



LAGOMORPHS (MAMMALIA) FROM THE EARLY PLIOCENE OF DORKOVO, BULGARIA

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Abstract: The vertebrate locality of Dorkovo yielded a rich mammalian assemblage of which some large mammals have been studied, but not smaller mammals. The previous investigations correlated this fauna to the early Pliocene (early Ruscinian, MN 14). The present paper describes lagomorph remains which consist of one fragment of mandible and 106 isolated teeth. Four species are identified: *Ochotona* cf. *antiqua*, *Prolagus sorbinii*, *Alilepus spassovi* n. sp. and *Trischizolagus crusafonti*. The new species is characterised by the derived pattern of its p3 which has trigonid more stretched, enamel infolding stronger than in any other species of *Alilepus*, and the p3 lacks anteroflexid. The presence of four species of lagomorphs at Dorkovo is in agreement with the diversity dynamics of lagomorphs toward the end of late Miocene and during the early Pliocene in Eurasia, and in particular in Eastern Europe. The time range of the Dorkovo lagomorphs encompasses the Miocene/Pliocene boundary, and this is in agreement with the previous age assignments, i.e., earliest Pliocene, or early part of MN 14 mammalian zone.

Key words: Lagomorpha, Ochotonidae, Prolagidae, Leporidae, early Pliocene, Bulgaria, dispersal

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Introduction

Lagomorphs are the common elements of Neogene and Quaternary mammalian assemblages in Eurasia. In late Miocene and Pliocene localities they usually occur as one ochotonid and one leporid species, in some cases altogether three, but exceptionally four species. As far as we found in the literature, only the karst locality of Muselievo (MN 15) in northern Bulgaria (Popov 2004) yielded two ochotonids and two leporids. Other late Miocene and Pliocene localities in eastern Europe are also well documented in lagomorphs, but the scarce detailed studies do not evidence their diversity. For example, Topachevsky et al. (1988) gave a list of nine lagomorph taxa, most of them undetermined, from the early Pliocene locality of Obukhovka-1, NE of Azov Sea. Nesin and Rekovets (1993) reduced this number to four in the list of taxa from this locality, although they did not study any of them. The occurrence of four species of lagomorphs makes Dorkovo one of the few localities where this order is the most diversified during the early Pliocene in Europe.

As rightly noted by López Martínez (2008), the systematics of fossil lagomorphs is mainly based on the characters of their dentition, and in particular on the third lower premolar (p3). For the genus *Prolagus*, the characters of upper cheek teeth also provide valuable criteria for species distinction. On the other hand, the lower molariform teeth of ochotonids and upper and lower molariform teeth of leporids are often neglected because considered non informative for

systematics of these groups. However, a close examination of these teeth revealed some characters that can be used for recognition of genera and even species. For instance, on the lower molariform teeth of *Prolagus*, some species have a labial notch on the talonid, while some others have not. Another example is given by the upper molariform teeth of the European leporids which have a uniform morphology. The degree and side of enamel plication around the hypoflexus is different from one genus to another, and also the shape of the entrance of hypoflexus as we will see here below.

The locality of Dorkovo is situated in southern Bulgaria, in the department of Pazardjik, about 100 km SE of Sofia and 1.6 km north to the center of Dorkovo village. The Chepino Basin in which this locality is included is one of the intramontane basins along the northern slopes of Rhodope Mountains. The stratigraphy of this basin is poorly documented due to the lack of outcrops (dense vegetation and/or cultivated lands), but also little interest of geologists. The Neogene deposits are distinguished as lower, middle and upper units, the Dorkovo fossil locality being included in the latter one (Thomas et al. 1986a, b). The fossiliferous site was discovered in 1982 by the geologist Milan Kaltchev from the Bulgarian Academy of Sciences, and it was excavated by a Bulgarian-French team between 1984 and 1987 under the leadership of Nikolai Spassov and Herbert Thomas. The fossiliferous bed is full of entangled mastodon bones

(Thomas et al. 1986a: fig. 2), while the remains of other mammals are scarce. Thomas et al. (1986a, b) provided a history of discoveries of vertebrate fossils in the Chepino Basin, the stratigraphy of Neogene and Quaternary deposits, and a preliminary list of vertebrate taxa from Dorkovo. From the fossils collected between 1984 and 1987 at Dorkovo, Boev (1998) studied birds, Delson et al. (2005) described cercopithecids and Alberdi and Alcalá (1999) hipparionine horses. Metz-Muller (1995, 2000) examined proboscidians for her PhD and published some dental remains of *Anancus arvernensis* (CROIZET et JOBERT, 1828). Rzebik-Kowalska and Popov (2005) established a list of 10 species of insectivores, without further study. The aim of the present study is to provide a detailed description of lagomorphs from Dorkovo and their input on the lagomorph dispersal at the Miocene/Pliocene transition.

Material and methods

The fossiliferous horizon contains more bones than sediment. All the matrix that can be obtained from excavation was screen washed on a sieve of 0.5 mm mesh. The residue consisted of about 80 % of bone fragments. The coarse fraction of the residue over 3 mm was sorted in the field using a head loupe, and the lower fraction under microscope by the author at the laboratory. After study, the material is housed at the National Museum of Natural History in Sofia, Bulgaria. The lagomorph remains consist of one fragment of mandible and 106 isolated teeth.

The terms anterior and mesial or posterior and distal are used indistinctly. The measurements are taken with a Mitutoyo measuring equipment on the wear plane of teeth, and they indicate maximum length and width of tooth on the sagittal and transverse axes, from the external margin of enamel on the occlusal face. All measurements are in millimetre. In the illustrations, enamel is represented in black, dentine in white and cement areas with dots. In all illustrations, the anterior is upward. Dental terminology follows Palacios Arribas and López Martínez (1980) for leporids, López Martínez (1989) and Angelone and Sesé (2009) for ochotonids (Text-fig. 1). Upper/lower premolars are abbreviated as P/p, and molars as M/m. All drawings have been made by the author with a camera lucida mounted on a Leica M3Z binocular microscope.

Systematic palaeontology

Order Lagomorpha BRANDT, 1855

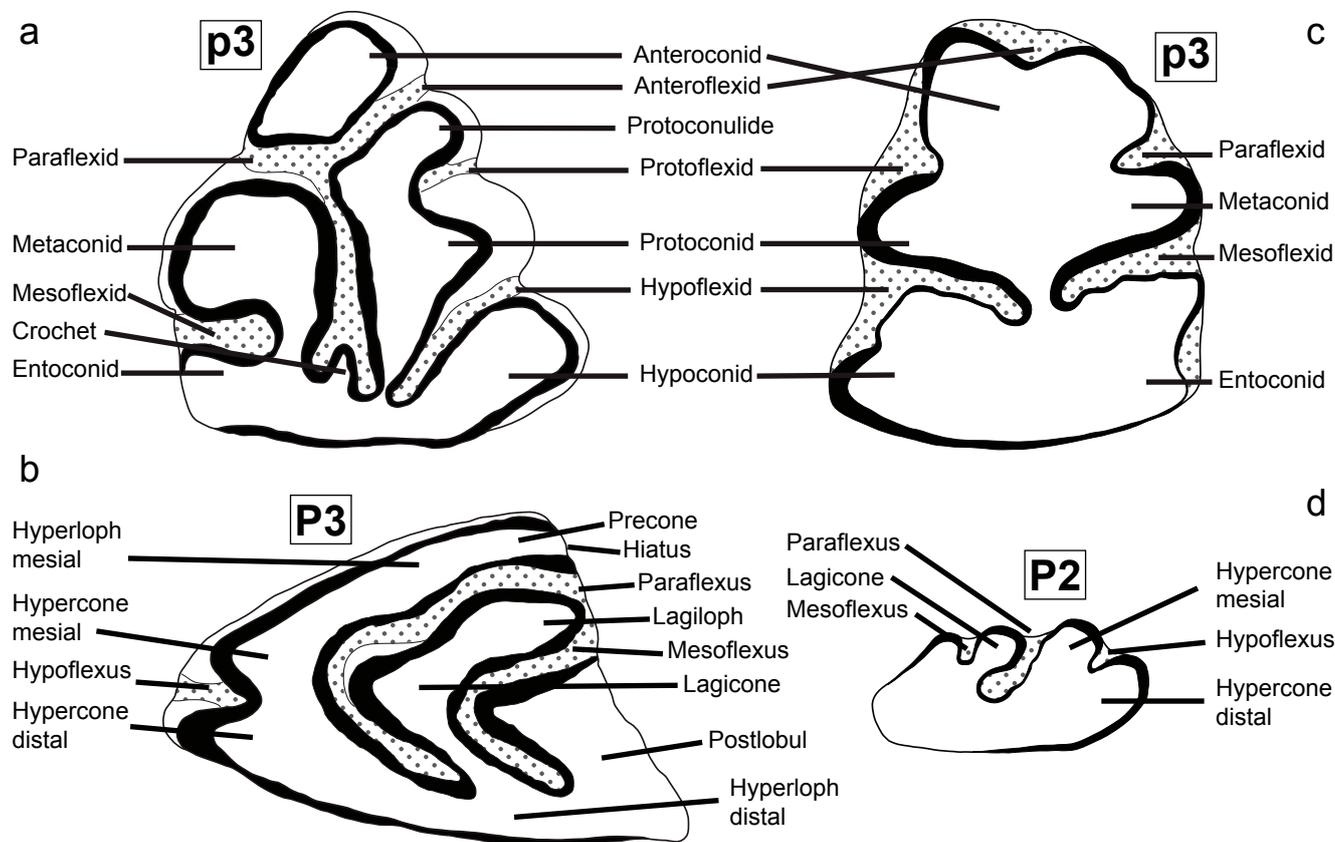
Family Ochotonidae THOMAS, 1897

Genus *Ochotona* LINK, 1795

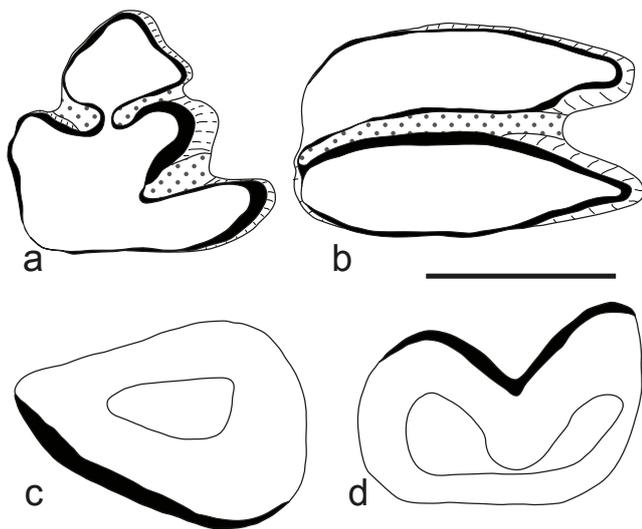
Ochotona cf. antiqua ARGYROPOULO et PIDOPLICHKO, 1939

Text-fig. 2

Material from Dorkovo. Isolated right p3 (length × width = 1.33 × 1.25, anteroconid length × width = 0.62 × 0.62), right upper molariform tooth (length = 1.16, anterior width = 1.81, posterior width = 1.87), fragment of



Text-fig. 1. Tooth terminology used in the present study to describe Prolagidae and Leporidae. Modified after Palacios et al. (1980), López Martínez (1989), and Angelone and Sesé (2009). a) right p3 of *Prolagus*, b) left P3 of *Prolagus*, c) left p3 of *Trischizolagus*, d) right P2 of *Trischizolagus*. Enamel is represented in black, dentine in white, and the parts covered with cement are dotted. Not to scale.



Text-fig. 2. *Ochotona* cf. *antiqua* from Dorkovo, Bulgaria. a) right p3 (DKV-1301), b) right upper molariform tooth (DKV-1303), c) section of left lower incisor, seen from the root side (DKV-1305), d) section of right upper incisor, seen from the root side (DKV-1306). The teeth are oriented anterior upward. Scale bar = 1 mm.

left P3, left lower incisor (1.10 × 1.58), right upper incisor (1.06 × 1.55), anterior portion of a lower molariform tooth (width = 1.29). Numbers DKV-1301 to DKV-1306).

Description. On the p3, the anteroconid is diamond shaped, without fold but with a slight depression on the labial side. The protoflexid is deeper than the paraflexid and both moderately oblique. The hypoflexid does not reach the half width. The enamel is thick on the labial sides of protoconid and hypoconid, but lacking on the distolingual corner. The molariform upper tooth has hypoflexid reaching the lingual margin. Both incisors are rather flat, the lower one with a triangular section, the upper one with a deep groove, which is rather central.

Comparison. The Dorkovo ochotonid belongs no doubt to the genus *Ochotona* in having small-sized cheek teeth, p3 with two labial and one lingual flexids, its anteroconid diamond-shaped and without groove and connected to the posterior complex by a narrow isthmus. The size is used as an important criterion to distinguish extinct species of *Ochotona*. Erbajeva (1988, 1994) grouped *Ochotona* species as small, medium and large. Later on, Fostowicz-Frelik et al. (2010) used this criterion in their phylogenetic analysis. The size of teeth from Dorkovo is small and is comparable with small-sized species which are numerous, such as *Ochotona pusilla* (PALLAS, 1769), *O. antiqua* ARGYROPULO et PIDOPLICHKO, 1939, *O. mediterranensis* SUATA-ALPASLAN, 2009, *O. polonica* SYCH, 1980, *O. horaceki* ČERMÁK, 2004 and *O. kormosi* FOSTOWICZ-FRELIK et al., 2010. Fostowicz-Frelik (2008) and Fostowicz-Frelik et al. (2010) synonymized *O. dehmi* ERBAJEVA, 2005 from Germany and *O. valerotae* ERBAJEVA et al., 2001 from France with *O. polonica* (see also Sen et al. 2017).

O. pusilla is different in having a peculiar occlusal pattern of p3, in particular the minute size of its anteroconid

associated with a wide junction with posteroconid. *O. polonica*, *O. dehmi* and *O. kormosi* have an elongated and narrow p3 with dissymmetric paraflexid and protoflexid. *O. mediterranensis* is known from its type locality İğdeli and from Çestepe, both in Central Anatolia and correlated to the early Pliocene (MN 14). This species has dentition similar to that of *O. antiqua* but its size is clearly smaller (Suata Alpaslan 2009, Sen et al. 2017).

In early species of *Ochotona*, such as *O. ozansoyi* SEN, 2003, the hypoflexus of upper molariforms does not reach the lingual margin, except M2, and the paraflexid and protoflexid of p3 are short and transverse (Sen 2003).

O. ursui SIMIONESCU, 1930 from Malusteni (early Pliocene, Romania) is badly documented. Description and sketchy illustration by its author and later by Radulescu and Samson (1995) do not give any clear picture of this species, hence its mention with some question mark in most papers dealing with Pliocene *Ochotona* from Eastern Europe. Čermák and Rekovets (2010) noted a number of differences from *O. antiqua*: shorter, taller, and more robust horizontal ramus of mandible, slightly elongated p3 alveolus pattern, derived morphology of paraflexid distally bent as in *Pliolagomys* ERBAJEVA in AGADJANIAN et ERBAJEVA, 1983. Waiting for a better knowledge of *O. ursui*, I suggest to maintain both species names, restricting however *O. ursui* to its type locality.

The scarce fossils from Dorkovo compare better with *O. antiqua*. Čermák and Rekovets (2010) restudied the type material from Novopetrovka (Odessa Province, Ukraine, early Pliocene, Ruscianian, MN 14) and also specimens from the neighbor localities of Frunzovka-1, Krasnopol and Grebenniki-2. In the pattern of p3, the Dorkovo pika is similar to *O. antiqua* from its type locality, but its size is slightly under the range of variation of this species (length between 1.39–1.67 mm, average 1.53 mm, contra 1.33 mm at Dorkovo). Čermák and Rekovets (2010) reviewed all record referred to this species, for instance from Kosyakino, and Nurnus. The material from Kosyakino (Stavropol Region, Russia, MN 14; Averianov and Tesakov 1998) and also from some other Moldavian localities (Erbajeva and Sushpanov 1988) fits in size and dental characters to *O. antiqua*. The four p3 illustrated by Melik-Adamyán (1986) from Nurnus (Armenia, MN 14/15), referred to *Ochotona* ex gr. *antiqua*, are smaller than the average values of *O. antiqua* from its type locality. The size of these teeth ranges between 1.25–1.50 mm for length and between 1.27–1.47 mm for width (measurements from illustrations). The size and characters of the unique p3 from Dorkovo fit with that of Nurnus.

In summary, the rare teeth of pika from Dorkovo have characters similar to that of *O. antiqua* from southeastern Europe and *O. mediterranensis* from Turkey. The proximity of Dorkovo to the localities in Moldova, Ukraine and southwestern Russia, where *O. antiqua* is a common element of early Pliocene (Ruscianian) assemblages, and similarities in dental pattern favor attribution of the scarce remains of pika from Dorkovo to as *Ochotona* cf. *antiqua*. *O. ursui*, pending its revision, is another early Pliocene species of the region, known from Malusteni (Romania). Lastly, Radulescu and Samson (2001) calibrated the age of this locality as close to the early/late Ruscianian boundary, i.e., a little older than 4.0 Ma.

Family Prolagidae GUREEV, 1960

Remark. The genus *Prolagus* and its relatives are either grouped in the family Ochotonidae THOMAS, 1897 or in the family Prolagidae GUREEV, 1960. Proponents of the first option consider Prolagidae synonymous with Ochotonidae, while other authors recognize both families, the Prolagidae being restricted to the genera *Piezodus* VIRET, 1929, *Prolagus* POMEL, 1853 and *Ptychoprolagus* TOBIEN, 1975. During the last 50 years, this issue was a serious subject of debate and disagreement in the conception of systematics principles between the western and eastern lagomorph specialists. Gureev (1960, 1964) defined a distinct subfamily for *Prolagus*, the Prolaginae that Erbajeva (1988) erected to the family level, and she also included the genus *Ptychoprolagus*. Unfortunately, the diagnostic features that Gureev (1960, 1964) and Erbajeva (1988) provided for the definition of the subfamily or family (upper incisor with rectangular cross section, hypsodont teeth compared to Oligocene genera, which have rooted and/or curved cheek teeth, the width of upper molariforms 1.6 to 2 time larger than the length, hypoflexus shorter than in other ochotonids, lack of m3) are far for a clear distinction of this group from the true Ochotonidae. Tobien (1975) analysed dental features of species referred to the genera *Piezodus*, *Prolagus* and *Ptychoprolagus*, demonstrated phylogenetic relationships of these genera, in particular between *Piezodus* and *Prolagus*, and he grouped them in the “*Prolagus*-Gruppe” included in the Ochotonidae. Later on several authors have expressed their opinion on the recognition of one or two families. Angelone et al. (2014) resumed the opinions of previous authors. Some arguments to refute the family Prolagidae border on the reasonable, such as “these attempts at subdivision have contributed neither to phylogenetic nor to palaeobiogeographic understanding of the order” (Dawson 2008: 295) or “this practice enhances the instability of the nomenclature because new information will influence the reconstruction of lineages and thereby the content of the (sub)families” (Bendoukidze et al. 2009: 347). One can wonder if the issue is rather an east-west conflict than a systematic question to enlighten the history of an evolutionary lineage that forms the “*Prolagus* group”, distinct from the “*Ochotona* group”. Angelone et al. (2014: 126), after reviewing the controversy, “recognized that (1) the descendants of *Piezodus*, the genera *Prolagus* and *Ptychoprolagus*, are indeed very peculiar and show features that distinguish them from the rest of the ochotonids; and (2) *Prolagus* has a long, independent, complex evolution and is very diverse”. However, they preferred “to follow the western and central European nomenclatorial custom, also followed by most of the revisions dealing with *Prolagus*, and place *Prolagus* in the family Ochotonidae”. Once more, we are entitled to ask whether it is objectivity based on palaeontological and phylogenetic arguments or obedience to a Western custom under the influence of some “authorities” of palaeontology. Finally, Hoffman and Smith (2005) in the famous book of “Mammal Species of the World” edited by Wilson and Reeder retained the family Prolagidae.

Compared to all other genera of the family Ochotonidae, the genera *Piezodus*, *Prolagus* and *Ptychoprolagus* have a peculiar dental pattern in having evergrowing hypselodont cheek teeth, i.e., continual replenishment of worn tooth

structures throughout the lifetime of the animal (except in the early species of *Piezodus* which may have small roots), at least two folds in P2, a complicated pattern of P3 and P4 in having a mesoflexus in addition to the hypoflexus and paraflexus, the presence on M1 and in some species on M2 an enamel island (mesofossette), the peculiar pattern of p3 with isolated anteroconid and several flexids deeply dividing occlusal outline, the talonid larger than the trigonid on the lower molariform teeth, and the fusion of m3 with the talonid of m2. As the fossil record shows, the three genera mentioned here above have a strict European, Eastern Mediterranean and North African distribution, while the representative of the true Ochotonidae are mainly dispersed in Asia and North America, except some genera of Asian origin that entered Europe: the lineage *Marcuinomys* LAVOCAT, 1951 – *Lagopsis* SCHLOSSER, 1884 – *Paludotona* DAWSON, 1959 during the Miocene, and the genera *Ochotona* and *Ochotonoma* SEN, 1998 from the latest Miocene up to the Pleistocene. Taking into consideration the peculiar dentition of the “*Prolagus* group” and its independent evolution during more than 20 million years in a well-defined territory (Europe, Anatolia and NW Africa), this group deserves a distinct family status, Prolagidae GUREEV, 1960.

Genus *Prolagus* POMEL, 1853

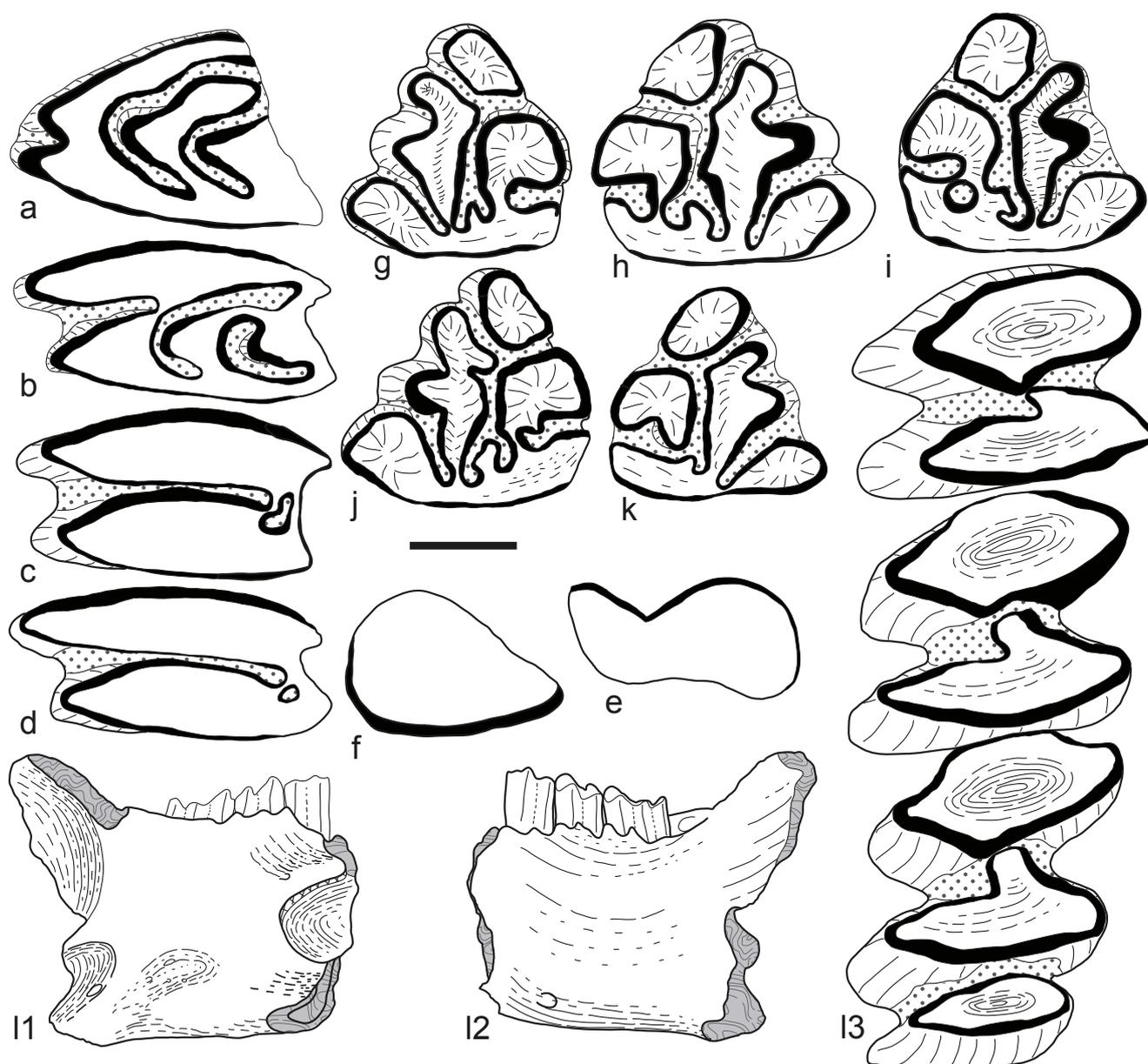
Prolagus sorbinii MASINI, 1989

Text-fig. 3

Material from Dorkovo. Fragment of left mandible bearing p4–m2 (DKV-1307), three lower incisors, one d4, five p3, four complete and two fragmentary lower molariform teeth, one fragment of m2, three upper incisors, one D3, one P3, one P4, two M1 and one M2, all numbered as DKV-1308 to DKV-1332.

Table 1. Measurements in millimetre of key specimens of *Prolagus sorbinii* from Dorkovo. Lantd – anteroconid length, Wantd – anteroconid width, Want – width of the anterior loph(id), Wpost – width of the posterior loph(id).

	Tooth	Length	Width	Lantd	Wantd
DKV-1309	p3	2.14	2.21	0.66	0.87
DKV-1310	p3	2.25	2.41	0.79	0.75
DKV-1311	p3	2.06	1.9	0.69	1.02
DKV-1312	p3	2.27	1.97	0.8	0.83
DKV-1313	p3	2.23	2.2	0.82	0.89
DKV-1331	Lower incisor	1.43	1.93	–	–
DKV-1332	Lower incisor	1.49	2.02	–	–
	Tooth	Length	Want	Wpost	–
	p4	2.03	2.12	2.28	–
DKV-1307	m1	2.2	2.36	2.48	–
	m2	2.91	2.23	2.14	–
DKV-1321	Upper incisor	1.07	1.95	–	–
DKV-1324	P3	1.86	3.06	–	–
DKV-1325	P4	1.5	2.88	2.67	–
DKV-1326	M1	1.64	3.17	2.75	–
DKV-1327	M1	1.63	3.1	2.58	–
DKV-1328	M2	1.44	2.73	2.49	–



Text-fig. 3. *Prolagus sorbinii* from Dorkovo, Bulgaria. a) left P3 (DKV-1324), b) left P4 (DKV-1325), c) left M1 (DKV-1326), d) left M1 or M2 (DKV-1328), e) section of right upper incisor, seen from the occlusal side (DKV-1321), f) section of left lower incisor, seen from the root side (DKV-1331), g) left p3 (DKV-1309), h) right p3 (DKV-1313), i) right p3 (DKV-1312), j) left p3 (DKV-1310), k) right p3 (DKV-1311), l) fragment of left mandible bearing p4–m2 (DKV- 1307) in lingual view (l1), labial view (l2) and occlusal view of p4–m2 (l3). The teeth are oriented anterior upward. Scale bar = 1 mm for teeth, 5 mm for mandible.

Measurements. See Table 1.

Description. The mandible fragment preserved the part under p4–m2 and the lower part of the ascending ramus. The body is high (about 10 mm), the lower margin almost linear, the labial face bears only one nutrient foramen. On the lingual face, the large fossette at the mid-depth of the jaw indicates that the distal end of the incisor reaches the limit between p4–m1. The pterygoid fossa is strongly delimited anteriorly by a sharp ridge far behind the m3. In dorsal view, the retroalveolar foramen is large (length × width = 1.3 × 1.0 mm). This mandible fragment bears p4–m2. Their length and width increase from p4 to m2 (Tab. 1). The mesial lophid is diamond shaped, mainly labially; the distal lophid is notched labially by a flexid next to the junction with the mesial lophid. The third lophid of m2 is short and wide.

The lower incisor has a drop-shaped section. The enamel covers the anterior and medial faces.

The p3 is quite variable in size and in the shape of occlusal outline (elongated or widened (see Tab. 1)). This is probably due to the individual age and the degree of attrition. The general shape of the occlusal outline is a triangle of which the tip is displaced labially. The maximum depth of the shaft is 11.1 mm (DKV-1312). The anteroconid is variable in shape, from oval to rather diamond shaped. It is smaller than the metaconid. The metaconid is round, connected to the posterolophid in four specimens over five by a narrow metaisthmus. The mesoflexid is rather deep and transverse. The crochet is present in all specimens next to the metaisthmus, but its size and orientation are variable. The hypoflexid is variably deep, strongly oblique, and it

almost reaches the distal margin in two specimens over five. One p3 has an enamel island behind the mesoflexid.

The upper incisor has a thin medial (1/3) and thick lateral (2/3) parts separated by a deep groove. The internal face is a little depressed. The enamel covers anterior and lateral faces.

The P3 is rather triangular in occlusal outline. Its hypoflexus is shallow but filled with cement. The paraflexus and mesoflexus are both hook shaped. The lagicone is large, and separated of the lagiloph by a slight mesial compression. The lagiloph reaches the labial margin.

On the P4, the hypoflexus is moderately deep, the paraflexus is hook shaped, stretched labially and almost reaches the anterolabial angle. The mesoflexus is also hook shaped, but with an opposite orientation, and it reaches the opposite labial angle.

The M1 has a deep hypoflexus and a reduced mesofossette situated distally to the hypoflexus.

The M2 is a little smaller than the previous molar, with a deep hypoflexus and a small mesofossette situated distally to the hypoflexus.

Comparison. The size of the specimens from Dorkovo fits with the middle-sized species. The length/width ratio of p3 is close to one. Consequently, the comparison will be limited to similar sized species that existed in Europe and Anatolia during the latest Miocene and Pliocene.

P. depereti LÓPEZ MARTÍNEZ in LÓPEZ MARTÍNEZ et THALER, 1975 is known from its type locality Perpignan (southern France, MN 15), and a neighbor locality, Villeneuve de la Raho (Mein and Aymar 1984). This species shares some characters with the Dorkovo sample such as oval-shaped anteroconid and metaconid, narrow protoisthmus and metaisthmus on the p3, labial notch of the talonid on the lower molariforms and rather triangular outline of the P3. However, *P. depereti* is different in having a rather oblique mesoflexid, stronger protoconulid, an anteroconid as large as or even larger than the metaconid, and the lack of crochet on the p3, U-shaped parafossette and mesofossette on the P4 and the lack of mesofossette on the upper molars.

P. michauxi LÓPEZ MARTÍNEZ in LÓPEZ MARTÍNEZ et THALER, 1975 is a medium-sized species quite common in latest Miocene and Pliocene localities of western Europe (reported from 46 localities in Spain and only from its type locality Sète and Vandargues (cf.) in France, according to NOW Database consulted on February 6, 2019). It was also reported from some North African localities and from Greece and Turkey. Attribution of North African and Eastern Mediterranean occurrences to *P. michauxi* should be considered with caution (see below). As for *P. depereti*, the Dorkovo sample shares the same features with *P. michauxi*, i.e., oval-shaped anteroconid and metaconid, narrow protoisthmus and metaisthmus, presence of crochet on the p3. However, this species is different in having an anteroconid short and wide, as large as or even larger than the metaconid and stretched lingually as a pinched spur, an oblique mesoflexid, stronger protoconulid, a crochet rather central on the p3, P3 with a distally bent mesial hyperloph, P4 with U-shaped parafossette and mesofossette, and lack of the notch in the hypoflexid of lower molariforms.

Averianov and Tesakov (1998) described a new species, *Prolagus caucasicus*, from the early Pliocene Kosyakino

Quarry in the vicinity of Stavropol, Russia. The size of its cheek teeth is smaller than that of Dorkovo, and it differs in the morphology of p3 in having an elongated triangle occlusal outline, the metaconid pear shaped and the mesoflexid deep and distally oblique.

Angelone and Čermák (2015) reported a new species, *P. latiuncinatus*, from Polgardi 2 (Hungary, MN 13). Although the material of Dorkovo shares several characters with this species, in particular similar size, *P. latiuncinatus* is different in having on the p3 a large and drop-shaped crochet and oblique mesoflexid, U-shaped parafossette and mesofossette on the P4, and lack of the mesofossette on the molars.

Masini (1989) described from the Messinian locality of Monte Castellaro in Italy an articulated skeleton as a new species, *P. sorbinii*. Angelone (2007), Angelone and Cavallo (2010) and Angelone and Rook (2012) enriched this species by a new study of the type material and description of new specimens from several other Messinian localities in Italy. In this species, p3 has anteroconid labially indented, crochet variable in size and situated next to the metaisthmus rather than central (contrary to *P. michauxi*), metaconid sometime isolated, mesoflexid rather transverse (directed backward in *P. michauxi*), P4 with verticalized and long parafossette, M2 with a round and small mesofossette.

The material from some Greek and Turkish localities was ascribed to either *P. michauxi* (van de Weerd 1979, Daams and van de Weerd 1980, Sen et al. 1989, Vasileiadou et al. 2003, 2012) or to *P. cf. sorbinii* (De Bruijn 1995, Angelone 2007, Angelone and Čermák 2015). What is true is that *Prolagus* is frequent but not abundant in late Miocene – early Pliocene localities of SE Europe and Anatolia. Some records clearly recall *P. michauxi* while the others rather similar to the type material of *P. sorbinii*. However, in these SE European and Anatolian localities, the material is limited in number of specimens and does not provide statistically valuable characters for clear species identification. The samples from Kessani and Silata fit well with *P. michauxi*, as did Vasileiadou et al. (2003, 2012) in having on p3 a large anteroconid, strong protolophid and distally oriented deep mesoflexid and, on P3 anterior hyperloph distally bent. On the other hand, the material from Ptolemais 1 and Maramena rather agree in much characters with *P. sorbinii*: p3 with a rounded anteroconid which has a labial indentation or depression, not stretched labially as in *P. michauxi*, transverse mesoflexid, crochet situated next to metaisthmus, and P3 triangular shaped on the Ptolemais 1 specimen, but trapezoidal in outline with a mesial hyperloph distally bent at Maramena. This is also the case of the scarce sample from the early Pliocene locality of Develi in Western Anatolia (Sen et al. 1989).

Tesakov and Averianov (2002) referred to *P. sorbinii* the material from the early Pliocene localities of Grebeniki-2 and Novaya Andriashevka in Moldova. As in Maramena, the specimens from these localities display the features discussed above, and their attribution to this species is the best option in the context of our present knowledge on the distinctive morphological characters and limited number of specimens that prevent to evidence variation of these characters in a statistically significant population. The specimens from Dorkovo recall those of Grebeniki-2 (Tesakov and Averianov 2002: fig. 1). On the contrary, a few teeth that these authors reported from Novaya Andriashevka (Tesakov and Averianov

2002: fig. 2) are clearly different in having drop-shaped metaconid, crochet centrally situated and oblique mesoflexid on the p3 and distally bent mesial hyperloph on the P3.

As seen here above, the species identification of southeastern European and Anatolian occurrences of *Prolagus* is rather conflicting for the assemblages from latest Miocene and Pliocene localities. This is partly due to the limited number of specimens in each locality, but also to the definition of the already known and well-established species such as *P. michauxi* and *P. sorbinii*. For instance, for the p3, the most used tooth for species definition, no data exist on its ontogenetic and individual variations from its type locality or from a reference locality where it is well represented. In the present state of knowledge, morphological similarities in the characters of skull and dentition of *P. michauxi* and *P. sorbinii* are intriguing and led palaeontologists to assign samples from the same age and same region to *P. michauxi* or to *P. sorbinii*. This is particularly true for records from southeastern Europe. For instance, Vasileiadou et al. (2003, 2012) assigned to *P. michauxi* samples from the localities of Silata and Kessani 1 and 2, while De Bruijn (1995) referred to *P. cf. sorbinii* the material of Maramena. These localities are all situated in the Macedonian Greece, and their age is determined as near the Miocene/Pliocene boundary. Taking into account the description and illustrations given by these authors, the samples from all these localities have anteroconid round or ellipsoidal, not flattened and stretched as in *P. michauxi*, neither angular with a lingual depression as in *P. sorbinii*, metaconid round or drop shaped, mesoflexid oblique in some specimens but transverse in some others, and so. Indeed, the samples from these localities, as well as from the Moldavian localities (Tesakov and Averianov 2002) have intermediate morphologies recalling the one species by some characters or the other by some other characters.

Angelone and Sesé (2009) used several morphological and biometrical parameters to distinguish *Prolagus* species. On the palate, the size, position and shape of the premolar foramen is one of them. This foramen is small in early species, and becomes progressively large in some lineages. It is situated next to P4, rather close to the anterior or posterior loph. Its shape may be round as in early species of *Prolagus*, or oval as observed in many Plio-Pleistocene representatives. Based on this character, these authors distinguished two lineages. The one consists of *P. oeningensis* – *P. crusafonti* – *P. michauxi* – *P. calpensis*, while the second is specific to Italy with *P. sorbinii* – *P. italicus*. Such an assessment is not in agreement with our observations. In *P. michauxi* and *P. sorbinii* this foramen is similar in size, situated next to P4, a little distal on the type specimen of *P. michauxi* than that of *P. sorbinii*, but the variation of its position is not known due to the limited number of palate to observe the characteristics of this foramen, and its shape is oval in both cases. Similar examples can also be derived from the dentition, thus altogether making doubtful the allocation to a species the occurrences from outside of the “home country” of these species.

Family Leporidae FISCHER, 1817

Remarks. The two leporids of Dorkovo are similar in size. As the material consists of isolated teeth, distinction

of some teeth belonging to one or other of these species is a risky task. It is easy to distinguish the p3s and lower molariform teeth belonging to each species thanks to their difference of pattern: folded enamel along the distal margin of hypoflexid and mesoflexid on p3, and folded enamel on the lower molariforms in *Alilepus*, contra smooth enamel on both teeth in *Trischizolagus*. The distinction is much less obvious for the m3 and upper molariform teeth. For this reason, in many studies on fossil leporids, these teeth are neglected when the material consisted of isolated teeth. However, a close observation of discrete characters of the dental pattern and comparisons with diverse species of these genera for which these teeth are represented in complete tooth rows, it is possible to find some criteria to attribute these teeth to the one or the other of the Dorkovo leporids. From eight m3 of leporid from Dorkovo, no one has enamel plication as expected in a derived species of *Alilepus* DICE, 1931. This molar has a half-moon shaped trigonid and a rounded talonid. Despite this simple outline, it is possible to distinguish two morphotypes in the Dorkovo sample: the one with trigonid oblique and hypoflexid open angled, the second with trigonid transverse and hypoflexid narrow. The first morphotype is tentatively ascribed to *Alilepus* and the second to *Trischizolagus* in comparison with assemblages where this tooth is known as part of tooth rows. The distinction of P2 between *Alilepus* and *Trischizolagus* seems much less obvious when enamel is not folded (as seen in some occurrences of *Alilepus*), probably due to the progressive change of occlusal pattern from juvenile to senile individuals. The distinctive characters of these teeth, identified first in the present study, will be discussed in the related paragraphs.

Genus *Alilepus* DICE, 1931

Alilepus spassovi n. sp.

Text-fig. 4

H o l o t y p e. Left p3 (3.48 × 3.28), DKV-1333 (will be housed at the National Museum of Natural History, Sofia, Bulgaria).

O t h e r s p e c i m e n s. One fragmentary p3, three lower molariform teeth, two m3; five upper molariform teeth, all numbered as DKV-1334 to DKV-1347.

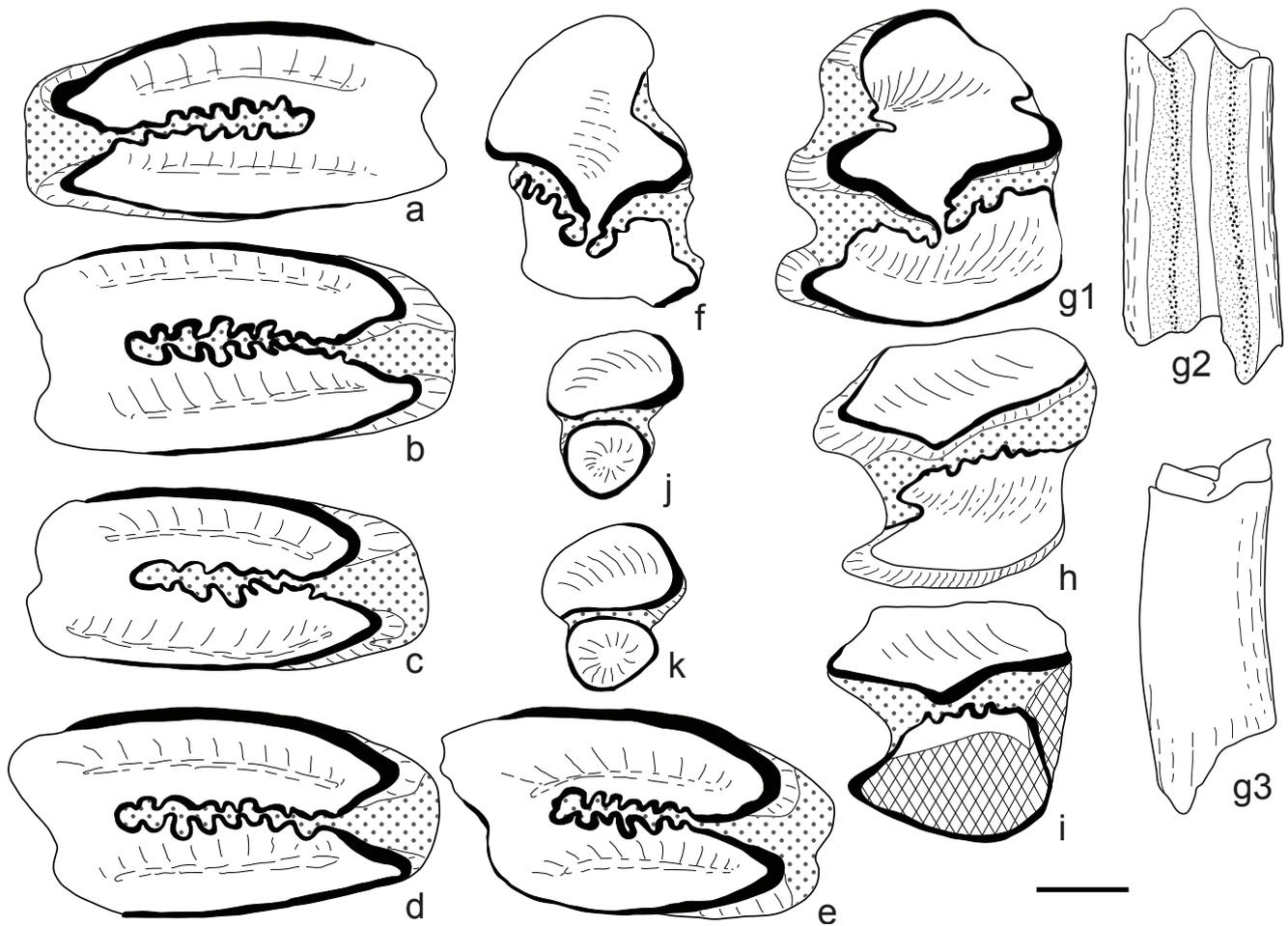
M e a s u r e m e n t s. See Table 2.

T y p e l o c a l i t y. Dorkovo, the Chepino Basin, southern Bulgaria, earliest Pliocene (MN 14).

E t y m o l o g y. Dedicated to Nikolai Spassov (National Natural History Museum, Sofia) who co-directed fieldwork at Dorkovo and greatly contributed to the knowledge of Neogene and Quaternary mammals and their environments in southeastern Europe.

D i a g n o s i s. Middle sized leporid; p3 with short protoflexid and paraflexid, anteroconid without anterior fold, enamel wrinkled along the distal walls of the hypoflexid and mesoflexid, but smooth on their mesial walls, upper molariform teeth with deep hypoflexus with mesial and distal enamel walls well crenulated.

D i f f e r e n t i a l d i a g n o s i s. This species differs from all species of *Pliopentalagus* by its smaller size, the



Text-fig. 4. *Alilepus spassovi* n. sp. from Dorkovo, Bulgaria. a) left molariform, possibly P4 (DKV-1347), b) right molariform, possibly P4 or M1 (DKV-1346), c) right molariform, possibly M1 (DKV-1345), d) right molariform, possibly M2 (DKV-1341), e) right molariform, possibly M2 (DKV-1342), f) fragment of right p3 (juvenile) (DKV-1334), g) left p3, holotype (DKV-1333) in occlusal (g1), labial (g2) and distal (g3) views, h) left lower molariform (DKV-1335), i) left lower molariform (DKV-1336), j) right m3 (DKV-1338), k) right m3 (DKV-1339). The teeth are oriented anterior upward. Scale bar represents 1 mm for occlusal views, 2 mm for labial and distal views.

lack of anterior fold on the trigonid, the shorter proto- and paraflexid, less crenulated enamel. It differs from most species of *Alilepus* in having strong enamel crenulation along the distal walls of hypo- and mesoflexid in lower cheek teeth, elongated trigonid on p3, deep hypoflexus on the upper molariform teeth and strong crenulation on its both walls.

Description. The shaft of p3 is curved lingually, and it may be very long (14.6 mm in DKV-1349). The occlusal surface displays equally deep hypoflexid and

mesoflexid which are directed backward. Between these flexids the isthmus connecting the trigonid to the talonid is narrow and rather oblique. Enamel is folded along the distal walls of hypoflexid and mesoflexid, more in the mesoflexid than in the hypoflexid, while along their mesial walls the enamel is smooth and thick. The protoflexid is short and wide (angle $> 90^\circ$) with one fold along its mesial margin. On the broken specimen, which apparently represent a younger individual, the protoflexid is wider than on the holotype, and enamel is smooth along its walls. The paraflexid is a tiny

Table 2. Measurements in millimetre of cheek teeth of *Alilepus spassovi* n. sp. from Dorkovo. N – number of measured specimens, Want – width of the anterior loph(id), Wpost – width of the posterior loph(id).

Tooth	N	Length		Want		Wpost	
		Range	Mean	Range	Mean	Range	Mean
p3	1	–	3.48	–	–	–	3.28
Lower molariforms	3	2.08–2.68	2.47	2.32–3.00	2.67	1.73–2.30	2.09
m3	2	1.81–1.89	1.85	1.48–1.86	1.67	0.91–0.92	0.92
Upper molariforms	8	2.14–2.35	2.26	3.51–4.25	3.89	3.12–4.25	3.67

fold filled with cement. The trigonid is twice longer than the talonid. The anteroconid is wide, inclined labially and lacks anteroflexid or any indentation.

The lower molariform teeth have talonid a little narrower than the trigonid. The enamel is well wrinkled along the mesial margin of the talonid. Labially, the hypoflexid is two folded due to the indentation of the talonid by a labial notch. The antero-external reentrant (AER) in p4–m2 sensu Tomida and Jin (2009) is missing.

Two m3 have been tentatively attributed to this species (see discussion below). This molar has a half-moon shaped trigonid and a rounded talonid. The trigonid is oblique and the hypoflexid has a V-shaped labial opening.

The P2 is not known. The upper cheek teeth ascribed to this species have deep hypoflexus with both enamel walls well wrinkled. The lingual opening of the hypoflexus is wide and V-shaped.

Comparison. This leporid from Dorkovo displays dental features of *Alilepus* DICE, 1931 and *Pliopentalagus* GUREEV et KONKOVA in GUREEV, 1964. *Alilepus* is one of the earliest leporid genera of the Old World where it appears at least during the early Turolian (Čermák et al. 2015), but known earlier in North America from the middle and late Miocene localities, before its dispersal toward the Old World (White 1991). Its type species *A. annectens* (SCHLOSSER, 1924) is from the latest Miocene of Ertemte in China.

The genus *Pliopentalagus* was first defined by Gureev and Konkova in Gureev (1964) with two species, *P. moldaviensis* (type species) from the Pliocene of Budei in Moldova and *P. dietrichi* (FEJFAR, 1961) from the early Pliocene locality of Ivanovce in Slovakia. *P. moldaviensis* is known with a fragmentary p3 and an upper molariform tooth. Daxner and Fejfar (1967) retained the genus name but synonymized this species with *P. dietrichi*, while Tomida and Jin (2009) and Čermák and Wagner (2013) recognize it as valid. In addition, four species from China were reported to *Pliopentalagus* (see below). Čermák and Wagner (2013) reviewed the European occurrences of *P. dietrichi*. The specimens from Dorkovo cannot be attributed to *P. dietrichi* because this species is clearly larger, and its p3 has an elongated anteroconid, anteroflexid, which lacks on the specimens from Dorkovo, and well-defined paraflexid. Out of Central Europe, *P. cf. dietrichi* was also mentioned from the early Pliocene locality of Dinar-Akçaköy in Turkey (Tobien 1974, Sickenberg et al. 1975). The Chinese species of *Pliopentalagus* are known from several late Miocene to early Pleistocene localities (Liu and Zheng 1997, Jin 2004, Tomida and Jin 2009). They are different from the Dorkovo specimens in being larger, and in having p3 with elongated anteroconid, deep anteroflexid, mesofossetid in place of mesoflexid (except in *P. progressivus* LIU et ZHENG, 1997 and some specimens of *P. anhuiensis* TOMIDA et JIN, 2009). *P. progressivus* from the late Pliocene or early Pleistocene of China (holotype) is represented by two isolated teeth from its type locality (karstic pits near Taizishan). It is distinguished from the other Pliocene species of the genus by larger measurements and deep folds on p3. In addition, in all Pliocene species from China, enamel is more wrinkled along the flexids and flexa, additional folds are frequent on the anteroconid of p3, and there is an antero-external reentrant in trigonids of p4–m2.

The genus *Alilepus* has a larger temporal and spatial distribution since it is reported from North America and all continents of the Old World between late Miocene and late Pliocene. The type species of *Alilepus*, *A. annectens* (SCHLOSSER, 1924), comes from Ertemte-2 in Inner Mongolia, China. Its p3 has an hour-glass shaped occlusal outline with a short trigonid, wide connection between the trigonid and talonid, without crenulation on the walls of hypo- and mesoflexid, and it lacks paraflexid on the trigonid. *A. longisinuus* QIU et HAN, 1986 from the hominoid locality of Lufeng in China is a species of the size of *A. annectens*, and with a similar p3 pattern, but in the Lufeng species the connection between the trigonid and talonid of p3 is weak or even absent, hence its species name. In this species as in *A. annectens*, the enamel is smooth on all lower cheek teeth and the hypoflexus is short and its walls are much less wrinkled on upper molariforms than in the Dorkovo specimens. Jin (2004) reported a new species, *A. lii*, from latest Miocene deposits of Laodong Cave in China, based on a single mandible fragment bearing p3–m1. The size of teeth is slightly larger than the Dorkovo leporid. The mesial enamel band of talonid is crenulated in all teeth, a character shared with the Dorkovo leporid. However, this species is different in having the trigonid less elongated and connected to the talonid by a large isthmus, and all lower teeth lacking labial indentation on the talonid.

Wu and Flynn (2017) described a new species, *A. parvus*, from a horizon dated between 6–6.5 Ma in the Yushe Basin (China). On the p3 the trigonid is somewhat elongated, but much less than on the p3 from Dorkovo; enamel is smooth along the flexids and flexa of lower and upper cheek teeth.

Čermák et al. (2015) give a complete account of the European species of *Alilepus*. They recognized five species, lasting in time from MN 10/11 (the localities of Palievo in Ukraine and Kainar in Moldova) to MN 15b (Odessa Catacombs). These species are *A. laskarewi* (KHOMENKO, 1914), *A. hungaricus* KORMOS, 1934, *A. ucrainicus* GUREEV, 1964, *A. turolensis* LÓPEZ MARTÍNEZ, 1977 and *A. meini* ANGELONE et ROOK, 2011. All these species are from the late Miocene (Turolian), except *A. ucrainicus* which is known in some early Pliocene localities of Odessa Catacombs (type locality). *Pratilepus ucrainicus* TOPACHEVSKI, 1980 from the early Pliocene of Kuchurgan deposits (Ukraine) is a junior synonyme of *Trischizolagus dumitrescuae* RADULESCO et SAMSON, 1967, as shown by Averianov and Tesakov (1997).

In some European species, e.g., *A. laskarewi*, *A. ucrainicus* and *A. tuoliensis*, Čermák et al. (2015) noted discrete undulations or even crenulations of enamel along the distal walls of hypoflexid and mesoflexid, mainly visible in juvenile individuals. However, there is no European *Alilepus* having strong crenulations on lower cheek teeth as on the specimens of Dorkovo. In addition, in all these European species, the trigonid of p3 is short, the paraflexid is absent or barely represented by a shallow depression (*A. ucrainicus*), the hypoflexus of upper cheek teeth is shorter, and on the upper molariform teeth enamel crenulation along the mesial and distal walls of hypoflexus is much less expressed than at Dorkovo.

Among the European species of *Alilepus*, *A. tuoliensis* has the largest spatial dispersal during the late Miocene (middle and late Turolian, MN12 and MN 13). Its type

locality is Arquillo in Spain. It was reported from several other localities in Spain, Italy, Greece and Turkey. In the youngest representatives of this species, the trigonid of p3 is somewhat elongated, and some tenous enamel undulations may occur along the distal wall of its hypo- and mesoflexid (e.g., Arquillo), although nothing comparable to that of the Dorkovo leporid. In addition, the p3 of this species has a narrow protoflexid and large isthmus between the trigonid and talonid.

The specimens from Dorkovo are better compared with *A. elongatus* WINKLER, FLYNN et TOMIDA, 2011 from the late Miocene (ca. 6.6–7.2 Ma) of the Siwaliks of Pakistan. They share several characters such as enamel wrinkled along the anterior margin of talonid in lower cheek teeth, the p3 with an elongated trigonid, the presence of paraflexid, P3 and P4 with a deep hypoflexus having walls well crenulated. One can wonder if this species fits with the diagnostic features of *Alilepus* (see White 1991: 69), or rather it deserves to be distinguished as a new genus. That said, it is different from the Dorkovo leporid in having a narrow anteroconid, rather transverse or slightly oblique hypo- and mesoflexid, an anterolabial indentation on some lower molariforms. Unfortunately, this species is poorly documented to allow further comparison.

Winkler (2003) and Winkler et al. (2011) reported two p3 from the late Miocene of Tugen Hills and Lothagam in Kenya, identified as *Alilepus* sp. These are similar in pattern to that of the Dorkovo specimens but much larger in size.

In summary, the leporid under study from Dorkovo cannot fit with any so far known species of *Alilepus*, although it share some typical characters with *A. elongatus* of Siwaliks,

A. lii from China and *Alilepus* sp. from Kenya, in addition to its similarities in the degree of enamel plication with the early species of *Pliopentalagus*. For all these reasons, the specimens from Dorkovo cannot be ascribed to any known species of *Alilepus*, and they are referred to a new species, *A. spassovi* n. sp.

Genus *Trischizolagus* RADULESCO et SAMSON, 1967

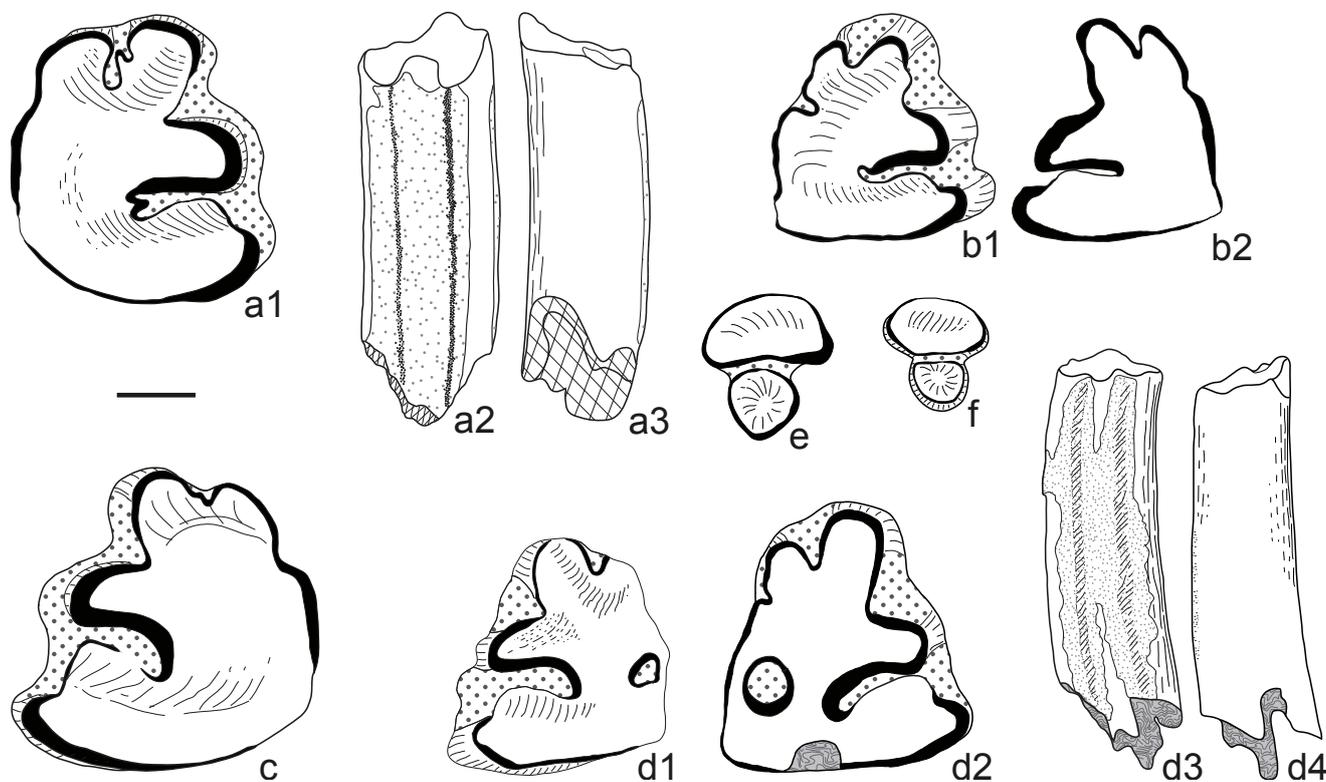
Trischizolagus crusafonti (JANVIER et MONTENAT, 1971)

Text-figs 5, 6

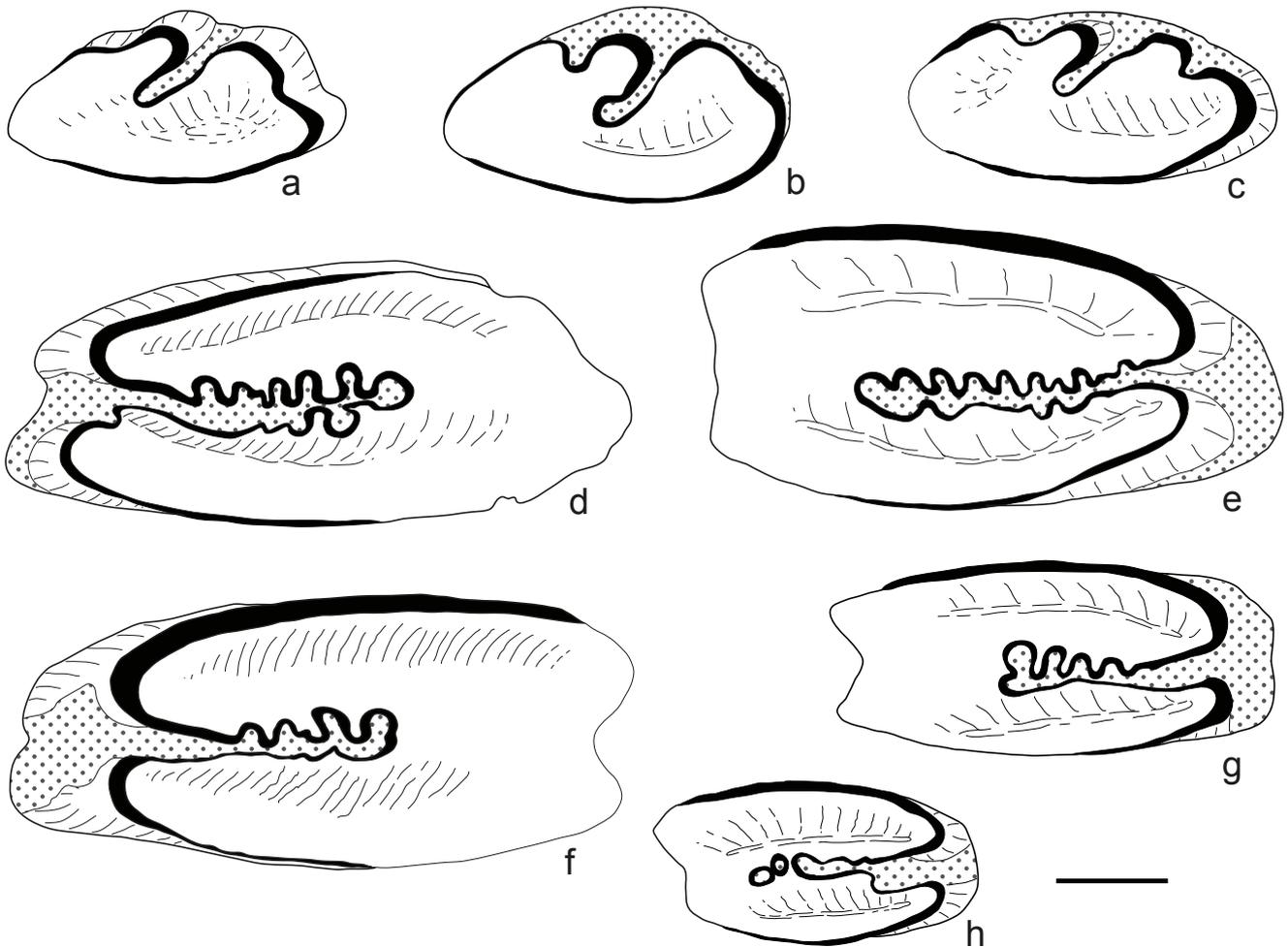
Material from Dorkovo. Four p3 (DKV-1348–1351), eight lower molariform teeth (DKV-1352–1359), six m3 (DKV-1360–1365), three P2 ((DKV-1366–1368), two P3 (DKV-1369–1370), seven P4 or M1 (DKV-1371–1377) two M2 (DKV-1378–1379), eleven fragmentary upper molariform teeth (DKV-1380–1390), seven upper (DKV-1391–1397) and ten lower incisors (DKV-1398–1407). Some of these incisors may well belong to *Alilepus*, but the distinction is not clear due to the lack of comparative data.

Measurements. See Table 3.

Description. There are four p3, belonging to two juvenile and two adult individuals. The occlusal outline is round in adult p3, but rather trapezoidal in juvenile specimens. The hypoflexid almost reaches the half width, enamel is smooth and thin along its distal wall and thick along its mesial wall. Only one specimen has a mesofossette all along the shaft, the other specimens lack mesoflexid or mesofossette. The protoflexid is right angled and filled with cement. The paraflexid is a short groove (2/4) or



Text-fig. 5. *Trischizolagus crusafonti* from Dorkovo, Bulgaria; lower cheek teeth. a) right p3 (DKV-1348) in occlusal (a1), labial (a2) and distal (a3) views, b) right p3 (DKV-1351) in occlusal (b1) and root side (b2) views, c) left p3 (DKV-1349), d) left p3 (DKV-1350) in occlusal (d1), root side (d2), labial (d3) and distal (d4) views, e) right m3 (DKV-1361), f) left m3 (DKV-1362). The teeth are oriented anterior upward. Scale bar = 1 mm for occlusal views, and 2 mm for labial and distal views.



Text-fig. 6. *Trischizolagus crusafonti* from Dorkovo, Bulgaria; upper cheek teeth in occlusal view. a) right P2 (DKV-1368), b) right P2 (DKV-1366), c) right P2 (DKV-1367), d) left P3 (DKV-1370), e) right P4 or M1 (DKV-1373), f) left P4 or M1 (DKV-1374), g) right P4 or M1 (DKV-1376), h) right M2 (DKV-1377). The teeth are oriented anterior upward. Scale bar = 1 mm.

a wide depression. The anteroflexid is simple, except in one specimen it bears an extra fold. It divides the anterior lobe in two unequal parts, the labial one being longer and broader than the lingual one. The lower molariform teeth have a deep hypoflexid and a thin enamel connection between trigonid and talonid on the lingual side. The m3 has a half-moon shaped trigonid and a round talonid.

Three P2 are referred to this species. The adult one (Text-fig. 6c) has three flexa of which the paraflexus is the deepest, while the hypoflexus and mesoflexus are shallow,

or even represented by a depression. The P3, P4 and M1 are similar in size in adult individuals while the M2 is smaller. The hypoflexus is deep in P3 and P4, extending on about 2/3 of the width, while in M1 and M2 its depth is about half width. Enamel is well crenulated along its anterior wall, but much less along its posterior wall. The degree of enamel crenulation decreases from P3 to M2.

C o m p a r i s o n. The size, the tree-fold trigonid of p3, lack of crenulation of enamel, the general pattern of lower

Table 3. Measurements in millimetre of cheek teeth of *Trischizolagus* sp. from Dorkovo. N – number of measured specimens, Want – width of the anterior loph(id), Wpost – width of the posterior loph(id).

Tooth	N	Length		Want		Wpost	
		Range	Mean	Range	Mean	Range	Mean
p3	4	2.58–3.60	3.14	–	–	2.53–3.91	3.11
Lower molariforms	6	2.51–2.90	2.67	2.31–3.36	3.02	2.42–2.64	2.49
m3	6	1.37–1.89	1.75	1.48–1.86	1.56	0.73–1.05	0.93
P2	3	1.49–1.55	1.53	2.89–3.07	2.96	–	–
P3	2	1.62–2.44	2.03	3.56–4.48	4.02	–	–
P4, M1	7	1.86–2.70	2.14	3.29–4.85	3.9	3.28–4.61	3.9
M2	2	1.53–2.09	1.81	2.67–3.87	3.27	2.23–3.41	2.82

and upper cheek teeth clearly support assignment of these specimens to the genus *Trischizolagus*. Čermák and Wagner (2013) presented a complete review of the species included in this genus and recognized six species: *T. dumitrescuae* RADULESCO et SAMSON, 1967, the type species, *T. crusafonti* (JANVIER et MONTENAT, 1971), *T. maritsae* DE BRUIJN, DAWSON et MEIN, 1970, *T. gambariani* (MELIK-ADAMYAN, 1986), *T. nihewanensis* (CAI, 1989), *T. mirificus* QIU et STORCH, 2000, and with a question mark *T. raynali* (GERAADS, 1994). Among these species, *T. nihewanensis* was initially referred to *Pliopentalagus* (one p3) because of its elongated trigonid and crenulated enamel walls of hypo- and mesoflexid. Tomida and Jin (2005) transferred it to *Trischizolagus*; they estimated that its less complicated pattern compared to other species of *Pliopentalagus*, despite its younger age, does not fit the evolutionary trend of this genus, and they considered it as a derived species of *Trischizolagus*. Anyway, the pattern of its p3, single tooth known, is different from those of Dorkovo, and thus it does not deserve further comparison.

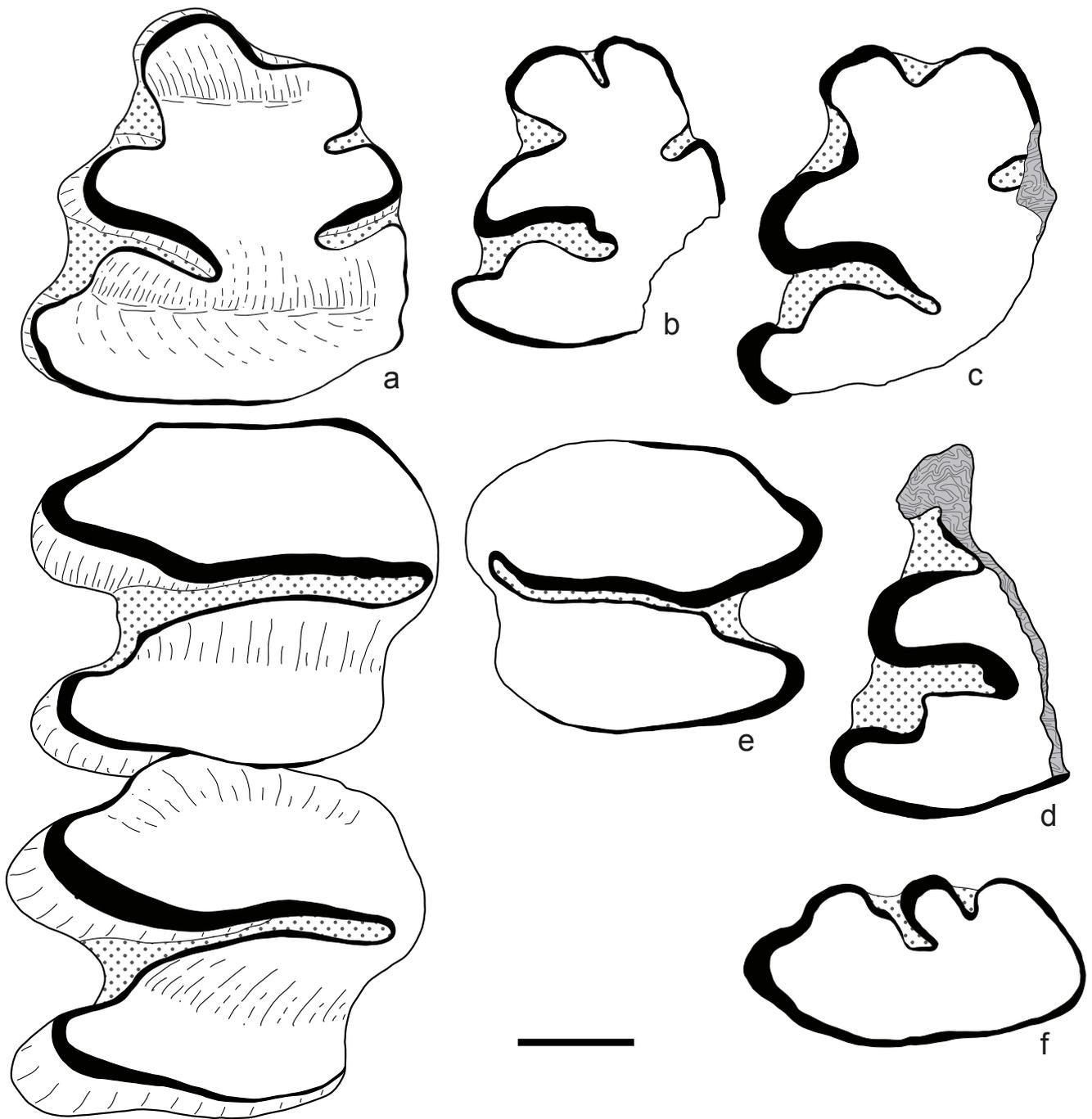
The other Chinese species *T. mirificus* is intermediate in size between the larger *T. dumitrescuae* and the smaller *T. maritsae* (Qiu and Storch 2000). Its p3 dominantly displays the “*Hypolagus* pattern”, i.e., the lack of mesoflexid in 50 % of specimens or its presence as a weak furrow in 27 % of p3s. The specimens from Dorkovo are a little larger than the measurements given by Qiu and Storch (2000). In *T. mirificus* the anteroconid of most p3 is not well defined due to the lack of shallowness of the anteroflexid. Despite these differences, *T. mirificus* shares several characters with the Dorkovo leporid, such as the lack of mesoflexid in most specimens, the pattern of P2 with well-defined paraflexus but mesoflexus and hypoflexus weak or absent, and smaller size compared to *T. dumitrescuae*.

The size is not an easy criterion to handle for species distinction. Averianov and Tesakov (1997: fig. 6) plotted on a diagram the length and width of p3 from all localities where *Trischizolagus* was known at that time. They observed a gradual size increase from the early to late Ruscinian and large overlap between the specimens referred to different species. They concluded (p. 149) that “this broad overlap of samples of different age allows us to ascribe all the material to the single species, *T. dumitrescuae*.” This statement was not followed by later students who recognized several species mainly based on the pattern of p3. As noted above, five to six species were assigned to this genus. In eastern and south-eastern Europe, the oldest known species is *T. maritsae* from Rhodos Island in Greece, which was defined from a limited number and mostly damaged specimens. The type mandible is useless to show the pattern of p3. From the other three p3, the one is an unworn juvenile, and the two others probably adult. The range of their length × width is 1.8–2.7 × 2.0–2.8 mm. The size of p3 as well as of the other teeth makes that *T. maritsae* is the smallest species referred to this genus, and out of the range of specimens from Dorkovo. One p3 of Maritsa has a well-defined mesoflexid, and the paraflexid is a deep fold. In all these characters the sample of Dorkovo cannot be assigned to *T. maritsae*. Out of its type locality, López Martínez (1989) and Piñero et al. (2017) tentatively referred to this species some scarce remains of leporids from several early Pliocene localities in Spain.

T. dumitrescuae RADULESCO et SAMSON, 1967 is well known from its type locality Malusteni, and also from the neighbour locality Beresti in Romania (Radulesco and Samson 1967, 1995, Daxner and Fejfar 1967) (Text-fig. 7a). In addition, it was reported from about 15 localities in the regions between southern Hungary, southern Ukraine and northern Greece (see map of distribution in Čermák and Wagner 2013: fig. 3), and even from northern China as *Trischizolagus* aff. *dumitrescuae* (Wu and Flynn 2017). All these localities are correlated to early Pliocene, i.e., MN 14 and MN 15 (Koufos and Koliadimou 1993, Averianov 1995, Radulesco and Samson 1995, Averianov and Tesakov 1997, 1998, Čermák and Wagner 2013). The dimensions of teeth from Dorkovo are smaller than that of *T. dumitrescuae* from its type locality Malusteni (Romania), also smaller than that of Beresti (Radulesco and Samson 1995), but in the range of variation of the specimens from Muselievo (Bulgaria; Popov 2004). On the p3 of this species, the trigonid is notched on its labial, mesial and lingual sides. In addition, a deep hypoflexid and a moderately deep mesoflexid separate the trigonid from the talonid. The mesoflexid is a variable structure in different species of *Trischizolagus* and its frequency is used as an important criterion for species distinction. Radulesco and Samson (1995) provided the ratio of morphotypes on a sample of 65 specimens from Beresti: mesoflexid open (59 %), enamel lake (32 %), open but becomes enamel lake at the base of the crown (6 %) and absent (3 %). Averianov and Tesakov (1997) distinguished three morphotypes of p3: *Alilepus*, *Nekrolagus* and *Hypolagus* morphotypes. This division is based on the shape or absence of the mesoflexid. In the first morphotype (*Alilepus*) the p3 has an open mesoflexid, in the second (*Nekrolagus*) there is a mesofossette in place of mesoflexid, and in the third morphotype this structure is absent. In all localities with *Trischizolagus dumitrescuae*, the “*Alilepus* pattern” dominates, followed by the “*Nekrolagus* pattern”. The “*Nekrolagus* pattern” is better represented in *T. gambariani* (MELIK-ADAMYAN, 1986) from Nurnus (Armenia) and Tepe Alagöz (Turkey), while the “*Hypolagus* pattern” in the specimens referred to *T. crusafonti* (JANVIER et MONTENAT, 1971) from Spain.

T. gambariani is similar in size, according to the measurements taken on illustrations of Melik-Adamyan (1986) and the measurements given by Čermák et al. (2019), to the specimens of Dorkovo. The p3 of this species has almost exclusively the “*Nekrolagus* pattern”, which is not the case in Dorkovo. In other characters of lower and upper cheek teeth, we did not observe any reliable differences.

T. crusafonti was defined from the latest Miocene (MN 13) locality of La Alberca in the Fortuna Basin, southern Spain, and Janvier and Monténat (1971) attributed it to a new genus *Hispanolagus*. López Martínez (1989: 202–203) re-evaluated the characters of the specimens from La Alberca and she concluded that “both p3 of *T. crusafonti* fall within the diagnosis of the genus *Trischizolagus* RADULESCO et SAMSON, 1967, and consequently *Hispanolagus* JANVIER et MONTENAT, 1971, should be considered synonymous with *Trischizolagus*, which has priority. *T. dumitrescuae* differs from *T. crusafonti* by its greater size and the frequent presence of mesoflexid or mesofossette”. When I studied leporids of Afghanistan in early 1980s (Sen 1983), I also examined



Text-fig. 7. Comparison of *Trischizolagus dumitrescuae* from Malusteni (Romania) and *T. crusafonti* from La Alberca (Spain). a) left p3–m1 of *T. dumitrescuae* (I. S. 6002), paratype, collections of Institutul de Speleologie Emil Racovita, Bucarest, Romania; b–f) *T. crusafonti* from La Alberca, Collections of Institut Català de Paleontologia Miquel Crusafont, Sabadell, Spain: b) left p3, n° 14, holotype, c) left p3, n° 15, d) labial part of left p3, unnumbered, e) right molariform tooth, n° 16, f) left P2, n° 2, paratype. The teeth are oriented anterior upward. Scale bar = 1 mm.

the specimens of La Alberca and made some drawings (Text-fig. 7b–f). These illustrations are somewhat different from that of Janvier and Monténat (1971). Philippe Janvier (personal communication on February 27, 2019) taught me that he used an old camera lucida to draw the teeth from La Alberca and that his drawings may have suffered in quality. In return, his measurements are perfectly in line with the one I made on these specimens. As seen in Text-fig. 7, the p3 of *T. crusafonti* from La Alberca has a deep hypoflexid that reaches the half width of the occlusal surface and it is curved backward in variable amount depending on specimens. The

two p3 that partly preserved the lingual part do not display any trace of mesoflexid or mesofossette (*Hypolagus* pattern of Averianov and Tesakov 1997). The re-entrant folds of the trigonid are moderately deep. The P2 has a deep paraflexus, not double-folded as Janvier and Monténat (1971: figs 1, 2) have illustrated, a shallow mesoflexus, and the hypoflexus as a wide depression. The adult P2 DKV-1367 from Dorkovo (Text-fig. 6c) shows an occlusal pattern very similar to this P2 of La Alberca. In all these characters the specimens of Dorkovo fit *T. crusafonti*.

Conclusions

The locality of Dorkovo in southern Bulgaria yielded four species of lagomorphs as evidenced by the present study: *Ochotona* cf. *antiqua*, *Prolagus sorbinii*, *Alilepus spassovi* n. sp. and *Trischizolagus crusafonti*. Such a lagomorph diversity in late Miocene and Pliocene localities is exceptionally encountered. This reflects the diversity and dynamics of lagomorphs around the Miocene/Pliocene boundary, particularly in eastern Europe, which is a transitional region between east and west.

The age of Dorkovo fauna was discussed by Delson et al. (2005). This locality yielded, in addition to the lagomorphs, rodents and insectivores, the following large mammals: *Dolichopithecus ruscinensis* DEPÉRET, 1889, *Mesopithecus monspessulanus* (GERVAIS, 1849), *Ursus* ex gr. *ruscinensis* DEPÉRET, 1890, Mustelidae indet., Hyaenidae indet. (size of *Chasmaporthetes* HAY, 1921), *Anancus arvernensis* (CROIZET et JOBERT, 1828), *Mammut borsoni* (HAYS, 1834), Cervidae indet., Suidae indet., Bovidae indet., *Stephanorhinus megarhinus* (DE CHRISTOL, 1834) and *Hipparion crassum* DEPÉRET, 1890 (Thomas et al. 1986a, b, Metz-Muller 1995, 2000, Alberdi and Alcalá 1999, Spassov 2003, 2005, Delson et al. 2005). All these authors conclude to its early Pliocene age (early Ruscinian, MN 14). Among the lagomorphs of Dorkovo, *Ochotona* cf. *antiqua* is a common element of Ruscinian faunas of south-eastern Europe, and it is best represented in early Ruscinian localities. *Prolagus sorbinii* was initially defined from the latest Turolian of Italy (Masini 1989, Angelone 2007, Angelone and Cavallo 2010, Angelone and Rook 2012). This species (or similar forms) from northern Greece, Moldova and Turkey was also reported by De Bruijn (1995), Tesakov and Averianov (2002) and Sen et al. (2019), in localities correlated to the Miocene/Pliocene transition (Maramena in Greece, Kale Tepe-2 in Turkey) or to the early Pliocene (Grebeniki-2 in Moldova, Develi in Turkey). The genus *Alilepus* is known in Europe in late Miocene and early Pliocene localities, as well as in China, Pakistan and East Africa. The latter lagomorph of Dorkovo was referred to *Trischizolagus crusafonti*, a species only recorded in its type locality La Alberca in Spain, which is correlated to the latest Messinian thanks to marine-continental correlations (Mein et al. 1973, De Bruijn et al. 1975). Its presence in Dorkovo could suggest an older age, close to the Miocene/Pliocene transition. However, the lack of knowledge on the spatial and temporal distribution of this species and its relationships with other species does not allow affirming that the Dorkovo assemblages may be anterior to the Miocene/Pliocene boundary. In summary, the available data suggest a basal Pliocene age, close to 5 Ma.

Evolutionary trends of leporid tooth pattern are debated at least since Dice (1929). Several lagomorph students proposed hypothesis to explain morphological changes in dentition, in particular in the pattern of p3, and they suggested lineages taking into account the trends of morphological changes. What is also true is that the p3, and in some extent the other teeth, show ontogenetic and individual variations, and the same assemblage may display several morphotypes although in different rates. It is out of the aim of the present study to enlarge this debate. The description

of the two species of leporids from Dorkovo, although limited in number of specimens, brings some elements to this issue. *Alilepus spassovi* n. sp. is one of the youngest representatives of its genus, and its cheek teeth have enamel much more crenulated than the older representatives of this genus, thus indicating that the increase of enamel infolding is an evolutionary trend, at least in the lineage to which this genus belongs. This species is also characterized by its larger size compared to other species of *Alilepus*, more stretched trigonid of p3, and the lack of its anteroflexid. In derived species of *Alilepus*, the p3 is shorter, and in particular infolding of enamel is absent or tenuous. In these respects, with its larger size, more crenulated cheek teeth and the lack of anteroflexid on p3, *A. spassovi* n. sp. of Dorkovo appears to be a younger representative of this genus.

Dorkovo is the first earliest Pliocene locality of Bulgaria with a rich mammalian assemblage. This country and the surrounding regions are of great interest for mammalian dispersals at the Miocene/Pliocene transition. My greatest wish is the development of multidisciplinary palaeontological research in this region to increase the data allowing to better understand the diversity crisis experienced by mammalian faunas around the Miocene/Pliocene boundary.

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References

- Agadjanian, A. K., Erbajeva, M. A. (1983): Pozdnekaynozozskie gryzuny i zaytseobraznye territorii SSSR [Late Cenozoic rodents and lagomorphs of the USSR]. – Nauka, Moscow, 189 pp. (in Russian)
- Alberdi, M. T., Alcalá, L. (1999): A study of the new samples of the Pliocene *Hipparion* (Equidae, Mammalia) from Spain and Bulgaria. – Transactions of the Royal Society of Edinburgh, Earth Sciences, 89: 167–186. <https://doi.org/10.1017/S0263593300007112>
- Angelone, C. (2007): Messinian *Prolagus* (Ochotonidae, Lagomorpha) of Italy – Geobios, 40: 407–421. <https://doi.org/10.1016/j.geobios.2006.04.004>
- Angelone, C., Cavallo, O. (2010): A new look to *Prolagus* (Ochotonidae, Lagomorpha) from the late Messinian of Ciabòt Cagna (Piedmont, NW Italy). – Rivista Italiana

- di Paleontologia e Stratigrafia (Research in Paleontology and Stratigraphy), 116(2): 267–270.
<https://doi.org/10.13130/2039-4942/5954>
- Angelone, C., Čermák, S. (2015): Two new species of *Prolagus* (Lagomorpha, Mammalia) from the late Miocene of Hungary: taxonomy, biochronology, and palaeobiogeography. – *Paläontologische Zeitschrift*, 89(4): 1023–1038.
<https://doi.org/10.1007/s12542-014-0247-z>
- Angelone, C., Prieto, J., Gross, M. (2014): Complement to the study of the pikas (Lagomorpha, Ochotonidae) from the middle Miocene of Gratkorn, Austria. – *Palaeobiodiversity and Palaeoenvironments*, 94(1): 125–134.
<https://doi.org/10.1007/s12549-013-0146-4>
- Angelone, C., Rook, L. (2011): *Alilepus meini* n. sp. (Palaeolaginae, Leporidae, Lagomorpha), a new leporid from the early Messinian of Tuscany (central-western Italy). – *Geobios*, 44: 151–156.
<https://doi.org/10.1016/j.geobios.2010.11.003>
- Angelone, C., Rook, L. (2012): Late Neogene and Quaternary lagomorphs from Tuscany: a revision based on specimens in Basel Naturhistorisches Museum and Florence University collections. – *Swiss Journal of Palaeontology*, 131(1): 127–145.
<https://doi.org/10.1007/s13358-011-0035-2>
- Angelone, C., Sesé, C. (2009): New characters for species discrimination within the genus *Prolagus* (Ochotonidae, Lagomorpha, Mammalia). – *Journal of Paleontology*, 83(1): 80–88.
<https://doi.org/10.1666/07-067R2.1>
- Argyropulo, A. I., Pidoplichko, I. G. (1939): Predstaviteli Ochotonidae (Duplicidentata, Mammalia) v pliocene SSSR [Representatives of Ochotonidae (Duplicidentata, Mammalia) in the Pliocene of the USSR]. – *Doklady Akademii nauk SSSR*, 24(7): 723–728. (in Russian)
- Averianov, A. O. (1995): Osteology and adaptations of the early Pliocene rabbit *Trischizolagus dumitrescuae* (Lagomorpha; Leporidae). – *Journal of Vertebrate Paleontology*, 15: 375–386.
<https://doi.org/10.1080/02724634.1995.10011236>
- Averianov, A. O., Tesakov, A. S. (1997): Evolutionary trends in Mio-Pliocene Leporinae, based on *Trischizolagus* (Mammalia, Lagomorpha). – *Paläontologische Zeitschrift*, 71: 145–153.
<https://doi.org/10.1007/BF03022556>
- Averianov, A. O., Tesakov, A. S. (1998): The Lagomorpha (Mammalia) from the early Pliocene Kosyakino locality of the Northern Caucasus. – *Paleontological Journal*, 32: 91–96.
- Bendukidze, O. G., de Bruijn, H., van den Hoek Ostende, L. W. (2009): A revision of late Oligocene associations of small mammals from the Aral Formation (Kazakhstan) in the National Museum of Georgia, Tbilisi. – *Palaeodiversity*, 2: 343–377.
- Boev, Z. (1998): Fossil birds of Dorkovo: an Early Pliocene site in the Rhodope Mts. (Southern Bulgaria). – *Geologica Balcanica*, 28: 53–60.
- Brandt, J. F. (1855): Beiträge zur näheren Kenntniss der Säugethiere Russlands. – *Mémoire de l'Académie impériale des Sciences, St. Petersburg, Physique, Mathématique et Naturalistique*, 6(9): 1–365.
- Cai, B. (1989): Fossil lagomorphs from the late Pliocene of Yangyuan and Yuxian, Hebei. – *Vertebrata Palasiatica*, 27: 170–181.
- Croizet, J. B., Jobert, A. (1828): Recherches sur les ossements fossiles du département du Puy-de-Dôme. – Dufour et Docagne, Paris, 224 pp.
- Čermák, S. (2004): A new ochotonid (Lagomorpha) from the Early Pleistocene of Slovakia. – *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 2004(11): 662–680.
<https://doi.org/10.1127/njgpm/2004/2004/662>
- Čermák, S., Angelone, C., Sinitsa, 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.
<https://doi.org/10.3140/bull.geosci.1523>
- Čermák, S., Joniak, P., Rojaj, B. (2019): A new early Pliocene locality Tepe Alagöz (Turkey) reveals a distinctive tooth phenotype of *Trischizolagus* (Lagomorpha, Leporidae) in Asia Minor. – *Palaeontologia Electronica*, 22.1.14A: 1–21.
<https://doi.org/10.26879/924>
- Čermák, S., Rekovets, L. I. (2010): Early Pliocene ochotonids (Mammalia, Lagomorpha) from Southern Ukraine. – *Geodiversitas*, 32(1): 107–120.
<https://doi.org/10.5252/g2010n1a3>
- 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(1): 97–111.
<https://doi.org/10.1127/0077-7749/2013/0321>
- Daams, R., van de Weerd, A. (1980): Early Pliocene small mammals from the Aegean island of Karpathos (Greece) and their palaeogeographic significance. – *Geologie en Mijnbouw*, 59: 327–331.
- Dawson, M. R. (1959): *Paludotona etruria*, a new ochotonid from the Pontian of Tuscany. – *Verhandlungen der Naturforschenden Gesellschaft in Basel*, 70(2): 157–166.
- Dawson, M. R. (2008): Lagomorpha. – In: Janis, C. M., Gunnell, G. F., Uhen, M. D. (eds), *Evolution of Tertiary mammals of North America. Volume 2: Small mammals, xenarthrans, and marine mammals*. Cambridge University Press, New York, pp. 293–310.
<https://doi.org/10.1017/CBO9780511541438.018>
- Daxner, G., Fejfar, O. (1967): Über die Gattungen *Alilepus* DICE, 1931 und *Pliopentalagus* GUREEV, 1964 (Lagomorpha, Mammalia). – *Annalen des Naturhistorischen Museums Wien*, 71: 37–55.
- De Bruijn, H. (1995): 11. Lagomorpha (Mammalia). – In: Schmidt-Kittler, N. (ed.), *The vertebrate locality Maromena (Macedonia, Greece) at the Turolian-Ruscinian boundary (Neogene)*. – *Münchener Geowissenschaftliche Abhandlungen, A*, 28: 87–102.
- De Bruijn, H., Dawson, M. R., Mein, P. (1970): Upper Pliocene Rodentia, Lagomorpha and Insectivora (Mammalia) from the Isle of Rhodes (Greece). – *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, B*, 73(5): 535–584.

- De Bruijn, H., Mein, P., Montenat, C., van de Weerd, A. (1975): Corrélations entre les gisements de rongeurs et les formations marines du Miocène terminal d'Espagne méridionale. I. (Provinces d'Alicante et Murcia). – Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, B, 78(4): 1–32.
- De Christol, J. (1834): Recherches sur les caractères des grandes espèces de Rhinocéros fossiles. – Jean Martel aîné, Montpellier, 70 pp.
<https://doi.org/10.5962/bhl.title.16189>
- Delson, E., Thomas, H., Spassov, N. (2005): Fossil Old World monkeys (Primates, Cercopithecidae) from the Pliocene of Dorkovo, Bulgaria. – Geodiversitas, 27(1): 159–166.
- Depéret, C. (1889): Sur le *Dolichopithecus rusciniensis*, nouveau singe fossile du Pliocène du Roussillon. – Comptes Rendus hebdomadaires des séances de l'Académie des Sciences, 109(26): 982–983.
<https://doi.org/10.5962/bhl.part.7904>
- Depéret, C. (1890): Les animaux pliocènes du Roussillon. – Mémoires de la Société géologique de France, 3: 7–195.
- Dice, L. R. (1929): The phylogeny of the Leporidae, with the description of a new genus. – Journal of Mammalogy, 10: 340–344.
<https://doi.org/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.
<https://doi.org/10.2307/1373916>
- Erbajeva, M. A. (1988): Pishchukhi kaynozoya (taksonomiya, sistematika, filogeniya) [Cenozoic Pikas (Taxonomy, Systematics, Phylogeny)]. – Nauka, Moscow, 224 pp. (in Russian)
- Erbajeva, M. A. (1994): Phylogeny and evolution of Ochotonidae with emphasis on Asian ochotonids. – In: Tomida, Y., Li, C. K., Setoguchi, T. (eds), Rodent and Lagomorph Families of Asian Origins and Diversification. National Science Museum Monographs, Tokyo, 8: 1–13.
- Erbajeva, M. A. (2005): New late Pliocene pika (Lagomorpha, Mammalia) from Germany. – Paleontological Journal, 3: 91–93.
- Erbajeva, M. A., Montuire, S., Chaline, J. (2001): New ochotonids (Lagomorpha) from the Pleistocene of France. – Geodiversitas, 23(3): 395–409.
- Erbajeva, M. A., Shushpanov, K. I. (1988): Pliotsenovy pishchukhi Moldavii [The Pliocene pikas of Moldavia]. – Vestnik zoologii, 4: 55–60. (in Russian)
- 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.
- Fischer, G. (1817): Adversaria zoologica, fasciculus primus. – Mémoires de la Société impériale des Naturalistes de Moscou, 5: 357–428.
- Fostowicz-Frelik, Ł. (2008): Review of the earliest Central European *Ochotona* (Mammalia: Lagomorpha), with description of a new species from Poland. – Mammalia, 72: 71–81.
<https://doi.org/10.1515/MAMM.2008.011>
- Fostowicz-Frelik, Ł., Frelik, G. J., Gasparik, M. (2010): Morphological phylogeny of pikas (Lagomorpha: *Ochotona*), with a description of a new species from the Pliocene/Pleistocene transition of Hungary. – Proceedings of the Academy of Natural Sciences of Philadelphia, 159: 97–118.
<https://doi.org/10.1635/053.159.0107>
- Geraads, D. (1994): Rongeurs et Lagomorphes du Pléistocène moyen de la “Grotte des Rhinocéros”, carrière Oulad Hamida 1, à Casablanca, Maroc. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 191:147–172.
- Gervais, P. (1849): Zoologie et Paléontologie Françaises, Volume 1. – Arthus Bertrand, Paris, 271 pp.
- Gureev, A. A. (1960): Zaytseobraznye (Lagomorpha) oligotsena Mongolii i Kazakhstana [Lagomorphs (Lagomorpha) of the Oligocene of Mongolia and Kazakhstan]. – in: Tretichnye mlekopitayushchie, part 4. Trudy Paleontologicheskogo instituta AN SSSR, 77: 5–34. (in Russian)
- Gureev, A. A. (1964): Zaytseobraznye (Lagomorpha) (Fauna SSSR, Mlekopitayushchie, tom 3, vyp. 10) [Lagomorphs (Lagomorpha) (Fauna of the USSR, Mammals, vol. 3, part 10)]. – Nauka, Moskva, Leningrad, 276 pp. (in Russian)
- Hay, O. P. (1921): Descriptions of species of Pleistocene Vertebrata, types or specimens of most of which are preserved in the United States National Museum. – Proceedings of U. S. National Museum, 59: 599–642.
<https://doi.org/10.5479/si.00963801.59-2391.599>
- Hays, I. (1834): Descriptions of the specimens of inferior maxillary bones of Mastodons in the cabinet of the American Philosophical Society, with remarks on the genus *Tetracaulodon* (Godman). – Transactions of the American Philosophical Society, 4: 317–339.
<https://doi.org/10.2307/1004835>
- Hoffmann, R. S., Smith, A. T. (2005): Order Lagomorpha. – In: Wilson, D. E., Reeder, D. M. (eds), Mammal Species of the World: A Taxonomic and Geographic Reference. The Johns Hopkins University Press, Baltimore, pp. 185–211.
- Janvier, P., Montenat, C. (1971): Le plus ancien Léporidé d'Europe occidentale, *Hispanolagus crusafonti* nov. gen. nov. sp. du Miocène supérieur de Murcia (Espagne). – Bulletin du Muséum national d'Histoire naturelle, Paris, 42(2): 780–788.
- Jin, C. Z. (2004): Fossil leporids (Mammalia, Lagomorpha) from Huainan, Anhui, China. – Vertebrata Palasiatica, 42(3): 230–245.
- Khomenko, I. P. (1914): La faune méotique du village Taraklia du district de Bendery: Fissipedia, Rodentia, Rhinocerotinae, Equinae, Suidae, Proboscidae. – Trudy Bessarabskoe Obshchestvo Estestvoispytatelei, Kishinev, 5: 1–55.
- Kormos, T. (1934): Az euráziai nyulak származástani problémája / Zur Frage der Abstammung eurasiatischer Hasen. – Állattani Közlemények, 31: 65–78.
- Koufos, G. D., Koliadimou, K. K. (1993): Two lagomorphs from the Pliocene of Macedonia, Greece. – Bulletin of the Geological Society of Greece, 28: 117–129.
- Lavocat, R. (1951): Révision de la faune des Mammifères oligocènes d'Auvergne et du Velay. – Science et Avenir, Paris, 154 pp.
- Link, H. F. (1795): Beiträge zur Naturgeschichte, vol. 2. – Karl Stiller, Rostock, Leipzig, 126 pp.

- Liu, L., Zheng S. H. (1997): Note on the late Cenozoic lagomorphs of Danjiang Reservoir area in Hubei and Henan. – *Vertebrata Palasiatica*, 35(2): 130–144.
- López Martínez, N. (1977): Nuevos lagomorfos (Mammalia) del Neógeno y Cuaternario español [New lagomorphs from the Neogene and Quaternary of Spain]. – *Trabajos sobre Neogeno-Cuaternario*, 8: 7–45. (in Spanish)
- López Martínez, N. (1989): Revisión sistemática y biostratigráfica de los Lagomorpha (Mammalia) del Terciario y Cuaternario de España [Systematic and biostratigraphic revision of Lagomorpha (Mammalia) from the Tertiary and Quaternary of Spain]. – *Memorias del Museo Paleontológico de la Universidad de Zaragoza*, 3: 1–342. (in Spanish)
- López Martínez, N. (2008): The lagomorph fossil record and the origin of the European rabbit. – In: Alves, P. C., Ferrand, N., Hackländer, K. (eds), *Lagomorph biology: evolution, ecology, and conservation*. Springer, Berlin, pp. 27–46.
https://doi.org/10.1007/978-3-540-72446-9_3
- López Martínez, N., Thaler, L. (1975): Biogéographie, évolution et compléments à la systématique du groupe d'Ochotonidés *Piezodus-Prolagus* (Mammalia, Lagomorpha). – *Bulletin de la Société géologique de France*, Sér. 7, 17: 850–866.
<https://doi.org/10.2113/gssgfbull.S7-XVII.5.850>
- Masini, F. (1989): *Prolagus sorbinii* n. sp., a new ochotonid (Mammalia, Lagomorpha) from the Messinian of Italy. – *Bollettino della Società Paleontologica Italiana*, 28: 295–306.
- Mein, P., Aymar, J. (1984): Découvertes récentes de mammifères dans le Pliocène du Roussillon. Note préliminaire. – *Nouvelles Archives du Muséum d'Histoire naturelle de Lyon*, 22(1): 69–71.
- Mein, P., Bizon, G., Bizon, J. J., Montenat, C. (1973): Le gisement de mammifères de La Alberca (Murcia, Espagne méridionale). Corrélations avec les formations marines du Miocène terminal. – *Comptes rendus de l'Académie des Sciences de Paris*, D, 276: 3077–3080.
- Melik-Adamyán, G. U. (1986): Novye danye o pliotsenovykh nazemnykh pozvonochnykh Armyanskoy SSR [New data on the Pliocene terrestrial vertebrates from the Armenian SSR]. – *Doklady Akademii nauk Armyanskoy SSR*, 83(3), 135–139. (in Russian)
- Metz-Muller, F. (1995): Mise en évidence d'une variation intra-spécifique des caractères dentaires chez *Anancus arvernensis* (Proboscidea, Mammalia) du gisement de Dorkovo (Pliocène ancien de Bulgarie, biozone MN14). – *Geobios*, 28(6): 737–743.
[https://doi.org/10.1016/S0016-6995\(95\)80069-7](https://doi.org/10.1016/S0016-6995(95)80069-7)
- Metz-Muller, F. (2000): La population d'*Anancus arvernensis* (Proboscidea, Mammalia) du Pliocène de Dorkovo (Bulgarie); étude des modalités évolutives d'*Anancus arvernensis* et phylogénie du genre *Anancus*; doctoral thesis. – MS, Muséum national d'Histoire naturelle, Paris, France, 306 pp. (copy study in the library of Muséum national d'Histoire naturelle, Paris)
- Nesin, V. A., Rekovets, L. I. (1993): Mikroteriofauna pliocenovykh mestonakhozhdeniy Shirokino i Obukhovka [Microtheriofauna of the Pliocene localities Shirokino and Obukhovka]. – In: Topachevsky, V. A. (ed.), *Mleko-pitayushchie Ukrainy [Mammals of the Ukraine]*. Naukova dumka, Kiev, pp. 23–39. (in Russian)
- NOW Database (2019): <http://www.helsinki.fi/science/now/database.html>
- Palacios Arribas, F., López Martínez, N. (1980): Morfología dentaria de las liebres europeas (Lagomorpha, Leporinae) [Dental morphology of European hares (Lagomorpha, Leporidae)]. – *Doñana, Acta Vertebrata*, 7: 61–81 (in Spanish)”.
Pallas, P. S. (1769) : *Decriptio Leporis pussilli*. – *Novi commentarii Academiae Scientiarum Imperialis Petropolitanae*, 13 : 531–538.
- Piñero, P., Agustí, J., Oms, O., Fierro, I., Montoya, P., Mansino, S., Ruiz-Sánchez, F., Alba, D. M., Alberdi, M. T., Blain, H.-A., Laplana, C., van der Made, J., Mazo, A. V., Morales, J., Murelaga, X., Pérez-García, A., Pérez-Valera, F., Pérez-Valera, J. A., Sevilla, P., Soria, J. M., Romero, G. (2017): Early Pliocene continental vertebrate fauna at Puerto de la Cadena (SE Spain) and its bearing on the marine-continental correlation of the late Neogene of Eastern Betics. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, 479: 102–114.
<https://doi.org/10.1016/j.palaeo.2017.04.020>
- Pomel, A. (1853): Catalogue méthodique et descriptif des vertébrés fossiles découverts dans le bassin hydrographique supérieur de la Loire, et surtout dans la vallée de son affluent principal, l'Allier. – J.-B. Baillière, Paris, 193 pp.
- Popov, V. V. (2004): Pliocene small mammals (Mammalia, Lipotyphla, Chiroptera, Lagomorpha, Rodentia) from Muselievo (North Bulgaria). – *Geodiversitas*, 26: 403–491.
- Qiu, Z., Han, D. (1986): Fossil Lagomorpha from the hominoid locality of Lufeng, Yunnan. – *Acta Anthropologica Sinica*, 5: 41–53.
- Qiu, Z., Storch, G. (2000): The early Pliocene micromammalian fauna of Bilike, Inner Mongolia, China (Mammalia: Lipotyphla, Chiroptera, Rodentia, Lagomorpha). – *Senckenbergiana lethaea*, 80: 173–229.
<https://doi.org/10.1007/BF03043669>
- Radulesco, C., Samson, P. (1967): Contributions à la connaissance du complexe faunique de Malusteni-Beresti (Pléistocène inférieur), Roumanie I. Ord. Lagomorpha, Fam. Leporidae. – *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 1967(9): 544–563.
- Radulescu, C., Samson, P. M. (1995): The mammals of the Dacian. – In: Marinescu, F., Papaianopo, L. I. (eds), *Dacien chronostratigraphie und Neostratotypen Neogen der Zentrale Paratethys*. Editura Academiei Române, București, pp. 506–518.
- Radulescu, C., Samson, P. M. (2001): Biochronology and evolution of the Early Pliocene to the Early Pleistocene mammalian faunas of Romania. – *Bollettino della Società Paleontologica Italiana*, 40: 285–291.
- Rzebik-Kowalska, B., Popov, V. V. (2005): Bulgaria. – In: van den Hoek Ostende, L. W., Doukas, C. S., Reumer, J. W. F. (eds), *The Fossil Record of the Eurasian Neogene Insectivores (Erinaceomorpha, Soricomorpha, Mammalia)*. Part I. *Scripta Geologica, Special Issue 5*: 31–35.
- Schlosser, M. (1884): Die Nager des europäischen Tertiärs: nebst Betrachtungen über die Organisation und die geschichtliche Entwicklung der Nager überhaupt. – *Palaeontographica*, 21: 19–162.

- Schlosser, M. (1924): Tertiary vertebrates from Mongolia. – *Palaeontologia Sinica*, Ser. C, 1(1): 1–133.
- Sen, S. (1983): Rongeurs et lagomorphes du gisement pliocène de Pul-e Charkhi, bassin de Kabul, Afghanistan. – *Bulletin du Muséum national d’Histoire naturelle*, C, 5: 33–74.
- Sen, S. (1998): Rodentia and Lagomorpha – In: Sen, S. (ed.), *Pliocene vertebrate locality of Çalta, Ankara, Turkey*. *Geodiversitas*, 20: 359–378.
- Sen, S. (2003): Lagomorpha. – In: Fortelius, M., Kappelman, J., Sen, S., Bernor, R. L. (eds), *Geology and Paleontology of the Miocene Sinap Formation, Turkey*. Columbia University Press, New York, pp. 163–178.
- Sen, S., Delfino, M., Kazanci, N. (2017): Çestepe, a new early Pliocene vertebrate locality in Central Anatolia and its stratigraphic context. – *Annales de Paléontologie*, 103: 149–163.
<https://doi.org/10.1016/j.annpal.2017.01.004>
- Sen, S., Jaeger, J.-J., Dalfes, N., Mazin, J.-M., Bocherens, H. (1989): Découverte d’une faune de petits mammifères pliocènes en Anatolie occidentale. – *Comptes Rendus de l’Académie des Sciences de Paris*, II, 309(17): 1729–1734.
- Sen, S., Karadenizli, L., Antoine, P. O., Saraç, G. (2019): Late Miocene-early Pliocene rodents and lagomorphs (Mammalia) from the southern part of Çankiri Basin, Turkey. – *Journal of Paleontology*, 93(1): 173–195.
<https://doi.org/10.1017/jpa.2018.60>
- Sickenberg, O., Becker-Platen, J. D., Benda, L., Berg, D., Engesser, B., Gaziry, W., Heissig, K., Hünermann, K. A., Sondaar, P. Y., Schmidt-Kittler, N., Staesche, K., Staesche, U., Steffens, P., Tobien, H. (1975): Die Gliederung des höheren Jungtertiärs und Altquartärs in der Türkei nach Vertebraten und ihre Bedeutung für die internationale Neogen-Stratigraphie. – *Geologisches Jahrbuch*, B, 15: 1–167.
- Simionescu, I. (1930): Vertebratele pliocene dela Mălușteni (Covurlui) [Pliocene vertebrates from Malusteni (Covurlui)]. – *Publicațiunile Fondului Vasile Adamachi, Academia Română*, 9(no. 49): 83–151. (in Romanian with French abstract)
- Spasov, N. (2003): The Plio-Pleistocene vertebrate fauna in South-Eastern Europe and the megafaunal migratory waves from the east to Europe. – *Revue de Paléobiologie*, 22: 197–229.
- Spasov, N. (2005): Brief review of the Pliocene ungulate fauna of Bulgaria. – *Quaternaire*, numéro spécial 2: 201–212.
- Suata-Alpaslan, F. (2009): *Ochotona mediterraneanensis* nov. sp. (Lagomorpha-Mammalia) from early Pliocene of İğdeli (Anatolia-Turkey). – In: 9th International Multidisciplinary Scientific GeoConference SGEM2009, Conference Proceedings, volume 1: 99–103.
- Sych, L. (1980): Lagomorpha (Mammalia) from the Pliocene and early Pleistocene of Poland. – *Folia Quaternaria*, 51: 57–64.
- Tesakov, A. S., Averianov, A. O. (2002): *Prolagus* (Lagomorpha, Prolagidae) from the Pliocene of Moldova and Ukraine. – *Paleontological Journal*, 36(1): 80–86.
- Thomas, H., Spasov, N., Kojungieva, E., Poidevin, J.-L., Popov, V., Sen, S., Tassy, P., Visset, D. (1986a): Résultats préliminaires de la première mission paléontologique franco-bulgare à Dorkovo (arrondissement de Pazardjik, Bulgarie). – *Comptes Rendus de l’Académie des Sciences*, II, 302: 1037–1042.
- Thomas, H., Spasov, N., Kojungieva, E., Poidevin, J.-L., Popov, V., Sen, S., Tassy, P., Visset, D. (1986b): Neogenovaya pozvonochnaya fauna iz s. Dorkovo, Zapadnye Rodopy (pervye rezul’taty) [Neogene vertebrate fauna from Dorkovo, West Rhodope Mountains (first results)]. – *Geologica Balcanica*, 16: 79–86. (in Russian)
- Thomas, O. (1897): On the genera of rodents: an attempt to bring up to date the current arrangement of the order. – *Proceedings of the Zoological Society of London*, 1896: 1012–1028.
<https://doi.org/10.1111/j.1096-3642.1896.tb03097.x>
- Tobien, H. (1974): Neue Säugerfaunen des Jungtertiärs aus Anatolien. – *Senckenbergiana lethaeae*, 55: 445–454.
- Tobien, H. (1975): Zur Gebißstruktur, Systematik und Evolution der Genera *Piezodus*, *Prolagus* und *Ptychoprolagus* (Lagomorpha, Mammalia) aus einigen Vorkommen im jüngeren Tertiär Mittel- und Westeuropas. – *Notizblatt des Hessischen Landesamtes für Bodenforschung zu Wiesbaden*, 103: 103–186.
- Tomida, Y., Jin, C. Z. (2005): Reconsideration of the generic assignment of “*Pliopentalagus nihewanensis*” from the late Pliocene of Hebei, China. – *Vertebrata Palasiatica*, 43(4): 297–303.
- Tomida, Y., Jin, C. Z. (2009): Two new species of *Pliopentalagus* (Leporidae, Lagomorpha) from the Pliocene of Anhui Province, China, with a revision of *Pl. huainanensis*. – *Vertebrata Palasiatica*, 47(1): 53–71.
- Topachevsky, V. A. (1980): Novye vidy roda *Pratilepus* (Lagomorpha, Leporidae) iz pliotsenovykh otlozheniy kuchurganskoy tolshchi [New species of genus *Pratilepus* (Lagomorpha, Leporidae) from Pliocene deposits of Kuchurgan sediments]. – *Vestnik zoologii*, 5: 37–40. (in Russian with English summary)
- Topachevsky, V. A., Nesin, V. A., Rekovets, L. I., Topachevsky, I. V., Pashkov, A. V. (1988): Novoe mestonakhozhdenie ostatkov melkikh mlekopitayushchikh (Mammalia) pliotsena Severnogo Priazov’ya [A new location of small mammalian remains in Pliocene of the northern Azov Sea area]. – *Doklady Akademii nauk Ukrainsskoy SSR*, Ser. B, 1988(11): 19–21. (in Russian)
- Vasileiadou, K., Konidaris, G., Koufos, G. D. (2012): New data on the micromammalian locality of Kessani (Thrace, Greece) at the Mio-Pliocene boundary. – *Palaeobiodiversity and Palaeoenvironments*, 92(2): 211–237.
<https://doi.org/10.1007/s12549-012-0075-7>
- Vasileiadou, K., Koufos, G. D., Syrides, G. E. (2003): Silata, a new locality with micromammals from the Miocene/Pliocene boundary of the Chalkidiki peninsula, Macedonia, Greece. – *Deinsea*, 10: 549–562.
- Viret, J. (1929): Les faunes des mammifères de l’Oligocène supérieur de la Limagne Bourbonnaise. – *Annales de l’Université de Lyon*, N. S., I. Sciences, Médecine, 47: 1–327.
- van de Weerd, A. (1979): Early Ruscinian rodents and lagomorphs (Mammalia) from the lignites near Ptolemais (Macedonia, Greece). – *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, B, 82(2): 127–170.

- White, J. A. (1991): North American Leporinae (Mammalia: Lagomorpha) from the late Miocene (Claredonian) to latest Pliocene (Blancan). – *Journal of Vertebrate Paleontology*, 11: 67–89.
<https://doi.org/10.1080/02724634.1991.10011376>
- Winkler, A. J. (2003): Rodents and lagomorphs from the Miocene and Pliocene of Lothagam, northern Kenya – In: Leakey, M. G., Harris, J. M. (eds), *Lothagam: the Dawn of Humanity in Eastern Africa*. Columbia University Press, New York, pp. 169–198.
<https://doi.org/10.7312/leak11870-010>
- Winkler, A. J., Flynn, L. J., Tomida, Y. (2011): Fossil lagomorphs from the Potwar Plateau, northern Pakistan. – *Palaeontologia Electronica*, 14(3): 38A (16 pp.).
- Wu, W.-Y., Flynn, L. J. (2017): The lagomorphs (Ochotonidae, Leporidae) of Yushe Basin. – In: Flynn, L. J., Wu, W.-Y. (eds), *Late Cenozoic Yushe Basin, Shanxi Province, China: Geology and Fossil Mammals. Volume II: Small Mammal Fossils of Yushe Basin* [series *Vertebrate Paleobiology and Paleoanthropology*]. Springer, Dordrecht, pp. 31–57.
https://doi.org/10.1007/978-94-024-1050-1_4