

Early *Paracamelus* (Mammalia, Tylopoda) in Eastern Europe

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Abstract. We describe some remains of late Miocene *Paracamelus* cf. *aguirrei* from Eastern Europe. The specimens originate from limestone deposits dated to the lower Pontian (the Novorossian substage) of the Black Sea marine stratigraphic scheme. These camel fossils are among the earliest in Europe. These late Miocene camels were ancestors of the Pliocene *Paracamelus*, whose remains are common in the numerous localities of the Black Sea and the Sea of Azov regions.

Key words: camels, *Paracamelus*, Late Miocene, Black Sea Region, Sea of Azov Region, evolution.

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I. INTRODUCTION

The history of Old World camels is very poorly known. Remains of early camels in Eurasia are extremely rare. Therefore, each find is of a real interest. Recently descriptions of late Miocene camels from Spain and Turkey have appeared. Upper teeth, an astragalus, a calcaneus, a cuboideum, a centrotarsale, and a first phalange have been found in Messinian deposits in Spain (MN 13), at the sites of Venta del Moro and Librilla (MORALES et al. 1980; PICKFORD et al. 1995). On the basis of this material the species *Paracamelus aguirrei* MORALES, 1984 was described (MORALES 1984). Also, three fragments of lower jaw of subadult *Paracamelus* cf. *aguirrei* individuals were described from the late Turolian locality of Çobanpinar in Turkey and also referred to the MN 13 stage (MADE et al. 2002).

On the African continent the most ancient findings of fossil camel are from sites such as Kossom Bougoudi (Chad) and Wadi Natrun (Egypt). The possible age of these localities is determined as Early Pliocene (PICKFORD et al. 1995; LIKIUS et al. 2003).

Several samples of the late Miocene camels are known from Eastern Europe (ALEXEEVA 1959, 1974; SVISTUN 1971). However, their descriptions are insufficient and are not well known to modern researchers. The *Paracamelus* remains in Eastern Europe originate from the near shore limestone deposits of the lower Pontian (the Novorossian substage) of the Black Sea marine stratigraphic scheme (late Miocene). These Pontian strata are widespread in the Black Sea and Sea

of Azov regions. They overlie upper Miocene terrestrial and marine sediments (Sarmatian and Meotian) and are usually overlain by Pliocene deposits. These limestones are formed from the molluscs *Dreissena simplex*, *D. tenuissima*, *Congerina novorossica*, *Prosodacna littoralis*, *Monodacna pseudocatillus*, and others (SEMENENKO & TESLENKO 1994). Isolated bones of *Paracamelus* are known from localities of the northern Sea of Azov and lower Don River regions (Sinyavskaya and a quarry near Novochoerkassk, Russia), the Crimea (the Mamay quarry near Eupatoria, Ukraine), and the northern Black Sea Region, near Odessa (Odessa limestone quarry; Yablioniya village, Ukraine) (Fig. 1; ALEXEEVA 1959, 1974; SVISTUN 1971). Other finds of Pontian camels are mentioned in the literature, such as a fragment of distal humerus from Buldynka village in the Odessa region, a lower jaw fragment from Poligarny village of Cherkassk Region (SVISTUN 1971) and a humerus from Simferopol (Crimea) (PIDOPLICHKO 1956, p. 79) but the determination of these remains is doubtful.



Fig. 1. Geographical position of localities with late Miocene *Paracamelus* in Eastern Europe: 1. Sinyavskaya, 2. Novochoerkassk, (Russia), 3. Eupatoria, 4. Odessa, 5. Buldynka, 6. Yablioniya (Ukraine).

In addition to many fish and reptile remains, the following large mammal taxa have also been found in the lower Pontian sites of the region mentioned (Table I): *Hypolagus igromovi*, *Machairodus* sp., *Mammot borsoni*, *Tetralophodon longirostris*, *Deinotherium* aff. *giganteum*, *Hipparion* sp., *Diceros "pachignatus"*, *Dicerorhinus schleiermacheri*, *Procapreolus* sp., *Helladotherium* sp., "*Palaeoryx*" *longicephalus*, *Neomegaloceros* sp. and others (KOROTKEVICH 1976, 1988; DUBROVO & KAPELIST 1979; LOGVINENKO 2000; BAJGUSHEVA et al. 2001). The lower Pontian (Fontanian) rodent complex is characterized by an increase in the Spalacidae and Muridae in comparison with previous complexes. *Baranarviomys admirabilis* is an index taxon for the lower Pontian (NESIN & NADACHOWSKI 2001). This late Turolian mammal association defines the Taurian Faunistic complex of Eastern Europe (a typical site of which is Shkodova gora near Odessa; KOROTKEVICH 1988).

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Table I

The list of mammal remains from some localities from the upper Miocene lower Pontian limestone deposits

Sinyavskaya	Novocherkassk	Razdorskaya	Shkodova gora	Odessa limestone quarry	16th Station of Bolshoy Fontan, Odessa	Mamay quarry, Crimea
Collections of Rostov-on-Don, Azov, Novocherkassk and Zoological RAS museums			DUBROVO, KAPELIST 1979	KOROTKEVICH 1976; DUBROVO, KAPELIST 1979	TOPACHEVSKIY et al. 1994; NESIN & NADACHOWSKI 2001	DUBROVO, KAPELIST 1979
Russia			Ukraine			
<i>Hipparion</i> sp., <i>Paracamelus</i> cf. <i>aguirrei</i>	<i>Paracamelus</i> cf. <i>aguirrei</i>	<i>Hypolagus igromovi</i> , <i>Machairodus</i> sp., Cervidae gen.	Cervidae gen., Giraffidae gen.	<i>Mammut borsoni</i> , <i>Tetralophodon longirostris</i> , <i>Hipparion</i> sp., <i>Diceros</i> cf. "pachygnatus", "Capra" cf. <i>cebennarum</i> , <i>Palaeomeryx minor</i> , <i>Delphinus</i> sp., <i>Paracamelus</i> cf. <i>aguirrei</i>	<i>Desmana</i> cf. <i>verestchagini</i> , <i>Amblycoptis</i> sp., <i>Veterilepus</i> cf. <i>hungaricus</i> , <i>Prolagus crusafonti</i> , <i>Nannospalax compositodontus</i> , <i>Prospalax</i> cf. <i>rumanus</i> , <i>Apodemus gorafensis</i> , <i>Apodemus dominans</i> , <i>Occitanomys neutrum</i> , <i>O. brailioni</i> , <i>Pseudocricetus kormosi</i> , <i>Micromys paricioi</i> , <i>Baranarviomys admirabilis</i> , <i>Trogontherium</i> aff. "minus", Castoridae gen. (large form)	<i>Hipparion</i> sp., <i>Palaeoryx longicephalus</i> , <i>Paracamelus</i> cf. <i>aguirrei</i>

II. SYSTEMATIC PALEONTOLOGY

Suborder Selenodontia

Infraorder Tylopoda

Family Camelidae GRAY, 1821

Subfamily Camelinae GRAY, 1821

Tribe Camelini GRAY, 1821

Genus *Paracamelus* SCHLOSSER, 1903

Paracamelus cf. *aguirrei* MORALES, 1984

Paracamelus sp.: ALEXEEVA 1959, p. 146-147; 1974, p. 53-54; BAIGUSHEVA et al. 2001, p. 133; PIDOPLI-CHKO 1956, p. 79, 98; DUBROVO & KAPELIST 1979, p.69, 72; KOROTKEVICH 1976, p. 69; MORALES et al. 1980, p. 139-141.

Gigantocamelus sp.: SVISTUN 1971, p. 64-68; KOROTKEVICH 1976, p. 69.

Paracamelus aguirrei: MORALES 1984, p. 135-161; MADE et al. 2002, p. 119.

M a t e r i a l. Fragment of a left lower jaw with p4-m3 (Odessa limestone catacombs, collection of the Geological Institute RAS, GIN, № 1127); right calcaneus (Novocherkassk quarry, collection of the Novocherkassk Museum of History of the Don Cossacks, № 5747); distal parts of metapodials: a metapodial fragment (Sinyavskaya village, Rostov region, Russia, AKM-OP-27213/53, collection of the Azov Regional Museum); a metatarsus (Mamay quarry near Eupatoria, Crimea, Ukraine, № 2137, collection of Eupatoria Regional Museum); a metatarsus (Yablonya village, Odessa region, Ukraine, № 41-780, collection of Kiev National Museum of Natural History).

D e s c r i p t i o n. The lower jaw is that of an adult camel. The anterior and posterior parts of the mandible are lacking. It was found by Dr. I.Ya. YATCKO in Pontian limestone of the Odessa stone quarries. The horizontal ramus is flat and deep; it is broken at the level of the p3-p1 diastema (Fig. 2, 3). Its lingual side is flat and the buccal surface slightly convex at the level of the m2-m3. The depth of the horizontal branch increases slightly from the anterior part of p4 to m3 (Table II). The thickness of the jaw increases slightly posteriorly. The diastemal crest on the mandible in front of the p3 is moderately high and sharp.



Fig. 2. *Paracamelus* cf. *aguirrei*. Teeth p4-m3 from left lower jaw (Pontian deposits, Odessa, Ukraine, GIN, № 1127). Occlusal view.

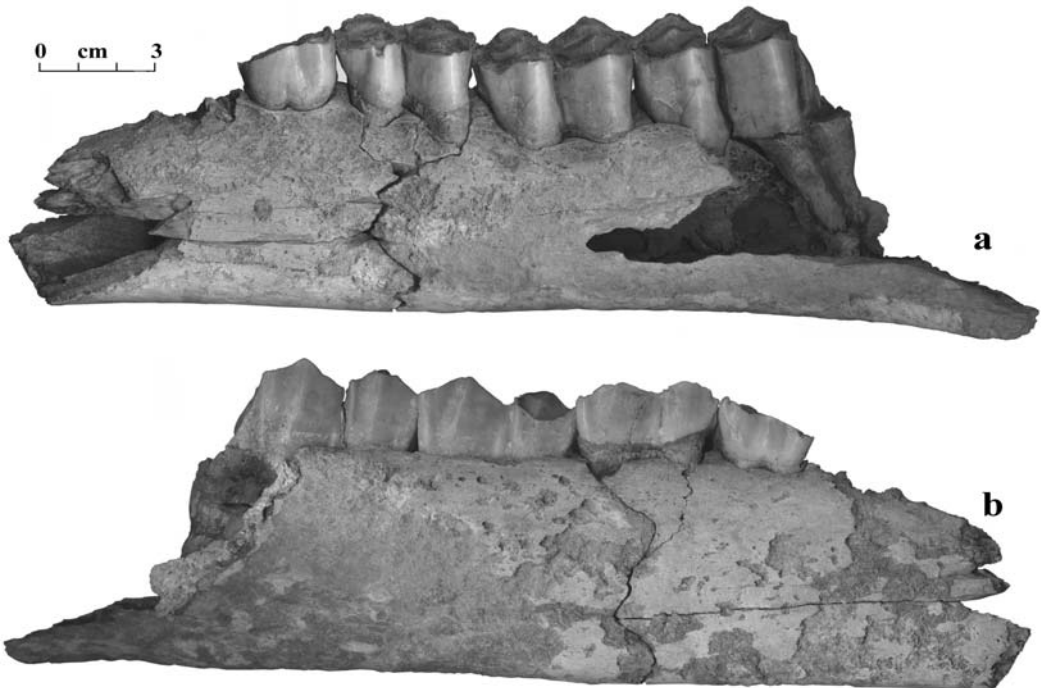


Fig. 3. *Paracamelus* cf. *aguirrei*. Left lower jaw with p4-m3 (Pontian deposits, Odessa, Ukraine, GIN, № 1127): a – Labial view; b – Lingual view.

Table II

The comparison of measurements of lower jaw and lower teeth of some large camels (measurements in square bracket are approximate due to damage). Data from: 1 – collection of GIN RAN (Moscow); 2 – MADE et al. 2002; 3 – LIKIUS et al. 2003; 4 – HAVESON 1954; LOGVINENKO 2000; 5 – collections of Rostov-on-Don Regional Museum and Azov Regional Museum; 6 – TEILHARD, TRASSAERT 1937; 7 – KHROMOV et al. 2001, collection of GIN-113; 8 – collection of Zoological Museum, Moscow State University

No	Mandible with teeth		Paracamelus						Camelus	
	Measurements [mm]	<i>P. cf. aguirrei</i>	<i>P. cf. gigas</i> ³ Kossov ³ Bougoudi KB3.97.316	<i>P. alexeevi</i> Odessa ⁴ catacomb, karst Min-(Mean)-Max	<i>P. altatensis</i> Liventsovka, ⁵ Khapry Min-(Mean)-Max	<i>P. gigas</i> China ⁶ Min-Max	<i>C. knoblochi</i> Lower Volga ⁷ Min-(Mean)-Max	<i>C. bactrianus</i> Recent ⁸ Min-(Mean)-Max		
1	Length p3-m3	al. [184]	[172]	153.0-(175.5)-182	132.6-145.7	168.0-188.0		–		
2	Length p4-m3	[163]	–	138.0-165.0	112.4-128.8			121.0-160.8		
3	Length p3- p4	[50]	[43]	33.5-(43.4)-50.0	29.2-42.4	40.0-[51]		–		
4	Length m1-m3	[138.5]	[127]	115.5-(126.6)-137	92.6-108.5	124.0-[142]	134.0; 140.0	101.8-133.1		
5	Length p3	al. [23.5]	al. [20]	15.0-(17.2)-21.0	12.4-18.6	18.0-[25]		–		
6	Width p3	–	–	8.0-(9.2)-10.0	9.2; 10.6	10.0-[12]		–		
7	Length p4	25.5	al. [26]	18.5-(22.7)-27.0	15.4-23.6	21.0-26.0		18.1-26.0		
8	Width p4	15.8	–	12.0-(13.0)-15.0	10.5-13.3	13.0-16.0		11.8-17.0		
9	Length m1	37.4	al. [33]	29.0-(38.0)-43.0	25.1-30.5	33.0-34.0		23.0-28.7		
10	Width m1	24.3	[22.2]; [22.8]	20.2-(22.5)-24.0	13.6-18.4	21.0-[28]		19.0-20.4		
11	Length m2	43.7	–	35.0-39.0	30.0-35.0	37.0-44.0	43.0; 47.0	33.5-43.0		
12	Width m2	25.0	23.7	22.0-25.0	15.0-21.0	23.0-29.0	30.0; 23.0	22.0- 27.0		
13	Length m3	[59.2]	54.4	48.0-(53.5)-56.5	39.2-47.2	40.0-62.0	61.0; 66.0; 74.0	45.8-61.2		
14	Width m3	24.3	21.5	20.5-(22.7)-26.0	13.5-18.8	22.0-28.0	25.0; 31; 42	15.0-27.0		
15	Jaw height at p4, lingual	60.0	–	48.0-(53.3)-64.0	32.0-40.2	[49]	52.0	–		
16	Jaw width at p4	24.0	–	24.0-(25.1)-27.0	19.5-26.4	–	–	–		
17	Jaw height at m1, lingual	72.0	55.0	52.0-(60.3)-69.0	32.0-44.0	–	–	36.0-57.0		
18	Jaw width at m1	30.0	–	30.0-(31.3)-32.0	24.4-32.8	–	–	25.0-32.0		
19	Jaw height at m2, lingual	72.8	–	58.0-(65.7)-74.0	40.8-(45.1)-48.8	–	–	–		
20	Jaw width at m2	[34.5]	–	35.0-(36.0)-38.0	32.1-(32.7)-33.9	–	–	–		
21	Jaw height at m3, lingual	71.2	59.0	62.0; 76.5	35.0-50.5	55.0	[58]	49.0-80.0		
22	Jaw width at m3	32.0	–	35.0-36.5	28.9-40.5	33.0	–	32.3-44.0		
23	Ratio 16/15, % at p4	40.0	–	42.0-(44.25)-46.0	57.1; 60.75	–	–	–		
24	Ratio 18/17, % at m1	41.7	–	44.0-(52.06)-56.0	58.8-(65.2)- 78.4	–	–	54.7-(69.0)-83.3		
25	Ratio 20/19, % at m2	[47.4]	–	52.0-(57.74)-63.0	65.8-(72.8)-78.9	–	–	–		
26	Ratio 22/21, % at m3	44.9	–	49.0-(53.4)-56.0	53.1-(63.5)-76.3	60.0	–	53.7-(60.3)-79.4		

The teeth are moderately hypsodont. There is no p2. The p3 on this specimen is missing, but two roots allow one to judge that this premolar was not large. The length of the p3 is 92 % that of the p4 length and 63 % that of the m1. The p4 is moderately large and slightly rounded on the labial side (Table II, III). The anterior part of the crown is broken, so it is not possible to observe the structure of antero-lingual corner of the tooth.

Table III

Teeth crown height of *P. cf. aguirrei* from Pontian deposits of Odessa (GIN-1127); teeth are in middle wear

Crown height, max, mm	p4	m1	m2	m3
Lingual	19.0	19.5	27.0	31.0
Labial	19.5	19.5	25.0	30.0

On the m2 and the m3 the metasyllids are well expressed. The m3 consists of 3 lobes. The crown of the third lobe is broken but was rounded. There is no evidence of anteroexternal styles on the molars. The anteroexternal style is weak on the m3. It is probable that on strongly worn teeth this fold usually disappears. But this feature is the result of significant individual variability among the various species of *Paracamelus* (*P. alexejevi*, *P. alutensis*). For example, on 7 out of 36 specimens of lower jaws of *P. alutensis* from Liventsovka such fold are absent (TITOV 2003).

A calcaneus was found in a limestone quarry in the neighborhood of Novocherkassk (Fig. I, Table IV). The transition from the sustentaculum tali to the body of the calcaneus is gradual with a small bend (Fig. 4). The maleolar facet is wide (its width is 62.5% its height). It is slightly oblique in relation to the main axis of the bone. The full width of the lateral surface is hollowed. In lateral view the body of the bone extends downward strongly (its diameter on tuber calcaneus is 73 % of its diameter on the level of coracoid process). The sustentaculum tali is relatively small with a crest on its top. On the plantar surface of the bone, at the level of the sustentaculum tali, there is a well expressed rugosity.

The distal ends of three large metapodials from different sites were studied. All of them were found in lower Pontian shelly limestone. These bones show the characteristic splayed and divergent condyles and a narrow intercondylar notch (Fig. 5). They are characterized by the extreme proximal divergence of metapodials III and IV (Table V). The distal condyles are relatively slender.

C o m p a r i s o n. The Pontian camel from Russia and Ukraine is similar to other *Paracamelus* in having a similar p3, slender metapodials and similar morphology of the calcaneus. The sizes of late Miocene camel from the Northern Black Sea Region are similar to those of the middle Pliocene *P. longipes* (AUBEKEROVA, 1974) from Kazakhstan (AUBEKEROVA 1974), *P. gigas* SCHLOSSER, 1903 from the late Pliocene of China (ZDANSKY 1926) and to the largest individuals of early Pliocene *P. alexejevi* HAVESSON, 1950 from the karstic features of the Odessa catacombs (early Pliocene; HAVESSON 1954). Other Eurasian representatives of this genus – *P. minor* LOGVYNENKO, 2001 (Odessa, early Pliocene), *P. alutensis* (STEFANESCU, 1895) (Eastern Europe, late Pliocene), *P. praebactrianus* (ORLOV, 1927) (Western Asia, middle-late Pliocene) and *P. trofimovi* SHARAPOV, 1986 (Kuruksay, Tajikistan, late Pliocene) are smaller (STEFANESCU 1910; ORLOV 1929; SHARAPOV 1986; LOGVYNENKO 2001; Table II).

Pontian camels clearly differ from Pleistocene and modern representatives of the genus *Camelus* by the presence of a large p3, rather narrow teeth (Table II), and by more slender metapodials with lengthened distal condyles. As a rule, late Miocene *Paracamelus* also differs from *Camelus* by its appreciably larger size, except perhaps from *C. knoblochi* POLJAKOV, 1881 from the middle - late Pleistocene of Eurasia (HAVESSON 1954; Table IV, V).

Table IV

The comparison of measurements of calcaneal bones of some camels. Data from: 1 – MADE et al. 2002; 2 – collection of Novochoerkassk Don Cossacks History Museum (Novochoerkassk, Russia); 3 – collection of Kiev National History Museum; 4 – HAVESSON 1954; LOGVINENKO 2000; 5 – collections of Rostov-on-Don Regional Museum and Azov Regional Museum; 6 – TEILHARD DE CHARDIN, TRASSAERT 1937; 7 – ORLOV 1929; HAVESSON 1954; 8 – GAUTIER 1966; 9 – HAVESSON 1954

No.	Calcaneus	Paracamelus						Camelus		
		<i>P. cf. aguirrei</i>		<i>P. alexejevi</i>		<i>P. alutensis</i>	<i>P. gigas</i>	<i>P. prae-bac-trianus</i>	<i>C. thomasi</i>	<i>C. bac-trianus</i> <i>ferus</i>
	Venta del Moro ¹		Novochoerkassk ²	Velikoploskoe, Kuchurgan ³	Odessa catacombs, carst ⁴	Khapry ⁵	China ⁶	Kazakhstan ⁷	Palikao (Algeria) ⁸	Recent ⁹
	ZV 277	NMIDK-5747			Min-(Mean)-Max	Min-Max		Min-Max		ZIN
1	Length maximal	167.0	192.8	168.5	148.0-(158.2)-169.0	129.0-142.0	181; 170; 189	134.0-157.8	198.0	152.0
2	Width maximal (latero-medially)	–	67.0	–	–	52.0	–	–	–	–
3	Minimal width bone's body (latero-medially)	23.0	30.0	27.0	22.0-(24.8)-30.0	19.2-21.8	30.5	18.5-30.5	36.0	22.0
4	Minimal anterior-posterior diameter of process anterior (heel tuber)	47.0	55.6	49.0	51.0-(57.8)-64.0	37.0-46.0	52.5	–	–	55.0
5	Minimal transversal diameter of process anterior (heel tuber)	46.0	58.7	50.0	41.0-57.0	31.0-39.7	57.0	–	–	–
6	Cuboidium articular surface length, maximal	–	54.4	45.0	40.0-(44.3)-47.0	36.0-39.0	–	35.0-44.5	–	45.0
7	Cuboidium articular surface width	–	25.8	18.0	16.0-(16.75)-18.0	10.5-15.4	–	–	–	16.0
8	Heel tuber (proc. anterior) diameter on the level condylus malleolaris, maximal	69.0	80.8	71.0	61.0-(66.4)-72.0	47.0-54.8	90.0; 80.0; 89.0	[59.5]-73.5	–	69.0
9	Condylus malleolaris width	–	24.4	21.0	21.0-(23.1)-26.0	14.2-19.6	–	16.5-21.5	–	19.5
10	Condylus malleolaris length	–	39.0	45.0	–	24.8-29.0	–	–	–	–
11	Ratio 3:1, %	13.77	15.56	16.02	14.0-(15.65)-19.0	–	16.85	–	–	14.47
12	Ratio 5:1, %	27.54	30.45	29.67	25.6-(29.1)-31.3	–	31.49	–	–	–
13	Ratio 8:1, %	41.32	41.91	42.14	40.0-(41.27)-43.0	–	47.06-49.7	–	–	45.39
14	Ratio 4:5, %	102.17	94.72	98.0	95.3-(104.0)-115.9	–	92.10	–	–	–
15	Ratio 7:8, %	–	31.93	25.35	22.5-(26.3)-29.2	–	–	–	–	23.19
16	Index of malleolar facet 9:10, %	–	57.43	46.67	–	47.62	–	–	–	–

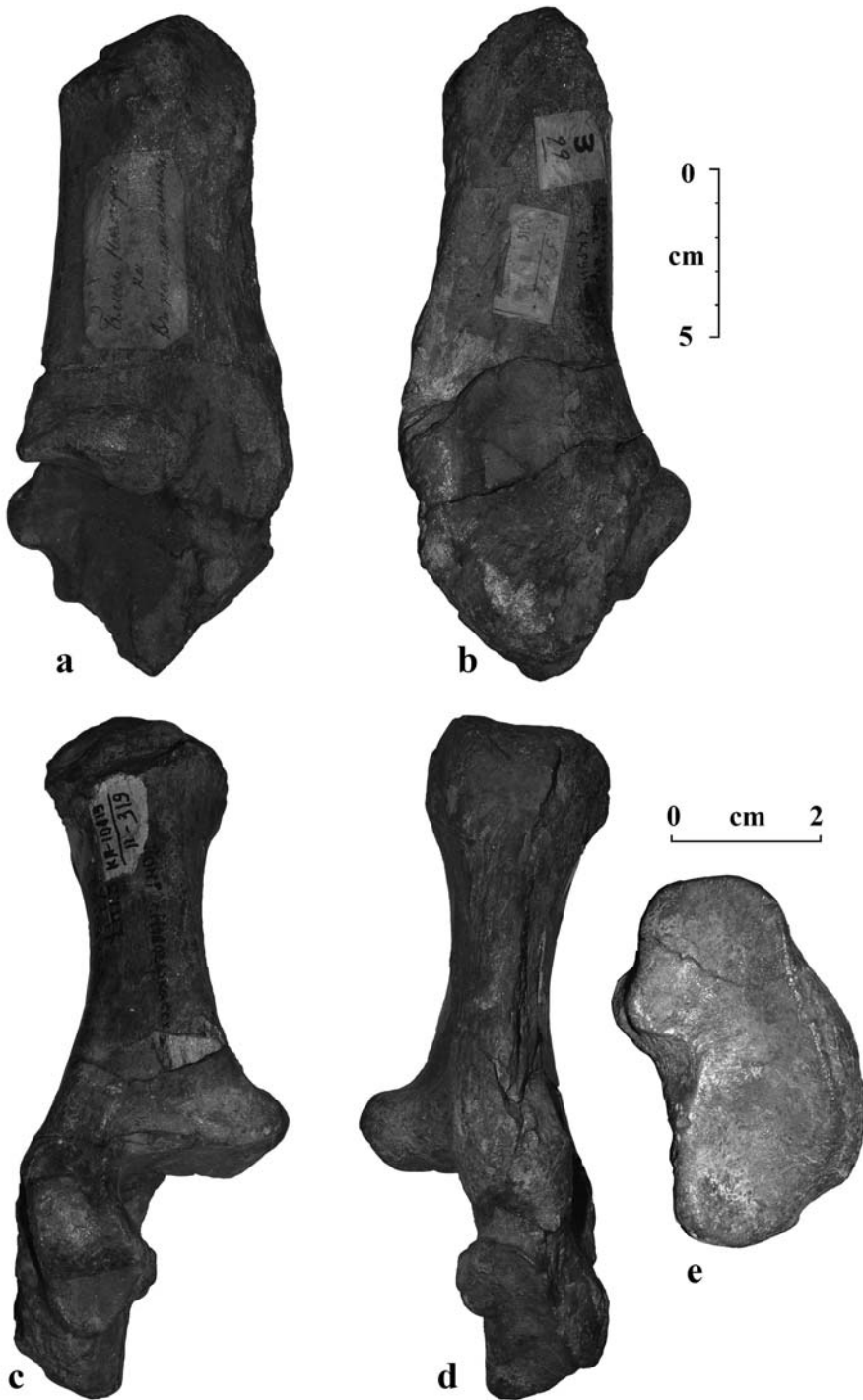


Fig. 4. *Paracamelus* cf. *aguirrei*. Right calcaneus (Pontian deposits, Novocherkassk, Rostov Region, Russia, NMHDC, № 5747): a – Medial view, b – Lateral view, c – Anterior view, d – Posterior view, e – Cuboidal facet.

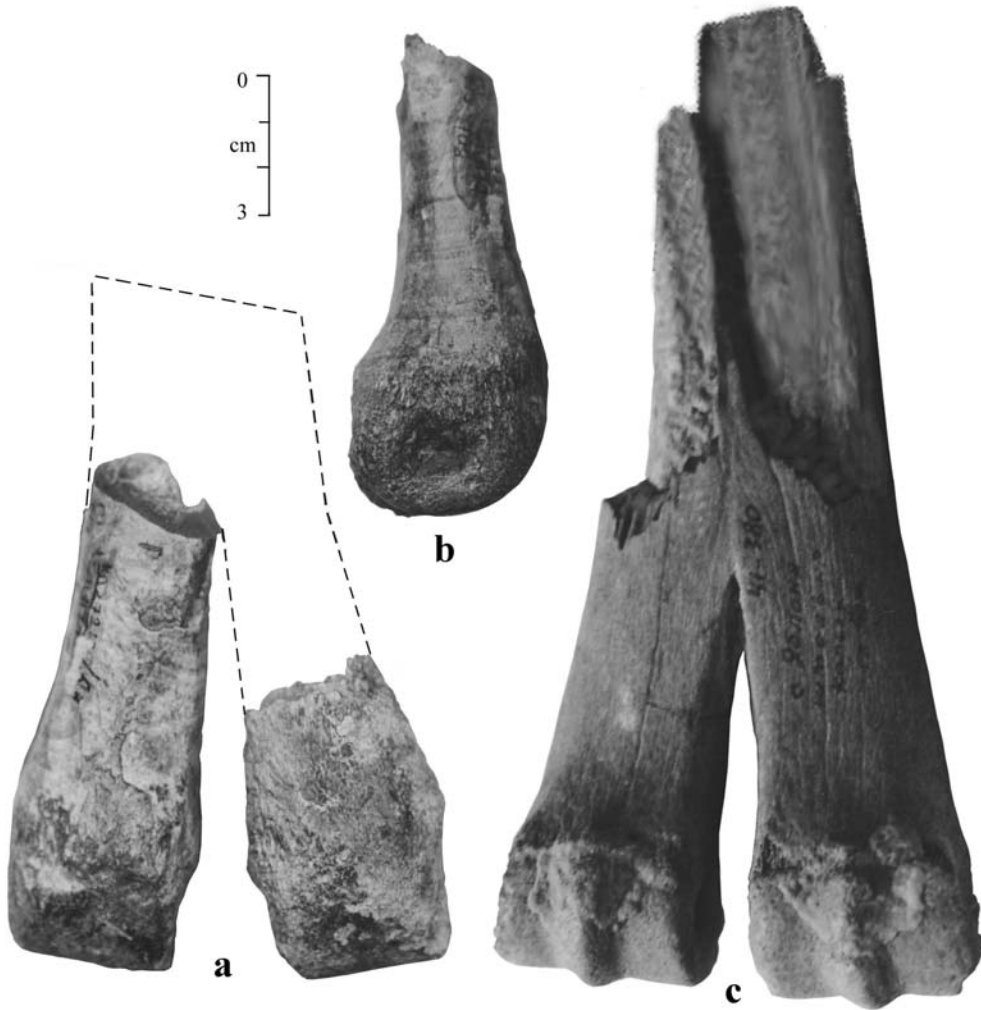


Fig. 5. *Paracamelus* cf. *aguirrei*. Distal part of metapodials (Sinyavskaya, Rostov Region, Russia, AKM, № OP-27213/53): a – Cranial view, b – Medial view. Distal part of metatarsus (Pontian deposits, Yablonya, Odessa Region, Ukraine, KMNH, № 41-780): c – Plantar view.

The horizontal branch of the lower jaw of the camel from the Odessa Pontian limestone is narrow and deep, and very distinct from most Eurasian Camelidae. However, jaws of *P. alexejevi* are more flat and higher in large males than in small specimens. The Pontian camel might also have had higher crowned teeth on the average.

In the calcaneus from the late Miocene of the Sea of Azov Region and Spain the transition from tuber to the sustentaculum tali has a more pronounced curve in comparison with that in *Paracamelus* and *Camelus*. The length of the plantar convex part of the maleolar facet of Pontian camels is almost equal to its dorsal concave part. This feature distinguishes late Miocene *Paracamelus* from other Pliocene-Pleistocene camels, which have a less concave part to the facet. The absolute sizes of the specimens from the Pontian of the Sea of Azov Region exceed those of all known finds of Tylopoda of Eurasia, including finds from the Messinian of Spain (Table IV). The calcaneus from Spain

Table V

The comparison of measurements of metapodials of some camels. Data from: 1 – ALEXEEVA 1959; 2 – collection of Azov Regional Museum; 3 – collection of Kiev National History Museum; 4 – HAVESSON 1954; LOGVINENKO 2000; 5 – collections of Rostov-on-Don Regional Museum and Azov Regional Museum; 6 – AUBEKEROVA 1974; 7 – TEILHARD DE CHARDIN, TRASSAERT 1937; 8 – HAVESSON 1954. * – calculated from fototable IV ZDANSKY 1926; TEILHARD DE CHARDIN, TRASSAERT 1937

	Paracamelus										Camelus	
	<i>P. cf. aguirrei</i>		<i>P. alexeejevi</i>		<i>P. alutensis</i>		<i>P. longipes</i>		<i>P. gigas</i>		<i>C. knoblochi</i>	
	Late Miocene, Pontian		Early Pliocene		Late Pliocene		Middle Pliocene		Late Pliocene		Late Pleistocene	
Metapodialis	Eupatoria ¹	Sinyavskaya ²	Yablonya ³	Odessa catacombs, carst ⁴		Liventsovka, Khapry ⁵	Esekartkan, Kazakhstan ⁶	China ⁷		Lower Volga ⁸		
	№ 2137, MT	AKMKP 27213/53	OF-904 / 41-780, MT	MC	MT	MC	MC	MC	MT	MC	MT	
Measurements, [mm]												
1	108.0	99.1	108.0	83.0-(90.5)-100.0	82.0-(87.0)-92.0	75.0-89.4	64.4-75.2	111.7	–	104.0	133.0-136.0	108.0
2	–	(26)	31.8	22.0-(26.2)-29.0	24.0-(27.1)-30.0	29.4-33.8	21.0-25.2	31.3	–	–	24.0-32.0	30.0
3	–	93.5	91.2	44.3-(53.9)-64.5	44.0; 50.0	48.0-56.5	58.4	–	–	–	–	–
4	48.0	(40)	49.5	40.0-(43.1)-46.0	35.0-(38.8)-44.0	34.0-40.0	26.0-33.0	48.5	–	46.0	49.0-61.0	48.0
	52.0	(49)	52.0	43.0-(45.5)-48.0	39.0-(42.5)-44.0	38.0-41.0	29.4-36.5	51.0	54.0	48.5	49.0-58.0	42.0
5	–	40.0	47.5	40.0-(44.2)-48.0	37.0-(39.2)-44.0	33.2-39.0	26.6-33.9	52.3	54.0	45.0	60.0-61.0	47.0
	–	34	52.0	44.0-(46.4)-49.0	39.0-(41.6)-43.0	37.0-40.8	29.8-37.0	53.0	55.0	48.5	54.0-60.0	43.0
6	–	94.3	84.4	47.3; 55.03; 65.7	48.6; 53.8	62.2-68.7	78.9	–	–	57.6-60.0*	–	–

seems to have a more slender body in comparison with that from Novocherkassk. However, we assume that these distinctions from the late Miocene camel of Venta-del-Moro are within the limits of individual and sexual variability.

The Pontian camel has, in keeping with *P. alexejevi* from a karst in Odessa's catacombs, a similar structure of the p3, similar proportions of the metapodials and calcaneus. Measurements of late Miocene camel bones, in general, are larger than those of *P. alexejevi* (Table II, IV, V).

The sizes and morphological characteristics of the camels from Pontian deposits are close to those of *P. cf. alexejevi* from the early Pliocene sites from the valley of the Kuchurgan River (Odessa region, Ukraine), Velikoploskoe and Grebeniki 2, dated to zone MN14 to the start of MN15 (VANGENGEIM et al. 1995; TOPACHEVSKIY et al., 1998).

The Pontian camel differs from late Pliocene *P. gigas* from Nihewan, Yushe (China) by having a higher and narrower lower jaw, longer distal condyles of the metapodials and a more slender calcaneus.

Taking into account the large dimensions, some of the morphological features, the similar age and the close geographic proximity, we attribute the camel from the lower Pontian beds of the Black Sea and the Sea of Azov regions to *Paracamelus cf. aguirrei*. However, the scarcity of the material hampers the final taxonomic decision. Unfortunately, remains of early camels from the Sea of Azov Region are hardly comparable with fossils from Spain and Turkey because of the scarcity and poor condition of the materials. It is likely that this form of *Paracamelus* was widespread in the Northern Mediterranean during the most of the late Miocene.

One can note many similar characters in the Miocene Eurasian camel and the North American *Megatylopus*. Early *Paracamelus* and *Megatylopus* share similar dimensions such as the depth of the horizontal ramus of the lower jaw, slender limb bones, especially the distal parts of metapodials, and relatively high-crowned molar. They had the same dental formula: canine-like I3, C1/c1 and P1/p1, p2 are absent, p3 and p4 are not large (HONEY et al. 1998). These features confirm the viewpoint of some investigators (MACDONALD 1956; HONEY et al. 1998) for a close relationship of these two taxa.

III. REMARKS

The similar proportions and morphology of bones, the identical dental formula, and belonging to adjacent territories, allows us to hypothesize a phyletic succession of several camel taxa in the Black Sea and Sea of Azov regions. The following evolutionary line looks likely: *P. aguirrei* – *P. khersonensis* (M. PAVLOW, 1904) – *P. alexejevi* – *P. alutensis*. The evolutionary trends might include: a gradual decrease of body size, a thickening of the horizontal branch of the lower jaw and the elongation of the facial parts of the skull. However, an appreciable reduction of p3 from early to late representatives of genus *Paracamelus* is not observed.

A g e. In general the Pontian strata of the Eastern Paratethys are correlated with the Messinian (SEMENENKO & TESLENKO 1994). Unfortunately, there is no clarity as to an exact correlation of the Messinian and the Pontian stages. Most researchers agree that these two divisions are close in age, but disagree about their lower boundaries. Lower Pontian sediments, according to some authors, are considered as equivalent (NEVESHKAYA et al. 2003), or to other authors, more ancient relation to Messinian ones from the Western Paratethys (Fig. 6). Lower Pontian strata have a reversed polarity and are attributed to Chron 6 of the magnetochronological scale (PEVZNER & VANGENGEIM 1984), or correspond to the uppermost Chron 7 (C4n) coupled with a greater portion of Chron 6 (C3Br–C3Ar) (PEVZNER et al. 2003). According to M. A. PEVZNER et al. (2003) the lower Pontian is correlated with the upper part of the Tortonian. The upper boundary of the lower Pontian coincides with the Tortonian-Messinian boundary. Using nannofossils, fission-track and paleomagnetic data the stratigraphic distribution of lower Pontian deposits is determined as 7.5–7.1 Ma (PEVZNER et al. 2003). In the CK95 scale the lower and upper limits of the Messinian correspond in age to 7.1 and

Time (Ma)	POLARITY	Polarity epoch	EPOCH	AGE	Localities							
					Africa	Western Europe	Eastern Europe	Asia				
4.5	Normal	Gilbert	PLIOCENE	EARLY	KIMMERIAN	MIDDLE	Ruscinian	Kuchurganian	Koobi Fora		Novopetrovka	
5	Normal								? Wadi Natrun Kossom Bougoudi		Kuchurgan (Velikoploskoe)	Beteke 1 (Kuskol'skaya formation)
6	Reversed	C3An Chron 5	MIOCENE	LATE	MESSINIAN	LOWER	Turolian	Vingra-dovskian		Venta del Moro Librilla		Hirgis-Nur 2 Çobanpinar
7	Normal	C3Br Chron 6							TORTONIAN	PONTIAN	LOWER UPPER	Taurian
	Normal	C4n Chron 7			MEOTIAN		Belkian					

Fig. 6. Stratigraphic position of some late Miocene sites with *Paracamelus* remains.

5.32 Ma respectively. So, based on the statement that lower Pontian layers of Eastern Paratethys are somewhat older than the Messinian ones, we suggest a more ancient age for the fauna from lower Pontian deposits than the Messinian mammal associations of the Western Paratethys.

There is no agreement about the age of the late Miocene fauna from the lower Pontian layers of the Eastern Paratethys. Some researchers correlate these associations of small and large mammals with MN 12 (PEVZNER & VANGENGEM 1984; PEVZNER et al. 2003), MN 13 (FEJFAR et al. 1997; NESIN & NADACHOWSKI 2001) or with lower part of MN 14 (TOPACHEVSKIY et al. 1998).

In Western Europe, the range of MN 12 and the beginning of MN 13 are variously defined. The ages of the upper and lower boundaries of MN 12 was determined as 8.24 and 7.3-7.1 Ma (STEININGER et al. 1996), 8.1 and 6.7 Ma (between Chron C4n.2n and Chron C3An.2n; OPDYKE et al. 1997), 7.7-8.1 and 7.1 Ma accordingly (between Chron C4n.2n and the polarity transition of Chrons C3Bn/C3Br.1r; SEN 1997). GARCÉS et al. (1998) prefer to consider the age for the MN 12/MN13 boundary older than 6.8 Ma (between 6.8-7.2 Ma) and correlated the beginning of MN 13 with the base of the Messinian stage. All of these coincide with the data of the lower Pontian.

All authors date the samples of mammals from the Messinian deposits of Spain to the late Turolian, mammal zone MN 13 (MORALES et al. 1980; MEIN 1990; PICKFORD et al. 1995; FEJFAR et al. 1997; OPDYKE et al. 1997; GARCÉS et al. 1998). The locality of Venta del Moro lies above a transition from a normal to reversed polarity and is situated in the Lower Gilbert Chron and has been dated to 5.8 Ma (OPDYKE et al. 1997; GARCÉS et al. 1998) or 6.5-5.9 Ma (STEININGER et al. 1996). Librilla is correlated with Chron C3An.1n at 6.1 Ma (GARCÉS et al. 1998).

Representative localities of large mammal remains from lower Pontian beds were not discovered hitherto. There are no reliable sites of large and small mammals of this age. The fragmentary nature of samples makes it difficult to determine the exact age of lower Pontian large mammal associations among the succession of late Turolian faunal complexes which were determined for Western Europe. However, this fauna is important stratigraphically, because it has an accurate association with marine lower Pontian deposits. Future revision and study may allow one to define more exactly its position.

According to data on MN zone boundaries, calibration the fauna from lower Pontian of Black Sea Region falls into MN 12. Taking into account the priority of faunal data in the determination of MN zone, we can relate the early Pontian faunas of the Eastern Paratethys to MN 13 of Western Europe. The presence of *Apodemus*, in the complex from the locality of 16th Station of Bolshoy Fontan (Odessa), does not allow us to attribute it easily with MN 12. However, taking into consideration the older age of the lower Pontian deposits, these faunas could be more ancient than the Lower Messinian sites of Western Europe. This may be related to the peculiarities of the geographical position of the Eastern Paratethys, and with the anisochronous appearance of some index forms in different parts of Europe.

M i g r a t i o n s. It is known that as a result of lower ocean levels in the late Miocene, a Beringian corridor allowed faunistic exchanges between Northern America and Eurasia. It is probable, some representatives of the genus *Megatylopus* managed to disperse into Asia across Beringia at that time, together with other American forms. This genus appeared at the end of the Miocene in Northern America (HARRISON 1985; MCKENNA & BELL 1998). These large animals could have quickly dispersed over Eurasia, occupying biotopes similar to those, in North America – open and semi-open landscapes of “savanna” type. From that time they evolved independently in Eurasia. Together with camels other representatives the New World fauna moved into the Old World.

The Miocene Eurasian “savanna” type landscapes was a widespread phenomenon, stretching from the Central Asia to the north of Africa. These territories were populated with associations of “hipparion” type. Camels quickly settled over the continent and reached the Western part of Europe, but they were never common. Later in the Pliocene with the increase in aridity of the area the distribution of the earliest Eurasian Tylopoda was broken up, and they adjusted to various ecological conditions in different parts of Eurasia. The development of camels adapted mainly to steppe and forest-steppe conditions occurred in the territory of the Black Sea Region and adjacent areas. In Asia camels of the genus *Paracamelus* adapted to the more arid conditions of steppe and semi-desert landscapes that developed in the Central and Western Asia.

The immigration from Northern America probably took place during zone MN12. Confirmations of this fact are camel remains from this age in Asia (locality Pavlodar; HAVESSON 1954; VANGENGEIM et al. 1993). Finds from the lower Pontian deposits of the Black Sea and the Sea of Azov regions are contemporaneous to these finds. The downturn in the sea-level of the world oceans caused the Messinian salinity crisis (KOLESNIKOV 1940; SEMENENKO & TESLENKO 1994). It is probable that the isolation of the Black Sea and the Caspian basins in contrast to a single Pontian basin occurred at this time (PEVZNER et al. 2003). During this period there was a penetration of camels to the territory of Western Mediterranean. Almost all researchers place the fauna of Venta-del-Moro and Librilla into MN13. It may be that the evidence shows that camels invaded the territory of the Western Mediterranean later than the Eastern Mediterranean.

There are no cogent arguments that late Miocene *Paracamelus* entered the territory of Western Europe from the African continent. There are no reliable finds of camels in the late Miocene localities of Africa. The migration route of camels to Western Europe most likely ran from the northern Mediterranean area in the late Miocene. Incidentally, camels have occupied both northern and southern coasts of the Eastern Paratethys and only in the early Pliocene did *Paracamelus* settle the African savannas, where they are known from several localities – Kossom Bougoudi (Chad; about 5 Ma), Koobi Fora (Kenya; 4,35-4,1 Ma), Laetoli (Tanzania; 3,8-3,5 Ma), Lac Ichkeul (Tunis) (PICK-

FORD et al. 1995; LIKIUS et al. 2003). At the beginning of the Pliocene the directions of *Paracamelus* expansion into Africa could be varied i.e. from the north of the continent and from Asia Minor.

Paleoecology. The period of the global cooling and aridification (in comparison with the earlier Meotian) is related to the beginning of the formation of the Pontian deposits (NEVESSKAYA et al. 2003; SEMENENKO & TESLENKO 1994). The Late Pontian and Messinian aridification caused the extension of the deserts and semidesert zones, and in the equatorial region, the replacement of rainforests by savannas. The Early Pontian Novorossian substage was characterized by almost a subtropical and semihumid climate in the Eastern Mediterranean. The typical Turolian fauna at this time, with an abundance of mastodons, hipparions, suids, antelopes and miscellaneous predators, indicates that the "savanna" type landscapes occurred in areas that today are in the arid zone. The small mammals of the Fontanian subcomplex of the lower Pontian indicate forest-steppe conditions, with moderate humidity, and elements of forest vegetation in the river valleys (TOPACHEVSKIY et al. 1994).

In the terminal Miocene all the arid area of today, from Northern Africa up to Western Mongolia and Tibet, were in a zone of Mediterranean subtropical climate with well defined seasonality (wet winters and dry summers) (ZUBAKOV 1990). The early Pontian of the Black Sea Region is marked by a mosaic landscape with various ecological floral and faunal elements (meadow-steppe, forest, wetland, savannah, marshland and other biotopes) (SZHEKINA 1979; NEGRU 1979; KOROTKEVICH 1988). The data on the early Pontian flora testify that widespread woodlands occurred that were insular in character. Forest associations consist mainly of deciduous trees, which did not form continuous woodlands, and covered north facing slopes and flood-plains. On wet soils there developed a local biotopes of boggy *Taxodium* forest. The grasses were represented by marshland taxa. There are palynological spectra testifying to the presence of mixed associations with a prevalence of representatives of the family Chenopodiaceae, a typical for steppe taxon (ANANOVA 1954; SZHEKINA 1979; NEGRU 1979).

The distinction of ecological conditions between the Western and Eastern Paratethys is marked. The Eastern Paratethys represented a zone of open landscapes to a greater degree. It stretched from the east of the lower reaches of the Dnieper River, and included the Northern Sea of Azov Region, the lower reaches of the Don River, and areas of the Transcaspian and southern areas of Ural River. The east and southeast borders of this zone were somewhere in Central Asia (SEMENENKO & TESLENKO 1994).

Therefore, in our opinion the early Eurasian camels mainly inhabited conditions of steppe and forest-steppe. Indirect confirmation for this thesis may be the fact that for many of the Northern American Camelinae habitats were typical the open savanna type landscapes (HONEY et al. 1998). Most likely, these animals combined browsing and grazing in their diet.

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