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Lower vertebrates of Late Paleogene and Neogene of Armenia

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Introduction

In spite of some earlier researches, paleontology in general and particularly paleontology of lower vertebrates is a very poorly investigated field in Armenia. In the territory of Armenia many localities with rich fossil faunas of Silurian to Holocene epochs have been found, which unfortunately were not studied systematically (Bogachev, 1936, 1938; Aslanyan, 1958; Atlas of fossil fauna of Armanian SSR, 1974). The main studies were focused on foraminifers, mollusks, fishes and mammals (Bogachev, 1936, 1938a, 1938b; Aslanyan, 1958; Gabielyan, 1964; Atlas of fossil fauna of Armanian SSR, 1974; Melik-Adamyan, 2003; Pipoyan, 2003; Pipoyan, Gabielyan, 1998, 2003 and etc).

One of the most interesting period for paleontological studies is the Late Paleogene and Neogene, when terrestrial development of the territory of republic and the formation of the Recent fauna were commenced (Alsanyan, 1958). During this time, the territory of Armenia both subsided and uplifted. The former caused sea expending and the latter sea retreating. These movements continued repeatedly, however there were also some land parts on the territory of the modern Armenia. Later in the Late Miocene, the brackish influenced inland water body disappeared. After a short period of erosion, freshwater sedimentation started and continued by the end of the Late Miocene (Aslanyan, 1958; Simonyan, 1999; Steininger et al. 1985; Popov et al. 2004). During this time many small lakes and rivers appeared in Armenia.

According to earlier records from Armenia, twenty-four lower vertebrate taxa, including fishes and amphibians are identified. From these, twenty-two taxa are reported from the Late Paleogene and Neogene sediments (e.g., Bogachev, 1936, 1938a, 1938b; Gabielyan, 1964; Melik-Adamyan, 2003; Pipoyan, 2003; Pipoyan, Gabielyan, 1998, 2003). In some of these works, no systematic descriptions and illustrations were provided, which make further investigations, including thorough taxonomy and critical analysis very difficult. Besides, in the last decades the classification of fish and amphibian families, genera and species has changed and significantly supplemented (e.g., Holčík et al., 1989; Cavender, Coburn, 1992; Sanchiz, 1998; Salmanov, Dorofeyeva, 2001; Mickoleit, 2004; Böhme M., 2007 etc).

In the territory of Armenia several zoogeographical provinces and subprovinces cross with the corresponding faunistic complexes. The Recent distribution of animals is the consequence of evolution in time and space of their ancestors (Sychevskaya 1986, 1989; Bănărescu, 1989). The study of late Paleogene and Neogene fish and amphibian remains permits to find the ancestral forms and to follow the development of the Recent lower vertebrate fauna of Armenia. Based on these studies, it is also possible to reconstruct the paleoenvironment and paleoecology of their habitats, as well as the possible development of the landscapes. Such studies has significantly increase our knowledge on biostratigraphy and paleoclimatology of these fossil groups (Uyeno and Miller, 1962).

Aim and objectives of the research. The aim of this study is to investigate the fossil lower vertebrates from the localities from the Oligocene - Pleistocene of Armenia, for ascertaining the formation and establishment of the fish and amphibian recent fauna and to reconstruct their paleoenvironment and biogeography. This will be achieved through the following objectives:

- Study of faunal composition (fishes and amphibians) of the Late Paleogene and Neogene of Armenia
- Comparative analysis of the lower vertebrates' species composition of Armenia with those from other localities of the neighboring territories,
- Paleoenvironmental analysis of fossil habitats
- to ascertain the formation and establishment of the recent fish and amphibian fauna of Armenia.

Scientific novelty of the study. Oligocene – Pleistocene fish and amphibian taxa represented by fourteen freshwater, four marine-brackish fish and 1 taxon of true frogs. For the first time, the remains of the Recent genus, *Garra* is described in present study, as well as the genus, *Enoplophthalmus* from the Eastern Paratethys. The present tudy have revealed the occurrence of *Alosa, Aphanius, Chondrostoma, Pseudophoxinus* and/or *Delminichthys,* also the order Perciformes (families Gobiidae and Percidae). The oldest brown trout *Salmo* cf. *trutta,* and *Chondrostoma* sp. from the Western Palaearctic are described.

It is shown, that the Recent fish and amphibian fauna of Armenia started to form from the end of Miocene, which was caused by the beginning of the terrestrial development of the territory of Armenia. It was found that, the possible incursion of the ancestral forms of recent lower vertebrate fauna into the territory of Armenia was occurred from the south and south-eastern parts of the neighboring regions.

CONTENTS

Chapter 1. The historical review of researches on lower vertebrate fauna of Armenia

In this chapter the fossil lower vertebrate fauna from the Trias to Pleistocene is described.

Chapter 2. Geological overview of the Late Paleogene and Neogene of Armenia

The chapter is composed of two parts (Late Paleogene and Neogene), where a geological overview of the region in the Oligocene-Holocene and detailed description of localities are given.

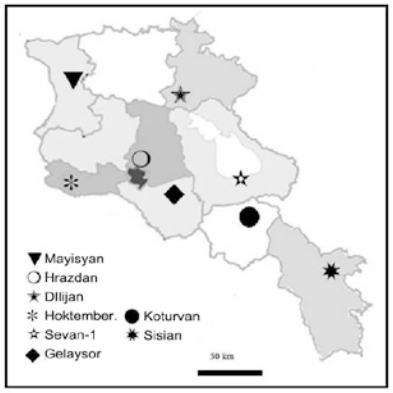

Fig. 1. Map of Armenia with studied localities

Chapter 3. Material and methods

3.1. Material. The material of the present study was collected from eight localities (See Figure 1 and Table 1), during several field works (2006-2009). Some other specimens were also obtained from the staff of the Institute of Geological Sciences NAS RA and Institute of Botany NAS RA, collected in several expeditions from 1940 to 2005. In Table 1, data on the localities and the collectors of the material are provided.

Table 1.

Material, studied in the present work.

Destrict	Locality	Age	Number of samples	Author/collector, year of collecting
Tavush	Dilijan	Middle-Late Oligocene	14	Gabrielyan, Pipoyan, 1993, 1998, 2008, 2009; Vasilyan 2008, 2009
Armavir	Oktemberyan	Early - Middle Miocene	8	Manukyan, 1963-1970
Kotayk	Hrazdan	Sarmat s. l./middle of the Middle and Late Miocene	13	Goghtuni, 1966
Shirak	Maisyan	Meot (Pontian?) /middle-end of late Miocene	31	Goghtuni, 1970
Vayots Dzor	Koturvan	Middle Pliocene	2	Goghtuni, 1959
Ararat	Gelaysor	Late Pliocene	75	Rukhkyan, 1986-1987; Gabilyan, Pipoyan, 2006-2008 and Vasilyan 2008, 2009
Syunic	Sisian	Early Pleictocene	98	Takhtajyan, Goghtuni, Gabrielyan, Pipoyan, Roiron etc., 1940, 1980, 1990-91, 2001-02, 2004-08
Gegargunik	Sevan-1	Middle Pleistocene	1	Gabrielyan, 2002

The studied material are deposited in the Institute of Zoology of Scientific centre of Zoology and Hydroecology NAS RA, Paleontological Museum of the Institute of Botany NAS RA, and VSEGEI

(Geological research institute Federal Agency of Mineral Resources, Russia).

3.2. Methods. Processing and registration of the fossil material is undertaken according to general methods of paleozoology and paleobotany (Müller, 1992). The morphometrical measurements is used the system of measures by J. Holčík et al. (1989). The last 2 branched rays of dorsal and anal fins are counted as one.

The terminology and systematic classification follow that of Obrhelová (1961), Sychevskya (1986), Rutte (1962) and Harder (1964) for the fish material and Böhme (1977) and Sanchiz et al. (1993) for the Anura.

The fossil remains were studied and photographed using a microscope Leica M125, with the digital camera Leica DFC300; Leitz 10 and C. Zeiss Stemi DV4, with digital camera Olympus FE290. The micrographs of fossils were taken using scanning electron microscope Leitz AMR 1200. The schematic drawings were made, using a Leica mirror connected to the microscope. Illustrations are digitally prepared in the Adobe Photoshop CS (version 3). The line art-works are generated in the Abobe Illustrator.

Chapter 4. Description of the fossil material

Systematic Paleontology

In this chapter it is given the detail description (osteological, morphological etc.) 18 studied fish and 1 amphibian taxa from the Oligocene – Pleistocene of Armenia. Below is the list of described taxa, according to their localities in the tabl. 2.

Table 2.

List of described taxa, according to their localities.

Locality	Taxa
Dilijan	*Palaeoleuciscus macrocephalus,* Perciformes gen. et sp. indet., *Enoplophthalmus* cf. *alsaticus*
Hoktemberyan	*Chondrostoma* sp. (Okt), Percidae gen. et sp. indet., Gobiidae gen. et sp. indet.
Hrazdan-1	*Alosa* sp., *Aphanius* sp.
Mayisyan	*Chondrostoma* sp. (Mays), *Pseudophoxinus* vel *Delminichthys* sp., Leuciscinae gen. et sp. indet. (Mays)
Gelaysor	*Leuciscus* cf. *souffia, Leuciscus* sp., *Capoeta* sp. (Gelays), *Garra* cf. *rufa, Pelophylax* cf. *ridibundus* (Gelays)
Koturvan	Leuciscinae gen. et sp. indet. (Kot)
Sisian	*Salmo* cf. *trutta*, *Pelophylax* cf. *ridibundus* (Sisian)
Sevan-1	*Capoeta* sp. (Sev)

Chapter 5. Lower vertebrate fauna from Armenia

5.1. Paleoichthyofauna from the Oligocene of Armenia

Literature data (Bogachev, 1962; Pipoyan, Gabrielyan 1998, 2003) and our studies revealed an Oligocene paleoichthyofauna, representing four fish taxa of the “freshwater” lake facies of Dijilan suite, *Palaeoleuciscus macrocephalus,* Perciformes gen. et sp. indet., *Enoplophthalmus* cf. *alsaticus* and *Prolebias armeniacus*. From the sediments of this lake, it was also mentioned *Lepidocottus* sp. (Cottidae) and *Clupea* sp. (Gabielyan A. et al., 1958), which we consider as Perciformes gen. et sp. indet. and *Enoplophthalmus* cf. *alsaticus* accordingly. For the first time it is shown the presence of fossil genus *Enoplophthalmus* from Eastern Paratethys and percids Perciformes gen. et sp. indet. from the Oligocene of Armenia.

***Paleoecology*.** In the shale member of Dilijan suite both large (adult) and little (juvenile?) specimens of *Enoplophthalmus* cf. *alsaticus* were found, representing of occurrences of diadromous and non-diadromous stocks of this species in the reservoir. So, the lake was their habitat as well as place for reproduction, as it is documented for the majority of species of this genus (Gaudant, Reichenbacher, 1999).

The occurrence of *Palaeoleuciscus macrocephalus* in these sediments indicates existence of shoal, rich in zooplankton in the coastal zone of the lake. In the lower part of the Dilijan suite there are two horizons, which have different species compositions. In the first one there are *Palaeoleuciscus macrocephalus* and *E.* cf. *alsaticus*, and in the second – *E.* cf. *alsaticus, Prolebias armeniacus* and Perciformes gen. et sp. indet. Based on the ecology and biology of these fishes, we suppose, that freshwater environment of the lake was changed to brackish, which could occur only in case of connection of this lake with the Maikop marine basin of the Kura depression.

***Paleogeography*.** So far the genus *Enoplophthalmus* with its seven known species was found from freshwater to brackish environments of the Tethys and Paratethys of the Oligocene and Early Miocene of Central, Western and Southern Europe (Gaudant, Reichenbacher, 1999; Martini, Reichenbacher, 2007). The find of *E.* cf. *alsaticus* from the "freshwater" Oligocene lake sediments of Armenia shows that the genus was distributed in the south – eastern coastal zone of the Paratethys, including freshwater bodies flowing into it.

The genus *Prolebias* was widely distributed in the reservoirs with the changing salinity, as well as in the lagoons of the Oligocene – Middle Miocene of France and Spain, in the Western Paratethys and the Upper Reingraben (totally 10 species) (Reichenbacher et al., 2004) and in the Oligocene – Miocene sediments of the Eastern Paratethys (4 species) (Bogachev, 1962). Hence, species of this genus were inhabiting not only in the Western, but also in the Eastern Paratethys, which confirms the the migration path of Cyprinidontids from Asia to Europe, through the Balkanian-Anatolian-Iranian archipelago (landmass), including Armenia, already proposed by Akhmetiev et al. (2004).

Small cyprinid fishes of the genus *Palaeoleuciscus* are the most numerous and widespread fishes of Oligocene and Miocene lakes in Central and Eastern Europe, as well as of Early Miocene of Western Asia (Böhme, 1996, 1997; Akhmetiev et al., 2005).

Probably, this genus was originated in Southern Asia, prior to Oligocene and two immigration waves from Asia to Europe through Balkanian-Anatolian-Iranian landmass could be recognized. The older at the Eocene-Oligocene boundary and the younger in the end of the Early Miocene (Böhme, 1996). As an evidence of these immigration waves, *P. macrocephalus* from the Oligocene of Armenia and *P. etilius* from the Early – Middle Miocene of Anatolia can be considered, respectively.

Fish paleocommunity of lake facies in the Dilijan Suite, including cyprinids, cyprinodonts, percids and osmerids, reveals similarities with the same faunas inhabiting the paleoreservoirs of Western Europe (Germany, France and Spain), where the ichthyofauna of continental water bodies and sea coastal zone (brackish environment) was represented by *Palaeoleuciscus, Gobius, Dapalis, Prolebias* and *Enoplophthalmus* (Böhme 1996). This faunal composition shows that the primary fish fauna of continental water bodies of Western Europe, and that of Armenia, consists of anadromorphous species and fishes of brackish environments. To this fauna, some freshwater forms joined, which were immigrated from the Western Asia through the Balkanian-Anatolian-Iranian archipelago into Europe.

Based on the above-mentioned, we conclude that the territory of Armenia, being a part of the landmass connecting Asia with Europe, was on the immigration path of freshwater fauna from Asia into Europe during the Oligocene.

5.2. Paleoichthyofauna from the Miocene of Armenia

5.2.1. Paleoichthyofauna of Hoktemberyan Suite. There are found fossil fishes *Chondrostoma* sp.

(Okt), Percidae gen. et sp. indet. and Gobiidae gen. et sp. indet. from the sediments of desalinated basin, which existed from Early to Middle Miocene on the south-western part of Armenia. For the first time the oldest remains of *Chondrostoma* and gobiid are described from the Western Palaearctic and Armenia.

Paleoecology. The presence of pharyngeal bones and teeth of *Chondrostoma* sp. (Okt) (Rutte, 1962), in different sizes as well as scales of Gobiidae gen. et sp. indet. of juvenile and adult stages support that these fishes were autochthonous of this paleoreservoir.

Most gobiids live in shallow marine environments. However, many forms can adapt to brackish and freshwater conditions, where they can develop into endemic species. For instance, this has been documented for the extant gobiids from the Ponto-Caspian realm (Simonovic, 1999, cited acc.: Reichenbacher et al., 2007). Freshwater environment of this water body can be evidenced by the finds of freshwater ostracods and mollusks in these sediments. Based on above mentioned, above, we suppose that the freshwater gobiid (Gobiidae gen. et sp. indet.) was inhabiting in this paleoreservoir .

It is known that it is possible to distinguish sediments from permanent water bodies with autochthon fish community (Böhme 2002). Therefore, the presence of freshwater ostracod and mollusk fauna from the sediments of the lower and upper subsuites of Hoktemberyan suite, as well as autochthon fishes support the stabile sedimentation of the freshwater (limnic and/or fluviatil) paleoreservoir of Early – Middle Miocene age in the south-western part of Armenia.

Paleobiogeography. The oldest known occurrences of *Chondrostoma* are documented from the Middle and Late Miocene of Mongolia (Sychevskaya, 1989), whereas in Europe they are known from the Late Miocene of Spain, Early Pliocene of Greece and Pliocene of Anatolia (Böhme et al., 2003).

Discovery of *Chondrostoma* from the Early and Middle Miocene of Armenia makes it as the oldest record of the genus, considering its distribution from Asia to Europe in the Miocene through the Balkanian-Anatolian-Iranian archipelago.

Gobiidae fish family is known from the Miocene of the Eastern Paratethys only by the species of genus *Gobius*. So, nine species of *Gobius* are known from marine sediments of the early Middle Miocene of Azerbaijan (the age of sediments is coeval with the lower subsuite of Hoktemberyan caving (Armenia) and eleven species of this genus are identified from the Pliocene – Middle Pleistocene of Azerbaijan (Djafarova, 2006).

The species of genus *Gobius* had wide distribution, their fossil remains are known from the Oligocene-Miocene marine sediments of the Eastern and Western Paratethys and Spain (Djafarova, 2006; Reicnehnbacher, 2007). However, there were also some finds of this genus from sediments of non marine environments of Germany (Reichenbacher, 2007). Thus, based on preceding we suggest that the gobiid appear in Eastern Paratethys in the Middle Miocene, then they became the dominant fish group of the water bodies (South-Eastern and Western Paratethys), and in some cases, probably, adapted to life in freshwater and/or saline environments.

5.2.2. Paleoichthyofauna of Hrazdan suite. A fish fauna in the clay and limestone sediments from localities Hrazdan-1 and Mangyus in the Hrazdan suite contains five taxa: *Alosa* sp., *Aphanius* sp., *Prolebias mutilus*, *Prolebias* sp. and *Atherina schelkovnikovi*, as well as “herrings” similar to *Clupea ventricosa* and *C. lanceolata*. Two former taxa are described for the first time from the territory of Armenia.

Paleoecology. *Atherina* are typical for sea coastal zone, rarely seen in fresh water bodies of tropical and boreal zones. They inhabit in brackish to hypersaline environments (Gabelaya, 1976; Reichenbacher,

2004).

The genus *Aphanius*, like *Prolebias*, is recognized in euryhaline environments, in coastal and brackish habitats along the Mediterranean Sea, the Red Sea, the Persian Gulf and the Arabian Sea, as well as in land-locked bodies of freshwater in these areas (Coad, 2000).

From the sediments containing *Aphanius* sp. there is one more cyprinodont species – *P. mutilus*. A sympatric occurrence of cyprinodontiform species (e.g., one or two *Prolebias* species and one *Aphanolebias* species) is common in oligohaline to brackish sediments of the late Early Miocene in the Western Paratethys (Reichenbacher 1993; Jost et al. 2006; Reichenbacher and Prieto, 2006) and the Upper Rhinegraben (Weiler 1963; Reichenbacher 2000).

The fragments of Middle Miocene cyprinodontiforms are scarcely recorded (for details see Reichenbacher, Kowalke, subm.), and sympatric occurrences of two cyprinodontiform species have not been documented to date. The presence of *Aphanius* sp. and *Prolebias mutilus* in early Upper Miocene sediments near Yerevan indicate that sympatric occurrences of cyprinodontiform species may have existed throughout the Miocene in euryhaline environments, at least in the Eastern Paratethys. This may be related to the absence of competition with other fish species in these habitats that are characterized by fluctuating salinity levels.

Comparison of recent and fossil species of genus *Alosa* (Fauna USSR, edt. Svetovidov, 1952; Grande, 1985; Gaudant, 1991) demonstrates, that the fossil specimens distinguished from recent ones with the lower number of vertebrae (34-40 vs. 47-53(57)) and, consequently, with poor development of caudal part of vertebrate. Thus, the fossil *Alosa* have lower number of caudal vertebrae (14-17(21) vs. 31-35), with the same or a little higher number of abdominal vertebrae. Poor development of caudal part of vertebrate supports hypothesis of Svetovidov (Fauna USSR, 1952), according to which the ancestral forms of herrings were rare “mobile”, then the recent, and could not make long migrations.

So, the co-occurrence of marine, brackish and freshwater fish, foraminifer and mollusc taxa (Gabrielyan A., 1964) indicates an euryhaline environment of Sarmat Yerevan basin.

***Paleobiogeography*.** The first found of *Atherina* are known from the Miocene of the Paratethys (Swichenskaya, 1973). From the Middle Miocene of the Eastern Paratethys, four species are known and only two species from the Western Paratethys. In the end of Miocene and in the Pliocene they appeared in basin of the Mediterranean Sea (Gaudant, 2002). After the Paratethys break-up to the basin of the Black, Caspian and Aralian seas in the Lower Pliocene and Early Pleistocene (Popov et al., 2004), the genus *Atherina*, which stay in these basins, became an origin for the recent species. The recent species of this genus occur in the basin of the mentioned seas, as well as in the Mediterranean Sea and the Atlantic Ocean.

Derived from paleontological data (Svichenskaya, 1973; Gabelaya, 1976; Gaudant, 2002) and modern distribution (Berg, 1949) of the genus *Atherina*, we can conclude that this genus has a Paratethys-Mediterranean origin.

First fossil *Aphanius* species find is documented from the early Late Miocene of Spain. Other species are known from the middle and Late Miocene of the Mediterranean region, Western and Central Paratethys. Only two species (*A. kirgisicus, A. longipinis*) were found from the Middle and the Late Miocene of the Eastern Paratethys (Kirgizia) (Yakovlev, 1959). Beside the *Aphanius*, there were found other cyprinodonts *Prolebias* sp., *P. mutilus* from Hrazdan suite. From Sarmatian sediments[1] of Nachijevan (Azerbaijan),

[1] from these locality clupeid fishes are known, which, according our unpublished data, belong to genus *Alosa*.

which are analogous to Hrazdan suite, *P. nepos* is known (Bogachev, 1962).

Hence, the dominant group of cyprinodonts of the fish fauna of coastal and brackish habitats along of Yerevan basin in Sarmat was *Prolebias*.

The fossil species of genus *Alosa* are found from the Oligocene to Pliocene of the Paratethys and the Mediterranean sea. The largest part of species (12) are found from the Paratethys, while from the Mediterranean region only 3-4 species are found (Gaudant, 1991, 2001). The recent species of this genus are distributed in the basin of the same seas, like their fossil forms, as well as in the Atlantic Ocean.

It is significant, that the beds with *Aphanius* sp., *Prolebias* sp., *P. mutilus* and *Atherina schelkovnikovi,* do not contain *Alosa* sp., and contrariwise. The first four taxa are recognized in coastal and brackish habitats, as well as in lagoons and in land-locked bodies of freshwater. *Alosa* inhabit, generally, in the pelagiac zone (Fauna USSR, edt. Svetovodov, 1952; Reichenbacher, 2004; Reichenbacher et al., 2004). Based on the above mentioned, we can conclude that during Sarmat the coastline and/or the depth of Yerevan marine-brackish basin changed.

5.2.3. Paleoichthyofauna of Mayisyan locality. Based on the pharyngeal teeth remains, the following ichthyofauna from Mayisyan locality were revealed: *Chondrostoma* sp. (Mays), *Pseudophoxinus* vel *Delminichthys* sp. and Leuciscinae gen. et sp. indet. (Mays) (subfam. Leuciscinae). This palaeocomunity is dominated by *Pseudophoxinus* vel *Delminichthys* sp., consisting 77 % of specimens.

***Paleoecology*.** Occurrence of isolated pharyngeal teeth of these fishes of different generations in sediments of Mayisyan locality indicates their autochthonous inhabiting in this paleoreservoir. Freshwater ostracods and mollusks are revealed from here (Aslanyan, 1958; Gabielyan A., 1964), which are common in lakes, as well as in slow flowing, broad rivers (Thienemann, 1950). The hydrological network Southern Armenia in Late Miocene consisted of the lakes and valleys of rivers, along latter there were forest swamps (Leie Ya., Leie Yu., 1960).

In conclusion, in Maeot there was a permanent water body – lake with the system of slow flowing rivers with marshland banks.

***Paleobiogeography*.** *Pseudophoxinus* vel *Delminichthys* sp. is an interesting species considering its paleobiogeography of the Eastern Anatolia and the Lesser Caucasus. The species of these genera are not documented from the basin of the Kura and Arax Rivers, to which belongs the modern hydrological network of Armenia. The latest studies demonstrate, that the genera *Pseudophoxinus* and *Delminichthys* are sister taxa, which diverged from one ancestral form (*Palaeoleuciscus*) in the Early Miocene (Freyhof et al., 2006; Perea et al., submitted). The fossil *Pseudophoxinus* vel *Delminichthys* (pharyngeal teeth) are known from the middle Early Miocene to the Middle Pliocene of Anatolia (Böhme et al., 2003; Rückert-Ülkümen et al., 2002).

As a conclusion, *Pseudophoxinus* vel *Delminichthys* sp. inhabited in the Late Miocene and Early Pliocene freshwater bodies of Anatolia, where in present they are distributed, as well as in paleoreservoirs of the Lesser Caucasus, where they were the dominant elements of ichthyocenoses.

5.3. Paleoichthyofauna from Pliocene of Armenia

5.3.1. Lower vertebrates paleofauna of Nurnus locality. Fauna of lower vertebrates of Nurnus locality consists of fish *Barbus* sp., *Alburnus* sp. and amphibian species *Pelophylax* cf. *ridibundus* and *Bufo* sp. (Melik-Adamyan, 2003).

Paleoecology of this locality was studied by Melik-Adamyan (2003). He showed, that the paleolake

was shallow, bad aerified, intensively turning into the swamp reservoir. There were reedstand and rushy at the lakeside. It was surrounded with poor rolling plain, savanna-steppe vegetation, probably of subtropical type, and with a positive annual temperature.

Paleogeography. *Barbus* sp. from this locality is an only find of the barbels from the territory of Armenia. *B. orientalis* was described from the Late Pliocene of Georgia (Gabelaya, 1976) and *Barbus* sp. from the Pliocene of Turkey (Böhme et al., 2003). Hence, taking the geographical position of the locality into account, we suggest that the genus *Barbus* appeared in the paleoreservoirs of Anatolia and the Lesser Caucasus in the Early Pliocene.

Genus *Alburnus* is known from the Miocene neither Armenia nor all of the Lesser Caucasus. The genus from Nurnus makes the oldest record for this region.

Pelophylax cf. *ridibundus* and *Bufo* sp. are the oldest remains of amphibians from the territory of Armenia. Genus *Pelophylax* were recorded from several localities as the followings: Neogene of Europe (Sanchiz, 1998; Tempfer, 2004), Miocene of Turkey, Pliocene of Kazakhstan and Eastern European plateau. Toads (*Bufo*) are also documented from the Neogene of Europe and the Pliocene of the Eastern European plateau (Ratnikov, 2001; Tempfer, 2004), but so far, there were not known from the Pliocene of the Lesser Caucasus and Anatolia.

Based on the preceding consideration and comparison, we propose that the appearance of modern fish and amphibian fauna elements in Armenia commenced from the Early Pliocene.

5.3.2. Pelaoichthyofauna of Koturvan locality. The Middle Miocene fauna of Koturvan locality composed of a single taxon, Leuciscinae gen. et sp. indet. (Kot).

5.3.3. Lower vertebrate paleofauna of Gelaysor locality. Paleofauna from Gelaysor consists of cyprinids including four taxa, *Leuciscus* sp., *L.* cf. *souffia*, *Capoeta* sp., *Garra* cf. *rufa* and a marsh frog *Pelophylax* cf. *ridibundus*. The assemblage is dominated by *Garra* cf. *rufa* and *Leuciscus* cf. *souffia*. For the first time the fossil records of recent genus *Garra* are found.

***Paleoecology*.** More than half of fossil records from Gelaysor locality consist of isolated pharyngeal teeth of different generations and pharyngeal bones, which belong to cyprinids. This indicates the long lasting occurrence of these fishes in this reservoir.

Analysis of anatomy and ecology of above mentioned taxa showed, that among them prevail benthophages and detritophages (*Garra*, *Capoeta*), which indicates a possible presence of well developed near-bottom vegetation and detritus on the bottom of the paleoreservoir. Occurrence of fossil *Garra* from here, makes this assumption that the climate in the end of the Pliocene of Armenia was warmer than that in present time and was closer to climate of Southern Anatolia, Mesopotamia, Near East and etc., where today occur the species majority of the complex *Garra rufa*.

Such paleoecologic idea is consistent with the paleoclimatic data from the Pliocene of Armenia recently revealed by Bruch, Gabrielyan (2004).

From the sediments of lakeside, which are characterized by the presence of mature gravels, as well as imprint of rhizoliths, we have found the knots of monocotyledonous plants (reed/rush) and the remains majority of marsh frog *Pelophylax* cf. *ridibundus* records.

***Paleobiogeography*.** Of a special interest is a record of genus *Garra* from Pliocene of Armenia. Up to now there was no fossil record on this genus. According to Menon (1964), the species of *Garra* probably originated in the Middle or Late Miocene in the Himalaya, then, the Latest Miocene and the Early Pliocene by series of waves they have migrated to the South and South-East, and then to the West. According to this

author, the species of this genus inhabiting the reservoirs of the Asia Minor and the Arabian Peninsula are descendants of one of these waves, namely «*tibanica – rufa – lamata*». We suppose that *Garra* cf. *rufa* from Gelaysor locality also belongs to the descendants of this wave.

Genus *Garra* does not occur neither in the recent ichthyofauna of Armenia, nor in the basin of the Arax and Kura Rivers. Probably *Garra* reached the paleohydrological network of the territory of Armenia in the Pliocene, when the territory of Armenia as well as the most part of Anatolia has mountainous (only 700-900 m above sea level) relief (Simonyan, 1999; Durand et al., 2000). Presumably the genus with its species existed on the territory of Armenia by the Pleistocene and they were disappeared from this territory, as a result of the glaciation period at the Early Pleistocene.

The fossil records of the genus *Capoeta* are known from the Late Pliocene of Georgia (*Capoeta nuntius* (Bogachev, 1938c) and the Pliocene of Anatolia *Capoeta* sp. (Böhme et al., 2003). The presence of *Capoeta* sp. (Gelays) in the Gelaysor locality, shows that the genus must have been occupied the Lesser Caucasus since Pliocene.

The recent distribution of *Capoeta* encompasses the Asian part of the Euro-Mediterranean subregion (Bănărescu, 1990). There are known 12 species of *Capoeta* (Turan et al., 2008), from them *C. capoeta* has the largest area. Probably, the fossil *Capoeta* sp. (Gelays) is an ancestral form of this species.

There are chub (*Leuciscus*) three taxa from the Pliocene of Armenia (*L. oswaldi*, *L.* cf. *souffia* and *L.* sp.). The last molecular genetical studies of *L. cephalus* and its sister taxa showed, that the *Leuciscus cephalus* s.l. may have originated from the Mesopotamia in the middle of Pliocene (3.5-3 myr). After this, chub radiated to the European continent (Durand et al., 2000). Probably, the fossil species from the territory of Armenia are the “derivative” forms from ancestral *L. cephalus*.

5.4. Lower vertebrate paleofauna from the Pleistocene of Armenia

5.4.1. Lower vertebrate paleofauna of Sisian suite. According to our and literature data the fossil fauna of the Sisian suite consists of *Salmo* cf. *trutta*, *Alburnus sisianensis* and *Pelophylax* cf. *ridibundus*. The most abundant remains in this suite belong to *Salmo* cf. *trutta* from this suite. *Salmo derzhavini* was described earlier by Vladimirov (1946) from diatoms near the Shamb village (Sisian suite), which we suggest to belong to *Salmo* cf. *trutta*. *Salmo* cf. *trutta* from the Pleistocene of Armenia of the oldest record of this species worldwide.

***Paleoecology*.** The majority of salmonid remains (*Salmo* cf. *trutta*) are represented by a disarticulated skeleton and isolated vertebrae and scales. These records of *Salmo* cf. *trutta* indicate the presence of lakes and fast flowing (mountainous) rivers, where they could be inhabited during their whole life.

So far, salmonids were not found from the Pre-Pleistocene horizons in Armenia. The appearance of these fishes could be probably only occurred under a colder paleoclimate as was in the Pre-Pleistocene time. This must be also considered into account that in the Pleistocene the climate of the Earth became colder and glaciation was initiated (Stanly, 2001).

The most number of organic remains (Gabrielyan's unpublished data), as well as the fishes (70%) is found from the diatom sediments of Shamb locality (Sisian suite). This indicates that the major part of Paleovorotan river basin water flowed together into the paleolake near the village Shamb.

***Paleobiogeography*.** Fossil genus *Salmo* are scarcely recorded. Three fossil species are documented from North America (Cavender, Miller, 1982; Wilson, Li, 1999). *Salmo* cf. *trutta* as a fossil, is only known from the Middle to the Late Pleistocene of Germany (Böhme, 1997, 1998).

Osteological similarities between fossil and Recent brown trout from Caspian sea basin suggest a

possible origin of trout of the Pleistocene and Recent water bodies of Armenia from the Caspian Sea, i.e. they are migrants from this sea.

Formation of brown trout and its subspecies in the Ponto-Caspian basin is closely related to the geological history of the basin evolution. The Ponto-Caspian basin is resulted from the Paratethys break-up to the Black, Caspian and Aral Seas basins 2 myr ago (Rögl, 1999; Popov et al., 2004). In all these basins, the most number of *Salmo trutta* subspecies are found.

There are several ideas on the origin of salmonid fishes (Berg, 1949; Rukhkyan, 1989). Rukhkyan (1989) considered Ponto-Caspian basin as one of the speciation centre for salmonid species, namely brown trout (*Salmo trutta*) and its subspecies. Evidence from the present study greatly supports this idea.

5.4.2. Paleoichthyofauna of Sevan-1 locality. From the clay sediments of the Middle Pleistocene age, situated at the southern shore of the Sevan Lake with the remains of bivalve *Dreissena diluvii* is found pharyngeal tooth of *Capoeta* sp. (Sev). Co-occurrence of these taxa supports the presence of lake and slow flowing river on a silty substrate.

5.5. Development of lower vertebrate fossil fauna of Late Paleogene and Neogene of Armenia

Development of Late Paleogene and Neogene lower vertebrate faunas is closely related to the orogenesis of the Caucasus in the Pre-Oligocene time, which caused the uplift of the earth's crust and emergence of a landmass in the southern part of Armenia, as a part of Balkanian-Anatolian-Iranian archipelago, connecting Asia with Europe.

In this landmass at the South Armenia, during the Oligocene a freshwater" lake was inhabited by *Palaeoleuciscus macrocephalus*. This species reached this reservoir, probably, from the South-Western Asia. Faunal composition of this reservoir of the Oligocene age also supplemented by the other fish species *Enoplophthalmus* cf. *alsaticus, Prolebias armeniacus* and Perciformes gen. et sp. indet. (tabl. 3), from the Maikopian marine basin of the Kura depression, which could be possible, only by the presence of connection between these two water bodies.

During the Early and Middle Miocene the tectonic movements in Armenia were continuing, as a result in the central and southern parts of Armenia arose a landmass. Here another freshwater body appeared. From the sediments of this desalinated paleoreservoir on the south-western part of Armenia the typical freshwater, as well as gobiid fishes are revealed (tabl. 3). The latter probably reached this reservoir from the East, from the marine basin of the Kura depression and formed here "freshwater" forms. In the sediments of the Late Middle and the early Late Miocene (Sarmat) there were changed the species composition of brackish-lagoon fishes *Aphanius* sp., *Prolebias mutilus, Prolebias sp., Atherina schelkovnikovi* to the marine-pelagial *Alosa* sp. (tabl. 3). This was probably related to sea level changes of of Yerevan marine basin.

The Latest Miocene is significant when the final uplifting stages of modern territory of Armenia were occurred and freshwater condition was established. From this moment the development of the recent freshwater fish and amphibian fauna of Armenia starts.

From the Late Pliocene freshwater sediments of North Armenia, fishes of Leuciscinae subfamily is appeared (tabl. 4). From them, we suggest *Chondrostoma* sp. (Mays) as a descendent of *Chondrostoma* sp. (Okt) from the Early Miocene of Hoktemberyan locality, and *Pseudophoxinus* vel *Delminichthys* sp. descendant of *Palaeoleuciscus macrocephalus* from the Middle – Late Oligocene.

From the Pliocene, a network of vast lakes was formed in the territory of Armenia, as well as neighboring territories and the Balkanian Peninsula. Here the ancestral forms of Recent fauna of mentioned

territories were developed (Aslanyan, 1958; Brinkmann, 1976; Lüttig, Steffens, 1976; Görür et al., 1995; Harzhauser, Mandic, 2008).

Table 3.

Fossil fishes from Middle Oligocene – Late Miocene of Armenia.

Отряд	Вид	Age and suite				**Total** amoun of taxsa	Reference
		Oligocene	Miocene				
		Middle-Late	Early	Middle	Late		
		Dilijan	Hoktemberyan		Hrazdan-1		
Osmeriformes	*Enoplophthalmus* cf. *alsaticus*	X	-	-	-	1	this work
Clupeiformes	*Clupea* sp. 1	-	-	-	x	4	Bogachev, 1936
	Clupea sp. 2	-	-	-	x		
	Clupeonella pliocenica	-	-	-	x		Gabelaya, 1976
	Alosa sp.	-	-	-	x		Our studies
Atheriniformes	*Atherina schelkovnikovi*	-	-	-	x	1	Bogachev, 1936
Cyprinidontiformes	*Prolebias armeniacus*	X	-	-	-	4	Bogachev1962
	Prolebias mutilus	-	-	-	x		
	Prolebias sp.	-	-	-	x		
	Aphanius sp.	-	-	-	x		this work
Cypriniformes	*Palaeoleuciscus macrocephalus*	X	-	-	-	2	
	Chondrostoma sp. (Okt)	-	x	x	-		
Perciformes	Perciformes gen. et sp. indet.	X	-	-	-	3	
	Percidae gen. et sp. indet	-	x	x	-		
	Gobiidae gen. et sp. indet	-	-	x	-		
Total (according to localities)		4	3		8	15/15	-

Data from Nurnus locality shows that barbins (*Barbus* sp.) and leuciscins (*Alburnus* sp.) were appeared in the Early Pliocene. From the locality, a marsh frog, *Pelophylax* cf. *ridibundus* and toad *Bufo* sp. were also found (Melik-Adamyan, 2003).

The Middle Pliocene fish fauna of the Koturvan locality is represented by Leuciscinae gen. et sp. indet. In the Gelaysor and Dzorakhbyur localities again the leuciscin fishes *Alburnus gambariani, Leuciscus* cf. *souffia, Leuciscus* sp., *Leuciscus oswaldi* are dominant. The following taxa are described: *Capoeta* sp., *Garra* cf. *rufa* and marsh frog *Pelophylax* cf. *ridibundus* (tabl. 4). Taking the ecological feathers of these species into account, we infer that the climate in the Late Pliocene was warmer than today.

From early Pleistocene sediments of Sisian suite (Armenia), *Salmo* cf. *trutta* and *Alburnus sisianensis* were found (tabl. 4). There were no prepleistocene fossil records of brown trout from the territory of Armenia., Their occurrence Probably was possible only under lower temperature than in the Pre-Pleistocene time.

The absence of the Pre-Pleistocene relatively rich lower vertebrate fauna in the Pleistocene, possibly was a result of climate cooling, which caused migration of fishes downstream to the Caspian sea, where during the glaciations the climate cooling were not strong. Probably, when the glaciers from the territory of Armenia retreated the fish fauna migrated upstream. However, for some fishes, which now inhabit only downstream of the Kura river, migration upstream was impossible.

The formation and development of the Late Paleogene and Neogene fish and amphibian faunas underwent under the influence of the Armenian geological evolution, paleoenvironmental changes and habitat paleoclimate. Based on available data, we infer that the beginning of Recent fish and amphibian species composition started from the Late Miocene and the Early Pliocene. Ichthyofauna of this time was presented by the fishes of Leuciscinae subfamily (tabl. 3). In the Pliocene the fauna was supplemented due to fish species from the subfamilies Leuciscinae, Barbinae and Cyprininae, as well as anurans (tabl. 4) from the South and South-East. The Pleistocene glaciations result was supplementation of fish fauna by the

Table 4.

Fossil fishes and amphibians from Late Miocene – Pleistocene of Armenia.

Higher taxa		Speices	Age and locality							Total amount oof taxa	Reference
			Miocene	Pliocene				Pleistocene			
			late	Early	Middle	Early		Early	Mddle		
			Maisyan	Nurnus	Koturvan	Gelaysor	Dzoraghbyur	Sisian	Sevan-1		
Fam. Salmonidae		*Salmo* cf. *trutta*	-	-	-	-	-	x	-	1	Our studies
fam. Cyprinidae	subfam Leuciscinae	Leuciscinae gen. et sp. indet. (Mays)	-	-	x	-	-	-	-	10	Our studies
		Leuciscinae gen. et sp. indet. (Kot)	x	-	-	-	-	-	-		
		Pseudophoxinus vel Delminichthys sp.	x	-	-	-	-	-	-		
		Chondrostoma sp. (Mays)	x	-	-	-	-	-	-		
		Alburnus sp.	-	x	-	-	-	-	-		Melik-Adamyan, 2003
		Alburnus sisianensis	-	-	-	-	-	x	-		Pipoyan 2003
		Alburnus gambariani	-	-	-	-	x	-	-		Bogachev, 1936
		Leuciscus oswaldi	-	-	-	-	x	-	-		
		Leuciscus cf. *souffia*	-	-	-	x	-	-	-		Our studies
		Leuciscus sp.	-	-	-	x	-	-	-		
	subfam. Barbinae	*Capoeta* sp. (Sev)	-	-	-	-	-	-	x	3	
		Capoeta sp. (Gelays)	-	-	-	x	-	-	-		
		Barbus sp.	-	x	-		-	-	-		Melik-Adamyan, 2003
	subfam. Cyprininae	*Garra* cf. *rufa*	-	-	-	x	-	-	-	1	Our studies
Order Anura	fam. Ranidae	*Pelophylax* cf. *ridibundus*	-	x	-	x	-	x	-	2	Our studies
	fam. Bufo-nidae	*Bufo* sp.	-	x	-	-	-	-	-		Melik-Adamyan 2003
Total (according to localities)			3	4	1	5	2	3	1	17 / 18	-

trouts (family Salmonidae). As a result of glaciers retreatment earlier formed fauna became partly extinct. After thaw a part of fish fauna returned to their earlier habitats and the final development of recent fish faunal composition started.

ՀՀ ԳԻՏՈՒԹՅՈՒՆՆԵՐԻ ԱԶԳԱՅԻՆ ԱԿԱԴԵՄԻԱ
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ՎԱՍԻԼՅԱՆ ԴԱՎԻԹ ՋՈՀՐԱԲԻ

ՀԱՅԱՍՏԱՆԻ ՈՒՇ ՊԱԼԵՈԳԵՆՅԱՆ ԵՎ ՆԵՈԳԵՆՅԱՆ ՍՏՈՐԱԿԱՐԳ ՈՂՆԱՇԱՐԱՎՈՐՆԵՐԸ

Գ.00.08 – «Կենդանաբանություն» մասնագիտությամբ
կենսաբանական գիտությունների թեկնածուի գիտական
աստիճանի հայցման ատենախոսության

Ս Ե Ղ Մ Ա Գ Ի Ր

ԵՐԵՎԱՆ – 2009

Ատենախոսության թեման հաստատվել է ՀՀ ԳԱԱ Կենդանաբանության և հիդրոէկոլոգիայի գիտական կենտրոնի Կենդանաբանության ինստիտուտում

Գիտական ղեկավար՝ կենսաբանական գիտությունների թեկնածու
Մ.Խ. Պիպոյան

Պաշտոնական ընդդիմախոսներ՝ կենսաբանական գիտությունների դոկտոր
Ն.Հ. Մանասերյան
կենսաբանական գիտությունների թեկնածու
Հ.Ռ. Ռուբենյան

Առաջատար կազմակերպություն՝ Երևանի պետական համալսարան

Պաշտպանությունը կայանալու է՝ «12» հունիսի 2009թ. ժամը 15:00
ՀՀ ԳԱԱ Կենդանաբանության և հիդրոէկոլոգիայի գիտական կենտրոնում գործող ԲՈՀ-ի 036 մասնագիտական խորհրդի նիստում:
Հասցեն՝ 0014, Երևան, Պ. Սևակի 7, e-mail: zoohec@sci.am
Ատենախոսությանը կարելի է ծանոթանալ ՀՀ ԳԱԱ Կենդանաբանության և հիդրոէկոլոգիայի գիտական կենտրոնի Կենդանաբանության ինստիտուտի գրադարանում:

Սեղմագիրն առաքված է՝ «12» մայիսի 2009թ.
Մասնագիտական խորհրդի գիտքարտուղար,
կենսաբանական գիտությունների թեկնածու Հ.Գ. ԽԱՉԱՏՐՅԱՆ

ԱՄՓՈՓՈՒՄ

Ատենախոսությունը նվիրված է Հայաստանի ուշ պալեոգենյան և նեոգենյան ժամանակաշրջանների նստվածքաշերտերում հայտնաբերված ձկների և երկկենցաղների բրածո ֆաունայի ուսումնասիրությանը, նրանց պալեոմիջավայրի նկարագրմանը և կենսաաշխարհագրական որոշ հարցերի պարզաբանմանը, ինչպես նաև բրածո ֆաունայի ուսումնասիրության հիման վրա Հայաստանի ժամանակակից ստորակարգ ողնաշարավորների ֆաունայի առաջացման և ձևավորման ուղիների պարզաբանմանը:

Կատարված հետազոտությունների արդյունքում նկարագրվել են Հայաստանի օլիգոցենյան-պլեյստոցենյան տարիքի ութ տեղավայրերի ստորակարգ ողնաշարավորների 19 տաքսոններ, որոնք ներկայացված են 14 քաղցիամ ու 4 աղի կամ աղիավուն ջրերի բնակիչ ձկների և իսկական գորտերի մեկ տաքսոնով: Դրանցից 11 տաքսոններ՝ *Alosa* sp., *Pseudophoxinus* vel *Delminichtys* sp., *Leuciscus* cf. *souffia*, *Leuciscus* sp., *Garra* cf. *rufa*, *Enoplophthalmus* cf. *alsaticus*, *Aphanius* sp., *Salmo* cf. *trutta*, Perciformes indet., Percidae gen. et sp. indet. և Gobiidae gen. et sp. indet., Հայաստանի բրածո ձկնաշխարհի համար նկարագրվում են առաջին անգամ:

Հնէաբանական տարեգրության մեջ առաջին անգամ նշվում են ժամանակակից ցեղ *Garra*-ն, իսկ բրածո ցեղ *Enoplophthalmus*-ը նշվում է Արևելյան Պարաթետիսից առաջին անգամ: Գտնվել են *Chondrostoma* ցեղի Արևմտյան Պալեարկտիկայի ամենահին բրածո ներկայացուցիչների մնացորդները (*Chondrostoma* sp. (Okt) և *Salmo trutta* տեսակի ամենահին մնացորդները:

Ցույց է տրվել, որ օլիգոցենում Հայաստանի ներկայիս տարածքը, հանդիսանալով Բալկանո-Անատոլա-Իրանական կղզիախմբի մասը, գտնվել է քաղցահամ ջրերի ձկնատեսակների Ասիայից Եվրոպա տարաբնակեցման ուղու վրա: Այդ ժամանակ Հայաստանի հյուսիսում գոյություն ունեցող քաղցրահամ ջրամբարը կապ է ունեցել Մայկոպյան ավազանի ծովային ջրերի հետ, որի մասին են վկայում այս ջրամբարի նստվածքաշերտերում հայտնաբերված աղիավուն ջրերի բնակիչ ձկների առկայությունը:

Սարմատի ընթացքում Երևանյան ավազանի ձկնաշխարհի ծովալճակային-աղիավուն ջրերի բնակիչ ձկները իրենց տեղը զիջում են ծովային պելագիալ ձկներին, ինչը պայմանավորված էր այս ջրավազանի խորության և/կամ ափեզրի փոփոխությամբ:

Հայաստանի տարածքում բրածո անուշահամ ձկնաշխարհի ձևավորման պահից (միջին օլիգոցեն) ձկների գերակայող խումբ էին հանդիսանում Leuciscinae ենթաընտանիքի ներկայացուցիչները: Ձկնաշխարհի կազմը, պահպանելով այս ենթաընտանիքին պատկանող տեսակների քանակական գերակայությունը, վաղ պլիոցենից, երբ սկսվում է Հայաստանի ժամանակակից ձկնաշխարհի ձևավորումը, համալրվում է Barbinae ենթաընտանիքի ձկնատեսակներով, իսկ վաղ պլեյստոցենում սաղմոնայիններով (Salmonidae): Ուշ պլեյստոցենում՝ վերջին սառցապատումից հետո, Հայաստանի ձկնաշխարհը մտնում է իր զարգացման վեջնական փուլ:

Ստացված տվյալները հետագայում թույլ կտան վերականգնել Հայաստանի ժամանակակից ձկների և երկկենցաղների ֆաունաների ձևավորման և նրանց պալեոմիջավայրի ամբողջական պատկերը: