

New Late Miocene *Alilepus* (Lagomorpha, Mammalia) from Eastern Europe – a new light on the evolution of the earliest Old World Leporinae

STANISLAV ČERMÁK, CHIARA ANGELONE & MAXIM V. SINITSIA



The leporid material from eight Late Miocene (MN11–13) localities of Ukraine and Moldova is described. The analysis is supported by a direct revision of type materials of *A. laskarewi*, *A. hungaricus* and *A. ucrainicus*. Lectotypes of *A. annectens* (type species of *Alilepus*), *A. laskarewi* and *A. hungaricus* are designated here. The new material from Egorovka 2 (MN12) allowed a detailed morphometric re-description and emended diagnosis of *A. laskarewi*, one of the least understood species of the Old World *Alilepus*. One of the peculiarities of *A. laskarewi* is the very high incidence of mesofossettid in p3. The oldest leporids of the study area are verified for the MN11 localities Palievo, UA and Keinar, MD, but the taxonomy for these very scanty records remains unclear. In the light of the new material presented here, (i) a synoptic survey and discussion on the presence of p3 mesofossettid and (ii) hypotheses on a possible evolution and dispersal among the Old and New World Leporinae are provided. • Key words: *Alilepus*, taxonomy, phylogeny, Late Miocene, Pliocene, Eastern Europe.

ČERMÁK, S., ANGELONE, C. & SINITSIA, M.V. 2015. New Late Miocene *Alilepus* (Lagomorpha, Mammalia) from Eastern Europe – a new light on the evolution of the earliest Old World Leporinae. *Bulletin of Geosciences* 90(2), 431–451 (6 figures, 2 tables). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received June 10, 2014; accepted in revised form November 6, 2014; published online March 9, 2015; issued March 23, 2015.

Stanislav Čermák, Institute of Geology, Academy of Sciences of the Czech Republic, v.v.i., Rozvojová 269, 165 00 Prague 6, Czech Republic; cermaks@gli.cas.cz • Chiara Angelone, Grup de recerca de Faunes del Neogen i Quaternari, Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICP, Campus de la UAB s/n, 08193 Cerdanyola del Vallès, Barcelona, Spain; chiara.angelone@icp.cat • Maxim V. Sinitsia, Paleontological Museum, National Museum of Natural History, National Academy of Sciences of Ukraine, Bohdan Khmelnytsky str. 15, 01-601 Kiev, Ukraine; sinitsimax@gmail.com

The genus *Alilepus* represents one of the most ancient forms of the Leporinae clade. Its origin can be traced back to the late Middle Miocene of North America (Voorhies & Timperley 1997). During the Late Miocene *Alilepus* arrived in Eurasia through Beringia. The widespread of leporids in Eurasia, the first of which most probably was *Alilepus*, marked a “revolution” in the ecosystems, determining the definitive decline of the ochotonids that since the Early Miocene dominated the Old World.

A century ago, Khomenko (1914) erected from the Moldovan locality Tarakliya (MN12) *Lepus laskarewi*, the species representing now the oldest available name among the Old World *Alilepus*. Since then neither the type nor other relevant material has been studied in detail to revise this poorly known species. The genus *Alilepus* was erected later by Dice (1931), as a new replacement name of *Allolagus* Dice 1929, based on the type species *Lepus annectens* Schlosser, 1924. Dice (1929, p. 342) diagnosed the new genus based on its p3 formed by “two columns

connected in the centre of the tooth by a bridge of dentine” [a direct quote from Schlosser (1924, p. 46)].

In spite of its importance for palaeobiogeography, biochronology and palaeoecology, *Alilepus* lacks a thorough revision in Eurasia. This paper is aimed to take stock of the situation of the genus *Alilepus* in Europe, in order to:

1) provide a taxonomic/nomenclatural basis for subsequent systematic considerations of European *Alilepus* by a revision of type materials of all available names of European species of *Alilepus*, with special respect to direct analysis and revision of the very poorly known type materials of *A. laskarewi*, *A. hungaricus* and *A. ucrainicus*;

2) provide a detailed morphometric re-description of *A. laskarewi* and formulate its emended diagnosis based on the new *Alilepus* material from eastern European localities;

3) provide in the Holoarctic context (a) a synoptic survey and discussion about the presence of the mesofossettid in the p3s of leporids, and (b) hypothesize a possible evolution and dispersal of the earliest Leporinae.

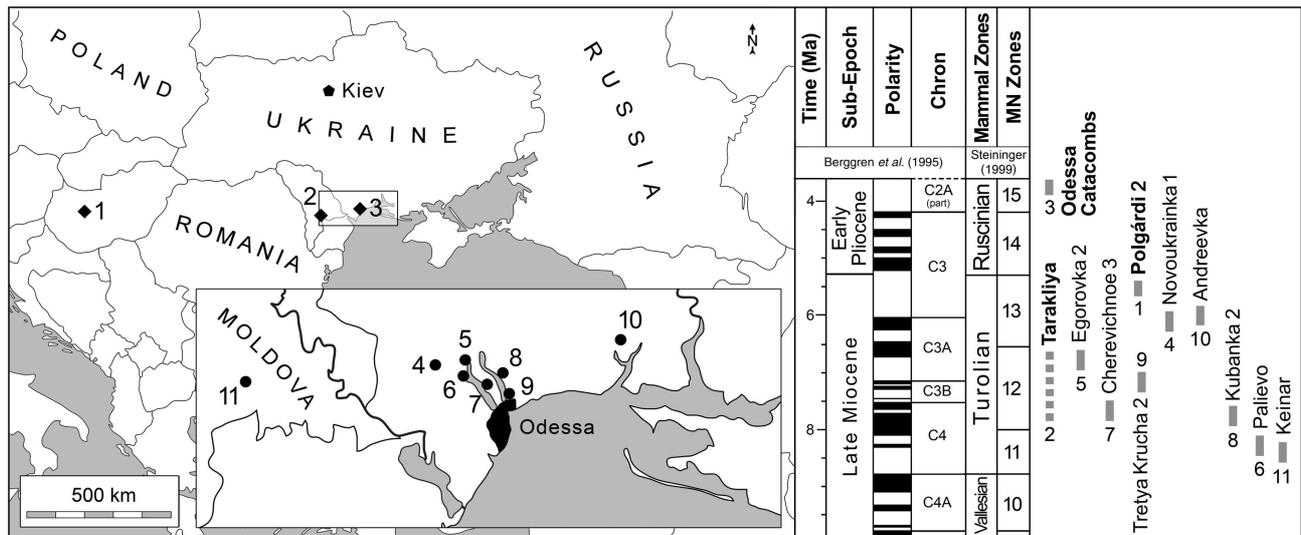


Figure 1. Geographical localization and age estimation of the fossil sites under study, including type localities Polgárdi 2, Tarakliya and Odessa Catacombs.

Geographical and geological setting of the new *Alilepus*-bearing fossil localities

The *Alilepus* material analyzed in this paper comes from eight Late Miocene (MN11–13) localities of Ukraine and Moldova. Their locations and chronologic relationships are illustrated in Fig. 1.

Andreevka [Андреевка]. – Thin lens of alluvial gravels embedded in a large sequence of Late Meotian siltstone and clay covered by a typical Upper Pontian shell limestone (Berezanski district, Nikolaev region, Ukraine). Association with *Pseudocricetus kormosi*, *Apodemus dominans*, *Apodemus gorafensis* and *Pliospalax (Nannospalax) compositodontus* suggests a Late Turolian (MN13) age.

Novoukrainka 1 [Новоукраинка 1]. – The locality (Razdelnyanski district, Odessa region, Ukraine) consists of several lenses of gravels and sandy gravels with a moderately rich fossil bed. The fossiliferous layer occurs within a large sequence of the Upper Chersonian, Meotian and Pontian siltstones, clays, sands and limestones. The faunal composition is identical with Andreevka, but *Pseudocricetus* shows an earlier evolutionary stage than in Andreevka.

Egorovka 2 [Егоровка 2]. – The locality is situated on the right riverbank of the Svinaya River near the village of Egorovka (Razdelnyanski district, Odessa region, Ukraine). The bones of small mammals were scattered in a thick lens of clayey gravels and siltstones. A very rich mammal assemblage is characterized by the predominance of *Pseudocricetus orienteuropaeus*, *Apodemus schaubi*, *A. cf. dominans* and *A. aff. lugdunensis*. Other taxa such as *Myomimus maritsensis*, *Muscardinus cf. pliocaenicus*, *Vasseuromys aff.*

pannonicus, “*Sciurotamias*” aff. *gromovi*, *Pliopetaurista* sp., *Euroxenomys minutum*, *Chalicomys* sp., anomalomyids, bats and lipotyphla form a minor part of this assemblage. The locality is noteworthy for the absence of ochotonids. The age of this small mammal community is correlated with the Middle Turolian (MN12), a slightly younger than Cherevichnoe 3, Tretya Krucha 2 and Kubanka 2.

Tretya Krucha 2 [Третья Круча 2]. – An abandoned artificial outcrop with a thick layer of Middle Meotian gravels exposed on the riverbank of Kuyalnitcki Liman (Kominternovski district, Odessa region, Ukraine). The moderately rich fossil bed contains a typical Middle Turolian (MN12) small mammal assemblage with *Pseudocricetus orienteuropaeus*, *A. lugdunensis* and *Apodemus cf. schaubi*.

Cherevichnoe 3 [Черевычное 3]. – The locality (Belyaevski district, Odessa region, Ukraine) is located in Lower Meotian gravels rich in small vertebrate fossils. Detailed information on the locality is given in Topachevski *et al.* (2000). Based on the predominance of *Pseudocricetus antiquus*, *Apodemus barbarae*, *A. lugdunensis*, *Vasseuromys cf. pannonicus* and the peculiar hamster *Stylocricetus*, this assemblage is believed to Middle Turolian in age (MN12).

Kubanka 2 [Кубанка 2]. – The locality is located in gravelly level(s) of a small abandoned sand quarry close to the Kubanka village (Kominternovski district, Odessa region, Ukraine). The small mammal fauna of Kubanka 2 is poorly investigated and understood, so a detailed biostratigraphic correlation of the locality is not yet possible. The presence of *Pseudocricetus aff. orienteuropaeus*, *Apodemus barbarae*, *A. lugdunensis*, *Vasseuromys pannonicus*, *Pliopetau-*

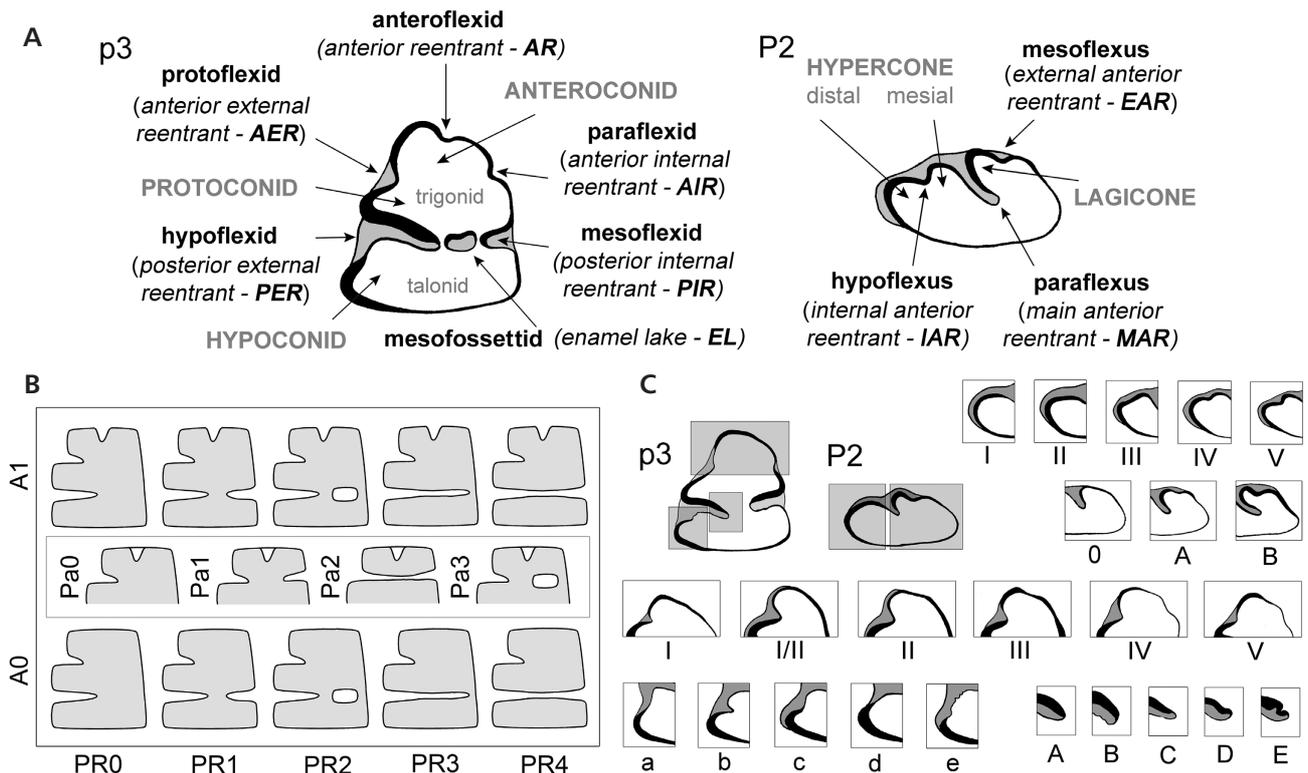


Figure 2. Dental terminology and morphology of leporid p3 and P2. • A – terminology and position of enamel structures in p3 and P2 (after Palacios & López Martínez 1980 supplemented with terminology by White 1991 – in parentheses). • B – categorization of basic enamel p3 patterns based on the combination of (1) presence/absence of anteroflexid (morphotypes A0–A1), (2) development of morphostructures between trigonid and talonid (morphotypes PR0–PR4) and (3) development of paraflexid (morphotypes Pa0–Pa3). • C – detailed morphological characterization of anterior and buccal enamel structures of p3 and P2 (after the scheme of morphological classes originally used for *Hypolagus* in Čermák [2009, fig. 5; based on Fladerer 1987 and/or Fladerer & Reiner 1996]).

rista cf. *bressana* and *Eozapus intermedius* suggests a Middle Turolian (MN12) age.

Palievo [Палиєво]. – The locality outcrops in the steep riverbank of the Khadzhibeiski Liman (Razdelnyanski district, Odessa region, Ukraine). Most fossil remains were recovered from a thin layer of gravel covered by Lower Chersonian oolithic limestone and greenish clay. The small mammal assemblage of *Apodemus barbarae*, *A. lugdunensis*, *Kowalskia progressa*, *Stylocricetus* sp., *Lophocricetus complicidens*, *Vasseuromys* aff. *pannonicus*, *Muscardinus* sp., *Ochotona* spp., *Prolagus* sp., *Schizogalerix* cf. *moedlingensis*, *Archaeodesmana* aff. *vinea* and “*Paenelimmocetus*” *repenningi* suggests an Early Turolian age (MN11).

Keinar [Cainari]. – The locality is situated on the right side of the Botna River, near the town of Keinar (Caușeni region, Moldova). Several thick (up to 1.5 m) layers and lenses of alluvial gravels are embedded in a large sequence of Late Sarmatian freshwater and marine deposits with abundant shells of mollusks (*Maetra caspia*, *M. bulgarica*, *Unio*, *Planorbis*, *Helix*). Lungu & Rzebik-Kowalska (2011) date the locality to the late Vallesian (MN10). How-

ever, the presence of *Apodemus lugdunensis* and species of *Kowalskia* similar to *K. skofleki* from Eichkogel (not to *K. falhbuschi* from Kohfidisch [M. Sinita, pers. obs. 2013]), excludes a Late Vallesian age. Thus the small mammalian fauna from Keinar is correlated here with the Early Turolian (MN11).

A list of the localities with brief characteristics, accompanied by major literature sources, is summarized in Table 1.

Material and methods

The type material of European *Alilepus* is in collections of the MFGI (*A. hungaricus*), MSN-UF (*A. meini*), PMONU (*A. laskarewi*), UM (*A. turolensis*) and ZIN RAS (*A. ucrainicus*). The newly described leporid material from the Late Miocene localities of Ukraine (Andreevka, Cherevichnoe 3, Egorovka 2, Novoukrainka 1, Kubanka 2, Palievo, Tretya Krucha 2) and Moldova (Keinar) is deposited in the collections of the NMNHU and FG TU, respectively. Comparative and/or additional material from Moldovan localities Chimishliya (MN12) and Gradishte (MN12) is deposited in the collections of the MENH and FG TU.

Table 1. List of Late Miocene localities with *Alilepus* studied in this paper. Explanatory notes: • A – name of the locality (country abbreviation). • B – biostratigraphic correlation (MN zones *sensu* Steininger 1999). • C – biostratigraphic significance of the mammalian record from the locality: 1 – abundant community samples in a continuous sequences and/or a very abundant point record (enabling a quantitative treatment), 2 – a sequence in which at least some samples allow a quantitative approach, or a representative point sample, 3 – a less representative point record. • D – state of preservation of fossil material: a – well preserved (*i.e.*, available fragments of skulls, teeth and parts of postcranial skeletons are abundant), b – moderately well preserved (*i.e.*, fragments of skulls are rare, isolated teeth are predominant), c – poorly preserved (*i.e.*, isolated teeth are available almost exclusively, moreover mostly corroded or damaged). • E – major references to the localities.

A	B	C	D	E
Andreevka (UA)	MN13	2	a	Topachevski & Skorik (1992), Nesin & Nadachovski (2001)
Novoukrainka 1 (UA)	MN13	2/3	b/c	Korotkevich (1988), Topachevski & Skorik (1992), Nesin & Nadachovski (2001)
Egorovka 2 (UA)	MN12	1	a	Sinitsa (2008, 2009a)
Tretya Krucha 2 (UA)	MN12	3	a	Sinitsa (2005)
Cherevichnoe 3 (UA)	MN12	1	b	Topachevski <i>et al.</i> (2000), Nesin & Nadachovski (2001), Nesin (2013)
Kubanka 2 (UA)	MN12	2	b	Sinitsa (2011)
Palievo (UA)	MN11	1	b	Sinitsa (2009b, 2012)
Keinar (MD)	MN11	2	b	Lungu (1980), Lungu & Rzebik-Kowalska (2011)

Dental terminology and metrics used to describe these structures follow Sych (1965) and Palacios & López Martínez (1980). The position of enamel structures in p3 and P2, supplemented with terminology by White (1991), is shown in Fig. 2A. The general enamel p3 pattern of Leporidae is categorized here based on the combination of presence/absence or degree of development of (1) anteroflexid (morphotypes A0–A1), (2) morphostructures between the trigonid and talonid (morphotypes PR0–PR4) and (3) paraflexid (morphotypes Pa0–Pa2). The classification scheme is summarized in Fig. 2B. Sequences (A0–A1, PR0–PR4, Pa0–Pa2) of structures in the scheme do not represent stages of morphoclines. More detailed morphological characterization of anterior and buccal enamel structures of p3 and P2 (Fig. 2C) follows the scheme of morphological classes originally used for *Hypolagus* in Čermák (2009, fig. 5; based on Fladerer 1987 and/or Fladerer & Reiner 1996). Here we reserve the formal term “Leporinae”, or informally “leporines” for a leporid group including *Alilepus* and their presumed descendants. For the group with taxa distantly related to that radiation, we use term “Leporidae”, or informally “leporids”.

Drawings and measurements were made with a camera lucida and ocular micrometer on a binocular microscope. Outline maps used in Figure 1 were taken from <http://d-maps.com/>. All measured data are given in millimeters. Biostratigraphic terminology follows Fejfar & Heinrich (1983), Semenenko (1987), Nesin (1996, 2004) and Fejfar *et al.* (1998). The North American fossil record is correlated also with the NALMA system (North American land mammal ages). All nomenclatural acts presented here conform to the mandatory provisions of the International Code of Zoological Nomenclature (ICZN 1999).

Abbreviations. – EL – enamel lake; FGTU – Faculty of Geography of Tiraspol State University, Department of

General Geography, Kishinev, Moldova; GLI – Institute of Geology AS CR, v.v.i., Prague, Czech Republic; L – length; Ltrig – trigonid length; Ltal – talonid length; M – mean; MENH – National Museum of Ethnography and Natural History, Kishinev, Moldova; MFGI – Magyar Földtani és Geofizikai Intézet (Hungarian Institute of Geology and Geophysics), Budapest, Hungary; MSN-UF – “Museo di Storia Naturale” (Geology and Palaeontology Section), University of Florence; N – number of specimens; NMNHU – National Museum of Natural History, V. Topachevsky Palaeontological Museum, Kiev, Ukraine; PMONU – Odessa I.I. Mechnikov National University, Palaeontological Museum, Odessa, Ukraine; OR – observed range; Wg – width of internal fault in I1; Wtrig – trigonid width; Wtal – talonid width; UM2 – University of Montpellier 2; ZIN RAS – Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia. Country abbreviations follow ISO 3166-1 alpha-2 codes. P/p (premolars) and M/m (molars) refer to upper and lower cheek-teeth, respectively.

Type material of European species of *Alilepus*

Before our systematic revision of studied taxonomic taxa from localities of Ukraine, we must clarify uncertainties in type materials of European *Alilepus* species. In the Miocene–Pliocene of Europe five available (fulfilling the conditions of Article 13.1.1 of ICZN 1999) species names of *Alilepus* have been described. With the exception of the recently erected *A. turolensis* and *A. meini*, European *Alilepus* (*i.e.*, *A. laskarewi*, *A. hungaricus* and *A. ucrainicus*) are described insufficiently, and their type material urges a revision. To further complicate the situation, the fossil record of European species of *Alilepus* is scanty and fragmentary,

represented mostly by dentition only. Moreover some species (*A. hungaricus*, *A. meini* and *A. ukrainicus*) are well proven only from their type localities by the original type series. Thus, an evaluation of the taxonomic validity of all European species, based on such limited material, cannot be resolved sufficiently, and is beyond the scope of this paper. The aim here is to review all nomenclaturally important data, including – if necessary – a proper name-bearing type fixation and, based on direct analysis of poorly known type materials of *A. laskarewi*, *A. hungaricus* and *A. ukrainicus*, to provide emended descriptions. For the sake of completeness we report here also details, with principal literature references, concerning the type materials of *A. turolensis* and *A. meini*.

Alilepus laskarewi (Khomenko, 1914)

Figure 3A1–A4

Type series. – The type material was collected by I.P. Khomenko from Tarakliya [Taraclia, Тараклия] in 1912. The exact location of the fossil site (situated in the northwestern part of Tarakliya village) is unknown (Delinschi pers. comm. 2013). The nominal taxon *Lepus laskarewi* was established by Khomenko (1914) based on the syntype (Article 73.2 of ICZN 1999) consisting of a right mandible with p3-m3 (Khomenko 1914, p. 12, pl. I, figs 19, 20) and two forelimb phalanges (Khomenko 1914, p. 12, pl. I, figs 9, 10). No single name-bearing type specimen was designated, neither originally (holotype [Article 73.1]) nor subsequently (lectotype [Article 74]). At present in the collections of the PMONU only a right mandible can undoubtedly be identified with the original material described by Khomenko (1914).

Name-bearing type. – Lectotype (designated in this paper) – right mandible with p3-m3 (No. 3403, Fig. 3A1–A4); collections of the PMONU.

Type locality and age. – Tarakliya (Keushen region), Moldova; Middle Turolian, MN12.

Emended description of the type material. – Mandible: Mandibular body with p3-m3, damaged in its ventral part. Its size and the cylindrical crown of the teeth indicate that it is an adult individual.

p3: The damage in the ventral part of the jaw reveals the “radical” part of the tooth, and shows that the A0/PR1/Pa0 morphotype is maintained along the whole tooth crown. The simple, unilobated anteroconid (morphotype II) is relatively long (about 1/3 of tooth length). The walls of the shallow protoflexid form a nearly right angle. The trigonid and talonid are connected by a thin isthmus, as the hypoflexid and mesoflexid are both quite deep. The

medial part of the hypoflexid is of the “C/D” morphotype. The labial part of hypoconid is of the “c” morphotype.

Lower molariforms: In p4-m3 no reentrant is present at the antero-buccal corner of the trigonids; the anterior and antero-buccal walls of talonids are without infoldings or undulation.

Measurements. – Mandible: alveolar length of p3-m3 = 13.4; p3: L = 3.20, W = 2.82; p4: L = 2.84, W_{trig} = 3.37, W_{tal} = 2.74; m1: L = 2.84, W_{trig} = 3.32, W_{tal} = 2.58; m2: L = 2.89, W_{trig} = 3.45, W_{tal} = 2.63; m3: L = 2.21, W_{trig} = 2.16, W_{tal} = 1.39.

Lectotype designation. – In the sense of Articles 74.7 and Declaration 44, we hereby designate the right mandible with p3-m3 (No. 3403, Fig. 3A1–A4) as a lectotype (Article 74.7.1 and Declaration 44) of the nominal taxon of *Lepus laskarewi* Khomenko, 1914 described from the Middle Turolian (MN12) locality Tarakliya (Moldova).

Remarks. – The species name “*laskarewi*” represents the oldest available species name within the Old World *Alilepus*. The correct original spelling of the species name (Article 32.1 of ICZN 1999) is *A. laskarewi*; thus, subsequent spellings *A. lascarevi*, *A. lascarewi*, or *A. laskarevi* reported in the literature (e.g., Kormos 1934, Gureev 1964, Daxner & Fejfar 1967, López Martínez 1976, Qiu & Han 1986, Jin 2004, Lungu *et al.* 2007, Jin *et al.* 2010) must be regarded as incorrect (Article 33.3 of ICZN 1999).

Alilepus hungaricus Kormos, 1934

Figure 3B1–C

Type series. – The type material was collected by T. Kormos in 1910 (Kormos 1911). The nominal taxon *Alilepus hungaricus* was established by Kormos (1934) based on the syntype (Article 73.2 of ICZN 1999) consisting of a left mandible with p3-m2 and a right maxilla with P3-M1. No single name-bearing type specimen was designated, neither originally (holotype [Article 73.1]) nor subsequently (lectotype [Article 74]). In the collections of the MFGI, we found both the specimens under the catalogue number Ob. 5068.

Name-bearing type. – Lectotype (designated in this paper) – left mandible with p3-m2 (Ob. 5068; Fig. 3B1–B5); collections of the MFGI.

Type locality and age. – Polgárdi 2, Hungary; Late Turolian, MN13.

Emended description of the type material. – Mandible: Lingually damaged mandibular body with p3-m2. The buccal surface of the body is fenestrated below p3-p4. The

root end of the lower incisive alveolus extends below the anterior border of p3. Available teeth are not conical attesting that this is an adult individual.

p3: The A0/PR1/Pa0 morphotype is maintained along the whole tooth crown. The anteroconid (between morphotypes II and III) is relatively short (less than 1/3 of tooth length) and markedly widened lingually. A very shallow, medially undulated protoflexid has walls forming an obtuse angle. The hypoflexid slightly indents the talonid and is crenulated in its distal side. The medial part of the hypoflexid is of the “B” morphotype. The mesoflexid end is bilobed and in radical view its distal side is undulated. The connection between the trigonid and talonid is relatively wide. The labial part of the hypoconid is of the “c” morphotype. The enamel band is thin.

Lower molariforms: The trigonid is short (Ltri < Ltal) in p4-m1; a reentrant at the antero-buccal corner of the trigonids is absent. The trigonids appear massive, prominent and rounded in the labial side, especially in p4-m1. In p4 the posterior wall of the trigonid is medially undulated and has a central tip oriented posteriorly. In all molariforms the anterior wall of the talonids is undulated, but without deep infoldings, and the degree of undulation decreases from p4 to m2; a small antero-buccal reentrant is present.

Maxilla: In ventral view, the incisive foramen extends to the posterior margin of the alveolus of P2. The choanae reach the P4/M2. The palatine occupies about 40% of the length of the palatal bridge. The major palatine foramen is located next to the hypostria of P4. The masseteric spine is thin and long, and does not expand laterally.

Upper molariforms (P3-M1): The internal reentrant (= hypostria) extends approximately halfway across the tooth and is crenulated on both sides.

Measurements. – Mandible: height at m2/m3 = 12.53; p3: L = 3.00, W = 2.97; p4: L = 2.72, Wtrig = 3.39, Wtal = 2.78; m1: L = 2.83, Wtrig = 3.22, Wtal = 2.50; m2: L = 2.72, Wtrig = 3.06, Wtal = 2.47; maxilla: alveolar length of P2-M3 = 15.54, minimum length of hard palate = 7.25; P3: L = 2.03, Want = 3.31, Wpost = 4.14; P4: L = 2.11, Want = 3.83, Wpost = 3.89; M1: L = 2.08, Want = 3.47, Wpost = 3.61.

Lectotype designation. – In the sense of Articles 74.7 and Declaration 44, we hereby designate the right mandible with p3-m2 (Ob. 5068, Fig. 3B1–B5) as a lectotype (Article 74.7.1 and Declaration 44) of the nominal taxon of *Alilepus hungaricus* Kormos, 1934, described from the Late Turolian (MN13) locality Polgárdi 2 (Hungary). In the context of the fixation of the left mandible (Ob. 5068) as a lectotype, the right maxilla (V.2013.49.1 – a new exclusive catalogue number) becomes a paralectotype (Article 74.1.3 of ICZN 1999).

Remarks. – In past years, *A. hungaricus* has been included in a different, monospecific genus: *Veterilepus* (*V. hungaricus* in Radulesco & Samson 1967). This was based on the crenulation of the distal part of the posterior flexids of p3, as those authors noticed that this condition was “different from all *Alilepus* s.s., in which the enamel of this tooth is smooth” (ib., p. 554). *Veterilepus* was considered to be the ancestor of a lineage independent from that of *A. annectens*.

Our opinion, based on our observation of Hungarian material and in the light of the present state of the art of fossil leporid taxonomy, is that the material from Polgárdi 2 is not distinctive enough to be considered a genus different from *Alilepus*. A comparable and even higher degree of enamel crenulation has been reported in other species of *Alilepus* (e.g., *Alilepus meini* from Europe and *A. lii* from Asia) and does not constitute a generic level character. Thus, we consider the leporid from Polgárdi 2 as pertaining to the genus *Alilepus*.

Alilepus ucrainicus Gureev, 1964

Figure 3D1–H3

Type series. – The type series (Articles 72.1.1 and 72.4.1) consists of two (glued together) maxillas (4998; Fig. 3H1) and four mandible fragments (4976–4979; Fig. 3D1–G2). The nominal taxon *Alilepus ucrainicus* was fixed in Gureev (1964, p. 124) by a holotype (*sensu* Article 73.1.1 of ICZN 1999).

Name-bearing type. – Holotype – right mandible with p3-p4, m2 (No. 4976, No. C. 61528; Fig. 3D1, D2); collections of the ZIN RAS.

Type locality and age. – Odessa Catacombs, Ukraine; Late Ruscinian, MN15b.

Emended description of the type material. – Mandible: The four mandibles belong probably to two individuals: specimens 4976 (holotype) and 4977 to an adult, and specimens 4978 and 4979 to a subadult (as their teeth appear to be conical in lateral view, Fig. 3F1, G2). The diastema is relatively long, about 20% longer than the alveolar length of p3-m3, and in buccal view it appears concave along its entire length. The dorsal surface of the mandibular body is convex, but without the distinctive swelling below p3-p4. The buccal surface of the mandibular body is richly fenestrated. The large antero-buccally directed mental foramen is on the dorso-buccal side about 2.7 mm (N = 2) beneath the p3.

p3: The A0/PR1/Pa0 morphotype is present in all available teeth, and in specimens 4978 and 4979 this morphotype is verifiable also in the “radical” end. The

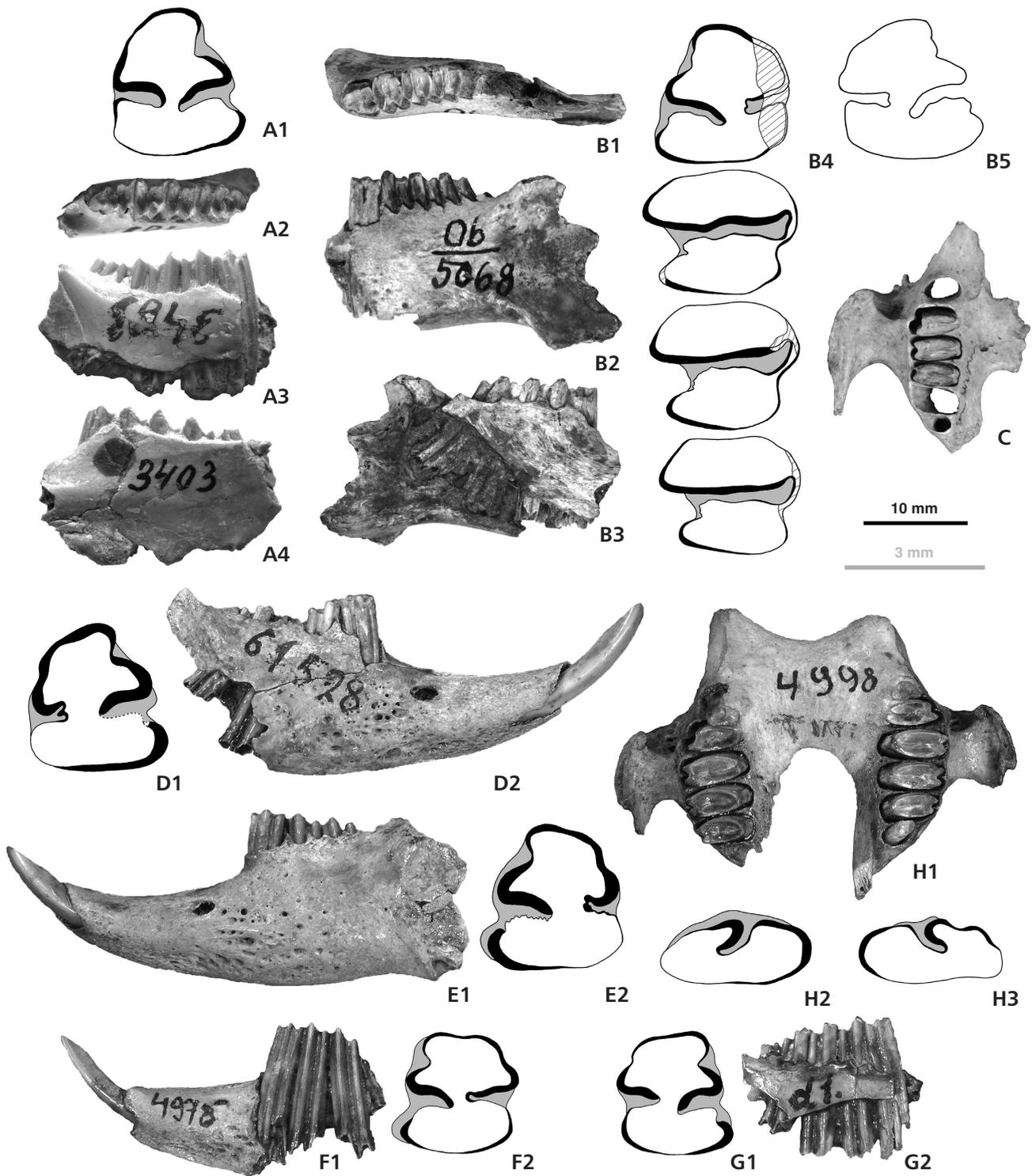


Figure 3. Type materials of Central and Eastern European *Alilepus* species. • A1–A4 – *Alilepus laskarewi* (Khomenko, 1914), lectotype (designated in this paper), right mandible with p3–m3 (No. 3403); A1 – p3 (occlusal view); A2–A4 – mandible; A2 – dorsal view; A3 – buccal view; A4 – lingual view. • B1–C – *Alilepus hungaricus* Kormos, 1934; B1–B5 – lectotype (designated in this paper), left mandible with p3–m2 (Ob. 5068); B1–B3 – mandible; B1 – dorsal view; B2 – buccal view; B3 – lingual view; B4–B5 – teeth; B4 – p3–m2, occlusal view; B5 – p3, radical view; C – right maxilla (V2013.49.1.) with P3–M1 ventral view. • D1–H3 – *Alilepus ukrainicus* Gureev, 1964; D1–G2 – mandibles (buccal views) and their p3s (occlusal views); D1, D2 – holotype, right mandible with p3–p4, m2 (No. 4976 [No. C. 61528]); E1, E2 – left mandible with p3–m1 (No. 4977); F1, F2 – left mandible with p3–m1 (No. 4978); G1, G2 – right mandible with p3–m3 (No. 4979); H1–H3 – two isolated upper jaws (No. 4998; glued together) with P2–M3 (left) and P2–M2 (right); H1 – upper jaw, ventral view; H2 – right P2, occlusal view; H3 – left P2, occlusal view. Scale bars: grey (3 mm) for teeth, black (10 mm) for jaws.

anteroconid (morphotype V in adult specimens, flattened and with shallow anteroflexid in juvenile individuals) is very short (about 1/4 of tooth length). The protoflexid walls form a right angle. The paraflexid is present, shallow in adults, more marked in juveniles. In adult specimens the hypoflexid is longer than the mesoflexid (medially with a bilobed tip), whereas in juveniles they have approximately the same depth. In adult specimens these two flexids are quite shallow, and therefore the isthmus connecting the trigonid and talonid is very wide (about 20% of tooth width). The posterior wall of both flexids is crenulated in 1 of 3 specimens (in specimen 4976 the enamel wall is not recognizable). In the medial part of the hypoflexid morphotype "A" predominates. The labial side of the hypoconid varies from morphotype "c" to "d".

Lower molariforms: No small reentrant is present at the antero-buccal corner of the trigonids of p4-m2; the anterior wall of the talonids is smooth.

Maxilla: The only available specimen (No. 4998) consists of two isolated upper jaws glued together (Fig. 3H1), thus no structures in the palatal bridge are recognizable. Both masseteric spines are broken.

P2: The hypercone has a very simple morphology and lacks a hypoflexus (morphotype II). An incipient mesoflexus is present in the lagicone (morphotype A).

Upper molariforms: The internal reentrant extends across approximately 2/3 the tooth width and is slightly crenulated on both sides.

Measurements. – Mandible (4976, 4977, 4978, 4979): alveolar length of p3-m3 = 14.39, 14.71, –, –; diastema length = 18.01, 18.05, –, –; height at p3 = 12.37, 12.65, –, –; p3 (LxW) = 3.10 × 2.95, 3.10 × 2.85, 2.60 × 2.35, 2.65 × 2.35; maxilla (4998): alveolar length of P2-M3 = 16.19; P2 (sin, dex): L = 1.50, 1.50; W = 3.05, 3.25.

***Alilepus turolensis* López Martínez, 1977**

Type series. – The type series (Articles 72.1.1 and 72.4.1) consists of 2 p3s and 1 P3 from El Arquillo and 1 P2, 1 M1 and 1 D3 from Los Mansuetos. The nominal taxon *Alilepus turolensis* was fixed in López Martínez (1977, p. 20) by a holotype (*sensu* Article 73.1.1 of ICZN 1999).

Name-bearing type. – Holotype – left p3 (ARQ-64); collections of the UM2.

Type locality and age. – El Arquillo (Rambla de Valdecebro 2), Spain; Late Turolian, MN13.

Description of the type material. – See López Martínez (1977).

Measurements. – p3 (holotype): L = 3.41, W = 2.98; additional material of type series: p3 (ARQ-65): L = –, W = 2.86.; P2 (LM-1001): L = 1.49, W = 3.30; M1 (LM-1002): L = 2.23, W = –; D3 (LM-1003): L = –, W = 1.72; (after López Martínez 1989).

***Alilepus meini* Angelone & Rook, 2011**

Type series. – Only the holotype (conforming Articles 16.4, 72.3 and 73.1 of ICZN 1999), without paratypes, was designated.

Name-bearing type. – Holotype – right p3 (IGF 9320v); collections of the UFM.

Type locality and age. – Ribardella (Baccinello–Cinigiano basin), Italy; Late Turolian, MN13.

Description of the type and of additional material. – See Angelone & Rook (2011).

Measurements. – p3 (holotype): L = 2.65, W = 2.58 (occlusal side); L = 3.00, W = 2.54 (radical side); additional material from the type locality: lower molariform (IGF 3222v): L = 2.71; lower molariform (IGF 3223v): L = 2.65, W_{trig} = 3.04; P3 (IGF 9321v): L = 2.21, W_{post} = 4.35.

Systematic palaeontology

Order Lagomorpha Brandt, 1855
Family Leporidae Fischer, 1817

Genus *Alilepus* Dice, 1931

Type species. – *Lepus annectens* Schlosser, 1924, by original designation.

Original diagnosis. – See Dice (1929, p. 342).

Emended diagnosis. – See White (1991, p. 69).

*Nomenclatural note and lectotype designation of *Lepus annectens*.* – The genus fixed by the type species *Lepus annectens* Schlosser, 1924, was first erected by Dice (1929) under the generic name *Allolagus*. However, the name *Allolagus* was preoccupied by *Allolagus* Ognev, 1929 with type species *Lepus mandshuricus* Radde, 1861. Subsequently, Dice (1931) erected *Alilepus* as a new replacement name. The nominal taxon of the type species was established by Schlosser (1924) based on the syntype (Article 73.2 of ICZN 1999) from Ertemte and Olan Chorea (Schlosser 1924, p. 45). No single

name-bearing type specimen has been designated till now.

The vast majority of syntype comes from Ertemte [1] discovered in 1919 by J.G. Anderson and excavated intensively in 1919 and 1920. Additional abundant leporid material from that area, about 400 m SSW of the original Anderson's locality, was recovered in 1980 from Ertemte 2 (Fahlbusch *et al.* 1983, Qiu 1987). Fossils from both localities, Ertemte [1] and 2, most probably belong to the same horizon and age, the Late Turolian, MN13 (Fahlbusch *et al.* 1983). Nevertheless only the original material published by Schlosser (1924) has nomenclatural relevance. The original material from Olan Chorea comprises only four fragments of postcranial bones not allowing a clear species attribution. Moreover, Olan Chorea appears to be younger than Ertemte [1] (Qiu 1987).

Due to the above, there is a need to fix a nominal taxon by a single name-bearing specimen. Thus, in the sense of Articles 74.7 and 74.4 and Declaration 44, we hereby designate the right mandible with p3-m2 figured (Article 74.4) in Schlosser (1924, pl. III, figs 37, 37a; Article 74.7.2) as a lectotype (Article 74.7.1 and Declaration 44) of the nominal taxon of *Lepus annectens* Schlosser, 1924, described from the Late Miocene (MN13) locality Ertemte [1].

Alilepus laskarewi (Khomenko, 1914)

Figures 4I1–R, T, V, X, 5

Locality and age. – Egorovka 2 (UA); MN12.

Referred material and measurements. – 3 p3 sin, L = 2.98, 2.69, 2.63 (juv.), W = 2.62, 2.88, 2.39 (juv.); 3 p3 dex, L = 2.69 (juv.), 2.91, 2.93, W = 2.71 (juv.), 2.66, –; P2 dex (juv.), L = 1.48, W = 2.82; d3 sin, L = 1.83, W = 1.60; tal p4 dex, Wtal = 2.55; p4 dex, L = 2.39, Wtrig = 2.66, Wtal = 2.16; m2 sin, L = 2.40, Wtrig = 2.85, Wtal = 2.24; m3 dex, L = 1.87, Wtrig = 1.79, Wtal = 1.08; trig p4 sin, Wtrig = 2.89; frag tal m1 dex; trig m2 dex, Wtrig = 2.69; i1 sin (juv.); tal p4 sin, Wtal = 2.04; I1 sin, L = 1.83, W = 2.70, Wg = 1.23; P4 or M1 sin, L = 2.26, Want = 3.78, Wpost = 3.86; M3 dex; L = 0.94, W = 1.56; 5 fragments of upper molariforms; fragment of masseteric spine; rostral part of sin and dex premaxillas; proximal part of radius; fragment of pelvis; talus; medial part of shaft of radius (NMNHU Egr-2-101–131).

Description. – p3: The available specimens are divided equally among morphotype PR1/A0/Pa0 (N = 3) and morphotype PR2/A0/Pa0 (N = 3). In all specimens the pattern of p3 is stable along the entire tooth crown (Fig. 4I1–N2). The anteroconid length ranges from 26% to 35% of total L (N = 6) and in some cases the anteroconid is widened lingu-ally. Morphotypes I/II, II and IV are present. The protofle-

xid is shallow. Its depth varies from 8% to 15% of the tooth width (averaging 11%; N = 5), with the angle formed by its walls ranging from a right to obtuse angle. The hypoflexid crosses on average 47% of the occlusal surface (ranging from 44% to 50%; N = 5), and is straight and horizontal. The medial part of the hypoflexid is variable within the sample, with morphotypes ranging from “A” to “D”. In the hypoconid morphotypes “b”, “c” and “e” are observed, with “e” predominant. In one specimen (Fig. 4K1, K2), the anterior wall of the hypoconid is deeply infolded. The mesoflexid is shallow, in general shallower than the hypoflexid, and with a simple labial end. When present (50% of individuals), the mesofossettid is irregularly oval, very large, with the lingual end almost reaching the tooth edge. The connection between trigonid and talonid is wide to very wide. Only in one specimen (Fig. 4K1, K2) is the protoisthmus narrow. There can be a very shallow paraflexid, in one case filled with cement.

d3: The tooth (Fig. 4O1, O2) is in an early stage of abrasion. It has the typical trilobed appearance of a juvenile. The buccally shifted anteroconid has a widened tip with a depression. The protoflexid is deep and its walls form an acute angle. A shallow concavity (paraflexid?) is present in the lingual border, between the anteroconid and trigonid. The talonid is hatchet-shaped with smooth enamel borders and indented by a notch on both sides.

Lower molariforms (Fig. 4P1–R): The trigonid is longer than the talonid. Neither a reentrant at the antero-buccal corner, nor a tip on their posterior side is present on the trigonids. The anterior and antero-buccal walls of the talonids range from smooth to moderately crenulated and a small antero-buccal reentrant is present.

P2: In the only specimen (Fig. 4V) the hypoflexus is not present (morphotype II), whereas an incipient mesoflexus is present (morphotype A). The paraflexus reaches half the tooth length.

Upper incisor (Fig. 4T): In cross section the first upper incisor is approximately rectangular. Its anterior enamel is thin. The groove on the anterior surface is simple with widely opened walls and is not filled with cement. The groove is located near the middle of the crown.

Upper molariforms: The hypostria is mildly to strongly crenulated on both sides and enters about 60% of the tooth.

Emended diagnosis. – Small-sized leporid; p3 of PR1/A0/Pa0 (slightly predominant) or PR2/A0/Pa0 morphotype, with long (about 1/3 of tooth length) morphologically variable anteroconid, shallow and wide protoflexid (about 10% of tooth width), wide connection between trigonid and talonid, short (less than 50% of tooth length) morphologically variable (morphotypes A to D) hypoflexid; anterior and antero-buccal walls of p3-m2 talonids ranging from smooth to moderately crenulated, p4-m2 trigonid without

antero-external reentrant; incisors with thin enamel, I1 without cement; P2 of simple morphology (III/A morphotype) with short paraflexus; P3-M2 hypostria short (about 60% of tooth width), mildly to moderately crenulated.

Stratigraphic and geographic distribution. – The proven record from the Late Turolian (MN12) of Ukraine and Moldova.

Comparison. – The attribution of the leporids from Egorovka 2 to the genus *Alilepus* is fully compatible with the diagnosis of the genus proposed by White (1991). The similarities between the *Alilepus* from Egorovka 2 and the lectotype of *A. laskarewi* from Tarakliya, the same age (MN12) and the close geographical proximity (*ca* 100 km) of these localities, justify the ascription of the leporid from Egorovka 2 to *A. laskarewi*.

The very high incidence of the mesofossettid (50%, similar incidence as presence of a mesoflexid) together with unilobated anteroconid on p3, discriminate this Late Miocene leporid from all other known Late Miocene and Pliocene *Alilepus* recorded from Europe and Asia. In addition to these characters, *Alilepus laskarewi* differs from:

1) *A. hungaricus* and *A. ucrainicus* in its p3 with relatively longer, anteriorly rounded and less wide anteroconid as well as shorter talonid; P2 with shorter paraflexus (compared to *A. ucrainicus*); lower molariforms with anterior walls of talonids more crenulated.

2) *A. turolensis* and *A. meini* in its p3 with longer anteroconid, much shallower, obtuse-angled protoflexus, much wider connection between trigonid and talonid, and straight entoconid; moreover, the p3 of *A. meini* is more crenulated.

3) *Alilepus annectens* (Schlosser, 1924) described from the Late Miocene (late Baodean, NMU 11, *i.e.*, comparable to the Late Turolian (MN13) in Europe [Fejfar *et al.* 2011; *cf. e.g.*, Fahlbusch *et al.* 1983, Qiu & Qiu 1995, Flynn *et al.* 1997, Qiu *et al.* 1999, Deng 2006]) Ertemte and Olan Chorea localities (Inner Mongolia, China) in its significantly smaller size and more developed posterointernal structures on p3; in *A. annectens* (based on the material from Ertemte [1] and 2; Schlosser 1924, Fahlbusch *et al.* 1983, Qiu 1987) the mesoflexid never extends more than about one-third of the tooth width, and the mesofossettid, if present (14% of cases, N = 14; material from Ertemte 2, Qiu 1987), is smaller and more gracile; the available lower and upper molariforms are less crenulated; the anteroconid of p3 is less variable in general shorter and of morphotype II.

4) *A. longisinuus* Qiu & Han, 1986, described from the Late Miocene Lufeng locality, Yunnan, China (currently estimated at 6.6–6.2 Ma [Qi *et al.* 2006]; *i.e.*, late Baodean, NMU 11) in its smaller average size and its wider connection between trigonid and talonid. *Alilepus longisinuus* has a significant tendency for reduction of

the connection between the trigonid and talonid on p3 (very weak in 15%, absent in 18%, N = 34; Qiu & Han 1986) – there is a presumed morphocline A0/PR1 => A0/PR4. *Alilepus longisinuus* commonly has a long hypoflexid (morphotype A0/PR3, probably derived from A0/PR2), rarely a mesofossettid (6%, N = 34; Qiu & Han 1986); talonids of lower teeth with less crenulated anterior walls, and P2 with larger, better-developed mesoflexus.

5) *Alilepus lii* Jin, 2004, known from a single mandible with p3-m1 from the latest Miocene (Late Baodean, NMU11; Deng 2006) deposits of Laodong Cave (Huainan, Anhui Province, China), for its larger anteroconid and less crenulated anterior walls of talonids in lower teeth.

6) *Alilepus elongatus* Winkler, Flynn & Tomida, 2011, from the Late Miocene (Middle Turolian, MN12, 7.35–6.5 Ma) deposits of Dhok Pathan Formation (Siwalik Group, Potwar Plateau, Pakistan) in its smaller size, wider but antero-posteriorly less elongated anteroconid, wider connection between trigonid and talonid, shorter mesoflexid, less crenulated hypo- and mesoflexid; absence of anteroexternal reentrant on the trigonid in all lower molariforms.

Remark. – A comparison with the material from the Early Pleistocene deposits of Zhoukoudian Cave (China) described by Cheng *et al.* (1995a, b) as *Alilepus zhoukoudianensis* was impossible due to lack of sufficient published data (Angelone & Rook 2011).

***Alilepus cf. hungaricus* Kormos, 1934**

Figure 4A–B2, F, G

Referred material and measurements. – Andreevka (UA), MN13 (NMNHU 33-1457–NMNHU 33-1464): p3 dex, L = 3.06, W = 2.82; p3 sin, L = 2.91, W = 2.87; i1 sin, L = 2.35, 2.31, W = 2.86, 3.09; m2 sin, L = 2.54, W_{trig} = 2.96, W_{tal} = 2.46; trig m1 dex, W_{trig} = 3.01; trig m2 dex, W_{trig} = 2.97; P3 sin, L = 2.23, W_{ant} = 3.42, W_{post} = 3.96.

Description. – p3 (Fig. 4A–B2): Adult individuals display the A0/PR1/Pa0 morphotype, maintained along the entire crown; a relatively short anteroconid (~30% of tooth length in adults) markedly widened lingually; protoflexid with right-angled walls; the hypoflexid (“B” morphotype in its medial part) slightly indents the talonid and is crenulated in its distal side; the labial end of the mesoflexid is simple (not bilobed); the connection between trigonid and talonid is relatively wide; the labial part of the hypoconid is of “c” morphotype.

Lower molariforms (Fig. 4G): L_{tri} > L_{tal}; the reentrant at the antero-buccal corner of the trigonid is not present. The trigonid appears labially prominent and rounded. In the talonid (available only in m2), the anterior wall is slightly undulated and a small antero-buccal reentrant is present.

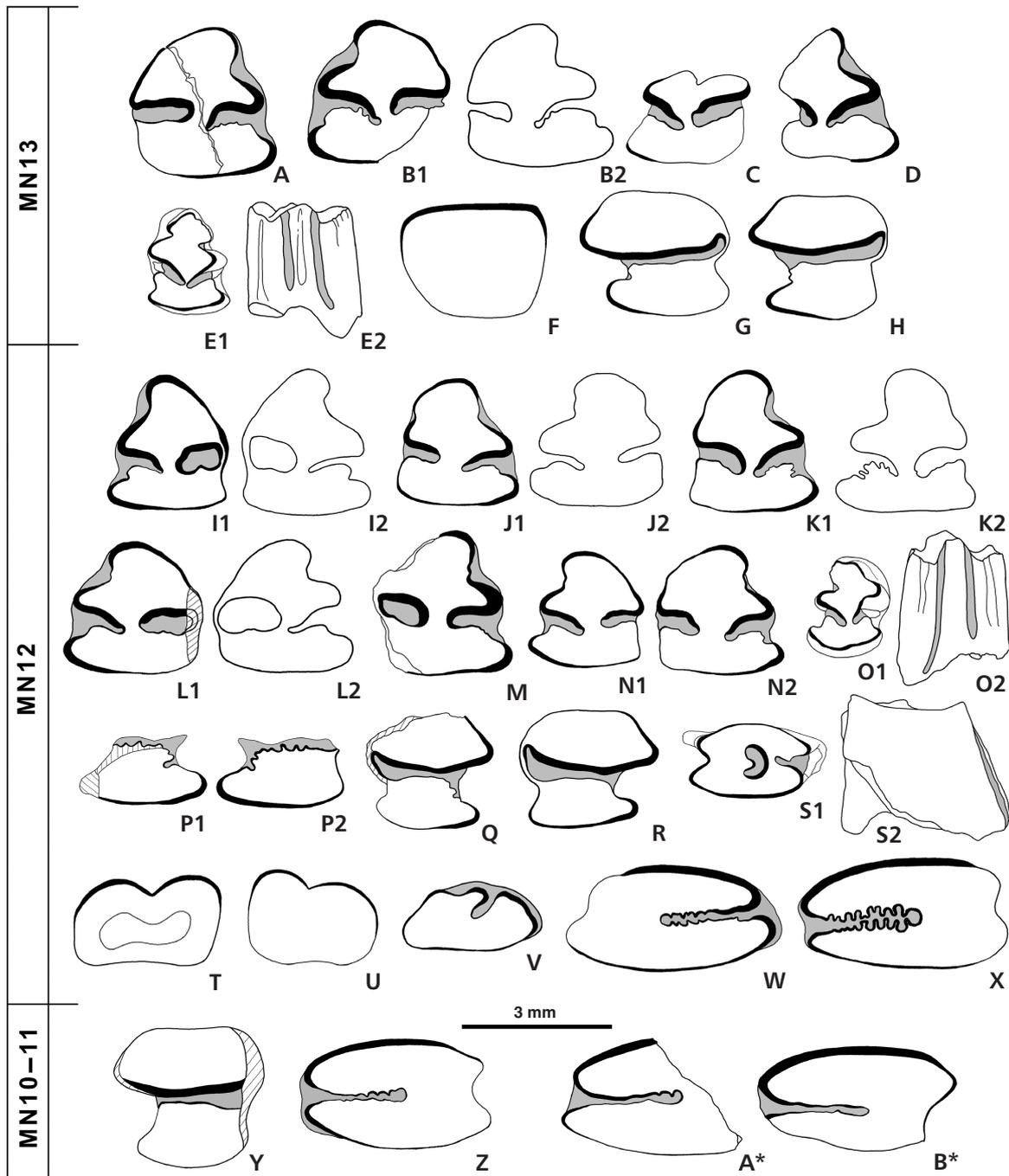


Figure 4. Leporid teeth from the Late Miocene (MN11–13) of Ukraine and Moldova. • A–B2, F, G – *Alilepus* cf. *hungaricus*, Andreevka; A – right p3 (NMNHU 33-1457); B1, B2 – left p3 (NMNHU 33-1458), occlusal and radical views; F – left i1 (NMNHU 33-1459); G – left m2 (NMNHU 33-1461). • C–E2, H – *Alilepus* sp., Novoukrainka 1; C – right p3 (NMNHU 38-2066), cross-section (radical view); D – left p3 (NMNHU 38-2067), cross-section (radical view); E1–E2 – right d3 (NMNHU 38-2068), occlusal and buccal views; H – left m1 (NMNHU 38-2066). • I1–R, T, V, X – *Alilepus laskarewi*, Egorovka 2; I1, I2 – left p3 (NMNHU Egr-2-101), occlusal and radical views; J1, J2 – right p3 (NMNHU Egr-2-102), occlusal and radical views; K1, K2 – right p3 (NMNHU Egr-2-103), occlusal and radical views; L1, L2 – left p3 (NMNHU Egr-2-104), occlusal and radical views; M – occlusal view of right p3 (NMNHU Egr-2-105); N1, N2 – left p3 (NMNHU Egr-2-106), occlusal and radical views; O1, O2 – left d3 (NMNHU Egr-2-108), occlusal and radical views; P1, P2 – talonid of right p4 (NMNHU Egr-2-109), occlusal and radical views; Q – right p4 (NMNHU Egr-2-110), occlusal view; R – left m2 (NMNHU Egr-2-111), radical view; T – left I1 (NMNHU Egr-2-118), cross-section; V – right P2 (NMNHU Egr-2-107), occlusal view; X – left P4/M1 (NMNHU Egr-2-119), occlusal view. • S1, S2, U, W – *Alilepus* sp., Cherevichnoe 3; S1, S2 – left D3 or D4 (NMNHU 45-5955), occlusal and rostral views; U – left I1 (NMNHU 45-5952), occlusal view; W – right P3 (NMNHU 45-5953), occlusal view. • Y–Z – ?*Alilepus* sp., Palievo; Y – right m1 (NMNHU Plv-03), cross-section (radical view); Z – left P4 or M1 (NMNHU Plv-04), occlusal view. • A*, B* – ?*Alilepus* sp., Keinar (MD); 2 left upper molariforms (FGTU 1–2 Lag/Knr), occlusal views.

i 1 (Fig. 4F): Trapezoidal shape, thin enamel on anterior part.

P3: Damaged and the only specimen; the hypostria is mildly crenulated on both sides.

Remarks. – The scarce material from Andreevka does not allow a definite specific determination; however, the dental features of p3 and the lower molariforms (*e.g.*, relatively short and markedly lingually widened anteroconid [morphotypes II and III] and the undulated anterior enamel of the hypoconid in p3, plus the labial shape of the trigonid and its relative proportions to the talonid) are compatible with the name-bearing type of *Alilepus hungaricus*. The age (MN13) of these specimens also supports their ascription to *A. hungaricus*. However, as shown above, the intraspecific variability of Late Miocene *Alilepus* from that area is very high, and the above-mentioned features may not represent dominant morphotypes in the population. Moreover, *A. hungaricus* is known only from its type material. Thus, until further relevant material of *Alilepus* from Andreevka is available, we refer this material tentatively to *Alilepus cf. hungaricus*.

***Alilepus* sp.**

Figure 4C–E2, H, S1–2, U, W

Referred material and measurements. – Cherevichnoe 3 (UA), MN12 (NMNHU 45-5951–45-5956): fragm. p3 dex; I1 sin, L = 1.84, W = 2.65, Wg = 1.07; P3 dex, L = 2.16, Want = 3.34, Wpost = 4.14; P4 or M1, L = 2.23, Want = 3.52, Wpost = 3.64; 2 D3 or D4 sin, L = 1.53, 1.50, Want = 2.03, 2.13, Wpost = 2.33, 2.27. Novoukrainka 1 (UA), MN13 (NMNHU 38-2066–38-2074): p3 dex (fragm.); p3 sin (fragm.); d3 dex, L = 2.00, W = 1.52; m1 sin, L = 2.56, Wtrig = 2.71, Wtal = 2.23; m2 dex (?juv.), L = 2.23, Wtrig = 2.49, Wtal = 1.83; P4 or M1 dex, L = 2.18, Want = 3.61, Wpost = 3.63; 2 upper molariforms; I1 dex (juv.).

?*Alilepus* sp.

Figure 4Y–B*

Referred material and measurements. – Keinar (MD), MN11 (FGTU 1–2 Lag/Knr): 2 upper molariforms sin. Palievo (UA), MN11 (NMNHU Plv-03, 04): m1 dex, L = 2.87, Wtrig = 3.14, Wtal = 2.42; P4 or M1 sin, L = 2.25, Want = 3.55, Wpost = 3.58. Kubanka 2 (UA), MN12 (NMNHU Kbn-2-01): I1 sin, L = 1.49, W = 2.58, Wg = 1.67. Tretya Krucha 2 (UA), MN12 (NMNHU TKr-1-01): fragment of upper molariform.

Remarks. – The scarce material from Cherevichnoe 3, No-

voukrainka 1, Keinar, Palievo, Kubanka 2 and Tretya Krucha 2 does not include sufficient diagnostic features and therefore is inadequate to confidently assign specimens to species or even to genus. The large age span of these findings, ranging from MN11–13, may support the presence of more than one species.

Discussion

The new Ukrainian and Moldovan leporids in the context of the most ancient Old World records

The appearance of Leporinae in Eurasia, and somewhat later in Africa, is a result of the Late Miocene migration from North America via the northern land connection of Beringia (López Martínez 2008 and references therein). Until the Late Miocene, there is no proven record of leporines in Europe (*cf.* Boon-Kristkoiz & Kristkoiz 1999). The relatively rapid spread of leporids across the Old World around 8 Ma was an important Turolian event and is called the “Leporid Datum” (Flynn *et al.* 2014). Whereas MN12 Old World records of Leporinae are relatively rare, and mostly limited to Europe, MN13 ones are relatively more common and available throughout the Old World. Only few, very fragmentary findings, date an appearance of advanced leporids in the Old World undoubtedly before MN12 (Flynn *et al.* 2014). There are also a few, still questionable fossil occurrences suggesting that leporids were present in Europe prior to MN11, however in many of these cases the relation of the leporid findings with the accompanying faunal assemblages is not clear and such findings need further evaluation of both age and taxonomy (see Flynn *et al.* 2014).

In the Late Miocene, Old World leporids already show a high phenotypic/taxonomic diversity. Four Archaeolaginae and Leporinae genera are recorded:

1) *Alilepus*: proven from MN12 (Flynn *et al.* 2014 and references herein);

2) *Hypolagus* Dice, 1917: proven from MN13 (Averianov 1996, Čermák 2009);

3) *Pliopentalagus* Gureev & Konkova *in* Gureev, 1964: proven from late MN13 (Tomida & Jin 2009);

4) *Trischizolagus* Radulesco & Samson, 1967: from ?MN13 (with PR0/A1/Pa0 morphotype), however the Late Miocene appearance of *Trischizolagus* is very poorly recorded and still remains questionable (López Martínez *et al.* 2007, Čermák & Wagner 2013).

Alilepus laskarewi represents the first-available described species of the Old World *Alilepus*, originally described as *Lepus laskarewi*. Nevertheless, since Kholmenco’s (1914) publication the phenotype considerations and species attributions have been made only based on insufficient species description and poorly figured type spec-

imens by Khomenko (1914), (e.g., cf. Kormos 1934; Gureev 1964; Radulesco & Samson 1967; López Martínez 1977, 1989; Angelone & Rook 2011; Winkler *et al.* 2011). At any rate, the type specimen (here designated as lectotype) possesses the typical *Alilepus* PR1/A0 morphotype, as seen in all published *Alilepus* European reports.

The new material of *Alilepus* from the MN12 locality Egorovka 2 shows a different p3 phenotype than presumed. A very high incidence of the PR2/A0 morphotype (= presence of mesofossettid) in p3 changes the view on the phenotype distribution in the earliest European Leporinae. In fact the “primitive” phenotype of leporines was thought to be the “classic” European *Alilepus* morphotype PR1/A0 (cf. Hibbard 1963, Averianov & Tesakov 1997). The p3 phenotype in the material from Egorovka 2 cannot be looked upon as exceptional or an accidental sampling of extreme morphotypes. A presence of PR2/A0 morphotype in *Alilepus* has been mentioned (without any further discussion) in a very recent paper by Delinschi (2014) from another MN12 locality, Chimishliya (situated in the close vicinity of the type locality Taracliya). Egorovka 2 and Chimishliya are coeval and situated in the presumed “*terra typica*” of *A. laskarewi*. Thus the high incidence of p3 mesofossettid in MN12 populations of *Alilepus* seems to be characteristic of the northwestern part of Eastern Paratethys.

Taxonomical notes on *Alilepus* species in Europe

Dice’s (1931) original description, followed Schlosser (1924), discriminating the taxon based on p3 consisting “of two columns connected in the centre of the tooth by a bridge of dentine”. The emended diagnosis by White (1991, p. 69), based on comprehensive revision of *Alilepus* from the late Miocene to Pliocene of North America, indicates a presence of mesofossettid in some *Alilepus* populations. The attribution of the newly described Late Miocene Ukrainian leporid populations to the genus *Alilepus* is fully compatible with the diagnosis proposed by White (1991).

As shown in “Systematic palaeontology” *Alilepus laskarewi* is a well-documented species, clearly discriminated from other European species. Its most peculiar distinctive trait is the high incidence of PR2/A0 morphotype in p3. This is in contrast with other European species, which show exclusively a p3 with clear A0/PR1 morphotype. Size relationships of p3s among *Alilepus laskarewi*, name-bearing specimens of European *Alilepus* species and leporines from the Early Pliocene (MN14–15) of Central and Eastern Europe is shown in Fig. 5.

Alilepus hungaricus, known only from its type locality Polgárdi 2 (MN13), seems to be differentiated by its short-

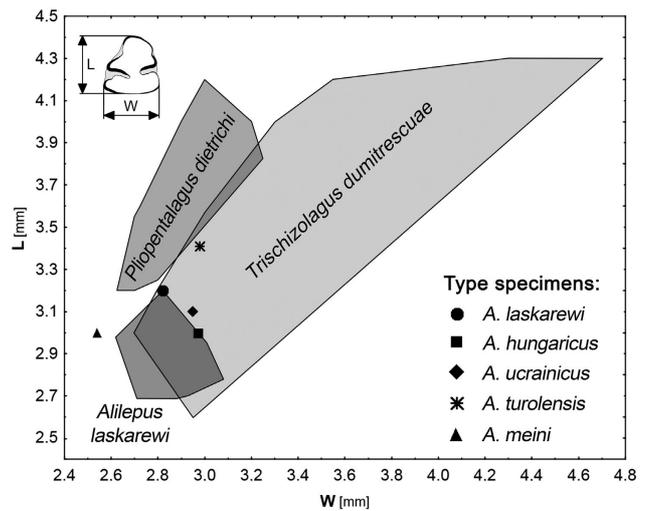


Figure 5. The p3 length-to-width scatterplot showing the size relationship among (1) *Alilepus laskarewi* (Egorovka 2, UA and Chimishliya, MD), (2) name-bearing specimens of European *Alilepus* species (*A. laskarewi* – Tarakliya, MD; *A. hungaricus* – Polgárdi 2, HU; *A. ucrainicus* – Odessa Catacombs, UA; *A. turoleensis* – El Arquillo, ES [data from López Martínez (1977)]; and *A. meini* – Ribardella, IT) and (3) leporines from the Early Pliocene (MN14–15) of Central and Eastern Europe; i.e., (a) *Trischizolagus dumitrescuae* (Beremend 39, HU; Berești, RO; Ciuperceni 2, RO; Grebeniki 2, UA; Lucheshty, MD; Mălușteni, RO; Megalo Emvolon 1, GR; Moskovei, MD; Muselievo, BG; Nikolskoe, MD; Novaya Andriashevka, MD; Stavnichevo, UA; Tatareshty, MD) and *Pliopentalagus dietrichi* (Budăi, MD; Ivanovce, SK; and Muselievo, BG), data from Čermák & Wagner (2013) and references therein.

ened and lingually widened p3 anteroconid and probably also the less crenulated anterior walls of talonids in lower molariforms. These features of *A. hungaricus* are in a good correspondence with those of *Alilepus* from Andreevka (MN13), described here as *Alilepus* cf. *hungaricus*. Nevertheless, based on the available material and, taking into account palaeoecological peculiarities of the Pannonian area, a relation of *Alilepus* from Andreevka to *A. hungaricus* cannot be fully resolved now and remains unclear. It is noteworthy that in the MN10/11 locality Csákvár, a few kilometers away from the type locality of *A. hungaricus*, Kretzoi (1954, p. 47; cf. Rabeder 1989) mentions the presence of “Lagomorpha indet. (*Alilepus*?)”. This identification was based on a fragment of long bone bearing no features attributable to *Alilepus*, not even to a leporid (SČ pers. obs.; MFGI 2013).

Alilepus ucrainicus from Odessa Catacombs (MN15b) is peculiar among other *Alilepus* species not only in its unusually formed anteroconid, but also in its distinctively younger age. The presence of the A0/PR1/Pa0 morphotype in p3 (in the verifiable cases – expressed along the entire crown) and relatively simple P2 support attribution to *Alilepus*. Note, however that incipient presence of an anteroflexid (as a depression), together with separation of the anteroconid from the rest of trigonid, are rarely present

also in *Trischizolagus* (particularly in subadult specimens). *Trischizolagus* is the leporid that dominated the area during the Pliocene (Čermák & Wagner 2013). On the other hand, crenulation of anterior walls of the talonids in lower molariforms (see p3, No. 4977; Fig. 3E2) would be very atypical for *Trischizolagus*. The available material does not provide a conclusive argument for an attribution to *Trischizolagus*, so attribution to a separate species of *Alilepus* is retained in this paper.

Alilepus turolensis is reported from some MN12–13 central-eastern Spanish localities (MN12; López Martínez 1977, 1989). *Alilepus* sp. from the MN13 of Lissieu (France; Mein 1988, 1999) likely pertains to this species. The very thin connection between the trigonid and talonid and the narrow protoflexid, that distinguish *A. turolensis*, characterize also the remains from the NE Greece localities Maramena (MN13) and Pikermi (MN12). Material from these localities was, respectively, classified as *A. turolensis* and *Alilepus* sp. by de Bruijn (1995) and López Martínez (1976). Taking into account the palaeobiogeographical context of such scanty material, a species determination of Greek *Alilepus* is unclear and needs further taxonomical evaluation based on additional material. Another Greek record (MN10–11, Elaiochoria 2; Hulva *et al.* 2007) is here excluded as it bears distinctive non-*Alilepus* features (SČ pers. obs.; GLI 2013).

Alilepus meini is known exclusively from its type locality, a geographically restricted area in central-western Italy in which lived several other continental isolated species of vertebrates together with “normal” taxa of wider European affinity (Angelone & Rook 2011 and references therein). Its morphological features reveal its affinity with *A. turolensis*, constituting a group distinct from the rest of European species.

The mesofossettid in Leporinae: Old vs New World

Postero-internal structures in p3 are a very important part of the tooth phenotype in Leporinae (Hibbard 1963, White 1991, Averianov & Tesakov 1997, López Martínez *et al.* 2007). These structures are never well developed in the sister clade to Leporinae, the Archaeolaginae. The oldest representatives of the Leporinae are recorded from the Middle Miocene (Late Barstovian, *ca* Late Astaracian; Late MN6, *ca* 13 Ma) of the Valentine Railway Quarries (Nebraska, USA). These specimens have a PR0/A0 morphotype with incipient para- and/or mesoflexid (/mesofossettid), and are generally referred to the genera *Alilepus* or *Pronotolagus* White, 1991 (Voorhies & Timperley 1997). Among these earliest representatives, a small mesofossettid was documented in two p3 (both of PR0/A0) from Stewart Quarry (the site of the Valentine Railway Quarries) referred by Voorhies & Timperley (1997) to *Alilepus* sp.

(Fig. 6). In one specimen (UNSM 117079), the mesofossettid was most probably derived from the mesoflexid, but in the other (UNSM 117069) the mesofossettid, adjacent to the lingual end of hypoflexid, seems to be derived from this structure or even independently. One of the six p3 of *Alilepus hibbardi* White, 1991, reported by White (1991) from the early Late Miocene (Late Clarendonian; *ca* MN10 equivalent) of California and Nevada (USA), possesses a small mesofossettid (p3 with PR2/A0). Taking into account its position near the lingual portion of tooth, a derivation from a weakly developed mesoflexid is likely.

The classical well-developed mesofossettid of North American Leporinae is documented from the Early Blancan in *A. vagus* Gazin, 1934 (*Pratilepus sensu* Hibbard, 1969; see White [1991] for arguments supporting the attribution to *Alilepus*), *Pratilepus kansassensis* Hibbard, 1939a and *Nekrolagus progressus* (Hibbard, 1939b). In all these taxa the PR2 p3 morphotype is clearly predominant (Fig. 6; Hibbard 1963, 1969; White 1991; White & Morgan 1995). In the latest Hemphillian (*ca* latest Turolian, MN13) in specimens assigned to *A. vagus* from Santee (Nevada) and *N. progressus* from the Upper Bone Valley (Florida), the presence of a mesofossettid was not documented (*cf.* White 1991, White & Morgan 1995). During the Blancan (*ca* Pliocene) a well-developed mesofossettid appeared also in *Aztlanolagus* Russell & Harris, 1986 (the structure shows a constant occurrence at 100% through time till the Late Rancholabrean [*ca* late Pleistocene]; Tomida 2008), *Aluralagus* Downey, 1968 and *Sylvilagus*. In all these Blancan forms the mesofossettid, if presents, is generally large and oval medio-lingually (Fig. 6).

A “closed enamel structure” (CES) may also appear in forms close to *Paranotolagus* Miller & Carranza-Castaneda, 1982 (p3 LACM106768 of ?*Paranotolagus* from the middle Blancan [*ca* Early Villányian], La Goleta locality, Mexico), but it is projected more anteriorly. The presence of this CES is most likely a result of the extreme development of the paraflexid, as in *Notolagus* Wilson, 1938 (*cf.* White 1991). A similar development of CES was documented by Russell & Harris (1986; Fig 2A, specimen MNM 5689-98-1) in the late Pleistocene records of *Aztlanolagus agilis*. The CES in these two taxa has nothing to do with the mesofossettid, which is related to postero-internal structures of p3.

In extant American taxa, the mesofossettid aberrantly/rarely appears in taxa such as *Sylvilagus audubonii*, *S. aquaticus*, *Lepus californicus* and *L. americanus*. Extremely large mesofossettids are observable in *Romerolagus diazi*.

The situation is different in the Old World fossil record, where the Late Miocene – Pliocene Leporinae are less diversified. The oldest Old World evidences of frequently occurring mesofossettid in p3 are documented from the middle–late MN12 of northwestern peri-Paratethyan area

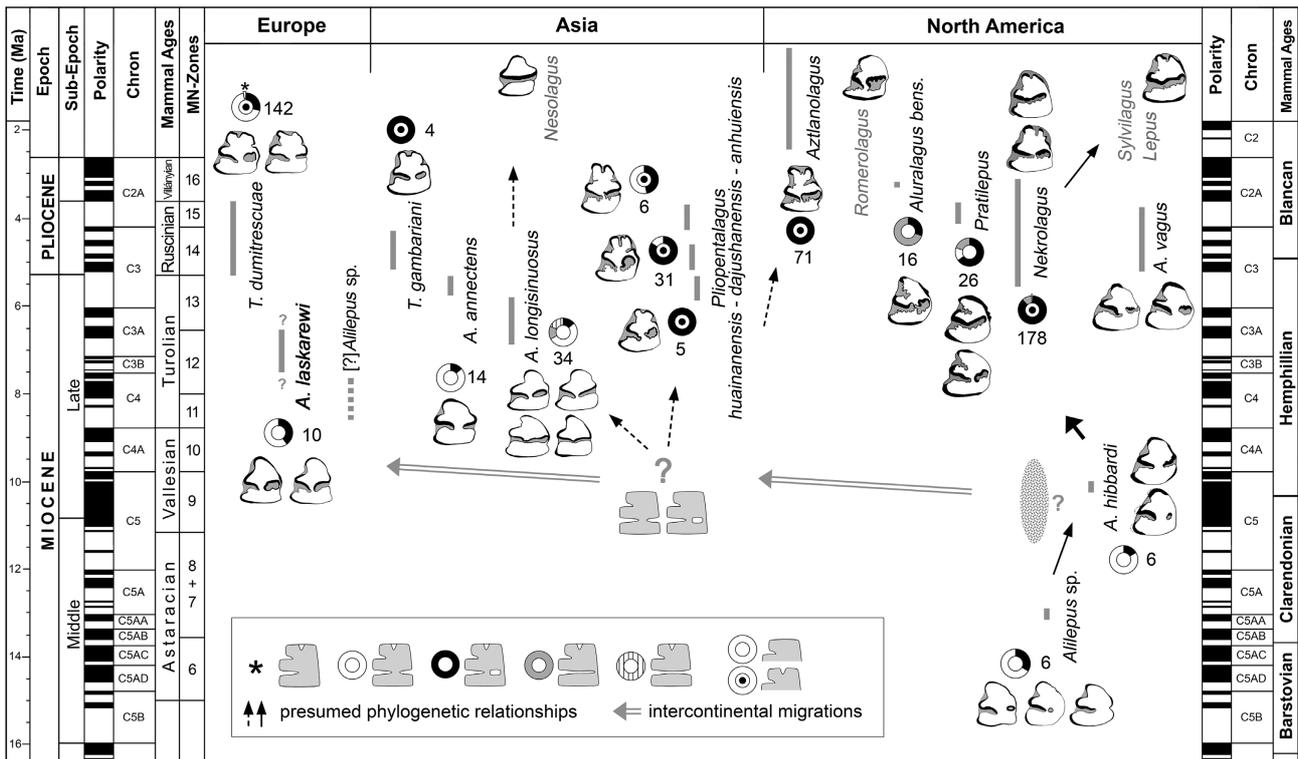


Figure 6. Distribution and diversity of p3 mesofossettid in Leporinae of North America and Eurasia with presumed phylogenetic relationship of selected taxa. For each species the circular symbol with number illustrates the p3 morphotype distribution and the number of specimens included. The vertical grey bar shows the stratigraphic span (data, p3 drawings and biostratigraphic chart from this paper and references herein). The recent genera are written in grey.

(i.e., *A. laskarewi*; Fig. 6). For its size and position this structure is comparable to similar structures documented in North American Blancan findings of *Alilepus vagus*, or in the more morphologically derived species *Nekrolagus progressus* and *Pratilepus kansansiensis*.

The rare presence of a mesofossettid can be observed also in *Alilepus longisinuus* from the Late Miocene (MN12/13) of Lufeng (Yunnan, China), that should be coeval or possibly slightly younger (Qi *et al.* 2006) than the peri-Paratethyan findings. Nevertheless this Asiatic form is clearly distinct from *A. laskarewi* and most probably belongs to a lineage evolving separately from other known *Alilepus* taxa (see below). The sporadic presence of a mesofossettid in *Alilepus annectens* from Ertemte (MN13) represents a clearly younger evidence of this structure (Fig. 6).

Among Asiatic Late Miocene–Pliocene leporid taxa the mesofossettid shows a high incidence only in the peculiar genus *Pliopentalagus*, whose earliest record dates back to the latest Miocene of Laodong Cave locality (China). It is noteworthy that within the latest Miocene–Late Pliocene lineage *P. huainanensis* Jin, 2004 – *P. dajushanensis* Tomida & Jin, 2009 – *P. anhuiensis* Tomida & Jin, 2009, presence of a mesofossettid is gradually reduced relative to presence of a mesoflexid (morphotype PR1), in a sequence 100% – 84% – 33% (Fig. 6; Tomida & Jin 2009). The only

European record of this genus is the Early Pliocene (MN15) *P. dietrichi* (Fejfar 1961), whose p3 exclusively has a morphotype PR1.

In the Pliocene (MN14–15) of Eastern Europe and the Middle East, the presence of a mesofossettid (morphotype PR2/A1) is common in the genus *Trischizolagus* (Fig. 6; Čermák & Wagner 2013). In the European species *T. dumitrescuae* no significant changes in the proportion of PR1/A1 to PR2/A1 p3 patterns were observed during the Pliocene (Čermák & Wagner 2013). Nevertheless, relatively large samples (of mixed ontogenetic age) from several localities of Eastern Europe show that on the occlusal surface of young individuals the mesofossettid is smaller (mesoflexid is shorter) than on the radical side. Thus, in occlusal view they look more archaic. The mesofossettid is almost exclusively placed lingually near the enamel border and its development is related to the mesoflexid. Pre-MN14 fossil findings assignable to *Trischizolagus* are very scarce and do not allow a reliable evaluation of morphotype composition.

A small mesofossettid is present very rarely in advanced European populations of Lower Pleistocene *Hypolagus* (PR0/A0 pattern), but this structure is derived from the medial end of the hypoflexid (*cf.* Fladerer & Reiner 1996) and has nothing to do with lingual structures.

The mesofossettid observed in a p3 (AFG 759; SČ pers. obs.) from the Lower Pliocene (cf. MN14) Pul-e Charkhi locality, Afghanistan (referred to *Trischizolagus* cf. *maritsae* in Şen 1983, *Trischizolagus* sp. in Averianov & Tesakov 1997; *Serengetilagus* sp. in Şen & Erbaeva 1995), likely has a similar origin.

In extant Old World species of *Lepus* (PR3/A1), the mesofossettid appears rarely (ca up to 1%; Averianov & Tesakov 1997). In European populations of *Oryctolagus cuniculus* (PR3/A1) an aberrant mesofossettid is also sometimes observed (Hibbard 1963).

The oldest leporid records in Africa are dated to the Late Miocene (ca 7.0–6.0 Ma). The p3 of these representatives, e.g., *Serengetilagus tchadensis* López Martínez *et al.*, 2007 (Chad), and *Alilepus* sp. (near *elongatus*, Kenya), are predominantly limited to PR0/A0–A1 (*Serengetilagus tchadensis*) and PR1/A0/Pa0–Pa1 morphotypes (cf. López Martínez *et al.* 2007, Winkler & Avery 2010, Winkler & Tomida 2012). During the Pliocene, advanced species of *Serengetilagus* may extremely rarely have a mesofossettid: *S. praecapensis* Dietrich, 1941, from Tanzania (in 0.7%, N = 143, Erbaeva & Angermann 1983) and from Egypt (Fejfar & Storch, unpubl. MS). The mesofossettid in these forms is large, antero-posteriorly elongated and almost square in shape. A well-developed mesofossettid is dominant in the leporid from the middle Pleistocene Grotte des Rhinocéros locality (Morocco), which, based on morphotype PR2/A1/Pa1 is referred generally to *Trischizolagus* (cf. e.g. Averianov & Tesakov 1997, López Martínez *et al.* 2007).

Notes on the evolution of the earliest Leporinae inferred from p3 phenotype: Old vs New World

The fossil record of earliest Leporinae is almost exclusively limited to dental remains. Pros and cons of using teeth in taxonomy of Leporidae are discussed in Čermák & Wagner (2013). The main evolutionary changes in the p3 of leporids are manifested predominantly in a selection in tooth patterns (/structural clusters) among the phylogenetic morphoclines leading to dominant p3 phenotypes. A continuous spectrum of morphologies between two particular features is less common and less obvious in leporids. During Late Miocene – Pliocene leporine evolution, the following main phylogenetic morphoclines were documented in p3: (1) mesoflexid => (isolated to) enamel lake, (2) mesofossettid => (merged with) hypoflexid, (3) enamel lake => (open to) lingual side, (4) reduction of connection between trigonid and talonid => PR4 pattern, (5) enlargement of anteroflexid, and (6) enlargement of paraflexid (exceptionally evolved to “closed enamel structure” or even to Pa2 trigonid pattern; cf. e.g. White 1991, Voorhies & Timperley 1997, Jin *et al.* 2010).

Voorhies & Timperley (1997, p. 736) suggested that *Hypolagus parviplicatus* Dawson, 1958, or a closely related species, likely gave rise to the Leporinae clade. They considered the oldest member of the Leporinae to be *Pronotolagus albus* Voorhies & Timperley, 1997. However, they also considered a coeval species, referred to *Alilepus* sp., to be close to *H. fontinalis* Dawson, 1958 (a more derived species than *H. parviplicatus*, and probably its direct descendant), and suggested their ancestor–descendant relationship. This taxonomic/phylogenetic model implies a diphyletic origin of Leporinae. At any rate, both *P. albus* and *Alilepus* sp. have significant complications of the lingual enamel pattern in p3 and it is very likely that the oldest leporine form comes from this stock, or a closely related form, by at least ca 14 Ma. The relationships of descendant taxa proposed by White (1991) and Voorhies & Timperley (1997) are more convincing and are supported here. The clade derived from *P. albus* comprises *P. apachensis* (Gazin, 1930) (Late Clarendonian–Early Hemphillian), and subsequently *Notolagus* and *Paranotolagus* (Hemphillian–Blancan). *Alilepus hibbardi* (derivable from *Alilepus* sp. from Stewart Quarry) most likely is the ancestor of Hemphillian – Blancan species of *Alilepus*, *Nekrolagus*, *Pratilepus*, *etc.* (see White 1991, Jin *et al.* 2010 for details). It is noteworthy that White (1991) assumed that *Alilepus*, *Nekrolagus*, *Pratilepus* and *Aztlanolagus* had similar development of postero-internal structures, following the sequence mesoflexid => mesofossettid => long hypoflexid (as proposed Hibbard 1963). In our view, this phenomenon is supported by the fossil record only in *Nekrolagus* and *Pratilepus*.

In contrast to the New World, proven Old World representatives of the earliest Leporinae appeared much later, during the Late Miocene (MN10–13; ca Late Clarendonian–Hemphillian). Forms with extensive enlargement of the paraflexid (morphological group *Notolagus–Paranotolagus*) never appeared in the Old World. The oldest Asian Leporinae are limited exclusively to *Alilepus* and evolved there in several phenotypic/evolutionary groups, each one corresponding to a presumed palaeobiogeographic path of dispersal:

1) First, a Far East group, is characterized by the reduction of the connection between trigonid and talonid, and the subsequent confluence of mesofossettid and hypoflexid (*i.e.*, PR1/A0 => PR4/A0). The clade is represented by *A. longisinuus*, which evolved into *Nesolagus* (Qiu & Han 1986 followed by Jin *et al.* 2010).

2) Second, another Far East group, is characterised by development of the anteroflexid and the crenulation of p3. According to Jin *et al.* 2010, this clade was derived from *A. lii* and evolved into *Pliopentalagus huainanensis* (PR2/A1/Pa1). *Pliopentalagus huainanensis* probably gave rise to three branches with different development of the mesofossettid: (a) a lineage leading to other *Pliopen-*

Table 2. Name-bearing types of European *Alilepus* species (* – designated in this paper).

Species	Name-bearing type	Type specimen	Type locality	Age
<i>Alilepus laskarewi</i> (Khomenko, 1914)	lectotype *	right mandible (p3-m3)	Tarakliya (MD)	MN12
<i>Alilepus hungaricus</i> Kormos, 1934	lectotype *	left mandible (p3-m2)	Polgárdi 2 (HU)	MN13
<i>Alilepus ucrainicus</i> Gureev, 1964	holotype	right mandible (p3-p4, m2)	Odessa Catacombs (UA)	MN15b
<i>Alilepus turolensis</i> López Martínez, 1977	holotype	isolated left p3	El Arquillo (ES)	MN13
<i>Alilepus meini</i> Angelone & Rook, 2011	holotype	isolated right p3	Ribardella (IT)	MN13

talagus species (PR2/A1/Pa1 => PR1/A1/Pa1); (b) a lineage leading to *Poelagus* and *Caprolagus* (PR2/A1/Pa1=> PR3/A1/Pa1); and (c) a lineage leading to *Aztlanolagus* (PR2/A1/Pa1 retained). In our view, based on the material presented here, it seems unlikely that *A. lii* can be the direct ancestor of *P. huainanensis*. Both species are almost coeval and the p3 pattern of *P. huainanensis* is limited exclusively to PR2/A1/Pa1. If the only specimen of *A. lii* does not represent an extreme morphotype, then one may expect in the ancestral taxon a significant presence of the mesofossettid. The new material of *A. laskarewi* presented here evidences a significant presence of the mesofossettid in the MN12 of Europe. Thus, similar forms may be expected in Asia at the same time, or even earlier. Moreover, as presented above, a tendency to tooth crenulation is also typical of these early forms. We expect in the ancestor of *P. huainanensis* (likely a pre-MN13 form) a significant presence of PR2/A1/Pa1 p3 morphotype together with a potential to tooth crenulation similar to that of *A. laskarewi*.

3) The third group, probably forming one separate clade, is represented by S Asiatic and NE African forms (i.e., *A. elongatus* from Pakistan and *Alilepus* sp. from Kenya) characterized by the elongation of the anteroconid with a potential to slight tooth crenulation.

4) At least one, probably north-Asiatic lineage, should lead to European *Alilepus* populations (cf. e.g., Jin *et al.* 2010, Flynn *et al.* 2014). Although *A. annectens* most likely belongs to this northern branch of *Alilepus*, taxonomical and palaeobiogeographical data presented here indicates that it cannot be linked directly with *A. laskarewi*. At any rate, a possible relationship of *A. annectens* with some other European *Alilepus* species cannot be excluded. Jin *et al.* (2010) suggested a close relationship of *A. annectens* with the ancestral type of *Trischizolagus*, but the new material presented here contradicts this hypothesis. The phenotypic compatibility of *A. laskarewi* with European populations of *Trischizolagus*, expressed particularly by the significant presence of p3 mesofossettid, may suggest their close relationship. The northern peri-Paratethyan distribution of both taxa also supports this hypothesis. In this perspective, it is not surprising that the development of the anteroflexid is a phenomenon that appeared independently several times in different lineages (White 1991). On the other hand, no intermediate forms with an incipient

anteroflexid together with the PR2 p3 pattern suggesting this morphocline, have yet been recorded. From a palaeobiogeographic point of view it is noteworthy that the material from Palievo (UA) and Keinar (MD), presented above, suggest that *A. laskarewi*, or its close forms, was present in the peri-Paratethyan area at least from MN11.

Conclusions

We analyzed new material referred to *Alilepus* from eight Late Miocene localities of Ukraine and Moldova. The taxonomic consideration of this material was supported by a revision of type materials of all available (*sensu* ICZN 1999) European species of *Alilepus*, particularly by a direct analysis and re-description of yet very poorly known type materials of *A. laskarewi*, *A. hungaricus* and *A. ucrainicus*. Lectotypes of *A. annectens* (type species of the genus), *A. laskarewi* and *A. hungaricus* were designated here. The present state of name-bearing types of European *Alilepus* species is synoptically summarized in Table 2.

The taxonomic analyses of the material under study resulted in individuation of *A. laskarewi* from MN12 locality Egorovka 2. The fragmentary and/or scarce materials from other studied localities are inadequate to confidently assign them to species or even to genus. Taking into account also their ages, the material from Andreevka (MN13) is tentatively assigned here as *A. cf. hungaricus*, the material from Cherevichnoe 3 (MN12) and Novoukrainka 1 (MN13) is tentatively assigned here as *Alilepus* sp., and the material from Keinar (MN11), Palievo (MN11), Kubanka 2 (MN12) and Tretya Krucha 2 (MN12) is tentatively assigned here as ?*Alilepus* sp.

Based on the new *Alilepus* material, particularly from Egorovka 2 and published relevant material from Chimishliya, Moldova (Delinschi 2014), we provided a re-description of *A. laskarewi* and formulated its emended diagnosis. These remains of *A. laskarewi* have a peculiar p3 phenotype, characterized by simple anteroconid and very high incidence of a mesofossettid (40% of PR2/A0 vs 60% of PR1/A0). These characters discriminate this Late Miocene (known since at least the second half of MN12) leporid species from all Late Miocene and Pliocene *Alilepus* of the Old World, and changes our view of the phenotypic distribution of earliest European Leporinae.

It can be assumed, that a similar p3 phenotype (*i.e.*, with significant presence of mesofossettid, potential to crenulation of anterior walls of talonids in lower molari-forms, variable development of the anteroconid) was in existence in the later MN12 or earlier in Eastern Asia (Fig. 6). This pre-MN12 hypothetical form of Asia may represent the root phenotype (at least for some lineages), appearing in Asia as a result of one of the earliest immigration waves of leporines from North America via Beringia. This hypothetical form may also have given rise to clades derived from *Alilepus longisinuosus* and *Pliopentalagus huainanensis* (Fig. 6). At any rate, pre-MN12 (yet the oldest) records from Eastern Europe with probable affinities to *Alilepus laskarewi* are reported here from MN11 Palievo (UA) and Keinar (MD).

In the context of dispersal scenarios of leporids into Eurasia as proposed by Flynn *et al.* (2014), the relatively early presence of *Alilepus* in Eastern Europe can be explained as a result of limited dispersal prior to the successful main late Miocene influx. Considering the general features of *A. laskarewi* in the palaeobiogeographic and biochronologic context of the Asiatic and North American leporid fossil record, the roots of the lineage leading to *A. laskarewi* can be traced to near the Clarendonian/Hemphillian boundary, to the phyletic proximity of *A. hibbardi* stock.

In light of identified p3 morphology in studied *Alilepus*, we provided a synoptic survey of the mesofossettid (including similar structures) in all Eurasian and North American leporid taxa. Predisposition to development of this structure is present already in the earliest forms of Leporinae; the initial appearance is recorded from the Middle Miocene (Late Barstovian; *ca* Late Astaracian, Late MN 6, *ca* 13 Ma) of North America. The available fossil record suggests differing origins of this structure; based on its size, morphology and position in p3, it seems in many cases that it originated independently of a lingual isolation of the mesoflexid. Moreover, p3 morphotype changes over time within presumed lineages suggest also their different morphoclines (note east Asiatic lineage of *Pliopentalagus*, Tomida & Jin 2009). The available data rather support limited validity of Hibbard's (1963) hypothesis proposing the development of postero-internal structures of p3 in the sequence mesoflexid => mesofossettid (although well documented in some North American leporines). In our view, this morphocline cannot be looked upon as a general phenomenon in all lineages of leporines.

Acknowledgements

We would like to express our thanks to Alexander O. Averianov (ZIN RAS), Emese Bodor (MFGI) and Adrian Delinschi (MENH) for access to collections in their care. A.O. Averianov

also provided precious information about the type material of *Alilepus ucrainicus*. Last but not least, we express thanks to the referees Alisa J. Winkler (Southern Methodist University, Dallas), Lawrence J. Flynn (Harvard University, Cambridge) and Yukimitsu Tomida (National Museum of Nature and Science, Tokyo) for their critical reading and helpful comments on the manuscript. The study was supported by the RVO67985831 of the Institute of Geology, Academy of Sciences of the Czech Republic, v.v.i. and the Spanish Ministerio de Economía y Competitividad (CGL2011-28681).

References

- ANGELONE, C. & ROOK, L. 2011. *Alilepus meini* n. sp., a new leporid (Leporidae, Lagomorpha) from the early Messinian of Tuscany (central western Italy). *Geobios* 44, 151–156. DOI 10.1016/j.geobios.2010.11.003
- AVERIANOV, A.O. 1996. The Neogene rabbit *Hypolagus igromovi* Gureev, 1964 (Lagomorpha, Leporidae) from southern European Russia. *Acta zoologica cracoviensia* 39(1), 61–66.
- AVERIANOV, A.O. & TESAKOV, A.S. 1997. Evolutionary trends in Mio–Pliocene Leporinae, based on *Trischizolagus* (Mammalia, Lagomorpha). *Paläontologische Zeitschrift* 71, 145–153. DOI 10.1007/BF03022556
- BERGGREN, W.A., KENT, D.V., SWISHER, C.C. & AUBRY, M.-P. 1995. A revised Cenozoic geochronology and chronostratigraphy, 129–212. In BERGGREN, W.A., KENT, D.V. & HARDENBOL, J. (eds) *Geochronology Time Scales and Global Stratigraphic Correlations: A Unified Temporal Framework for a Historical Geology*. *SEPM Special Publication No. 54*. SEPM, Tulsa.
- BOON-KRISTKOIZ, E. & KRISTKOIZ, A.R. 1999. Order Lagomorpha, 259–262. In RÖSSNER, G. & HEISSIG, K. (eds) *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München.
- BRANDT, J.F. 1855. Beiträge zur näheren Kenntniss der Säugethiere Russlands. *Mémoire de l'Académie impériale des Sciences, St. Petersburg, Physique, Mathématique, et Naturalistique Série* 6(9), 1–365.
- BRUIN, H. DE 1995. The vertebrate locality Maramena (Macedonia, Greece) at the Turolian–Ruscinian boundary (Neogene). 11 – Lagomorpha (Mammalia). *Münchener Geowissenschaftliche Abhandlungen A* 28, 133–136.
- ČERMÁK, S. 2009. The Plio-Pleistocene record of *Hypolagus* (Lagomorpha, Leporidae) from the Czech and Slovak Republics with comments on systematics and classification of the genus. *Bulletin of Geosciences* 84(3), 497–524. DOI 10.3140/bull.geosci.1104
- ČERMÁK, S. & WAGNER, J. 2013. The Pliocene record of *Trischizolagus* and *Pliopentalagus* (Leporidae, Lagomorpha, Mammalia) in Central Europe with comments on taxonomy and evolutionary history of Leporinae. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 268, 97–111. DOI 10.1127/0077-7749/2013/0321
- CHENG, J., CAO, B., TIAN, M. & LI, L. 1995a. A new early Pleistocene Mammalian fauna from Zhoukoudian. *Earth Science (Wuhan)* 20, 497–504.

- CHENG, J., CAO, B., TIAN, M., YUAN, L., ZHAO, Z., LI, L., LI, C. & CHEN, L. 1995b. Early Pleistocene cave deposits with fossil mammals at Zhoukoudian. *Geoscience* 9, 441–449.
- DAWSON, M. 1958. Late Tertiary Leporidae of North America. *University of Kansas Paleontological Contributions* 6, 1–75.
- DAXNER, G. & FEJFAR, O. 1967. Über die Gattung *Alilepus* Dice, 1931 und *Pliopentalagus* Gureev, 1964 (Lagomorpha, Mammalia). *Annalen des Naturhistorischen Museums Wien* 71, 37–55.
- DELINSCHI, A. 2014. Late Miocene lagomorphs from the Republic of Moldova. *Annales de Paléontologie* 100, 157–163. DOI 10.1016/j.annpal.2013.10.004
- DENG, T. 2006. Chinese Neogene mammal biochronology. *Vertebrata Palasiatica* 44, 143–163.
- DIETRICH, W.O. 1941. Die säugetierepaläontologischen Erhebungen der Kohl-Larsen'schen Expedition 1937–1939 in nördlichen Deutsch-Ostafrika. *Zeitblatt Mineralogie B* 8, 217–223.
- DICE, L.R. 1917. Systematic position of several tertiary lagomorphs. *University of California Publications, Bulletin of the Department of Geology* 10, 179–183.
- DICE, L.R. 1929. The phylogeny of the Leporidae, with description of a new genus. *Journal of Mammalogy* 10, 340–344. DOI 10.2307/1374124
- DICE, L.R. 1931. *Alilepus*, a new name to replace *Allolagus* Dice, preoccupied, and notes on several species of fossil hares. *Journal of Mammalogy* 12, 159–160. DOI 10.2307/1373916
- DOWNEY, J.S. 1968. Late Pliocene Lagomorphs of the San Pedro Valley, Arizona. *United States Geological Survey, Professional Paper 600D*, 169–173.
- ERBAEVA, M.A. & ANGERMANN, R. 1983. Das Originalmaterial von *Serengetilagus praecapensis* Dietrich, 1941 – ergänzende Beschreibung und vergleichende Diskussion. *Schriftenreihe für geologische Wissenschaften* 19/20, 39–60.
- FAHLBUSCH, V., QIU, Z.-D. & STORCH, G. 1983. The Neogene mammalian faunas of Ertemte and Harr Obo in Nei Mongol, China. – I. Report on field work in 1980 and preliminary results. *Scientia Sinica B* 26, 205–224.
- FEJFAR, O. 1961. Die plio-pleistozänen Wirbeltierfaunen von Hajnáčka und Ivanovce (Slowakei), ČSSR. III. Lagomorpha. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1961(5), 267–282.
- FEJFAR, O. & HEINRICH, W.-D. 1983. Arvicoliden-Sukzession und Biostratigraphie des Oberpliozäns und Quartärs in Europa. *Schriftenreihe für Geologische Wissenschaften* 19/20, 61–109.
- FEJFAR, O., HEINRICH, W.-D. & LINDSAY, E.H. 1998. Updating the Neogene Rodent biochronology in Europe. *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO* 60, 533–554.
- FEJFAR, O., HEINRICH, W.-D., KORDOS, L. & MAUL, L.C. 2011. Microtoid cricetids and the early history of arvicolids (Mammalia, Rodentia). *Palaeontologia Electronica* 14(3), 27A: 1–38; palaeo-electronica.org/2011_3/6_fejfar/index.html
- FISCHER, J.G. 1817. Adversaria zoologica. *Mémoires de la Société Impériale Naturelle (Moscow)* 5, 368–428.
- FLADERER, F.A. 1987. Beitrag zur Entwicklung von *Hypolagus* und *Lepus* (Lagomorpha, Mammalia) im Pliopleistozän von Mitteleuropa. *Sitzungsberichte der Österreichische Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse, Abteilung I* 196, 123–138.
- FLADERER, F.A. & REINER, G. 1996. Evolutionary shifts in the first premolar pattern of *Hypolagus beremendensis* (Petényi, 1964) (Lagomorpha, Mammalia) in the Plio-Pleistocene of Central Europe. *Acta zoologica cracoviensia* 39, 147–160.
- FLYNN, L.J., WINKLER, A.J., ERBAEVA, M., ALEXEEVA, N., ANDERS, U., ANGELONE, C., ČERMÁK, S., FLADERER, F.A., KRAATZ, B., RUEDAS, L.A., RUF, I., TOMIDA, Y., VEITSCHEGGER, V. & ZHANG, Z. 2014. The Leporid Datum: A late Miocene biotic marker. *Mammal Review* 44(3–4), 164–176. DOI 10.1111/mam.12016
- FLYNN, L.J., WU, W.Y. & DOWNS, W.R. 1997. Dating vertebrate microfaunas in the late Neogene record of Northern China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 133, 227–242. DOI 10.1016/S0031-0182(97)00082-5
- GAZIN, C.L. 1930. A Tertiary vertebrate fauna from the upper Cuyama drainage basin, California. *Carnegie Institution of Washington* 404, 55–76.
- GAZIN, C.L. 1934. Fossil Hares from the Late Pliocene of Southern Idaho. *Proceedings of the United States National Museum* 83(2976), 111–121. DOI 10.5479/si.00963801.83-2976.111
- GUREEV, A.A. 1964. *Fauna of the USSR (Lagomorpha), Vol. 3 (10)*. 276 pp. Nauka, Moscow & Leningrad. [in Russian]
- HIBBARD, C.W. 1939a. Four new rabbits from the upper Pliocene of Kansas. *American Midland Naturalist* 21(2), 506–513. DOI 10.2307/2420552
- HIBBARD, C.W. 1939b. *Nekrolagus*, new name for *Pediolagus* Hibbard, not Marelli. *American Midland Naturalist* 21(3), Table of Contents.
- HIBBARD, C.W. 1963. The origin of the p3 pattern of *Sylvilagus*, *Caprolagus*, *Oryctolagus* and *Lepus*. *Journal of Mammalogy* 44, 1–15. DOI 10.2307/1377162
- HIBBARD, C.W. 1969. The rabbits (*Hypolagus* and *Pratilepus*) from the Upper Pliocene, Hagerman Local Fauna of Idaho. *Papers of the Michigan Academy of Science, Arts, and Letters* 1(1), 81–97.
- HULVA, P., HORÁČEK, I. & BENDA, P. 2007. Molecules, morphometrics and new fossils provide an integrated view of the evolutionary history of Rhinopomatidae (Mammalia: Chiroptera). *BMC Evolutionary Biology* 7, 165, 1–28.
- ICZN 1999. *International Code of Zoological Nomenclature, 4th Edition*. XXIX + 306 pp. International Trust for Zoological Nomenclature, London.
- JIN, C.Z. 2004. Fossil leporids (Mammalia, Lagomorpha) from Huainan, Anhui, China. *Vertebrata Palasiatica* 42, 230–245. [in Chinese, English summary]
- JIN, C.Z., TOMIDA, Y., WANG, Y. & ZHANG, Y. 2010. First discovery of fossil *Nesolagus* (Leporidae, Lagomorpha) from South-east Asia. *Science China Earth Sciences* 53, 1134–1140. DOI 10.1007/s11430-010-4010-3
- KHOMENKO, J. 1914. La faune méotique du village Taraklia du district de Bendery. *Travaux de la Société des Naturalistes et des Amateurs des Sciences Naturelles de Bessarabie* 5, 1–55.
- KORMOS, T. 1911. Der pliozäne Knochenfund bei Polgárdi (Vorläufiger Bericht). *Földtani Közlemény* 41, 171–189.
- KORMOS, T. 1934. Az euráziai nyulak származástani problémája – Zur Frage der Abstammung eurasiatischer Hasen. *Allatani Közlemények* 31, 65–78.

- KOROTKEVICH, E.L. 1988. *A history of foundation of hipparion fauna of Eastern Europe*. 164 pp. Naukova dumka, Kiev. [in Russian]
- KRETZOI, M. 1954. Befejező jelentés a Csakvári barlang őslénytani feltásáról [Final report on the paleontological findings in the cave of Csakvár]. *A Magyar Állami Földtani Intézet Évi Jelentése az 1952 Évről 1952*, 37–69. [in Hungarian]
- LÓPEZ MARTÍNEZ, N. 1976. Lagomorpha from the Turolian of Pikermi (Greece). *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen* 79, 235–244.
- LÓPEZ MARTÍNEZ, N. 1977. Nuevos Lagomorfos (Mammalia) del Neógeno y Cuaternario español. *Trabajos sobre Neógeno-Cuaternario* 8, 7–45.
- LÓPEZ MARTÍNEZ, N. 1989. Revisión sistemática y biostratigráfica de los Lagomorpha (Mammalia) del Terciario y Cuaternario de España. *Memorias del Museo Paleontológico de la Universidad de Zaragoza* 3, 1–342.
- LÓPEZ MARTÍNEZ, N. 2008. The lagomorph fossil record and the origin of the European rabbit, 27–46. In ALVES, P.C., FERRAND, N. & HACKLÄNDER, K. (eds) *Lagomorph Biology: Evolution, Ecology and Conservation*. Springer-Verlag, Berlin & Heidelberg.
- LÓPEZ MARTÍNEZ, N., LIKIUS, A., MACKAYE, H.T., VIGNAUD, P. & BRUNET, M. 2007. A new Lagomorph from the Late Miocene of Chad (Central Africa). *Revista Española de Paleontología* 22, 1–20.
- LUNGU, A. 1980. New records of the Sarmatian land vertebrate fauna in Moldavia, 3–8. In *Quaternary and neogene faunas and floras of Moldavian SSR*. Shtiintsa, Kishinev. [in Russian]
- LUNGU, A. & RZEBIK-KOWALSKA, B. 2011. *Faunal assemblages, stratigraphy and taphonomy of the Late Miocene localities in the Republic of Moldova*. 62 pp. Institute of Systematics and Evolution of Animals Polish Academy of Sciences, Krakow.
- LUNGU, A., DELINSCHI, A. & NICOARA, I. 2007. Some dates about studies representative order Lagomorpha from hipparion fauna, of superior Miocen from Republic of Moldova. *Scientific Bulletin of National Museum of Ethnography and Natural History of Moldova. Ethnography, Natural Sciences and Museology* 6(19), 141–143.
- MEIN, P. 1988. Continental faunas at the Miocene–Pliocene boundary. La gisement karstique turolien de Lissieu (Rhône). *International Workshop “Continental Faunas at the Miocene/Pliocene Boundary”*. *Proceedings, Faenza*, 25.
- MEIN, P. 1999. The late Miocene small mammal succession from France, with emphasis on the Rhône Valley localities, 140–164. In AGUSTÍ, J., ROOK, L. & ANDREWS, P. (eds) *The Evolution of Terrestrial Ecosystems in Europe, Volume 1. Hominoid Evolution and Climatic Change in Europe*. Cambridge University Press, Cambridge.
- MILLER, W.E. & CARRANZA-CASTANEDA, O. 1982. New lagomorphs from the Pliocene of central Mexico. *Journal of Vertebrate Paleontology* 2, 95–107.
DOI 10.1080/02724634.1982.10011920
- NESIN, V.A. 1996. Lower Pliocene rodents of Ukraine and problems of Pontian biostratigraphy. *Acta zoologica cracoviensia* 39(1), 395–399.
- NESIN, V.A. 2004. Stratigraphical position of the Late Neogene localities of the microtheriofauna in Ukraine, 195–199. In GOZHI, P.F. (ed.) *Problemy stratigrafii i fanerozooyu Ukrainy*. Institut geologichnikh nauk, Kiev. [in Russian]
- NESIN, V.A. 2013. *The Neogene Murinae (Rodentia, Muridae) of Ukraine*. 174 pp. University book, Sumy. [in Russian, English summary]
- NESIN, V.A. & NADACHOWSKI, A. 2001. Late Miocene and Pliocene small mammal faunas (Insectivora, Lagomorpha, Rodentia) of Southeastern Europe. *Acta zoologica cracoviensia* 44(2), 107–135.
- OGNEV, S.I. 1929. Zur Systematic der russischen Hasen. *Zoologischer Anzeiger* 84, 68–83.
- PALACIOS, F. & LÓPEZ MARTÍNEZ, N. 1980. Morfología dentaria de las liebres europeas (Lagomorpha, Leporidae). *Doñana Acta Vertebrata* 7, 61–81.
- QI, G.-Q., DONG, W., ZHENG, L., ZHAO, L., GAO, F., YUE, L.-P. & ZHANG, Y.-X. 2006. Taxonomy, age and environment status of the Yuanmou hominoids. *Chinese Science Bulletin* 51, 704–712. DOI 10.1007/s11434-006-0704-5
- QIU, Z.-D. 1987. The Neogene mammalian faunas of Ertemte and Harr Obo in Inner Mongolia (Nei Mongol), China. 6. Hares and pikas – Lagomorpha: Leporidae and Ochotonidae. *Senckenbergiana lethaea* 67, 375–399.
- QIU, Z. & HAN, D. 1986. Fossil Lagomorpha from the hominoid locality of Lufeng, Yunnan. *Acta Anthropologica Sinica* 5, 41–53. [in Chinese, English summary]
- QIU, Z. & QIU, Z. 1995. Chronological sequence and subdivision of Chinese Neogene mammalian faunas. *Palaeogeography, Palaeoclimatology, Palaeoecology* 116, 41–70.
DOI 10.1016/0031-0182(94)00095-P
- QIU, Z., WU, W. & QIU, Z. 1999. Miocene mammal faunal sequence of China: paleozoogeography and Eurasian relationships, 443–445. In RÖSSNER, G.E. & HEISSIG, K. (eds) *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München.
- RABEDER, G. 1989. Die Säugetiere des Pontien in Österreich und Ungarn. *Jugoslawische Akademie der Wissenschaften und Künste* 8, 821–836.
- RADDE, G. 1861. Neue Säugethier-Arten aus Ost-Sibirien. *Mélanges Biologiques tirés du Bulletin Physico-Mathématique de l'Académie Impériale des Sciences de St. Petersburg* 3, 676–687.
- RADULESCO, C. & SAMSON, P. 1967. Contribution à la connaissance du complexe faunistique de Malusteni-Beresti (Pléistocène inférieur), Roumanie I. Ord. Lagomorpha, Fam. Leporidae. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1967(9), 544–563.
- RUSSELS, B.D. & HARRIS, A.H. 1986. A new leporine (Lagomorpha: Leporidae) from Wisconsinan deposits of the Chihuahuan Desert. *Journal of Mammalogy* 67, 632–639.
DOI 10.2307/1381125
- SCHLOSSER, M. 1924. Tertiary vertebrates from Mongolia. *Palaeontologia Sinica, Series C* 1(1), 1–133.
- ŞEN, Ş. 1983. Rongeurs et lagomorphes du gisement Pliocène de Pul-e Charkhi, basin de Kabul, Afghanistan. *Bulletin du Museum National d'Histoire Naturelle, Paris, 5e série, 5C(1)*, 33–74.
- ŞEN, Ş. & ERBAEVA, M. 1995. Early Pliocene leporids (Mammalia, Lagomorpha) from Afghanistan. *Comptes Rendus de l'Académie des Sciences de Paris, Sér. II* 320, 1225–1231.
- SEMENENKO, V.N. 1987. [Stratigraphical Correlation of the Upper Miocene and Pliocene of the Eastern Paratethys and Tethys]. 230 pp. Naukova dumka, Kiev. [in Russian]

- SINITSА, M.V. 2005. The small mammal fauna (Insectivora, Lagomorpha, Rodentia) from the Meotian deposits of Kuyalnik River. *Proceedings of the museum Brauner's foundation 11(4)*, 11–17. [in Russian]
- SINITSА, M.V. 2008. Meotian small mammals from the Egorovka locality, 285–289. In GOZHИK, P.F. (ed.) *Biostratigraphic fundamentals of creating the stratigraphic schemes of the Phanerozoic of Ukraine*. Proceedings of the Institute of Geological Sciences of the NAS of Ukraine, Kyiv. [in Russian, English summary]
- SINITSА, M.V. 2009a. Cricetids (Rodentia, Mammalia) from the Upper Miocene of Egorovka locality. *Vestnik zoologii 44*, 209–225. [in Russian, English summary]
- SINITSА, M.V. 2009b. A new small mammal fauna from the Lower Turolian (MN11) of the Southern Ukraine, 181–182. In CODREANU, I. (ed.) *Materialele simpozionului jubiliar internațional 'Mediul și dezvoltarea durabilă'*. Labirint, Chișinău.
- SINITSА, M.V. 2011. *Pliopetaurista* (Mammalia, Rodentia) from the Neogene of Ukraine. *Vestnik zoologii 45*, 19–33. [in Russian, English summary]
- SINITSА, M.V. 2012. Cricetids (Mammalia, Rodentia) from the Late Miocene locality Palievo, Southern Ukraine. *Vestnik zoologii 46*, 137–147. [in Russian, English summary]
- STEININGER, F.F. 1999. The Continental European Miocene. Chronostratigraphy, Geochronology and Biostratigraphy of the Miocene “European Land Mammal Mega-Zones” (ELMMZ) and the Miocene “Mammal-Zones (MN-Zones)”, 9–24. In RÖSSNER, G.E. & HEISSIG, K. (eds) *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München.
- SYCH, L. 1965. Fossil Leporidae from the Pliocene and the Pleistocene of Poland. *Acta zoologica cracoviensia 10*, 1–88.
- TOMIDA, Y. 2008. Can morphological differences among extinct species be explained by means of genetics? An example from fossil rabbits. *Journal of Vertebrate Paleontology 28* (3, Supplement), 152A.
- TOMIDA, Y. & JIN, C.-Z. 2009. Two new species of *Pliopentailagus* (Leporidae, Lagomorpha) from the Pliocene of Anhui Province, China, with a revision of *Pl. huainanensis*. *Vertebrata Palasiatica 47(1)*, 53–71.
- TOPACHEVSKI, V.A. & SKORIK, A.F. 1992. *The Neogene and Pleistocene lower cricetids of SE Europe*. 242 pp. Naukova dumka, Kiev. [in Russian, English summary]
- TOPACHEVSKI, V.A., NESIN, V.A. & TOPACHEVSKI, I.V. 2000. A small mammal oryctocenoses in the Meotian of the Cherevichnoe section. *Proceedings of the National Academy of Sciences of Ukraine 10*, 192–195. [in Russian, English summary]
- VOORHIES, M.R. & TIMPERLEY, C.L. 1997. A new *Pronotolagus* (Lagomorpha: Leporidae) and other leporids from the Valentine Railway Quarries (Barstovian, Nebraska), and the archaeolagine-leporine transition. *Journal of Vertebrate Paleontology 17*, 725–737.
DOI 10.1080/02724634.1997.10011020
- WHITE, J.A. 1991. North American Leporinae (Mammalia: Lagomorpha) from late Miocene (Clarendonian) to latest Pliocene (Blancan). *Journal of Vertebrate Paleontology 11*, 67–89. DOI 10.1080/02724634.1991.10011376
- WHITE, J.A. & MORGAN, N.H. 1995. The Leporidae (Mammalia: Lagomorpha) from the Blancan (Pliocene) Taunton Local Fauna of Washington. *Journal of Vertebrate Paleontology 15*, 366–374. DOI 10.1080/02724634.1995.10011235
- WILSON, R.W. 1938. A new genus of lagomorph from the Pliocene of Mexico. *Bulletin of the Southern California Academy of Sciences 36(3)*, 98–104.
- WINKLER, A.J. & AVERY, M. 2010. Lagomorpha, 305–317. In WERDELIN, L. & SANDERS, W.J. (eds) *Cenozoic Mammals of Africa*. University of California Press, Berkeley.
- WINKLER, A.J. & TOMIDA, Y. 2012. The fossil record of African leporids. 4th World Lagomorph Conference, Proceedings, Vienna, 139.
- WINKLER, A.J., FLYNN, L.J. & TOMIDA, Y. 2011. Fossil lagomorphs from the Potwar Plateau, northern Pakistan. *Palaeontologia Electronica 14(3)*, 38A, 1–16;
palaeo-electronica.org/2011_3/17_winkler/index.html