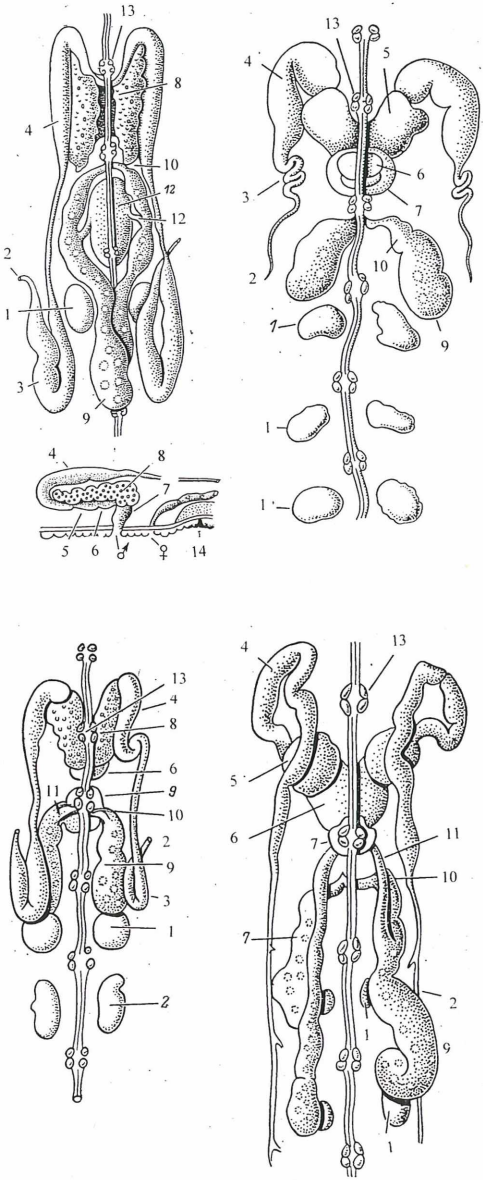

Fig. 6: Types of the structure of reproductive systems of Piscicolinae. A = *Piscicola*-type (*P. geometra*) B = *Limnotrachelobdella*-type (*L. sinensis*) C = *Caspiobdella*-type (*C. fadejewi*) D = *Cystobranchus*-type (*C. mammillatus*). 1 = testes, 2 = vasa deferentia, 3 = seminal vesicles, 4 = ejaculatory ducts, 5 = terminal parts of the ejaculatory ducts (= "cornua" of the atrium), 6 = common part of the atrium (= ejaculatory bulb), 7 = bursa, 8 = prostatic glands, 9 = ovaries, 10 = oviducts, 11 = conducting strands, 12 = vector tissue, 13 = V ganglion of the ventral nerve cord, 14 = spermatheca, = gonopores. (from Epshtein 1987)

9 Summary

1) The genus *Piscicola* is distributed in the Holarctic. Evidently, this genus is the most ancient representative of freshwater Piscicolidae.
2) In ancient lakes from Baikal to Aral sea inclusive a series of *Limnotrachelobdella* species are present. It can be supposed that contemporary fish leeches of Baikal are the result of divergence from general ancestor, who was connected with *Limnotrachelobdella* by the common origin; the similarity of baikalian Piscicolidae with *Piscicola* is a result of convergence.
3) On the territory of East Europe in waters deriving from the Tethys Sea the Caspian fauna had developed, which includes the piscicolid genera *Caspiobdella* and others, sharply different from previous one due to the construction of the reproductive system.
4) The fourth element of the piscicolid fauna of Holarctic is *Cystobranchus mammilatus*, invading into continental waters in the time of quaternary transgression of the Arctic ocean. Some continental waters are referred to species of the marine subfamily Platybdellinae (lakes Chilka and Tanganyika; North America).

Types of the reproductive systems of the mentioned Piscicolidae-groups are presented in figure 6.

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Received: 2004-11-13