



## Article

# Plio-Pleistocene Small Mammal-Based Biochronology of Eastern Anatolia and Transcaucasus

Alexey S. Tesakov <sup>1,\*</sup>, Pavel Frolov <sup>1</sup>, Alexandra Simakova <sup>1</sup>, Albina Yakimova <sup>1</sup>, Vadim Titov <sup>2</sup> , Pranav Ranjan <sup>1</sup> , Hasan Çelik <sup>3</sup> and Vladimir Trifonov <sup>1</sup>

<sup>1</sup> Geological Institute, Russian Academy of Sciences, Pyzhevsky 7, 119017 Moscow, Russia; pavlenty987@mail.ru (P.F.); simak2001@mail.ru (A.S.); albina.yakimova@ginras.ru (A.Y.); pranavranjan42@gmail.com (P.R.); trifonov@ginras.ru (V.T.)

<sup>2</sup> Southern Scientific Centre, Russian Academy of Sciences, Chekhova 41, 344006 Rostov-on-Don, Russia; vvtitov@yandex.ru

<sup>3</sup> Geological Engineering Department, Engineering Faculty, Firat University, Elâzığ 23119, Türkiye; hasancelik@firat.edu.tr

\* Correspondence: tesak@ginras.ru

**Abstract:** The known Plio-Pleistocene mammalian record, mainly represented by small mammals, and its biotic and geological context in the vast region of Eastern Turkey and Transcaucasus provides a sound base for regional biochronology. Recently obtained faunal associations and the main evolutionary lineages found in the region support direct correlations to the European (ELMA/MN/MQ) and the Eastern European (faunal complexes/MQR-MNR) biochronological systems. Important data on palynology, aquatic and terrestrial mollusks, and magnetostratigraphy integrate the reviewed material into a robust local biochronology. The range of standard biochrons of Early Pliocene through late Early Pleistocene and the regional Anatolian zones M-P are reliably detected. The Early Pleistocene time range (zone P) is refined based on rhizodont lagurines *Borsodia* and Euro-Asian larger voles *Mimomys* ex gr. *pliocaenicus*. The successive zone R for Early Pleistocene faunas with early rootless *Microtini* is proposed.

**Keywords:** mammals; biochronology; eastern Turkey; transcaucasus; pliocene; early pleistocene; middle pleistocene



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## 1. Introduction

Fossil mammals and particularly smaller forms, such as rodents, are well known for their importance in biochronology because of their rapid evolution, wide distribution, and abundant fossil record, e.g., [1,2]. Following the pioneering works on Neogene and early Quaternary mammals by Fikret Ozansoy [3] and others, Otto Sickenberg and his colleagues continued studies on fossil mammalian faunas of Turkey [4–7]. These studies paved the way for later studies of primarily Neogene mammals and mammalian biochronology. Large mammals of the Pliocene and Pleistocene of Anatolia, particularly proboscideans, carnivorans, and ungulates, are constantly in the focus of recent studies [8–10].

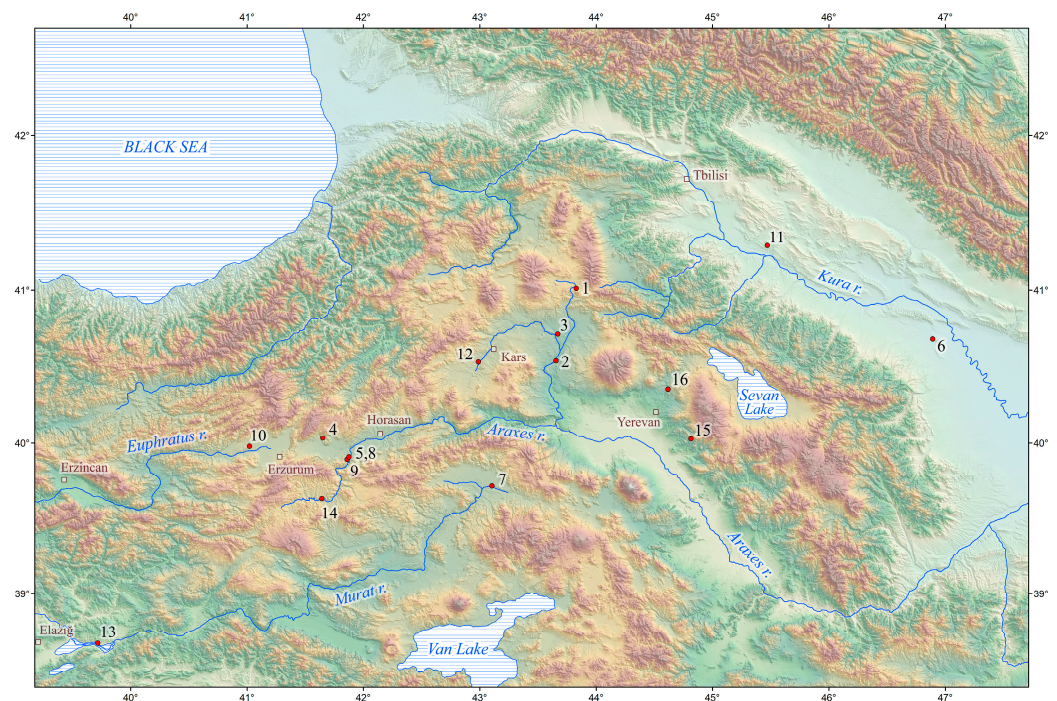
After several decades of research, the Plio-Pleistocene small mammals of Asiatic Turkey are relatively well studied [11–15] and many others. Important new data on this and adjacent regions accumulated recently [16–22].

The last decade brought informative new fossil material on small mammals, particularly from the Plio-Pleistocene of east Anatolia and adjacent areas of Transcaucasus [23–29]. Though not exceptionally rich and continuous, this record presents a contribution to the knowledge of the small mammal history and enables a needed modern review of regional mammalian biostratigraphy and its integration with the European (MN/Q/ELMA) [1], Eastern European (faunal complexes/MQR-MNR) [30], and Anatolian [31] biochronological systems. The goal of this contribution is a review of new data relevant to the update

and revision of the regional mammalian Plio-Pleistocene biochronology of Eastern Turkey and Transcaucasus.

## 2. Material and Methods

This study is based on fossil material from East Anatolia and adjacent regions of Transcaucasus in Armenia and Azerbaijan both originally collected in the field, studied in scientific collections, or reviewed from the literature. The bulk of data from Eastern Anatolia were collected by the joint Russian–Turkish cooperation project of the Geological Institute RAS in Moscow and the Firat University of Elâzığ. Data on the localities Tekman, Kümbetli, Pekecik B and C, Agri-East, and Duzdag are published for the first time. The geographic positions of the studied sites are shown in Figure 1. All key fossil collections are stored in the institution’s acronym as GIN, Geological Institute of the Russian Academy of Sciences in Moscow; EU, Firat University of Elâzığ; MTA, General Directorate of Mineral Research and Exploration, Ankara.



**Figure 1.** Schematic map showing the geographic position of the reviewed Pli-Pleistocene localities. 1. Krasar, 2. Haykadzor, 3. Demirkent, 4. Pasinler-A, 5. Pekecik C, 6. Duzdag, 7. Agri-East, 8. Pekecik B, 9. Pekecik A, 10. Paşayurdu, 11. Kushkuna, 12. Kümbetli, 13. Karangibaşı, 14. Tekman, 15. Jradzor, 16. Nurnus.

Mostly arvicolids (Arvicolinae, Cricetidae, Rodentia) are included in the review because this is the dominant and most important for biostratigraphical studies of small mammal group for the Plio-Pleistocene of the region. The utilized terminology of the European mammal biochronology follows Fejfar et al. [1] for mammal ages and MQ zones, and the regional zonation for the Pliocene follows Ünay et al. [31] and de Bruijn et al. [32].

In the text, most generalized Early Pliocene voles are referred to as *Promimomys*, diagnosed by low hypsodonty, the undifferentiated thickness of the enamel wall, lack of the external cement, predominantly two enamel islets in M3, compact anteroconid of m1 with integral T4–T5 and with a deep enamel islet. Generic differentiation of Early Pliocene voles based on merely the shape of anteroconid, with its triangular shape indicating *Promimomys* and trifoliate shape (with developed incoming angles BRA3 and LRA4) signaling *Mimomys*, is discouraged. Many of thus understood primitive voles of the Ruscinian are, in fact,

unrelated to true Villanyian *Mimomys* and may represent stem groups of multiple genera of Plio-Pleistocene arvicolines (see the discussion in [19] (p. 314)).

### 3. Results

#### Plio-Pleistocene biotic record.

In this section we review the most important mammalian associations of the studied region. Their correlation with standard and regional stratigraphic charts is shown in Figure 2. Necessary short notes on the most important correlative faunas of the neighbouring regions are given.

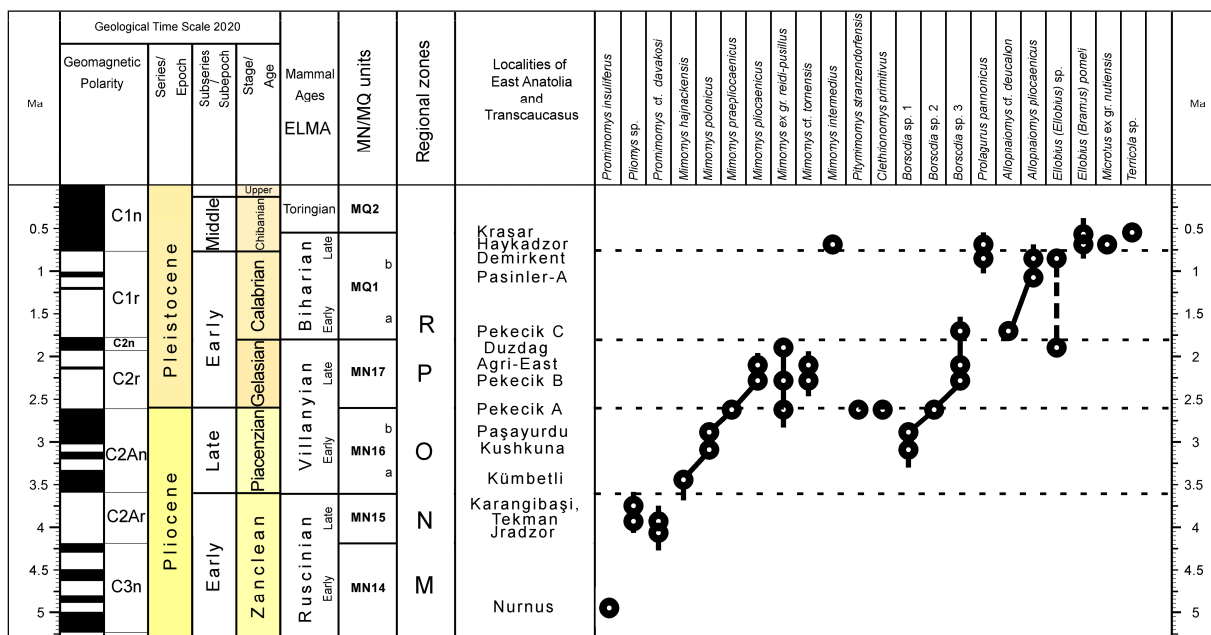


Figure 2. Stratigraphic chart showing the sequence of mammalian localities, occurrences of forms of Arvicolinae and their phyletic connections. Regional zones are after [31].

#### 3.1. Early Pliocene (Early Ruscinian) Nurnus

Located in central Armenia in an abandoned diatomite pit 6 km north of Yerevan (40°21'27.9" N 44°37'08.1" E), this site provided the only fauna of the earliest Pliocene age in the region. The scanty material, including bones of hipparionine horse, rhino, and fish imprints, has long been attributed to the Pliocene. It was the excavation and research by Melik-Adamyan [24] that ultimately refined the age of the fauna as Early Pliocene based on small mammal remains. Still, insufficiently published fauna includes a pika, close to *Ochotona meditteranensis* Suata-Alpaslan, 2015 from İğdeli, a rabbit *Trischizolagus gambariani* Melik-Adamyan, 1986, and a primitive arvicoline *Promimomys cf. insuliferus* shortly described as *Polonomys* sp. in [23] The evolutionary level of this vole places this fauna in the unit MN14.

Correlative faunas. In contrast to the detailed sequential Ruscinian record of the Ptolemais Basin in Greece [33], mammalian faunas of the Early Pliocene age are relatively rare and patchy in Anatolia. The oldest faunas of this age document the primitive vole *Promimomys cf. insuliferus* in İğdeli [34] and Nasrettinhoca 2 [22]. Faunas from Hacısam and Aşağı Page in central and eastern Anatolia appear to be close in age, based on the morphology of voles with a poorly differentiated triangular anteroconid [15]. The fauna of Çeştepe in Kazan Basin near Ankara is presumably close in age [20]. The oldest known early Ruscinian faunal association of Dinar-Akçaköy, according to the recent revision [35], includes the primitive vole *Promimomys enginae* Suata-Alpaslan, 2015. This form shows some characters, such as squared anteroconid, known in later European voles of the genus

*Germanomys*. The presence of these voles enables the attribution of these faunas to the unit MN14 and zone M of the Anatolian regional biozonation.

### 3.2. Early Pliocene (Late Ruscinian)

#### 3.2.1. Jradzor

The site is located in central Armenia (40°1'42.53" N 44°48'53.92" E). Smaller vertebrate fauna originated from an extensive stratigraphic sequence of lake sediments strongly influenced by pyroclastic material. Paleomagnetic and radiometric analyses provide a rare case of accurate placement of fossiliferous beds to upper Lower Pliocene, in the time range between 3.9 and 4.1 Ma [36]. Illustrated voles *Promimomys* sp. and *Mimomys* cf. *davakosi* (level JZ-3, ca. 4.1–4.0 Ma) belong to a medium-size generalized form *Promimomys* ex gr. *moldavicus-davakosi*, more advanced in hypsodonty than in lower Pliocene levels of the Ptolemais sequence [33]. Of the preliminary illustrated coeval forms from Jradzor [36], especially important are the leporid *Trischizolagus* cf. *dumitrescuae*, the glirid *Myomimus* cf. *maritsensis*, the murid *Occitanomys* sp., the gerbil *Pseudomeriones* cf. *tchaltensis*, and the cricetid *Neocricetodon* sp. The fauna is correlated with early Late Ruscinian, MN15.

#### 3.2.2. Karangibaşı

The site belongs to the Mio-Pliocene Çaybağı Formation and is located 16 km west of Palu town on the right bank of the Murat River (38°39'51.80" N 39°43'07.12" E). Small mammal fauna includes *Amblycoptus* sp., Desmaninae gen., *Ochotona* sp., Leporidae gen., cf. *Propliomys*. Scanty arvicoline remains to represent a brachiodont vole resembling late Early Pliocene *Propliomys* [37].

#### 3.2.3. Tekman

The fossil locality is situated on the right bank of the Araxes River near the bridge on the road from Hacıömer to Tekman. The site was reported by Sickenberg et al. [5] with the original faunal list including *Promimomys* sp. and *Castillomys* sp. Subsequently, a more detailed revised species list, strangely with reference to the same source, was published by Suata-Alpaslan [38]. This presumably revised list includes the vole *Mimomys* sp. and murids *Occitanomys* sp. and *Orientalomys*. The same site was reported under the name Çevirme, referred to the Pliocene Işıklar Formation in a publication devoted to fossil *Capoeta* fish from the original collections in Tübingen University [39]. As a result of our studies, a small outcrop of lacustrine deposits at the bank of the Araxes River (39°37'48.97" N 41°38'43.37" E) yielded a very small collection of micromammals, including Ochotonidae gen., *Promimomys* cf. *moldavicus-davakosi* and *Propliomys* sp. The low hypsodonty suggests an Early Pliocene age; the presence of pliomyoid vole points to the late Ruscinian, MN15 biochronological unit.

Correlative faunas. The most studied of coeval small mammalian faunas in north-central Anatolia is the reference fauna of Çalta [11,12]. The single arvicolid form in this locality was originally referred to *Mimomys gracilis* Kretzoi, 1959 [11], and later to *Mimomys davakosi* van de Weerd, 1979 [12]. The morphology of this vole with the deep *Mimomys* reentrant (BRA3), which insulates late in the wear process [11], indicates an early stage of the pliomyine evolutionary trend. Early morphological stages of late Early Pliocene *Propliomys* voles of the peri-Black Sea region, for example *Propliomys destinatus* (Tesakov, 2005) [40] from Odessa Catacombs or *Mimomys moldavicus/Propliomys* from Dranic-2 [41], show high similarity to the vole from Çalta.

Recently a small late Early Pliocene (MN15) cricetine assemblage was described from Afşar 1 in western Anatolia [42]. Arvicolines were referred to as *Mimomys* cf. *gracilis* and *Pliomys* sp. This is well supported by the morphology of M3. The late Early Pliocene *Propliomys* was also reported from central Anatolia in Ortalica [15]. The locality of Ericek in western Anatolia [19] documents a large vole, "*Mimomys*" *occitanus* Thaler, 1955. It can represent either a late Ruscinian early member of a large *Mimomys* group related to *M. plioaenicus* of Plio-Pleistocene or an endemic short-lived lineage of the *Promimomys* evolu-

tionary grade. The biochron of Late Ruscinian is also characterized in Anatolia by faunas of Tozaklar and Zirnak ("*Mimomys*" cf. *occitanus*), Sürsürü (medium-size *Promimomys* with pliomyine variability), Taşova (primitive *Promimomys*) [15].

### 3.3. Late Pliocene (Early Villanyan)

#### 3.3.1. Kümbetli

A roadside 5 m thick section of sandy-silty fluvial deposits of the Pliocene infill of the Kars sedimentary basin (40°31'51.47" N 42°59'22.43" E) yielded microvertebrate remains, including fragmentary shells of turtles, bones of anurans, and few molars of a larger vole *Mimomys hajnackensis* (= *hassiacus*). This is the first record of early Late Pliocene arvicolines in eastern Turkey. It may represent the MN16a unit in the region.

#### 3.3.2. Kushkuna

This site is located in western Azerbaijan, at the left bank of the Kura River valley (41°17'36.71" N 45°28'21.90" E). The site exposes a thick sequence of the marine deposits of the Caspian Sea Akchagylian transgression of the Late Pliocene age [43]. Small mammal assemblage includes a large form *Mimomys polonicus* and a scanty smaller vole *Borsodia* sp. 1 (reported as *B. ex gr. steklovi-novoasovica* [44]). The evolutionary level of the larger vole *Mimomys* and the geological constraints of the section indicate the correlation of this micromammal fauna to the Late Pliocene, the biostratigraphic unit MN16b, and the regional Anatolian zone O.

#### 3.3.3. Paşayurdu

Recently studied section of Late Pliocene paleo-delta fluvial deposits at the margin of the Erzurum intermontane Basin (39°58'44.82" N 41°01'19.72" E) between the villages Paşayurdu and Çigdemli. This site yielded a small mammal association with *Mimomys* cf. *polonicus* and *Borsodia* sp. [28]. The hypsodonty level of the larger *Mimomys* matches that of the type *M. polonicus* Kowalski, 1961 Rebielice Królewski in Poland. *Borsodia* from Paşayurdu is characterized by uniformly thick enamel, low dentine tracts (HH-index of m1, ca. 1.6), and a very short posterior lobe of M3. All these characters can be regarded as primitive. This record of *Borsodia* appears to be the oldest known in Anatolia. The fauna of small mammals from Paşayurdu-Çigdemli dates between 3.0 and 2.6 Ma. The lower age limit is controlled by the lower boundary of the MN16b biochronological zone, which is estimated to be close to 3.0 Ma [1].

Correlative faunas. The earlier part of the Early Villanyan (MN16a) in central Anatolia is represented by the fauna from Kadiözü, with large brachyodont *Mimomys* cf. *hajnackensis* (reported as *Mimomys* sp.) [15], and by the faunas from Hoyhoytepe and Mercan 1, also with *M. cf. hajnackensis* [22].

The properly described fauna of Afşar 2 in western Anatolia [42] includes larger *Mimomys* cf. *hajnackensis* (reported as *M. hassiacus*), medium-size *Mimomys* cf. *stehlini* (as *M. gracilis*), and *Propliomys graecus* (as *Pliomys*). Lower hypsodonty levels of the voles indicate a correlation with the MN16a biochronological unit.

The later part of the Late Pliocene (MN16b) in the published faunas is difficult to recognize because of the lack of conspicuous records of large *Mimomys* of the *M. polonicus* grade. The late Early Villanyan age may be presumed for Yenice-1 with rather advanced M3 of *Propliomys graecus* [15].

### 3.4. Early Pleistocene (Late Villanyan)

Pekecik A. The small mammal fauna of the lignite-rich lacustrine deposits near the village of Pekecik (39°53'35.79" N 41°51'41.09" E) at the right bank of the Araxes River in the Horasan Basin (Yolüstü or Horasan Formation) was first briefly reported by Ünay and de Bruijn [15] with *Mimomys pliocaenicus*, *Borsodia* sp., and *Clethrionomys* sp. The fauna was dated to the late Villanyan. The revision of the original collection (MTA) and additional material collected from this level led to a revised list including *Allocricetus* sp., *Mimomys*

*praepliocaenicus* Rabeder, 1981 (HH-index ca. 3), *Mimomys reidi* Hinton, 1910, *Borsodia* sp. 2 (HH-index ca. 2.5), *Pitymimomys stranzendorfensis* Rabeder, 1981, and *Clethrionomys primitivus* Popov, 2000 [32] (Simakova et al., 2021). The paleomagnetic constraints of normally magnetized host deposits indicate the chronological position of this fauna in the uppermost part of the Gauss Chron and an age slightly older than 2.6 Ma. The taxonomic content of the fauna matches the MN17a unit. This part of the section contains direct palynological evidence (brackish-water dinocysts) of the deep inland penetration of the Akchagylian marine transgression into the Horasan Basin. The maximal stage of the transgression is recorded close to the Pliocene–Pleistocene boundary. It gives an additional stratigraphic constraint to the Pekecik sequence [32,35].

Pekecik B. Higher in the section of Horasan Formation in Pekecik (39°54′18.79″ N 41°52′21.48″ E), several successive levels document *Mimomys pliocaenicus*, *Mimomys* ex gr. *reidi-pusillus*, *Mimomys* cf. *tornensis*, and *Borsodia* sp. 3.

Agri-East. The volcano–sedimentary infill of the Agri intermontane basin in the sections at the eastern margins of the town of Agri (39°42′53.33″ N 43°06′21.48″ E) yielded a micromammalian fauna similar to Pekecik B with *Mimomys pliocaenicus*, *Mimomys* cf. *tornensis*, and hypsodont *Borsodia* sp. 3.

The coeval faunas of Pekecik B and Agri-East correspond to the early-middle Gelasian and the middle part of late Villanyian, MN17b.

Duzdag. This section is situated in the central part of the Kura River valley in Azerbaijan (40°40′56.66″ N 46°53′40.09″ E). This several hundred-meters-thick section is one of the most studied sequences documenting the Plio-Pleistocene of Akchagylian and Apsheronian marine transgressions in the Caspian region [45]. The early Apsheronian stratigraphic member was recently regionally constrained to the late Gelasian time slice between the Reunion and Olduvai subchrons [36]. Fluvial freshwater deposits in this part of the section yielded micromammalian remains, including *Ellobius* (*Ellobius*) sp. similar to *E. kujalnikensis* Topachevsky, 1965, and *Mimomys* ex gr. *reidi-pusillus*.

Correlative faunas. The older part of Villanyian is documented by the mammalian fauna of Sarikol Tepe in central Anatolia [8]. This fauna was the first to show the presence of rhizodont lagurines *Borsodia* in Anatolia. *Borsodia* sp. from this site is more advanced in hypsodonty and shows deeper incurving reentrants than *Borsodia* sp. 1 from late early Villanyian Paşayurdu fauna [28]. The review in [15] described several faunas referred to the late Villanyian. The older faunas (Ziyaret, Sivricek, Karasapaca, Çatakli) show the presence of hypsodont *Mimomys pliocaenicus*. The assemblage of Ziyaret shows a probable taphonomic admixture of more primitive *M. hajnackensis*. *Mimomys* sp. 2 from Ziyaret and *Borsodia* sp. from Çatakli may represent *Clethrionomys* sp.

The later faunas of Havutçulu, Şevketin Dağı, and Kartaltepe, along with large hypsodont *Mimomys*, document the first appearance of endemic Aegean–Anatolian rootless lagurine voles *Kalymnomys* [15,46]. *Kalymnomys* datum preceding the migrational appearance of rootless Microtini of the *Allophaiomys* grade and other Lagurini (*Lagurodon arankae* Kretzoi, 1954, *Prolagurus*) is recorded in the diverse fauna of Biçakçi in western Anatolia. This fauna includes hypsodont *Mimomys pliocaenicus* (HH-index 5–6), *Mimomys tornensis* Janossy et van der Meulen, 1975, *Pitymimomys pitymyoides* (Rabeder, 1981), *Borsodia* gr. *newtoni-arankoides*, *Kalymnomys* sp., and *Clethrionomys kretzoi* (Kowalski, 1958) [22].

### 3.5. Early Pleistocene (Early Biharian)

Pekecik C. The high level of the Pekecik sequence some 300 m above the Pekecik A level (39°54′18.08″ N 41°52′28.83″ E) yielded an assemblage of *Beremendia fissidens*, *Allophaiomys* cf. *deucalion*, and *Borsodia* sp. 3 resembling *B.* ex gr. *newtoni-arankoides*.

Pasinler-A. Early Pleistocene lacustrine deposits north of Pasinler produce a small material of *Allophaiomys* cf. *pliocaenicus* [25]. This vole, showing an undifferentiated enamel band and early stage of anteroconid complication in m1, fits the evolutionary stage of Microtini dated to the late Early Pleistocene between 1 and 0.8 Ma. Additional material (2017) of the third upper molar of this vole, with shallow postero-lingual reentrant

LRA4, supports the conclusions. The specific fauna of freshwater mollusks of the Pasinler Formation [25] with sculptured pyrgulids is very close in composition with the assemblage of the late Early Pleistocene Ani Formation of the Shirak Basin at the Turkish–Armenian boundary [28]. A similar molluscan assemblage was recovered from the uppermost levels of the Pekecik sequence above the datum of *Allophaiomys* cf. *deucalion*.

Demirkent. This reference section (40°42'53.83" N 43°40'22.01" E) documents the penetration of the Akchagylian transgression of the Caspian Sea into the Shirak Basin as evidenced by brackish-water dinocyst assemblage of the Akchagylian type [27]. The lacustrine deposits of the lower part of the section are correlated to the Late Pliocene (Piacenzian) based on palynology and normal magnetization of the deposit. Higher in the section, fluvio-lacustrine deposits of the Ani Formation yielded a very small material of micromammals, including *Prolagurus pannonicus* and *Microtini* cf. *Allophaiomys* sp., and cf. *Ellobius* sp. This late early Biharian association indicates the late Early Pleistocene age of this part of the section.

Correlative faunas. Important early Biharian faunas in central and western Anatolia include Hamamayađı, Deđirmendere, Krttepe, and Kemalpařa Mahallesi-I [15,47]. The post-Villanyian age is indicated by the presence of primitive rootless *Microtini*, *Allophaiomys*, or larger endemic *Tibericola* voles. The latter may represent basal stages of the snow voles *Chionomys*. Most of these faunas also represent rootless endemic lagurines *Kalymnomys*. One of the youngest Early Pleistocene small mammal faunas of central Anatolia comes from the Early Palaeolithic site Dursunlu [48]. The vole fauna includes advanced *Allophaiomys nutiensis* Chaline, 1972, lagurine *Lagurodon arankae*, water vole *Mimomys intermedius* (Newton, 1881), and a mole vole *Ellobius* (*Bramus*) sp. This fauna correlates to micromammals of the Ani and Pasinler Formations, the late early Biharian, late Calabrian, and late Early Pleistocene age.

### 3.6. Early Middle Pleistocene (Late Biharian)

Haykadzor. Fluvial deposits of the Arapi formation in the Shirak Basin in western Armenia (40°32'16.04" N 43°39'21.05" E) yielded arvicoline fauna with *Ellobius* (*Bramus*) *pomeli* Tesakov, 1916, *Prolagurus pannonicus transylvanicus* Terzea, 1989, *Mimomys intermedius*, and *Microtus* ex gr. *nutiensis* [19]. This locality is bracketed between the Matuyama–Brunhes paleomagnetic reversal below (0.78 Ma) and the overlying ashes of the Aragats volcano radiometrically dated to 0.6–0.7 Ma. This position gives the time range of 0.78–0.6 Ma [19]. The biochronological position of this fauna matches the Cromerian of NW Europe, Tiraspolian mammal unit of Eastern Europe, late Biharian, early Cibanian, and early Middle Pleistocene age.

Krasar. Fluvial deposits of the Upper Akhuryan Basin in western Armenia (41°00'45.22" N 43°49'52.28" E). Arvicoline assemblage from Krasar includes *Ellobius pomeli* and *Terricola* sp. [19]. The fauna of this locality is close in age or slightly younger than Haykadzor.

Correlative faunas. Emirkaya 2 is a presumably early Middle Pleistocene fauna from a fissure filling in Central Anatolia [49] as indicated by the co-occurrence of *Mimomys intermedius* (reported as *M. savini*), and *Microtus* and *Terricola*. The presence of *Arvicola* may indicate a mixing of early and late Middle Pleistocene material.

## 4. Discussion

### 4.1. Regional Anatolian Biozonation

The regional biochronological zonation of Neogene of Anatolia was proposed by nay, de Bruijn, Sarac, and Hordijk [15,31,32]. The lowering of the Pliocene–Pleistocene boundary to 2.6 Ma by the International Commission on Stratigraphy (2009) transferred the uppermost zone P of this scheme, originally correlated to MN17, into the Early Pleistocene. This Early Pleistocene zone P is characterized by *Mimomys pliocaenicus/ostramosensis* and *Tibericola sakaryaensis* from the reference localities Hamamayađı and Yađmurlu [31]. The latter fauna likely belongs to an older Pliocene time [50]. In fact, in its original content

zone P corresponds to two different zonal units. The lower subunit is characterized by the faunas with dominant Late Villanyan hypsodont rhizodont arvicolines of the *Mimomys* group, such as the *Mimomys pliocaencus* group, co-occurring with advanced *Borsodia*, and first primitive *Kalymnomys* in western Anatolia (e.g., Bıçakçı, Kartaltepe 1, Havutçulu). In eastern Anatolia, the proper match is the new fauna of Agri-East without *Kalymnomys*. The upper subunit includes later faunas with dominant first primitive (*Allophaiomys* grade) arvicolines with rootless molars (e.g., Hamamayağı, Değirmendere, Pekecik C). Rhizodont voles are nearly missing. This later unit corresponds to early Biharian time. We propose to restrict the usage of zone P to the older late Villanyan faunas with the type fauna of Bıçakçı [18]. The immediately chronologically subsequent zone is expedient to denote as zone R with the type fauna of Hamamayağı. More data are needed to extend this zonation into the early Middle Pleistocene.

#### 4.2. East European Biochronology

The regional biochronological system of MNR/MQR units of Eastern Europe [30,40] was established based on the principle of concurrent range zones of several self-checking lineages of arvicoline rodents. In the time periods of a stable, well-differentiated, and homogeneous fauna of small mammals, such as in the Late Pliocene and early Early Pleistocene, this zonation is easily applicable to the fossil record of all Europe and Western Asia, giving a reliable increase in accuracy and more details in the biostratigraphic subdivision of continental deposits [18,51,52]. The eastern Anatolian record shows the stable presence of the most important small mammal groups and the identical sequence of evolutionary events as compared to the East European record. More data are needed to resolve endemic or universal lineages of rhizodont lagurines, *Borsodia*. Some morphological characters, such as more robust molars and more uniformly thick enamel, may indicate an independent development of a *Borsodia* lineage in the eastern Anatolian region in the Late Pliocene and earliest Pleistocene. No reliable evidence on the origin of Aegean–Anatolian endemic *Kalymnomys* lagurines of the Early Pleistocene is yet available.

#### 4.3. European Biochronology

The overviewed sequence of small mammal faunas in the Anatolia and western Transcaucasus shows a very important and growingly reliable information basis for regional stratigraphy and elaboration of the bio-climatic history of the region in Pliocene and Early Pleistocene. The unique geological structure of the region features numerous intermontane basins experiencing long-term subsiding and accumulating long sedimentary sequences of continental deposits. The paleontological record of these basins, most importantly, the record of land mammals, thus can be studied in its continuous geological content. Ruscinian arvicoline faunas of Asia Minor and Transcaucasus, still insufficiently known, present the common evolutionary trends known elsewhere in the Holarctic Realm: brachiodont *Promimomys* grade voles gradually increase their hypsodonty, and by the second half of Early Pliocene show evidence of phyletic radiation and genus-level differentiation. Villanyan arvicoline faunas show stages of radiation of mimomyian voles and some endemic Anatolian lineages (*Borsodia*). Presumably aquatic, large voles of the *Mimomys hajnackensis-pliocaenicus* group are very widespread in the region. This group most efficiently provides interregional and intracontinental biostratigraphic correlations in Piacenzian and Gelasian. Biharian arvicoline faunas of the region document the global *Allophaiomys* dispersal and parallel endemic evolution of other lineages of rootless voles. The present-day state of the art in the understanding of the history of micromammalian faunas in the westernmost part of Asia enables bright perspectives of a further increase in our knowledge.

### 5. Conclusions

The fossil record of Eastern Anatolia and Transcaucasus enables a recognition of a dozen consecutive biochronological levels from the Early Pliocene to the early Middle Pleistocene. In contrast to the older Neogene fossil record [32], the Plio-Pleistocene biotic



record of Anatolia shows a low level of endemism, which makes it important and applicable for the extensive regions of Northern Eurasia. The region seems to be easily penetrated by continental-wide migration waves of Arvicolinae. The local development of vole faunas shows the main evolutionary events of the group: the Early Pliocene *Promimomys* stage, late Ruscinian vole radiation, Villanyian *Mimomys* radiation, and dispersal of *Borsodia*, the *Allophaiomys* datum at the Villanyian-Biharian transition, and the beginning of the Biharian Microtini radiation. The availability of radiometric age control of some faunas provides precious calibration points of regional and continental biostratigraphic data. The reviewed record is thus easily correlated both to the standard European biochronology (ELMA, MN/MQ units) and regional sequences of Western [2,51,53] and Eastern Europe [52] and Western and central Anatolia [31]. The position of the region at the crossroads between Eastern Europe and the Caucasus and South and Western Europe makes it crucial for studies in the historical biogeography, faunistics, and elaboration and calibration of the Eurasian continental biochronology.

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