

Early-Middle Pleistocene environmental and biotic transition in north-western Armenia, southern Caucasus

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ABSTRACT

Quaternary biota of north-western Armenia is studied from several localities in the Ani and Arapi fluvial formations of the Shirak and Upper Akhuryan sedimentary basins. Palynology of lacustrine deposits of the Ani Formation indicates cyclic alternation of forest-steppe and steppe coenoses in the Shirak Depression. The patchy pollen record from the sections of the Arapi Formation indicates forest-steppe coenoses. Aquatic molluscs from the Ani Formation are dominated by gastropods and dreissenid bivalves. Molluscs of the Arapi Formation are characterised by limnophilic freshwater species with mostly extant forms. The Arapi deposits yielded remains of fishes, amphibians, and small mammals. The freshwater fish assemblage comprises cyprinid species that derived from the earlier Plio-Pleistocene fish communities of Armenia. The assemblage indicates lacustrine and river habitats with rocky bottoms and the presence of water plants overgrowth. The herpetofauna from the Arapi Formation includes remains of anuran amphibians that indicate aquatic habitats. Small mammals include *Sorex* cf. *runtonensis*, *Neomys* cf. *hintoni*, *Ochotona* sp., *Mimomys intermedius*, *Terricola* sp., *Microtus* gr. *nutiensis*, *Prolagurus pannonicus transylvanicus*, and *Ellobius pomeli*. This fauna characterises the Leninakan (Gyumri) faunal assemblage correlated to the late Biharian of the European land mammal biochronology, Tiraspol faunal complex of Eastern Europe, and the Cromerian of NW Europe. The studied record has an important biogeographic significance for the southern rim of the Ponto-Caspian region. It shows the complex history of the biotic exchanges and polygenous origin of the terrestrial communities in the southern Caucasus. Radiometric, paleomagnetic, and biotic control make it possible to date the Ani deposits to late Early and earliest Middle Pleistocene. The age of the Arapi formation is early Middle Pleistocene older than 0.6 Ma. The main trend of landscape evolution in the region between ca. 1.5-0.7 Ma is a transition from forest-steppe to steppe conditions.

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INTRODUCTION

The Quaternary terrestrial biotic record of north-western Armenia is crucial for stratigraphy and correlations, and for understanding the development of Pleistocene biota under conditions of fluctuating climate, volcanic activity, and general neotectonic uplift of the Lesser Caucasus. Sedimentary filling of the depositional basins along the Akhuryan valley in Armenia are under study for a long time. The successive Ani and Arapi formations are traditionally recognised in the Shirak basin (Sayadyan, 1972). According to the paleontological and paleomagnetic data, the two formations correspond to late Early Pleistocene (the Ani Formation, Fm) and earliest Middle Pleistocene (Arapi Fm) (Sayadyan, 2009; Shalaeva et al., 2019).

Recent study of stratigraphy and neotectonics of NW Armeina based on several reference sections (Shalaeva et al., 2019) brought new diverse paleontological materials. In this contribution we specifically focus on the biotic record of the Ani and Arapi deposits. Fossils were analysed from sections Voghji and Haykavan (Ani unit, palynology, molluscs), Lusaghbyur and Haykadzor (Arapi unit, molluscs, fishes, amphibians, and mammals), and Krasar (Kurtan unit, palynology, mammals) (Figures 1-2). The data on palynology and molluscs are reviewed on the level of assemblages. The for-

mal paleontological description of vertebrates is given separately.

The general aim of the paper is accurate documentation of the new paleontological record of late Early and early Middle Pleistocene of western Armenia as a basis for regional stratigraphy, history of climate and environment, and biogeographic connections in the broad Ponto-Caspian region, and for refining the mammalian biochronology of western Asia.

Our research is backed by important results of the previous studies, especially in palynology and fossil mammals. Palynological study of the lacustrine-fluviatile deposits of the Shirak Depression was first conducted by Sayadyan (1972, 2009) and Zaikina et al. (1969a, b). The deposits of substantially clayey Ani Fm record the main period of the development of the Shirak Paleolake. The study of these deposits showed a cyclic change of vegetation in the Ani time from forest-steppe phase through a steppe period to a well expressed forested phase at the top of the formation (Sayadyan, 1972). Data on Pleistocene diatom assemblages of the Shirak Depression was obtained from the lacustrine diatomaceous deposits of the Ani unit in the sections of Arapi and the Marmashen borehole 6 (Zaikina et al., 1969a, b). Additional diatom materials were recently studied in the Ani sections of Haykavan (lower part) and Arapi deposits of the



FIGURE 1. Schematic map showing the position of the studied sections.

Haykadzor section (beds 6-7) (Shalaeva et al., 2019). The general revealed trend is from assemblages with higher representation of planktonic forms in lower parts of the Ani Fm towards associations with growing role of bottom and littoral forms higher in the Ani sequences and in the Arapi Fm. This picture supports a concept of a shallowing of the Pleistocene Shirak Lake (Sayadyan, 2009) from late Early to early Middle Pleistocene.

The fluvial deposits of the Arapi formation in the Shirak Basin of western Armenia yielded a large mammal assemblage, with the elephant *Mammuthus trogontherii* (Pohlig, 1885) and other forms, defined as the Leninakan (later, Gyumri) faunal complex (Avakyan, 1959) correlated to late Middle Pleistocene (Sayadyan, 1970, 2009; Alekseeva, 1977). The remains of Quaternary small mammals from the same fluvial formation in western Armenia were studied by Melik-Adamyanyan and Agadjanyan (Agadjanyan, Melik-Adamyanyan, 1985; Melik-Adamyanyan, 1985, 1994, 2003, 2004).

The composition of this fauna with *Mimomys intermedius*, advanced *Prolagurus pannonicus*, and basal *Terricola* clearly indicated an older, early Middle Pleistocene age of the Gyumri assemblage (Agadjanyan, Melik-Adamyanyan, 1985; Melik-Adamyanyan, 2004). Likewise, Forsten (1999) based on the morphology of horse remains from the Leninakan assemblage questioned the original age estimations as too late “for such a large stenorid horse” and argued for an early Middle Pleistocene age. She also rejected an assignment of these horses by Alexeeva (1977) to caballoid forms (Forsten, 1999). The additional age control was provided by the geochronology of the Leninakan tuffs covering or interfingering with Arapi deposits yielding dates in the range of 0.65–0.7 Ma (Melik-Adamyanyan, 2016; Shalaeva et al., 2019) and normal polarity (Brunhes Chron) of these deposits (Sayadyan, 2009; Trifonov et al., 2017; Shalaeva et al., 2019). Recently small mammals of the Gyumri appearance were found in the Krasar (bed 2) section in Upper Akhuryan basin of western Armenia (Trifonov et al., 2016; Tesakov, 2016). In 2015-2016 the relatively abundant association of small mammals was recovered from the Arapi deposits near the village of Haykadzor, in bed 4 of the Haykadzor section (Shalaeva et al., 2019).

GEOLOGICAL SETTING

Early and early Middle Pleistocene deposits fill the Upper Akhuryan and more southern Shirak basins (Figure 1). The latter extends to the adjacent part of North-Eastern Turkey. These deposits are differentiated into the Karakhach, Ani, and Arapi sedimentary units (formations) in the Shirak Basin (Sayadyan, 2009; Trifonov et al., 2017). In the northern margin of the Shirak Basin, the Lower Pleistocene Karakhach unit occupies the highest topographic position. The 6 m thick analog of Ani and Arapi units (Kurtan unit) is incised into the upper terrace composed by the Karakhach unit near the Kaps village (Trifonov et al., 2017). The surface of the Kurtan unit terrace is 60–70 m lower than the Karakhach unit terrace. Just to the south, the Ani unit thickness abruptly increases on the W–E-trending Kaps flexure-fault zone (Trifonov et al., 2017) and reaches 137 m in the northern Shirak Basin, in the borehole 6 near the Marmashen village (Sayadyan, 2009). The Arapi unit is incised into the Ani unit terrace, and the Arapi unit surface is situated ca. 50 m lower than the Ani unit terrace (Trifonov et al., 2017). In the central Shirak Basin, the Karakhach unit thins out, and the Ani unit covers the basaltic trachyandesites with the K/Ar and

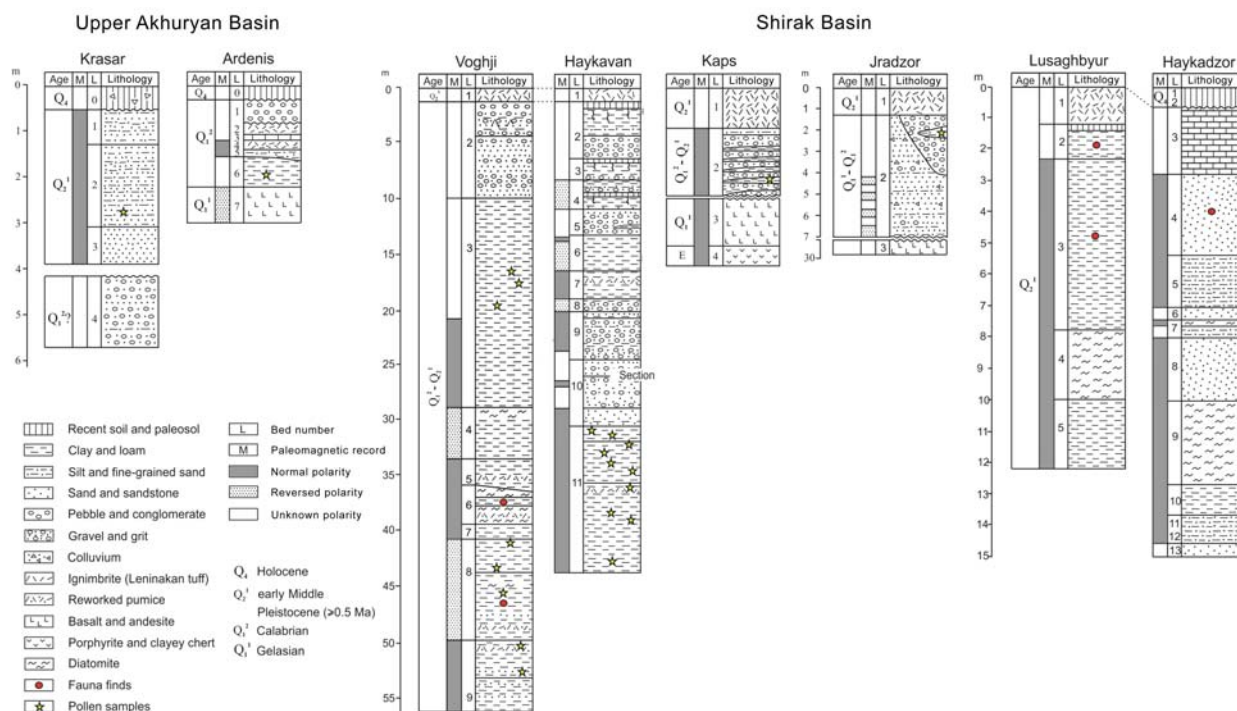


FIGURE 2. Main studied sections of Quaternary deposits in north-western Armenia (modified after Shalaeva et al., 2019).

$^{40}\text{Ar}/^{39}\text{Ar}$ dates of 2.0–2.3 Ma that underlie the Karakhach unit in the northern margin of the basin (Ritz et al., 2016; Trifonov et al., 2017; Shalaeva et al., 2019). Farther to the south, the Arapi unit covers the Ani unit in the Lusaghbyur locality. In this section deformed by a fault, the Ani deposits are exposed in the diapir piercing the Arapi sequence (Shalaeva et al., 2019). In the southern margin of the basin, in the section of Haykadzor, the Arapi unit overlies Early Pliocene basaltic andesites (the K/Ar dates 5.60 ± 0.15 Ma to 4.26 ± 0.12 Ma) (Shalaeva et al., 2019). Therefore, the Karakhach unit is older than the Ani one, and the Arapi unit is the youngest.

The deposits that are attributed to the Karakhach unit in the Shirak Basin are correlated with the unit stratotype in the Karakhach quarry in the south-western Lori Basin, where the unit is dated to 1.9–1.7 Ma by the SIMS $^{238}\text{U}/^{206}\text{Pb}$ method with using volcanic zircons and by the remanent magnetic polarity analysis (Presnyakov et al., 2012; Trifonov et al., 2016). These deposits are characterised by similar lithology (mountain alluvium), archaeological finds (earliest Paleolithic), and magnetic polarity with a normal zone in the lower part (Olduvai Subchron) and a reverse one in the upper part (the lowest part of Upper Matuyama Chron), although the lower part of the unit with nor-

mal magnetic polarity is reduced in the Shirak Basin.

The detailed description of geological setting of late Early and early Middle Pleistocene deposits of the Shirak Basin is given in the paper of Shalaeva et al. (2019). Both Ani and Arapi units are mainly composed of lacustrine deposits in the lower and middle parts and of the fluvial sediments in the uppermost part. The lower part of the Ani unit shows alternating beds with reverse and normal magnetic polarity in the Voghji and Haykavan sections (Figure 2). The magnetization of the upper part of the Ani unit was examined only in the Voghji section and showed normal polarity. All studied Arapi unit sections show normal magnetic polarity. The Arapi unit is covered by trachydacitic ignimbrites (so called Leninakan tuffs) with $^{40}\text{Ar}/^{39}\text{Ar}$ date of 0.65 ± 0.04 Ma (Gevorgyan et al., 2018) and K/Ar dates 0.68 ± 0.05 Ma (Shalaeva et al., 2019). Melik-Adamyanyan (2003), however, reported the upper layers of the Arapi unit covering this tuff near the Gyumri Airport. The molluscan association of the Arapi unit contains mostly Recent limnic species contrary to the Ani mollusc fauna represented mainly by extinct fresh water species (Shalaeva et al., 2019). The combination of these data gives a possibility to date the Ani unit within the time interval ca. 1.5–0.8 (?0.75) Ma and

the Arapi unit at 0.70–0.65 Ma. The paleontological data presented below support these estimates.

In the Upper Akhuryan Basin, the late Early and early Middle Pleistocene deposits form the Kurtan unit (Trifonov et al., 2016). Its stratotype is situated in the south-eastern Lori Basin, where the Kurtan unit overlies reversely magnetised ash and pumice layers. The pumice fills a small depression incised into the eroded surface of basaltic trachyandesites with K/Ar date 2.08 ± 0.10 (Trifonov et al., 2016). The SIMS U-Pb and $^{39}\text{Ar}/^{40}\text{Ar}$ dates of the pumice are 1.495 ± 0.021 Ma and 1.49 ± 0.01 Ma, correspondingly, and the SIMS U-Pb date of the ash is 1.432 ± 0.028 Ma (Presnyakov et al., 2012). The lower part of the Kurtan unit shows reverse magnetic polarity with a short interval of normal polarity (Jaramillo Subchron) and the upper part of the unit shows normal magnetic polarity (Trifonov et al., 2016, 2017). The fragmentary left humerus of southern elephant *Archidiskodon ex gr. meridionalis* (Nesti, 1825) was found in the lower part of the unit. The Krasar section in the Upper Akhuryan Basin (Figure 2) belongs to the upper part of the Kurtan unit. The section deposits show normal magnetic polarity and contain remains of mammals. Combining the chronological information from large and small mammals and the paleomagnetic data, an early Middle Pleistocene age of the section seems to be the most plausible (Trifonov et al., 2016).

MATERIALS AND METHODS

Palynological studies were based on more than 200 samples from 16 sections. The revealed concentration of palynomorphs strongly varied. The highest content of pollen (80–322 grains) was found in clayey deposits of the Ani Fm in sections of Ardenis, Marmashen, Arapi, Haykavan, and Voghji. In silty, gravely and sandy, and diatomaceous deposits in the sections of Lusaghbyur, Haykadzor, and Gyumry (Airport) we found only single pollen grains or none at all. Some samples in loamy deposits in the youngest sections of Haykadzor, Kaps, and Jradzor yielded up to 100 grains.

Preparation of samples was carried out according to the modified separation method. It includes a treatment with 10% hydrochloric acid (HCl) to remove carbonates, washing samples by adding distilled water until neutral reaction, processing samples with hot 10% disodium phosphate (Na_2HPO_4), removing clay particles by washing out the sediment with distilled water, separation of the resulting precipitate in heavy liquid potassium

tetraiodocadmate ($\text{K}_2[\text{CdI}_4]$) with a density of 2.25 to extract fossil palynomorphs. In addition the sediment was treated with hydrofluoric acid (HF). Palynological preparations were studied under Motic VA 400 optical microscope equipped with Moticam 2300 camera, at magnification of $\times 400$. Pollen diagrams were compiled using Tilia 2.0.41 software.

The molluscan and microvertebrate remains were collected in the field in 2013–2016 by the field team of the Geological Institute of the Russian Academy of Sciences headed by V. Trifonov in collaboration with geologists from the Institute of Geological Sciences of the National Academy of Sciences of Republic of Armenia. The standard technique of dry screening with the use of 0.7 and 1.0 mm mesh size sieves was utilized. The microvertebrate concentrate was separated in several size fractions and manually sorted in the laboratory. The geographic positions of the studied sections are given in captions to Figure 1.

Geographic positions of the studied sections: Ardenis ($41^\circ 03' 54.78''\text{N}$ $43^\circ 42' 43.14''\text{E}$), Krasar ($41^\circ 00' 45.18''\text{N}$ $43^\circ 49' 52.32''\text{E}$), Jradzor ($40^\circ 54' 29.80''\text{N}$ $43^\circ 46' 16.59''\text{E}$), Kaps ($40^\circ 52' 22.33''\text{N}$ $43^\circ 45' 02.13''\text{E}$), Marmashen ($40^\circ 50' 26.26''\text{N}$ $43^\circ 45' 30.23''\text{E}$), Voghji ($40^\circ 49' 34.63''\text{N}$ $43^\circ 44' 44.16''\text{E}$), Haykavan ($40^\circ 48' 50.51''\text{N}$ $43^\circ 44' 54.64''\text{E}$), Arapi ($40^\circ 46' 26.58''\text{N}$ $43^\circ 48' 22.14''\text{E}$), Lusaghbyur ($40^\circ 38' 38.22''\text{N}$ $43^\circ 44' 30.42''\text{E}$), Haykadzor ($40^\circ 32' 16.02''\text{N}$ $43^\circ 39' 21.13''\text{E}$).

The terminology of the fish pharyngeal teeth follows the system of Rutte (1962) partially modified by Sytchevskaya (1986). The morphological terminology of anuran bones is after Bolkay (1919). The terminology of equine premolar is according to Gromova (1949) and Eisenmann (1981). The terminology of arvicoline molars follows van der Meulen (1973) and Rabeder (1981). The terminology of arvicoline enamel differentiation patterns and indexes follows Heinrich (1982). All measurements are in mm.

The violin diagram was produced using the Past software v.3.19 (Hammer et al., 2001).

The authors of this paper contributed to the study of small mammals and biochronology (A.S. Tesakov), palynology (A.N. Simakova), molluscs (P.D. Frolov), fishes (E.K. Sytchevskaya), amphibians (E.V. Syromyatnikova), large mammals (I.V. Foronova), and geological setting (E.A. Shalaeva and V.G. Trifonov).

Paleontological materials described in this paper are preserved in the Geological Institute of the Russian Academy of Sciences, GIN (GIN-1141,

1142, 1172: molluscs, amphibians, small mammals) and Paleontological Institute of the Russian Academy of Sciences, PIN (PIN-5595: fishes) in Moscow.

BIOTIC RECORD

Palynology

In our work we studied the palynology of two sections of lacustrine deposits of the Ani Fm, Voghji and Haykavan and several sections exposing younger deposits of the Arapi Formation. According to the paleomagnetic data, the Ani Fm is dated to the late Early and earliest Middle Pleistocene (Shalaeva et al., 2019). Palynological data were obtained from eight sections (Figure 3) of the Early-early Middle Pleistocene units of Shirak and Upper Akhuryan basins. The oldest spectra came from a loam bed underlain by basaltic andesites with K-Ar date of 2.00 ± 0.10 Ma (Trifonov et al., 2016) in the quarry southwest of the Ardenis village in the Upper Akhuryan Basin (Figure 2). The spectrum is dominated by coniferous pollen (90%) mainly represented by pine, including *Pinus* sect. *Strobus*, *Pinus* cf. *excelsa*, and birch (16%). Also encountered is the pollen of *Picea*, *Podocarpus*. Also present are single grains of *Quercus*, *Tilia*, *Salix*, Ericales, Chenopodiaceae, and Filicales. These data indicate the widespread pine-birch forests.

In the Shirak Basin, the oldest palynological records came from the dark olive-coloured clays of the Ani Fm in the section near the Marmashen monastery (Shalaeva et al., 2019; Figure 4) The 65 m thick clays overlie basaltic andesite outcropping in the channel of Akhuryan River. Another location of an older record is the section exposed in the roadcut near the village of Arapi (Shalaeva et al., 2019; Figure 4). Clays in Marmashen show a spectrum dominated by pollen of trees as *Pinus*, *Picea* (98%), with additions of pollen of *Cedrus*, *Podocarpus*, and *Abies*. These data evidence the widespread pine-spruce forests gradually replaced by pine forests with rare occurrence of *Picea* and *Tsuga* (olive-coloured clays of the Arapi roadcut section) interpreted as the onset of aridisation. Pollen data on these three sections indicate moist temperate continental climatic period possibly matching climatically based stratons (climatoliths) 11 or 13 of regional climatical periodisation defined by Sayadyan (2009).

The overlying sediments of the Ani Formation in sections of Haykavan and Voghji (Figure 2) contain clayey diatomites, dark-brown clays with abun-

dant molluscan remains strongly dominated by *Dreissena* and interlayers of volcanic material. The pollen spectra of the lower parts of the sections (Figures 2-4; Shalaeva et al., 2019) show a high share of Chenopodiaceae, Asteraceae, and *Ephedra*. The content of arboreal pollen amounts to 15-50%. The spectra are specific in high diversity of conifers: *Taxodium*, *Podocarpus*, *Tsuga canadensis*, cf. *Tsuga sieboldii*, *Tsuga aculeata*, *Tsuga diversifolia*, *Abies*, *Picea*, *Pinus*, and broadleaved trees: *Acer*, *Castanea*, *Carya*, Juglandaceae, Moraceae, *Carpinus*, Fagaceae, *Tilia*, *Ulmus*, *Liquidambar*, *Myrica*, and *Quercus*. The spectra indicate a presence of altitudinal zonation manifested in the regular change of plant communities. The association of higher altitudinal zones is characterised by *Sciadopitys*, *Podocarpus*, *Cedrus*, *Tsuga*, *Picea*, and *Abies*. Lower belts were dominated by mixed pine and broad-leaved forests. The low elevations were covered by meadow-steppe vegetation in a relatively warm temperate climate. Lower parts of Haykavan and Voghji sections indicating an interval of predominant forest-steppe under conditions of semi-humid temperate climate we correlate with the climatolith 15 of the scheme elaborated by Sayadyan (2009).

The amount of pollen of grasses and shrubs (Chenopodiaceae, Asteraceae, *Ephedra*) increases upsection in Haykavan. At the same time the spectra show a decreasing amount of *Picea* and *Pinus*, and disappearance of *Cedrus*, *Abies*, *Podocarpus*, and *Carya*. The leaved trees and shrubs are represented by *Ilex*, *Acer*, Moraceae, Fagaceae, *Lonicera*, *Salix*, and *Quercus*. Also present are spores of freshwater algae *Cosmarium* and spores of *Sphagnum*. These indicate the presence of swampy areas that could possibly originate during the shallowing of the paleolake. Steppe vegetation expanded, and this stage can be correlated with climatolith 16 (semi-arid steppes and forest-steppe) of Sayadyan (2009). Similar spectra were obtained from the clays of the lower part of borehole 6 near the village of Marmashen, interpreted as the deposits of the 6th terrace of the Akhuryan River at the depth of 30-50 m (Zaikina et al., 1969).

The upper part of the Voghji section (Figure 2) documents an interval with increasing amount of pollen of *Pinus* and *Tsuga*. Deciduous trees are represented by the pollen of *Castanea*, *Betula*, *Ulmus*, and *Quercus*. The representation of Chenopodiaceae and *Ephedra* decreases. This is a period of expansion of coniferous forests (pine and spruce-tsuga) during colder and wet climatic conditions. The uppermost part of the Voghji section is

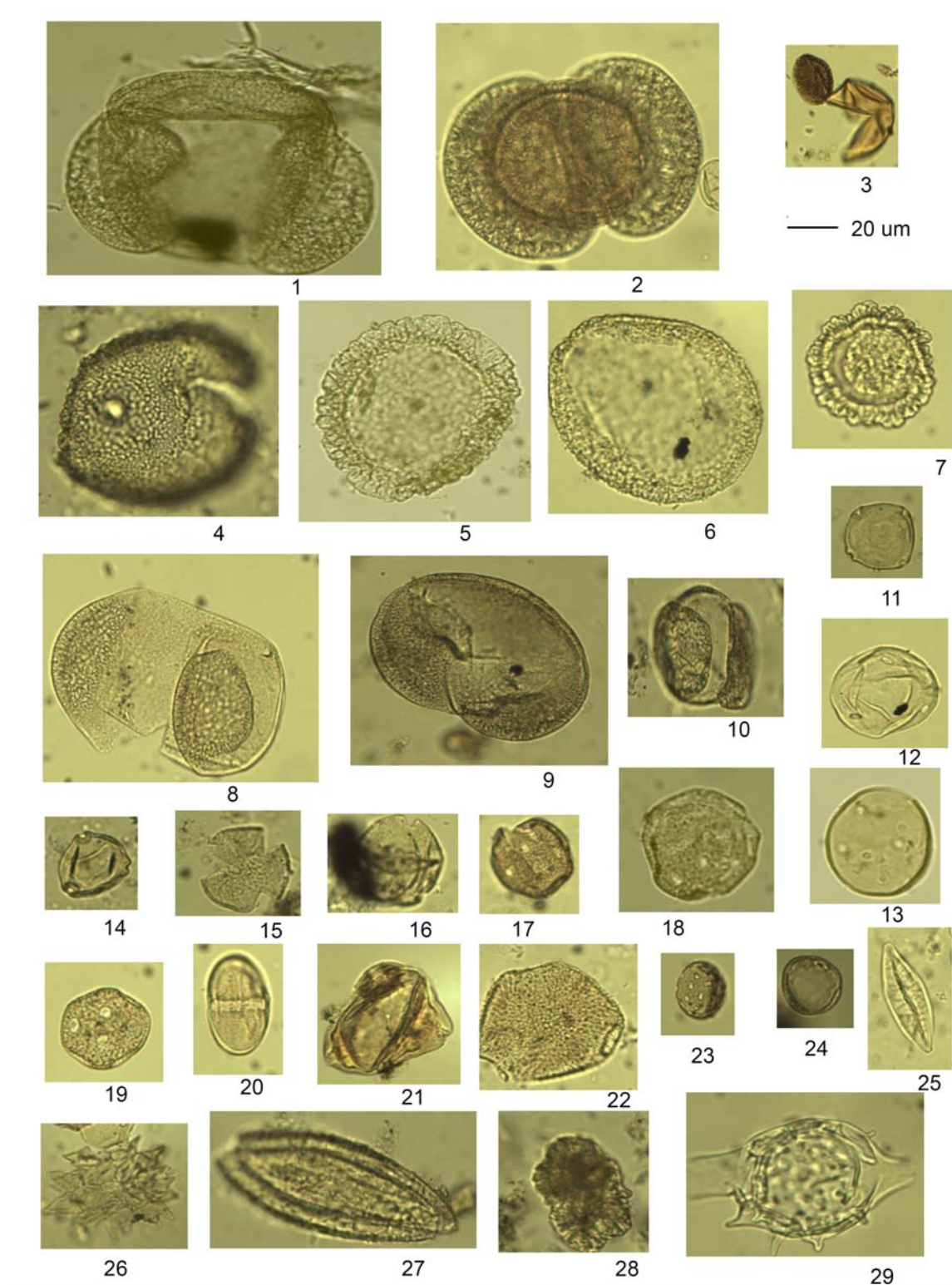


FIGURE 3. Characteristic palynomorphs of the Quaternary deposits of the Ani Formation, north-western Armenia. 1. *Abies* sp.; 2. *Podocarpus* sp.; 3. Taxodiaceae; 4. *Tsuga canadensis*; 5. *Tsuga diversifolia*; 6. *Tsuga aculeata*; 7. *Tsuga sieboldii*; 8. *Picea* sect. *Eupicea*; 9. *Picea* sect. *Omorica*; 10. *Pinus* sp.; 11. *Pterocarya* aff. *stenoptera*; 12. *Carya* sp. 13. *Juglans* sp.; 14. *Betula* sp.; 15. *Acer* sp.; 16. *Fagus* sp.; 17. cf. *Altingia*; 18. *Liquidambar* sp.; 19. Caryophyllaceae; 20. Boraginaceae; 21. Onograceae; 22. *Scabiosa* sp.; 23. Chenopodiaceae; 24. Poaceae; 25. *Ephedra* sp.; 26. *Pediastrum*; 27. *Spirogyra*; 28. *Botryococcus*; 29. unidentified.

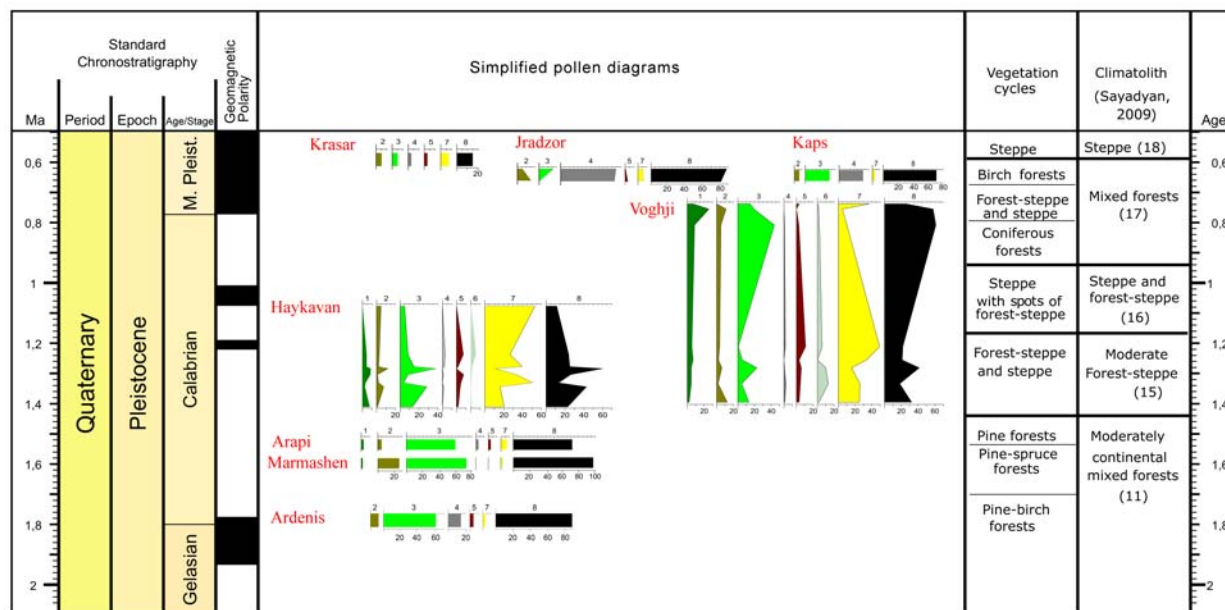


FIGURE 4. Palynological subdivision of the late Early – early Middle Quaternary deposits of north-western Armenia. Stratigraphic positions and ranges of the sequences are tentatively modeled based on data from Trifonov et al. (2016, 2017) and Shalaeva et al. (2019). I – Krasar; II – Jradzor (Shirak Province); III – Kaps; IV – Haykavan; V – Voghji; VI – Arapi; VII – Marmashen; VIII – Ardenis; 1 – *Podocarpus*, *Sciadopitys*, *Tsuga*, *Taxodium*; 2 – *Picea*, *Abies*, *Cedrus*; 3 – *Pinus*, 4 – *Betula*, *Salix*, *Alnus*; 5 – broad-leaved trees; 6 – *Ephedra*, 7 – *Artemisia*, Chenopodiaceae; 8 – arboreal pollen relative to total pollen sum.

characterised by an increase in grass pollen (Chenopodiaceae and Asteraceae) representative of the widespread steppe coenoses under dry and cool climate.

Palynological characteristics for the Arapi Formation were obtained from alluvial deposits capped by the Leninakan tuff on the northern side of the Shirak Depression, in sections Kaps and Jradzor (Figure 2). The spectra contain up to 75% of arboreal pollen (*Pinus* and *Betula*) indicating dominant pine-birch forests. These spectra lack exotics elements common for assemblages of the Ani Fm. The deposits of Kaps and Jradzor indicating humid and moderately continental climate can be compared with the climatolith 17 of Sayadyan (2009).

The youngest spectra of the Arapi Fm were obtained from the lacustrine-alluvial deposits of the Middle Pleistocene in the section of the Krasar (Upper Akhuryan Depression). Grass pollen (Asteraceae and Chenopodiaceae) dominates in the assemblage. Pollen of *Pinus*, *Picea*, *Betula*, and *Ulmus* are represented by single grains. The content of arboreal pollen is less than 20% of the pollen sum. These spectra indicate a predominance of meadow-steppe landscapes. According to palynological data, the deposits of Krasar can be

correlated with the semiarid climatolith 18 and the upper lacustrine-alluvial complex of the Middle Pleistocene of the Shirak Basin (Sayadyan, 1972, 2009).

The presence of a significant number of arboreal species not common (“exotic”) to the recent flora of the studied region (Figure 3) in the palynological spectra of the Ani Formation (*Tsuga aculeata*, *Tsuga canadensis*, *Tsuga diversifolia*, cf. *Tsuga sieboldii*, *Podocarpus*, *Cedrus*, *Abies alba*, *Abies nordmanniana*, *Taxus*, *Liquidambar*, *Castanea*, and *Carya*) indicate the ancient age of the lacustrine sediments of the Shirak and Upper Akhuryan depressions. A comparison with the palynological record of the neighbouring regions shows similar trends regardless of possible regional differences. The vegetation of the south and southeast Armenia in the second half of the early Pleistocene (1.41-0.94 Ma) had a mosaic structure combining mixed forests and open areas with steppe plant communities (Joannin et al., 2010; Scharrer, 2013). Palynological spectra of late Early Pleistocene in Georgia (early Chaudian) (Mchedlishvili, 1984, Chochieva, 1999; Shatilova, et al., 2011) are characterised by diverse and abundant *Tsuga*, as well as by the presence of *Podocarpus* and *Pseudotsuga*, which do not occur

in younger sediments. The record of Azerbaijan also shows an expansion of forest vegetation edited by birch, alder, spruce and tsuga in late Early Pleistocene (0.95-0.77 Ma). Thus, the pollen spectra of the Ani Formation of northeastern Armenia reflect a common climatic trend in late Early Pleistocene of the southern Caucasus and the adjacent Caspian region (Zaikina et al., 1969a, b, Filippova, 1997; Shatilova, 1974; Joannin et al., 2010; Tagieva, 2011; Shatilova, et al., 2011; Scharrer, 2013). In general, the vegetation of Armenia during late Early Pleistocene had a mosaic structure and combined mixed forests and open areas with steppe vegetation. In colder stages, the meadow-steppe vegetation shows a predominance of Asteraceae, Chenopodiaceae, and *Artemisia*. Forests of that time were dominated mainly by coniferous trees *Pinus*, *Tsuga*, *Abies*, and *Sciadopitys*. In warmer periods the mountain slopes hosted sparse mesophilic forests with *Quercus*, *Carpinus*, *Juglans*, Ulmaceae, *Picea*, and *Tsuga*, and the open spaces were covered with herbaceous steppes.

At the beginning of the Middle Pleistocene, in contrast to Western Georgia (Shatilova et al., 2011), relict arboreal elements nearly disappeared in pollen spectra from the Shirak and Upper Akhuryan Basin (Sayadan, 1972, 2009; Trifonov et al., 2016) succeeded by assemblages with widespread forest-steppe and meadow-steppe vegetation.

Molluscs

Six molluscan associations from four sections were studied from deposits of the Ani and Arapi formations (Table 1). The fauna of the Ani Fm is represented by the assemblages of Voghji, Haykavan, and that of the diapir beds of Lusaghbyur. The assemblage derived from beds, which confine the diapir in the Lusaghbyur section, is regarded as malacologically transitional between faunas of Ani and Arapi formations. The assemblages sampled from the upper part of Lusaghbyur section and from Haykadzor section characterise the fauna of the Arapi Fm.

Aquatic molluscs from the Ani Fm (Figures 5-6) are co-dominated by extinct species *Falsipyrgula sieversi* and *Dreissena diluvii*. This association is similar to the fauna with sculptured pyrgulids previously described from the middle level of the Leninakan/Gyumri Lake deposits in northwestern Shirak Depression (Akramowski, 1956) and Early Pleistocene molluscan fauna from eastern Turkey (Vasilyan et al., 2014). The most representative of the Ani Fm assemblages is that from the section of

Voghji. It includes abundant hydrobiid gastropods and the fossil bivalve *Dreissena diluvii*.

The abundant hydrobiid shells are represented by the genera *Shadinia* Akramowski, 1976, and *Falsipyrgula* Radoman, 1973 (Figure 6).

The genus *Shadinia* contains three modern species: *S. terpoghassiani* (Shadin, 1952), *S. akramowskii* (Shadin, 1952), and *S. bjniensis* Bößneck, Walther and Neiber, 2016 (Zhadin, 1952; Glöer et al., 2016; Anistratenko et al., 2017). In our materials there are elongated shells reminiscent of *S. terpoghassiani* and more squat forms resembling *S. cf. akramowskii*. These shells differ from the modern species in more convex whorls. One of these forms, *S. terpoghassiani*, represents the modern species. It is possible that the other one will be later described as a new species.

Pyrgula-like shells are referred to the genus *Falsipyrgula* Radoman, 1973, following Schütt and Yildirim (1999). In his preceding works Schütt (1991, 1997) referred these shells to the genus *Pyrgula*. When describing the genus *Falsipyrgula*, Radoman (1973) noted the characters of soft body as the main distinction from the closely related *Pyrgula*, *Diana*, and *Xestopyrgula*; the shell structure showed very little differentiation. Anistratenko (2008), however, remarked that *Falsipyrgula* is characteristic in a clear keel above the suture. In our materials there are several forms of this genus: *Falsipyrgula shadini* (Akramowski, 1956), *F. sieversi* (Boettger, 1881), *F. cf. shuetti* Yildirim, 1999, and *F. sp.*

In the Voghji locality, shells of *F. sieversi* are the most numerous. They are quite variable as was noted by Akramowski (1956). Our material shows all transitional forms from shells nearly lacking a keel to the shells with a well-developed keel, with a gradual flattening of the whorls. Today *F. sieversi* occurs in the eastern region of Turkey (Yildirim, 1999).

Falsipyrgula shadini was described from a sand pit near Byurakn (formerly Gyullibulagh) village in the Shirak province of Armenia, 12 km north-west of Gyumri (Akramowski, 1956). The enclosing deposits obviously correspond to the Ani Formation. Another fossil record comes from the Yayladag site (Pasinler Basin, Turkey), which is correlated with late Early Pleistocene (Schütt, 1997; Schütt and Yildirim, 1999; Vasilyan et al., 2014).

Falsipyrgula shuetti was described from the eastern shore of Lake Beyşehir (Central Anatolia, Turkey). Since the authors found only empty

TABLE 1. Molluscs from the late Early and early Middle Pleistocene localities of north-western Armenia.

Localities Taxa	Formations					
	Ani Formation		?transitional beds		Arapi Formation	
	Voghji	Haykavan	Lusaghbyur (diapir)	Lusaghbyur (member enclosing diapir)	Lusaghbyur (overthrust wing)	Haykadzor
<i>Valvata piscinalis</i> (Müller, 1774)	+	-	-	-	+	+
<i>Valvata piscinalis</i> cf. <i>alpestris</i> (Küster, 1853)	-	+	-	+	-	-
<i>Valvata pulchella</i> (Studer, 1820)	-	-	-	+	-	+
<i>Valvata cristata</i> (Müller, 1774)	-	-	-	-	-	+
<i>Shadinia</i> cf. <i>terpoghassiani</i> (Shadin, 1952)	+	-	-	-	-	-
<i>Shadinia</i> spp.	+	-	-	-	-	-
? <i>Pyrgorientalia</i> sp.	+	-	-	-	-	-
<i>Falsipyrgula sieversi</i> (Boettger 1881)	+	-	+	-	-	-
<i>Falsipyrgula shadini</i> (Akramowski, 1956)	+	-	-	-	-	-
<i>Falsipyrgula</i> cf. <i>shuetti</i> Yildirim, 1999	+	-	-	-	-	-
<i>Falsipyrgula</i> cf. <i>bakhtarana</i> ? (Schütt et Mansoorian, 1999)	+	-	-	-	-	-
<i>Falsipyrgula</i> spp.	+	-	-	-	-	-
<i>Pseudamnicola</i> spp.	+	-	-	+	-	+
<i>Bithynia</i> sp.	-	+	+	+	-	+
Succineidae indet.	-	-	-	-	-	+
<i>Lymnaea</i> spp.	-	-	-	-	-	+
<i>Planorbis planorbis</i> (Linnaeus, 1758)	-	-	-	-	-	+
<i>Anisus spirorbis</i> (Linnaeus, 1758)	-	-	-	-	-	+
<i>Gyraulus</i> spp.	-	-	-	-	-	+
<i>Armiger crista</i> (Linnaeus, 1758)	-	-	-	-	-	+
<i>Pisidium</i> (<i>Europisidium</i>) cf. <i>tenuilineatum</i> (Stelfox, 1918)	+	+	-	-	-	-
<i>Pisidium</i> (<i>Neopisidium</i>) <i>moitessierianum</i> (Paladilhe, 1866)	-	-	-	+	-	+
<i>Pisidium</i> (<i>Odhneripisidium</i>) <i>stewarti</i> (Preston, 1909)	-	-	-	-	-	+
<i>Euglesa</i> (<i>Euglesa</i>) <i>casertana ponderosa</i> (Stelfox, 1918)	+	-	-	+	+	+
<i>Euglesa</i> (<i>Cingulipisidium</i>) <i>nitida</i> (Jenyns, 1832)	-	-	-	+	+	+
<i>Euglesa</i> (<i>Cyclocalyx</i>) <i>obtusale</i> (Lamarck, 1818)	-	-	-	-	+	+
<i>Euglesa</i> (<i>Henslowiana</i>) <i>henslowana</i> (Leach and Sheppard, 1823)	-	-	-	-	-	+
<i>Dreissena diluvii</i> (Abich, 1859)	+	+	+	-	-	+

shells, it is possible that this is a Holocene species (Schütt and Yildirim, 1999; Yildirim et al., 2006).

Our material also presents a form resembling *Falsipyrgula* cf. *bakhtarana* Schütt and Mansoorian, 1999, originally described from Iran (Schütt and Mansoorian, 1999).

The Voghji assemblage also includes a characteristic small bivalve (Figure 5.3), *Pisidium* cf. *tenuilineatum* (Stelfox, 1918). Compared to the extant species, absent in the fauna of Armenia but occurring in western Transcaucasia, the fossil form shows more pronounced and sparse ribs on the

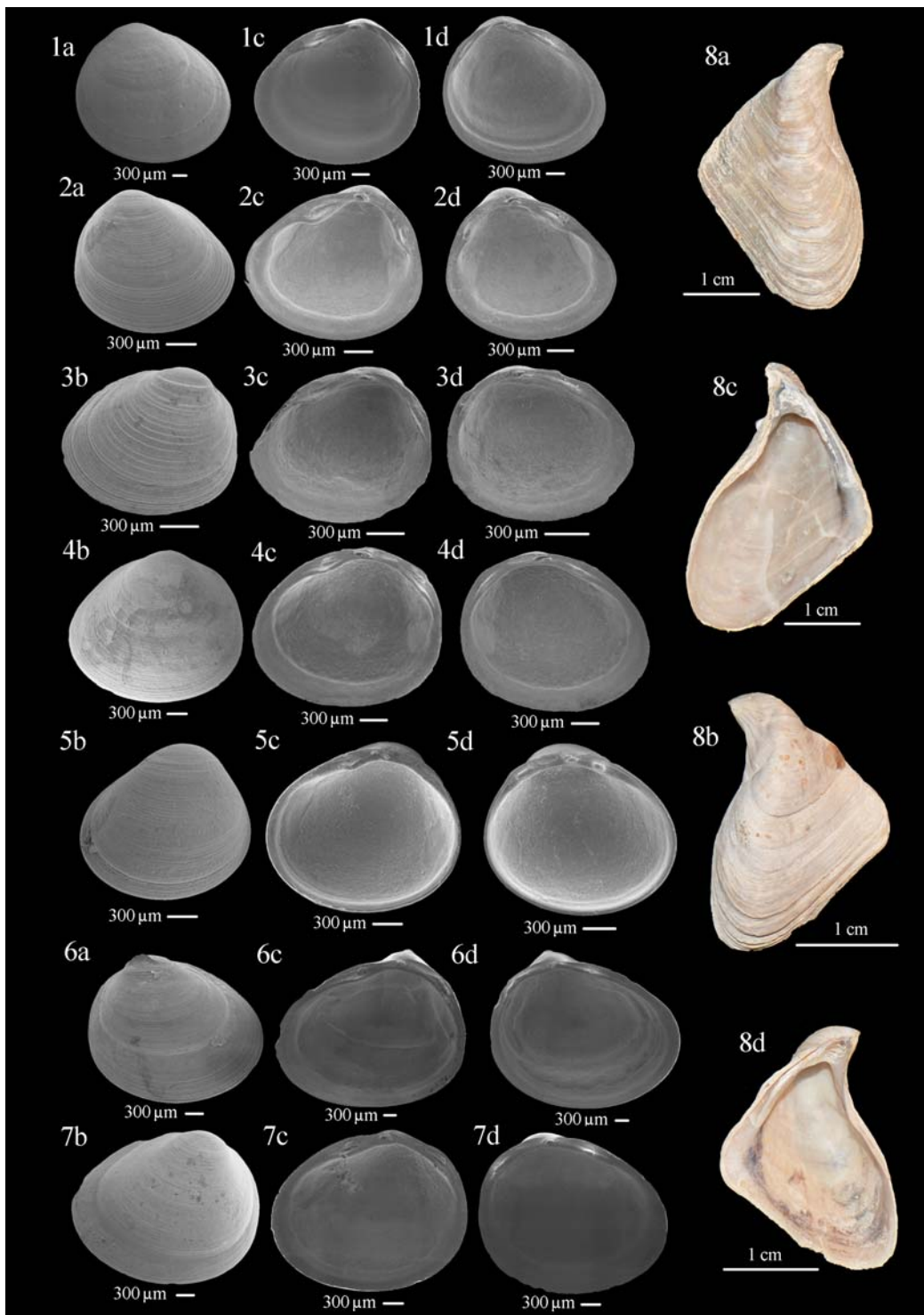


FIGURE 5. Bivalve molluscs from the late Early and early Middle Quaternary deposits of north-western Armenia. 1. *Pisidium (Odhneripisidium) stewarti*, GIN-1142/151; 2. *Pisidium (Neopisidium) moitessierianum*, GIN-1142/152; 3. *Pisidium (Europisidium) cf. tenuilineatum*, GIN-1172/19; 4. *Euglesa (Cingulipisidium) nitida*, GIN-1142/154; 5. *Euglesa (Cyclocalyx) obtusale*, GIN-1142/155; 6. *Euglesa (Henslowiana) henslowiana*, GIN-1142/156; 7. *Euglesa (Euglesa) casertana ponderosa*, GIN-1142/157; 8. *Dreissena diluvii*, GIN-1172/20. 1-2, 4-7 – Haykadzor, bed 4; 3 – Voghji, bed 8; 8 – Voghji, bed 6. a, outer surface of the right valve; b, outer surface of the left valve; c, inner surface of the right valve; d, inner surface of the left valve.

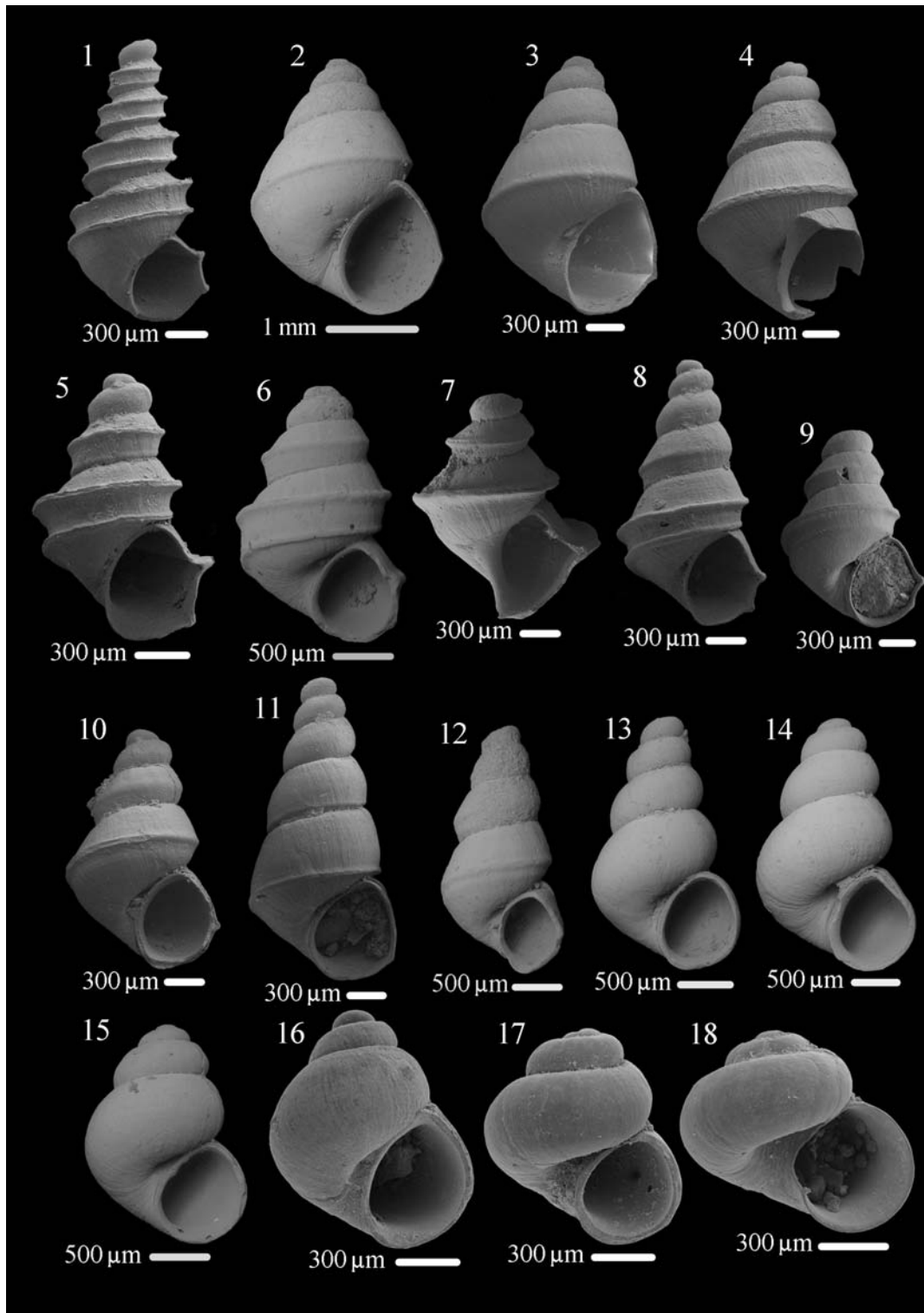


FIGURE 6. Gastropods from the late Early Quaternary deposits of north-western Armenia. 1. ?*Pyrgorientalia* sp., GIN-1172/1; 2-4. *Falsipyrgula sieversi*, GIN-1172/2-4; 5. *Falsipyrgula shadini*, GIN-1172/5; 6. *Falsipyrgula* cf. *shuetti*, GIN-1172/6; 7. ?*Falsipyrgula* cf. *bakhtarana*, GIN-1172/7; 8. *Falsipyrgula* sp. 1, GIN-1172/8; 9. *Falsipyrgula* sp. 2, GIN-1172/9; 10. *Falsipyrgula* sp. 3, GIN-1172/10; 11. *Falsipyrgula* sp. 4, GIN-1172/11; 12. *Shadinia* cf. *terpoghassiani* (Shadin, 1952), GIN-1172/12; 13. *Shadinia* sp. 1, GIN-1172/13; 14. *Shadinia* sp. 2, GIN-1172/14; 15. *Pseudamnicola* sp. 1, GIN-1172/15; 16. *Pseudamnicola* sp. 2, GIN-1172/16; 17. *Pseudamnicola* sp. 3, GIN-1172/17; 18. *Pseudamnicola* sp. 4, GIN-1172/18. 1-18 – Voghji, bed 8.

outer surface of the shell, and an additional delimitation of the umbo. The extant form is completely devoid of ribs on the outer surface of the shell.

Two other Ani Fm molluscan associations from Haykavan and the diapir of the Lusaghpyur are more species poor but reliably correlated with the Voghji fauna by co-occurring *P. cf. tenuilineatum* (Haykavan) and *F. sieversi* (diapir of Lusaghbyur).

According to the composition of molluscan fauna, the beds which confine the diapir in the Lusaghbyur section may span the uppermost part of the Ani Fm and contain a transitional assemblage corresponding to a reorganization time of the malacofauna of Ani and Arapi formations. The presence of *Valvata piscinalis cf. alpestris* and *Bithynia* sp. is similar with the Haykavan fauna, and the composition of bivalve molluscs is close to that of the Haykadzor assemblage.

Molluscs of the Arapi Fm are characterised by modern limnophilic freshwater species with abundant and diverse sphaeriid bivalves (Figure 5). The most representative Arapi malacofauna is studied in the Haykadzor section. All species in this association, except *Dreissena diluvii*, are extant. *Euglesa obtusale* and *E. nitida* are known from Pleistocene of Turkey (Schütt, 1991, 1997). *Pisidium stewarti*, *P. moitessierianum*, and *Euglesa henslowana* have not been previously known in the Caucasus, Transcaucasia, or Anatolia. Other species are known from Transcaucasia and/or from the Near East. The typical feature of this fauna is its abundant and diverse freshwater pulmonate gastropods (Lymnaeidae, Planorbidae). The Arapi fauna of the overthrust part of the Lusaghbyur section features the characteristic sphaeriid assemblage but lacks pulmonate gastropods.

The succession of Ani (Voghji) and Arapi (Haykadzor) mollusc faunas shows the transition of hydrobiid-dreissenid dominated fauna of the large and relatively deep freshwater Ani-time lake to the assemblage combining sphaeriid bivalves and pulmonate gastropods indicating the conditions of a large freshwater lake with shallow, overgrown areas with silty bottom in the Arapi time. The Ani assemblage contains several extinct forms (*Shadinia* spp., *Dreissena diluvii*), whereas the Arapi assemblage includes mostly extant species (except *D. diluvii*) and resembles the modern type lacustrine malacofauna of Armenia. It is yet to be established which of the malacological distinctions between Ani and Arapi are controlled by chronological or/and environmental/facies factors but a more modern appearance of the Arapi malacofauna (prevailing modern species) supports a

younger, early Middle Pleistocene age of this formation.

Vertebrates

Fishes, amphibians, and mammals were found in the sections of the Arapi Fm (Table 2).

Remains of Pleistocene fishes from the southern part of the Shirak Basin in western Armenia were obtained from two localities of the Arapi Fm: Lusaghbyur, bed 2, and Haykadzor, bed 4 (Figure 2). Fishes are represented by scattered fragments of the skull bones and isolated pharyngeal teeth. Judging from the mode of preservation, the bones were buried near the site of fish death and underwent significant maceration.

The herpetofaunal remains are relatively scarce and represented by the two amphibian taxa: *Bufo viridis* s. l. and *Rana* sp. recorded in microvertebrate material from Haykadzor, bed 2. The modern herpetofauna of Armenia is highly diverse and includes seven amphibian and 51 reptilian species (Tadevosyan, 2004–2009; Arakelyan et al., 2011). The fossil herpetofauna of this region is poorly known and represented only by a few records, mostly from the Plio-Pleistocene. Among them, amphibians are represented by *Bufo* sp. and *Pelophylax cf. ridibundus* from the early Pliocene of Nurnus (Melik-Adamyanyan et al., 1988). *Pelophylax cf. ridibundus* are also known from the Pliocene fauna of Jradzor (= Gelaysor, Ararat Province), and from the Early Pleistocene of Sisian (Vasilyan et al., 2009; Vasilyan and Carnevale, 2013) and Syunik (Palaeo-Vorotan) (Gabrielyan et al. 2004; Arakelyan et al., 2011). The remains of *Bufo viridis* s. l. (as *Bufo variabilis*) and *Rana* (as *Rana macrocnemis*) were previously mentioned only from the Upper Paleolithic of Aghitu-3 Cave (Kandel et al., 2017).

The fluvial deposits of the Arapi formation in the Shirak Basin of western Armenia yielded a large mammal assemblage, with the elephant *Mammuthus trogontherii* and other forms, defined as the Leninakan (later, Gyumri) faunal complex (Avakyan, 1959) correlated to late Middle Pleistocene (Sayadyan, 1970, 2009; Alekseeva, 1977). The remains of Quaternary small mammals from the same fluvial formation in western Armenia were studied by Melik-Adamyanyan and Agadjanyan (Agadjanyan, Melik-Adamyanyan, 1985; Melik-Adamyanyan, 1985, 1994, 2003, 2004). The composition of this fauna with *Mimomys intermedius*, advanced *Prologurus pannonicus*, and basal *Terri-Cola* clearly indicated an older, early Middle Pleistocene age of the Gyumri assemblage (Agadjanyan,

TABLE 2. Composition of early Middle Pleistocene vertebrates in faunas of north-western Armenia.

Taxa	Localities		
	Haykadzor	Lusaghbyur	Krasar
Pisces			
<i>Telestes cf. souffia</i>	+	+	–
<i>Pseudalburnus sp.</i>	+	+	–
<i>Capoeta sp.</i>	+	+	–
Amphibia			
<i>Bufo viridis sensu lato</i>	+	–	–
<i>Rana sp.</i>	+	–	–
Mammalia			
<i>Equus cf. stenorhis</i>	–	+	–
<i>Sorex cf. runtonensis</i>	+	–	–
<i>Neomys cf. hintoni</i>	+	–	–
<i>Ochotona sp.</i>	–	–	+
<i>Ellobius pomeli</i>	+	–	+
<i>Mimomys intermedius</i>	+	–	–
<i>Microtus ex gr. nutiensis</i>	+	–	–
<i>Terricola sp.</i>	–	–	+
<i>Prolagurus pannonicus transylvanicus</i>	+	–	–

Melik-Adamyany, 1985; Melik-Adamyany, 2004). Likewise, Forsten (1999) based on the morphology of horse remains from the Leninakan assemblage questioned the original age estimations as too late “for such a large stenorhis horse” and argued for an early Middle Pleistocene age. She also rejected an assignment of these horses by Alexeeva (1977) to caballoid forms (Forsten, 1999). The additional age control was provided by the geochronology of the Leninakan tuffs covering or interfingering with Arapi deposits yielding dates in the range of 0.65–0.7 Ma (Melik-Adamyany, 2016; Shalaeva et al., 2019) and normal polarity (Brunhes Chron) of these deposits (Sayadyan, 2009; Trifonov et al., 2017; Shalaeva et al., 2019). Recently small mammals of the Gyumri appearance were found in the Krasar (bed 2) section in Upper Akhuryan basin of western Armenia (Trifonov et al., 2016; Tesakov, 2016). In 2015–2016 the relatively abundant association of small mammals was recovered from the Arapi deposits near the village of Haykadzor, in bed 4 of the Haykadzor section (Shalaeva et al., 2019). This fauna contributes to the knowledge of biodiversity and refines the biostratigraphic position of the Gyumri faunal complex.

SYSTEMATIC PALEONTOLOGY

Order CYPRINIFORMES Bleeker, 1859

Family CYPRINIDAE Rafinesque, 1820

Subfamily LEUCISCINAE Bonaparte, 1835

Genus *TELESTES* Bonaparte 1837

Telestes cf. souffia (Risso, 1826)

Figure 7.1

Material. Three pharyngeal teeth, coll. PIN 5595.

Locality. Haykadzor and Lusaghbyur localities.

Measurements. Pharyngeal teeth of main row range in height from 4.0 to 4.5 mm.

Description. Teeth of the main row are slender, narrow, straight; hook at the apex with a tip directed at right angle to the tooth axis. Anterior margin of the crown is oblique and serrate (bearing up to five serrations), the abdomen rounded, with a slight anterior compression at the neck region (Figure 7.1). In general, the teeth are similar to those from the presumably Pliocene locality Gelayzor (Jradzor) of the Ararat Depression (Vasilyan, 2008a, p. 116. fig. 3; Vasilyan and Carnevale, 2013) and to the teeth of the recent *Telestes souffia* (Risso, 1826).

Comments. Recent population area of *Telestes souffia* (Risso, 1826) is confined to European part of the Mediterranean basin and does not extend eastwards of the Tissa River basin in Romania and Ukraine. The species inhabits fresh waters with unstable flow regime and rocky bottom. The above described fossils, similar to modern representatives of this species, indicate a wider range of its close relatives in the Pleistocene.

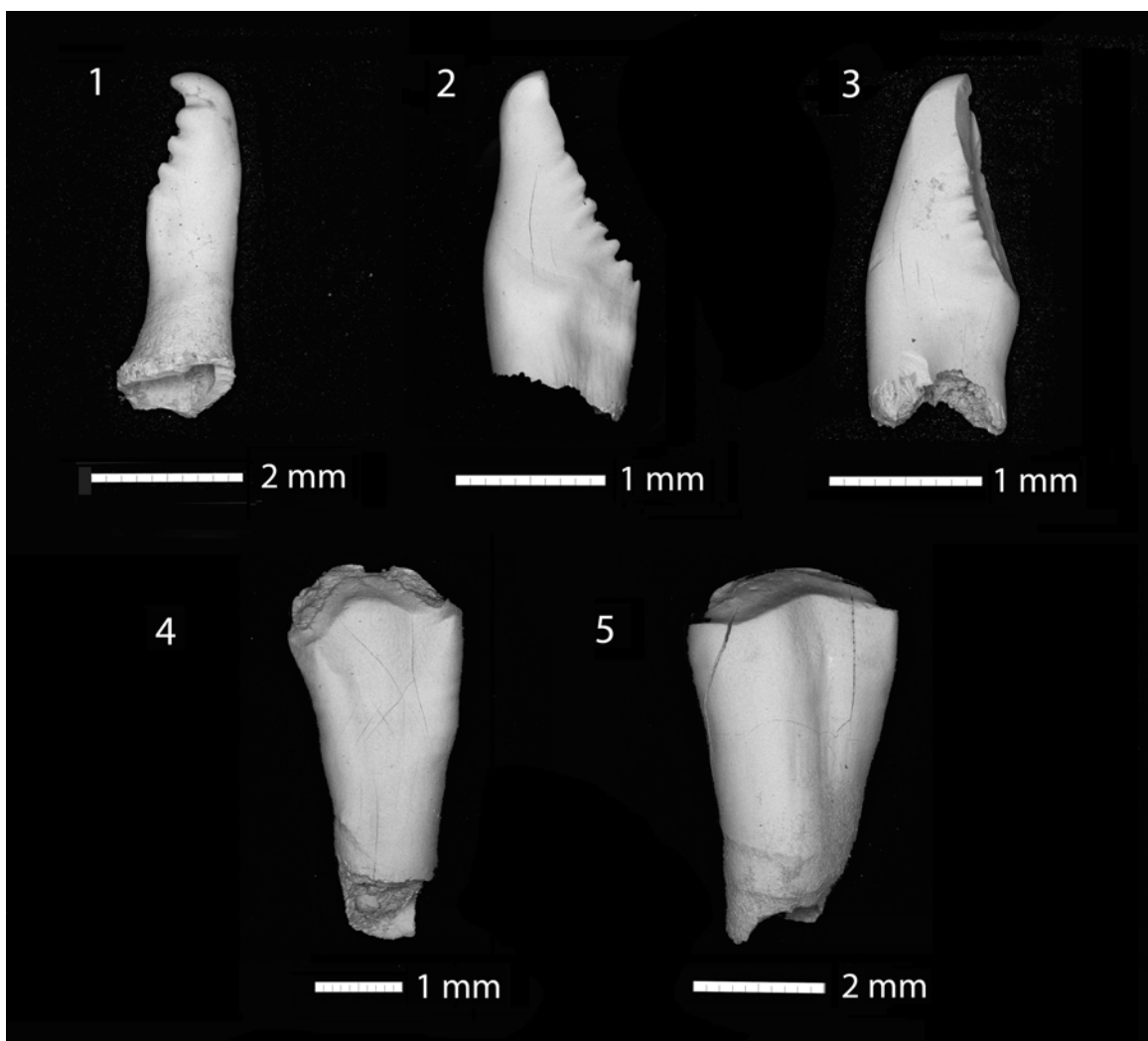


FIGURE 7. Fish remains from Haykadzor and Lusaghbyur localities, north-western Armenia. 1. *Telestes* cf. *souffia*, PIN 5595/201, pharyngeal tooth; 2-3. *Pseudalburnus* sp., PIN 5595/202, 203, pharyngeal teeth; 4-5. *Capoeta* sp., PIN 5595/204, 205, pharyngeal teeth.

Genus *PSEUDALBURNUS* Sytchevskaya, 1989

Pseudalburnus sp.

Figure 7.2-3

Material. Nine pharyngeal teeth, coll. PIN 5595.

Locality. Lusaghbyur, bed 2, and Haykadzor, bed 4

Measurements. Pharyngeal teeth of main row range in height from 2.0 to 2.4 mm.

Description. Teeth small, with tapered crowns slightly inflated towards the abdomen. The tooth stem is short. The hook is weakly expressed, barely projecting beyond the chewing surface level. The back of tooth is bent at the hook and above the neck, slightly deflected in the middle part. Chewing surface elongate, moderately narrowed, with

slightly jagged external edge; the internal edge with gently wavy contour.

Comments. In general, the teeth are similar with those of *Pseudalburnus* Sytchevskaya from the Pliocene of Mongolia, differing from them mainly by narrower crown and chewing surface. Occurrence of *Pseudalburnus* sp. in the Middle Pleistocene of Armenia may suggest some faunal links between the Caucasian region and Central Asia at that time. A kind of indirect evidence in favour of such assumption can be derived from the wide latitudinal dispersal of the genus *Alburnus* in the Neogene. Its common occurrence in the Pliocene-Pleistocene of Armenia (Bogachev, 1938; Vasilyan, 2008b) is paralleled by its finds in Pliocene of Sibe-

ria (Sytchevskaya, 1989) and in the Miocene of Germany (Kinkelin, 1884).

Subfamily BARBINAЕ Bleeker, 1859
Genus *CAPOETA* Valenciennes, 1842
Capoeta sp.
Figure 7.4-5

Material. 17 pharyngeal teeth, coll. PIN 5595.

Locality. Lusaghbyur, bed 2, and Haykadzor, bed 4

Measurements. Pharyngeal teeth of main row range in height from 16 to 19 mm.

Description. Teeth of main row are large, long, chisel-shaped, flattened, with a crown markedly widened upwards and narrowed towards the tooth neck (Figure 7.4-5). The chewing surface is slightly sloped to the abdomen.

Comments. The teeth are similar to those of *Capoeta* sp. from the Pliocene Ericek locality in Turkey (van den Hoek Ostende et al., 2015, figure 4-c), as well as to the teeth of the modern *Capoeta aculeata* (Valenciennes, 1844) from Iran. In fresh waters of West Asia (Iraq, Syria, Iran, Turkey, Transcaucasia) the genus is represented by at least 10 species inhabiting the basins with rocky bottom, rich water vegetation and well-warmed bank zone (Ayzazyan et al., 2018).

Order ANURA Fischer, 1813
Family BUFONIDAE Gray, 1825
Genus BUFOTES Rafinesque, 1815
Bufo *viridis* sensu lato (Laurenti, 1768)
Figure 8.1

Material. One fragmentary scapula, one coracoid, and two ilia, coll. GIN-1142.

Locality. Haykadzor, Armenia, early Middle Pleistocene.

Description and comments. The scapula is not complete, but longer than wide. The collum scapulae is relatively narrow and only slightly curved. The fossa supraglenoidalis is shallow as in *B. viridis* s. l. The coracoid is thick in the middle part and has a poorly expanded pars epicoracoidalis.

The ilia show the presence of two distinct bulges on the anterolateral side of the tuber superior and well-developed preacetabular fossa. These features are typical for *B. viridis* s. l. (Böhme, 1977). *Bufo* *viridis* s. l. (or *B. viridis* species group) is widely distributed and includes several species. The green toads from Balkans, Anatolia, and Caucasus were assigned to *B. variabilis* (Pallas, 1769) (Stöck et al., 2006, 2008). There are no published accounts providing osteological characters to support its taxonomic identification. Therefore, here we use *B. viridis* s. l. in the

traditional sense, encompassing *B. variabilis* and other species of the group. *Bufo* *viridis* s. l. is present in the extant fauna of Armenia and is widespread throughout the region; it prefers open landscapes with moderately arid climatic conditions (Arakelyan et al., 2011).

Family RANIDAE Rafinesque, 1814
Genus RANA Linnaeus, 1758
Rana sp.
Figure 8.2-3

Material. One scapula, ten fragmentary ilia, coll. GIN-1142.

Locality. Haykadzor, Armenia, early Middle Pleistocene.

Description and comments. The scapula is relatively short and wide. The crista supraglenoidalis is long and well-pronounced. The ilia are represented mostly by the acetabular parts. The dorsal crest is relatively high. The tuber superior is poorly developed and bears one laterally projected tubercle. The characters of scapula and ilia listed above allow their attribution to the genus of brown frogs *Rana* (Böhme, 1977; Ratnikov, 2001). But due to fragmentary preservation the precise taxonomic identification of the material is impossible. Within the genus *Rana*, the only *Rana macrocnemis* Boulenger, 1885, is currently known in Armenia. It occurs in humid and dry places along ravines of small rivers and streams (Arakelyan et al., 2011; Kuzmin, 2012). Besides, the fragments of two ranid humeri are revealed in Haykadzor. They are relatively large and possibly belonging to the green frogs of the genus *Pelophylax*.

Order PERISSODACTYLA Owen, 1848
Genus EQUUS Linnaeus, 1758
Subgenus ALLOHIPPIUS Kretzoi, 1938
Equus sp. ex gr. *E. stenonis* Cocchi, 1867
Figure 9

Material. Lower left premolar, p3 or p4, coll. GIN, unnumbered specimen.

Locality. Lusaghbyur, surface find near the Arapi deposits exposure, Armenia, ?early Middle Pleistocene.

Measurements. Occlusal length and width, 32.5 x 20. Height of the tooth ca. 75 mm.

Description. The molar is large and well-preserved, medium-worn. The double knot is of typical "stenonid" structure. Its composing elements, metaconid and metastylid, are almost symmetrical and have convex inner walls. Metaconid, especially the outer wall, is rounded and has a relatively broad opening (2 mm). Matastylid is more elliptic, has a narrow opening; its posteroexternal wall has

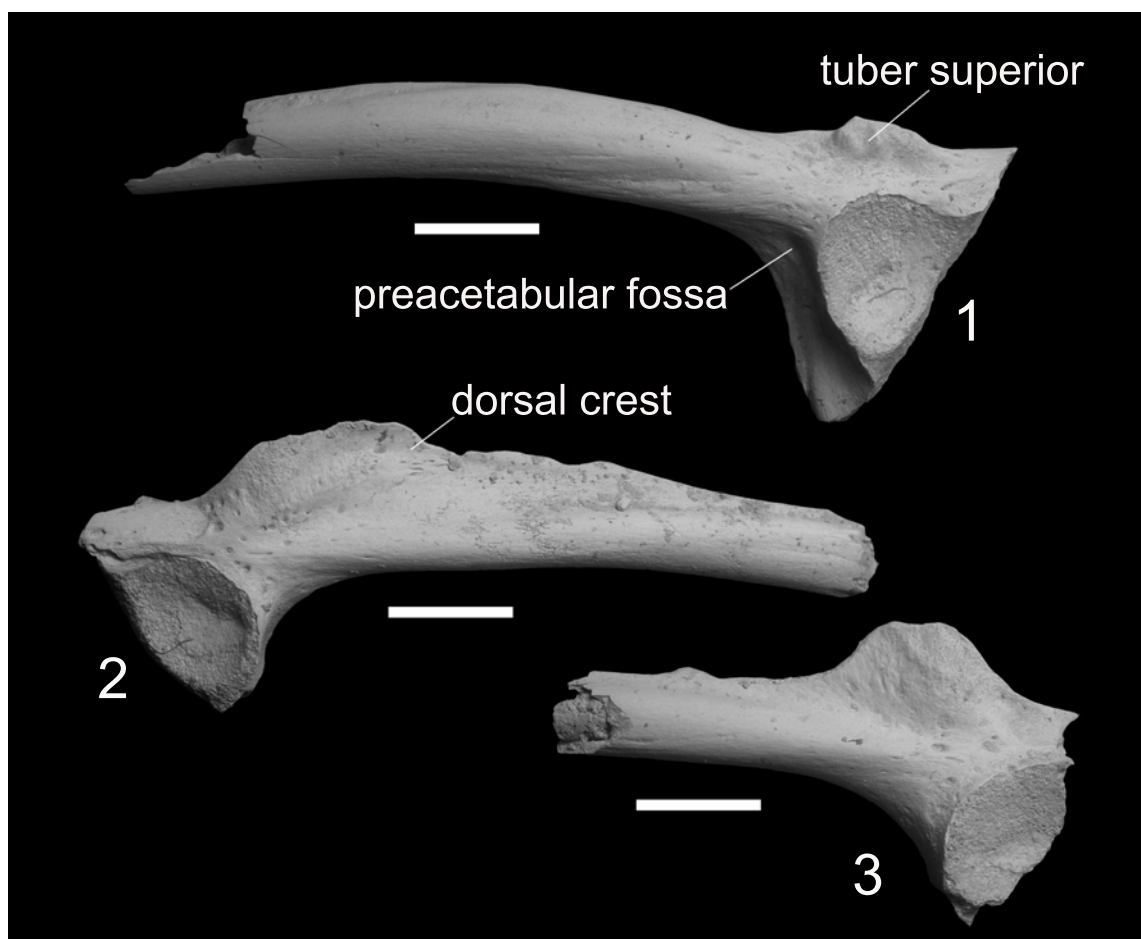


FIGURE 8. Amphibian remains from early Middle Pleistocene Haykadzor locality, Armenia. 1. *Buftotes viridis* s. l., GIN-1142/120, left ilium of lateral view; 2. *Rana* sp., GIN-1142/121, right ilium of lateral view; 3. *Rana* sp., GIN-1142/122, left ilium of lateral view. Scale bars are 1 mm.

a well-pronounced fold, posterointernal part is slightly pointed.

The linguaflexid has a distinct V-shape, similarly to all representatives of *E. stenorhis* s.l. Ectoflexid with a subtle “spur” is rather long. It approaches to the isthmus, not penetrating it (similarly to all premolars and slightly worn teeth). Entoconid with rounded inner wall and an anteroexternal beak-shaped bulge. The enamel is slightly thickened (1.0-1.2 mm), weakly plicated, with several (up to 3) smaller folds on the postflexid. The outer walls of protoconid and hypoconid are convex, similarly to stenonid horses of European subspecies. The latter, along with weakly plicated enamel of postflexid, is regarded as an archaic feature.

In addition to morphology of the double knot, it is the postflexid and postflexid index (IF index: postflexid length/tooth length) that are the most

characteristic elements of lower cheek teeth. In our case, the length of the postflexid is 15.0 mm and IF=46.1. This value exactly corresponds to the IF values in P3 and P4 of *E. stenorhis vireti* Prat from Saint-Vallier (Eisenmann, 1981) and is relatively close to IF in P4 of *E. stenorhis bactrianus* Zhegallo (47.0) from Tajikistan (Zhegallo, 1988). It is important that IF of the form under study substantially differs from IF in P3 and P4 of *E. suessenbornensis* Wüst (IF=48.0), the large archaic horse of late Early Pleistocene and early Late Pleistocene. This form was widespread from the southern Western Europe (Musil, 1969) to Eastern Europe and western Asia, including Transcaucasia (Akhalkhalaki, Georgia) (Vekua, 1962, 1986; Gabunia, Vekua, 1989; Alexeeva, 1977, and others), to Western Siberia (Foronova, 1990, 1998, 2001), Kazakhstan (Kozhamkulova, 1967), and probably Eastern Siberia (Sher, 1971; Forsten, 1986, and others).

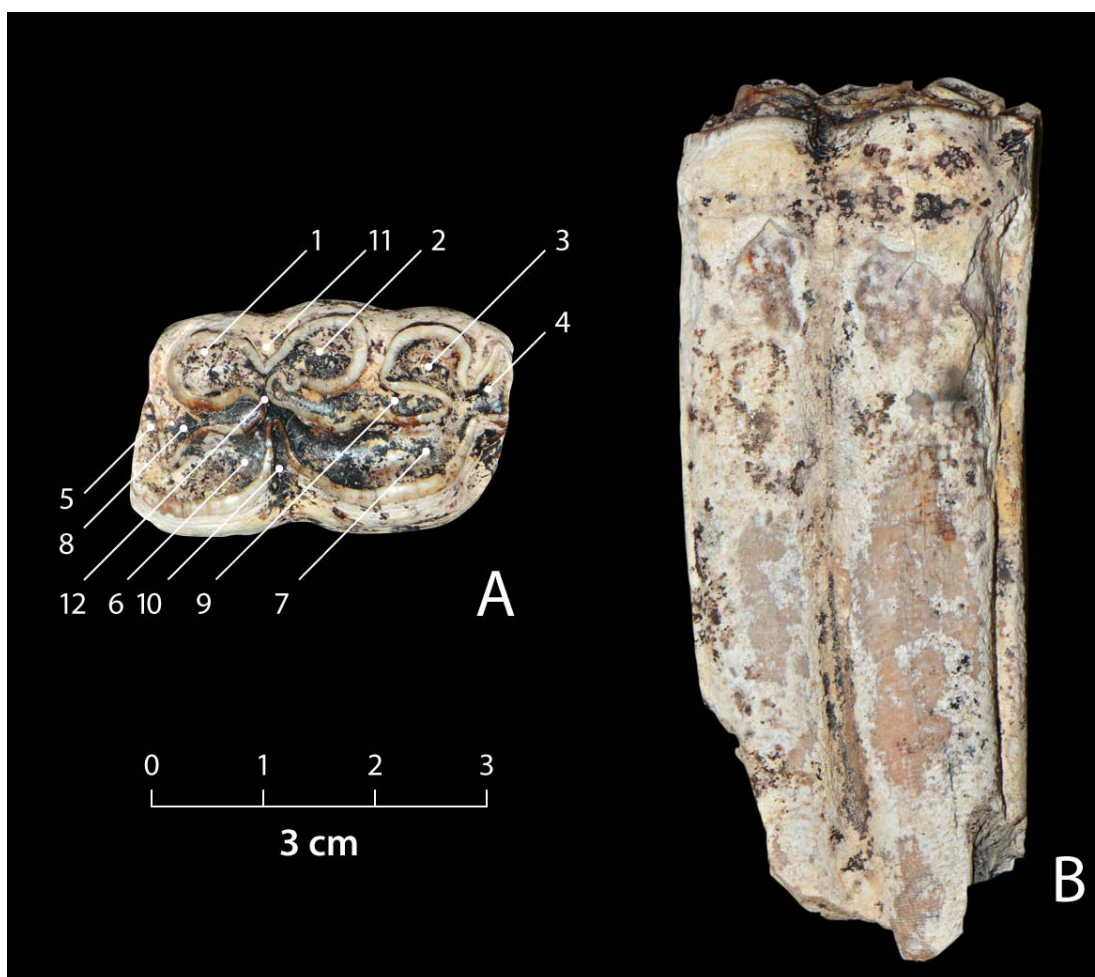


FIGURE 9. *Equus* sp. ex gr. *E. stenorius*, GIN, unnumbered specimen, Lower left p3? or p4, Lusaghbyur, Arapi Fm, Shirak Depression, early Middle Pleistocene, Armenia. A. Occlusal view with indicated elements of the tooth. 1. metaconid; 2. metastylid; 3. entoconid; 4. talonid; 5. paraconid; 6. protoconid; 7. hypoconid; 8. fossa anterior; 9. fossa posterior (postflexid); 10. ectoflexid; 11. linguaflexid; 12. isthmus. B. Buccal view.

Moreover, the horse from Shirak Depression markedly differs from *E. suessenbornensis* in composition of the double knot, especially its metastylid (it is always sub-triangular) and other dental elements. Peculiar angular outlines of all dental elements of *E. suessenbornensis* are determined by extremely high folding of the enamel, especially on lower cheek teeth.

Finally, this form has the most significant differences from caballoid horses, the group *Equus* (*Equus*) *mosbachensis* Reichenau, widespread in Eurasia at the very end of Early and in Middle Pleistocene. Unlike stenonid forms, caballoid horses show typically caballine, sharply asymmetric double knot with wide and low-sloping recess. Its metaconid is of oval or irregular shape and has

a long stem; metastylid is elongated and has an extended and sharpened posterointernal part.

Thus, the morphology of the studied tooth considerably differs from that of Suessenborn and Mosbach horses and fits that of the *E. stenorius* group. It is possible that it represents one of the late forms of stenonid horses studied by many researchers (Gromova, 1949; Musil, 1969; De Giuli, 1972, 1986; Azzaroli, 1987, and others). The West European sequence of species includes *E. stenorius vireti* – *E. stenorius stenorius* – *E. stenorius senezensis* Prat; the Asian record documents *E. stenorius bactrianus* Zhegallo. The described horse of Armenia can be reliably determined as *Equus* (*Allohippus*) sp. (ex gr. *E. stenorius*). It dates to early Middle Pleistocene and most likely inhabited open steppe-like landscapes.

Comments. Fossil horses are known from several localities in Transcaucasus. The Late Villafranchian fauna of Dmanisi documents a larger and smaller stenorid horses (Azzaroli, 1983; Forsten, 1999; Gabunia, Vekua, 1989, and others), the latest Villafranchian fauna of Akhalkalaki includes *E. suessenbornensis* Wüst (Vekua, 1962, 1986; Alexeeva, 1977, and others). There is no common opinion on the origin of *E. suessenbornensis* with alternatives ranging from a direct descent from *E. stenonis* (Gromova, 1949; Azzaroli, 1982, 1987) to the migrational hypothesis based on a lack of affinities of *E. suessenbornensis* with any early European horses and a substantial dissimilarities from *E. stenonis* in a number of characters (Musil, 1969). In Armenia, the horse of the Gyumri complex has been assigned to *E. stenonis* (Avakyan, 1957, 1959). Sayadyan (1972) refers to the personal communication of L.I. Alexeeva that “the horse in question is younger than *stenonis* typical for the Khapry faunal complex.”

Order EULYPOTYPHILA Waddell, Okada,
Hasegawa, 1999

Family SORICIDAE Fischer, 1814

Genus NEOMYS Kaup, 1829

Neomys cf. hintoni Zaitsev and Baryshnikov, 2002
Figure 10.1

Material. 1 fragmentary left mandible, GIN-1142/2.
Locality. Haykadzor, Armenia, early Middle Pleistocene.

Measurements. Height of ascending ramus = 3.6; articular process height = 1.85; upper facet width = 0.6; lower facet width = 1.17; basal width of internal temporal fossa = 1.0.

Comments. Small size, the single mandibular foramen, and especially a fossa on the buccal side of the ascending ramus anterior to the condyle fit the morphology of *N. hintoni* from the mid Middle Pleistocene level of the lowermost bed 7 of the Treugolnaya Cave in the North Caucasus (Zaitsev and Baryshnikov, 2002). The described form is also similar in size and morphology to *N. newtoni* Hinton from early Middle Pleistocene of upper freshwater bed of West Runton (Hinton, 1911; Maul and Parfitt, 2010). The variability of buccal fossa in *N. hintoni*, the character differentiating it from *N. newtoni*, is not known. A slight concavity on the buccal side of the ascending ramus is illustrated for one specimen of topotypic *N. newtoni* (Maul and Parfitt, 2010: figure 2, H). The Armenian smaller *Neomys* is among the oldest records of this group in Europe and western Asia. It clearly differs from Recent *N. anomalus* in slightly smaller size, single mandib-

ular foramen, and the presence of the buccal fossa.

Genus SOREX Linnaeus, 1758
Sorex cf. runtonensis Hinton, 1911
Figure 10.2

Material. Fragmentary right mandible with m1-m2 and ascending ramus, GIN-1142/3; fragment of mandible with m2, GIN-1142/4.

Locality. Haykadzor, Armenia, early Middle Pleistocene.

Measurements. Height of ascending ramus >3.0; articular process height = 1.7; upper facet width = 0.72; lower facet width = 1.1; mandibular length from the base of ascending ramus to mental foramen = 4.65; length m1-m3 = ca. 3.5; length m1 = 1.5; length m2 = 1.25, 1.2; mandibular height below m2 = 1.25, 1.20.

Comments. The medium size soricid, and in structure of condyle generally matches *S. runtonensis* from Middle Pleistocene of Europe and Caucasus (Hinton, 1911; Rzhelik-Kowalska, 1991; Zaitsev and Baryshnikov, 2002; Maul and Parfitt, 2010).

Order RODENTIA Bowdich, 1821

Family CRICETIDAE Fischer, 1817

Subfamily ARVICOLINAE Gray, 1821

Genus MIMOMYS F. Major, 1902

Subgenus MICROTOMYS Méhely, 1914

Mimomys intermedius (Newton, 1881)

Figures 11-13, Tables 3-8

non 1845a *Arvicola intermedia* Bonaparte, p. 350:
nomen nudum

non 1845b *Arvicola intermedia* Bonaparte, p. 30:
nomen nudum

1881 *Arvicola (Evotomys) intermedia* Newton, p. 258.

1882 *Arvicola intermedia* Newton, partim, p. 83,
pl. XIII, figs. 1-3, 12.

1902 *Mimomys intermedius* (Newton); F. Major, p. 104-107,
figs. 1, 11-13, 21-26.

1910 *Mimomys savini* Hinton, p. 491.

1910 *Mimomys majori* Hinton, p. 491.

1914 *Microtomys intermedius* (Newton); Méhely,
p. 211-214, taf. VI, figs. 8, 9.

1958 *Mimomys milleri* Kretzoi, p. 55.

1965 *Mimomys intermedius* (Newton);
Topachevsky, p. 112-118, figs. 28, 29.

Material. 12 m1, 12 m2, 11 m3, 16 M1, 18 M2, 9 M3, GIN-1141/5-80.

Locality. Haykadzor, Armenia, early Middle Pleistocene

Measurements. See Tables 3-8.

Description. The large size water vole with rhizodonty strongly shifted to early stages of root forma-

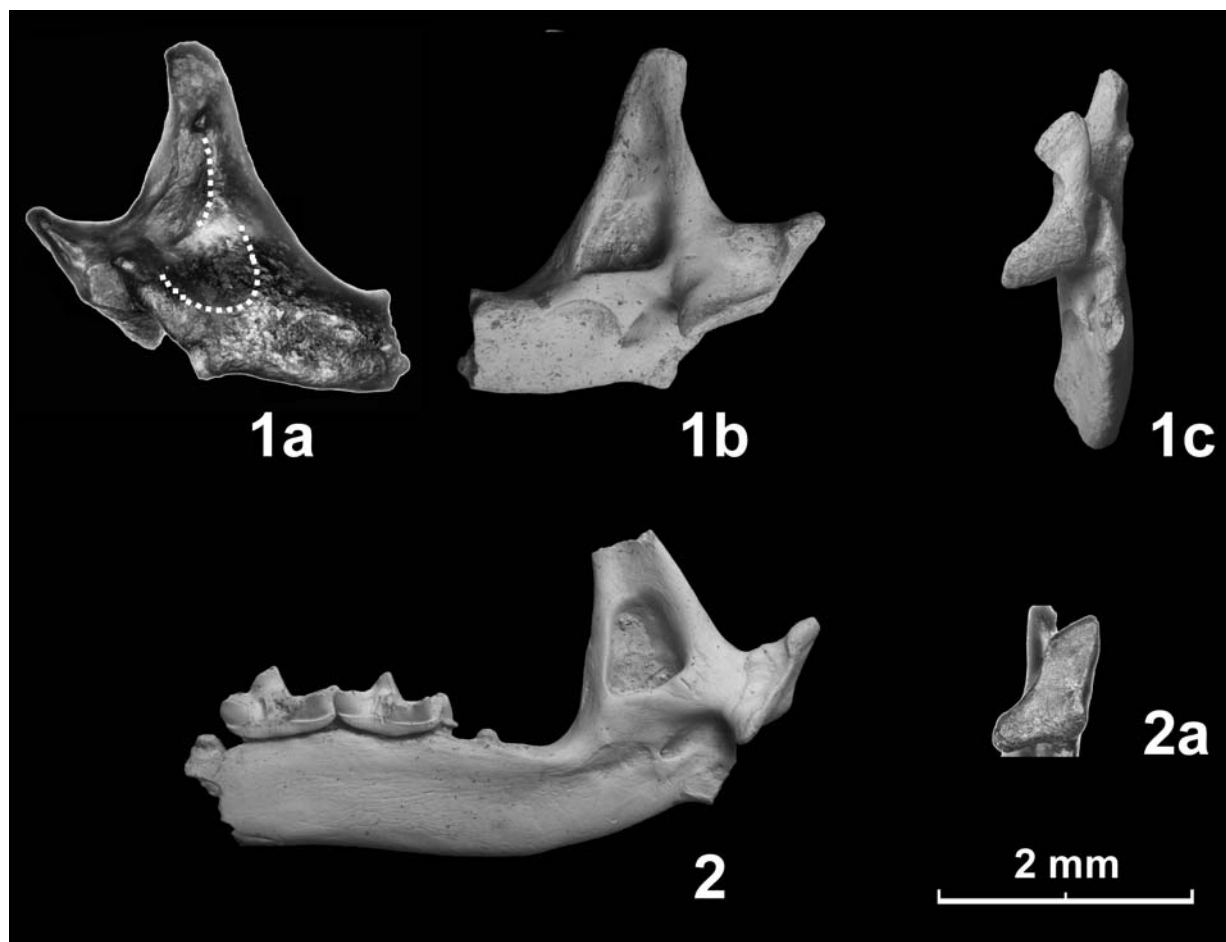


FIGURE 10. Soricidae from early Middle Pleistocene, Haykadzor, Armenia. 1. *Neomys* cf. *hintoni*, GIN-1142/2, ascending branch of fragmentary right mandible, 1a. lingual view with buccal fossa indicated by dashed line, 1b. labial view, 1c. condyle view; reversed. 2. *Sorex* cf. *runtonensis*, GIN-1142/3, right mandible, lingual view, 2a. condyle view.

tion, well expressed pleurorhiz position of roots in m2, two-rooted upper molars, with the protocone root of M1 broadly fused with the anterior root, very high but still measurable dentine tracts, mimomyine features (islet, *Mimomys*-ridge) expressed in youngest specimens of m1. The sample shows a predominance of younger, higher crowned specimens as shown in the violin diagram (Figure 13).

m1. The ontogenetically younger specimens shows the crown heights around 5 mm. Several youngest molars (n=3, Figure 11) show enamel islets, oval to circular in shape. *Mimomys* ridge is weakly expressed in the upper parts of crowns in several youngest specimens (n=3, Figure 11). Enamel differentiation changes from nearly undifferentiated condition at juvenile rootless stage to strongly negatively (= *Mimomys* type with thicker trailing edges) differentiated in more worn specimens with well developed roots.

M3. Third upper molars show typical structure (Figure 12) with deep, posterolingual reentrant angle (LRA3) filled with cement and without signs of insulation. The posterior lobe is rounded at early stages and grades to more triangular shaped with wear.

Comparison. The small sample of *M. intermedius* from Haykadzor is generally close in size and morphology to other known Cromerian populations described from Europe (Agadjanian and Kondrashov, 2007; Maul and Parfitt, 2010). The somewhat smaller mean values of occlusal length in m1 and M3 may account for the earliest Cromerian age of the Armenian sample, and, alternatively, may be related to the higher share of occlusally smaller molars at younger age stages in this sample (Figure 13). The size of m1 in *Mimomys* from Armenia is notably smaller than described for successive late Early Pleistocene samples of archaic water voles in Spain (Lozano-Fernández et al., 2013a, b).

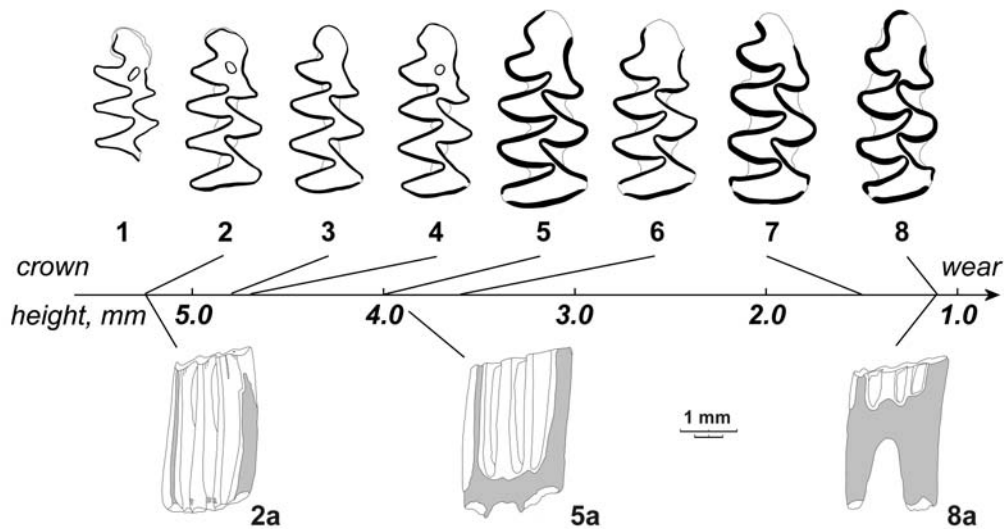


FIGURE 11. Dental morphology of the fossil water vole *Mimomys intermedius*, early Middle Pleistocene, Haykadzor, Armenia. 1-8. GIN-1142/5-12, first lower molar, m1, occlusal view; a, labial view. All molars are shown as right side, numbers 1, 5 are reversed. Horizontal axis illustrates decreasing crown heights in the course of wear (higher crowned, younger specimens are to the right, more worn, to the left). Occlusal and lateral scales, 1 mm.

This clearly shows that regional size differences in ancient water voles probably override the general evolutionary trend to size increase in this species and cannot be used for accurate long distance correlations. More reliable for comparisons between

separate fossil samples are likely size independent evolving characters like hypsodonty (e.g., crown height/length ratio, Agadjanian and Kondrashov, 2007), and especially the enamel differentiation index. Indeed, the mean SDQ value of the studied

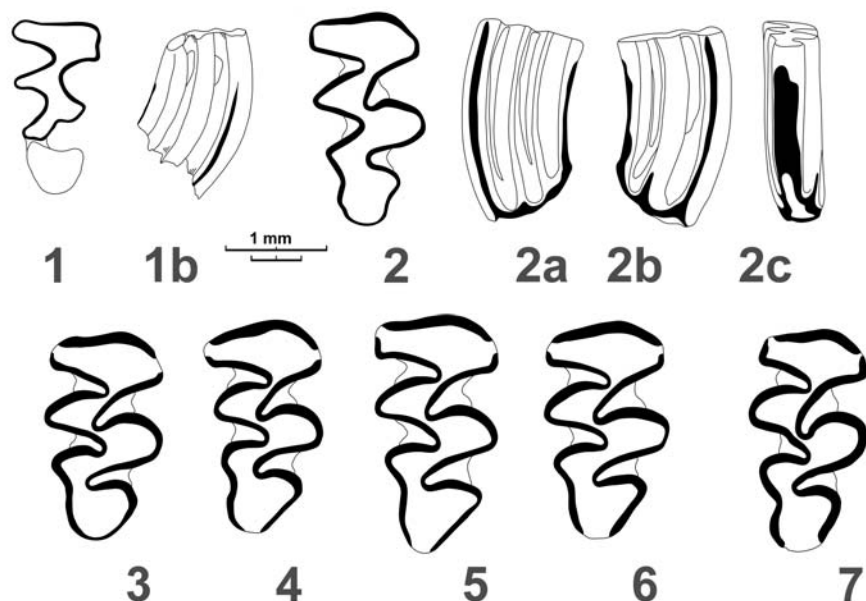


FIGURE 12. Dental morphology of the fossil water vole *Mimomys intermedius*, early Middle Pleistocene, Haykadzor, Armenia. 1-7. GIN-1142/68-75, third upper molar, M3, occlusal view; a, labial view; b, lingual view; c, posterior view. All molars are shown as right side, numbers 4, 6, 7 are reversed. Occlusal and lateral scales, 1 mm.

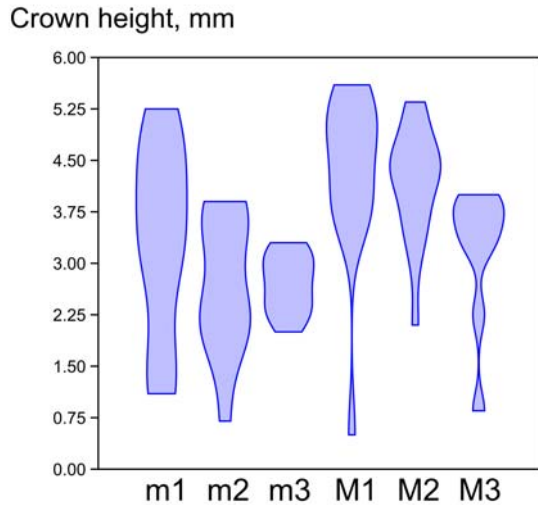


FIGURE 13. *Mimomys intermedius*, early Middle Pleistocene, Haykadzor, Armenia. Violin diagram showing distribution of frequencies of crown heights in molar types.

sample generally fits the range 130-140 observed in middle European *Mimomys intermedius* from early Middle Pleistocene (Maul et al., 2000; Maul and Parfitt, 2010). Notably higher (e.g., more archaic) SDQ values, ranging between 140 and 160, are known for Early Pleistocene populations in south-western (Fernández et al., 2013b) and northern (Maul et al., 2000) Europe.

Taxonomic comment. The name *Mimomys intermedius* (Newton, 1881) has a priority over *Mimomys savini* Hinton, 1910, due to the name *Arvicola*

intermedia Bonaparte, 1845, that was regarded a senior synonym of *A. intermedia* Newton, 1881 (e.g., Kretzoi, 1958), that was never validly described. It was first stated by Miller (1912: p. 672) and later by Ellerman and Morrison-Scott (1966: p. 703). Based on this information, Topachevsky (1965) clearly stated the validity of *M. intermedius* (Newton, 1881) for fossil water voles with rhizodont molars. We checked relevant publications of Bonaparte (Bonaparte, 1845a, b). Both of these, published in Milan in the proceedings of the Italian scientific congress and as a separate edition, are reiterations of the same taxonomic inventory of European mammals. Indeed, none of these papers contains anything but listing *A. intermedia*, without giving any characters, as a questionable synonym to *Arvicola bailloni* (now regarded as a younger synonym of *Microtus agrestis*) with the reference to the usage of Sélys-Longchamps. None of the arvicolid papers of Sélys-Longchamps of that period contain any references to “*Arvicola intermedia*”, including the checklist of European voles immediately preceding in the book the vole list of 1845b by Bonaparte (Sélys-Longchamps, 1845). We, therefore, regard “*A. intermedia* Bonaparte, 1845” a nomen nudum. The origin of the name “*intermedia*”, regarding the British fossil water voles, ascends to the work of Owen (1846) who noted that the form coming from “older pliocene crag near Norwich” is intermediate in size between the recent “Water vole (*Arvicola amphibia*,) and the Field-vole (*Arvicola arvalis*)”. Newton (1881) when coining a new name for this vole referred to “the intermediate position which it

TABLE 3. Measurements and indices, m1, *Mimomys intermedius*, Haykadzor.

	n	Mean	SE	Min	Max	SD	CV
L	10	3.17	0.0667	2.85	3.45	0.2109	6.65
W	12	1.44	0.0377	1.15	1.6	0.1309	9.09
A	12	1.285	0.0220	1.2	1.45	0.0762	5.93
Height	12	3.35	0.4084	1.1	5.25	1.4149	42.28
Asd	5	>4.58	-	>4	4.58	-	-
Hsd	5	>4.57	-	>4	4.85	-	-
Hsld	5	>4.75	-	>4.4	5	-	-
HH-index	5	>4.32	-	>4.1	4.4	-	-
Hsd/L	5	>1.47	-	>1.2	1.7	-	-
Lbas	10	3.33	0.0442	3.15	3.6	0.1398	4.19
A/L	10	40.6	0.7770	37.3	44.3	2.4571	6.04
SDQ	10	133.89	3.8511	118.63	157.79	12.1781	9.09
BTQ	11	131.84	5.0729	105.10	162.11	16.8250	12.76

TABLE 4. Measurements and indices, m2, *Mimomys intermedius*, Haykadzor.

	n	Mean	SE	Min	Max	SD	CV
L	10	1.99	0.0380	1.8	2.2	0.1202	6.03
W	12	1.31	0.0371	1	1.45	0.1286	9.81
Height	12	2.69	0.2879	0.7	3.9	0.9974	37.06
Asd	4	>4.19	-	>4	>4.4	-	-
Hsd	4	>3.64	-	>3.4	>3.9	-	-
Hsld	4	>3.77	-	>3.6	>4.1	-	-
HH-index	4	>3.85	-	>3.77	>3.94	-	-
Hsd/L	3	>1.86	-	>1.74	>1.95	-	-
Lbas	8	2.17	0.0422	1.95	2.3	0.1193	5.5

TABLE 5. Measurements and indices, m3, *Mimomys intermedius*, Haykadzor.

	n	Mean	SE	Min	Max	SD	CV
L	7	1.82	0.0359	1.65	1.9	0.0951	5.22
W	11	1.04	0.0208	0.9	1.11	0.0690	6.65
Height	11	2.69	0.1302	2	3.3	0.4321	16.03
Asd	3	>3.6	-	>3.5	>3.7	-	-
Hsd	3	>2.77	-	2.5	>3.2	-	-
Hsld	3	>2.7	-	2.7	>2.7	-	-
HH-index	2	>3.34	-	>3.25	>3.43	-	-
Hsd/L	2	>3.87	-	>3.79	>3.93	-	-
Lbas	7	1.84	0.1059	1.73	1.95	0.1498	8.12

TABLE 6. Measurements and indices, M1, *Mimomys intermedius*, Haykadzor.

	n	Mean	SE	Min	Max	SD	CV
L	12	2.69	0.0369	2.5	2.91	0.1274	4.73
W	16	1.65	0.0250	1.5	1.8	0.1001	6.07
Height	16	4.33	0.3090	0.5	5.6	1.2360	28.51
As	4	>5.09	-	4.85	>5.6	-	-
Asl	4	>5.6	-	>5.5	>5.8	-	-
Prs	4	>5.6	-	4.45	>4.75	-	-
Ds	4	>5.5	-	>5.5	>5.87	-	-
PA-index	4	>4.62	-	>4.55	>4.77	-	-
As/L	3	>1.89	-	>1.82	>1.96	-	-
Lbas	12	2.67	0.0361	2.55	3	0.1249	4.68

occupies between the *Arvicola amphibia* and *Arvicola (Evotomys) glareola*.”

The name *Mimomys savini* Hinton, 1910, widely, but not overwhelmingly (see Méhely, 1914, Topachevsky, 1965, and others) used in the European literature, is a younger synonym of *M. intermedius* (Newton, 1881). Méhely (1914) attributed *M. intermedius* to his new genus *Microtomys* where he placed rhizodont mimomyine voles with the lateral position of the posterior root in m2 relative to the incisor (pleurorhiz condition). Topachevsky (1965, p.111) considered *Microtomys*

as a subgenus of *Mimomys*, and in the sense of the International Code of Zoological Nomenclature established its type species by subsequent designation (ICZN, 1999: 69.1) fixing *Arvicola (Evotomys) intermedius* Newton, 1881, as the type species of the genus *Microtomys* Méhely, 1914.

Genus *Terricola* Fatio, 1867

Terricola sp.

Figure 14

Material. 1 m1, 2 m1 fragments, 1M1, 1M2, GIN-1141/2-7

TABLE 7. Measurements and indices, M2, *Mimomys intermedius*, Haykadzor.

	n	Mean	SE	Min	Max	SD	CV
L	14	2.17	0.0256	1.92	2.3	0.0959	4.43
W	18	1.36	0.03	1.05	1.52	0.1095	8.05
Height	18	4.17	0.1924	2.1	5.35	0.82	19.55
As	3	>5.08	-	4.7	>5.35	-	0
Prs	3	>4.53	-	4.3	>4.8	-	0
Ds	4	>4.5	-	>4.2	>4.8	-	0
PA-index	2	>4.37	-	>4.2	>4.51	-	0
As/L	3	>2.33	-	>2.14	>2.48	-	0
Lbas	14	2.14	0.0261	1.95	2.3	0.0978	4.56

TABLE 8. Measurements and indices, M3, *Mimomys intermedius*, Haykadzor.

	n	Mean	SE	Min	Max	SD	CV
L	9	2.18	0.0587	1.7	2.3	8.3097	8.31
W	9	1.14	0.0319	0.9	1.23	8.4365	8.44
P	9	0.93	0.025	0.8	1.05	0.075	8.04
Height	9	3.18	0.3405	0.85	4	32.1409	32.14
Prs	4	3.65	0.1190	3.4	3.9	6.5218	6.52
As	4	3.85	0.0736	3.7	4	3.8232	3.82
Ds	4	2.56	0.1434	2.15	2.8	11.1947	11.19
PA-index	4	3.87	0.0492	3.77	3.96	2.5418	2.54
As/L	4	1.82	0.0364	1.76	1.93	0.0729	3.99
P/L	9	44.14	0.7034	40.91	47.73	2.1102	4.78
Lbas	9	2.08	0.0430	1.9	2.3	0.1291	6.21

Locality. Krasar, Armenia, early Middle Pleistocene.

Description. The microtine vole from this site shows well-developed positive (*Microtus* type) enamel differentiation (BTQ = 43, 9, SDQ = 60, n=1), broadly fused triangles T4-T5 forming the “*Pitymys*-rhombus”, and initial complication of posterior side (T4) of upper molars. The well-preserved first lower molar (L= 2.47; W= 0.94; A=1.27; A/L=51.4) and two fragmentary m1 (W, A: 0.9 x 1.5; 0.94 x 1.27) show characteristic confluent T4-T5 with somewhat incurving tip of third reentrant (LRA3). In one specimen (Figure 14.3), T6-T7 show an incomplete alternation. Upper molars (M1 and M2, L, W: 2.01 x 1.16; 1.56 x 0.98) demonstrate initial complication at the posterior side (Figure 14.4-5).

Comparison. The vole from Krasar shows shorter (A/L=51, n=1) and more compact anteroconid cap with more shallow reentrants BRA4 and LRA5 than any extant *Terricola* of the Caucasus and Asia Minor (Kryštufek and Vohralík, 2005). The relative anteroconid length (A/L) in recent subterranean voles of the region well exceeds 51 in most individ-

uals. The Armenian vole is also less advanced in complication degree of the anteroconid than Late Pleistocene *T. majori* from Kudaro Cave (Baryshnikov and Baranova, 1983).

Comments. *Terricola* from early Middle Pleistocene deposits of Shirak Fm were described by Agadjanan and Melik-Adamyán (1985) and Melik-Adamyán (1994). Noting short and poorly dissected anteroconid cap in this vole these authors assigned it to most morphologically primitive of the extant subterranean voles, *Pitymys duodecimcostatus*. Having in mind the geological antiquity and geographic remoteness of Armenia from the Mediterranean region, this assignment is obviously very approximate. The single M3 so far described for the Armenian vole (Melik-Adamyán, 1994) fits modern *Terricola* morphology in confluent T2 and T3, and in “*principalis*” morphotype with two lingual salient angles (LSA4 and LSA5) on the posterior lobe. We would rather favour a detection of a very primitive stage of the Caucasus *Terricola*. The basal position of the modern *T. majori* in the molecular tree of *Terricola* (Martinková et al., 2007; Tougaard, 2017) suggests an early presence of the

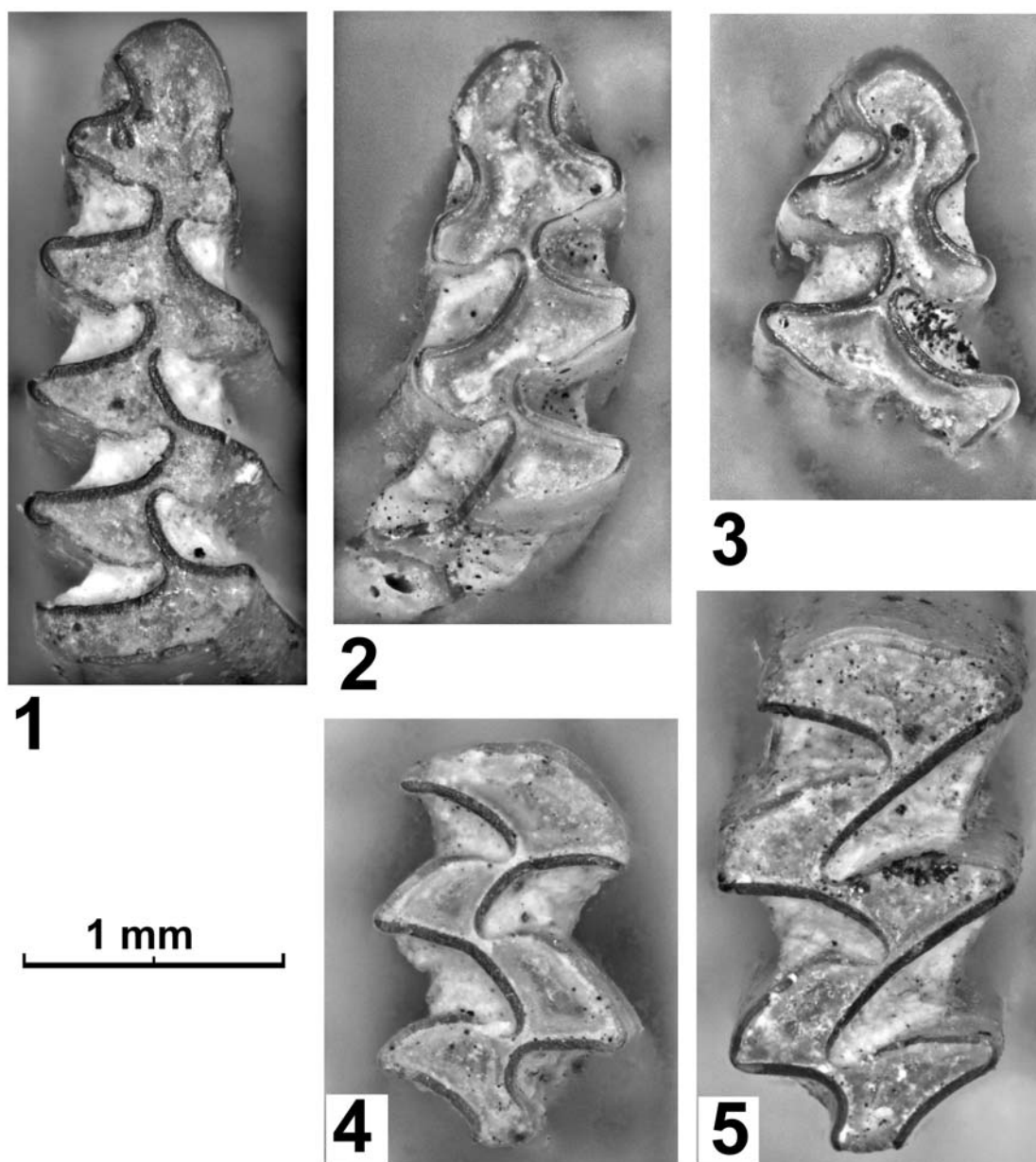


FIGURE 14. Dental morphology of the fossil vole *Terricola* sp., early Middle Pleistocene, Krasar, Armenia. 1-3. GIN-1141/2-4, first lower molar, m1; 4. GIN-1141/5, second upper molar, M2; 5. GIN-1141/6, first upper molar, M1. Occlusal view. All molars are shown as left side, numbers 1, 3, 4 are reversed. Scale equals 1 mm.

group in the Caucasus. The morphological archaism of the described forms, however, hampers a reliable attribution to any of the extant species, e.g., *T. majori* and *T. daghestanicus*, and implies an existence of a new chronospecies to be described in future when more complete material will be available. The state of evolution of the vole from Krasar (upper Akhuryan basin) is very close to that hitherto described from early Middle Pleistocene sites of Shirak Fm. We, therefore, infer a sim-

ilar age for the fauna of Krasar (Trifonov et al., 2016). Our initial interpretation of one incomplete specimen (Figure 14.3) as belonging to ?*Chionomys*, based on a slightly larger size and more dissected anteroconid cap, is questionable. Many of its characters are indeed close to other *Terricola* specimens from Krasar but more material is needed for a reliable taxonomic placement.

Microtus ex gr. *nutiensis* Chaline, 1972

Figure 15, Table 9

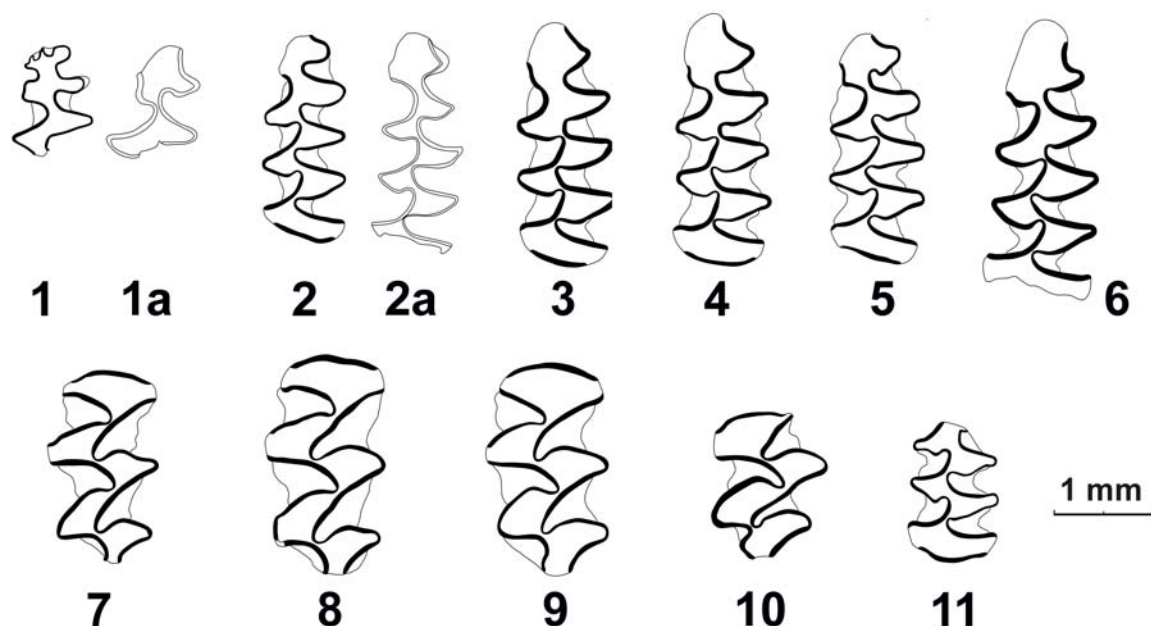


FIGURE 15. Dental morphology of the fossil vole *Microtus* ex gr. *nutiensis*, early Middle Pleistocene, Haykadzor, Armenia. 1-6. GIN-1142/90-95, first lower molar, m1; 7-10. GIN-1142/96-99, first upper molar, M1; 11. GIN-1142/100, second lower molar, m2; occlusal view; a, alveolar view. All molars are shown as left side, numbers 1, 5, 7 are reversed. Scale equals 1 mm.

Material. 3 m1, 3 fragmentary m1, 1 m2, 3M1, 1 fragmentary M1, GIN-1142/90-101.

Locality. Haykadzor, Armenia, early Middle Pleistocene

Measurements. See Table 9 for dimensions of m1.

Description. The microtine vole with the transitional morphology between the *Allophaiomys* and *Microtus* conditions. Lower m1 with communicating T4-T5 ("Pitymys-rhombus") not completely disconnected from the anteroconid cap. The anteroconid cap shows better developed lingual salient angle (LSA5) and incipient labial salient angle (BSA4). The relative length of anteroconid is on the average less than 50. Enamel differentiation is of positive type, though trailing edges are still quite thick. Lower m2 (L=1.42; W=0.95) shows communicating

T1-T2 and T3-T4 (Figure 15.11). First upper molars (L/W: 1.95 x 1.12; 2.2 x 1.17; 2.15 x 1.2;-x 1.2) show initial signs of complication at posterior side of T4 in three of four specimens.

Comparison. The sample of microtoid vole from Haykadzor looks somewhat less advanced than so far described materials from Arapi Fm (Kazachii Post, Arapi 1 and 2, Airport) and from the upper Akhuryan basin (Krasar) in less complex anteroconid structure, and possibly in less differentiated enamel. This may be evidence of a slightly older age of the Haykadzor fauna or a difference in taxonomy. One of the well-described forms with similar morphology is *Allophaiomys nutiensis* from Early Pleistocene locality Valerot in France (Chaline, 1972). Another morphologically close

TABLE 9. Measurements and indices, m1, *Microtus* ex gr. *nutiensis*, Haykadzor.

	n	Mean	SE	Min	Max	SD	CV
L	5	2.43	0.1164	2.1	2.8	0.2603	10.70
W	6	0.94	0.0420	0.78	1.07	0.1028	10.92
A	6	1.14	0.0670	0.9	1.4	0.1642	14.34
A/L	5	47.21	1.1965	42.86	50	2.6754	5.67
BTQ	5	75.03	4.8882	59.02	86.20	10.9303	14.57
SDQ	5	83.44	4.2994	67.82	93.08	9.6138	11.52

form was described from late Early Pleistocene karstic site Monte Peglia in Italy (van der Meulen, 1973). Another similar form from a geographically close region was described as *M. nutiensis* from Early Pleistocene locality Dursunlu in central Turkey (Ünay, 1998). A single lower m1 of similar morphology was described as *Allophaiomys* cf. *plioacaenicus* from Pasinler A (Yaladag) locality in the neighbouring region of eastern Turkey (Vasilyan et al., 2014), in deposits malacologically similar to the Ani Fm underlying the Arapi Fm deposits. The sample from Haykadzor is obviously chronologically younger than all those forms, but somewhat dissimilar in less complicated and more asymmetric anteroconid cap.

Comments. A transitional morphological stage of first lower molar in Microtini between the plesiomorphic condition with three closed triangles and broadly confluent anteroconid, known as the “*Allophaiomys*” condition (late Early Pleistocene), and the advanced stage with five closed triangles and a trifoliate anteroconid cap, called the “arvaloid” condition (late Middle Pleistocene to the Recent), are generally addressed as “*Pitymys*”-like stage. This transitional morphology is characterised by three closed triangles, two fused or incompletely closed triangles and rounded to slightly trifoliate anteroconid cap. Several evolutionary lineages of Microtini could pass this stage in late Early and early Middle Pleistocene thus obscuring the phyletic relationships of fossil forms. The morphology of the taxon “*Allophaiomys nutiensis*” is a good match for this intermediate stage but it could easily contain multiple unrelated forms. A thorough revision of this grade of Microtini from latest Early and early Middle Pleistocene of Europe and western Asia (e.g., samples attributed to *A. nutiensis*, *M. thenii*, *M. hintoni*, etc.) with accurate documentation of all molars of the toothrow and enamel differentiation quotient is needed.

The vole from Haykadzor may be related to *Terricola*, as suggested by morphotypes of m1 with “*Pitymys*-rhombus” (Figure 15.6), confluence pattern in m2, and incipient LSA4 in M1. It may show the way of transformation of *Allophaiomys* dental pattern into that of *Terricola*. The origin and early evolution of *Terricola* is still poorly known and generally related with Early Pleistocene *Allophaiomys* (Chaline, 1972; Rabeder, 1981; Rekovets and Nadachowski, 1995). The study of morphometry of lower m1 in Middle and Late Pleistocene subterranean voles in Europe put forward a hypothesis of the group affinity with Early Pleistocene *Allophaiomys*-grade Microtini as *A. pitymyoides* Chaline, *A.*

nutiensis Chaline, *A. praehintoni* Rabeder (Brunet-Lecomte and Chaline, 1991). A credible hypothesis interpreting *Allophaiomys laguroides* Kormos from Early Pleistocene of Betfia 2 as an early stage of *Terricola* was proposed by Rekovets and Nadachowski (1995). Popular taxonomic practice relates primitive transitional stages of multiple lineages of Microtini (*Microtus* s.str., *Terricola*, *Stenocranius*, etc.) with confluent T4-T5 to *Terricola*. According to a widespread concept, the Middle and Late Pleistocene *Terricola* descended from early Middle Pleistocene *Microtus arvalidens* Kretzoi (e.g., Maul and Markova, 2007; Maul et al., 2007, etc.). Rekovets and Nadachowski (1995), though placed *M. arvalidens* in *Terricola*, argued against the direct phyletic connection of *M. arvalidens* and *T. subterraneus*. Indeed, the topotypic *M. arvalidens* (= *M. arvaloides* Hinton) from Cromerian of West Runton (Maul and Parfitt, 2010) and large synchronous samples from Eastern Europe as Tikhonovka 1 in Ukraine (Rekovets and Nadachowski, 1995) and Port-Katon 4 (Tesakov et al., 2007) show a range of variation uncommon to later *Terricola*, and rather suggesting a phyletic link with *Microtus arvalis* s.l. In general, early Middle Pleistocene voles attributed throughout Europe to *M. arvalidens* are clearly heterogeneous, representing in different sites either an arvaloid *Microtus* (e.g., West Runton), true *Terricola* (e.g., Subpiatră: Hír and Venczel, 1992) or a mixture of different forms (e.g., Betfia 5: Kretzoi, 1941 and Terzea, 1970; Futjova Cave: Popov, 2017). Most Toringian records of *M. arvalidens* in Europe likely represent *Terricola* gr. *subterraneus*. A modern revision of the group is needed.

Genus PROLAGURUS Kormos, 1938

Prolagurus pannonicus transylvanicus Terzea, 1989

Figure 16.1-3

Material. 1 m1, 1 fragmentary m1, 1 m3, 3M1, 1 M2, GIN-1142/105-112.

Locality. Haykadzor, Armenia

Measurements. m1: L=2,25, W=0,87, A=1,15; m1 fragm.: W=1,0; m3: L=1,6, W=0,8; M1 L,W: 1,9 x 1,0, 1,95 x 1,16; M2 L,W: 1,85 x 1,12.

Description. Lower m1 (Figure 16.1) has widely fused anteroconid triangles well-separated from rounded cap with a slightly expressed antero-labial reentrant (BRA4). This reentrant fold becomes deeper with wear (Figure 16.1a, viewed from alveolar side of the molar). The lagurine additional anteroconid tract is present on the labial side of the cap. The enamel band is positively differentiated. Three M1 show moderately developed lagurine

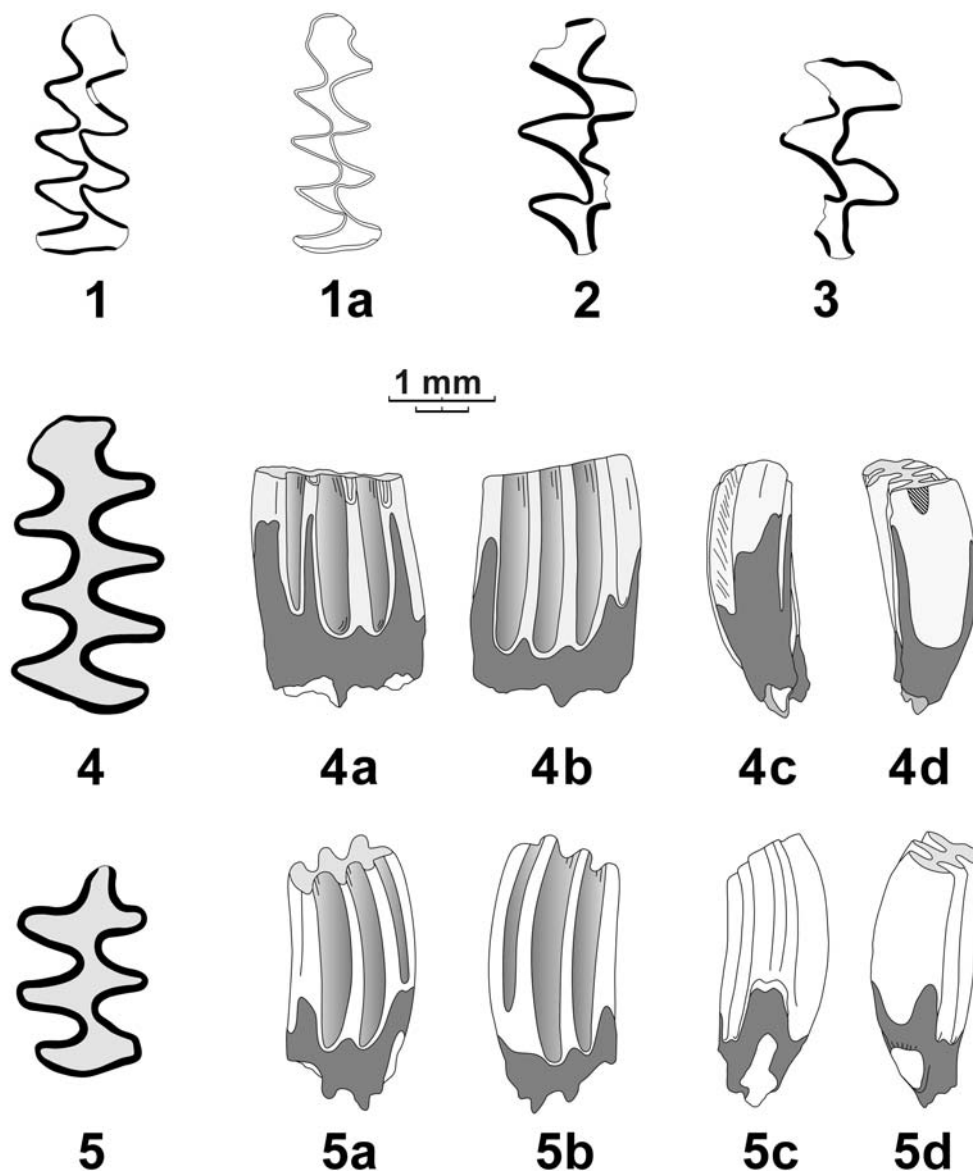


FIGURE 16. Dental morphology of the fossil voles from early Middle Pleistocene of Armenia. *Prolagurus transylvanicus*, Haykadzor. 1. GIN-1142/105, first lower molar, m1, right side; 1a, the same molar in occlusal view; 2. GIN-1142/108, first upper molar, M1; 3. GIN-1142/111, second upper molar, M2; a, alveolar view. *Ellobius pomeli* (after Tesakov, 2016), 4. Krasar, GIN-1141/1, first lower molar, m1, left side; 5. Haykadzor, GIN-1142/1, second lower molar, m2, right side, occlusal view; 4a and 5a, labial; 4b and 4b, lingual; 4c and 5c, anterior; 4d and 5d, posterior view. Numbers 2 and 3 are reversed. Scale equals 1 mm.

denticles (Figure 16.2). A single incompletely preserved specimen of M2 has a characteristic smooth lagurine denticle in the depth of the LRA2 (Figure 16.3).

Comments. The morphology of *Prolagurus pannonicus* Kormos from Haykadzor fits that of the sample from Kazachii Post, Arapi 1 and 2, and Airport sites of the Arapi Fm (Agadjanian and Melik-

Adamyam, 1985; Melik-Adamyam, 1994). This form is characterised by the rounded anteroconid cap with well developed antero-labial salient angle (BSA4) with lagurine tract. The evolutionary sequence of morphospecies in Pleistocene *Prolagurus-Lagurus* was established in numerous publications (e.g., Zazhigin, 1970; Markova, 1974; Rekovets and Nadachowski, 1995; Agadjanian,

2009, etc.). According to Rekovets and Nadachowski (1995), the lineage of rootless smaller lagurines includes *Prolagurus ternopolitanus* (earliest Biharian) with widely fused anteroconid cap and triangles, *P. pannonicus* (late early-early late Biharian) with dominant morphotype with broadly confluent anteroconid triangles separated from rounded cap, *Lagurus transiens* (late Biharian) with separated anteroconid triangles and slightly trifoliate cap, and *L. lagurus* (Toringian) with separated anteroconid triangles and strongly trifoliate cap. For advanced *P. pannonicus* of late Early to early Middle Pleistocene with anteroconid cap showing incipient labial reentrant (BRA4) Terzea (1989) described the species *P. transylvanicus*. We follow Rekovets and Nadachowski (1995) in its subspecies rank, *P. pannonicus transylvanicus*. This taxon is a perfect taxonomic and chronological match for the lagurine from Armenia.

Genus ELLOBIUS Fischer, 1814
Subgenus BRAMUS Pomel, 1892
Ellobius pomeli Tesakov, 2016
Figure 16.4-5

Material. 1 m1, GIN-1141/1; 1m2, GIN-1142/2.

Locality. Krasar (m1), Haykadzor (m2).

Measurements. m1: L = 2.8, W = 1.35, A = 1.15, H = 2.9, R = 1.25, ASD = 2.3, MIM = 2.4, HSD = 2.32, HSLD = 2.25, Lbas = 3.1, HH-index = 3.23; m2: L = 2.0, W = 1.16, H = 1.55, R = 1.0, ASD = 1.2, HSD = 1.05, HSLD = 1.1, Lbas = 2.3, HH-index = 1.52.

Description. The morphologically archaic mole vole intermediate in hypsodonty stage between

mid Early Pleistocene (early-mid Calabrian) *Ellobius tarchancutensis* Topachevsky from Crimea and lower Don River area and late Middle Pleistocene to Recent southern mole vole *E. lutescens* Thomas of Transcaucasus, Near East and eastern Anatolia (see the details in Tesakov, 2016).

Comments. The hypsodonty of m2 from Haykadzor looks slightly less advanced than in m1 from Krasar. Although the variability range of hypsodonty features is not known for *E. pomeli*, the observed difference may account for somewhat older geological age of the Haykadzor fauna relative to the Krasar assemblage also suggested by morphology of Microtini voles in both localities.

BIOCHRONOLOGY

The composition of the Haykadzor fauna, the fauna of Krasar (Trifonov et al., 2016) and other published faunas of the Arapi Fm near Gyumri (Agadjanyan and Melik-Adamyanyan, 1985, 2016; Melik-Adamyanyan, 1985, 1994, 2003, 2004, 2017) represents a compact assemblage of small mammals (Table 10).

The faunal assemblage of the Arapi Fm clearly indicates a broadly synchronous fauna of early Middle Pleistocene age. Geologically it is bracketed by the Matuyama-Brunhes reversal at the bottom (0.78 Ma) and the *Arvicola* datum estimated as ca.0.5-0.6 Ma (von Koenigswald, van Kolfschoten, 1996; Maul et al., 2000) from above. The evolutionary level of *Mimomys intermedius* from Haykadzor is comparable to populations of

TABLE 10. Composition of early Middle Pleistocene small mammal faunas of north-western Armenia.

Taxa	Localities						
	Haykadzor	Kazachiy Post	Arapi 1, 2	Aeroport	Bayandur	Lusaghbyur	Krasar
<i>Sorex</i> sp.	-	+	-	-	-	-	-
<i>Sorex</i> cf. <i>runtonensis</i>	+	-	-	-	-	-	-
<i>Neomys</i> cf. <i>hintoni</i>	+	-	-	-	-	-	-
<i>Ochotona</i> sp.	-	-	-	-	-	-	+
<i>Ellobius pomeli</i>	+	-	-	-	-	+	+
<i>Mimomys intermedius</i>	+	+	-	-	-	-	-
<i>Microtus</i> ex gr. <i>nutiensis</i>	+	-	-	-	-	-	-
<i>Terricola</i> sp.	-	+	+	+	-	+	+
<i>Prolagurus pannonicus transylvanicus</i>	+	+	+	+	+	+	-
<i>Eolagurus</i> sp.	-	+	-	+	-	-	-

water vole from Cromerian correlated deposits of Western and Eastern Europe with values of size and hypsodonty indicating an early part of early Middle Pleistocene. *Prolagurus pannonicus transylvanicus* from the Arapi Fm precisely coincides in its evolutionary level with lagurines of late Early – early Middle Pleistocene faunas of Eastern and Central Europe. Smaller lagurines of Tiraspolian faunal complex of Eastern Europe (ca. 0.8-0.6 Ma) show the evolutionary transition from *P. pannonicus* dominated morphotypes in early Tiraspolian faunas to *Lagurus transiens* dominated morphotypes in latest Tiraspolian assemblages (Agadjanian, 2009). In biozonal chart of Eastern Europe (Vangengeim et al., 2001) this corresponds to the upper part of zone MQR7 (concurrent range zone of *Prolagurus pannonicus* and *Stenocranius hintoni*), spanning the very beginning of the early Middle Pleistocene. It is thus possible to correlate the faunas of the Arapi Fm to early Tiraspolian faunal complex. The yellow lagurine, *Eolagurus* sp. (cf. *argyropuloi* Gromov and Parfenova) also matches the evolutionary level of the Tiraspolian faunas of Eastern Europe. Subterranean voles *Terricola* of the Upper Akhuryan basin (Krasar) show a primitive evolutionary stage, clearly more primitive than recent and mid Middle Pleistocene *Terricola* species from the Caucasus. *Microtus* gr. *nutiensis* from Arapi Fm (Haykadzor) belongs to a morphological grade common in Europe at latest Early and early Middle Pleistocene. The same intermediate evolutionary position between Early Pleistocene and late Middle to Late Pleistocene and Recent forms occupies the mole vole *Ellobius pomeli* from the Arapi and synchronous deposits of western Armenia. Having in mind also absolute dates of 0.6-0.7 Ma obtained from Aragats ashes overlying and interfingering with Arapi deposits, their normal polarity interpreted as Bruhnes Chron, considered together with the evolutionary level of arvicolines from this formation, the age of the Arapi deposits and faunas can be reliably dated in the range of 0.78-0.6 Ma. In this range, a correspondence to a glacial/interglacial stage cannot be defined with certainty yet. Nevertheless, the notable arid elements in pollen flora and small mammals may favour a correlation to a glacial time, with MIS18 and, less likely, MIS16 being plausible time matches.

Combined biotic, paleomagnetic, and radiometric control makes the studied biotic sequence a reference point for the knowledge of geological, paleoclimatic, and biological evolution of the southern Caucasus in the Quaternary.

PALAEOENVIRONMENT

The available biotic record from fluvial formations of western Armenia enables a synthetic overview of the environmental conditions of regional late Early to early Middle Pleistocene transition.

Palynological data from diatomaceous clays of the Ani Fm indicate forest-steppe landscapes with more forested phases and a general trend towards more open biotopes in the Arapi time. Data on Pleistocene diatom assemblages of the Shirak Depression was obtained from the lacustrine diatomaceous deposits of the Ani unit in the sections of Arapi and the Marmashen borehole 6 (Zaikina et al., 1969a, b.). Later, additional material was studied in the Ani sections of Haykavan (lower part) and Arapi deposits of the Haykadzor section (beds 6-7) (Shalaeva et al., 2019). The general revealed trend is from assemblages with higher representation of planktonic forms in lower parts of the Ani Fm towards associations with growing role of bottom and littoral forms higher in the Ani sequences and in the Arapi Fm. This picture supports a concept of a progressing shallowing of the Pleistocene Shirak Lake (Sayadyan, 2009; Shalaeva et al., 2019) from late Early to early Middle Pleistocene. Molluscan and fish assemblages indicate conditions of a large lake with rich aquatic vegetation and a varying depth. Small mammalian fossils from the Arapi Fm indicate open steppe-like landscapes (lagurines, pika), meadows (mole voles, subterranean voles, *Sorex*), and periaquatic (ancient water voles *Mimomys intermedius*, water shrew) biotopes. The differences in composition of the Arapi faunas (e.g., dominant *Mimomys* in Haykadzor versus prevailing lagurines in Kazachii Post) can reflect both local taphonomy and/or environmental oscillations. The important role of small mammals adapted to open, arid biotopes in the Arapi sites can be an indication of a glacial climatic stage as the time of deposition of this unit.

DISCUSSION AND CONCLUSIONS

Palynological data on the lacustrine deposits of the Ani Fm indicate extensive development of forest-steppe and steppe coenoses in the Shirak Depression grading into birch forest and steppe associations in Arapi time (Figure 3). The reconstructed landscape trend in the range of ca. 1.5-0.6 Ma features the general transition from forest-steppe to steppe conditions. The high number of “exotic” arboreal species (not currently occurring in the Shirak region) in the Ani deposits, like *Tsuga* spp., *Podocarpus*, *Cedrus*, *Abies alba*, *Taxus*, *Liq-*

uidambar, *Altingia*, *Castanea*, *Carya* (Figure 4), does not contradict to the late Early Pleistocene – early Middle Pleistocene age of the main stage of the ancient Shirak lacustrine-fluvial sedimentary sequence.

The association of malacofauna from the Arapi unit exclusively contains Recent limnic species and can hardly be older than Middle Pleistocene. The Ani mollusc fauna is represented mainly by extinct fresh water species. This testifies that the Ani fauna is older and belongs to Calabrian and, perhaps, the lowest Middle Pleistocene. The hydrobiid *Falsipyrgula* of the Ani molluscan fauna sheds light on the historical biogeography and dispersal routes of freshwater fauna in the region. *Falsipyrgula* has a Ponto-Caspian origin, as shown by Wilke et al., 2007, based on the extant endemic *Falsipyrgula pfeiferi* (Weber, 1927) occurring in western Taurus Lake District. The migration pathways of the freshwater Ponto-Caspian fauna in this region are still controversial. For forms of the genus *Dreissena*, a Pliocene colonisation from Mesopotamia via central Anatolian lake area is inferred (Wilke et al., 2007). Finds of *Falsipyrgula* in Early Pleistocene of Armenia and Eastern Turkey (Vasilyan et al., 2014) show the probable migration routes of this genus through the early-middle Pleistocene lake systems of the Western Caucasus and Eastern Turkey, and also suggest an earlier divergence from the Ponto-Caspian genera *Euxinipyrgula*, *Turricaspia*, and '*Micromelania*' than the estimate of 0.42 ± 0.18 Ma suggested by Wilke et al. (2007).

The fish material from two sites of the Arapi Fm (Lusaghbyur and Haykadzor) provides evidence of a depleted cyprinid community dominated by the Barbinae (*Capoeta* sp., scraper) and *Pseudalburnus* sp., whereas the Leuciscinae (*Telestes* cf. *souffia*), documented by pharyngeal teeth, is extremely rare. This assemblage characterises the lacustrine and river habitats with rocky bottom,

well-warmed coastal zone, and the presence of intensive fouling produced by water vegetation. Occurrence of the above-listed taxa points to the continuity of the local ichthyofauna with the earlier Plio-Pleistocene fish communities known from Armenia (Bogachev, 1938; Vasilyan, 2008 a, b).

The mammalian faunas of Haykadzor and Krasar contribute to the knowledge of biodiversity and refines the biostratigraphic position of the Gyumri faunal complex.

Combined biotic, paleomagnetic, and radiometric control makes the studied biotic sequence a reference point for the knowledge of geological, paleoclimatic, and biological evolution of the southern Caucasus, and the entire Ponto-Caspian region in the Quaternary.

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