

## Late Pliocene Carnivores from Včeláre 2 (Southeastern Slovakia)

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**Abstract**—Carnivores from the Late Pliocene site of Včeláre 2 are described and their taxonomy is discussed. The carnivore assemblage includes nine specimens of the families Felidae (*Homotherium crenatidens*), Ursidae (*Ursus minimus*), and Ailuridae (*Parailurus* sp.). The scimitar-toothed cat and ursid are common representatives of the Pliocene European fauna, whereas the lesser panda is probably a new species of *Parailurus*, which differs from both Pliocene species, *P. anglicus* and *P. hungaricus*. As a part of a more or less uniform Pliocene carnivore fauna of the Northern Hemisphere, the Včeláre 2 assemblage represents a forest and (or) open grassland environment.

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**Key words:** *Homotherium*, *Ursus*, *Parailurus*, Pliocene, Včeláre 2, Slovakia.

### INTRODUCTION

The Pliocene is a very important geological period from the viewpoint of the origin of modern Eurasian carnivore genera. However, in Slovakia, only a few Pliocene sites are known where carnivore fossils have been found. Včeláre is one of three or four Slovak Pliocene sites yielding carnivore remains. The site is an open quarry situated in the southeastern part of the Slovak Karst on the Dolný Vrch Range south of the village of Včeláre near the town of Turňa nad Bodvou (geographic coordinates of the site are 48°36' N and 20°47' E) (Fig. 1). The section consists of the Ladinian Wetterstein limestone with some systems of karst fissures filled with terra rossa sediments along with angular fragments and blocks of limestone (ranging in size from several cm to tens of cm). The fissures are several meters wide and could have been natural traps for various animals.

At present, seven complexes of fissures are known, but only a few have yielded fossil vertebrates, mostly mammals. Fossil assemblages from two sites (Včeláre 3 and Včeláre 4) have already been described in detail. The assemblage from Včeláre 3 represents a Villanyian fauna (MN17), whereas the fossiliferous fissure fillings of the Včeláre 4 assemblage are dated Early Biharian (MQ1) (Fejfar and Horáček, 1983).

The Včeláre carnivores described come from the site Včeláre 2 (Horáček, 1985). Although this site was discovered in 1977, only partial faunal lists have been published (Holec, 1982, 1988; Horáček, 1985); and its rich mammal fauna has never been described in detail (except for proboscideans; Holec, 1985). However, the examination of all mammalian groups (including lagomorphs, rodents, primates, or ungulates) is currently in progress. Based on preliminary analysis of the mammal assemblage, which includes *Villanyia exilis*, *Borsodia hungarica*, *Tapirus arvernensis*, and *Anancus arvernensis*, the site was dated Late Pliocene, probably corresponding to a somewhat later age than that of the Hajnáčka site (MN16a).

### MATERIALS AND METHODS

The material examined is a part of the paleontological collection of the Slovak National Museum–Natural History Museum (SNM-NHM). The specimens figured were photographed with digital cameras and enhanced using COREL PHOTO-PAINT and ADOBE PHOTO-SHOP software. The measurements were taken to the nearest 0.05 mm using engineering vernier callipers capable of reading to the nearest 0.01 mm. The terminology for the main tooth cusps follows Ginsburg (1999), and that for the bear, Rabeder (1999). The Late Cenozoic biochronology follows Fejfar et al. (1998).

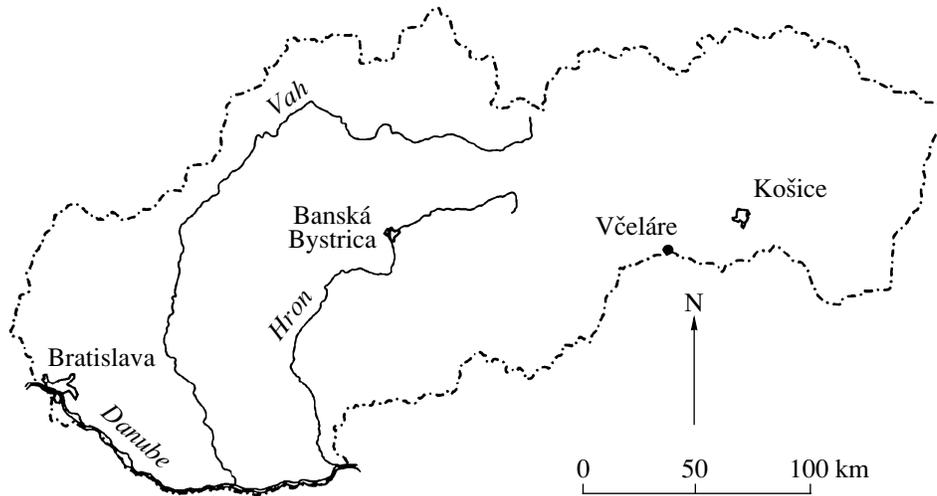


Fig. 1. Geographical position of the Včeláre site in Slovakia.

## SYSTEMATIC PALEONTOLOGY

### Family Felidae Fischer von Waldheim, 1817

Subfamily Machairodontinae Gill, 1872

### Tribe Machairodontini Gill, 1872

### Genus *Homotherium* Fabrini, 1890

*Homotherium crenatidens* (Fabrini, 1890)

Plate 8, figs. 1 and 2.

*Machairodus crenatidens*: Fabrini, 1890, pp. 162–172, pl. V, figs. 4–6, pl. VI, figs. 3–5;

*Epimachairodus crenatidens*: Kretzoi, 1929, p. 1310;

*Homotherium crenatidens*: Simpson, 1945, p. 121.

**H o l o t y p e.** A holotype was not designated. Syn-types are housed in the Museum of Geology and Paleontology, nos. IGF 817 and IGF 820, two left upper canines; Italy, Val d'Arno Superiore; Lower Pleistocene, Lower Biharian, MQ1.

**D e s c r i p t i o n.** The crowns of both lower teeth examined are almost unworn, with a coarse surface.  $P_4$  is faintly damaged; the crown is inclined posteriorly, consists of three main cusps and one small cuspid. The anterior cusp (= paraconid) with its semicircular cutting edge is well separated from the main cusp (= protoconid) by a deep notch. The distinct main cusp is pointed, with a nonserrated anterior cutting edge, which is longer than the posterior edge. It is also separated from the posterior cusp (= hypoconid) by a distinct notch. The pointed posterior cusp is approximately as large as the anterior one, and it has a distinct posterior crest. The small accessory cuspid is situated near the posterior cusp as a part of the cingulum at the posterolingual side of the tooth. In the tooth row, the posterior part of  $P_4$  crown is overlapped by the paraconid of  $M_1$ .

The large lower carnassial is damaged, mostly on the labial side, and also in the area of the anterior protoconid cutting edge, and the top part of the paraconid

is broken off. The posterior crest of the protoconid is declined almost perpendicularly to a faint trace of the posterior cingulum. The distinct notch, which separates the paraconid from the protoconid, continues into the U-shaped lingual depression with a tiny accessory cuspid at its base. The metaconid and the talonid are not developed.

**M e a s u r e m e n t s,** mm.  $P_4$ , length, 25.9; maximum width, 11.7; premolar crown height at the labial side of the protoconid, 17.6.  $M_1$ : length, 32.2; maximum width, 12.3.

**C o m p a r i s o n a n d r e m a r k s.** According to Bonis (1976), the ancestors of homotheres lived in Asia. To date, the oldest European representatives of *Homotherium* have only been recorded in the Odessa Catacombs in Ukraine; they are dated to the terminal part of Zone MN15 (Alekseev, 1945, Sotnikova, 2004). These early homotheres, along with Early Villanyian ones found in the Udunga site in Transbaikalia (MN16a; Sotnikova and Kalmykov, 1991) and the Kva-bebi site in Georgian (MN16; Vekua, 1972), are characterized by lesser average dimensions. They have a slightly reduced  $P_3$  (Sotnikova et al., 2002) and an unreduced or only slightly reduced  $P_4$  (Sotnikova et al., 2002). They also differ from homotheres of later periods in the lesser difference in length of  $P_4$  and  $M_1$  (Fig. 4); in later homotheres,  $P_4$  became gradually shorter relative to  $M_1$  (Sotnikova et al., 2002).

However, the taxonomic position of Late Pliocene and Pleistocene Eurasian homotheres remains unresolved. Ficarelli's revision (1979) of the Tuscan record from the Val d'Arno Superiore indicated no differences between *H. nestianum* and *H. crenatidens*. The material demonstrates only individual variability within a single *Homotherium* species resulting from sexual dimorphism. Based on this, Pons-Moyá and Moyá-Solá (1992) interpreted all Pliocene and Pleis-

tocene European homotheres species as synonyms of *H. crenatidens*. Sotnikova (1989) also assigned Asian forms to this species.

However, Turner and Antón (1997) take a different view. They assigned all known Eurasian (and probably also African) species (*H. nestianum*, *H. sainzelli*, *H. crenatidens*, *H. nihowanensis*, *H. ultimum*) to *H. latidens*, attributing certain morphological and metric differences to intraspecific variability. This conclusion is followed by Antón and Galobart (1999) and Reumer et al. (2003). Reumer et al., however, assigned only European forms from the Middle Pleistocene along with the latest finds from the bottom of the North Sea dated to the Denekamp interstadial ( $31\,300 \pm 400$ – $26\,700 \pm 240$  BP) to *H. latidens*. Pleistocene homotheres (*H. moravicum*, syn. *H. hungaricum*) from central Europe (Bohemia, Moravia, Slovakia, Hungary, Austria, and Germany) probably also belong to *H. latidens*, since they mostly only differ from Pliocene *Homotherium* in the absence of the parastyle in  $P^4$  (Kretzoi, 1938, Thenius, 1972).

Overall, the Eurasian material demonstrates wide variability in the dimensions of the skull, upper canines, and diastema  $C$ – $P_3$ , in the development of  $P_3$  and the diastema between  $P_3$  and  $P_4$ . Apart from sexual dimorphism, in most cases, this variability also indicates evolutionary changes, such as the reduction in dimensions and morphology of the lower premolars (Sotnikova et al., 2002). This enables the division of homotheres into two chronospecies, the earlier Pliocene–Early Pleistocene species *H. crenatidens*, with a well developed mental flange, a slightly reduced  $P_4$  (Sotnikova and Titov, 2002), and with a parastyle on  $P_4$ , and the later post-Pliocene–Early Pleistocene species *H. latidens*. Ballesio (1963) proposed a similar division. He distinguished Pliocene forms (*H. crenatidens*, *H. nestianus*) from Pleistocene representatives (*H. latidens*) of the genus. Furthermore, Sotnikova et al. (2002) divided Pliocene homotheres based on the relative lengths of  $P_4$  and  $M_1$  into two groups, Late Villanyian–Early Biharian (“Middle to Late Villafranchian”) and Late Ruscinian–Early/Late Villanyian (“Terminal Ruscinian to Early Villafranchian”) forms; the latter probably represents a separate *Homotherium* species.

The Včeláre 2 record displays only a slightly reduced  $P_4$  and a metric similarity mostly with the Late Pliocene forms (Figs. 2 and 3). Based on this, it is assigned to the species *H. crenatidens*.

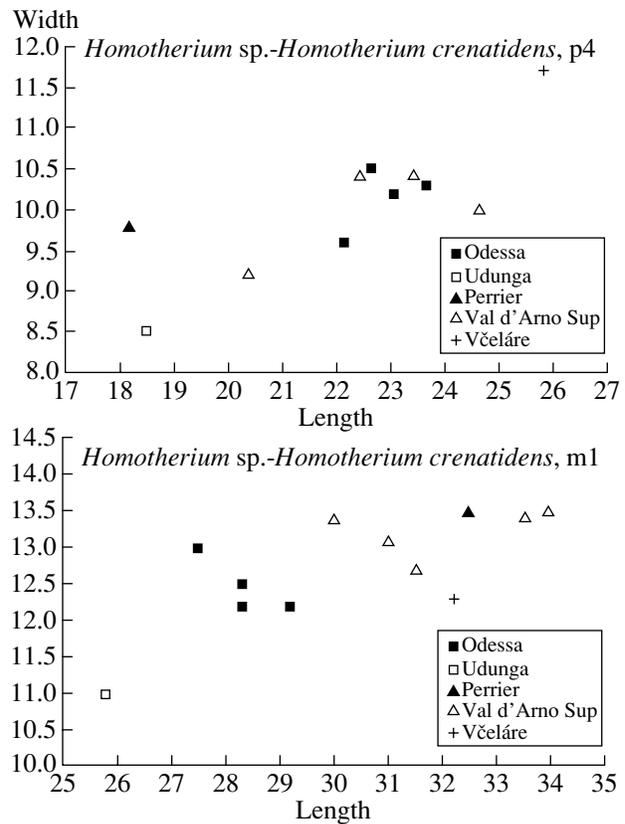
**Occurrence.** Europe, Asia (?); Lower Villanyian–Lower Biharian, MN16–MQ1.

**Material.** Two fragments of left dentaries with (Z-25237)  $P_4$  and (Z-25236)  $M_1$ .

#### Family Ursidae Fischer von Waldheim, 1817

Subfamily Ursinae Fischer von Waldheim, 1817

#### Genus *Ursus*, Linnaeus 1758



**Fig. 2.** Scatter diagram of  $P_4$  length and  $M_1$  length of Pliocene and Pleistocene homotheres (Sotnikova et al., 2002, modified).

#### *Ursus minimus* Devèze et Bouillet, 1827

Plate 8, figs. 3–6.

*Ursus minimus*: Devèze and Bouillet, 1827, p. 75, pl. XIII, figs. 1 and 2;

*Ursus arvernensis*: Croizet and Jobert, 1828, p. 188, pl. I, figs. 2–5;

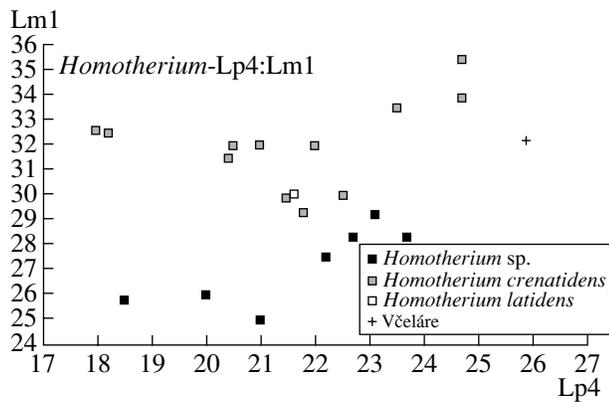
*Ursus wenzensis*: Stach, 1953, pp. 105–117, pls. I–IV;

*Ursus yinanensis*: Li, 1993; p. 44, pls. I and II.

**Holotype.** Claude Bernard University, Lyon 1, no. 211227, skull; France, Étouaires; Lower Pliocene, Villanyian, probably MN16b (?).

**Description.** Only a small mandibular fragment with  $P_4$ – $M_2$  is preserved. In front of  $P_4$ , damaged remains of  $P_3$  alveolus are present. All teeth are heavily worn. The enamel is fossilized in a whitish color and the bone is gray.

In the anterolingual part of the crown base of  $P_4$ , the enamel is missing. The dominant cusp is a conical protoconid, with the posterior arm sloping downwards more gradually than the anterior arm. The posterior end of the tooth has a well-developed hypoconid. In lingual view, the tooth is similar in outline to that of typical *U. minimus* sensu Erdbrink (1953, p. 172). Other cusps are absent.



**Fig. 3.** Biostratigraphical framework of the Pliocene and Pleistocene of Central and Western Europe (after Fejfar et al., 1998, on the left; Masini and Sala in Masini and Abbazzi, 2006, in the middle; and INQUA-ICS from 2007, with the base of the Pleistocene Series at 2.6 Ma, modified, on the right).

The first lower molar ( $M_1$ ) is slightly damaged in the trigonid part, where it is cracked. This crack is filled by calcite, which has somewhat distorted the trigonid, particularly in the buccal part. The paraconid has only a buccal arm. The protoconid is the dominant cusp of the trigonid part. The well-developed metaconid is markedly displaced distally. Its anterior end is situated distal to the top of the protoconid; it was probably connected to the central part of the protoconid, the medial slope of which forms most of the trigonid lingual portion. The posterior arm of the metaconid is turned abruptly medially, whereas that of the protoconid is turned only slightly. A small accessory cusp of the protoconid complex is placed between the posterior end of the protoconid and the anterior end of the hypoconid complex. The hypoconid is very large, with a small hypostylid. The main cusp of the entoconid complex (entoconid 1) is placed at the posterolingual corner of the tooth. From the top of this main cusp, an edge with two weak accessory cusps runs anteriorly. There is no obvious hypoconulid. A very weak cingulum is located on the buccal side under the hypoconid and on the posterior part of the protoconid (Plate 8, figs. 4a, 4b).

The last preserved tooth,  $M_2$ , is heavily worn and damaged, with most of the lingual and posterior parts of the buccal wall missing. Therefore, only a few morphological characteristics are available. A well-developed anterior metastylid is present. In front of this stylid (at the anterolingual corner), a large cusp is developed. It

probably belongs to the structures of the mesial margin. Regarding the inner field, only a mesolophid and probably a part of the enthyoconid are preserved. Generally, the morphology of the teeth seems to be simple, with relatively steep inner sloping of the main cusps (Plate 8, figs. 3–6).

**Measurements, mm.**  $P_4$ : maximum length, 12.0; maximum width, 7.0.  $M_1$ : maximum length, 21.5; buccal length of the trigonid, 14.2; lingual length of the trigonid, 14.0; trigonid width, 8.2; talonid width, 9.1; and constriction width, 8.4.  $M_2$ : maximum length, 19.2; buccal length of the trigonid, 12.1; and trigonid width, more than 11.0.

**Comparison and remarks.** Based on the faunal assemblage, which is similar to that of Hajnáčka, the site in question was dated Early Villanyian, MN16 (Horáček, 1985). Holec (1988) reported an isolated tooth and mandibular fragment of a bear from this locality, which he assigned to *Ursus deningeri*. Later, he redetermined the bear from Včeláre 2 as *Ursus cf. minimus* (Holec, personal communication).

Based on both metrical and morphological characteristics, this Včeláre 2 bear seems to be similar to the Late Ruscinian–Early Villanyian forms of *Ursus ex gr. minimus–thibetanus* sensu Mazza et Rustioni (1994). Its molars are small (with  $M_1$  longer than  $M_2$ ), within the variability of Pliocene black bears (see, e.g., Berzi, 1966, Ryziewicz, 1969), but outside the variation range of *Ursus etruscus* sensu lato (e.g., Viret, 1954, Mazza and Rustioni, 1992; Mazza and Rustioni, 1992, who mentioned only one  $M_1$  of *Ursus etruscus* sensu stricto, with the maximum length less than 21.5 mm, but respective  $M_2$  was relatively large and longer than  $M_1$ ).

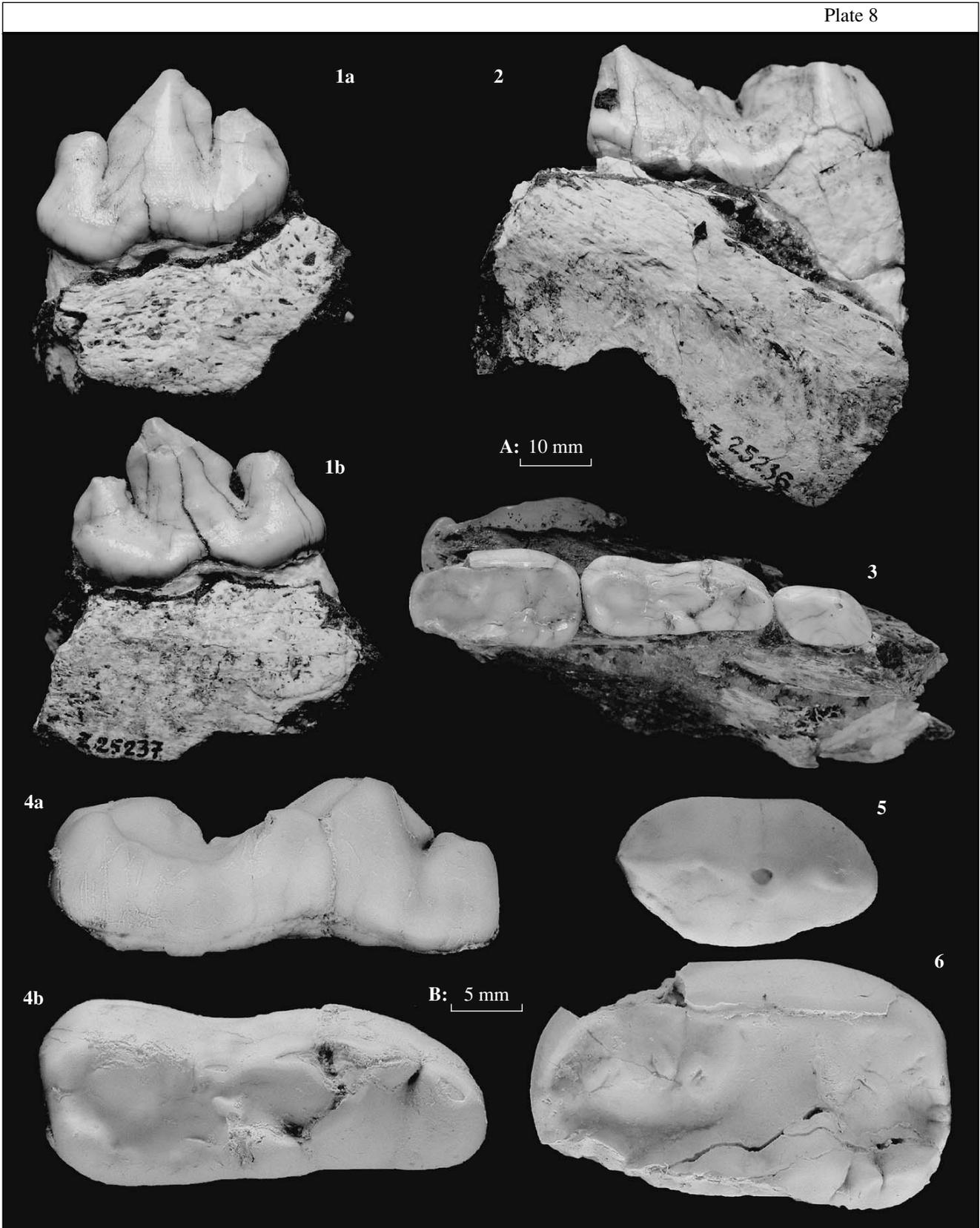
From the taxonomic point of view, the morphology of  $M_1$  plays an important role. Although this tooth is generally similar to  $M_1$  from the other MN15b–MN16b localities (e.g., from Wéze, Wölfersheim, Odessa Catcombs, Gaville, and Osztromos 7), there are some interesting differences. The posterior position of the metaconid top relative to the protoconid top, the absence of premetaconid structures, and the presence of the entoconid with a bicuspid anterior edge are rather characteristic of forms from MN14. However, the bear from Včeláre 2 is more similar to the more advanced forms in the larger dimensions and structure of the molars (e.g., the distal arm of the protoconid lacks a medial turning and has a hypostylid).

#### Explanation of Plate 8

Late Pliocene carnivores from Včeláre 2.

**Figs. 1 and 2.** *Homotherium crenatidens* (Fabrini, 1890): (1) specimen no. Z-25237, left  $P_4$ : (1a) buccal and (1b) lingual views; (2) specimen no. Z-25236, left  $M_1$ , lingual view.

**Figs. 3–6.** *Ursus minimus* Devèze et Bouillet, 1827, specimen no. Z-26702: (3) general appearance on the left dentary fragment with dentition, occlusal view; (4) left  $M_1$ : (4a) lingual and (4b) occlusal views; (5) left  $P_4$ , occlusal view; (6) left  $M_2$ , occlusal view.



Based on the above, it is possible to infer that the bear from Včeláre 2 belongs to *Ursus* gr. *minimus*–*thibetanus* sensu Mazza and Rustioni (1994). In spite of the scarcity of available material, we propose to assign this bear to *Ursus minimus* Devèze et Bouillet, 1827. This is the first well preserved evidence of this species in Slovak territory. Fejfar and Sabol (2004) and Sabol (2004) mentioned the possible occurrence of this species in Hajnáčka (MN16b); however, only one anterior premolar is known from this locality (the previously listed occurrence of *U. boeckhi* in Hajnáčka (Fejfar, 1961) was not confirmed by further revision). In relation to the Včeláre 2 bear it is also beneficial to recall the occurrence of *Ursus minimus* in the Hungarian locality of Osztramos 7 (MN16b) (Jánossy, 1978; revised by the authors), which is situated only a few kilometers from Včeláre.

In addition to the comparisons and results presented above, it is still necessary to elucidate our taxonomic concept of *U. minimus*. Within the interval from MN14 to MN16, several taxa of fossil black bears have been described in the Northern Hemisphere. Morlo and Kundrát (2001) proposed that all European bears from this period belonged to a single species *U. minimus*, represented by two chronosubspecies *U. m. boeckhi* (the older one) and *U. m. minimus*. They also proposed that Asiatic (*U. yinanensis* and *U. sinomalayanus*) and North American (*U. abstrusus*) forms may belong to this species. However, in the case of *U. sinomalayanus* we support the opinion of Thenius (1947) that this bear belongs exclusively to the *malayanus* lineage. Due to morphological (in particular, morphology of the entoconid complex of  $M_1$ ) and paleobiogeographical reasons, we do not suppose the conspecificity of *U. minimus* and *U. abstrusus* (at least until new material of *U. abstrusus* is described). Concerning MN14 specimens (including *U. boeckhi*), we agree with Montoya et al. (2006) that it should be assigned to a different taxon. Based on our data, it seems that MN14 bears differ from typical *U. minimus*, e.g., in the morphometry of  $M_1$  (different character of the entoconid and variation of the maximum lengths). However, because of the small number of MN14 specimens, this is only a preliminary conclusion. The specification of the taxonomic position of the crucial MN15a bears (Perpignan) requires further study and remains an open question.

**Occurrence.** Europe, including the Caucasus, northern Asia, North America (?); Upper Ruscinian–Lower Villanyian, MN15–MN16.

**Material.** A left mandibular fragment with  $P_4$ – $M_2$  (specimen Z-26702).

#### DESCRIPTION AND CONSIDERATION OF THE MATERIAL OF *PARAILURUS*

The material of the lesser panda from Včeláre 2 (Pl. 9) is described in open nomenclature as *Parailurus* sp. (the genus *Parailurus* Schlosser, 1899: Ailurinae, Ailuridae). It includes a right maxillary fragment with unerupted  $P^3$  and  $P^4$  (specimen Z-26703/1); fragment of right  $M^1$  (Z-26703/2); fragment of left  $P_4$  (Z-26704/2); left dentary fragment with damaged  $M_1$  (Z-26704/1); right dentary fragment with  $P_3$  (damaged),  $P_4$ , and  $M_1$  (damaged) (Z-26705/2); and a fragment of right  $M_2$  in a mandible fragment (Z-26705/1).

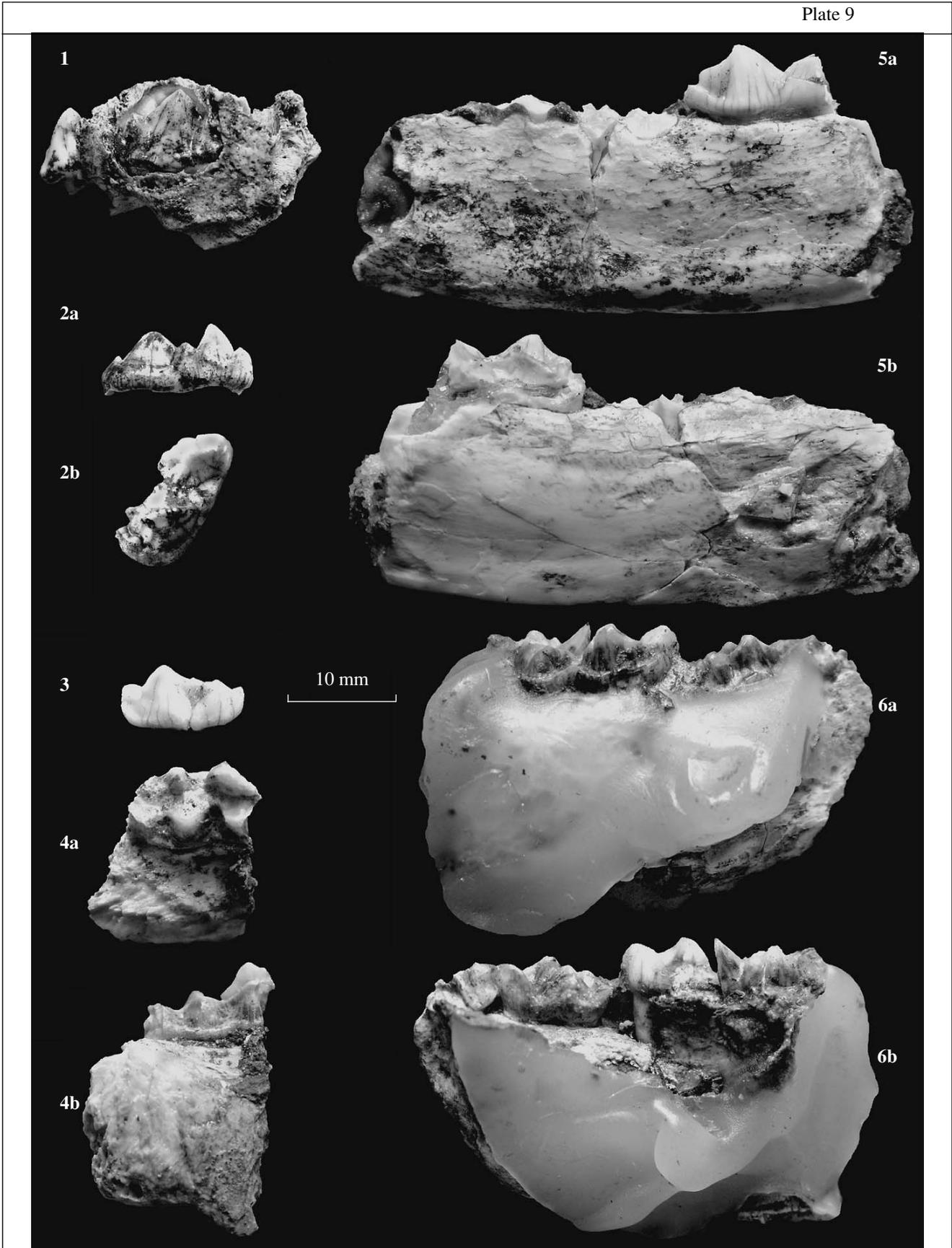
Unerupted right  $P^3$  consists only of an unworn rootless crown. The crown is oval in occlusal view with a faint lingual extension, which probably results from premolar molarization. The main cusp (= paracone) is high and robust, with distinct anterior and posterior crests, which form a shearing edge. The anterior crest of this cusp is faintly arched in its lower part, substituting the missing parastyle. The strong medial ridge of the main cusp, ending near the lingual cingulum, divides the lingual crown area into the anterolingually pointed and lingually pointed walls. The second is approximately twice as large as the first. The hump-like posterior cusp (= metacone or metastyle) is situated behind the main cusp and separated from it by an indistinct notch. It is shifted slightly labially. The labial cingulum is weak, whereas the lingual cingulum is massive and humped in its posterior part, where it is probably turned towards the posterior cingulum. The maximum width of  $P^3$  (specimen no. Z-26703/1) is 5.0 mm, and its paracone is 6.0 mm high on the labial side.

Only the labial side of the unworn crown of rootless right  $P^4$  is exposed. The anterior and posterior crests of the robust paracone form a conspicuous carnassial edge. The well-developed parastyle is situated in front of the paracone and separated from the main cusp by a narrow notch and restricted anteriorly by a rim-like cingulum (or cingular ectoparastyle). The metacone (metastyle) is smaller than, or as large as, the parastyle. It is separated from the paracone by a weak notch, which is continued by a narrow labial groove. The labial cingulum is poorly developed, faintly shelf-shaped in the area below the groove, which runs

#### Explanation of Plate 9

*Parailurus* sp. from Upper Pliocene of Včeláre, Slovakia.

**Figs. 1–6.** (1) specimen no. Z-26703/1, right maxillary fragment with unerupted  $P^3$  and  $P^4$ , buccal view; (2) specimen no. Z-26703/2, fragment of right  $M^1$ : (2a) mesial and (2b) occlusal views; (3) specimen no. Z-26704/2, fragment of left  $P_4$ , buccal view; (4) specimen no. Z-26705/1, fragment of right  $M_2$  in the mandible fragment: (4a) occlusal and (4b) buccal views; (5) specimen no. Z-26704/1, left dentary fragment with damaged  $M_1$ : (5a) buccal and (5b) lingual views; (6) specimen no. Z-26705/2, right dentary fragment with  $P_3$ ,  $P_4$ , and  $M_1$ : (6a) buccal and (6b) lingual views.



between the paracone and the metacone. On the labial side, the paracone of P<sup>4</sup> (specimen no. Z-26703/1) is 6.2 mm high.

The fragment of the unworn crown of rootless right M<sup>1</sup>, which probably belonged to the same juvenile animal as the above-mentioned premolars, consists of only the mesial part, with the parastyle, paracone, protocone, and paraconule. The mesial angle is about 60°. The paracone is conical, higher than the protocone, with a conspicuous sharp, blade-like posterior (part of the centrocrista) and anterior (or anterolabial) crests along with a small crestlike accessory cusp at the base of the inner side near the protocone. The surface of the paracone is smooth and faintly wrinkled only at the base of its inner side. The distinct parastyle is separated from the paracone by a deep notch. Its short posterolingual crest is not fused with the paracone anterior one, while the long arched anterolabial–labial crest ends near the bottom of a labial groove-shaped depression between this cusp and the paracone. Another short ridge runs mesially from the parastyle tip towards a small accessory cusp situated close to the parastyle at the anterolabial corner of the crown. From this accessory cusp, a crest runs along the anterior crown margin towards the paraconule to the tiny intermediate cusp, thus, dividing it from the arched, humped anterolabial crest of the paraconule. The ridge-shaped paraconule is conspicuous, approximately as high as the parastyle, with a short posterolingual crest and a long anterolabial crest. The cusp is distinctly separated from the paracone by a groove and from the protocone by a narrow, but marked notch. The protocone is large, extensive, but lower than the paracone, faintly wrinkled at the base of its inner side. It has a crest running anterolabially from its posterolingual border through the weakly humped tip towards the paraconule. The lingual part of the crown is rounded. The inner cingulum is distinctly developed only on the lingual side, where it surrounds the anterolingual base of the protocone, with a series of six or seven cusps at its upper margin. The greatest width of M<sup>1</sup> (specimen no. Z-26703/2) is 11.55 mm.

Only the posterior crown part of double-rooted right P<sub>3</sub> is preserved. The crown fragment has a blunt posterior cusp (= hypoconid) and a lingual talonid basin bordered by a crest-shaped cingulum. The tooth is somewhat overlapped in the tooth row by the anterior cusp of P<sub>4</sub>.

The undamaged crowns preserved of right and left double-rooted P<sub>4</sub>s show an advanced stage of molarization. The conspicuous anterior cusp (= paraconid) with lingual and labial crests is shifted slightly lingually and tilted more anteriorly. The lingual crest of the cusp ends near the lingual opening of the nearly circular trigonid basin, whereas the labial crest is separated from the anterior crest of the main cusp (= protoconid) by an indistinct notch. The high main cusp is less massive than the lingual cusp (= metaconid). Its posterior crest runs towards the notch separating it from the posterior

cusp (= hypoconid). The medial crest of the main cusp is substituted by a crest-shaped accessory cusp, separating it from the medial crest of the lingual cusp. The lingual cusp is large, trilateral, with flat anteromedial, flat posteromedial, and convex labial walls. In addition to the medial crest, the posterior crest is present. It is separated by a notch from the posterolingual crest-shaped cingulum. The conical blunt posterior cusp is the smallest cusp of the crown. It, along with the main cusp, lingual cusp, and posterolingual cingulum border the relatively deep and wide V-shaped talonid basin, which is slightly larger than the trigonid basin. The anterolabial cingulum is either weak or shaped as a shelf-shaped crest under the labial wall of the anterior cusp. A weak cingulum is also developed at the crown base in the area between the main and posterior cusps. The crown fragment of left P<sub>4</sub> probably belongs to the left dentary fragment with M<sub>1</sub>. The maximum lengths of P<sub>4</sub> are 10.75 mm in specimen no. Z-26704/2 and 10.3 mm in specimen no. Z-26705/2; the maximum width is (specimen no. Z-26705/2).

The trigonid of both M<sub>1</sub> is larger than the talonid. Both crown portions are arched labially, making the labial crown side bilobate in occlusal view. The lingually and anteriorly shifted paraconid (the smallest cusp of the trigonid) is a conspicuous, trilateral cusp, with a distinct lingual crest and a blunt labial crest terminating in a notch, which separates it from the anterior protoconid crest. The posterior crest of the conical protoconid is bifurcated; one branch turns medially towards the metaconid and the second runs posteriorly to the nearby cusp base. Here it turns labially, verging into a crest-shaped to shelf-shaped humped structure, forming the labial border of the basin between the protoconid and the hypoconid. The metaconid is separated from the entoconid by a distinct notch and lingual groove. The trigonid basin is wide, relatively shallow and probably opens lingually. The hypoconid is a blunt, wide conical cusp. It either possesses a small accessory cusp on the anterolingual side, which turns into a humped crest, forming a lingual border of the basin between the protoconid and the hypoconid, or lacks an accessory cusp. The small entoconid is separated from the conical entoconid by a notch. Behind the latter cusp, which is smaller than the hypoconid, the blunt hypoconulid is situated as the smallest talonid cusp, forming the end of the posterior cingulum. The talonid basin is shallow and narrow, and oriented anteroposteriorly. The lingual cingulum only forms a crest-shaped structure below the end of the lingual paraconid ridge, while the labial cingulum is massive, bordering the crown base from the paraconid to the hypoconid. In specimen no. Z-26705/2, M<sub>1</sub>, the greatest length is 14.3 mm and the greatest width is 7.5 mm.

The fragment of the unworn crown of right M<sub>2</sub> consists of a damaged protoconid, metaconid, and entoconid, while the hypoconid is complete. The lingual cusps are separated from the labial cusps by a distinct

**Table 1.** Teeth measurements of lesser pandas (after Morlo and Kunderát, 2001; Fejfar and Sabol, 2004; Wallace and Wang, 2004); lengths and widths, in mm; angle A is the angle between the anterior and labial crown sides

	P <sub>4</sub>		M <sub>1</sub>		M <sup>1</sup>		
	length	width	length	width	length	width	angle A, deg
<i>Ailurus fulgens</i> (Recent)							
females	–	–	11.5	6.0	9.2	11.0	85
	–	–	11.9	6.0	9.6	11.2	77
males	–	–	11.9	6.3	9.2	11.8	72
	–	–	11.3	6.2	9.5	11.0	70
<i>Pristinailurus bristoli</i> (MN13–MN14)							
Gray Fossil Site (USA)	–	–	–	–	11.4	12.3	–
<i>Parailurus anglicus</i> (MN14–MN15)							
Barault-Capeni (RO)	–	–	15.0	8.7	13.3–13.8	14.0–14.2	–
	–	–	17.4	8.8	–	–	–
	–	–	15.8	8.1	–	–	–
Boyton (GB)	–	–	–	–	14.5	14.5	–
Wölfersheim (D)	10.75	6.85	18.55	9.45	14.25	14.25	71
	10.8	6.8	(14.8)	(8.40)	(14.45)	(14.45)	–
	9.5	6.1	–	–	–	–	–
<i>Parailurus hungaricus</i> (MN16)							
Hajnáčka (SK)	–	–	20.5	11.6	15.4	15.6	83
<i>Parailurus</i> sp.							
Včeláre (SK)	10.3	5.25	14.3	7.5	–	11.55	~60
	10.75	–	–	–	–	–	–

sagittal depression. The posterior crests alone are preserved of the trigonid cusps and the entoconid is only represented by the superior and inner surfaces. The conical hypoconid, with its anterior, posterior, and medial crests is wide. It is separated from the protoconid and hypoconulid by synclinal depressions. At the base of the crown labial side, a distinct cingulum fragment is preserved. The dentary fragment with M<sub>2</sub> and the above-mentioned fragment of the right dentary with P<sub>3</sub>–M<sub>1</sub> probably belong to the same specimen of a lesser panda. The fragment of the left dentary shows a relatively slender horizontal ramus, with a slightly concave labial side and a convex lingual side. The two mental foramina preserved are relatively large, located below the alveolus of the posterior root of P<sub>2</sub> or below the posterior root of P<sub>3</sub>. Judging from the shape of the alveolus, the root of the lower canine was lateromedially flattened. The depth of the left dentary at M<sub>1</sub> on the labial side is 17 mm.

To date, five or six lesser panda species have been recorded in the Pliocene; they occur from North America (*Pristinailurus bristoli* from Gray Fossil Site (Wallace and Wang, 2004) and *Parailurus* sp. from Taunton (Tedford and Gustafson, 1977)) through Asia (*Parailurus* sp. from Tochio (Sasagawa et al., 2003) and *Parailurus* sp. from Udunga (Sotnikova, 2006)) to Europe

(*Parailurus anglicus* from Felixtowe-Red Crag (Dawkins, 1888), Boyton (Newton, 1890), Wölfersheim (Morlo and Kunderát, 2001), Ivanovce (Fejfar and Sabol, 2004), and Barault-Capeni (Schlosser, 1899); and *Parailurus hungaricus* from Hajnáčka (Kormos, 1935, Fejfar, 1964, Fejfar and Sabol, 2004) and Aronelli (Berzi et al., 1967)). From a paleobiogeographical point of view, the Slovak western Carpathians played an important role, since both European Pliocene species of the lesser pandas have been found here (Ivanovce, Hajnáčka), as well as the form from the Včeláre 2 site.

These new panda fossils display a relatively unusual combination of primitive and derived characters, differentiating them from *P. anglicus* and *P. hungaricus*.

The lesser panda from Včeláre 2 differs from *P. anglicus* in having (1) smaller tooth measurements (Table 1); (2) a smaller mesial angle of M<sub>1</sub>, with the paracone higher than the protocone, the paraconule distinctly separated from the protocone, and the less projecting inner cingulum; and (3) larger anterior cusp and more massive lingual cusp of P<sub>4</sub>. It differs from *P. hungaricus* in the smaller tooth measurements (Table 1); the smaller mesial angle of M<sub>1</sub>, with the protocone not

**Table 2.** Carnivore faunas of various Pliocene sites: (1) Barault Capeni (Schlosser, 1899), (2) Wölfersheim (Morlo and Kundrát, 2001), (3) Wèze 1, (4) Ivanovce (Fejfar and Sabol, 2004), (5) Odessa (Sotnikova, 2004), (6) Villaroya (Turner, 1987), (7) Les Étouaires, (8) Arondelli/Triversa (de Bruijn et al., 1992), (9) Hajnáčka (Fejfar and Sabol, 2004), (10) Udunga (Sotnikova, 2006), (11) Valverde (Kurtén and Crusafont-Pairó, 1977), (12) Chagny (Argant, 1991), (13) Saint-Vallier (de Bruijn et al., 1992), (14) Senèze (Delson et al., 2006), and (15) Včeláre 2

Taxon/locality	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Lynx issiodorensis</i>							+			+			+		
<i>Lynx</i> sp.					+										
<i>Puma pardoides</i>											+		+		
<i>Dinofelis</i> cf. <i>abeli</i>					+										
<i>Megantereon cultridens</i>						+	+				+		+	+	
<i>Megantereon</i> sp.									+						
<i>Homotherium crenatidens</i>						+	+					+	+	+	+
<i>Homotherium</i> sp.					+					+					
<i>Acinonyx pardinensis</i>							+	+					+	+	
<i>Viverra</i> cf. <i>prepratxi</i>								+							
<i>Hesperoviverra carpathorum</i>				+											
Viverridae indet.				+											
<i>Pliocracuta pyrenaica</i>					+					+					
<i>Pliocracuta perrieri</i>						+	+		+			+	+	+	
<i>Chasmaporthetes lunensis</i>					+		+	+					+	+	
?Hyaenidae indet.				+											
" <i>Eucyon</i> " <i>odessanus</i>					+										
<i>Nyctereutes megamastoides</i>						+	+				+		+	+	
<i>Nyctereutes sinensis</i>			+												
<i>Nyctereutes</i> sp.										+					
<i>Vulpes alopecoides</i>													+	?	
<i>Vulpes praecorsac</i>					+										
<i>Canis senezensis</i>														+	
Canidae indet.			+												
<i>Ursus minimus</i>	+	+	+		+					+		+			+
<i>Ursus etruscus</i>													+	+	
<i>Agriotherium intermedium</i>			+												
Ursidae indet.				+					+						
<i>Baranogale helbingi</i>			+					+					+		
<i>Baranogale</i> sp.		+			+										
<i>Mustela pliocaenica</i>			+												
<i>Mustela plioerminea</i>		+	+												
<i>Mustela</i> sp.									+						
<i>Martes wenzensis</i>			+												
<i>Martes</i> sp.					+										
<i>Arctomeles ferus</i>					+										
<i>Arctomeles pliocaenicus</i>			+												
<i>Parameles suillus</i>										+					
<i>Meles thoralis</i>													+		
Melinae indet.										+					
<i>Gulo minor</i>										+					
<i>Pannonictis</i> sp.		cf.													
<i>Enhydriactis ardea</i>		+											+		
<i>Lutra bravardi</i>									cf.				+		
<i>Lutra</i> sp.				+											
Mustelidae indet.				+											
<i>Parailurus anglicus</i>	+	+		cf.											
<i>Parailurus hungaricus</i>								cf.	+						
<i>Parailurus</i> sp.										+					+

shifted mesially; and in the less projecting inner cingulum.

*Parailurus* sp. from Včeláre 2 differs from *Ailurus fulgens* in the advanced morphology. Its paraconule is distinctly separated from the protocone and has a less projecting inner cingulum of M<sup>1</sup>. This seems to support the hypothesis of Wang (1997) that *Parailurus* is too derived to be the ancestor of *Ailurus*. Since the differences in tooth size could have reflected valid taxonomic differences (Sasagawa et al., 2003), the record from Včeláre 2 may represent a new European species of the lesser panda. Moreover, it shows a certain similarity in the morphology of M<sup>1</sup> to the North American *Parailurus* sp. from the Lower Pliocene of Taunton. However, the different age of these sites and their large geographical distance, in all likelihood preclude the possibility of including the forms from Včeláre 2 and North America to the same lesser panda species.

An almost complete skull with the dentition of a lesser panda was found in 1992 in the same East Slovakian site as the above-mentioned material (Kundrát, 1996). Both records probably belong to the same Late Pliocene panda species, and a description based on the skull discovered is being prepared by Dr. M. Kundrát. From this viewpoint and because of the scarcity of material, at present, it is only possible to assign the jaw fragments and teeth described from Včeláre 2 to *Parailurus* sp.

#### REMARKS ON PALEOBIOGEOGRAPHY, PALEOECOLOGY, AND THE AGE OF THE SITE

The Včeláre 2 site has yielded fossils of three Late Pliocene carnivore genera (*Homotherium*, *Ursus*, and *Parailurus*; Table 2). This record is unique due mostly to the presence of fossil remains of a lesser panda, which probably represents a new Late Pliocene species of *Parailurus* in Europe.

Lesser pandas are rarely found in European Pliocene sites. Apart from Včeláre 2, they have only been found in seven localities in England (Felixtowed Red Crag and Boyton), Germany (Wölfersheim), Italy (Arondelli), Romania (Barault-Capeni), and Slovakia (Ivanovce and Hajnáčka). However, their geographical range during the Pliocene period covered the whole area of the northern continents from Europe (*Parailurus*) through Asia (*Parailurus*) to North America (*Pristinailurus*, *Parailurus*).

However, *Homotherium* and *Ursus* are common in the Late Pliocene faunas of Europe and their presence in Včeláre 2 is more or less expected. Thus, the Včeláre 3 Carnivore Assemblage (Canidae gen. indet., *Ursus* sp., *Mustela* cf. *nivalis*), which Fejfar and Horáček (1983) referred to MN17, forms the terminal member of the Pliocene faunal succession in the Western Carpathians. The Ivanovce Assemblage (MN15b) forms the beginning and the Hajnáčka (MN16a) and Včeláre 2 (prob-

ably MN16b) assemblages are intermediate members of this sequence. This also fits well with other Pliocene carnivore faunas from Western and Central Europe.

The European Late Pliocene carnivore fauna was a result of faunal turnover during the Early/Late Pliocene Period (Late Ruscinian/Early Villanyian, MN15/MN16), when "true" canids appeared mostly in connection with the extinction of hyenids and probably also of large viverrids. At the same time, large machairodontine felids, such as *Homotherium* or *Megantereon*, probably spread from Eastern Europe to other European areas and some ancient carnivore elements (e.g., agriotheriines, which are not known in Europe after MN15) gradually became extinct. Surprisingly, the lesser pandas (*Parailurus*) were present in Europe during the whole of this turnover period, and they probably died out at the end of the Early Villanyian (MN16).

Although these carnivore faunas are more or less uniform (Table 2), it is possible to find some differences between the assemblages from Central and Western Europe (Morlo and Kundrát, 2001). However, the presence of some genera (e.g., *Ursus*, *Eucyon*, *Homotherium*, *Megantereon*, *Chasmaporthetes*, and *Parailurus*) in both Asia and North America shows that the whole carnivore fauna of the Northern Hemisphere was ecologically uniform (Alroy et al., 1998), differing mostly at the species level and due to some endemic taxa (Morlo and Kundrát, 2001).

From an ecological viewpoint, the referred taxa of carnivores from the Včeláre 2 site correspond to forest (*Ursus* and *Parailurus*) and open grassland (*Homotherium*) habitats. This is supported by records of other mammals, such as *Macaca sylvanus florentina*, *Tapirus arvernensis*, *Anancus arvernensis*, and *Hypolagus*. The mammal assemblage recorded in the Late Pliocene Včeláre 3 site, including reptiles, erinaceids, talpids, soricids, bats, arvicoline and cricetine rodents, anomomyids, murids, glirids, dipodids, lagomorphs, primates, canids, ursids, mustelids, and horses (Fejfar and Horáček, 1983), indicates similar paleoenvironments, although they could have been drier and more open. Thus, the whole mammalian assemblage from the site under study is most similar in ecology to that of Hajnáčka and in general corresponds to humid forest habitats.

Based on this and morphometric analysis of the above-mentioned carnivore fossils, it is possible to speculate that the site is probably younger than the Hajnáčka site, but older than the Včeláre 3 site. Thus, the Včeláre 2 site should be dated MN16b (or MN16/MN17?).

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