

Early Middle Pleistocene *Ellobius* (Rodentia, Cricetidae, Arvicolinae) from Armenia

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ABSTRACT. A large mole vole from the early Middle Pleistocene of Armenia shows morphological features and hypsodonty intermediate between basal Early Pleistocene *E. tarchancutensis* and the late Middle Pleistocene to Recent southern mole vole *E. lutescens*. The occlusal morphology of the first lower molar is similar to Early Pleistocene forms but hypsodonty values do not overlap either with Early Pleistocene mole voles (higher in the described form) or with extant *E. lutescens* (lower in the described form); these features characterise the Armenian form as a new chronospecies *Ellobius (Bramus) pomeli* sp.n., ancestral to the extant southern mole vole. Three phyletic lineages leading to two extant Asian species and to Pleistocene North African group of mole voles are suggested within *Ellobius (Bramus)*.

KEY WORDS: *Ellobius*, *Bramus*, phylogeny, early Middle Pleistocene, Armenia.

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Слепушонка *Ellobius* (Rodentia, Cricetidae, Arvicolinae) начала среднего плейстоцена Армении

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РЕЗЮМЕ. Ископаемая крупная слепушонка из отложений начала среднего плейстоцена Армении по морфологии и гипсодонтии занимает промежуточное положение между раннеплейстоценовыми *E. tarchancutensis* и современной закавказской слепушонкой *E. lutescens*. По строению жевательной поверхности армянская форма близка к раннеплейстоценовым слепушонкам, а значения гипсодонтии у этой формы занимают промежуточное положение и не перекрываются ни с формами раннего плейстоцена (выше у описываемой формы), ни с современной *E. lutescens* (ниже у армянской формы). Эти признаки характеризуют новый хроновид *Ellobius (Bramus) pomeli* sp.n., предковый по отношению к современной *E. lutescens*. Предложено рассматривать внутри *Ellobius (Bramus)* три филетические линии, ведущие к современным азиатским видам и ископаемым плейстоценовым слепушонкам Северной Африки.

КЛЮЧЕВЫЕ СЛОВА: *Ellobius*, *Bramus*, филогения, начало среднего плейстоцена, Армения.

Introduction

Mole voles (Ellobiusini, Arvicolinae, Cricetidae) are highly specialised burrowing cricetid rodents. The combination of specific cranial structure and molar teeth with plesiomorphic features (e.g. root formation and moderate hypsodonty) suggested for some systematists a position of mole voles outside the subfamily Arvicolinae (Miller, 1896). In their thorough revision of voles, Gromov & Polyakov (1992) considered mole voles as vole-toothed cricetines convergent with arvicolines in dental morphology. In many other revisions Ellobiusini were included in the family/subfamily Arvicolidae (Hinton, 1926; Stehlin & Schaub, 1951; Kretzoi, 1969). Recent data on molecular phylogeny of the Arvicolinae show a close sister-group relationships of Ellobiusini, Lagurini, and Microtini, thus supporting the hypothesis of mole voles being a part of the second

(Early Pliocene) radiation of Arvicolinae (Abramson *et al.*, 2009a, b). Therefore, most specific features of mole voles developed due to a strong burrowing specialization (incisor digging, molar enamel thickening and partial reduction of molars) so that Early Pleistocene forms still show much more arvicoline-looking molars with some mimomyoid characters (e.g. *Mimomys*-ridge and relics of enamel islets). As with many rapidly evolving arvicoline phylums, molar evolution in mole voles shows a progressive hypsodonty increase from Early Pleistocene to Recent forms expressed in lengthening of dentine tracts of enamel-dentine boundary (Topachevsky & Rekovets, 1982; Zazhigin, 1988; Tesakov, 2008; Fig. 2). Two main branches of mole voles are recognised (Fig. 3). The nominotypical subgenus *Ellobius (Ellobius)* Fischer, 1814 combines smaller mole voles with the fossil record ranging from Early Pleistocene to recent (Topachevsky & Rekovets, 1982; Tjutkova, 1989;

Tesakov, 2008). The group of larger forms is included in the subgenus *Bramus* Pomel, 1892. This name has a priority over *Afganomys* Topachevsky, 1965 commonly used for this group in the literature (Tesakov, 2008). This subgenus is represented by two extant species of western and central Asia, the southern (*E. lutescens* Thomas, 1897) and Afghan (*E. fuscocapillus* Blyth, 1842) mole voles. These species were often considered conspecific (Ognev, 1950), but substantial chromosomal and marked morphological differences support their status as distinct species (Vorontsov *et al.*, 1980; Carleton & Musser, 2005).

The fossil record of *E. (Bramus)* is patchy. The most impressive is the Early to Middle Pleistocene record of the group in North Africa where after a migration from Asia a short but conspicuous endemic evolution occurred with several successive species known (Pomel, 1892; Jaeger, 1988; Geraads, 2002; Stoetzel, 2013).

In the range and adjacent areas of the recent Afghan mole vole, there are records of a basal form from the early Early Pleistocene (Gelasian) of Kazakhstan, *E. primigenius* Savinov, and late Early Pleistocene species from Tadjikistan, *E. lakhutensis* Zazhigin (Lytchev & Savinov, 1974; Zazhigin, 1988). In the south of Eastern Europe there are several records of Early Pleistocene (Calabrian) *E. tarchancutensis* Topachevsky (Topachevsky, 1963; Tesakov, 2008). The morphology of this vole tentatively points to its ancestral position relative to the recent southern vole *E. lutescens* of Transcaucasus, northern Iran, and eastern Asia Minor (Tesakov, 2008). Fossil records of late Middle to Late Pleistocene *E. lutescens* are known from archaeological sites of the Near East (Bate, 1937; Tchernov, 1968; Maul *et al.*, 2015); these were originally considered as a separate species *E. pedorychus* Bate, 1937 or a subspecies of the southern mole vole. The new record of a larger mole vole from Armenia sheds light on a ca. 1 Myr gap in the known history of *Ellobius (Bramus)* in the western Asia.

The early Middle Pleistocene deposits of the Shirak Depression exposed in numerous outcrops near the city of Gyumri in western Armenia are assigned to the fluvio-lacustrine Arapi Formation (Sayadyan, 2009; Trifonov *et al.*, 2016). These deposits have yielded a rich biotic record including large and small mammals and freshwater molluscs (Akramowski, 1956; Avakyan, 1959; Melik-Adamyanyan, 1994, 2004; Agadjanyan & Melik-Adamyanyan, 1985). On the basis of the large mammals, notably *Mammuthus trogontherii* (Pohlig), the deposits were assigned to the Leninakan or, later, Gyumri faunal complex (assemblage) correlated with mid Middle Pleistocene Singilian assemblage of Eastern Europe (Sayadyan, 1970, 2009; Alekseeva, 1977). Melik-Adamyanyan (1994, 2004) argued for an older age of the Arapi deposits. Based on the composition of the small mammal faunas and radiometric dates he correlated the Gyumri assemblage to the early Middle Pleistocene, Cromerian of Western Europe, and Tiraspolian com-

plex (assemblage) of Eastern Europe. The records of *Mammuthus trogontherii* (Alekseeva, 1977), small mammals with basal *Terricola*, advanced *Prolagurus pannonicus* Kormos and *Mimomys intermedius* Newton (Agadjanyan & Melik-Adamyanyan, 1985), radiometric dates of 0.6–0.7 Ma for “Leninakan tuffs” covering or interfingering with Arapi deposits, and normal polarity (Brunhes Chron) of these deposits (Trifonov *et al.*, 2016) point to the early Middle Pleistocene age of the Gyumri faunal assemblage.

In 2013, a new early Middle Pleistocene mammalian fauna was discovered by the expedition of the Geological Institute of the Russian Academy of Sciences headed by V.G. Trifonov. A four meters thick fluvial deposits exposed in a sandpit near Krasar settlement in the upper Akhurian Basin yielded a mammalian assemblage including *Ochotona* sp., *Terricola* cf. *majori* Thomas, *Microtus* sp., *Ellobius (Bramus) pomeli* sp.n., Elephantidae gen. indet., *Praemegaceros* cf. *verticornis* (Dawkins), cf. *Bison* sp. (Trifonov *et al.*, 2016, and additional data). Normal polarity of the deposits and their faunal composition point to the correlation to the Arapi Formation of western Armenia. Additional material on mole vole has been collected in 2016 from the Arapi deposits of Haykadzor locality located in the Shirak Basin. This site yielded remains of *Terricola* ex gr. *majori*, *Mimomys intermedius*, *Prolagurus pannonicus transylvanicus* Terzea, and *Ellobius pomeli* sp.n.

The find of isolated molars of mole vole from early Middle Pleistocene deposits of Armenia is an important record for reconstructing the history of this group of arvicolines. In 2013, remains of a large mole vole (a damaged M2) was found in another early Middle Pleistocene locality in the Shirak Basin, Armenia, at Lusaghbyur (Agadjanyan & Melik-Adamyanyan, 2016).

Material and methods

Remains of small mammals were collected in the field using standard dry-sieving techniques with the mesh size of 1 mm. Occlusal elements of vole mole molars are named according to van der Meulen (1973). Measurements are after Tesakov (2004). Terms for dentine tracts (sinuous enamel-dentine boundary folds) in dentitions of rhizodont voles follow G. Rabeder (1981): HH-index, the square root of the sum of squared heights of dentine tracts of hypoconid and hypoconulid in lower molars; ASD — anterosinuid, HSD — hyposinuid, HSLD — hyposinulid, MIM — mimosinuid. Lower case m stands for lower molars; upper case M, for upper molars. T stands for dental triangle; A, anteroconid length; H, labial height; R, root height in labial view; Lbas, basal length. All measurements are in mm. Institutional abbreviation: GIN, Geological Institute of the Russian Academy of Sciences, Moscow; ZISP, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg.

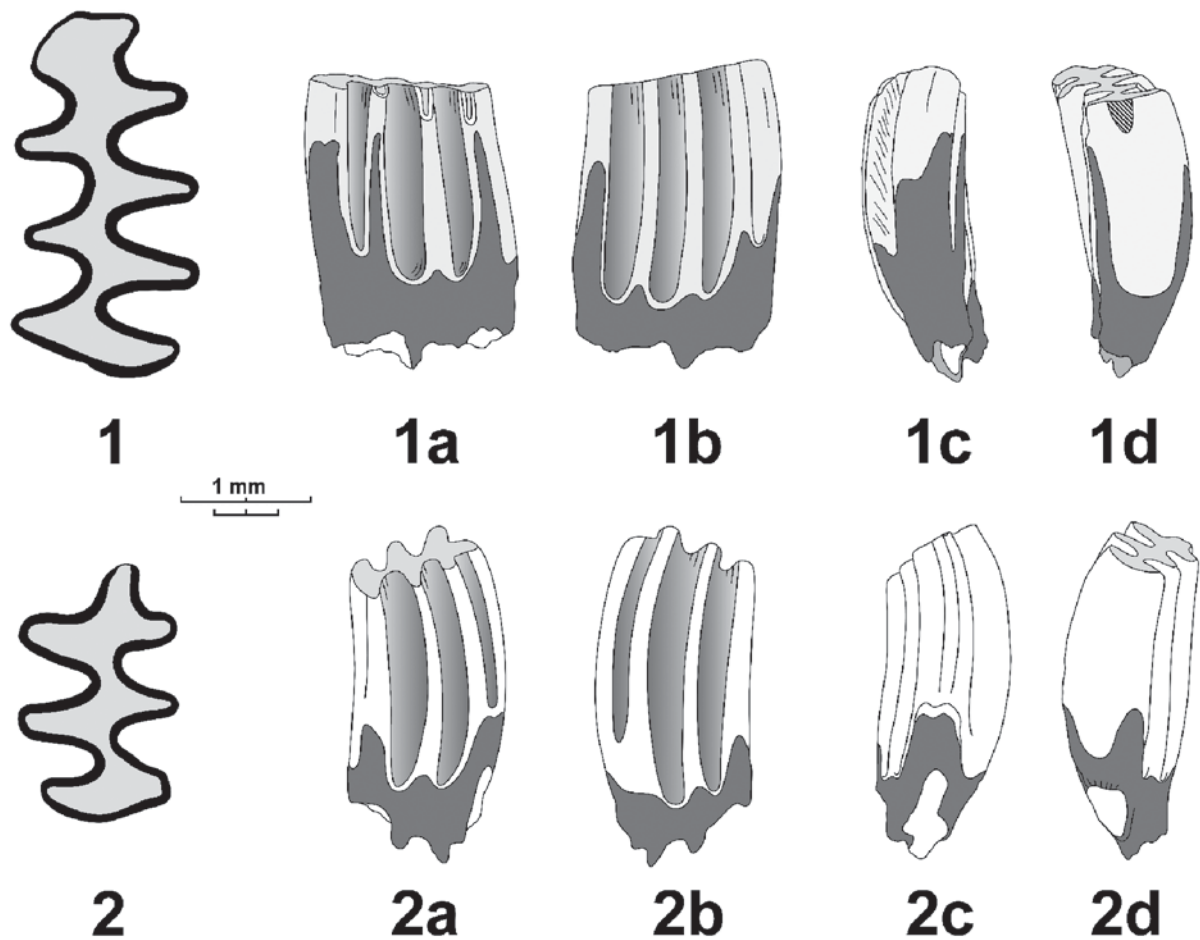


Fig. 1. *Ellobius (Bramus) pomeli* sp.n. 1 — first lower molar, m1, left side, occlusal view, Krasar; 2 — second lower molar, m2, right side, Haykadzor. Lateral views: a — labial; b — lingual; c — anterior; d — posterior. Scale bars for occlusal (upper) and lateral (lower) views equal 1 mm.

Systematic paleontology

Order Rodentia Bowdich, 1821
 Family Cricetidae Fischer, 1817
 Subfamily Arvicolinae Gray, 1821
 Tribe Ellobiusini Gill, 1872
 Genus *Ellobius* Fischer, 1814
 Subgenus *Bramus* Pomel, 1892

Ellobius (Bramus) pomeli sp.n.

Fig. 1.

Ellobius ex gr. *lutescens*: Trifonov *et al.*, 2016: p.12, fig. 9: 1.

Ellobius (Bramus) ex gr. *lutescens*: Tesakov, 2016: p.420.

Etymology: In honour of Auguste Pomel, eminent French paleontologist who made an important contribution to the study of Pleistocene larger Ellobiusini.

Holotype: GIN-1141/1, isolated right first lower molar, 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.

Type locality and geological age. Krasar (N41°00.753', E43°49.872'; H = 1981 m a.s.l.), Arapi Formation, Upper Akhurian Basin, north-western Armenia; early Middle Pleistocene, late Biharian, Tiraspolian faunal complex, East European regional biochronological unit MQR7.

Additional material: GIN-1142/1, isolated left second lower molar, 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. Haykadzor (N41°32.26', E43°39.31'; H = 1488 m a.s.l.), Arapi Formation, Shirak Basin, north-western Armenia; early Middle Pleistocene, late Biharian, Tiraspolian faunal complex, East European regional biochronological unit MQR7.

Diagnosis. Medium size *Bramus* with hypsodonty HH-index near 3, short anteroconid, and occlusal confluence between of T4 and T5 broader than that of T3 and T4.

Differential diagnosis. The new species differs from Early Pleistocene forms *E.(B.) primigenius* Lytchev et Savinov, 1974 of Kazakhstan (Gelasian), *E.(B.) tarchancutensis* Topachevsky, 1963 (early to mid Calabrian)

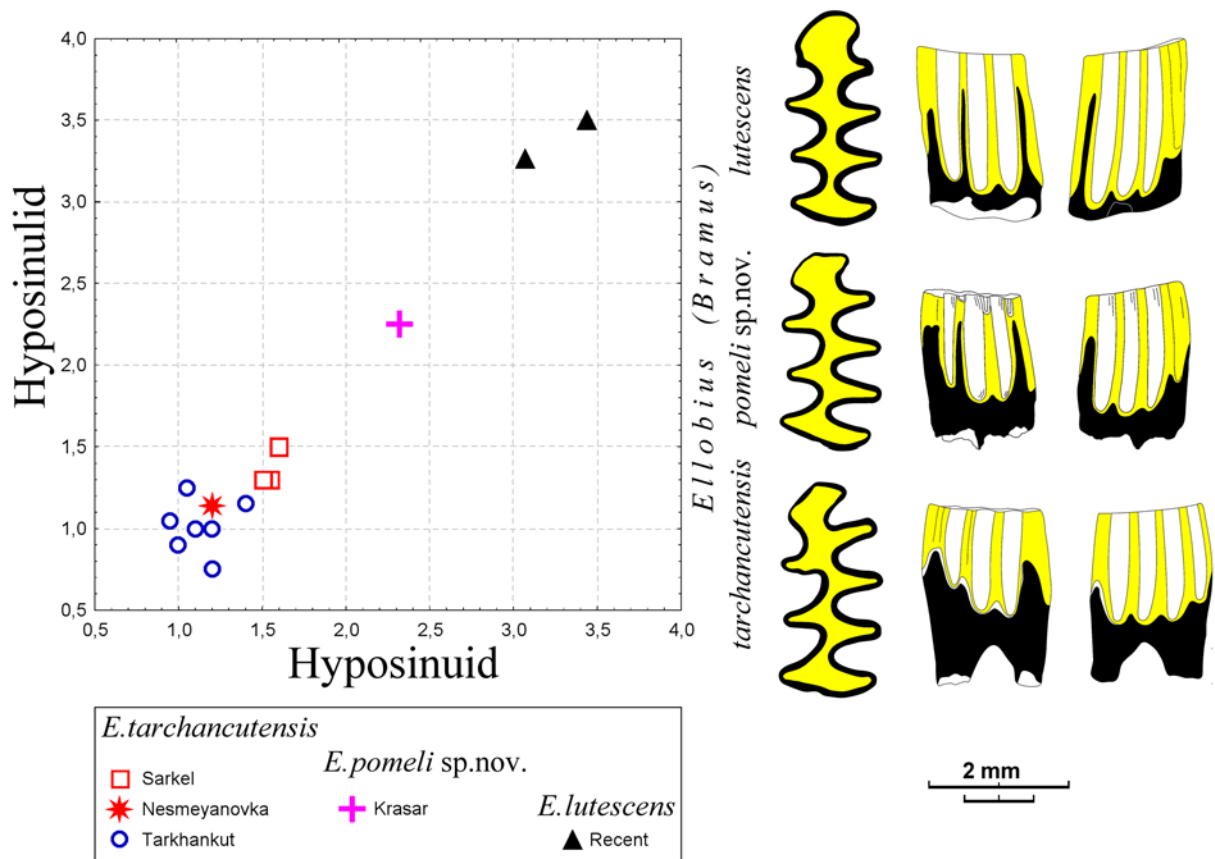


Fig. 2. Hypsodonty diagram of some fossil and recent mole voles *Ellobius (Bramus)*. Hyposinuid, labial dentine tract of posterior loop of m1, mm; hyposinulid, lingual dentine tract of posterior loop of m1, mm. Note a difference in dentine tract height, as a marker of hypsodonty, in Early Pleistocene *E. tarchancutensis* (Sarkel locality, GIN-EMM-139/21) through early Middle Pleistocene *E. pomeli* sp.n. to Recent *E. lutescens* (ZISP-35390, Vedi, Armenia).

of southern Eastern Europe, and *E.(B.) africanus* Jaeger, 1988 from North Africa (late Calabrian?) in higher hypsodonty (HH-index = 3.2 compared to ≤ 1.5). *Ellobius (Bramus) pomeli* sp.n. differs from late Middle to recent *Ellobius lutescens* Thomas, 1897 including *E. lutescens pedorychus* Bate, 1937 in lower hypsodonty (HH-index = 3.2 vs > 4 in compared forms) and in stronger alternating basic triangles (T1–T3) and more opposing anteroconid triangles (T4–T5). The described species differs from late Early Pleistocene *Ellobius lakhtensis* Zazhigin, 1988 from Tadjikistan and from recent Afghan mole vole *E. fuscocapillus* Blyth, 1842 in smaller size, lower hypsodonty (HH-index = 3.2 vs ≥ 4 in the compared forms), and from the latter form in more alternating basic triangles. From North African Middle-Late Pleistocene species, *E. pomeli* sp. nov. differs in smaller size and higher hypsodonty.

Description. The first lower molar (Fig. 1: 1) shows moderately high crown and two roots. The enamel is mostly uniformly thick with a notable thinning along the anterolabial side of the anteroconid cap. The closing enamel of the posterior lobe bears an attritional facet of m2. The molar has a well developed posterior lobe, three basic triangles (T1–T3), anteroconid trian-

gles T4–T5, and a slightly transversely elongated sub-oval anteroconid cap (Fig. 1). Occlusal dentine fields broadly communicate, with broadest connections between T1–T2 and anteroconid elements. The reentrant angles are U-shaped. Dentine tracts are of medium height. Hyposinuid is somewhat higher than hyposinulid. Mimosinuid is well developed, matching the height of hyposinuid. The tip of anterosinuid is slightly bilobate. The anterosinuid bears a notable indentation on the anterior side of the anteroconid. Apart from hyposinulid, the tracts of the lingual side are low, except for a slightly higher tract of LSA4 (1.1 mm).

Lower m2 from Haykadzor (Fig. 1: 2) has a relatively high crown and two distinct roots. The enamel is thick, with some thinning in the corners of reentrant angles, and at the tips of salient elements. The molar has two pairs of occlusal triangles (T1–T2 and T3–T4) and posterior loop. All occlusal elements broadly communicate, with the triangles showing broader pair-wise confluence. At the same time the triangles display notable alternation with labial elements shifted in an anterior direction compared to their lingual counterparts. The anterior portion of the molar has a distinct, pointed anteroconid delimited by two deep reentrants, BRA3

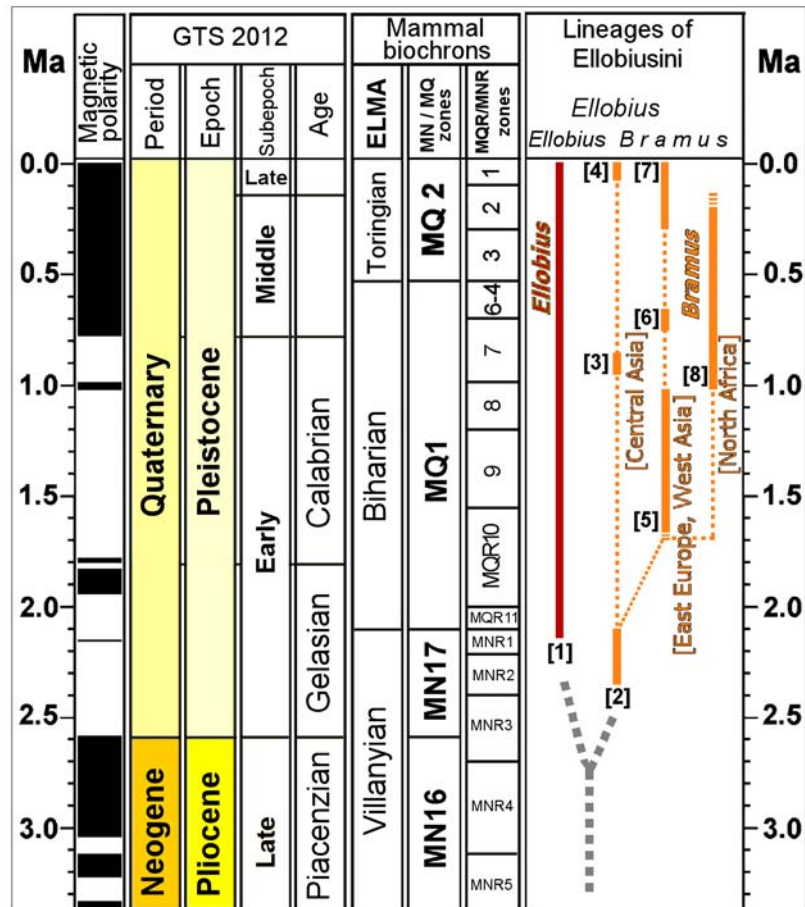


Fig. 3. Chronology of reconstructed phyletic lineages of *Ellobius* (*Bramus*). Documented intervals of the lineages: nominative subgenus *Ellobius* (*Ellobius*), smaller mole voles: [1]; subgenus of larger mole voles, *Ellobius* (*Bramus*): [2] *E. primigenius* (early Early Pleistocene, southern Kazakhstan, Turkmenistan), archetypal ancestor of larger mole voles; [3] *E. lakhutensis* (latest Early Pleistocene, Tadjikistan); [4] *E. fuscocapillus* (Recent, Central Asia); [5] *E. tarchancutensis* (late Early Pleistocene, East Europe, West Asia, ?North Africa); [6] *E. pomeli* sp.n. (early Middle Pleistocene, Armenia); [7] *E. lutescens* (late Middle to Late Pleistocene, Recent, West Asia); [8] *E. spp.* (late Early to Middle Pleistocene, North Africa). Geochronologic and paleomagnetic scales are according to Geological Time Scale 2012 (Hilgen *et al.*, 2012; Pillans & Gibbard, 2012). Mammal biochrons are according to Pevzner *et al.* (2001) modified; Tesakov *et al.* (2007), modified; Hilgen *et al.* (2012); Tesakov & Titov (2013).

and LRA3. Dentine tracts are clearly expressed. The tip of anterosinuid is bilobate.

Discussion

The mole vole *Ellobius* (*Bramus*) *pomeli* sp.n. in hypsodonty of m1 has an intermediate position (Fig. 2) between the Early Pleistocene (Calabrian) *Ellobius tarchancutensis* Topachevsky of Eastern Europe (Crimea, lower Don River area) (Tesakov, 2008) and the extant southern mole vole *Ellobius lutescens* (Transcaucasus, eastern Turkey, north-western Iran) and its fossil forms including late Middle Pleistocene *E. lutescens* from Azykh (Azokh) Cave in eastern Transcaucasus (Markova, 1982; Parfitt, 2016), and late Middle Pleistocene to Late Pleistocene *Ellobius lutescens* pe-

dorychus Bate from Israel (Bate, 1937; Tchernov, 1968). These former forms include the type *E. l. pedorychus* from Late Pleistocene Levallois-Mousterian beds of Tabun Cave and an older form from late Middle Pleistocene Acheulian beds of the Oumm-Qatafa archaeological site (Tchernov, 1968). On the other hand, in occlusal structure with well alternating triangles and well separated anteroconid, early Middle Pleistocene *Ellobius pomeli* sp.n. is most similar to advanced *E. tarchancutensis* from Early Pleistocene fauna of Sarkel (Tesakov, 2008). It differs from late Middle Pleistocene to Recent forms of *E. lutescens* (e.g. Markova, 1982; Kryštufek & Vohralík, 2005; Coşkun, 2016) which show a broad confluence of dental triangles with a trend to pair-wise opposing of T1–T2 and T3–T4, and separation of T5 getting confluent to the anteroconid cap.

In fact, a placement of ancient mole voles from Europe and Asia to the lineages of either of the two extant Eurasian species is hampered by plesiomorphic traits in the fossil forms. The dental differences apparent between recent *E. lutescens* and *E. fuscocapillus* are not easily traceable back in time. For example, *E. lutescens* is slightly smaller than *E. fuscocapillus* (Moradi Gharkheloo & Kivanç, 2003), *E. lutescens* has a less anteroposteriorly extended m1, and a slightly less pairwise opposed T1–T2 and T3–T4. More differences are apparent in cranial and dental characters (Ognev, 1950; Kryštufek & Vohralík, 2005). In this situation, the geographic occurrence coupled with morphological evidence is the only way to set up a phyletic hypothesis. Thus the Transcaucasian location of *E. pomeli* sp. nov. combined with its intermediate hypsodonty suggests that the Armenian form is a chronological stage of the lineage of recent *E. lutescens*. The reconstructed lineage of *E. pimigenius*–*E. tarchankutensis*–*E. pomeli* sp.n.–*E. lutescens* then shows a relatively uniform increase of hypsodonty through time. On the other hand, most of occlusal changes from alternating to opposing triangles conditions should have occurred in a short period between early and late Middle Pleistocene. A form only slightly older than the Armenian mole vole, the late Early Pleistocene *E. lakhutensis* Zazhigin from Tajikistan shows characters not compatible with the lineage considered above. Firstly, regardless of its older age, the Tajik form is somewhat larger and more hypsodont than *E. pomeli* sp.n. Secondly, *E. lakhutensis* has a more robust anteroconid in m1. It makes sense to regard this form as a part of another lineage leading to extant *E. fuscocapillus*.

Lineages of *Ellobius* (*Bramus*)

The basal Early Pleistocene forms of *Ellobius* (*Bramus*) include the oldest and archetypically basal *E. primigenius* from Gelasian Kiiikbai fauna of southern Kazakhstan (Lytchev & Savinov, 1974), the Tarkhankut vole, *E. tarchankutensis*, known from several Calabrian localities in southern Eastern Europe, and morphologically very similar to East European forms *E. africanus* Jaeger from latest Early Pleistocene Tighenif (Ternifine) locality in Algeria (North Africa).

Three distinct post-Early Pleistocene lineages are clearly defined in the group. Two lineages are definable for the recent species of *Ellobius* (*Bramus*). The lineage of the Afghan mole vole includes latest Early Pleistocene *E. lakhutensis* from Lakhuti 2 site in Tajikistan (Zazhigin, 1988) and the recent *E. fuscocapillus*. The lineage of the southern mole vole includes *E. pomeli* sp. nov. from early Middle Pleistocene of Transcaucasus, *E. l. pedorychus* from late Middle to Late Pleistocene of the Near East, and the recent *E. lutescens*. The third one is Middle to Late Pleistocene extinct lineage from North Africa including *E. atlanticus* Jaeger, *E. barbarus* Pomel, and *E. zimae* Jaeger (Jaeger, 1988; Geraads, 1994, 2002). It was suggested

that the North African group can in turn be split into two lineages (Jaeger, 1988). The origin of the African lineage by a migration of an Asian form is suggested (Jaeger, 1988). The earliest known East European and African forms (*E. tarchankutensis* and *E. africanus* respectively) share an almost identical plesiomorphic morphology and stage of evolution indicating a possible conspecificity of these forms. Therefore, the dispersal event of mole voles to Africa can be biochronologically dated to at least the middle part of the Early Pleistocene (Tesakov & Geraads, 2009). The proposed lineages are illustrated in Fig. 3.

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