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Prolagus (Lagomorpha, Prolagidae) from the Pliocene of Moldova and Ukraine

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Abstract—Two species of the genus *Prolagus*, *P. sorbinii* Masini (Early Ruscinian) and *P. bilobus* Heller (Late Ruscinian) are determined from the Pliocene of Ukraine and Moldova for the first time. *Prolagus* fossils from the Upper Ruscinian of Moldova and Ukraine, which were previously referred to as *Prolagus* cf. *oeningensis*, are assigned to *P. bilobus.* In Eastern Europe, *P. sorbinii* became extinct and *P. bilobus* widely distributed at the boundary between the Early and Late Ruscinian.

INTRODUCTION

Prolagids compose a small group of lagomorphs resembling pikas. They developed in the Early Miocene to the Late Holocene mainly in the Mediterranean Region and occurred in Europe, North Africa, Asia Minor, and the region of Lake Baikal. Late prolagids (genus *Prolagus*) are characterized by an enlarged premolar foramen, hypsodont teeth, reduced m3, detached hypoconulid on m2 (this tooth consists of three prisms), increased p3 with a well-pronounced anteroconid, and by a number of primitive features of the upper cheek teeth. *Prolagus* is common in the Neogene and Pleistocene faunas from western Europe and abundant in a number of localities. In eastern Europe and the former Soviet Union, *Prolagus* is less common. In Ukraine, *Prolagus* was first determined by Kontkevich (1887) and Lungershausen (1934). These identifications were questioned by Argiropulo and Pidoplichko (1939). Subsequently, *Prolagus* fossils were registered in the following Neogene localities of Moldova and Ukraine: in MN 11 (12?), Novoelizarovka 2 (Topachevsky *et al.*, 1998); in MN 12, Novoukrainovka, Cherevichnoe 3, and Andreevka (according to Topachevsky *et al.*, 1988 and Nesin, 1996, MN 13) (Dubrovo and Kapelist, 1979; Topachevsky *et al.*, 1987, 1988, 1998); in MN 13, Odessa (Bolshoi Fontan), Frunzovka 2, Vinogradovka, Orekhovka, and Mugureny (Prisyazhnyuk and Shevchenko, 1987; Topachevsky *et al.*, 1988, 1990, 1994; Vangengeim *et al.*, 1995); in MN 14, Kamenskoe and Novaya Andriashevka (Topachevsky, 1962; Dubrovo and Kapelist, 1979; Vangengeim *et al.*, 1995); in MN 15, Salchiya and Grebeniki 2 (David *et al.*, 1988; Vangengeim *et al.*, 1995); and in MN16 (?), Novaya Etuliya 3 (Godina and David, 1973).

The teeth from the Middle Sarmatian (MN 9) of the Buzhory locality (Lungu, 1978, p. 22; 1979, p. 36; 1981, pp. 44–45, pl. 5, fig. 1), which were identified as m2 of *Prolagus* sp., are most likely deciduous teeth (d3) of pikas, probably, *Ochotona kalfense* (Lungu, 1981). This inference follows from the absence of other identifiable *Prolagus* fossils in the Sarmatian of Moldova. The presence of the genus *Prolagus* in the Middle Sarmatian Kalfa locality was proposed by Topachevsky (1987, p. 86); however, this was not substantiated by a description or figures.

Prolagus remains (*Prolagus* sp. and *P.* cf. *aeningensis* [sic]) found in the Pleistocene of Ukraine (Morozovka 2, Bolshevik, and Ozernoe 2 localities) were probably redeposited from earlier beds (Topachevsky *et al.*, 1975; Rekovets, 1991; Rekovets and Nadachowski, 1995). Several teeth of *Prolagus* sp. (three p3 and one P3 collected by L.P. Aleksandrova, GIN) found in Bed 19 of the Kolkotova Balka locality among the forms characteristic of the Tiraspol Faunal Assemblage (Early Neopleistocene according to the Russian Stratigraphic Chart, i.e., early Middle Pleistocene according to the International Stratigraphic Chart) were probably redeposited from the Mio-Pliocene beds.

In all the studies cited above (except for Lungu, 1981), specimens were not determined to the species rank and descriptions or figures were absent. To date, the figures of the following *Prolagus* forms from the former Soviet Union have been published: (1) p3 of *Prolagus* sp. from the Pliocene of the village of Kamenskoe, Ukraine [Topachevsky, 1962, text-fig. 1 (2)]; (2) p3 from Pliocene Lake Olkhon near Lake Baikal (Mats and Pokatilov, 1982, pl. 3, fig. 14); (3) p3 of *Prolagus* from the Pliocene Kotlovina locality, Ukraine (Agadjanian and Erbajeva, 1983, text-fig. 19, fig. 1); (4) one p3 from the Early Pliocene Tanatary locality, Moldova (Erbajeva, 1988, text-fig. 20, fig. 9; Erbajeva and Shushpanov, 1988, text-fig. 17); and (5) a new species, *Prolagus caucasicus*, described from the Early Pliocene Kosyakino locality, northern Caucasus (Averianov and Tesakov, 1998, text-figs. 1d–1h). In addition

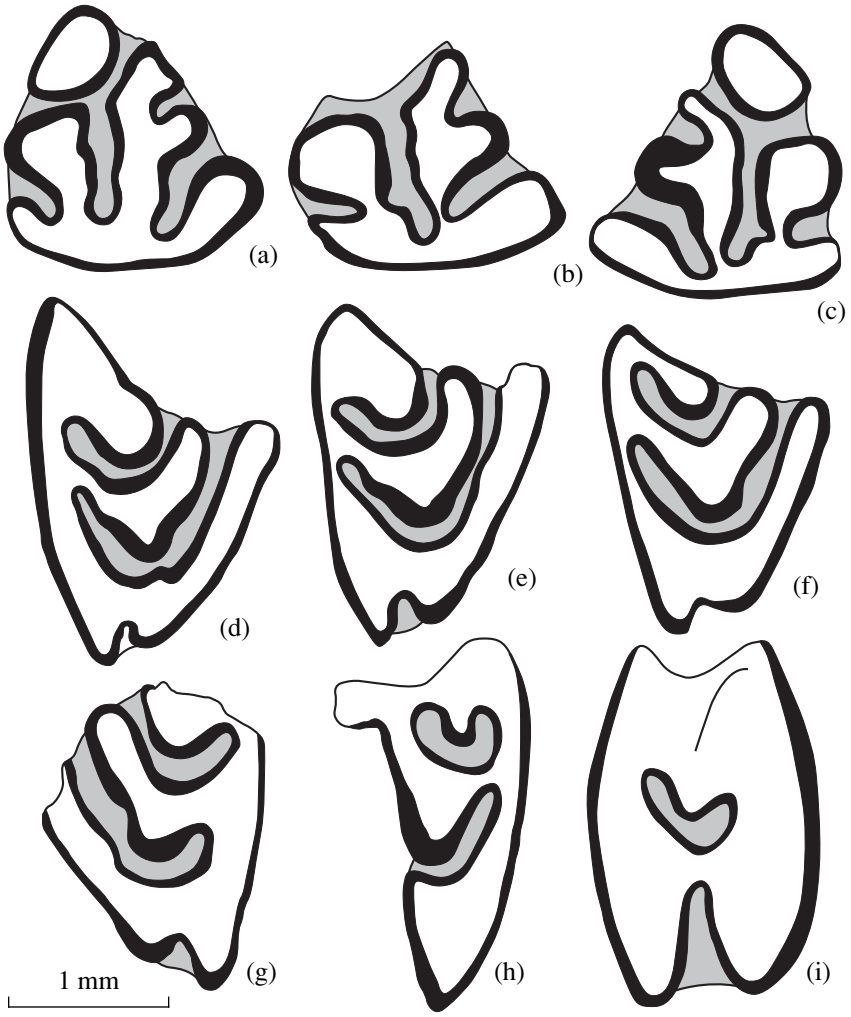

Fig. 1. Occlusal surface of isolated teeth of *Prolagus sorbinii* from Grebeniki 2, Lower Ruscinian: (a, b) GIN, nos. 1074/157 and 158, right p3; (c) GIN, no. 1074/156, left p3; (d)–(f) GIN, nos. 1074/150, 160, and 161, right P3; (g) GIN, no. 1074/159, left P3; (h) GIN, no. 1074/162, fragmentary left P4; and (i) GIN, no. 1074/163, left M1. Scale bar, 1 mm.

to *Prolagus* from the Caucasus, only the specimens from the Kotlovina and Tanatary localities were identified to the species rank, namely, designated as *Prolagus* cf. *oeningensis.* In the present study, this identification is revised. In addition, new material on *Prolagus* from the Pliocene of the Grebeniki 2 (Ukraine) and the Novaya Andriyashevka and Tatareshty (Moldova) localities is described and pictured. To date, *Prolagus* has not been registered in the Tatareshty locality (Aleksandrova, 1971; Godina and David, 1973; David, 1983; David *et al.*, 1989).

The material examined in the present study is housed at the Geological Institute of the Russian Academy of Sciences, Moscow (GIN) and in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZIN).

The teeth were measured with a vernier caliper to within 0.05 mm. The measurements are given in mm. In the figures, enamel is black, dentin is white, and tooth cementum is gray. Capital P and M designate upper premolars and molars, respectively; lower case p and m are lower premolars and molars, respectively. The morphological structures of molars are designated according to the terminology used by Lopez Martinez and Thaler (1975).

SYSTEMATIC PALEONTOLOGY

Order Lagomorpha Brandt, 1855

Family Prolagidae Gureev, 1962

Genus *Prolagus* Pomel, 1853

***Prolagus sorbinii* Masini, 1989**

Prolagus cf. *crusafonti*: Lopez Martinez, 1976, p. 235, text-fig. 2, pl. 1, figs. 1–14.

Prolagus cf. *michauxi*: van de Weerd, 1979, p. 165, pl. 4, figs. 1–4; Daams and van de Weerd, 1980, p. 329, pl. 1, figs. 10 and 11.

Prolagus sorbinii: Masini, 1989, p. 300, text-fig. 3B, pls. 1 and 2, pl. 3, figs. 1, 2, and 4.

Prolagus cf. *sorbinii*: Masini, 1989, p. 302, pl. 3, figs. 5–11, pl. 4.

Prolagus michauxi: Şen *et al.*, 1989, p. 1731, text-figs. m–q.

Prolagus cf. *sorbinii*: de Bruijn, 1995, p. 135, figs. 1–13.

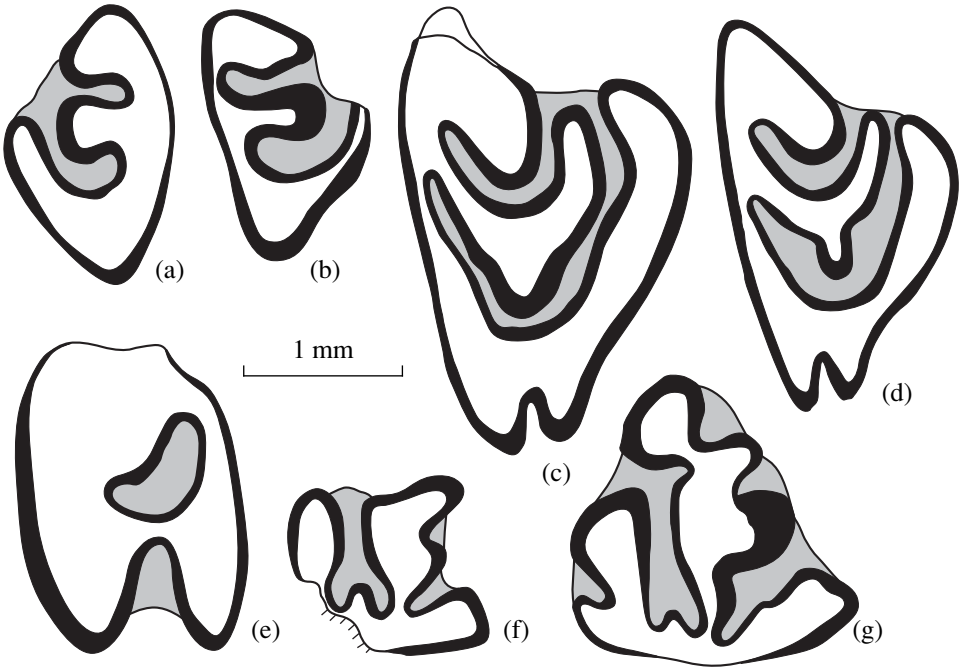

Fig. 2. Occlusal surface of isolated teeth: (a)–(e) *Prolagus sorbinii* from Novaya Andriyashevka, Lower Ruscinian, and (f, g) *P. bilobus* from Tatareshty, Upper Ruscinian: (a) GIN, no. EMM-15/101, left P2; (b) GIN, no. EMM-15/102, right P2; (c, d) GIN, nos. EMM-15/103 and 104, right P3; (e) GIN, no. EMM-15/105, right M1; (f) ZIN, no. 84001, fragmentary right p3; and (g) ZIN, no. 84000, right p3. Scale bar, 1 mm.

Holotype. Museum of Natural History, Verona, no. V7026, articulated skeleton, including skull; Italy, Monte Castellaro; Upper Miocene, Turolian, MN 13, Gessozo-Solfifera Formation.

Description (Figs. 1, 2a–2e). P2 has a long precone reaching buccally the middle of the crown. The centrocone and postcone are approximately equal in size. P2 lacks a hypostria (hypoflexus). Two out of six specimens have a hiatus of enamel on the precone of P3. P3 has a hypostria, which is relatively long and usually filled by cementum. The postcone ranges in size from relatively large to small. The parafossette and metafossette of P4 are relatively very large; the parafossette is approximately twice as large as the metafossette. The hypostria of P4 is short. In M1, the parafossette is relatively large and the hypostria is short; the metafossette is absent. On p3, the crochet is absent. The anteroconid of p3 is usually oval. The protolophid is not discontinuous. The protoconulid is narrow and long, usually longer than the protoconid. The protoflexid is deep. The mesoflexid is oriented posterobuccally or buccally.

Measurements, mm. Novaya Andriyashevka locality: P2 length, 1.05 and 1.10; P2 width, 1.55 and 2.00; P3 length, 1.55 and 1.80; P3 width, 2.40 and 2.85; M1 length, 1.65; and M1 width, 2.35. Grebeniki 2 locality: P3 length, 1.50–1.65 (on the average, 1.56 ± 0.04, $n = 4$); P3 width, 2.00–2.65 (2.34 ± 0.14, $n = 4$); P4 width, 2.50; M1 length, 1.70; and M1 width, 2.85. The measurements of p3 are in Table 1.

Comparison and remarks. The specimens examined in the present study were referred to as *P. sorbinii* based on the following diagnostic characters: (1) relatively large measurements; (2) the hypostria of P3 is relatively long; (3) the weakly worn M1 and M2 have fassettes; (4) p3 usually lacks crochet; (5) the anteroconid of p3 is usually oval; and (6) the protoconulid is narrow and long, usually longer than the protoconid. The specimens described above differ from *P. sorbinii* by the predominance of the P3 morphotype, in which enamel on the precone lacks a hiatus; a relatively short hypostria on the P3; and by substantially stronger developed fassettes on the P4 and M1. The latter character shows the evolutionary advantage of this form and is associated with consecutive fetalization of the dental system of *Prolagus* (Averianov, 1999). This agrees with a later geological age of the samples from Moldova (Table 1). *P. sorbinii* was previously found in the Late Miocene (Turolian) to the Early Pliocene (Ruscinian) of Italy, Greece, and Turkey and probably in the Ruscinian of Bulgaria (Dorkovo). The specimens from Grebeniki 2 are extremely similar to the *Prolagus* teeth from Develi, Turkey (MN 14), initially determined as *Prolagus michauxi* (Şen *et al.*, 1989, text-figs. m–q). The similarity is especially well pronounced in the P4 structure, i.e., the large fassettes and a short hypostria of this tooth. The same structure is characteristic of the *Prolagus* teeth from Pikermi, Cavo Monticino, and Maramena (Lopez Martinez, 1976; Masini, 1989; de

Table 1. Measurements of p3 in *Prolagus* from the Mio-Pliocene of Moldova, Ukraine, Italy, Greece, and Germany

Species, locality	Length of p3		Width of p3		Reference
	lim	$M \pm m$	lim	$M \pm m$	
Prolagus sorbinii					
Pikermi, MN 12, $n = 18$	1.1–1.8	1.55	1.1–2.0	1.60	Lopez Martinez, 1976
Monte Castellaro, MN 13, holotype	2.20		2.17		Masini, 1989
Cavo Monticino, MN 13, $n = 15$	1.5–2.3	1.87 ± 0.06	1.4–2.1	1.81 ± 0.06	Masini, 1989
Maramena, MN 13, $n = 17$	1.4–2.0	1.72	1.4–2.0	1.64	De Bruijn, 1995
Grebeniki 2, MN 15, $n = 2$–3	1.75, 1.75		1.70–1.75	1.73 ± 0.02	this study
Prolagus bilobus					
Gundersheim, MN 15, holotype	2.9?		2.5?		based on (Heller, 1936, fig. 3)
Tanatary, MN 15, $n = 1$	1.8		1.7		Erbajeva and Shushpanov, 1988
Tatareshty, MN 15, $n = 1$	1.95		1.93		this study
Kotlovina, MN 15–16, $n = 1$	2.58		2.54		based on (Agadjanian and Erbajeva, 1983, text-fig. 19, fig. 1)

Bruijn, 1995). This allows for the assignment of these forms to the same species, *P. sorbinii*.

The measurements of p3 from the Grebeniki locality are intermediate between those from Pikermi (MN 12) and Cavo Monticino (MN 13) and smaller than those from Maramena (MN 13) (Table 1, Fig. 3).

O c c u r r e n c e. Italy, Greece, Turkey, Moldova, Ukraine, and probably Bulgaria; Upper Miocene (Turolian) to Lower Pliocene (Ruscinian).

M a t e r i a l. Collection GIN, no. j EMM-15: two P2, two P3, and one M1, Novaya Andriyashevka locality, right bank of the Kuchurgan River near the village of Novaya Andriyashevka, Tiraspol District, Moldova; Lower Ruscinian, lower part of the MN 14 Zone. Collection GIN, no. 1074 (collected by Tesakov and colleagues): three p3, four P3, one P4, and one M1, Grebeniki 2 locality, Velikomikhailovskii District, Odessa Region, Ukraine; Lower Ruscinian, upper part of the MN 14 Zone.

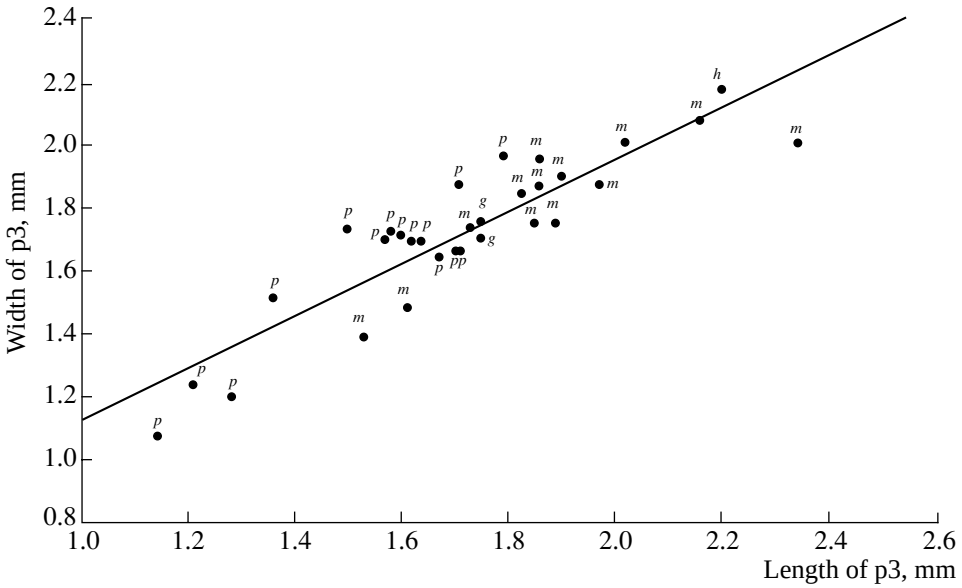

Fig. 3. Scatterplot of length against width of p3 in *Prolagus sorbinii* from the following samples: (*h*) holotype (after Masini, 1989), (*g*) Grebeniki 2, (*m*) Cavo Monticino (after Masini, 1989), and (*p*) Pikermi (after Lopez Martinez, 1976).

***Prolagus bilobus* Heller, 1936**

Prolagus bilobus: Heller, 1936, p. 139, text-fig. 3.

Prolagus sp.: Topachevsky, 1962, p. 108, text-fig. 1 (2).

?Prolagus sp.: Tobien, 1963, text-fig. 13.

Prolagus bilobus: Berzi, 1967, text-fig. 9.

Prolagus cf. *oeningensis*: Agadjanian and Erbajeva, 1983, p. 83, text-fig. 19, fig. 1; Erbajeva, 1988, text-fig. 20, fig. 9; Erbajeva and Shushpanov, 1988, p. 55, text-fig. 17.

Lectotype (first indicated in this paper). Right p3 (Heller, 1936, text-fig. 3; no. not available), Germany, Gundersheim; Lower Pliocene, MN 15.

Description (Figs. 2f–2g). The anteroconid of p3 is relatively small. In one specimen, the anteroconid fused with the protoconulid on the occlusal surface; however, on the side of the tooth root, these elements are separated from each other by the anteroflexid (Fig. 2g, a rare morphotype, probably belonging to a young individual). The protolophid is straight and positioned in the central part of the tooth crown. A crochet that looks like a hooked blade is present and relatively large. The protoflexid is deep and relatively very broad. The protoconulid is long and narrow. The mesoflexid is relatively short and oriented buccally.

Measurements. See Table 1.

Comparison and remarks. The specimens described above are referred to as *P. bilobus* based on the combination of the following diagnostic characters: (1) the crochet is present and well developed, (2) the protoflexid is deep, and (3) the protoconulid is long and narrow. The p3 specimen from the Tatareshty locality differs from the holotype *P. bilobus* by a substantially smaller anteroconid, a shorter mesoflexid lacking posterior extension, and smaller sizes (exact measurements of the holotype are not available). The anteroconid merged with the protoconulid occurs as a variant in *P. sorbinii* from the Late Turolian of Maramena, Greece (de Bruijn, 1995, text-fig. 11). The endemic species *Prolagus apricenicus* Mazza, 1987 (which is rather similar to *P. bilobus*) found in the Pliocene karstic cavities of the Gargano Peninsula (Italy) occasionally has the p3 morphotype, in which the anteroconid merged with the metaconid (Mazza, 1987a, text-fig. 13; 1987b, pl. 2, fig. 2).

The p3 specimen from the Kamenskoe locality, which was initially determined as *Prolagus* sp. [Topachevsky, 1962, text-fig. 1 (2)], is characterized by a large crochet and a longitudinally extended anteroconid. The structural details show that it has much in common with the holotype *P. bilobus* and should be assigned to this species. The measurements of this specimen are not available.

The p3 specimen from the Tanatary locality (Erbajeva, 1988, text-fig. 20 (9); Erbajeva and Shushpanov, 1988, text-fig. 17) is almost identical in morphology to the holotype *P. bilobus* and differs from the latter by only the lingually closed mesoflexid (ontogenetic variation) and, probably, smaller measurements. This specimen was initially determined as *Prolagus* cf. *oeningensis*. It is actually similar to p3 of this species (to the *oeningensis* morphotype characterized by an undivided metalophid); however, it is distinguished by somewhat larger measurements and a stronger developed crochet. *P. oeningensis* was registered in the Early to the beginning of the Late Miocene (Orleanian–Vallesian, MN 3–MN10) of Portugal, Spain, France, Germany, Switzerland, and Turkey. Apparently, the specimen from Tanatary would be more properly referred to as Late Miocene–Pliocene *P. bilobus*, previously found in Germany and, possibly, in Hungary (Polgardi), since they are similar in the extent to which the crochet is developed.

The specimen from the Kotlovina locality was initially determined in the text as *Prolagus* cf. *oeningensis* and in the figure caption as *Prolagus* sp. (Agadjanian and Erbajeva, 1983, p. 83, text-fig. 19, fig. 1). In general, this specimen is similar to the holotype *P. bilobus*; however, it is distinguished by a narrower anteroconid, the absence of crochet, and the lack of posterior extension on the mesoflexid. These characters are rather variable in *Prolagus*; therefore, *Prolagus* from the Kotlovina locality should be referred to as *P. bilobus* until additional material is available. This statement is supported by large measurements of this specimen (Table 1). Kotlovina is a multilayer locality that includes Ruscinian and two Middle Villafranchian levels (Topachevsky and Nesin, 1989). The stratigraphical position of the *Prolagus* find is not known with certainty.

Occurrence. Lower Pliocene (Ruscinian to Lower Villafranchian) of Germany, Moldova, and Ukraine and probably the Upper Miocene of Hungary.

Material. ZIN, nos. 84000 and 84001, two p3 from Tatareshty, Kagul'skii District, Moldova; Upper Ruscinian, MN 15; collected by L.I. Khozatskii.

DISCUSSION

This study allowed us to determine two *Prolagus* species from Moldova and Ukraine, i.e., *P. sorbinii* from the Early Ruscinian (MN 14) of the Novaya Andriyashevka and Grebeniki 2 localities and *P. bilobus* from the Late Ruscinian (MN 15) of the Tatareshty, Tanatary, and (?) Kotlovina localities, and, probably, from the Early Villafranchian (MN 16) of (?) Kotlovina.

Apparently, *Prolagus* first appeared in this region in the Middle Turolian (Meotian, MN 12). In the Vallesian faunas (Middle and Late Sarmatian, MN 9–MN 11) from the Black Sea Region, *Prolagus* has not been registered with certainty. The *Prolagus* specimens from the Upper Miocene of this region have not been examined nor determined to species. In the Early Ruscinian, the eastern part of the Black Sea Region, northern Caucasus, was inhabited by the endemic species *P. caucasicus*. The latter differs from *P. sorbinii* by weaker developed fassettes on P4 and, in particular, on M1 (a primitive feature); a well-developed crochet on p3 (the crochet is observed in 23.8% of *P. sorbinii* specimens from the Late Turolian Cavo Monticino locality,

Italy, $n = 21$); and by a deep and almost longitudinally oriented mesoflexid on p3 (an autapomorphy of this species). In the Early Ruscinian, the range of *P. sorbinii* included not only Ukraine and Moldova but also Turkey, Greece, and probably Bulgaria. In the Late Ruscinian, this species disappeared and was replaced by the larger and probably more archaic *P. bilobus*. In addition to Moldova and Ukraine, the latter inhabited Germany and probably Hungary. Apparently, this species also occurs in the Early Villafranchian (MN 16) of the Kislang locality, Hungary (Kretzoi, 1954). If this is the case, the *P. bilobus* tooth from the Kotlovina locality could have come from either Ruscinian or Villafranchian levels. It is likely that, in this region, we deal with an actual replacement of *Prolagus* species (*P. sorbinii* is replaced by *P. bilobus*) at the boundary between the Early and Late Ruscinian. This can be used for biostratigraphic purposes. The change most likely occurred by the extinction of *P. sorbinii* and expansion of *P. bilobus* over the vacant space. Note that *P. bilobus* is probably known as early as the Late Turolian (Polgardi). The moment of the *Prolagus* extinction in this region is not known with certainty, since the specimens found in the Lower and Middle Pleistocene beds could be redeposited.

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