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The first record of *Amphimachairodus horribilis* from the Late Miocene of Mongolia

Marina V. Sotnikova* & Alexander V. Sizov

ABSTRACT. Mandibular fragments of a large-sized sabre-toothed cat from the Late Miocene (MN12/MN13) of the locality Khyargas Nuur 2 (=Khirgis-Nur-2) in northwestern Mongolia are described. They are included in the hypodigm of the species *Amphimachairodus horribilis*, a common member of the Late Turolian (Late Baodean) fauna of Central Asia and China. The attribution to this species is based on the large size of the cheek teeth, the presence of slight serrations along their cristids, and the morphology of the metaconid-talonid complex on m1, with a slender, cutting, ventrally rounded, and well-differentiated metaconid, as seen in the lectotype of *A. horribilis*. Comparative analysis of the Mongolian remains and the morphologically close *Amphimachairodus irtyshensis,* from the nearby locality of Pavlodar (MN12) in Kazakhstan, suggested that the latter taxon is an independent, relatively more primitive species, rather than a synonym of more advanced *A. horribilis.* This is the first report of *A. horribilis* from Mongolia and, so far, the northernmost occurrence of this species in Eurasia. This work also reconsiders the phylogeny of Eurasian representatives of *Amphimachairodus*.

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Первая находка *Amphimachairodus horribilis* из позднего миоцена Монголии

М.В. Сотникова*, А.В. Сизов

РЕЗЮМЕ. Описаны фрагменты нижней челюсти крупного саблезубого кошачьего из позднего миоцена (MN12/MN13) местонахождения Хиргис-Нур-2 на северо-западе Монголии, которые отнесены к *Amphimachairodus horribilis*, обычному представителю позднетуролийской (поздний баодэ) фауны региона Центральной Азии (Китай). Отнесение к этому виду основано на крупных размерах щечных зубов, наличии легкой зазубренности их килей, а также на форме метаконид-талонидного комплекса у m1, который имеет тонкий, режущий, вентрально округлый и хорошо дифференцированный метаконид, как у голотипа *A. horribilis.* Сравнительный анализ монгольской формы и морфологически близкого *Amphimachairodus irtyshensis* из близлежащего местонахождения Павлодар (MN12) в Казахстане позволил нам рассматривать последний таксон как самостоятельный вид, а не синонимизировать примитивный *A. irtyshensis* с более продвинутым *A. horribilis*. С территории Монголии *A. horribilis* указывается впервые и, таким образом, демонстрирует самое северное распространение этого вида в Евразии. В этой работе был также пересмотрен взгляд на филогению евразийских представителей рода *Amphimachairodus.*

КЛЮЧЕВЫЕ СЛОВА: саблезубая кошка, махайрод, нижняя челюсть, зубы, верхний миоцен, туролий, Хиргис-Нур, Монголия.

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Introduction

Numerous important localities containing remains of both large and small mammals from the Late Miocene have been identified across Mongolia. These fossils are crucial for defining specific stratigraphic levels within the Miocene, providing key insights into the region's biostratigraphic and paleoenvironmental framework (Devyatkin & Zhegallo, 1974; Devyatkin, 1981). Among these, the Khyargas Nuur 2 (=Khirgis-Nur-2; Mongolian: Хяргас нуур 2; Russian: Хиргис-Нур-2) section is of particular interest, as it serves as the stratotype of the Late Miocene Khyargas Nuur Formation (=Khirgis-Nur Formation). Situated at the base of the Khan Khukhii Ridge, near the Khar Termes spring on the northern shore of Khyargas Lake in northwestern Mongolia, the Khyargas Nuur 2 section is considered a reference section not only for Mongolia but for Central Asia as a whole. It is notable for its well-preserved biostratigraphic record, spanning over 100 metres, with clearly defined, faunally well-characterised levels. These faunal assemblages are correlated with MN13, and may possibly at their base also span the transitional zone between MN12 and MN13. These levels yield valuable biostratigraphic markers, especially referring to large mammals (Godina, 1974; Dmitrieva, 1977; Zhegallo, 1978; Vislobokova, 1983; Forsten, 1997; Sotnikova & Rook, 2010). These data delineate the temporal succession within the Late Miocene and elucidate the evolution of ecosystems during this period. The site is located in extensive badlands exposing Neogene-Quaternary sediments and offers a rare, detailed window into the geological history of the region.

The sedimentary succession exposed at the Khyargas Nuur 2 section (Fig. 1) is subdivided into four or five formations (from base to top): Oshin, Altan Teeli (?), Khyargas Nuur, Tuin Gol, and Goshu, spanning a period from the Early Miocene to the Middle Pleistocene. A more detailed description is provided elsewhere (Sizov *et al.*, 2024).

Fossil remains of Machairodus have been identified in the lower part of a faunally characterised sequence within the Khyargas Nuur Formation (levels 0–10), which consists of alluvial-proluvial deposits. Some researchers distinguish these sediments as the Altan Teeli Formation (Devyatkin & Zhegallo, 1974; Devyatkin, 1981). Although relatively thin, measuring approximately 10 metres, the precise age of this sequence remains a subject of debate. Based on the associated faunal assemblages, their age is tentatively placed in the Late Turolian (latest MN12 to MN13).

The mammal fossil remains previously found in these sediments have been tentatively identified as *Chilotherium* sp., *Samotherium* cf. *irtyshense*, *Gazella dorcadoides* Schlosser, 1903, *Gazella blacki* Teilhard de Chardin & Young, 1931, *Tragoceras* sp., and *Cervavitus* sp. (Godina, 1974; Devyatkin & Zhegallo, 1974; Dmitrieva, 1977). As mentioned above, these taxa are common in Eurasian faunas of the second half of the Turolian, within MN12–MN13.

The remains of the sabre-toothed felid consist of fragments of the mandible in matrix. These fragments display a significant deformation of the mandibular body. The well-preserved cheek teeth, with visible serrations, allowed identification of the specimen as a member of the subfamily Machairodontinae. This material has not been prepared before and, therefore, has not been thoroughly described or examined.

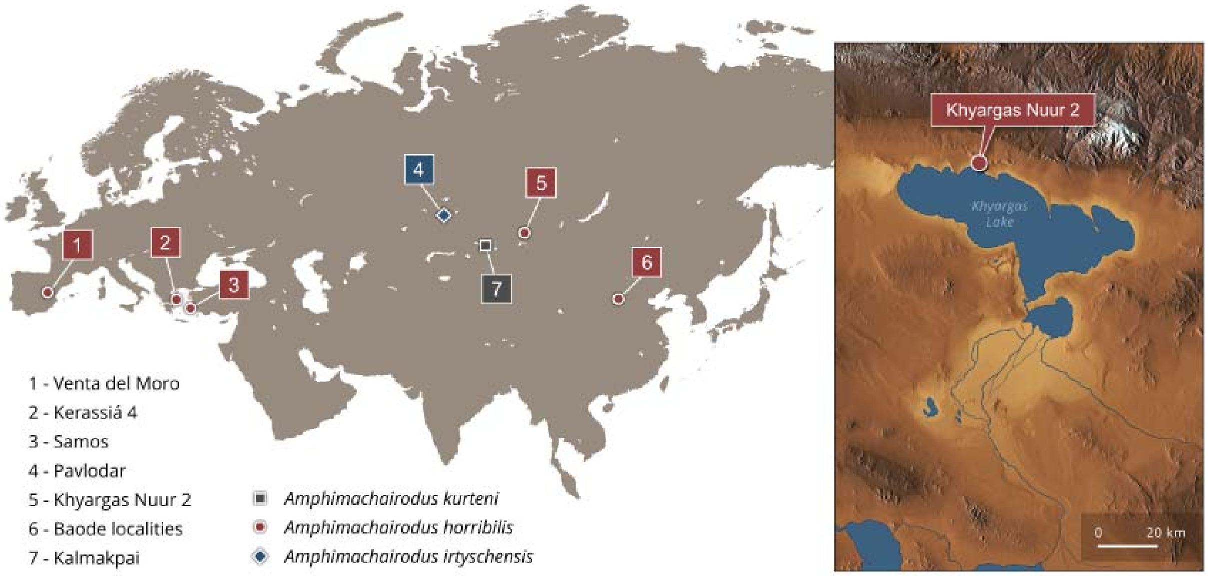

Fig. 1. Late Miocene localities that yielded the *Amphimachairodus* remains described in this paper.

After preparation, it was determined that the Mongolian sabre-toothed felid more closely resembles the larger representatives of the genus *Amphimachairodus*, a common member of the tribe Machairodontini, rather than Homotheriini (according to the taxonomic revision by McKenna & Bell, 1997). This tribe unites large sabre-toothed carnivorans characterised by several specific features associated with the development of long, sabre-like upper canines. Machairodontini first appeared in the Middle Miocene and reached the peak of their diversity towards the end of the Miocene (Turner & Antón, 1997; Antón *et al.*, 2004; Werdelin *et al.*, 2010). The Plio-Pleistocene history of these felids is also well documented, but it is represented by other, more specialised genera now classified into the subtribe Homotheriina (Jiangzuo *et al.*, 2022).

Machairodontini represent a geographically widespread group, with a fossil history in both the Old World (Eurasia, Africa) and the New World (Americas). This tribe includes large forms that reach the size of a lion and are characterised by long, flat, and relatively broad upper canines with serrated keels, other teeth with varying degrees of serration, and a variably developed mandibular flange prominence (Turner & Antón, 1997).

Our knowledge of the tribe Machairodontini has rapidly expanded and deepened over the past 25 years. In the phylogenetic framework proposed by Turner & Antón (1997), the tribe Homotheriini (currently Machairodontini) of the Old World comprised only two genera: *Machairodus* and *Homotherium*. The recent phylogeny by Jiangzuo *et al.* (2022) recognises eight genera in this tribe, including four Eurasian, two African, and two American. Among the most notable genera of this tribe are Late Miocene *Machairodus* and *Amphimachairodus*, and Plio-Pleistocene *Homotherium*, all of which had Holarctic ranges. Traditionally, these three taxa have been considered part of a single lineage, originating with generalised *Machairodus*, progressing through *Amphimachairodus* (once considered a subgenus of *Machairodus*), and culminating in highly specialised *Homotherium* (Beaumont, 1975; Turner & Antón, 1997; Antón *et al.*, 2004; Werdelin *et al.*, 2010; Jiangzuo *et al.*, 2022).

However, recent discoveries have expanded and modified this evolutionary concept, as new taxa with unusual morphology have been identified within this tribe. Among them are the Plio-Pleistocene American genera *Xenosmilus* and *Ischyrosmilus*, the leopard-sized genus *Taowu* from the Early Pliocene of northern China, the primitive yet specialised genus *Lokotunjailurus*, and giant *Adeilosmilus* from the Late Miocene of Africa (Martin *et al.*, 2000; Werdelin, 2003; Jiangzuo *et al.*, 2022). The exact phylogenetic relationships of these forms to the main Machairodontini lineage (*Machairodus–Amphimachairodus–Homotherium*) remain somewhat uncertain. Still, they suggest that the evolutionary trends in Machairodontini were not limited to the unidirectional specialisation but also included diversification (Jiangzuo *et al.*, 2022). These forms likely adapted to distinct ecological niches in geographically distant regions. The present study extends the already broad geographical range of these sabre-toothed cats during the Late Miocene. We describe a large representative of Machairodontini from the Khyargas Nuur 2 section in Mongolia. The specimen, never before documented, represents the first record of a machairodont cat in Mongolia.

Material and methods

Specimens examined. The mandibular fragments of *Amphimachairodus horribilis* (Schlosser, 1903), PIN 3222/730, were excavated in 1971 by members of the Joint Soviet-Mongolian Geological and Palaeontological Expeditions. The material remained embedded in matrix until it was prepared in 2024 at the Laboratory of Quaternary Stratigraphy of the Geological Institute of the Russian Academy of Sciences. The comparative material studied includes *Amphimachairodus irtyschensis* (Orlov, 1936) PIN 2413/115 (holotype), originally described from the Irtysh River valley at the Pavlodar locality (MN12) in Kazakhstan, and *Amphimachairodus kurteni* (Sotnikova, 1992) PIN 2433/287 and 2433/524 (mandibles from the type series) originally described from the Turolian (MN13) of Kalmakpai, Kazakhstan. All the material is stored at the Borissiak Paleontological Institute of the Russian Academy of Sciences in Moscow. Additional comparisons are based on the literature.

Abbreviations. General abbreviations: ELMA, European Land Mammal Ages; ALMA, Asian Land Mammal Ages; MN, biochronological zones (units) of Neogene Mammals; KhN2 — Khyargas Nuur 2 locality. Dental abbreviations: c1, lower canine; p2, lower 2nd premolar; P3, upper 3rd premolar; p3, lower 3rd premolar; P4, upper 4th premolar; p4, lower 4th premolar; m1, lower 1st molar; alv., alveolar measurement.

Institutional abbreviations. GIN RAS, Geological Institute of the Russian Academy of Sciences (Moscow, Russia); PIN RAS, Borissiak Paleontological Institute of the Russian Academy of Sciences (Moscow, Russia); SMGPE, the Joint Soviet-Mongolian Geological and Paleontological expedition; AMNH, American Museum of Natural History, New York, NY, USA; SNSB-BSPG, Staatliche Naturwissenschaftliche Sammlungen Bayerns — Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany.

Measurements. Most measurements in this research are the standard measurements of maximum lengths and widths accepted in the literature. Measurements were taken with digital callipers Lefavor SH-20. In this study, we used the standard terminology adopted for the dental characteristics of the Felidae.

3D-rendering and tomography. The mandibular specimens were scanned with a precision of up to 0.1 mm and a resolution of 0.1 mm using the Artec Space Spider at the GIN RAS. The digital model was acquired using the Artec Studio 17 Professional software, subsequently converted into an OBJ file, and further processed in the Autodesk 3ds Max software to create a relief image. The final rendering was saved in the PNG format.

The μCT-scans (computed microtomography) were carried out to better visualise external morphological details and reveal the internal morphology of the remains. The μCT-scans were performed on a NEOSCAN N80 (Belgium) X-ray scanner at the PIN RAS. The scanning parameters were as follows: source voltage 101 kV (right hemi-mandible) and 110 (left hemi-mandible); current 159 μA (right hemi-mandible) or 146 (left hemi-mandible); image resolution 37.3 μm/pixel; frame averaging 6 (right hemi-mandible) or 5 (left hemi-mandible); rotation step 0.3°; and a 0.5 mm Cu filter (right hemi-mandible) or a 1 mm Cu filter (left hemi-mandible). Cross-sections were reconstructed using Neoscan (Belgium) software.

Scanning electron micrographs were taken with a backscattered electron detector of a Tescan Vega3 (Brno, Czech Republic) scanning electron microscope (SEM) operated at the low vacuum mode, at the PIN RAS.

Systematic Palaeontology

Order CARNIVORA Bowdich, 1821
Suborder FELIFORMIA Kretzoi, 1945
Family FELIDAE Batsch, 1788
Subfamily MACHAIRODONTINAE Gill, 1872
Tribe MACHAIRODONTINI Gill, 1872
AMPHIMACHAIRODUS HORRIBILIS (Schlosser, 1903)
Figs. 2–3; Tab. 1.

Lectotype. Left m1 (Schlosser, 1903, pl. 115–116; Fig. 6B–C of this paper).

Referred Material. PIN 3222/730, fragments of the right and left branches of the mandible with p3, p4, and m1.

Locality and geological age. Khyargas Nuur 2 (=Khirgis-Nur-2; Mongolian: Хяргас нуур 2, Russian: Хиргис-Нур-2) locality (KhN2), Great Lakes Depression, Northwestern Mongolia. The lower part of the Khyargas Nuur Formation (levels 010). Late Turolian (latest MN12 to early MN13).

Description. The mandible is fragmented and slightly crushed due to taphonomic processes. Only parts of the right and left mandibular corpora, bearing the cheek teeth, remain from both branches. The dorsal margins of these branches are partially broken off, and the symphyseal part and the regions of the coronoid, articular, and angular processes are completely absent. On the right branch, the posterior part of the ventral ridge, running along the diastema between the canine and p3, and the base of the coronoid process, with a fragment of the ridge surrounding the ventral part of the masseteric fossa, are preserved. The left branch is broken similarly to the right one, but it has preserved the anterior part of the deep masseteric fossa with its anterior border reaching the level of the m1 posterior root (Fig. 3B).

The dental row is relatively straight, with the cheek teeth positioned nearly in line, except for p3, which sits at a slight angle relative to p4 and m1, with its anterior part turned slightly lingually. There is a diastema between p3 and p4 (3.2 mm on the right corpus and 4.5 mm on the left). The posterior edge of p4 and the anterior edge of m1 slightly overlap but do not come into direct contact. All teeth have traces of slight serrations, which are most noticeable on the posterior ridge of m1 and the anterior ridges of the premolars.

The long, four-cusped p3 has a large main cusp with the anterior cristid being noticeably longer than the posterior one. This anterior cristid is serrated in its upper, more vertical portion, but is less sharp, slightly lingually directed, and unserrated in its lower portion, which joins the base of the anterior cusp (see a lingual view of the right p3, Fig. 3).

The anterior part of p3 is unusually elongated, so that the crown length from the anterior margin to the level of the apex of the main cusp is nearly equal to the length of the remaining tooth. A small, poorly pronounced anterior cusp, lacking cristids, is situated at the base of the main cusp. This cusp is shifted towards the lingual side of the crown, where the cingulid is absent. On the buccal side, a small, slightly concave space separates the cusp from a weak buccal cingulid.

The posterior accessory cusp in p3 is almost twice the size of the anterior one. It has weakly defined anterior and posterior ridges and a smoothed, slightly rounded apex, with no gaps separating it from the adjoining cusps. The fourth posterior cusp is small and appears to be of cingulid origin. Its apex is at the level of the anterior cusp. In occlusal view, the crown of p3 has an oval outline, with a much narrower mesial than a distal part. The basal portion of the crown is supported by two long roots of equal size, both directed mesially (Fig. 2A, 3A).

The long, blade-like p4 also has four cusps, with the main cusp being large and tall, slightly serrated along the anterior ridge, while the two accessory cusps (mesial and distal) are much smaller. They are of similar height, but the mesial cusp is larger and has a rounded apex and sharp, slightly serrated anterior ridge. There is a significant gap between the main and third cusps, but between the first and main cusp, this gap is less noticeable. The fourth, smallest cusp is closely pressed against the third.

In buccal view, all cusps of p4 show a slight distal inclination, while its two long roots are angled forwards. There is a noticeable concavity between the poorly differentiated anterior cingulid and the base of the mesial ridge of the first cusp (Fig. 5, the arrow on A–C), which has a rounded apex and a sharp, slightly serrated anterior ridge. Hereafter it is termed “the concavity of the mesial wall of p4”.

The posterior cingulid around the distal accessory cusp extends from its lingual to its buccal border, showing a distinct widening and bearing two small cuspids positioned lingually and buccally to the fourth cusp. All three discussed cusps are of cingulid origin. In the oc-

Table 1. Dental measurements (in mm) of *A. irtyschensis* PIN 2413/115 (this paper), *A. horribilis* PIN 3222/730 (this paper), *A. horribilis* from Baode IVPP V15643, *A. horribilis* from Baode SNSB-BSPG 1900 XII 15 (Qiu et al. 2008), *A. horribilis* from Venta del Moro VM 53 (Morales 1988), *A. horribilis* from Kerassiá 4 K4/Δ69/1 (Roussiakis & Theodorou, 2003), *A. horribilis* from Samos AMNH 20606 (Kurtén 1976), *A. kurteni* from Kalmakpai PIN 2433/287 (this paper), *A. kurteni* from Kalmakpai PIN 2433/524 (this paper).

No	Measurements	Pavlodar PIN 2413/115, right branch	KhN2 PIN 3222/730, right branch	KhN2 PIN 3222/730, left branch	Baode IVPP V15643	Lectotype from Baode SNSB-BSPG 1900 XII 15	Venta del Moro VM 53	Kerassiá 4 K4/Δ69/1	Samos AMNH 20606	Kalmakpai PIN 2433/287	Kalmakpai PIN 2433/524, left branch
1	p3 L	21	19.5	–	20	–	21	18.8	21.4	alv. 17	17.5
2	p3 ant. W	8.2	7.1	–	–	–	–	–	–	–	7
3	p3 post. W	10.5	8.6	9	9.9	–	–	9	9.5	–	7.6
4	p3 H at main cusp	10.5	10	10	14.4	–	–	–	–	–	–
5	Distance between the anterior edge of p3 and the main cusp	10.9	10.2	–	–	–	–	–	–	–	8.2
6	3 / 1 (%)	50	44.1	–	49.5	–	–	–	–	–	–
7	4 / 1 (%)	50	51.2	–	72	–	–	–	–	–	–
8	p4 L	31.9	32.1	31.2	31.7	–	29.8	28.3	29.2	26.7	25
9	p4 ant. W	12	10.9	–	12.4	–	–	–	–	9.6	9.9
10	p4 post. W	13.7	12.8	12.5	13.5	–	13.2	12.9	12.7	11.1	11.1
11	p4 H at main cusp	16.3	18	17.1	>17	–	–	–	–	–	–
12	10 / 8 (%)	42.9	39.8	40	42.6	–	44.2	45.5	43.4	41.5	44.4
13	11 / 8 (%)	51	56	54.8	>53.6	–	–	–	–	–	–
14	m1 L	35.5	35	34.4	36.7	35.5	35.5	35.6	32.8	31	31.1
15	m1 max. W	15.7	13.9	14.3	15.5	15	14.2	15.1	14.7	12.9	13.7
16	m1 H at post. end of protoconid	~17.1	~18	~19	20	–	–	–	–	19	–
17	15 / 14 (%)	44.2	39.7	41.5	40	42.3	40	42.4	44.8	41.6	44
18	16 / 14 (%)	48.1	51.4	55.2	54.5	–	–	–	–	61.2	–
19	1 / 8 (%)	65.8	60.7	–	63.1	–	70.4	66.4	73.2	–	70
20	1 / 14 (%)	59.1	55.7	–	54.5	–	59.1	51.9	65.2	–	56.2
21	8 / 14 (%)	89.8	91.7	90.6	86.4	–	83.9	79.5	89	–	80.3
22	Dia. c–p3	59	–	–	–	–	50	58	–	alv. 34	46.9
23	Lp3–m1	91	87.5	~85	–	–	–	81.4	–	alv. 77	70

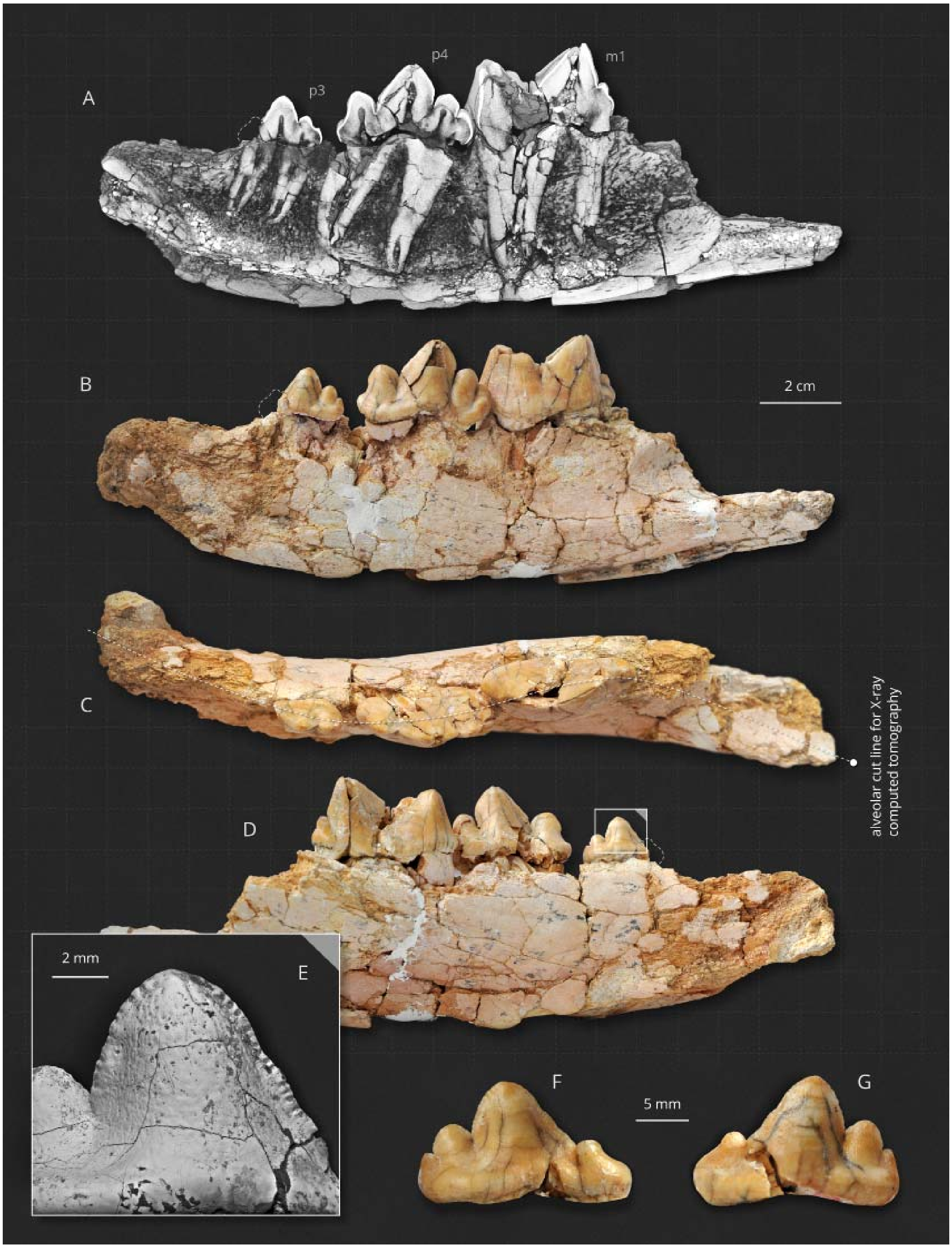

Fig. 2. Left hemi-mandible of *Amphimachairodus horribilis* from Khyargas Nuur 2 PIN 3222/730. A — alveolar section of the hemi-mandible by X-ray computed tomography (the path of this section is indicated with a dashed line in C); B — buccal view; C — occlusal view; D — lingual view; E — SEM image of a serrated anterior cristid of the main cusp of p3; F, G — p3 reconstructed by combining photographs of the right and left branches of the mandible; F — lingual view; G — buccal view.

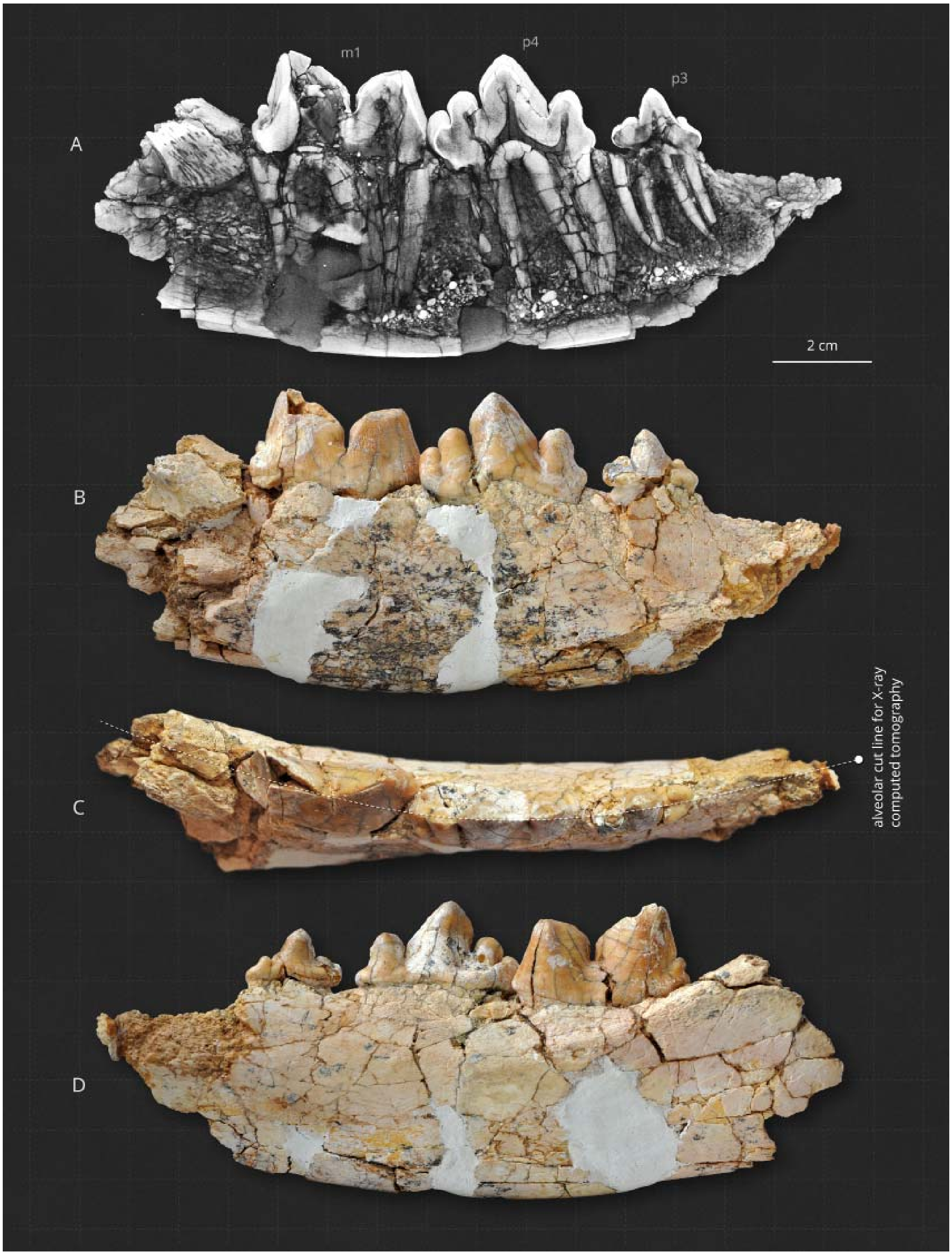

Fig. 3. Right hemi-mandible of *Amphimachairodus horribilis* from Khyargas Nuur 2 PIN 3222/730. A — alveolar section of the hemi-mandible by X-ray computed tomography (the path of this section is indicated with a dashed line in C); B — buccal view; C — occlusal view; D — lingual view.

clusal view, p4 has an oval outline, with its distal width greater than the mesial one.

The long and narrow first molar, m1, displays the paraconid which is slightly lower and mesiodistally shorter than the protoconid. There is a large and wide carnassial notch between the two cusps. The lingual fold of enamel is expressed on the paraconid in its ventral part; this fold is not visible on the protoconid. The sharp, cutting posterior crest of the protoconid bears poorly developed serrations. A small but distinct metaconid is situated on the posterior ridge of the protoconid just above the talonid; the latter does not extend distal to the metaconid. The rounded apex of the metaconid is offset from the protoconid ridge and separated from it by a shallow and narrow, yet distinct gap. The sharp posterior ridge of the metaconid runs down to the posterior projection of the talonid. The distal outline of the metaconid/talonid complex shows a notable concavity between the upper part of the talonid and the base of the metaconid, demarcating the boundary between these cusps. A similar shape of the metaconid and a similar degree of its differentiation from other cusps are characteristic of *A. horribilis* and can be observed in its lectotype (Fig. 6, B–C).

The m1 possesses two roots. The anterior one, supporting the paraconid and the mesial portion of the protoconid, is long, robust, and vertically oriented. The posterior one, associated with the distal part of the protoconid and talonid, is significantly shorter and narrower, yet also vertically positioned.

Comparison and discussion

The specimen PIN 3222/730 from KhN2, as described above, displays distinct machairodontine characteristics, including serrated edges of the cheek teeth and a ventral enamel fold (lingual ridge of paraconid) on the lingual side of the m1 paraconid. Its large size and overall dental morphology, particularly the structure of p3, closely resemble those of the Late Miocene Asian species "*Machairodus" irtyschensis* Orlov, 1936, and "*Machairodus" horribilis* Schlosser, 1903, as described by Orlov (1936) and Qiu *et al.* (2008). Thus, our comparisons primarily focus on the Late Miocene large sabre-tooth felids from neighbouring regions of Kazakhstan and China. At present, all of these species are attributed to the genus *Amphimachairodus* Kretzoi, 1929 (Sotnikova & Tleuberdina, 2023; Wang *et al.*, 2023).

The Eurasian history of the genus *Amphimachairodus*

This genus was established for the species *"M." palanderi* Zdansky, 1924 from the Baode fauna of North China (Kretzoi, 1929). However, it initially received limited attention and was occasionally treated as a subgenus for *M. giganteus* (Beaumont, 1975). In the 1980s, Morales (1984), based on dental characters, cautiously suggested the existence of two genera of machairods, which were later vastly reinforced by craniomandibular features identified in the new material from Batallones-1 (Vallesian, Spain) (Antón *et al.*, 2004). These authors noted that the differences in the degree of machairodont specialisation between the Vallesian *M. aphanistus* (Kaup, 1832) and the Turolian *M. giganteus* (Wagner, 1848) are at least as important as those separating *M. giganteus* from the Plio-Pleistocene genus *Homotherium*. They proposed the recognition of *Amphimachairodus* as a valid generic name for the Turolian species *M. giganteus* (Antón *et al.*, 2004). Christiansen (2013) formalised this distinction through cladistic analysis, confirming the conclusions of earlier researchers.

According to the latest phylogenetic revision, both genera are included within the tribe Machairodontini, where they represent distinct stratigraphic intervals, the Vallesian and the Turolian, respectively (Jiangzuo *et al.*, 2022).

Amphimachairodus was widespread across the Old and New Worlds during the second half of the Turolian (Wang *et al.*, 2023). Although the remains of these predators have been discovered on almost every continent except Antarctica, their phylogenetic relationships and species-level taxonomy remain subjects of ongoing debate. In many cases, uncertainty stems from the incomplete fossil record and the fact that numerous specimens originate from historical collections made without strict documentation of their geological or stratigraphic context. As a result, closely related forms have sometimes been described under different species names, while conversely, some species have been recognised as polyphyletic (Zdansky, 1924; Beaumont, 1975; Qiu *et al.*, 2008; Wang *et al.*, 2023).

"Machairodus" palanderi from the Baode fauna of China is the type species of the genus *Amphimachairodus* (Kretzoi, 1929). This taxon closely resembles *A. giganteus* (Wagner, 1848) from the Pikermi fauna of Greece (MN12–MN13) and is sometimes considered synonymous with that species (Beaumont, 1975; Antón *et al.*, 2004; Turner & Antón, 1997). Additionally, other Late Turolian species, such as "*M.*" *tarakliensis* Riabinin, 1929, "*M.*" *tingii* Zdansky, 1924 and "*M.*" *irtyschensis* have also been included under *A. giganteus* (Beaumont, 1975).

Due to the lack of clearly defined morphological criteria during the early stages of research, many scholars, following Beaumont's concept, grouped nearly all Late Turolian Eurasian species under the synonymy of *A. giganteus*. These species were sometimes treated as part of the informal "*giganteus* group". This perspective prevailed until the early 2000s, with many authors attributing the alleged differences among these species to sexual dimorphism (Turner & Antón, 1997; Antón *et al.*, 2004; Peigné *et al.*, 2005). However, the Asian species "*M." horribilis* Schlosser was excluded from these discussions due to its unclear systematic position.

A revision of Chinese specimens undertaken in the 2000s helped clarify and reduce the number of Turolian species identified in Asia. This progress was facilitated by description of new material and reassessment of existing collections conducted or endorsed

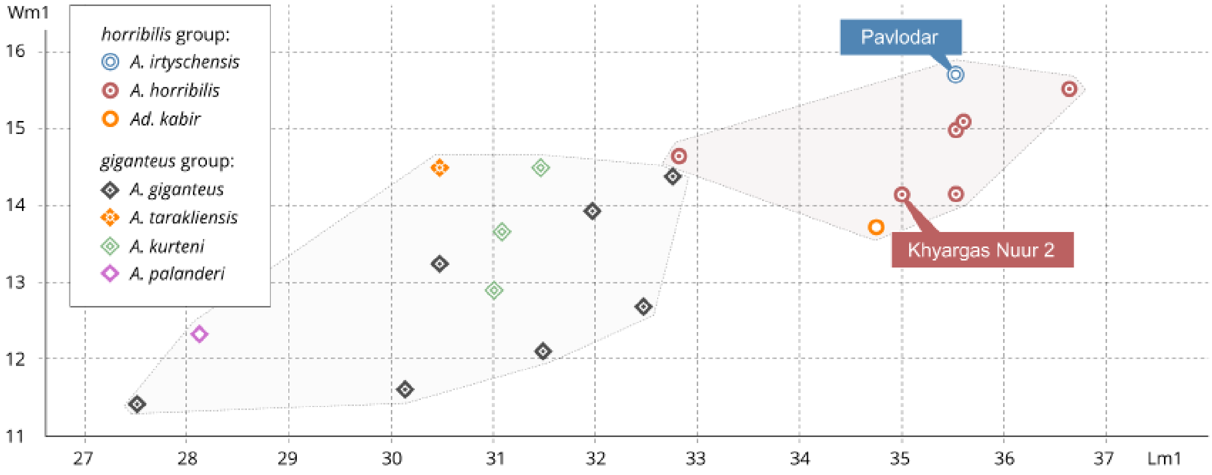

Fig. 4. Bivariate plot of m1 length and width of *Amphimachairodus* based on data in Table 1 and data from Kurten (1976), Morales (1988), Morlo & Semenov (2004), Peigné *et al.* (2005) and Qiu *et al.* (2008).

by Qiu *et al.* (2008). These studies revealed that the type series for *A. palanderi* (Zdansky) and *A. horribilis* (Schlosser) were heterogeneous. The taxonomic status of most specimens was clarified, with lectotypes designated for the best-known Chinese species (*A. palanderi* and *A. horribilis*). Additionally, some species, such as *M. tingii*, were synonymised or considered invalid (Qiu *et al.*, 2008).

Systematisation of the type materials by Qiu *et al.* (2008) significantly facilitated identification of Asian taxa. It became evident that the Asian representatives of *Amphimachairodus* fall into two distinct groups. The first group, consisting of smaller forms, including *A. palanderi* and *A. kurteni*, is closely related to the European *A. giganteus*. The second group consists of giant forms previously unparalleled among European specimens (Fig. 4). This group encompasses *A. horribilis* from China and *A. irtyschensis* from Kazakhstan (Qiu *et al.*, 2008).

Amphimachairodus irtyschensis and its comparison with remains from KhN2

The species *Amphimachairodus irtyschensis* (Lm1 = 35.5 mm) from Pavlodar is based on two branches of a single mandible, PIN 2413/115, having a complete lower dentition and a well-preserved symphysis, along with numerous postcranial remains (Orlov, 1936, Fig. 1/1). In his description, Orlov (1936) emphasised the substantial size of the specimen and noted its similarity to the Chinese species *A. horribilis*. However, due to the heterogeneous nature of the type series for *A. horribilis*, a definitive conclusion regarding this resemblance was not possible at the time. Subsequently, the material of A. irtyschensis has not been revised.

The Pavlodar specimen has taken on an entirely new significance following the revision of Schlosser's Chinese materials and the designation of a single lower molar SNSB-BSPG 1900 XII 15 from the type series as a lectotype for the species *A. horribilis* (Qiu *et al.*, 2008). While discussing the species *A. irtyschensis*, Qiu and colleagues (2008) noted similarities between the Chinese and Pavlodar forms. Still, they retained the name *A. irtyschensis* due to observed differences in the occlusal morphology of the lower molar, as depicted in Orlov's photograph (1936, Pl. 1).

Subsequently, Wang *et al.* (2023) questioned the validity of these morphological distinctions, attributing them to potential artefacts in Orlov's (1936) photograph and, as a result, proposed *A. irtyschensis* as a junior synonym of *A. horribilis*. The species *A. irtyschensis* was not considered in the genus *Amphimachairodus* by Jiangzuo *et al.* (2022) either.

Since Orlov's original description in 1936, the morphology of *A. irtyschensis* has never been revisited at a modern analytical level, except for its brief characterisation in Sotnikova & Tleuberdina (2023, in Russian). To better understand its morphology and potentially restore the species status of *A. irtyschensis*, we present a detailed dental analysis of this taxon in comparison with the new Mongolian material.

Our examination of the Pavlodar material and the mandibular remains from KhN2 reveals many shared traits, such as the large tooth size, the presence of a pronounced diastema between p3 and p4, weak serrations on the anterior ridges of premolars and the lingual posterior ridge of m1, the presence of a metaconid-talonid complex on m1, and a concavity of the mesial wall of p4. In the distal portion of the premolars in both forms, there is a notable bucco-lingual expansion of the crown, which is of cingulid origin.

The advanced traits shared by both Asian sabre-toothed cats include a large p3 with a relatively low crown, which is unusually elongated anterior to the mesial accessory cusp; as well as bucco-lingually flattened and rounded apices of accessory cusps on the premolars. There is also a tendency towards the development of vertical gaps and notches between the non-cingulid cusps of the cheek teeth. Additionally, a weak vertical groove between the paraconid and the talonid on the buccal side of m1 is also present.

However, unlike the KhN2 specimen, *A. irtyschensis* possesses more robust and lower-crowned cheek teeth, p3 with a weaker developed mesial cusp, p4 with less rounded apices of the anterior and posterior accessory cusps, and a posterior cingulid lacking lateral elements. Both premolars also show a more developed, bulbous expansion of the distal cingulid. The carnassial of *A. irtyschensis* displays a less-developed lingual paraconid ridge (=lingual fold on the paraconid). Although its metaconid has a thin and slightly rounded apex, it is less differentiated and not separated from the posterior protoconid ridge (Fig. 6A). All these features are more primitive than those of *A. horribilis* from KhN2.

Thus, our morphological analysis of dental characters suggests that *Amphimachairodus* from Mongolia is more derived than the generalised one from Kazakhstan, for which the original species name *irtyschensis* proposed by Orlov (1936) should be reinstated.

Amphimachairodus horribilis and its comparison with remains from KhN2

Inadequate information on the type specimen of *A. horribilis* has led to ongoing debate and controversy regarding its taxonomic position. As was noted above, Qiu *et al.* (2008) made a serious attempt to resurrect the species *horribilis*. From Schlosser's collection in Munich they selected the lower carnassial SNSB-BSPG 1900 XII 15 (Lm1 = 35.5 mm) and designated it as the lectotype.

Two well-preserved skulls and one mandible from the latest Miocene deposits in the Baode region were also assigned to this species (Qiu *et al.*, 2008). Later, Deng and colleagues described a skull of a very large Late Miocene sabre-toothed felid and also included it in the hypodigm of *A. horribilis*. Based on these materials it was found that this taxon had a primitive cranial shape (Deng *et al.*, 2016) and a p3 morphology that is very different from p4, which also sharply differentiates this form from the *A. giganteus* group (Qiu *et al.*, 2008).

Our comparison of the lower carnassial from the Mongolian mandible with the lectotype of *A. horribilis* revealed their close similarity. They have nearly identical linear dimensions of m1 (Table 1) and its main cusps, the paraconid and protoconid. In both cases, these cusps display an open carnassial notch and a lingual paraconid fold.

The greatest similarity between PIN 2413/115 and the lectotype is observed in the structure of the metaconid-talonid complex. These specimens share the most characteristic traits of the species, specifically a moderately developed metaconid positioned directly above the talonid, with their boundary marked by a distinct notch on the posterior wall of this complex. Additionally, the metaconid is rounded on three sides and separated from the posterior ridge of the protoconid by a clear gap, an unquestionably advanced trait absent in more primitive *A. irtyschensis*.

Based on its complete morphological and metric congruence with the m1 of the *A. horribilis* lectotype, we assign the KhN2 specimen PIN 3222/730 to *A. horribilis*. Furthermore, we assert that both specimens display characteristics that are more derived than those of *A. irtyschensis*.

The description of new material (two skulls and a mandible) from the Late Miocene deposits in the Baode region (Qiu *et al.*, 2008) significantly expanded the concept of the species *A. horribilis*. For our comparative study, the most important specimen is the well-preserved mandible V-15643, with its m1 being 36.7 mm in length, the largest recorded for *A. horribilis*.

The diagnostic dental features exhibited by this mandible include the long and mesially narrow p3 (Fig. 5D), very large and five-cusped p4, and m1 with lingual ridges. The morphology of m1 resembles *A. horribilis* in the presence of a moderately developed metaconid-talonid complex, with a small rounded metaconid situated just above the talonid and separated by gap from the posterior ridge of the m1 protoconid.

Our comparison revealed that IVPP V-15643 is more derived than PIN 3222/730. The former demonstrates the presence of the anterior cingulid of p4 as a true high cuspid, which is clearly separated from the other cusps, and the presence of the mesial cusp of p4, which is strongly vertically oriented, more rounded ventrally, and thinner buccolingually. In addition, V-15643 has wider and more open dental gaps and notches than other members of *A. horribilis*, which is also interpreted as an advanced condition.

Regarding the morphology of the V-15643 mandibular body, it is low, slender, nearly straight ventrally, and thin bucco-lingually. It shows no trace of a mental flange, while its symphyseal portion is strongly verticalised. These traits sharply differentiate this mandible from that of *A. irtyschensis*, which, in contrast to V-15643, is higher and more robust, has a more horizontally oriented symphysis and evidence of a developed mental flange. In all these features, apart from the absence of a mental flange, the mandible V-15643 demonstrates a more derived condition.

Other *Amphimachairodus* from the *irtyschensis-horribilis* group

Another significant point is that *A. horribilis* was long thought to be confined to Asia. However, Wang *et al.* (2023) suggested that the lower jaw VM53 from the Venta del Moro locality in Spain (MN13) could also be attributed to *A. horribilis* based on m1 length of 35.5 mm and the elongated shape of the mandible. Initially, this material was described by Morales (1984) as *Amphimachairodus giganteus*. According to his description, the ridges of the cheek teeth are serrated, the p3 alveolus is elongated, the p4 displays a slightly curved basal outline with well-developed accessory cusps and a prominent cingulid with posterior cuspid, and the m1, as in *A. horribilis*, exhibits a wide carnassial notch between the paraconid and protoconid, along with a well-developed metaconid-talonid complex. Considering the large size and the dental description by Morales (1984), as well as the stratigraphic position of these remains, it is reasonable to suggest that this mandible belongs to *A. horribilis*.

Our survey of other European finds suggests that the mandible with an m1 measuring 35.6 mm from Kerassiá 4, Greece (MN12–MN13), may also belong to this group. Initially, this mandible (K4/Δ69/1) was attributed to *A. giganteus* (Roussiakis & Theodorou,

Fig. 5. Comparison of mandibles of *Amphimachairodus irtyschensis* (A), *Amphimachairodus horribilis* (B–D) and *Amphimachairodus kurteni* (E) from A — Pavlodar PIN 2413/115; B –- Samos AMNH 20606; C — Khyargas Nuur 2 PIN 3222/730, D — Baode IVPP V15643 (Qiu *et al.*, 2008. Fig. 2); D' — p3 from the occlusal side (IVPP V15643); E — Kalmakpai PIN 2433/287. The arrow in A–C indicates the concavity of the mesial wall of p4.

2003). However, our comparison revealed significant similarities with the mandible of *A. horribilis* (IVPP V15643) from China. These similarities are evident not only in the large size but also in the morphology of the dorsal part of the symphysis, which is notably elongated and flattened in both specimens, as well as in the pronounced arching of the incisor row and the complete absence of diastemata between the incisors.

Nevertheless, the Kerassiá 4 mandible is distinguished by the presence of a mandibular flange. Some dental traits described by Roussiakis & Theodorou (2003, Pl. 4, Fig. 1–2) are also consistent with *A. horribilis*, including an elongated p3 with a small but developed anterior cusp. Additionally, p4 is four-cusped with a well-developed posterior cingulid, while m1 exhibits a moderately developed metaconid-talonid complex. Judging from the Figure (Pl.4, Fig. 1–2), the apex of the metaconid is slightly rounded and subtly separated from the posterior ridge of the protoconid.

The mandible AMNH 20606 from Samos, Greece (MN12–MN13), was discussed and attributed to *Machairodus giganteus* by Beaumont (1975, Fig. 6f). The following characteristics support its assignment to *A. horribilis*: large size (Lp3 = 21.4 mm; Lp4 = 29.2 mm; Lm1 = 32.8 mm), the diastema between p3 and p4, long and four-cusped p3 with a large mesial space in front of the anterior cusp and rounded tips of all additional cusps, four-cusped p4 with distinct gaps between all cusps, high and rounded additional cusps. The metaconid-talonid complex is moderately developed, its structure is similar to that of *A. horribilis* from KhN2 (Fig. 5B).

The large machairodont (Lm1 = 34.7 mm) from the African Late Miocene was initially described as *Machairodus kabir* by Peigné *et al.* (2005), based on the mandible TM-266-02-102 from the Toros-Menalla locality in Chad. Subsequently, this specimen was referred to the genus *Amphimachairodus*. However, it has recently been designated as the type of a newly established genus, *Adeilosmilus* (Jiangzuo *et al.*, 2022).

Many researchers have highlighted the derived characteristics of TM-266-02-102, including the prominent mandibular flange, reduced p3, and pronounced posterior inclination of the cheek teeth. Despite these advanced traits, it primitively retains a moderately developed metaconid-talonid complex, described by Peigné *et al.* (2005) as "separated from the protoconid by a shallow groove." This feature, alongside others, such as the substantial gap between the mesial and main cusp on p4, sharp upper edges of the premolar cusps, a carnassial notch on m1, and the elongated mandibular body, places this specimen close to *A. horribilis*.

Comparison with the Asian members of the *giganteus* group (*kurteni–palanderi*)

Qiu and colleagues were the first to demonstrate that two distinct groups of large machairodont cats emerged during the Late Turolian in Asia (Qiu *et al.*, 2008). The first group, closely related to the European *A. giganteus*, included *A. palanderi* and *A. kurteni*. The second group comprised giant forms, such as *A. irtyschensis* and *A. horribilis*, which lacked European representatives. While the authors noted differences in the morphology of p3 between these two groups, they did not provide a detailed analysis of these distinctions.

To gain a deeper understanding of the differences between the A. *irtyschensis-horribilis* group and the species related to *A. giganteus*, such as *A. palanderi* and *A. kurteni*, we compared cheek tooth morphology of our material from Khyargas Nuur 2 to that of *A. kurteni*, previously described from the Kalmakpai locality (MN13) in Kazakhstan (Sotnikova, 1992).

In the p3 of *A. kurteni* (PIN 2433/524) (Fig. 5E, Fig. 6H), the mesial accessory cusp is well-developed, with no anterior elongation of the crown ahead of the cusp—a feature characteristic of *A. irtyschensis-horribilis*. The mesial and distal accessory cusps of p3 in *A. kurteni* are relatively large and comparable in size. In contrast, in *A. horribilis*, the mesial cusp is so small that it is only comparable to the distal cingulid cusp. All features noted for the p3 of *A. kurteni* are also observed in the p3 of the mandible PMU 3851, the lectotype of *A. palanderi* (Wang *et al.*, 2023, Fig. 12b). Such an asymmetrical p3 structure is characteristic of basal felids, whereas in *A. irtyschensis-horribilis* a more derived condition is observed, with the tooth being more evenly divided at the level of the main cusp apex.

The p4 of *A. kurteni* (PIN 2433/287) closely resembles that of *A. horribilis* except for some notable distinctions. In *A. kurteni*, the mesial cingulid is developed as a small cusp, whereas in *A. horribilis* it almost entirely merges with the main crown. The additional cusps of the p4 in *A. kurteni* are less differentiated than in *A. horribilis*. In the latter, a pronounced tendency for a fan-like arrangement of accessory cusps is evident, particularly in the mandible of *A. horribilis* IVPP V15643 from China (Fig. 5D, Fig. 6G).

The distal cingulid in *A. horribilis* forms a platform on which three cingulid cusps are situated, while in *A. kurteni* the distal cingulid is not complicated by additional elements. The distal part of the crown is greatly expanded in *A. horribilis*, in contrast to *A. kurteni*, in which the posterior width of the crown is only slightly less than the anterior. The lower carnassial tooth (m1) of *A. kurteni* (PIN 2433/287) has well-developed lingual ridges, which form an arc, and a closed carnassial notch, the latter also observed in the lectotype of *A. palanderi* (PMU 3851). In nearly all specimens of sabre-toothed cats from the *A. giganteus* group, the metaconid-talonid complex is either absent or represented only by a slight thickening of enamel at the base of the protoconid posterior ridge (Fig. 5E). In *A. horribilis*, the carnassial retains a moderately developed metaconid-talonid complex, and a lingual ridge is developed only on the paraconid.

Conclusions

The Late Turolian was a pivotal period of the Late Miocene, spanning approximately 7 to 5 million years ago. This epoch was characterised by significant faunal transformations that laid the foundation for the emergence of Pliocene faunas. It was marked by intensive faunal exchanges between regions and high biodiversity across various taxa.

Among the defining elements of the Late Turolian ecosystems were the sabre-toothed cats of the genus *Amphimachairodus*. These large predators reached their peak diversity during this period but eventually became extinct by its end, giving way to new Pliocene taxa. In this study, the genus *Amphimachairodus* is examined based on fragments of a mandible with cheek teeth from the Late Miocene Khyargas Nuur 2 section in Mongolia. This material includes previously unpublished specimens, which significantly advance our understanding of the evolutionary history of the genus. Our analysis reveals that the Mongolian material differs markedly from a more primitive *A. irtyschensis* from Pavlodar, Kazakhstan (MN12), and instead corresponds to *A. horribilis*, showing a nearly complete morphological congruence to its lectotype.

The comparative analysis suggests that large Late Turolian sabre-toothed cats from Eurasia can be divided into two major groups. The first group comprises giant forms, including *A. irtyschensis* and *A. horribilis*. The second, known as the "*giganteus* group," includes species closely related to *A. giganteus* such as *A. tarakliensis, A. palanderi* and *A. kurteni*. The hypothesis of these two groups was first proposed by Qiu and colleagues,

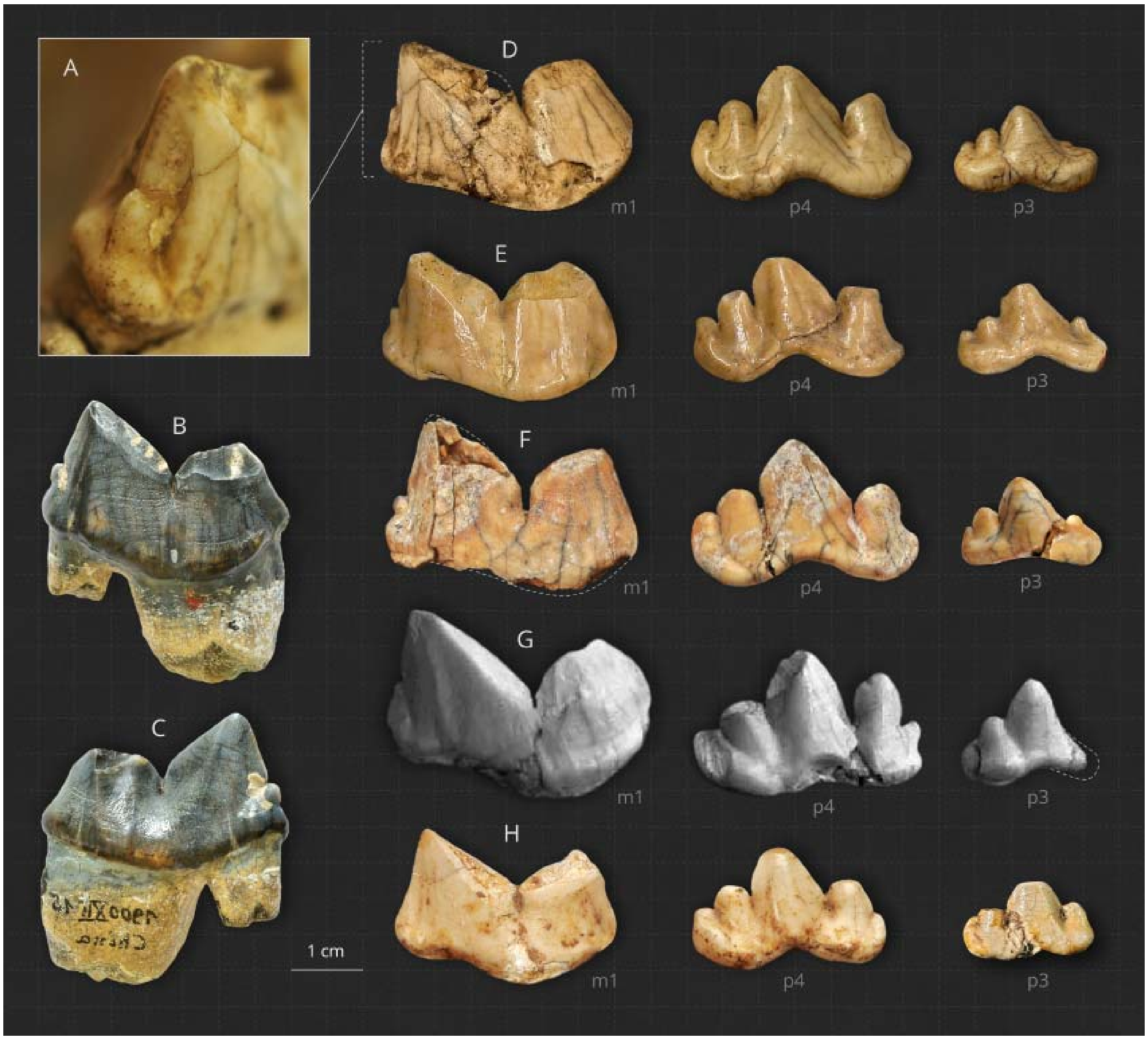

Fig. 6. Dental comparison. A — metaconid-talonid complex on m1 of *Amphimachairodus irtyschensis*; B–C — mirrored lectotype of *Amphimachairodus horribilis* SNSB-BSPG 1900 XII 15 (Wang *et al.*, 2022, Fig.9); B — buccal view; C — lingual view. Buccal views of dental raws: D — holotype of *Amphimachairodus irtyschensis* from Pavlodar PIN 2413/115; E — *Amphimachairodus horribilis* from Samos AMNH 20606; F — *Amphimachairodus horribilis* from Khyargas Nuur 2 PIN 3222/730; G — *Amphimachairodus horribilis* from Baode IVPP V15643 (Qiu *et al.*, 2008. Fig. 2); H — *Amphimachairodus kurteni* from Kalmakpai PIN 2433/287.

who suggested that the *A. irtyschensis-horribilis* group was confined to the Asian region (Qiu *et al.*, 2008).

However, our study demonstrated that members of that group also occurred in Europe. The first evidence of *A. horribilis* in Europe was provided by Wang *et al.* (2023), who attributed the specimen from Venta del Moro, Spain (MN13), to this species. Our study confirms this hypothesis and further substantiates the inclusion of additional European specimens in this group, specifically from the localities of Samos and Kerassiá 4 in Greece (MN12–MN13).

We found that both groups, *A. irtyschensis-horribilis* and *A. giganteus*, differ not only metrically (Fig. 4) but also exhibit a complex mosaic of dental traits, combining apomorphic and plesiomorphic states. In the *giganteus* group, primitive features are more pronounced in the premolars, while the carnassial tooth, lacking a metaconid-talonid complex, displays a more derived condition. In contrast, the *A. irtyschensis-horribilis* group exhibits more derived premolars, while their carnassial primitively retains a well-developed metaconid-talonid complex. Furthermore, this second group of machairodontine cats shares a unique autapomorphy: the symmetrical appearance of p3, as opposed to the asymmetrical one in other members of the Machairodontini. The divergent evolutionary trajectories of dental traits suggest no direct ancestral relationships between these two groups of machairodontines.

An intriguing implication of this study results from our placement of two giant forms — one found in China (Qiu *et al.*, 2008) and another in Africa (Peigné *et al.*, 2005) in the *A. irtyschensis-horribilis* group. The first one was described as *A. horribilis*, while the other was later assigned to a newly established genus, *Adeilosmilus* (Jiangzuo *et al.*, 2022). The Chinese mandible exhibits advanced characteristics that may warrant its recognition as a separate species. The African taxon, *Ad. kabir*, shares many traits with the *A. irtyschensis-horribilis* group but is distinguished by a set of unique derived features, including a prominently developed mental flange and a reduced p3. These considerations underscore the necessity of generic differentiation between the two groups of machairodontines. Given that *A. palanderi*, a member of the *giganteus* group, is the type species of *Amphimachairodus*, the *irtyschensis-horribilis* group requires its own generic designation. If future studies support the inclusion of *Ad. kabir* in this group, the generic name *Adeilosmilus* could potentially be applied to all its members. However, resolving this taxonomic issue will require a more detailed morphological analysis incorporating a broader range of traits, including cranial features.

Although the significant research by Kaakinen *et al.* (2013) has clarified many stratigraphic issues associated with Late Miocene sites in the Baode region, often hindered by the lack of precise geological context, certain questions remain unresolved. For instance, the exact provenance of the lectotype of *A. horribilis* and other material described by Qiu *et al.* (2008) is yet to be determined. In this respect, Mongolian and Kazakhstan localities, such as Pavlodar, Kalmakpai, and Khyargas Nuur 2, offer a distinct advantage due to their well-defined stratigraphic contexts. Specimens from these sites are accompanied by rich associated faunas, including birds, fish, and small and large mammals, facilitating more accurate comparisons and reconstructions (Devyatkin & Zhegallo, 1974; Devyatkin, 1981; Vangengeim *et al.*, 1993; Sizov *et al.*, 2024).

The results of this study not only confirm the existence of two parallel evolutionary lineages of machairodontines in the Late Turolian but also shed new light on the phylogeny of the genus *Amphimachairodus*. These results highlight the complex mosaic of adaptations and evolutionary transformations characteristic of this period.

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