PalZ (2017) 91:409–426
DOI 10.1007/s12542-017-0371-7

RESEARCH PAPER

A new species of *Paramachaerodus* (Mammalia, Carnivora, Felidae) from the late Miocene of China and Bulgaria, and revision of *Promegantereon* Kretzoi, 1938 and *Paramachaerodus* Pilgrim, 1913

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Received: 17 March 2016 / Accepted: 10 June 2017 / Published online: 18 August 2017

Abstract New Machairodontinae material from the late Miocene localities of Hezheng (China) and Hadjidimovo (Bulgaria) represents a new species of *Paramachaerodus* Pilgrim. Both localities are similar in age and suggest that the new species had a very large geographic range extending from northwestern China adjacent to the Tibetan Plateau (Gansu Province) to southeastern Europe or probably to all of southern Europe. The new species—*Paramachaerodus transasiaticus* sp. nov is characterized by a combination of features of "*Promegantereon*" and *Paramachaerodus*. This specific morphology, as well as the age of the Hezheng and Hadjidimovo (early Turolian, after the European Land Mammal Ages) put the new species in intermediary position between "*Promegantereon*" and *Paramachaerodus*. The new felid material give grounds to discuss and revise in a new light the systematic and evolution of the "*Promegantereon*"–*Paramachaerodus* lineage, which should represent successive stages of one and the same genus: *Paramachaerodus* Pilgrim.

Handling editor: Irina Ruf.

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Keywords Machairodontinae · *Paramachaerodus transasiaticus* sp. nov. · *Promegantereon* · Late Miocene · China · Bulgaria

Kurzfassung Neues Material von Machairodontinae aus den obermiozänen Fundstellen Hezheng (China) und Hadjidimovo (Bulgarien) repräsentiert eine neue Art, die der Gattung *Paramachaerodus* Pilgrim zugeordnet werden kann. Die beiden Fundstellen sind altersgleich und deuten darauf hin, dass die neue Art ein sehr ausgedehntes Areal von Nordwest-China, im benachbarten Hochland von Tibet (Provinz Gansu), bis Südost-Europa oder möglicherweise auch ganz Südeuropa besiedelt hat. Die neue Art – *Paramachaerodus transasiaticus* sp. nov. – wird durch eine Kombination der Merkmale von *Promegantereon* und *Paramachaerodus* charakterisiert. Sowohl die spezifische Morphologie als auch das Alter von Hezheng und Hadjidimovo (Unteres Turolium, nach der europäischen Landsäugetier-Chronologie) stellen die neue Art in eine Zwischenposition zwischen *Promegantereon* und *Paramachaerodus*. Das neue Feliden-Material bietet eine Diskussionsgrundlage und rückt die Systematik und Evolution der Abstammungsgruppe *Promegantereon–Paramachaerodus* in ein anderes Licht, die nachfolgende Stadien von ein und derselben Gattung (*Paramachaerodus* Pilgrim) repräsentieren soll.

Schlüsselwörter Machairodontinae · *Paramachaerodus transasiaticus* sp. nov. · *Promegantereon* · spätes Miozän · China · Bulgarien

Institutional abbreviations

IVPP (V) Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China

NMNH-A	Paleontological museum-Assenovgrad, branch of the National Museum of Natural History—Sofia, Bulgaria
NHMW	Naturhistorisches Museum Vienna, Austria
PMU (M)	Collection of the Evolution Museum of Uppsala University, Sweden

Anatomical abbreviations

C	Upper canine
c	Lower canine
I	Upper incisor
i	Lower incisor
M	Upper molar
m	Lower molar
PM	Upper premolar
pm	Lower premolar
DIA	Diastema
L	Mesiodistal length
W	Bucco-lingual width
H	Crown height
PadH	Height of the paraconid
PadL	Length of the paraconid
PrdH	Height of the protoconid
PrdL	Length of the protoconid

Measurement abbreviations
Cranium

BU	Maximum length of the tympanic bullae
LAL	Length from the rostral border of the lacrimal bone to the rostral border of the premaxilla
LB	Length from the caudal border of the foramen magnum to the rostral border of the premaxilla
LBO	Dorsal length from the caudal border of the occipital to the rostral border of the sagittal crest
LDT	Maximal dorsal length
LNB	Length from the rostral border of the sagittal crest to the caudal border of the nasals
LNO	Length from the caudal border of the nasals to the caudal border of the occipital
LO	Length from the rostral border of the lacrimal bone to the postorbital process of the zygomatic
LP	Length from the rostral border of the lacrimal bone to the postorbital process of the frontal bone
LPA	Length from the rostral border of the premaxilla to the caudal border of the palate
LPL	Length from the caudal border of the occipital to the rostral border of the lacrimal bone
LPP	Length from the caudal border of the palate to the caudal border of the foramen magnum
LPPF	Length from the caudal border of the occipital to the rostral border of the postorbital process of the frontal bone
LR	Length from the caudal border of the nasals to the rostral border of the premaxilla
LSD	Length of the upper dental series
TFL	Length from the postorbital process of the frontal bone to the caudal border of the occipital
WN	Width of the nasals
WSU	Skull width across buccal margins of the upper canines
WSP	Skull width across distal buccal margins of PM4 s

Measurement abbreviations
Mandible

CM1	Length from the mesial border of the lower canine to the distal border of m1
COM1	Length from the carnassial notch of m1 to the caudal border of the mandibular condyle
DMS	Depth of the mandibular symphysis distally of the lower canine
DMM	Depth of the mandible under m1 (labially)
HRM	Height of the mandibular ramus
LCOR	Length from the mesial border of the incisors to the caudal border of the coronoid process
LM	Length from the rostral border of the mandibular symphysis to the caudal border of the mandibular condyle
LSY	Length of the lower jugal series
MAM	Height from the dorsal border of the mandibular condyle to the central border of the angular process
TDM	Transverse diameter of the mandible at m1

Other abbreviations

HD	Hadjidimovo locality, Bulgaria
LX	Indication for localities in Linxia Basin

Introduction

Paramachaerodus Pilgrim (1913) is a machairodontine felid. That genus and its close relatives were poorly known until the discovery of the Batallones-1 locality (Spain) with its abundant material (Salesa et al. 2003). Until the revision of the genus, stimulated by the discovery of the important material from Batallones-1 (Salesa et al. 2010), two, and eventually three, *Paramachaerodus* species were accepted in the more recent taxonomic studies as valid for this genus: *Pa. ogygia* from the Vallesian, *Pa. orientalis* from the early to middle Turolian and (eventually) *Pa. maximiliani* from the late Turolian (Beaumont 1975; Morales 1984; Morlo 1997; Ginsburg 1999; Salesa et al. 2003, and references therein). The study of the rich fossil material

from Batallones-1 led to the concept of the existence of two genera with close features—*Promegantereon* Kretzoi known mostly in Vallesian time and the more evolved *Paramachaerodus* Pilgrim, which replace *Promegantereon* in Turolian (Salesa et al. 2010). Thus, *Promegantereon* Kretzoi, considered at the time of this study as a synonym of *Paramachaerodus* was resurrected. New material from Hezheng district (Gansu Province, China) and Hadjidimovo (South Bulgaria) give the opportunity to develop further ideas about the taxonomy and evolution of the primitive *Promegantereon–Paramachaerodus* saber-toothed felid lineage.

Materials and methods

The Chinese specimens (a skull and a semimandible from two different individuals) are collected from the Chinese late Miocene site of Shilei locality (Fig. 1a) and housed in the IVPP. The Bulgarian material (two partial mandibular rami, a separate pm3, and a separate upper canine) was excavated by D. Kovachev in the 1980s, came from the Bulgarian Turolian site of Hadjidimovo-1 (Fig. 1b), and is stored in the NMNH-A.

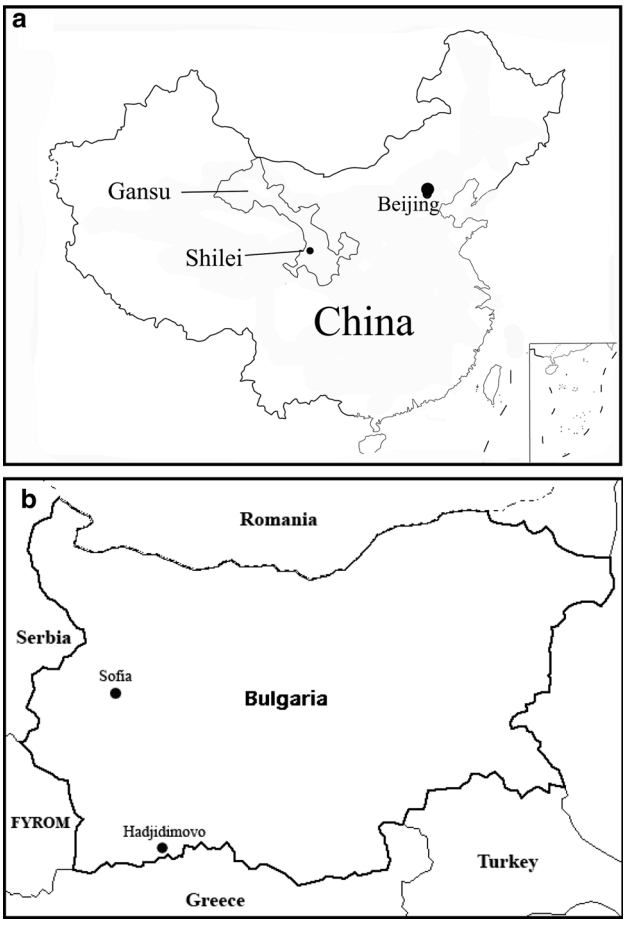

Fig. 1 Locations of the localities on the map. **a** The location of Shilei locality in Hezheng district, Linxia Basin (Gansu Province, China); **b** The location of Hadjidimovo in southwestern Bulgaria

The finds were compared to other similar fossils and in particular to the species of *Paramachaerodus* and *Promegantereon*, discussed in the comprehensive work of Salesa et al. (2010). Comparisons with fossil specimens are based on direct examination of the specimens, on figures and descriptions from the literature, and on excellent photos kindly provided by M. Salesa.

The morphological descriptions follow the terminology used by Merriam and Stock (1932), Salesa et al. (2010), and Berta (1987) with some modifications (Fig. 2a). Measurements (in mm) (Fig. 2b; Tables 1, 2, 3) were taken with a digital caliper.

For the cladistic analysis, 18 cranio-mandibular characters (Appendix) were scored across six taxa (*Proailurus lemanensis*, "*Promegantereon*" *ogygia*, *Paramachaerodus orientalis*, *Paramachaerodus maximiliani*, *Paramachaerodus transasiaticus* sp. nov (Hadjidimovo material), and *Pa. transasiaticus* sp. nov (Hezheng material), using *Proailurus lemanensis* as an outgroup. Most of the characters analyzed are modified from the revision of the genus *Paramachaerodus* by Salesa et al. (2010). Supplemental characters reflect some additional features, which we consider in our taxonomical approach as important in the evolution of the mentioned taxa. The data matrix was compiled in Mesquite version 3.04 (Maddison and Maddison 2015) and the cladistic parsimony analyses were carried out in the program TNT version 1.1 (Tree Analysis using New Technology; Goloboff et al. 2008).

Fossil localities

The skull V 20106 and the mandible V 20107 were collected at Shilei locality in Guanfang village of Guanghe county, Hezheng district in the Linxia Basin, southeastern part of Gansu Province, China (Fig. 1a). This district preserves a continuous and well-developed sedimentary sequence from the Oligocene to the Holocene, which yield abundant mammal fossils (Deng et al. 2004). Thanks to the effort of Z.-X. Qiu and T. Deng from IVPP, who organized a lot of field work and fossil investigation in that district, more than 100 localities have been found, and many new fossil remains of mammals have been reported in Linxia Basin since the 1980s (Deng et al. 2013).

Fossils from Shilei locality were discovered in red clay of the upper part of Liushu Formation, where the thickness of sediments approaches 150 m and is overlain by younger Malan loess. The lithology of the outcrops shows medium brown (5YR4/4 after GSA Rock Color Chart 1991) and dark yellowish orange (10YR6/6) silty mudstone and

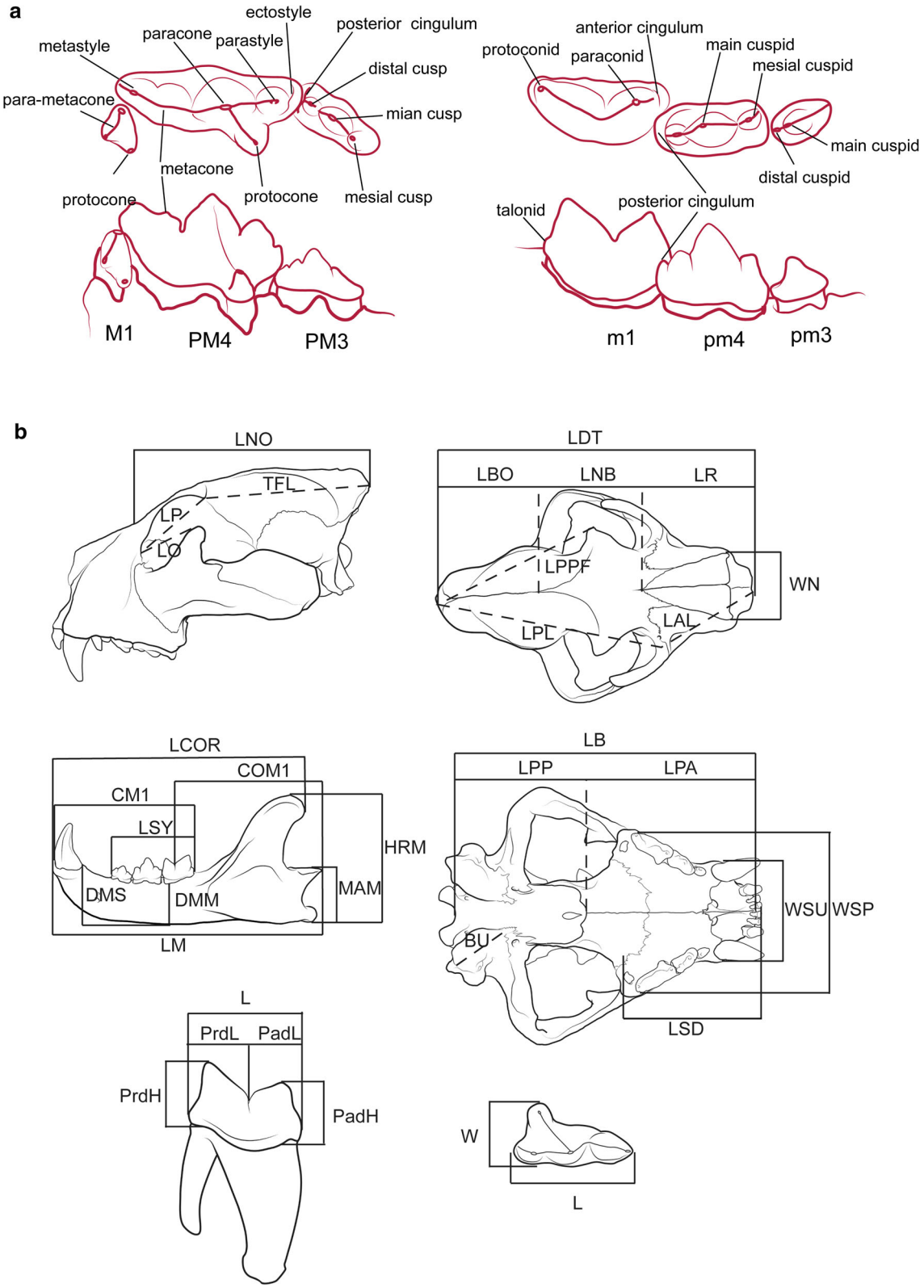

Fig. 2 **a** Nomenclature of teeth used in this work (after Berta 1987 with some modifications); **b** explanation of cranial and mandibular measurements taken (after Merriam and Stock 1932; see Salesa et al. 2010, with some modifications)

Table 1 Comparative skull and mandible dimensions of Hezheng and Hadjidimovo specimens of *Paramachaerodus transasiaticus* sp. nov. and "*Promegantereon*" *ogygia* (Batellones-1, Spain)

Measurement	*Pa. transasiaticus*			*"Pr." ogygia* (Salesa et al. 2010)		
	V 20106/7	HD 9227	HD 9228	Max.	Min.	Average
LAL	65.0	–	–	73.9	53.6	65.0
LPL	135.0	–	–	148.5	125.6	137.8
LR	80.0	–	–	90.8	70.4	79.2
LNB	60.0	–	–	73.7	61.0	65.9
LBO	70.0	–	–	84.2	60.5	73.1
LDT	186.0	–	–	209.8	174.2	194.2
LPPF	103.0	–	–	124.7	106.3	115.1
LNO	120.0	–	–	143.9	131.9	137.9
TFL	101.0	–	–	112.3	108.7	110.6
LP	40.0	–	–	34.0	30.6	32.2
LO	34.5	–	–	37.0	33.7	36.0
LB	155.0	–	–	176.7	153.1	166.1
LPA	75.0	–	–	93.0	73.3	84.3
LPP	80.0	–	–	88.3	78.7	85.2
LSD	74.0	–	–	85.2	73.3	80.2
BU	32.0	–	–	33.2	28.4	32.2
WN	26.8	–	–	–	–	–
WSU	48*	–	–	–	–	–
WSP	74*	–	–	–	–	–
LCOR	120.0	–	–	135.3	111.5	118.5
CM1	74.2	73.9	–	75.0	68.2	71.6
COM1	61.1	–	56.1	65.5	53.7	59.0
LSY	52.7	50.6	–	48.4	41.5	45.0
HRM	56.8	–	49.8	60.8	50.8	55.7
MAM	26.4	–	24.9	27.9	25.2	26.5
LM	124.0	–	–	132.3	110.9	122.1
DMS	28.2	26.5	–	–	–	–
DMM	20.0	18.6	18.3	–	–	–
TDM	12.5	12.2	12.0	–	–	–

* Estimated value

calcareous argillaceous siltstone with calcium nodules varying in size. Many mammal fossils are discovered in this locality including the felid materials described below, which were collected by T. Deng in 2001. The fossils from that locality are placed in the Yangjiashan Fauna as the result of detailed stratigraphic and associated mammal fauna comparisons, such as *Chilotherium wimani*, *Tapirus hezhengensis*, *Machairodus palanderi* (Deng et al. 2004, 2008, 2013). The Yangjiashan Fauna is placed in the Bahe Stage of the late Miocene (NMU 10), and is a Chinese equivalent of the European Turolian, in particular the MN11 zone of Europe, 8.7–8 Ma (Deng 2006; Deng et al. 2013).

HD 9226, HD 9227, HD 9227-2, and HD 9228 were collected at the Hadjidimovo-1 locality in southwestern Bulgaria (Fig. 1b). Hadjidimovo is situated in the Mesta River valley, close to the eastern end of the Pirin Ridge, not far from the Greek border. Four fossiliferous sites are known in that area, and the most important is Hadjidimovo-1 (Hadjidimovo-Girizite), a fossiliferous horizon with light clayey sands belonging to the Nevrokop Formation (Vatsev 1980). HD-1 has produced more than 20,000 fossils, now housed in NMNH-A), representing approximately 30 species of mammals (Primates, Rodentia, Carnivora, Proboscidea, Perissodactyla, Artiodactyla), including the felid described below, making it one of the richest late Miocene sites of the eastern Mediterranean and peri-Pontic areas (Spassov 2002; Geraads and Spassov 2009). Although the Hadjidomovo fossiliferous area was first mentioned by Nikolov (1973, 1985) (the exact locality discovered by him remains unknown), this huge collection was mostly accumulated and cared mainly between 1985 and 1998 thanks to the efforts of D. Kovachev. Hadjidimovo-1 is older than Pikermi, as indicated by the

Table 2 Measurements of upper dentition of *Paramachaerodus transasiaticus* sp. nov. and other species

Measurement	*Pa. transasiaticus*		*"Pr." ogygia* (Salesa et al. 2010)			*Pa. orientalis* (Salesa et al. 2010)	*Pa. maximiliani* (Zdansky 1924)
	V 20106	HD 9226	Max.	Min.	Average	NHMW2007Z0172/0001	PMU M 69
I3							
L	7.4	–	–	–	–	–	10.7
W	5.8	–	–	–	–	–	10.2
C							
L	16.0	15.9	16.6	13.4	14.9	17.0	18.0/20.5
W	8.5	7.7	9.5	7.8	8.9	9.6	11.0/11.0
H	40.0	39.6	40.2	30.4	35.8	41.4	–
DIA C-PM3	5.6	–	–	–	–	8.7*	11.5
PM3							
L	18.2	–	17.7	11.5	15.4	15.0	16.3
W	8.4	–	8.7	5.4	7.8	7.1	7.2
H	10.0	–	8.4	6.8	7.6	–	–
PM4							
L	28.6	–	27.5	22.8	25.2	28.0	29.0
W	15.3	–	13.4	12.0	12.6	13.8	13.3
H	14.4	–	13.2	10.3	12.0	–	–

Localities: *Pa. orientalis*, Maragheh (Iran); *Pa. maximiliani*, Shangyingou (China)

* Calculated from the photograph used in Salesa et al. (2010)

Table 3 Measurements of lower dentition of *Paramachaerodus transasiaticus* sp. nov. and other species

Measurement	*Pa. transasiaticus*			*"Pr." ogygia* (Salesa et al. 2010)			*Pa. ogygia* (Beaumont 1975)	*Pa. orientalis* (Salesa et al. 2010)	*Pa. maximiliani* (Zdansky 1924)
	V 20107	HD 9227	HD 9228	Max.	Min.	Average		M 8959	
c									
L	12.6	10.8	–	11.9	9.4	10.8	10.0–11.0	14.0	13.3
W	8.0	8.0	–	8.3	6.5	7.6	7.0	9.5	9.5
H	23.0	–	–	24.0	17.4	20.9	–	–	–
pm3									
L	13.6	12.4	–	13.4	10.5	11.9	10.3	14.0	–
W	6.7	6.4	–	6.9	4.8	5.6	5.4	–	–
H	7.5	–	–	7.8	5.1	6.2	–	–	–
DIA c-pm3	9.5	13.0	–	–	–	–	17.0	20.0*	–
PM4									
L	19.6	17.8	–	18.7	15.0	16.5	15.2	19.0	–
W	8.2	8.0	–	8.2	6.7	7.3	6.5	–	8.2
H	11.6	–	–	10.9	7.5	9.4	–	–	–
M1									
L	21.8	22.5	22.4	20.9	17.6	19.3	–	22.0	21.5
PadL	10.0	–	8.2	9.6	7.5	8.8	–	–	–
PrdL	10.7	14.1	–	11.3	9.3	10.1	–	12.8*	11.8*
W	8.5	8.1	–	8.7	7.6	8.2	–	9.5	9.9
PadH	11.8	10.6	–	12.6	9.5	10.6	–	–	–
PrdH	12.0	11.1	–	11.2	9.8	10.5	–	13.0*	13.2*

Localities: *Pa. ogygia*, type specimen, Eppelsheim; *Pa. orientalis*, Pikermi; *Pa. maximiliani*, Shangyingou

* Calculated from the photograph used in Salesa et al. (2010)

evolutionary stages of *Mesopithecus* (Koufos et al. 2003), *Hipparion* (*Cremohipparion*) *mediterraneum* (Hristova and Spassov 2005), and *Adcrocuta eximia* (pers. obs. NS), as well as by the presence of *Tragoportax rugosifrons* (Spassov and Geraads 2004). Spassov (2002) suggested that the locality likely could be placed near the MN11/MN12 boundary, and recent faunal analysis demonstrates that the locality must be early Turolian in age (Hristova et al. 2013). It could be included within MN11, and probably in the second half/the end of the zone.

Systematic palaeontology

Order **Carnivora** Bowdich, 1821
Family **Felidae** Fischer von Waldheim, 1817
Subfamily **Machairodontinae** Gill, 1872
Genus ***Paramachaerodus*** Pilgrim, 1913

Type species. *Felis ogygia* Kaup, 1832, by original designation.

Other species included: *P. orientalis* (Kittl, 1887), *P. maximiliani* (Zdansky, 1924).

Paramachaerodus transasiaticus sp. nov.
Figures 3–5.

Etymology. From "trans-Asia" (i.e. "across", "beyond" Asia), in relation to the discovery of this species in the eastern part of Central Asia and eastern Europe.

Holotype. A skull (IVPP V 20106) with its left zygomatic arch missing, occipital and left side of the frontal region damaged, with right I3, right canine broken at the tip, PM3, and right PM4.

Type locality and horizon. Shilei, Guanghe County, Gansu Province (China), Liushu Formation, Turolian (late Miocene, MN11).

Referred material. Chinese material: A slightly damaged skull (IVPP V 20106) and a complete left mandibular ramus (IVPP V 20107) that are not derived from the same individual. Bulgarian material: Two partial mandibular rami from Hadjidimovo-1, HD 9227 (left side, with c1, pm4-m1, and a separate pm3 only preserved as a cast from the same hemi-mandible, HD 9227-2) and HD 9228 (right side, with m1 and a fragment of pm4 from the same individual as HD 9227); and a complete right upper canine crown—HD 9226.

Stratigraphic and geographic distribution. From southern (southeastern) Europe to Central Asia (China) in the time equivalent to the early Turolian (MN11) (second half of the early Turolian?) (after the European Neogene Land Mammal ages).

Diagnosis. Skull with moderately developed sagittal crest and relatively short neurocranium. Teeth with mixed features of *Paramachaerodus* and *Promegantereon* (sensu Salesa et al. 2010) such as: presence of crenulations on the upper canines, but not regularly on the lower ones and generally on all upper and lower cheek-teeth; although all crenulations are rather weak. PM3 is very long with elongated and constricted mesial part and strong disto-lingual expansion, there is a small mesial cusp on its antero-lingual part. The buccal border of PM4 is sinusoidal, with strongly expanded mesio-labial part of parastyle, indicating the beginning (a rudiment) of an ectostyle; the protocone of PM4 is relatively large and mesio-distally elongated. PM4 is much longer than PM3. PM3 and PM4 are not aligned in occlusal view. M1 is with two roots. Very short c-pm3 diastema. Possible presence of a strongly reduced, vestigial pm2. Low and elongated cutting m1 with an extremely elongated talonid and a well-marked metaconid. Mandible symphysis rostral surface is moderately verticalized, with incipient mandible flange and moderately marked mental crest on its antero-lateral margin. The coronoid process is high with more vertical anterior edge.

Differential diagnosis. Paramachaerodus transasiaticus sp. nov. differs from *Pa. ogygia* by its slightly larger size, by the relatively short neurocranium and weaker expressed sagittal and temporal crests, the narrower nasal aperture, the shorter and rounded zygomatic process of the fontal bones, the weaker mastoid process, the regular presence of thin crenulations on nearly all teeth (which are missing as a rule in *Pa. ogygia*), the more elongated PM3 (in particular the mesial part), the presence of a rudimentary ectostyle, the PM4 more elongate than PM3, the shorter c-pm3 diastema, the elongated talonid-metaconid complex of m1 with a larger metaconid, the incipient flange on the mandibular symphysis, and the more marked mental crest on the antero-lateral margin. The new species differs from *Paramachaerodus orientalis* by the straight anterior border of the nasal bones (without a distal projection in dorsal view), the narrower nasal aperture, the weaker tooth crenulations, a PM3 with a disto-lingual expansion, a PM4 with a much less developed ectostyle and a sinusoidal rather than straight buccal border, the reduced protocone of PM4, the longer M1 with two roots, the much shorter c-pm3 diastema, the much more developed m1 talonid-metaconid complex (with an elongate talonid and larger metaconid), the mandible coronoid process with more vertical anterior edge. Compared to *Pa. maximiliani*, *Pa. transasiaticus* sp. nov. differs by its smaller overall size, the distinctly smaller I3 and upper canine, the markedly weaker tooth crenulations, the longer PM3 (more elongated mesially), the much less developed PM4 ectostyle, the sinusoidal rather than straight PM4 buccal border, the more

developed and forwardly situated PM4 protocone, the longer M1 with two roots, and the m1 with much more elongate talonid and metaconid.

Description. *Cranium.* As *Paramachaerodus ogygia* (see in: Salesa et al. 2010), the cranium V 20106 is similar in size (Table 1) and proportions to that of an extant puma (*Puma concolor*), but relatively lower. It is slightly compressed by external lateral stress, its right half part is almost completely preserved (Fig. 3a-A). The nasals are sub-rectangular in shape, with rostral margin wider than the caudal one and with convex caudal border. They are pinched in the middle part and medio-laterally convex in dorsal view. The anterior border of the nasals is rather straight. The nasal aperture is relatively narrow, close to piriform in shape (Fig. 3a-B). The rostral part of the premaxilla is damaged and unclear in shape. The muzzle is short and broad. The frontal region is wide and flat, possibly slightly compressed. The zygomatic processes are short and blunt. The infraorbital foramina are relatively large, higher than wider and placed at the level of the mesial part of the parastyle of PM4 (Fig. 3a-C). The postorbital constriction is well marked. The neurocranium is short and bulged laterally. Spina nasalis caudalis is not marked on the choanae aperture (Fig. 3a-D). The temporal and sagittal crests join at the level above the glenoid fossa. They are relatively weak, especially the temporal ones. The transversal crest is strong. The occipital surface is close to an equilateral triangle. In lateral view, the orbital surface is oval, post-upwards oriented. The zygomatic arch is robust as in *Paramachaerodus ogygia*. The postorbital process of the zygomatic arch is low and rounded, positioned anteriorly to that of the frontal one. Judging from the right

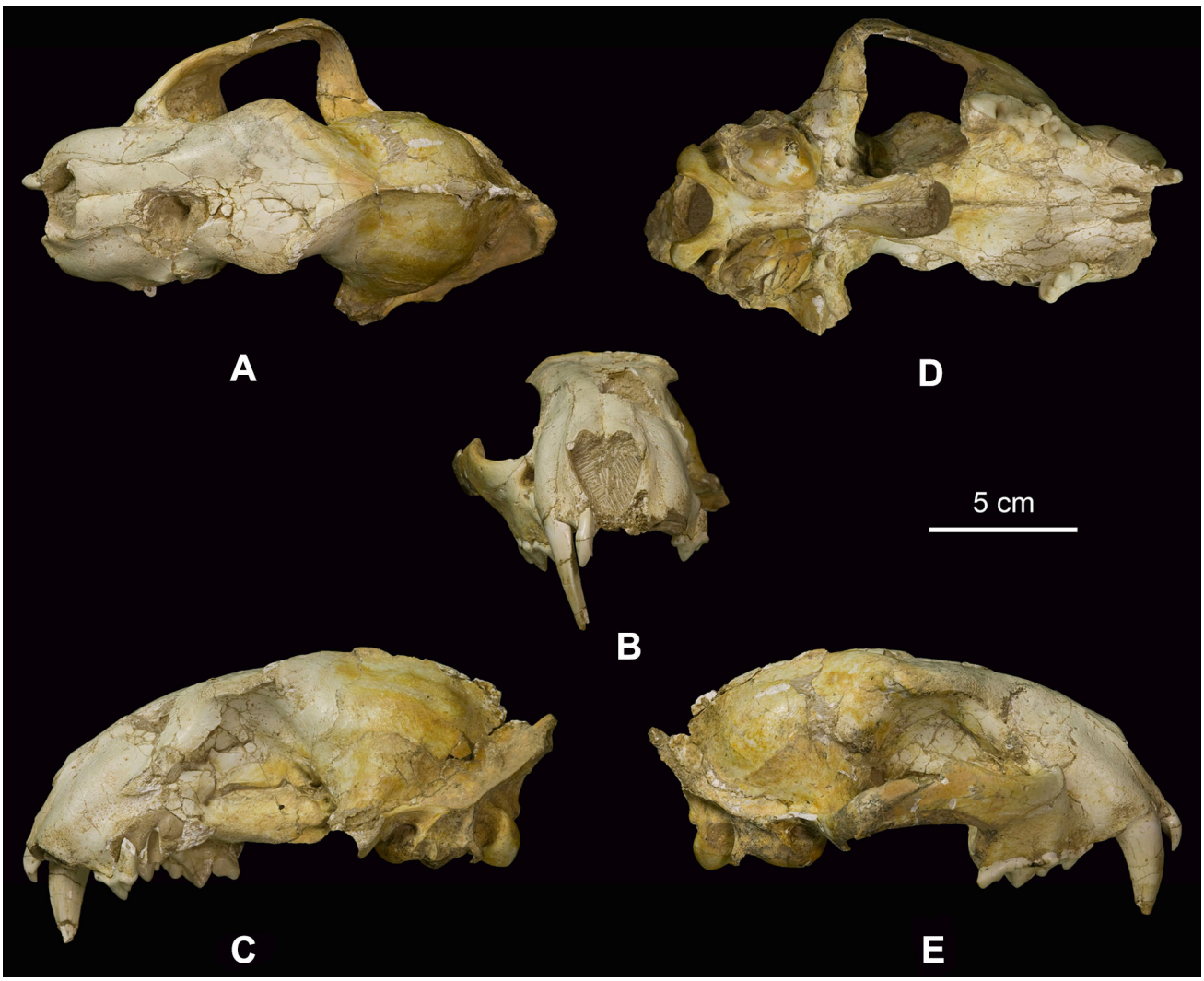

Fig. 3 **a** *Paramachaerodus transasiaticus* sp. nov., holotype (skull—IVPP (V) 20106) from Shilei, China: *A* dorsal view; *B* rostral view; *C* right lateral view; *D* ventral view; *E* left lateral view. **b** *Paramachaerodus transasiaticus* sp. nov., left hemi-mandibular ramus IVPP (V) 20107 from Shilei, China: *A* buccal view; *B* occlusal view; *C* lingual view

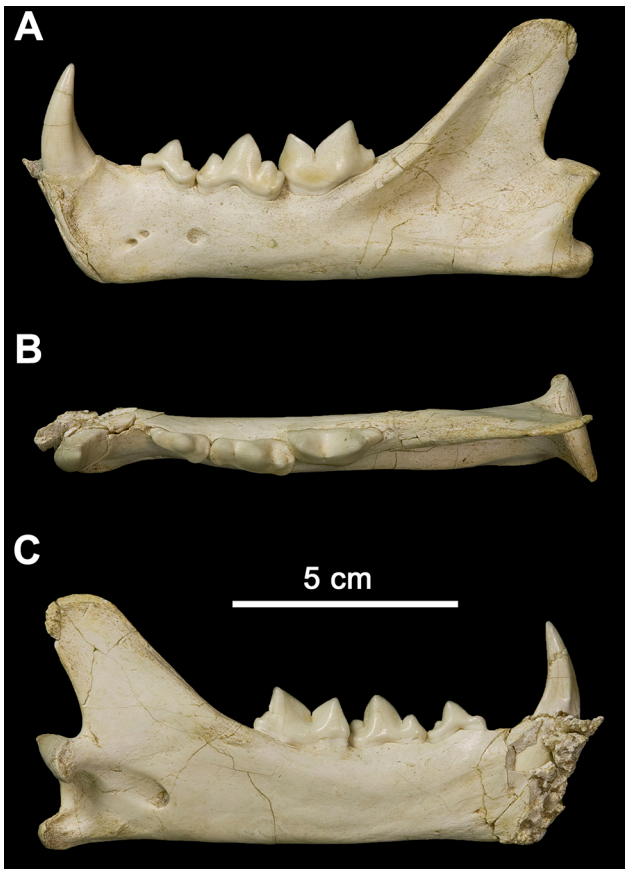

Fig. 3 continued

zygomatic arch, this structure has a maximum width near to the caudal part. The posterior palatine foramen is situated antero-ventrally to the sphenopalatine one, and they are similar in size, unlike in the *Paramachaerodus ogygia* (see also Salesa et al. 2010), where the former is much smaller than the latter. Like *Pa. ogygia*, the optic foramen and the orbit fissure are placed as in a pantherine cat. The places of foramen rotundum and the oval foramen are placed also as in *Pa. ogygia* (see also Salesa et al. 2010) (Fig. 3a-E). The tympanic bullae are rather bulged. The mastoid process is relatively weak compared to *Pa. ogygia*. The jugular process is reduced in size when compared with that of pantherines but close in size and shape to *Pa. ogygia*. Its apex don't reach ventrally the level of the occipital condyle border.

Upper incisor. I3 is large with caniniform crown. Its disto-buccal ridge is more marked than the mesial one. Its detailed morphology is similar to the ones of *Pa. ogygia* (see also Salesa et al. 2010): the distal surface bears a marked cingulum, which developed into a large mesial, basal cusplet. There is a short diastema, approximately 3 mm long between I3 and the upper canine.

Upper canines (Figs. 3a, 4a, b). The crown is laterally flattened and slightly curves backwards. The buccal surface is smooth and convex (in cross section), the lingual one is slightly concave on its mesial surface and become slightly convex in its middle portion. Both mesial and distal cutting edges are well developed, the mesial edge is lingually deflected at the base and slightly arched laterally after toward the apex; the distal one is sharper. There are very thin crenulations on both edges.

PM3. As in *Pa. ogygia* (see Salesa et al. 2010), the crown is mesio-distally lengthened, with a straight buccal border and a marked disto-lingual expansion, showing a marked constriction at the level of the anterior part of the main cusp. There is a small, but distinct mesial cusp on the mesio-lingual side of the teeth, whereas the distal cusp and the main one are strong. Very thin crenulations can be seen on the anterior edge of the main cusp. There is a cingulum around the distal border, which forms a small distal tubercle straightly behind the distal cusp.

PM4. The upper carnassial has a relatively large protocone, mesio-distally elongated, placed between the parastyle and the paracone. The parastyle is well developed, its height is about the half of the height of the paracone. Thin crenulations can be seen on the anterior edge of the paracone. The buccal border of PM4 is sinusoidal, with strongly expanded mesio-labial part of the parastyle, indicating the beginning of the ectostyle. The metacone-metastyle blade is much shorter than the parastyle-paracone. PM3 and PM4 are not aligned and form a slight angle in occlusive view.

M1. Absent but preserved two alveoli.

Mandibles (Figs. 3b, 4f–k). They are relatively short and stout. V 20107 has three mental foramina, the first one being placed at the level of the postcanine diastema, the main one is at the level between pm3/pm4. The foramina number in HD 9227 is not very clear because of the slightly damaged surface, but the main one is under pm3. Mandible symphysis rostral surface is close to vertical (the angle between the anterior and the ventral border of the horizontal ramus is about 110°), with incipient mandible flange and moderately marked mental crest (but better marked than in *Pa. ogygia*) on its antero-lateral margin. The masseteric fossa is wide and deep, its anterior border reaches the level of the protoconid of m1, its ventral border has a prominent ridge, extending to the lateral end of the condyle. The coronoid process exceeds in height the level of the lower canine and is with only slightly inclined anterior edge.

Lower canine. Relatively reduced, clearly smaller than the upper one. It is slightly compressed and curved backwards, its lingual face is flat, whereas the buccal face is smooth and convex. The distal ridge is more marked than the

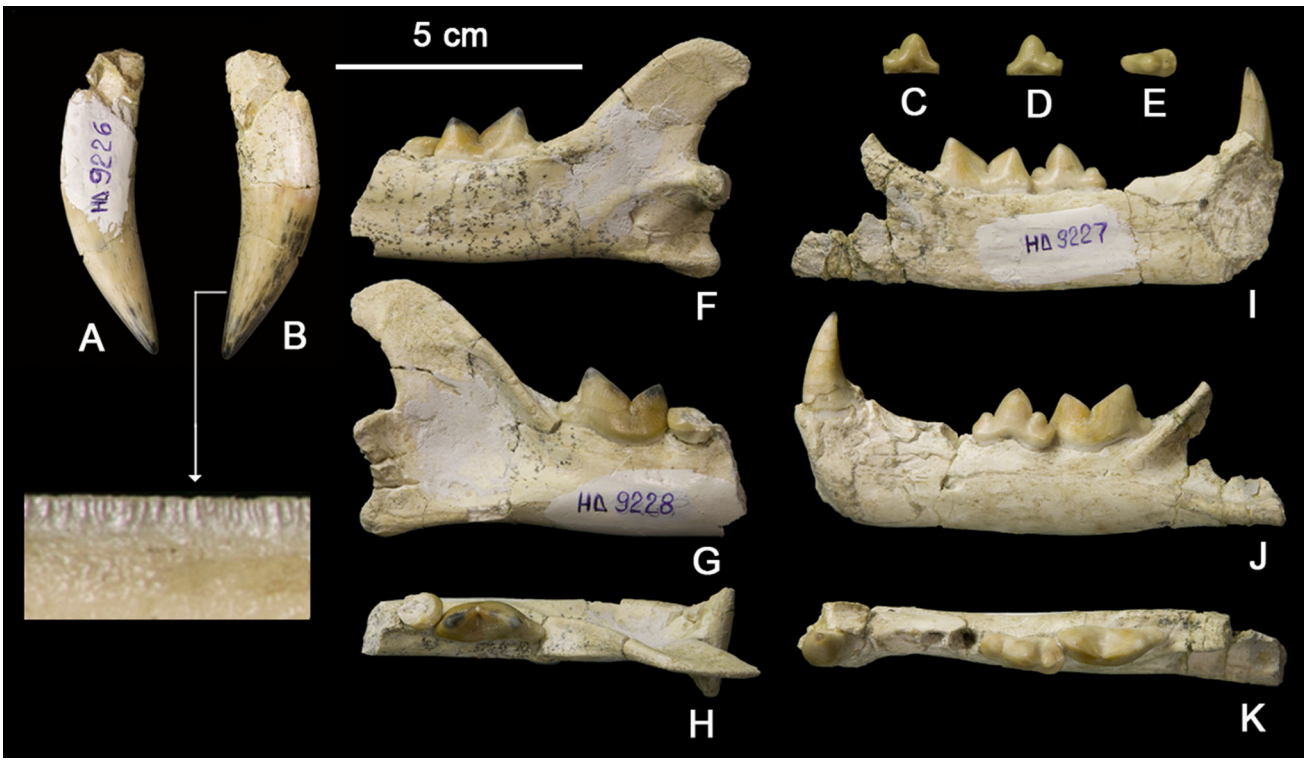

Fig. 4 *Paramachaerodus transasiaticus* sp. nov. from Hadjidimovo-1 (Bulgaria). *a*, *b*, HD 9226, *right* upper canine, in *a* lingual and *b* buccal views. *c*, *d* HD 9227-2, left p3 (cast), in *c* lingual, *d* buccal and *e* occlusive views; *f–h* HD 9228, fragment of right hemimandible, in *f* lingual view, *g* buccal view and *h* occlusive views; *i–k* HD 9227, *left* hemi mandibular ramus, in *i* lingual view, *j* buccal view, and *k* occlusive views

mesio-lingual one, thin crenulations on both ridges can be seen clearly on the Hezheng mandible but not on the Hadjidimovo one.

pm2. Practically absent. In the Hezheng and Hadjidimovo mandibles, there is a very small hollow in front of pm3, which could be a vestigial alveolus of pm2, especially in the case of Hezheng fossil.

pm3. The crown is elongated distally and triangularly shaped in occlusal view—the distal part markedly wider than the mesial part. It is slightly concave at the middle part of both the lingual and buccal faces. It dos not have an additional mesial cuspid, and the distal one is reduced. There is a smooth posterior cingulid. Very thin crenulations are observed on the anterior edge of the main cuspid. This tooth is slightly oblique in relation to pm4 in Hezheng mandible.

pm4. The crown is very long and blade like, 4-cusped. The main cuspid is well developed, much higher than the mesial and distal ones and highly positioned in relation to paraconid of m1. It presents very slight crenulations on the mesial edge. The mesial and distal cuspids are almost the same size. The marked posterior cingulid forms a small distal cusplet. A mesio-buccal basal expansion is present in the tooth of the Hezheng mandible. pm4 is not aligned with m1.

m1. The lower carnassial is remarkably elongated and relatively low, the protoconid is significantly longer than the paraconid and separated from it with strongly marked notch. The tanolid-metaconid complex is very well developed (Fig. 5). The metaconid is well expressed and separated from the upper part of the distal edge of the protoconid by a visible horizontal groove. The talonid is crest-like and very elongated. Very thin crenulations are visible on the paraconid-protoconid blade (Hadjidimovo) and on the distal edge of the protoconid.

Comparisons

The characters of the known mandibles from Hezheng and Hadjidimovo are almost identical, with only minor differences. The mandible V 20107 seems to have more securely a vestigial pm2, which is possibly absent in the Hadjidimovo one, but the range of the variation of this feature (presence/absence of pm2) in "*Promegantereon*" from the Batallones-1 sample (in which pm2 is absent in some specimens) is not smaller. Furthermore, in the Hezheng specimen V 20107, the lower canine is crenulated (crenulations present in both specimens are very thin and present in the cheek-teeth), and this difference might just be individual variation. In the

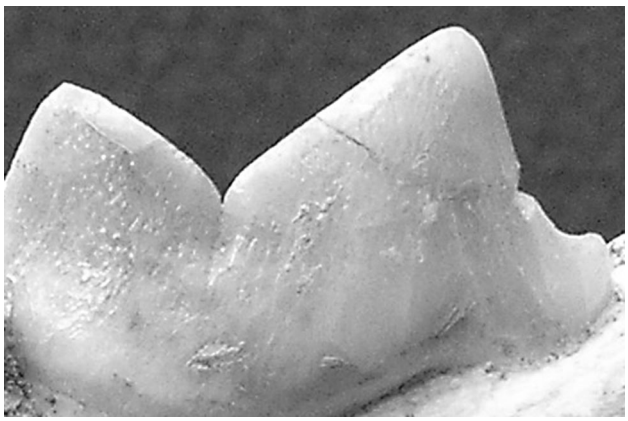

Fig. 5 M1 of HD 9227 showing the very well developed tanolid-metaconid complex

Hezheng mandible V 20107, pm3 is slightly more mesio-distally elongated, the size of the mandible is slightly larger (Table 1), and the mesio-buccal basal expansion of pm4 is much stronger. All of these characters might be the result of individual, geographic (subspecific), or sexually dimorphic variation. The most important shared features among the material from Hezheng (China: V 20106 and V 20107) and Hadjidimovo (Bulgaria: HD 9226, HD 9227, and HD 9228) include the very elongated m1 with an extremely developed talonid-metaconid complex and the presence of very thin enamel crenulations. Those shared features give us the opportunity to unite the Chinese and Bulgarian specimen into one species.

The skull and mandibles of the new species present typical machairodont characters, including the elongated and mediolaterally compressed upper canines, the crenulation of teeth edges, the existence of a (incipient) mandible flange, and a marked mental crest on the symphysial mesio-buccal margin. With these characters, the fossils described above can be separated clearly from *Yoshi* Spassov and Geraads (2015), *Pristifelis attica* (Wagner 1857), *Styriofelis* Kretzoi (1929), the oldest Pantherinae *Felis pamiri* Ozansoy 1965, and *Panthera blytheae* (Tseng et al. 2014). In other words, the new species differs from the conical-toothed cats of the late Miocene of Eurasia (Spassov and Geraads 2015). Given that our new species is half the size of *Machairodus*/*Amphimachairodus* (Tables 1, 2), *Paramachaerodus transasiaticus* will be compared here only with contemporaneous and similar sized taxa of Machairodontinae with crenulated teeth, and excluding the so-called Metailurini (see Salesa et al. 2010; Spassov and Geraads 2015).

Thus, the comparison will focus on the "*Promegantereon*"–*Paramachaerodus* group discussed in details by Salesa et al. (2010) in their comprehensive work, where they presented a review of the systematics of the genus *Paramachaerodus* and a detailed description of the fossils from Batallones-1, attributed by them to *Promegatereon ogygia.*

Comparison with "*Promegantereon*" *ogygia*. Compared to the holotype of *Paramachaerodus ogygia* (Kaup, 1832), a fragment of right hemi-mandible with c1-pm4 from Eppelsheim, Germany (Beaumont 1975), all measurements of *Paramachaerodus transasiaticus* are slightly larger, except for the much shorter c-pm3 diastema in our new species (Table 3). *Pa. transasiaticus* has (weak) crenulations on the upper and lower canines and on all borders of the teeth, and this contrasts to the state in the Eppelsheim material where they are consistently absent. The pm3 of the new species also is rather narrow mesially, and the mandible has a more marked mental crest on the anterolateral margin. Compared with "*Promegantereon*" *ogygia* fossils from Batallones-1 (Salesa et al. 2010), most of the general features of the cranium from Hezheng are rather similar to the Batallones specimens, but the new species displays several advanced features. Some of those differences include, a relatively short neurocranium and weaker expressed sagittal and temporal crests, a narrow nasal aperture (assessed by comparison with the photos provided by M. Salesa), the shorter and rounded zygomatic process of the fontal bones, the weaker mastoid process, the thin crenulations on nearly all teeth, the more elongated PM3 (in particular the mesial part), the rudimentary ectostyle formed by a mesio-buccal expansion of the buccal border of PM4, the slightly shorter protocone of PM4, the PM4 more elongate than PM3, the shorter c-pm3 diastema, the elongated talonid-metaconid complex of m1 with a larger metaconid, the incipient flange on the mandibular symphysis, and a more marked mental crest on the antero-lateral margin.

Comparison with *Paramachaerodus orientalis*. Compared with *Pa. orientalis* from Maragheh (Iran) and Pikermi (Greece) (Kittl 1887; Salesa et al. 2010), *Paramachaerodus transasiaticus* exhibits some more primitive features and several other differences, including a straight anterior border of the nasal bones (without a distal projection in dorsal view), a narrower nasal aperture, weaker tooth crenulations (canines included, although some teeth may lack crenulations, see description above), a PM3 with a disto-lingual expansion, a PM4 with a much less developed ectostyle (only a rudimental one), and a sinusoidal rather than straight buccal border, a reduced protocone of PM4, a longer M1 with two roots, a much shorter c-pm3 diastema, a more developed m1 talonid-metaconid complex (with an elongate talonid and larger metaconid), and a coronoid process is with more vertical anterior edge.

Comparison with *Paramachaerodus maximiliani*. As compared to *Pa. maximiliani* from Shangyingou (Henan

Province, China) (Zdansky 1924) and Venta del Moro (Spain) (Salesa et al. 2010), *Pa. transasiaticus* shows a number of primitive features and differences including a smaller overall size, a distinctly smaller I3 and upper canine (Table 2), much weaker tooth crenulations, a longer PM3 (more elongated mesially), a much less developed PM4 ectostyle (only a rudimentary one), a sinusoidal rather than straight PM4 buccal border, a more developed and forwardly situated PM4 protocone, a longer M1 with two roots, and a m1 with a much more elongate talonid and a metaconid.

Discussion

Taxonomy of the "*Promegantereon*"-*Paramachaerodus* lineage. *Paramachaerodus* was established by Pilgrim (1913) to encompass several published felid fossils, including *Machairodus orientalis* Kittl, 1887, *Machairodus schlosseri* Weithoffer, 1888, and *Felis ogygia* Kaup, 1832, from the late Miocene of Maragheh (Iran), Pikermi (Greece), and Eppelsheim (Germany). In 1929, Kretzoi created the genus *Pontosmilus* for a number of taxa (as *Po. ogygia*, *Po. hungaricus*, *Po. schlosseri*, *Po. orientalis* and *Po. indicus*). He restricted *Paramachaerodus* to the single species *Pa. pilgrimi* which is now excluded from this genus by Salesa et al. (2010). Meanwhile, Pilgrim (1931) considered *Pontosmilus* as a synonym of *Paramachaerodus*. Later, Kretzoi (1938) established the new genus *Promegantereon* to accommodate "*Felis*" *ogygia*. More recently, *Promegantereon* has been considered a junior synonym of *Paramachaerodus* (Beaumont 1975, 1978), and (as we mentioned above) few species were accepted as valid for this latter genus: *Pa. ogygia* from the Vallesian, *Pa. orientalis* from the early to middle Turolian and (eventually) *Pa. maximiliani* from the late Turolian. Thus, *Pa. hungaricus* and *Pa. shlosseri* were considered synonyms of *Pa. orientalis* (Beaumont 1975, 1978; Morales and Soria 1977; McKenna and Bell 1997; Montoya 1994; Morlo 1997; Ginsburg 1999; Salesa et al. 2003; see more details in Salesa et al. 2010). The taxonomic concept, according to which *Promegantereon* represents a synonym of *Paramachaerodus* lasted in a long time until the discovery of a large number of fossils of a *Paramachaerodus*-like sabre-toothed cat from Batallones-1 (Spain). The abundant Batallones-1 machairodontine material was studied by Salesa et al. (2003, 2005a, b, 2010). Their work led to the concept of the existence of two closely related, but successive in time genera (*Promegantereon* and *Paramachaerodus*) in the late Miocene, and to the resurrection of *Promegantereon* Kretzoi (Salesa et al. 2010).

As we noted above, the fossils from Hezheng and Hadjidimovo are almost identical with some very small differences which we consider as individual/sexual or/and subspecific (geographic) and all this material must be assigned to one and the same species of the "*Promegantereon*"–*Paramachaerodus* lineage, i.e. of the genus *Paramachaerodus*. It is characterized by the low and very elongated m1 with extremely developed talonid-metaconid complex (Fig. 5, 6); the presence of very thin crenulations on teeth (as these crenulation are very thin; they could lack in some cases as the case of c1 in HD); a combination of an elongated PM3 but with strong disto-lingual expansion; PM4 with a combination of a rudimental ectostyle and sinusoidal rather than straight buccal border; the very short c-pm3 diastema; relatively short neurocranium and moderately developed sagittal crest.

The distribution of the features which differentiate "*Promegantereon*" *ogygia* from *Paramachaerodus*

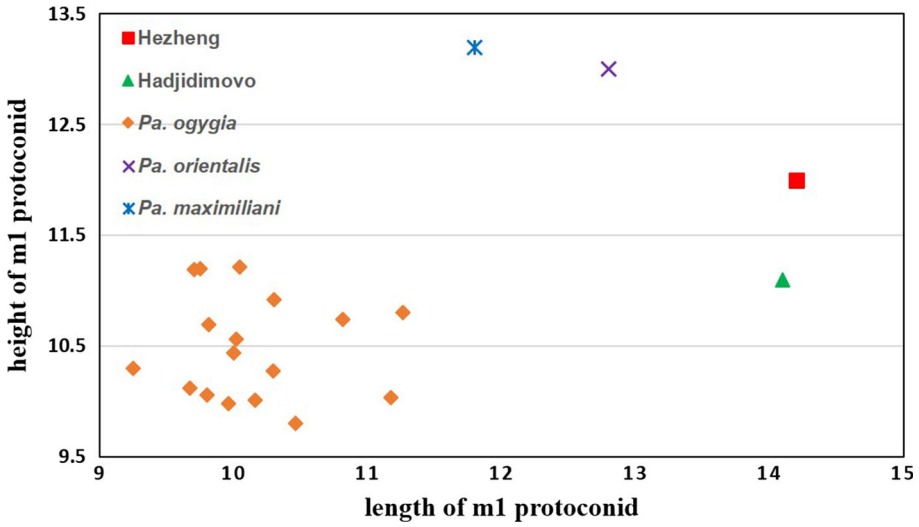

Fig. 6 Comparative visualization of the ratio length/height of the m1 protoconid (including the talonid-metaconid complex) of *Paramachaerodus transasiaticus* sp. nov

Table 4 Comparison of feature diagnosis after Salesa et al. (2010) with some details added by us

Feature/taxa	"*Promegantereon*" *ogygia*	Hezheng (China)	Hadjidimovo (Bulgaria)	*Paramachaerodus*
Crenulation on canines	No crenulations	Thin, present in all borders without exceptions on canines	Thin, present in all borders with exceptions on lower canines	Strong in borders of upper and lower canines
Shape of canines	Smoothly and laterally flattened crown*	Flattened with sharp ridges	Flattened with sharp ridge	Smoothly and laterally flattened
Length of PM3	Short and wide	Rather elongated with elongated mesial part	No data	Mesial-distally elongated
PM3 mesial cusp	Absent or with a minute cusp	With a minute mesial cusp	No data	Generally without mesial cusp**
PM3 distal-lingual part	Expansion	Expansion	No data	No expansion in *Pa. orientalis*, present in *Pa. maximiliani*
Buccal border of PM4	Sinusoidal***	Sinusoidal, with strongly expanded mesial-labial edge	No data	Straight
Ectostyle of PM4	Not present	Very rudimentary	No data	Present
Protocone of PM4	Big and elongated mesial-distally	As in "*Pr.*" *ogygia*, but slightly shorter	No data	Reduced, situated backward in *Pa. maximiliani*
Angle between PM3/PM4	PM3&PM4 aligned	Not aligned	No data	Aligned in *Pa. maximiliani* but not in *Pa. orientalis*
Relative size of PM4-PM3	PM4/PM3 index $\leq$1.5	PM4/PM3 index >1.5	No data	PM4/PM3 index >1.5
M1	Two roots, elongated	Two roots, elongated	No data	One single root or in any case short if it has two roots
pm2	Minute in size, but exist with some exceptions	?****A minute pm2 is probably present	?****A minute pm2 is probably present	Absent
Length of c-pm3 DIA	Long	Very short	Very short	Long
pm4 mesio-buccal basal expansion	Absent	Exist	Exist but weak	Exist in *Pa. Orientalis*
Proportion of m1	Relatively low and elongated	Low and very elongated	Low and very elongated	Relatively short and high
Talonid-metaconid complex of m1	Long, smoothly expressed metaconid	Very elongated with big metaconid	Very elongated with big metaconid	Short without metaconid in *Pa. Orientalis* and with high positioned metaconid in *Pa. Maximiliani*
Mandible symphysis	Without flange and with smooth mental crest	As in *Pa. Orientalis*	As in *Pa. Orientalis*	Incipient mandible flange and more marked mandible mental crest
Coronoid process	High and more verticle anterior edge of the coronoid process	As in "*Pr.*" *Ogygia*	As in "*Pr.*" *Ogygia*	Low and more inclined anterior edge of the coronoid process
Sagittal crest	Strong	Moderately developed	No data	Moderately developed

* After our calculations the upper canines of "*Promegantereon*" *ogygia* are not less flattened than *Paramachaerodus*

** In *Pa. orientalis* it is absent and unclear in the *Pa. maximiliani*

*** After our observations

****? Maybe a very reduced, vestigial alveolus

diagnosed by Salesa et al. (2010) are shown in Table 4. *Paramachaerodus transasiaticus* sp. nov. has mixture of features showing an intermediary situation, thus the difference between "*Promegantereon*" and *Paramachaerodus* becomes invisible, as also shown in the cladogram C (Fig. 7). A gradual evolution of the features exists in time from "*Promegantereon*" *ogygia* through *Pa. transasiaticus* to *Pa. orientalis* and after to *Pa. maximiliani*, so it is hard to separate the taxa on generic level. It is interesting to note that the gradual evolution of crenulations started here in the same genus from forms without tooth crenulations until forms with well-marked crenulations. The same kind of development of the crenulatuons with time was shown recently for the different stages of the evolution of the genus *Metailurus* (Li 2015). We consider that the more logical taxonomic decision could be the inclusion of all the

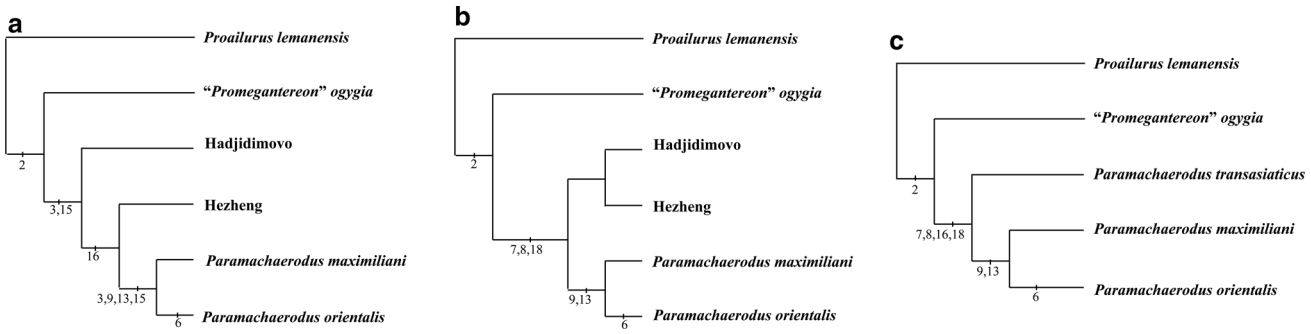

Fig. 7 Cladograms showing the phylogenetic relationships. **a** based on the matrix of six taxa and 18 characters (Supplementary 1); **b** based on the same matrix, but the 16th character is deleted; **c** based on the same matrix but unifying Hezheng and Hadjidimovo. All characters are treated as additive (ordered). The *numbers* indicate which characters support each clade

Table 5 Data matrix used in the phylogenetic analysis

Taxa	Character																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Proailurus lemanensis	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Promegantereon ogygia	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0
Hadjidimovo	?	1	1	?	?	?	?	?	?	?	?	?	?	2	1	0	2	?
Hezheng	1	1	1	1	1	0	1	1	0	1	1	1	0	2	1	1	2	1
Paramachaerodus orientalis	2	1	2	1	0	1	1	1	1	2	2	2	1	2	2	1	4	?
Paramachaerodus maximiliani	2	1	2	0	?	0	1	1	1	2	2	2	1	2	2	?	3	1

previously mentioned forms in one and the same genus, the name of which by priority must be *Paramachaerodus* Pilgrim. Thus, the genus contains four valid and successive species: *Paramachaerodus ogygia*, *Paramachaerodus transasiaticus* sp. nov., *Paramachaerodus orientalis*, and *Pamachaerodus maximiliani*. The talonid-metaconid complex of m1 of *Paramachaerodus transasiaticus* sp. nov. shows in general primitive features, retaining a large metaconid and elongated talonid. In the same time, this extremely enlargement of the talonid-metaconid complex can suggest a secondary evolution of this structure is relation to its cutting function. Such kind of secondary m1 talonid evolution was proposed for the lynx lower carnassial tooth (Werdelin 1981).

Cladistic analysis

First, we prepared two analysis methods, using feature 16 (p4 mesio-buccal basal expansion in the crown, which shows some evolutionary trend, but must be strongly related to individual variation) and another lacking this feature. After our opinion, this feature does not have a high taxonomic value and could be present in the population of *Paramachaerodus transasiaticus* sp. nov. only in some of the individuals of this species [possibly the number of the individuals with this feature in Hezheng population (subspecies?) prevailed]. Using TNT, treating all characters as additive (ordered), a parsimonious tree of each method was obtained, whatever the search options used (Fig. 7). In cladogram A, the Hezheng sample is in a common clade as the sister group of both *Paramachaerodus–Pa. orientalis* and *Pa. maximiliani*, and diverge by Hadjidimovo sample by one apomorphy, which is feature 16. In cladogram B, Hezheng and Hadjidimovo are close together, which could be regarded as appurtenance to one and the same species. Feature 16 is the only difference (in fact a very small difference) between Hezheng and Hadjidimovo samples. It is probably an apomorphy (Salesa et al. 2010), but we don't think only one feature like this could characterize another species; it could be in the case of Hezheng and Hadjidimovo due to individual or subspecific (geographic/geologic age) differences (see above). Thus, we unify Hezheng and Hadjidimovo (in the cladogram A and B both localities are coded separately) to the same new species *Paramachaerodus transasiaticus* sp. nov. as shown in cladogram C, using all 18 characters (Appendix; Table 5),

concluding that there is no distinct apomorphy that can separate *Promeganteron* from *Paramachaerodus*.

Geological and geographical range of *Paramachaerodus* species. The most primitive form *Paramachaerodus ogygia* is known from Europe only and is in general a Vallesian form, but possibly reach the beginning of the early Turolian (Crevillente-2) (Salesa et al. 2010). *Pa. orientalis* is known from the second half of the early Turolian of upper Maragheh (Iran), but in Europe, it is a typical middle Turolian form (Salesa et al. 2010), and we hypothesize that it reached this continent most probably at the beginning of the MN12. The youngest and most evolved form *Pa. maximiliani* probably had a very wide distribution from Central Asia (China) to southwestern Europe (Spain) (Salesa et al. 2010). After the biochronology of Hadjidimovo (second half of the early Turolian) and Hezheng (cf. MN11) (see above), *Paramachaerodus transasiaticus* sp. nov. must be related to the early Turolian after the European land mammal ages. It was also largely spread, as *Pa. maximiliani*, from Central Asia to southern (southeastern) Europe. In southern Europe, it lived in the time span between the time of the existence of *Pa. ogygia* and the arrival of *Pa. orientalis*. Keeping in mind the development of tooth crenulation in *Pa. transasiaticus* sp. nov., we can assume that the Puente Minero (Spain, MN11) upper canines (Alcalá et al. 1991) are related to this species. In Asia, the new species probably coexisted (but geographically separated) with the more evolved *Pa. orientalis*. The strongly reduced, but high positioned metaconid of m1 of *Pa. maximiliani* give us the opportunity to suggest that the new, described here species could be an ancestral for *Pa. maximiliani* form. *Pa. orientalis* shows a more evolved condition than *Pa. transasiaticus*, but the very specialized talonid-metaconid complex of m1 (see above) of the latter do not suggest an evolution from this form in direction to *Pa. orientalis*.

The paleohabitat of *Paramachaerodus transasiaticus*. The paleoenvironment of Hadjidimovo-1 is discussed by Spassov (2002), who interpreted the landscape of this locality (based on the study of the rich mammal fauna), as a forest-steppe mosaic, resembling a forest-savanna mix. This opinion also was supported by Merceron et al. (2006) and Clavel et al. (2012), who both indicated that the Turolian paleohabitats of southwestern Bulgaria were dominated by open wooded landscapes and a relatively dry climate, with a continuum of habitats ranging from slightly wooded areas to relatively open landscapes. Other fossils found at the Shilei locality (Hezheng) are *Ictitherium* sp., *Hyaenictitherium hyaenoides*, *Machairodus palanderi*, *Felis* sp., *Hipparion* sp., *Acerorhinus hezhengensis*, *Chilotherium wimani*, *Chleuastochoerus stehlini*, *Palaeotragus microdon*, *Gazella* sp., *Tapirus hezhengensis* (Deng et al. 2008), and *Struthio linxiaensis* (Hou et al. 2005). All of those taxa are typical of the Hipparion Fauna found in the late Miocene of northern China, and they point to a hot and semi-arid savanna-like paleoenvironment (Deng 2004). This inferred paleoenvironmental difference likely was not an obstacle for *Paramachaerodus* because it is well known that extant large felids occupy a wide variety of environs. For example, the puma (*Puma concolor*) occupies the different habitats from Argentina north to Alaska (USA). The hunting behavior of this new *Paramachaerodus* species (Fig. 8) might have been similar to the behavior of the ambush predators such as the extant solitary pantherines (jaguars or leopards), as indicated for *Pa. ogygia* by Salesa et al. (2006).

Fig. 8 Life appearance of *Paramachaerodus transasiaticus* sp. nov. Reconstruction of the head with the position of the skull (after the skull—IVPP (V) 20106 and the mandibles—IVPP (V) 20107 and HD 9227) (reconstruction: Velizar Simeonovski, Field Museum of Natural History, Chicago & National Museum of Natural History, Sofia)

Conclusions

The analysis shows that Hezheng and Hadjidimovo machairodontine samples are almost identical. They show only some small differences which is reasonable to consider as individual, sexual, and geographic/subspecific differences, thus it is logical to assign all these geographically separated fossils as remains of one and the same species.

Both samples from Hezheng and Hadjidimovo represent a new species of the "*Promegantereon*"–*Paramachaerodus* lineage–*Paramachaerodus transasiaticus* sp. nov., characterized by: the presence of very thin crenulations on teeth (as these crenulation are very thin, they could lack in some cases as the case of c1 in HD); the low and very elongated m1 with extremely developed talonid-metaconid complex; a combination of an elongated PM3, but with strong disto-lingual expansion; PM4 with a combination of a rudimental ectostyle and sinusoidal rather than straight buccal border; the very short c-pm3 diastema; relatively short neurocranium.

The combination of all this mixture of features between "*Promegantereon*" and *Paramachaerodus*, as well as the age of the Hezheng and Hadjidimovo (early Turolian, after the European Land Mammal Ages) put *Paramachaerodus transasiaticus* sp. nov in intermediary position between the representatives of *Promegantereon* (sensu Salesa et al. 2010) and *Paramachaerodus.* Thus, it is hard to separate "*Promegantereon*" *ogygia* in generic level from the representatives of *Paramachaerodus* and all species of "*Promegantereon*"–*Paramachaerodus* lineage could be regarded as species of one and the same genus—*Paramachaerodus* Pilgrim.

Acknowledgements We (especially N.S.) are very grateful to Manuel Salesa for the photos and data, and to Jorge Morales for access to the collections in the National Museum of Natural Sciences, Madrid. We (especially Y. L.) are very grateful also to Zhanxiang Qiu (IVPP) for providing the Chinese specimen and for his advises in this research, to Tao Deng (IVPP) for funding support for the cooperation work, to Shiqi Wang and Qinqin Shi (IVPP) for their help in the field work, to Thomas Stidham (IVPP) for his help in English improving and his useful comments, to Guo Xiaocong (IVPP) for her help in drawing of some pictures and Gao Wei (IVPP) for photographing. We are indebted to Velizar Simeonovski (Field Museum, Chicago and National Museum of Natural History, Sofia) who agreed to prepare the reconstruction of the life appearance of the new species described. The detailed comments by the reviewers Michael Morlo, an anonymous reviewer, and the editor Mike Reich much improved our manuscript. This work was supported by the National Natural Science Foundation of China (Grant Number 41430102), the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB03020104), and the Ministry of Science and Technology of China (2012CB821906).

Appendix: Character analysis

Definition of characters used in the cladogram (after Salesa et al. 2010) with some additions and modifications:

1. Nasal bones shape. 0, close to rectangular, relatively narrow. 1, sub-rectangular. 2, rectangular, relatively wide.
2. Shape of upper canine crown. 0, moderately flattened. 1, markedly flattened.
3. Upper canine crenulations. 0, absent. 1, thin crenulations. 2, well-marked crenulations.
4. Orientation of PM3 and PM4. 0, aligned. 1, not aligned.
5. Mesial cusp of PM3. 0, absent. 1, present.
6. PM3, disto-lingual basal expansion of crown. 0, present. 1, absent.
7. PM3, mesio-distal elongation of crown. 0, absent. 1, present.
8. Relative size PM4-PM3. 0, PM4/PM3 index $\leq$1.50. 1, PM4/PM3 index >1.50.
9. Place of PM4 protocone. 0, protocone of PM4 situated close to the mesial edge of the parastyle. 1, situated backwards.
10. Buccal border of PM4. 0, sinusoidal. 1, sinusoidal with strongly expanded mesial-labial edge. 2, straight.
11. Protocone of PM4. 0, big and elongated mesiodistally. 1, moderately elongated mesiodistally. 2, reduced.
12. PM4 ectostyle. 0, absent. 1, rudimentary one. 2, well-marked.
13. M1 crown. 0, bucco-lingually elongated. 1, shortened (rounded).
14. Mandibular symphysis outline. 0, without flange and without mental crest. 1, without flange and with smooth mental crest. 2, verticalized with incipient mandible flange and marked crest.
15. pm2. 0, present. 1, present but very rudimentary. 2, absent.
16. pm4 mesio-buccal basal expansion in the crown. 0, absent. 1, present.
17. m1 talonid. 0, elongated with very big metaconid.1, elongated with morderate metaconid. 2, very elongated with morderate metaconid (we regard this as an apomorphy as secondary cutting edge). 3, short with morderate metaconid. 4, short without metaconid.
18. Sagittal crest. 0, strongly prominent. 1, moderately developed.

References

Alcalá, L., C. Sesé, E. Herráez, and R. Adrover. 1991. Mamíferos del Turoliense inferior de Puente Minero (Teruel, España). *Boletín Real Sociedad Española de Historia Natural* 86 (1–4): 205–251.

Berta, A. 1987. The sabercat *Smilodon gracilis* from Florida and a discussion of its relationships (Mammalia, Felidae, Smilodontini). *Bulletin of the Florida State Museum, Biological Science* 31 (1): 1–63.

Beaumont, G. 1975. Recherches sur les félidés (Mammifères, Carnivores) du Pliocène inférieur des sables à Dinotherium des environs d'Eppelsheim (Rheinhessen). *Archives des Sciences, Genève* 28: 369–405.

Beaumont, G. 1978. Notes complémentaires sur quelques félidés (Carnivores). *Archives des Sciences, Genève* 31: 219–227.

Bowdich, T.E. 1821. *An analysis of the natural classifications of Mammalia, for the use of students and travellers*, 1–115. Paris: J. Smith.

Clavel, J., G. Merceron, L. Hristova, N. Spassov, D. Kovachev, and G. Escarguel. 2012. On *Mesopithecus* habitat: insights from late Miocene fossil vertebrate localities of Bulgaria. *Journal of Human Evolution* 63: 162–179.

Deng, T. 2004. Evolution of the late Cenozoic mammalian faunas in the Linxia Basin and its background relevant to the uplift of the Qinghai-Xizang Plateau. *Quaternary Sciences* 24 (4): 413–420. (Chinese with English abstract).

Deng, T., X.-M. Wang, X.-J. Ni, and L.-P. Liu. 2004. Cenozoic stratigraphic sequence of the Linxia Basin in Gansu, China and its evidence from mammal fossils. *Vertebrata PalAsiatica* 42 (1): 45–66. (Chinese and English).

Deng, T. 2006. *Chinese Neogene mammal biochronology. Vertebrata PalAsiatica* 44 (2): 143–163.

Deng, T., W. He, and S.-Q. Chen. 2008. A new species of the Late Miocene tapirs (Perissodactyla, Tapiridae) from the Linxia Basin in Gansu, China. *Vertebrata PalAsiatica* 46 (3): 190–209. (Chinese and English).

Deng, T., Z.-X. Qiu, B.-Y. Wang, X.-M. Wang, and S.-K. Hou. 2013. Late Cenozoic biostratigraphy of the Linxia Basin, northwestern China. In *Fossil mammals of Asia: neogene biostratigraphy and chronology*, ed. X.-M. Wang, L.J. Flynn, and M. Fortelius, 243–273. Columbia: Columbia University Press.

Fischer von Waldheim, G. 1817. Adversaria zoologica. *Mémoires de la Société Impériale des Naturalistes de Moscou* 5: 357–428.

Geraads, D., and N. Spassov. 2009. Rhinocerotidae (Mammalia) from the late Miocene of Bulgaria. *Palaeontographica* 287: 99–122.

Gill, T. 1872. Arrangement of the families of mammals with analytical tables. *Smithsonian Micellaneous Collections* 11(4): 1–98.

Ginsburg, L. 1999. Order Carnivora. In *The Miocene land mammals of Europe*, eds. G.E. Rössner, and K. Heißig, 109–148. München: Pfeil-Verlag.

Goloboff, P.A., J.S. Farris, and K.C. Nixon. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786.

GSA Rock Color Chart. 1991. *The Geological Society of America Rock-Color Chart with Genuine Munsell Color Chips*. USA: Munsell Color.

Hou, L.H., Z.-H. Zhou, F.-C. Zhang, and Z. Wang. 2005. A Miocene ostrich fossil from Gansu Province, northwest China. *Chinese Science Bulletin* 50 (16): 1808–1810.

Hristova, L., and N. Spassov. 2005. *Taxonomy and Ecology of the late Miocene Hipparions of Bulgaria: Implication to the questions of the Balkans Turolian stratigraphy and environmental changes*, 24. Institute of Botany, Bulgarian Academy of Sciences, Abstracts: In Annual NECLIME Meeting.

Hristova, L., D. Geraads, G. Markov, and N. Spassov. 2013. Late Miocene mammals from Kocherinovo. *Southwestern Bulgaria. Acta Zoologica Bulgarica* 65 (4): 517–529.

Kaup, J. 1832. Vier neue Arten urweltlicher Raubthiere welche im zoologischen Museum zu Darmstadt aufbewart werden. *Archiv für Mineralogie* 5: 150–158.

Kittl, E. 1887. Beiträge zur Kenntnis der fossilen Säugethiere von Maragha in Persien. *Annalen des Kaiserlich Königlichen Naturhistorischen Hofmuseums Wien* 1: 317–338.

Kretzoi, N. 1929. Materialien zur phylogenetischen Klassifikation der Aeluroïdeen. *X Congres International de Zoologie, Budapest* 2: 1293–1355.

Kretzoi, N. 1938. Die Raubtiere von Gombaszög nebst einer Übersicht der Gesamtfauna. *Annales Historico-Naturales Musei Nationalis Hungarici* 31: 88–157.

Koufos, G., N. Spassov, and D. Kovatchev. 2003. Study of *Mesopithecus* (Primates, Cercopithecoidea) from the Late Miocene of Bulgaria. *Palaeontographica Abteilung A* 269 (1–3): 39–91.

Li, Y. 2015. Restudy of *Metailurus major* from Yushe Basin, Shanxi Province reported by Teilhard de Chardin and Leroy. *Vertebrata PalAsiatica* 52 (4): 467–485.

Maddison, W.P., and D.R. Maddison. 2015. Mesquite: a modular system for evolutionary analysis. Version 3.04. Available: http://mesquiteproject.org.

McKenna, M.C., and S.K. Bell. 1997. *Classification of mammals above the species level*. New York: Columbia University Press.

Merceron, G., A. Zazzo, N. Spassov, D. Geraads, and D. Kovachev. 2006. Bovid paleoecology and paleoenvironments from the Late Miocene of Bulgaria: evidence from dental microwear and stable isotopes. *Palaeogeography, Palaeoclimatology, Palaeoecology* 241 (3–4): 637–654.

Merriam, J.C., and C. Stock. 1932. The Felidae of Rancho La Brea. *Carnegie Institution of Washington* 22: 1–231.

Montoya, P. 1994. *Los Macromamíferos del Mioceno superior del área de Crevillente (Alicante)*. Unpublished PhD thesis. Universitat de València, 421 pp.

Morlo, M. 1997. Die Raubtiere (Mammalia, Carnivora) aus dem Turolium von Dorn-Dürkheim 1 (Rheinhessen). Teil 1: Mustelidae, Hyaenidae, Percrocutidae. *Felidae. Courier Forschungs-Institut Senckenberg* 197: 11–47.

Morales, J., and D. Soria. 1977. Presencia de la asociación *Machairodus-Paramachairodus* en Concud (Teruel). *Teruel* 57–58: 1–9.

Morales, J. 1984. *Venta del Moro: su macrofauna de mamíferos y biostratigrafía continental del Mioceno terminal mediterráneo*, 1–340. Madrid: Universidad Complutense.

Nikolov, I. 1973. The Genus *Hipparion* in Bulgaria. *Ph.D. Thesis. Institute of Geology, Bulgarian Acadamy of Sciences (Bulgarian)*.

Ozansoy, F. 1965. Étude des gisements continentaux et de mammifères du Cénozoique de Turquie. *Mémoire de la Societée Géologique de France (n. série)* 44:1–92.

Nikolov, I. 1985. Catalogue of the localities of tertiary Mammals in Bulgaria. *Bulgarian Academy of Sciences* 21: 43–62.

Pilgrim, G. 1913. The correlation of the siwaliks with Mammal Horizons of Europe. *Records of the Geological Survey of India* 43: 264–326.

Pilgrim, G. 1931. *Catalogue of the Pontian Carnivora of Europe in the Department of Geology*. London: British Museum of Natural History.

Salesa, M.J., P. Montoya, L. Alcalá, and J. Morales. 2003. El género *Paramachairodus* Pilgrim, 1913 (Felidae, Machairodontinae) en el Mioceno superior Española. *Coloquios de Paleontología, Volumen Extraordinario* 1: 603–615.

Salesa, M.J., M. Antón, A. Turner, and J. Morales. 2005a. El origen de los félidos machairodontinos: aspectos funcionales de la anatomía cráneo-cervical de *Paramachairodus ogygia* (Kaup, 1832) (Felidae, Machairodontinae) de Batallones-1 (Vallesiense, MN 10). *Revista Española de Paleontología* 20 (2): 133–141.

Salesa, M.J., M. Antón, A. Turner, and J. Morales. 2005b. Aspects of the functional morphology in the cranial and cervical skeleton of the sabre-toothed cat *Paramachairodus ogygia* (Kaup, 1832) (Felidae, Machairodontinae) from the Late Miocene of Spain: implications for the origins of the machairodont killing bite. *Zoological Journal of the Linnean Society* 144: 363–377.

Salesa, M.J., M. Antón, A. Turner, and J. Morales. 2006. Inferred behaviour and ecology of the primitive sabre-toothed cat *Paramachairodus ogygia* (Felidae, Machairodontinae) from the Late Miocene of Spain. *Journal of Zoology* 268: 243–254.

Salesa, M.J., M. Antón, A. Turner, L. Alcalá, P. Montoya, and J. Morales. 2010. Systematic revision of the Late Miocene sabre-toothed felid *Paramachaerodus* in Spain. *Palaeontology* 53: 1369–1391.

Spassov, N. 2002. The Turolian Megafauna of West Bulgaria and the character of the Late Miocene "Pikermian biome". *Bollettino della Societa Paleontologica Italiana* 41 (1): 69–81.

Spassov, N., and D. Geraads. 2004. *Tragoportax* Pilgrim and *Miotragocerus* Stromer (Mammalia, Bovidae) from the Turolian of Hadjidimovo, Bulgaria, and a revision of the Late Miocene Mediterranean Boselaphini. *Geodiversitas* 26 (2): 339–370.

Spassov, N., and D. Geraads. 2015. A new felid from the late Miocene of the Balkans and the contents of the genus *Metailurus* Zdsndky, 1924 (Carnivora, Felidae). *Journal of Mammalian Evolution* 22 (1): 45–56.

Tseng, Z.-J., X.-M. Wang, G.J. Slater, G.T. Takeuchi, Q. Li, J. Liu, and G.-P. Xie. 2014. Himalayan fossils of the oldest known pantherine establish ancient origin of big cats. *Proceedings of the Royal Society B* 281: 20132686.

Vatsev, M. 1980. Lithostratigraphy of the Neogene sedimentary rocks of the Gotse Delchev basin. *Annual of the Higher Institute of Mine and Geology* 25: 103–115.

Wagner, A. 1857. Neue Beiträge zur Kenntniss der fossilen Säugthier-Ueberreste von Pikermi. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftlichen Klasse* 8: 111–158.

Weithoffer, K. 1888. Beiträge zur Kenntniss der Fauna von Pikermi bei Athen. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients* 6: 225–292.

Werdelin, L. 1981. The evolution of lynxes. *Annales Zoologici Fennici* 18: 37–71.

Zdansky, O. 1924. Jungtertiäre Carnivoren Chinas. *Palaeontologica Sinica* 2: 1–149.