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Fast spread followed by anagenetic evolution in Eurasian and North American *Amphimachairodus*

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ABSTRACT

The charismatic sabretooth cat *Amphimachairodus* has numerous but largely fragmentary records across late Miocene deposits of Africa, Eurasia and North America. The genus has a complex taxonomic history, and the majority of *Amphimachairodus* materials come from isolated localities, often studied without stratigraphic context. Here, we analyse the long, continuous records from the classic Chinese Baode strata, which produce *Amphimachairodus* throughout the section, and demonstrate that an *A. palanderi-horribilis* chronospecies succession represents a continuum of *in situ* anagenetic evolution of increasing size. We then synthesise chronological occurrences of *Amphimachairodus* from all Holarctic records and reframe their evolution as a case of chronospecies succession. Two parallel anagenetic lineages are evident: a Eurasian *A. giganteus-palanderi-horribilis* chronospecies succession and second, a North American *A. coloradensis-alvarezi* chronospecies succession following an immigration event in the early Hemphillian. In addition to greater hypercarnivory evidenced by dental specialisation, the Eurasian lineage shows a trend towards a large body size, whereas the North American lineage decreases in size. We take this opportunity to describe materials of *Amphimachairodus alvarezi* from Yepómera (latest Hemphillian) in the state of Chihuahua, Mexico, and previously undescribed materials from San Miguel de Allende Basin. We review taxonomic status of Chinese *A. horribilis* and related taxa.

Introduction

Amphimachairodus is a tiger-sized sabretooth felid and a primitive member of the tribe Homotheriini (Felidae, Machairodontinae). The genus was initially established by Kretzoi (1929) based on a late Miocene Chinese species, *A. palanderi* (Zdansky 1924). It did not gain much subsequent consideration until Beaumont (1975, 1978) began to refer the Chinese materials to a Pikermi (Greece) species, *Machairodus giganteus* (Wagner 1848), which is now widely referred under *Amphimachairodus* Kretzoi.

In recent years, there has been a general agreement for a homotheriine clade that consists of *Amphimachairodus* at the base plus the terminal taxa *Homotherium* and *Xenosmilus* (Antón et al. 2004, 2014; Christiansen 2013; Werdelin and Flink 2018). *Machairodus*, as represented by type species *M. aphanistus*, on the other hand, is considered to be either within the homotheriine clade (Antón and Galobart 1999; Antón et al. 2004), just outside of a homotheriine-smilodontine clade (Werdelin and Flink 2018), or basal to all machairodontines (Christiansen 2013). Taxa assigned to *Amphimachairodus* appear to constitute a paraphyletic species complex that gave rise to the *Homotherium* lineage (Sotnikova 1991; Antón et al. 2004; Geraads et al. 2004; Werdelin and Sardella 2006). However, enough morphological and chronological gaps remain to prevent a good sense of where, when and from which lineage *Homotherium* was derived.

As part of a larger project of reviewing late Cenozoic Mexican faunas, we describe in detail materials from Yepómera, Chihuahua, Mexico, which despite having been mentioned in the early literature

as the first Mexican machairodont, were never fully documented. In reviewing the literature, we recognise two parallel anagenetic lineages of *Amphimachairodus* in Eurasia and North America, with the North American lineage representing an immigration event from Eurasia. In this article, we demonstrate that two chronospecies successions best describe the known records: *A. giganteus-palanderi-horribilis* lineage in Eurasia and *A. coloradensis-alvarezi* lineage in North America. We also review the nomenclatural status of Chinese species, *A. horribilis, A. palanderi* and *A. tingii*. Our systematic synthesis is built on recent examinations of specimens from all northern continents (Qiu et al. 2008; Antón et al. 2013; Ruiz-Ramoni et al. 2019; Jiangzuo and Hulbert 2021).

Materials and methods

Institutional abbreviations

AMNH: Division of Vertebrate Palaeontology, American Museum of Natural History, New York, New York, USA; DMNH: Denver Museum of Nature and Science, Denver, Colorado, USA; F:AM: Frick Collection, American Museum of Natural History, New York, New York, USA; IGCU: Instituto de Geología Ciudad Universitaria, Mexico City, Mexico; IGM: Museo María del Carmen Perrilliat, Instituto de Geología, Universidad Nacional Autónoma de México (UNAM), Mexico City, Mexico; IVPP: Institute of Vertebrate Palaeontology and Palaeoanthropology, Chinese Academy of Sciences, Beijing, China; LACM CIT: California Institute of Technology collection, now in Natural History Museum of Los

Angeles County, Los Angeles, California, USA; MPGJ: Museo de Paleontoogía Geociencias Juriquilla, Querétaro, Mexico; MWSU: Midwestern State University Collection of Fossil Vertebrates, Wichita Fall, Texas, now part of Jackson School Museum of Earth History collection at University of Texas at Austin; PIN: Institute of Palaeontology, Russian Academy of Sciences, Moscow, Russia; PMU: Lagrelius Collection, Palaeontological Museum Uppsala, Uppsala, Sweden; SNSB-BSPG: Staatliche Naturwissenschaftliche Sammlungen Bayerns – Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; UEK: Museum of Izmir University, Izmir, Turkey; UF: University of Florida, Gainesville, Florida, USA; UNSM: University of Nebraska State Museum, Lincoln, Nebraska, USA.

Specimens examined

Amphimachairodus alvarezi, LACM CIT 3541, LACM CIT 30237, LACM CIT 30209, MPGJ-274, MPGJ-276, IGCU-7156; *A. horribilis*, SNSB-BSPG 1900 XII 15, lectotype; *A. palanderi*, PMU 3850, PMU 3851, lectotype. Most other fossil records are based on literature reviews.

Measurements

Most measurements in Table 1 and text are derived from standard measurements of maximum lengths and widths in the literature. Measurements taken in this study were performed using a Mitutoyo Absolute Digimatic digital caliper.

3D model by laser scans

A left dentary of *Amphimachairodus alvarezi* (LACM CIT 3541) and left m1 of *A. horribilis* (SNSB-BSPG 1900 XII 15, lectotype) were scanned using a NextEngine scanner (model 2020i) in combination with ScanStudio software (version 2.0.2). Specimens were usually scanned in the highest resolution possible in the 'Macro' setting, which has a 0.005" accuracy (~40,000–160,000 points/square inch). Typically, two sets of 360° scans (at intervals of 22.5°) were obtained and manually aligned and fused into a single model. Scans were saved in the PLY format that preserves texture information. Size scale was captured by built-in calibrations of the NextEngine scanner. These 3D models are available for download (see below).

MorphoSource repository

MorphoSource is a repository platform (www.morphosource. org) that holds digital data of biological specimens and cultural heritage objects contributed by museums, researchers and scholars. We have placed above 3D model files into this site to make them broadly available. A left dentary of *Amphimachairodus alvarezi* (LACM CIT 3541) model is assigned a media number of 000424109 in MorphoSource (https://www.morphosource.org/concern/media/000424109? locale=en), and a left m1 of *A. horribilis* (SNSB-BSPG 1900 XII 15, lectotype) is assigned a media number of 000424126 (https://www.morphosource.org/concern/media/000424126? locale=en).

Systematic palaeontology

Class Mammalia Linnaeus, 1758
 Order Carnivora Bowdich 1821

Family Felidae Fischer von Waldheim 1817
Subfamily Machairodontinae Gill 1872
Tribe Homotheriini; Kurtén 1962
***Amphimachairodus* Kretzoi, 1929**

Type species
Machairodus palanderi; Zdansky, 1924.

Included species
Amphimachairodus giganteus (Wagner, 1848); *A. palanderi* (Zdansky, 1924); *A. horribilis* (Schlosser, 1903); *A. coloradensis* (Cook, 1922); *A. kabir* (Peigné et al. 2005), *A. alvarezi* Ruiz-Ramoni, Rincón, Montellano-Ballesteros, 2019.

Chronological range and geographic distribution
MN12-13 of Europe and Turkey, late Miocene of Africa, Baodean of Central and East Asia and Hemphillian of North America.

Emended diagnosis
Large P4 preparastyle that is in line with parastyle; presence of a shallow depression on rostral face of the mandibular ramus; large and high crowned caniniform i3 (can be slightly higher than lower canine in advanced species); lower canine and i3 with serration, presence of a lingual ridge on m1 paraconid, and to a lesser extent, on m1 protoconid; m1 having a very small talonid, which is lost in advanced species; large and deep mental foramina and a variable mandibular flange (modified from Ruiz-Ramoni et al. 2019; Jiangzuo and Hulbert 2021).

Taxonomic remarks
One of the major advancements in our understanding of the machairodontines was the recovery of a rich sample of *Machairodus aphanistus* from Batallones-1 in Spain (Antón et al. 2004). With this new knowledge, the genus *Machairodus* is increasingly reserved for the type species, *M. aphanistus*, whereas most species previously referred to the *Machairodus* are assigned to other genera, including *Amphimachairodus.* In recent years, there seemed a general agreement that *Amphimachairodus* is related in some way to *Homotherium* and *Xenosmilus* (Antón et al. 2004, 2014; Werdelin and Sardella 2006; Christiansen 2013; Werdelin and Flink 2018), but see Geraads et al. (2004), Martin et al. (2011a), Wallace and Hulbert (2013) and Deng et al. (2016) for alternative phylogenetic arrangements. Antón et al. (2013) may be the first to link some North American late Miocene form (such as *A. coloradensis*) to the Eurasian *Amphimachairodus.* Such an extension of *Amphimachairodus* to North American forms was followed by more recent authors (Ruiz-Ramoni et al. 2019; Jiangzuo and Hulbert 2021), which permits a more explicit test of relationships between old and new world forms.

In the species taxonomy, there is a divergence of opinions between European palaeontologists, who view all Eurasian forms as representing a single species of *Amphimachairodus giganteus*, and Chinese and Russian palaeontologists, who still use regional names, such as *A. horribilis, A. palanderi, A. irtyschensis* and *A. kurteni.* Some recent authors even extended *A. horribilis* to North American forms (Jiangzuo and Hulbert 2021). We examine the taxonomic status of the Chinese forms and related European taxa. We also review the nomenclatural status of *A. horribilis* and attempt to reconcile the various viewpoints under a chronospecies framework.

Table 1. Dental measurements (in mm). Sources of measurements are: *A. giganteus* from AMNH (Kurtén 1976), *A. giganteus* from UEK (Geraads et al. 2004), *A. giganteus* from PIN (Sotnikova 1991), *A. palanderi* from PMU (Zdansky 1924), *A. horribilis* from Pavlodar (Orlov 1936), *A. horribilis* from IVPP (Chang 1957; Qiu et al. 2008), *A. horribilis* from Venta del Moro and from Las Casiones (Salesa et al. 2012), *A. coloradensis* from DMNH (Cook 1922), *A. coloradensis* from UNSM (Martin and Schultz 1975) and *A. alvarezi* from IGM (Ruiz-Ramoni et al. 2019). * indicates an estimate.

	Eurasia														North America						
	A. giganteus-palanderi grade						A. horribilis								A. coloradensis				A. alvarezi		
	Samos	Kemiklitepe	Kalmakpay		Baode		Venta del Moro	Las Casiones	Pavlodar	Drug store	Baode		Withlacoochee		Wray		Kimball Fm.	Ash Hollow Fm.	Yepómera	Rinconada	
	AMNH 20606	UEK-124	PIN 2433/287	PIN 2433/524	PMU 3851 (Ex 2)	A. tingi Ex. 1	Mean	Mean	2413/115	SNSB-BSPG 1900 XII 15	IVPP V906	IVPP V15643	UF 133906	UF 133905	DMNH 207	DMNH 208	UNSM 26086	UNSM 25510	LACM CIT 3541	IGM 6414	MPGJ-276
i3 length		9.2		10.4	9.9	10.6			10.0			11.8						9.5	8.8		
i3 width		7.8		8.6	9.2	9.2												9.1	7.9		
c length		15.0	16.2	15.2	14.3	17.6		15.4	19.5			21.2					19.2	15.5	12.5		
c width		11.1	11.6	12.2	10.3	12.0		11.2	13.0			14.4					12.8	13.2	9.5		
p3 length	21.4	18.5	17.5*	17.5	15.1	18.8			21.5		21.0	20.0	20.3*	20.0*	19.0	20.0	19.6	20.0	15.5*	14.9	
p3 width	9.5	7.5	7.9	7.9	7.4	8.4			10.5		10.0	9.9			6.0	9.0	7.9	7.8	5.8*	6.9	
p4 length	29.2	27.2	26.8	25.5	25.7	29.0	32.0	29.4	32.0		29.0	31.7	29.0*	25.5	21.0	23.0	26.3	26.4	26.0*	24.4	
p4 width	12.7	11.2	11.5	11.1	10.4	12.4*	13.0	12.7	14.0		12.0	13.5		10.6	9.0	10.0	10.5	10.2	9.9*	9.2	
m1 length	32.8		31.2	31.3	28.8		35.8	32.9	35.5	35.5	33.0	36.7	29.5	33.9	30.0		32.0	31.9	27.2	27.6	22.7
m1 width	14.4		13.0	13.5	12.9		14.2	15.6	15.5	16.0	14.0	14.7	11.9	13.5	12.0		12.6	14.0	11.5	11.2	9.7

Amphimachairodus alvarezi Ruiz-Ramoni, Rincón, and Montellano-Ballesteros, 2019

Machairodus catocopis Cope 1887: Lance 1950, p. 9; Ferrusquía-Villafranca 1978, p. 235; Lindsay and Jacobs 1985, p. 4; Lindsay et al. 2006, p. 25.

Machairodus sp.: Dalquest and Mooser 1980, p. 3; Miller and Carranza-Castañeda 1984, p. 233; Carranza-Castañeda 1992, p. 183.

Nimravides catocopis (Cope 1887): Lindsay 1984, p. 212.

Machairodus cf. *M. coloradensis* Cook, 1922: Carranza-Castañeda and Miller 1996, p. 510.

Homotherium sp.: Hodnett 2010, p. 72.

Amphimachairodus coloradensis (Cook, 1922): Antón et al. 2013, p. 1205.

Amphimachairodus alvarezi Ruiz-Ramoni et al., 2019: Jiangzuo and Hulbert 2021, p. 725.

Holotype

IGM 6414, incomplete left and right dentaries with i3, c1, p3, p4 and m1.

Referred specimen

LACM CIT 3541, left and right dentaries, from LACM CIT 276 locality, Arroyo de las Burras (Patterson's R-4 quarry) (Lindsay et al. 2006: Figs. 1, 2; McLeod 2006: Figs. 5, 6), Chihuahua, Mexico (3D model download at https://www.morphosource.org/concern/media/000424109?locale=en); LACM CIT 30237, anterior half of m1, from LACM CIT 276 locality, Arroyo de las Burras; LACM CIT 30209, left I3, from LACM CIT 276 locality, Arroyo de las Burras; IGM 6666, a left P4 and IGM 6667, a partial left upper C from Arroyo Tepalcates, Guanajuato, Mexico; MPGJ-274, right maxillary fragment with P2 alveolus, P3-P4, from GTO 43 locality, Rinconada section of San Miguel de Allende Basin; MPGJ-276, isolated left m1, from GTO 43 locality, and IGCU-7156, left maxillary fragment with P3, GTO 43 locality.

Type locality

Rinconada (GTO 43) in Los Galvánes area, 18 km north of the city of San Miguel de Allende, in San Miguel de Allende Basin, Guanajuato, México (Carranza-Castañeda and Miller 1996; Carranza-Castañeda 2006).

LACM CIT 276 Locality

Located in western Chihuahua, the Yepómera area (also referred to as Rincon in the earlier literature) was first excavated by staff from the California Institute of Technology in 1936–1939 (Stock 1948; Lindsay 1984) (Figure 1; see the History section below). The LACM CIT 276 locality (John W. Patterson's R-4 quarry) in Arroyo de las Burras is in the Río Papigóchic drainage basin, and it is one of the most productive among Yepómera fossil sites (Lindsay et al. 2006; McLeod 2006). Around 4,450 catalogued LACM specimens were produced from this quarry, many of them being isolated horse teeth. The Arroyo de las Burras section is not more than 20 m thick (Lindsay et al. 2006:Fig. 3), and the productive layer in the quarry is mostly less than 2 m (McLeod 2006:Fig. 5). The sediments in the Arroyo de las Burras section are unsuitable for palaeomagnetic sampling, and using marker beds, Lindsay et al. (2006:Fig. 4) was able to correlate the beds with a normal zone in the much longer SH Arroyo section nearby. Lindsay et al. further correlated this normal zone with C3n.4 n, i.e. 4.997–5.235 Ma in the earliest Pliocene (Hilgen et al. 2012), latest Hemphillian (Hh4).

Emended diagnosis

In addition to having all the characters in the diagnosis of the genus, *Amphimachairodus alvarezi* is the smallest among all known species but has the deepest mandibular flange. Showing its derived status, *A. alvarezi* has a large and high crowned caniniform i3 that is slightly higher than lower canine. m1 has no metaconid and lacks the talonid altogether, which is present in more primitive species.

Distribution

Arroyo Tepalcates Local Fauna of Rancho Viejo, Rinconada of Los Galvánes and Arroyo de las Burras of Yepómera, latest Hemphillian North American Land Mammal age, Mexico.

History of studies of *Amphimachairodus* from Mexico

So far, two Mexican fossil sites have yielded materials of *Amphimachairodus*. Lance (1950) first mentioned *Machairodus catocopis* from the Yepómera, presumably based on LACM CIT 3541. Subsequently, this taxon has been listed in Yepómera Fauna as *Machairodus catocopis* by Ferrusquía-Villafranca (1978), as *Machairodus* by Miller and Carranza-Castañeda (1984), as *Nimravides catocopis* by Lindsay (1984) and Lindsay and Jacobs (1985) and as *Machairodus catocopis* by Lindsay et al. (2006). Despite the earlier discovery of the Yepómera record, the materials have never been formally described and figured, and they have not been linked to *Amphimachairodus*.

A second fossil site yielding *Amphimachairodus* was first mentioned by Dalquest and Mooser (1980) based on a lower carnassial of *Machairodus* sp. (MWSU 11063, 28.0×11.8 mm; this specimen is not catalogued in TMM, which has accepted all Neogene collections from the MWSU) from Rancho El Ocote, San Miguel de Allende Basin, Guanajuato, Mexico. In their faunal list of late Cenozoic mammals from central Mexico, Miller and Carranza-Castañeda (1984) listed *Machairodus* from both Yepómera and Rancho El Ocote. Carranza-Castañeda (1992) first described *Machairodus* sp. left and right dentaries (IGM 6414 and 6415) probably belonging to the same individual from Rinconada Locality (GTO 43) in Los Galvánes area, 18 km north of the city of San Miguel de Allende, in San Miguel de Allende Basin. Adding a left P4 (IGM 6666) and a left C (IGM 6667) from Arroyo Tepalcates Local Fauna, 3 km east of the village of Rancho Viejo, Carranza-Castañeda and Miller (1996) more specifically referred the San Miguel de Allande materials to *Machairodus* cf. *M. coloradensis* Cook, 1922. The lower jaws were later the subject of a cover illustration in Carranza-Castañeda and Lindsay (2006). In the same volume, Carranza-Castañeda (2006:Fig. 2) placed the GTO 43 in the latest Hemphillian, as also did Carranza-Castañeda et al. (2013). Hodnett (2010) remarked that the Guanajuato jaws are similar to *Megantereon*, but overall, the Mexican form is more closely related to *Homotherium*. Antón et al. (2013) referred the Arroyo Tepalcates materials to *Amphimachairodus coloradensis*. Ruiz-Ramoni et al. (2019) re-evaluated the materials in Carranza-Castañeda and Miller (1996) and named a new species, *A. alvarezi*. Jiangzuo and Hulbert (2021) remarked that their *Amphimachairodus* cf. *A. horribilis* from the Withlacoochee River 4A locality in Florida is larger than *A. alvarezi* and has smaller mandibular flange. They concluded that the Florida form represents the earliest arrival from Eurasia of *Amphimachairodus* in late early Hemphillian (Hh2).

Description of Yepómera materials (Figures 2 -6)

Despite the fact that Yepómera machairodonts were the first known machairodont in Mexico, going back as early as Lance (1950), these materials have never been described. We thus provide a detailed description below.

Figure 1. a, image of Arroyo de las Burras, looking upstream (easterly) by California Institute of Technology field crew Sebenius on 21 July 1947 (LACM CIT photo number 1348). b, Google Earth (2020) image of Yepómera area drainage (arroyos; highlighted by light blue lines) where LACM CIT fossils were collected.

Both the left and right dentaries are missing part of the ascending rami, but they are otherwise quite well preserved, showing little sign of damage and distortion. The specimen represents a young adult with fully erupted permanent dentitions, but most of the teeth were not strongly anchored to the alveoli and lost before burial. Possibly also due to its young age, the symphysial joint is not fused, permitting examination of the structure of the symphysis.

The dentary is overall strongly constructed with the widest horizontal ramus at p4-m1 on the left dentary (15.6 mm at the p4-m1 junction) and at the anterior root of m1 on the right dentary (maximum width of 18.4 mm) – the right dentary shows a swelling at this spot as compared to that of the left dentary. The depth of the ramus is the shallowest at left p4 (27.3 mm, measured at the p4 posterior root on the lingual side) and at right p4-m1 (27.2 mm, measured at

the p4-m1 junction on the lingual side). From here, the rami gradually deepen towards anterior and posterior ends. At the symphysis, the rami reach their maximum depth of 45.6 mm for symphysial joint and 53.6 mm for total depth (including the flange) on the left side and 48.5 mm and 54.0 mm, respectively, on the right side.

A modest mandibular flange exists extending slightly below the symphysis (Figures 2, 3), much less so than those in the holotype (Ruiz-Ramoni et al. 2019:Fig. 1), but this is likely due to a relatively young individual. The flange extrudes laterally and forms a gentle ridge, which delineates a small dimple just below the canine root, anterodorsal to the mental foramen. This lateral ridge also surrounds a gentle depression on the anterior face of the mandible. The flange lacks a horizontal ridge extending backward from the 'chin' to the middle of the horizontal ramus in lateral view, as seen

in many *Homotherium* species. Nor is there any indication of a posterior ridge extending forward from the angular process, as also seen in *Homotherium*.

Two mental foramina are present. The anterior one is large (8.2 mm in maximum diameter on the left side), rounded, deep and located at the diastema between c and p3. The posterior one is much smaller (3.3 mm in maximum diameter on the left side) and located between the roots of the p3. Both ascending rami are broken off anterior to the tips, and their heights are unknown. The anterior rim of the masseteric fossa reaches the posterior edge of the m1 protoconid.

Despite the lack of preservation of all right lower teeth and several left ones, their alveoli are all well preserved. The diameters of incisors roots increase in i1 through i3. The i1 root (8.5 x 2.6 mm) is highly compressed mediolaterally. The i2 root cross-section (8.5 x 6.2 mm) is rectangular and is twice as wide as that of the i1. The i3 root (8.8 x 7.9 mm) is much wider anteriorly and its posterior width. The canine alveolus is oval in cross-section (12.5 x 9.5 mm) and strongly splayed laterally. The maximum alveolar distance of i1-m1 is 112.3 mm, and that for p3-m1 is 66.5 mm on the right side. The c-p3 diastema is 22.3 mm.

Figure 2. *Amphimachairodus alvarezi*, LACM CIT 3541, left dentary with i3-c and m1. a, lingual and b, labial views. Photograph by X. Wang.

Figure 3. *Amphimachairodus alvarezi*, LACM CIT 3541, edentulous right dentary. a, lingual and b, labial views. Photograph by X. Wang.

The left i3 is high-crowned, with a maximum crown height of 19.8 mm (measured from the enamel-dentine junction on the labial side). The tip of the i3 is about 1.5 mm higher than that of the canine. The anteromedial and posterior edges are blade-like with fine serrations throughout their edge (Figure 5). These blades also bend lingually to form shallow grooves along the inner sides of the blade. At the base of these blades is a slight swelling, more prominent on the posterior one. The conical i3 is recumbent and hooks backwards gently.

The lower canine is similar to the i3 in both size and morphology, with a maximum crown height of 24.2 mm (measured from the enamel-dentine junction on the labial side). As in the i3, the canine also has sharp anterior and posterior ridges or blades with fine serrations throughout its length (Figure 5). Also, like the i3, the blades wrap lingually to form shallow grooves. However, unlike the i3, the bases of the blades do not swell. The canine is slightly more recumbent than in the i3 – despite its higher crown height, and its tip is 1.5 mm lower than that of the i3. In dorsal view, the i3-c strongly splay laterally and forward, a homotheriine character.

The maximum length and width of p3 alveolus are 15.5 × 5.8 mm as compared to 26.0 × 9.9 mm for the p4 alveolus (measured on the right jaw), with a p3/p4 length ratio of 0.60, suggesting a modest reduction of the p3. The left m1 shows signs of having been loosened during burial and might have fallen out

Figure 4. *Amphimachairodus alvarezi*, LACM CIT 3541, left and right dentary. Occlusal view in stereo. Photograph by X. Wang.
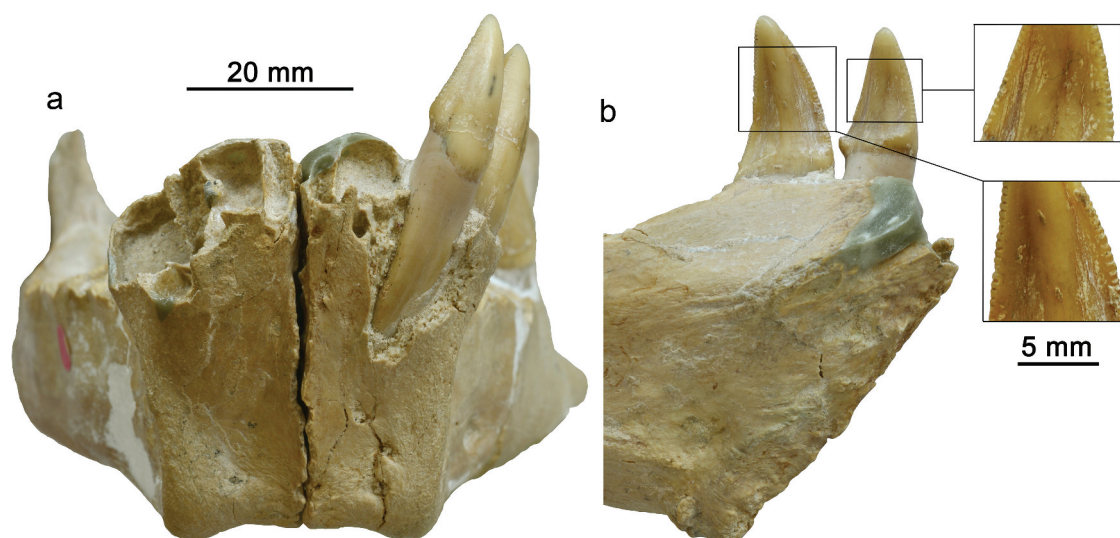

Figure 5. *Amphimachairodus alvarezi*, LACM CIT 3541. a, anterior view of left and right dentary; b, lingual view of i3 and c with closeups and enhanced contrast to show serrations. Photograph by X. Wang.

(note white plaster surrounding the roots in Figure 2), again probably due to a relatively young age. The m1 (27.2 x 11.5 mm for maximum length and width, and maximum crown height 20.0) suffers only slight wear at its cutting blade. Its anterior edge is nearly vertical except the top 1/3, which reclines slightly. The posterior edge is slightly procumbent. On the lingual side of both paraconid and protoconid, there are strong ridges that form a U shape on lingual view. A metaconid/talonid is not present, although a basal swelling, especially on the lingual side, is readily visible.

As in the i3, isolated left I3 is also recumbent. A distinct anteromedial and posterior blade is present with fine serrations throughout, although the serrations are worn smooth near the tip. The blades wrap lingually to form a shallow groove on the inner side. Unlike i3, the labial surface of the I3 also has a shallow, indistinct groove just anterior to the posterior blade, which is present in *Homotherium*. At the base of the anterior blade is a distinct cingulum (Figure 6), which is also present in *A. palanderi* and *A. horribilis* (Qiu et al. 2008:Fig. 2), as well as in *Homotherium* but not in *Xenosmilus*.

Comparison

The Yepómera materials possess the following characteristics that support its membership within *Amphimachairodus*: an anterior depression of jaw, large and high crowned caniniform i3, a rounded ridge on the lingual surface of m1 paraconid and protoconid and large and deep mental foramina, characteristics that are summarised by Jiangzuo and Hulbert (2021). In addition, the Yepómera specimens are more favourably compared to the holotype of *A. alvarezi* from San Miguel de Allende Basin in terms of its relatively small size, but it has a less reduced p3 relative to p4 (p3/p4 = 15.5/26.0 = 0.596 in Yepómera form, as compared to 14.9/24.4 = 0.610 in the holotype from Rinconada; measurements from Table 1), suggesting a slightly more primitive status in this northern form. The main difference of the Yepómera jaws from the holotype is the former's relatively shallow mandibular flange. We interpret this weakness of a flange in the Yepómera specimen to be due to its relatively

young age. Therefore, on account of its age variation, morphology, geography and chronology, the Yepómera cat is undoubtedly referrable to *A. alvarezi*.

New materials from Rinconada, San Miguel de Allende Basin (MPGJ-274, MPGJ-276 and IGCU-7156) add some sense of size and morphologic variations to the population from the type locality of *Amphimachairodus alvarezi*. The upper teeth in MPGJ-274 (P3: 17.5×8.5 mm; P4: 36.8×13.2 mm) are smaller than those in IGM 6666 (P4: 40.4×13.0 mm) (Ruiz-Ramoni et al. 2019:Table 1). The m1 of MPGJ-276 (22.7 x 9.7 mm) is the smallest of all known individuals of this species (Table 1). Morphologically, MPGJ-276 has a lingual ridge on m1 paraconid and protoconid, as well as a very small talonid, consistent with this genus. We thus regard MPGJ-276 as a very small individual of this species that was trending towards body size reduction.

Jiangzuo and Hulbert (2021) suggested that the Withlacoochee machairodont is slightly more primitive than *A. coloradensis* in its relatively robust P4 with a relatively large protocone and a large and narrower lower canine. Such differences were deemed sufficient to refer the Withlacoochee form to a Chinese species, *A.* cf. *A. horribilis*, a novel taxonomic treatment. However, Jiangzuo and Hulbert also remarked that the Withlacoochee materials possess relatively narrow m1 and shorter postcanine diastema, characteristics that are more derived than *A. horribilis*. In the end, they settled for *A.* cf. *A. horribilis* 'prior to the speciation event that resulted in the North American *A. coloradensis*' (Jiangzuo and Hulbert 2021, p. 726).

Amphimachairodus alvarezi (Figure 2) has a striking resemblance to the recumbent, high-crowned lower incisor-canine arcade of *Xenosmilus hodsonae* (Martin et al. 2011b:Figs. 4.8, 4.9) and species of *Homotherium*. Martin et al. (2011b) coined the term 'cookie cutter' cat for this prominently procumbent incisor arch, envisioning a killing role for the protruding incisors associated with short limbs for ambush (Martin et al. 2000). This incisor arcade is also seen in *Barbourofelis fricki* (Martin et al. 2011c:Fig. 9.7) and must have been convergently developed from homotheriines. Within the homotheriines, the morphological similarity is striking enough that taken at face value and may suggest relationship
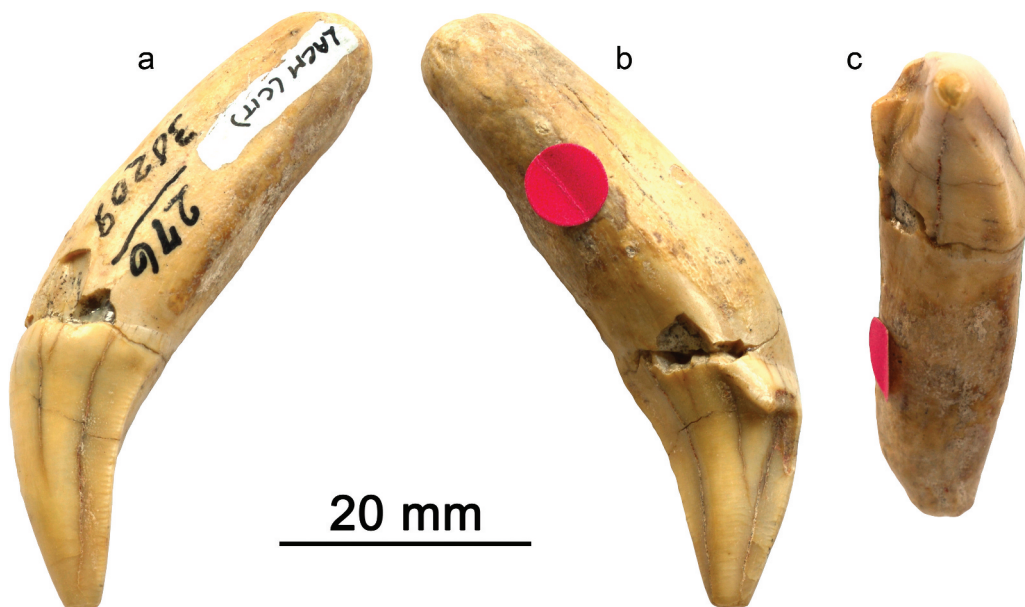

Figure 6. *Amphimachairodus alvarezi*, LACM CIT 30209, left I3. a, labial; b, lingual and c, occlusal views. Photograph by X. Wang.

between *Amphimachairodus alvarezi* and *Xenosmilus* and *Homotherium*, although a more comprehensive phylogenetic analysis is required to resolve that question.

Most recently, Orcutt and Calede (2021) named a large felid *Machairodus lahayishupup* from the early Hemphillian Chalk Hills Formation of Idaho. Mandibular and dental morphology of the Idaho form indicates an affinity to *Nimravides*, a controversial large felid that possibly independently evolved sabretooth adaptations. Dentally, it has a robust lower canine and relatively small i3 (Orcutt and Calede 2021:fig. 1) and a lower carnassial that has no lingual ridges but appears to have a small metaconid-talonid complex. The mandible is also typical of *Nimravides* in having no flange.

Nomenclature and lectotype of *Amphimachairodus horribilis* and comments on *A. irtyschensis*

The resurrection of *Amphimachairodus horribilis* by Qiu et al. (2008) demands a re-examination of the taxonomic status of this species. Schlosser (1903) named *Machairodus horribilis* based on a rostral fragment and a few isolated teeth purchased from Chinese drugstores by K. A. Haberer in 1899–1901. With poorly preserved syntype series without provenance, this species never gained much attention in the literature during its nearly 120 years of history, except for early workers such as Zdansky (1924) and Kretzoi (1929), plus an occasional mention in a few subsequent studies (Hemmer 1965; Werdelin and Lewis 2001). Qiu et al. (2008) made a serious attempt to revive and stabilise *Machairodus horribilis* by designating a lectotype and referring to this species two well-preserved skulls and one lower jaw from Baode Basin. In doing so, Qiu et al. (2008), however, confused the catalogue numbers of their lectotype and left the type locality matter unresolved, although they made a suggestion for a potential future mitigation. Here, we trace the history of this taxon, clarify catalogue numbers and discuss the remaining nomenclatural problems.

The syntype series of *Machairodus horribilis* was based on a rostral fragment with three incisors and alveoli of cheek teeth acquired from a Beijing drugstore (SNSB-BSPG 1900 XII 507–508), plus five isolated teeth including a partial upper canine (SNSB-BSPG 1900 XII 505), a right lower canine (SNSB-BSPG 1900 XII 509), two halves of P4s (SNSB-BSPG 1900 XII 502–503) belonging to two different individuals (possibly belonging to a felid and a hyaenid according to Qiu et al. 2008), a left p4 (SNSB-BSPG 1900 XII 501; Figure 7) and a left m1 (SNSB-BSPG 1900 XII 15; Figure 8; 3D model download at https://www.morphosource.org/concern/media/000424126?locale=en) that were purchased from a drugstore in Tianjin, North China. No type specimen was initially declared by Schlosser. Kretzoi (1929) was the first to narrow the 'type' to the left p4 and m1. However, this designation was apparently invalid because it does not satisfy the ICZN rule for lectotype (International Commission on Zoological Nomenclature 1999), i.e. Article 74 requiring (1) the explicit use of the term 'lectotype' and (2) the designated lectotype represented by a single individual – the isolated p4 and m1 are evidently represented by two individuals due to their different colour of preservation and morphology (Figures 7, 8) (the p4 may or may not be a machairodontine, as observed by Qiu et al. 2008). Without mentioning Kretzoi's early attempt at fixing a lectotype, Qiu et al. (2008) rectified Kretzoi's unsatisfactory designation by expressly choosing the left m1 as the 'lectotype', a designation that does satisfy both conditions of the ICZN code. Qiu et al. listed '1900 XII 501' as the lectotype, which was the catalogue number of the left p4, not the m1 that was actually labelled 1900 XII 15 (Figure 8). Qiu et al.'s intention, however, was not in doubt (they clearly stated that Schlosser's original

concept of this species must have been based on the m1, which was figured by Qiu et al.), and we thus correct this error by reassigning SNSB-BSPG 1900 XII 15 as the lectotype.

Fixing the lectotype still leaves unresolved the matter of the poor preservation of the designated specimen and the lack of provenance for the type locality. Qiu et al. (2008) next attempted to stabilise *Amphimachairodus horribilis* by referring two well-preserved specimens, IVPP V15642 and V15643, from Baode Basin. Of these two new specimens, only one, IVPP V15643, has a lower jaw with an m1 comparable to the lectotype, which was 'collected from Baode by IVPP staff Wu Ying in 1965', but detailed locality information is lost (Qiu et al. 2008, p. 265). The new specimens were likely acquired from local fossil hunters, as was the case for nearly all well-preserved specimens from Baode, where a long tradition of 'dragon bone' collecting exists. Assuming that is the case, the exact stratigraphic horizon for IVPP V15642 and V15643 is also unknown, but that it was from the Baode Basin is not in doubt.

Despite the above efforts, the problems of a poor lectotype without provenance seem to present a major nomenclatural difficulty. To this obstacle, Qiu et al. (2008, p. 276) suggested that 'in the future, maybe we should fix IVPP V15643 as the neotype and IVPP V15642 as the allotype'. We note, however, that Article 75 of the ICZN requires that a neotype is considered either because the original syntype series is lost or failing that, a special petition is submitted to the Commission (International Commission on Zoological Nomenclature 1999). In the present case, the syntype series is not lost and a petition is the only available course of action.

Before a petition is considered, a question naturally arises regarding the distinctness of the lectotype. Is the lectotype sufficiently diagnostic by a single lower carnassial? In other words, could *Machairodus horribilis* Schlosser be considered a *nomen dubium* (Chorn and Whetstone 1978; International Commission on Zoological Nomenclature 1999)? The answer to this question will be subjective and likely controversial. However, it seems that *A. horribilis*, as defined by its lectotype, is sufficiently diagnostic, i.e. the general morphology of SNSB-BSPG 1900 XII 15 seems to be indicative of *Amphimachairodus*, such as the presence of lingual ridges on the paraconid and protoconid and a small metaconid-talonid complex, as suggested by Jiangzuo and Hulbert (2021). As for species distinctions, Qiu et al. (2008) pointed out its large size relative to *A. palanderi*. In addition, a reclined anterior border of paraconid in the lectotype (Figure 8) is typically seen in advanced machairodontines. Given the above, the lectotype of *A. horribilis* does seem to meet the minimum criteria of being diagnostic enough as an advanced species of *Amphimachairodus*.

It remains to be seen if Qiu et al.'s (2008) fixing of the lectotype and referral of IVPP V15642 will stabilise *Amphimachairodus horribilis* in the long run. Qiu et al. further expanded the concept of *A. horribilis* by synonymising Zdansky's *A. tingi* under *A. horribilis* and included Zdansky's Ex. 3 (of his *A. palanderi*) as well as specimens from Yushe (Teilhard de Chardin and Leroy 1945; Chang 1957) under *A. horribilis*. Teilhard de Chardin and Leroy (1945) remarked that the Yushe machairodontines (their *Epimachairodus*) are all from the 'Pontian' (i.e., Mahui Formation) part of the Yushe strata, which seems confined to the upper part of C3A (Flynn and Qiu 2013), although their presence in Gaozhuang Formation is uncertain.

In their comparisons with 'Chinese materials', Qiu et al. (2008) singled out *Amphimachairodus irtyschensis* (Orlov 1936) from Pavlodar, Kazakhstan, as a potentially distinct species from Chinese forms. In addition to *A. irtyschensis* being also of large size (m1 length 35.5 mm), comparable to that of *A. horribilis*, the main reason for Qiu et al.'s perceived distinction is an apparently labially arched m1 outline in contrast to a relatively straight lingual
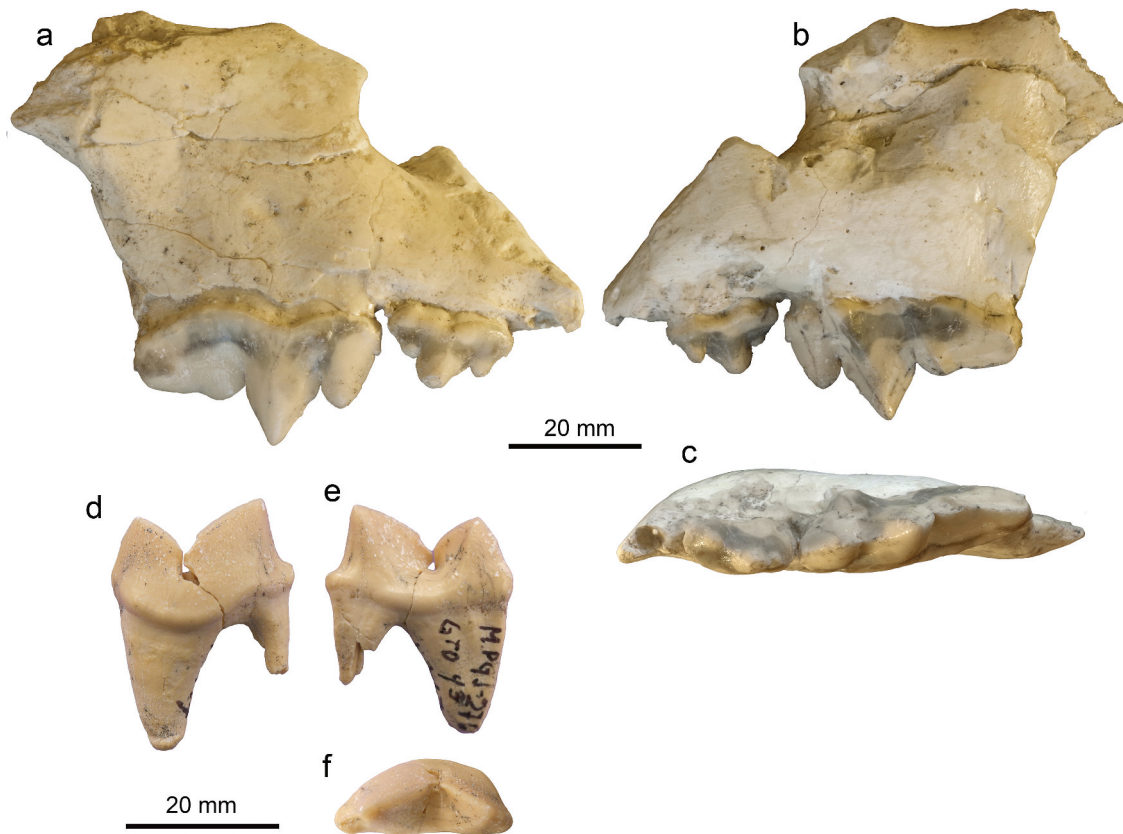
Figure 7. *Amphimachairodus alvarezi*, MPGJ-274, right maxillary fragment with P2 alveolus, P3-P4, from GTO 43 locality, a, labial; b, lingual and c, occlusal views. MPGJ-276, isolated left m1, from GTO 43 locality, d, labial; e, lingual and f, occlusal views. Photograph by Jesus Silva Corona and X. Wang.

border. However, part of what Qiu et al. observed as 'peculiarity' is likely due to an artefact of photographic angle (camera leaning towards the labial side of the specimen, exaggerating the arch) in Orlov's Figure 1 of his photographic plate. Furthermore, Orlov has trimmed the outline of his m1 along the enamel-dentine junction, which itself forms an arc and thus may further enhance the sense of this 'arch'. To what extent this is the case will not be answered without personal observations (or by taking another photo), but we suspect the actual arch, if present, is far less than that has been portrayed by Orlov. Qiu et al. also observed more reduced accessory cusps in p3 and p4 of *A. irtyschensis*. However, the size, crown height and degree of forward leaning of the i3 (relative to those in c) in *A. irtyschensis* are all comparable to the referred specimens of *A. horribilis* by Qiu et al. We treat *A. irtyschensis* as a junior synonym of *A. horribilis*.

Status of *Amphimachairodus palanderi* and *A. tingii*

Following de Beaumont (1975, 1978), many European carnivore palaeontologists have accepted the view that Chinese late Miocene machairodontines belong to a single Eurasia-wide *Amphimachairodus giganteus* (Turner and Antón 1996; Koufos 2000; Antón et al. 2004; Morlo and Semenov 2004; Peigné et al. 2005; Sardella and Werdelin 2007), which thus subsumes such Chinese species as *A. palanderi* and *A. tingii*. Most Chinese vertebrate palaeontologists, on the other hand, treated these two species as distinct (Chang 1957; Tong et al. 1975; Deng et al. 2016; Li 2021), as well as some western scholars such as Teilhard de Chardin and Leroy (1945), Melentis (1968) and Werdelin (2003). Churcher

(1984) even regarded *palanderi* as a species of *Homotherium*. Since *A. palanderi* is the type species of the genus (Kretzoi 1929), it is a matter of some importance to review its status here.

Among the five specimens (Ex. 1–5) described, Zdansky (1924) did not specify a type for his *Machairodus palanderi*. As recently as 2005, Peigné et al. (2005:Table 1) still used a syntype series for this species, although they singled out the skull from Loc. 113 in their measurements. Qiu et al. (2008) fixed the type problem by selecting as the lectotype Ex 2 from locality 113 (PMU 3850, skull and 3851, left and right jaws; Figures 9–11). In addition to the lectotype, Qiu et al. included in *A. palanderi* Zdansky's Ex 1 (Locality 30), plus another skull from Baode (IVPP V905) described by Chang (1957). Zdansky's Ex 3 from Locality 30, somewhat larger in size, however, was assigned by Qiu et al. to *A. horribilis*. Qiu et al. (2008) further synonymised *M. tingi* Zdansky 1924 (which was also based on two specimens, Ex 1 and 2, both from Locality 30) as a junior synonym of *M. horribilis*, further strengthening the idea that most individuals at top of Baode Formation (Loc. 30) have reached the size of *A. horribilis*. Finally, Qiu et al. referred a skull from Huoxian, Shanxi, described by Tong et al. (1975) to *A. horribilis*.

Qiu et al. (2008) further pointed out additional cranial and dental distinctions between *A. horribilis* and *A. palanderi*, mostly based on his newly described referred specimens from Baode. However, a full evaluation of interspecific variations awaits examination of several undescribed specimens in the F:AM collection from Baode and Yushe (Teilhard de Chardin and Leroy 1945). Following Qiu et al. (2008), Chinese vertebrate palaeontologists began to resurrect *Machairodus horribilis*, but its concept has been substituted by IVPP V15642 from Baode (Deng et al. 2016; Li
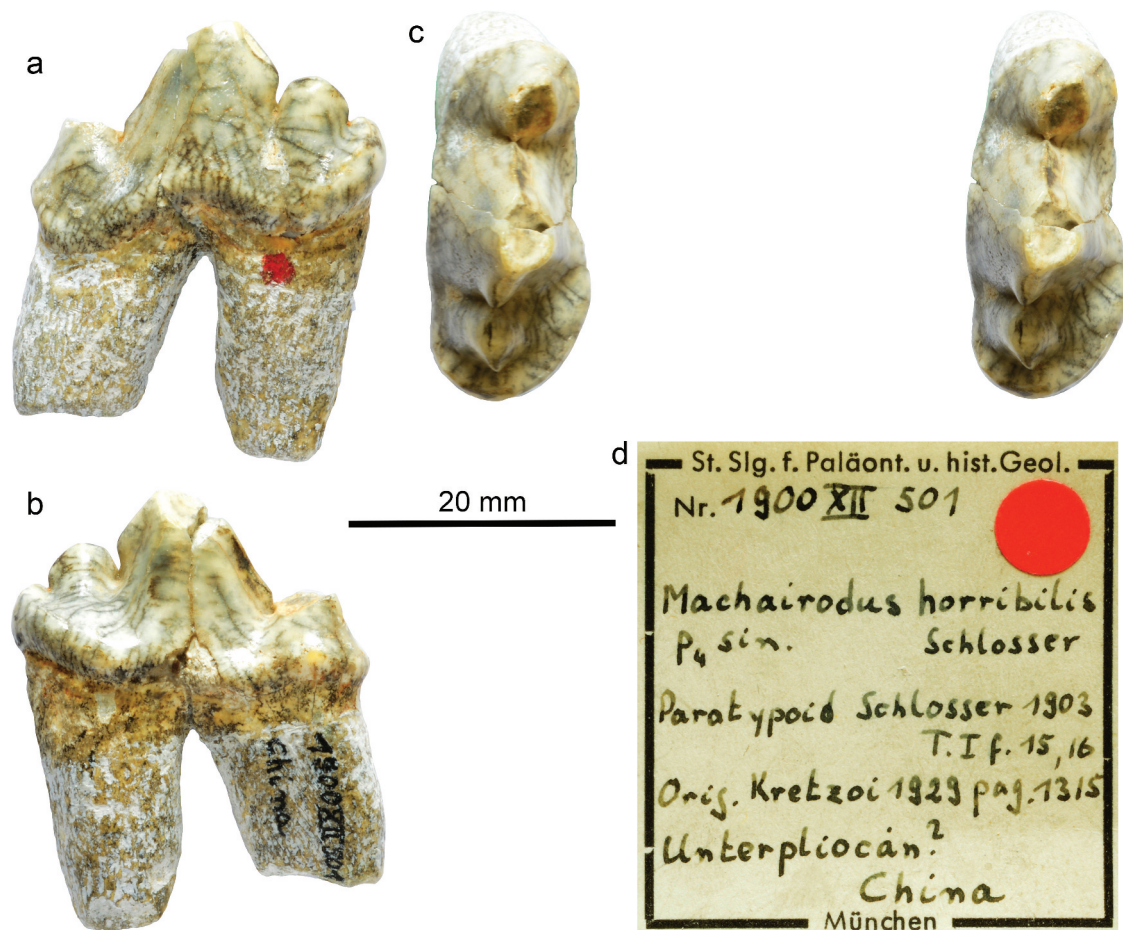
Figure 8. *Amphimachairodus horribilis* (Schlosser, 1903), SNSB-BSPG 1900 XII 501, left p4, syntype series incorrectly assigned to lectotype by Kretzoi (1929), purchased from a drugstore in Tianjin by K. A. Haberer in 1899–1901. a, labial; b, lingual; c, occlusal (in stereo) views and D, SNSB-BSPG specimen label (note the same ink number on the specimen). Photograph by X. Wang with permission from Gertrud Rössner of SNSB-BSPG.

2021). Jiangzuo and Hulbert (2021) even used this taxon for North American materials, but they appear to synonymise both *A. palanderi* and *A. tingii* under *A. horribilis*.

Chronospecies succession of *Amphimachairodus* spp. in Eurasia

The Chinese Baode Basin not only produces the best preserved and most numerous skulls and jaws of *Amphimachairodus* but also has a long and continuous record of this genus spanning much of the Baode Formation, a stratigraphic succession found nowhere else. Largely due to the fact that the Baode region has a long tradition of 'dragon bone' hunting (for profit excavations of fossils that were sold to traditional Chinese medicine stores), from the beginning of the fossil acquisition in Baode area for the Lagrelius Collection, Zdansky (1923) had the foresight to devise a system of locality numbers that mapped the locations of horizontal tunnels, which mostly follow fossiliferous horizons. As a result, these tunnel entrances roughly capture a sequence of stratigraphic records as Baode strata are largely flat-lying. In essence, Zdansky's locality numbers permit a sense of local stratigraphy and manage to preserve some information on provenance otherwise lost. These locality numbers are recently field-verified by a team of Chinese and Finnish palaeontologists and geologists and placed in their modern biostratigraphic and magnetostratigraphic frameworks (Kaakinen et al. 2013). Kaakinen et al.'s work

suggests that the *Hipparion* red clays from Baode, often exceeding 50 m thickness in key sections, span from 7.2 to 5.5 Ma, representing ~1.7 million years in depositional history, in contrast to earlier interpretations (Yue et al. 2004).

From Kaakinen and colleagues' work, three major fossiliferous horizons can be recognised, represented by Locality 30 at the top (5.7 Ma), Locality 108 in the middle (6.5 Ma) and Locality 49 near the bottom (7.0 Ma). Fortunately, *Amphimachairodus* are produced from all three horizons, representing three nominal species of *Amphimachairodus*: *A. horribilis* (referred specimens from Baode by Qiu et al. 2008), *A. tingii* (three specimens from Loc. 30) and *A. palanderi* (one from Loc. 49, one from Loc. 108, one from Loc. 113 and two from Loc. 30, as originally recorded by Zdansky, but see below for reasons that Loc. 30 specimens are more suitably referred to *A. horribilis*).

Loc 113 is important because it is the type locality for *Amphimachairodus palanderi* and by extension, for the genus *Amphimachairodus*. Unfortunately Zdansky's (1924) Loc. 113 (he made a mistake of placing Loc. 113 in 'Chi-Chia-Kou', which is really located in Tai-Chia-Kou according to his 1923 map) produced only one carnivoran specimen and its stratigraphic position is unaccounted for by Kaakinen et al. (2013). According to Zdansky's (1923) map, the closest locality to Loc. 113 is Loc. 108 on the opposite side of an east-west oriented ridge, and these two localities are at approximately the same elevation, i.e. belonging to similar stratigraphic levels (Zdansky's topographic contours are
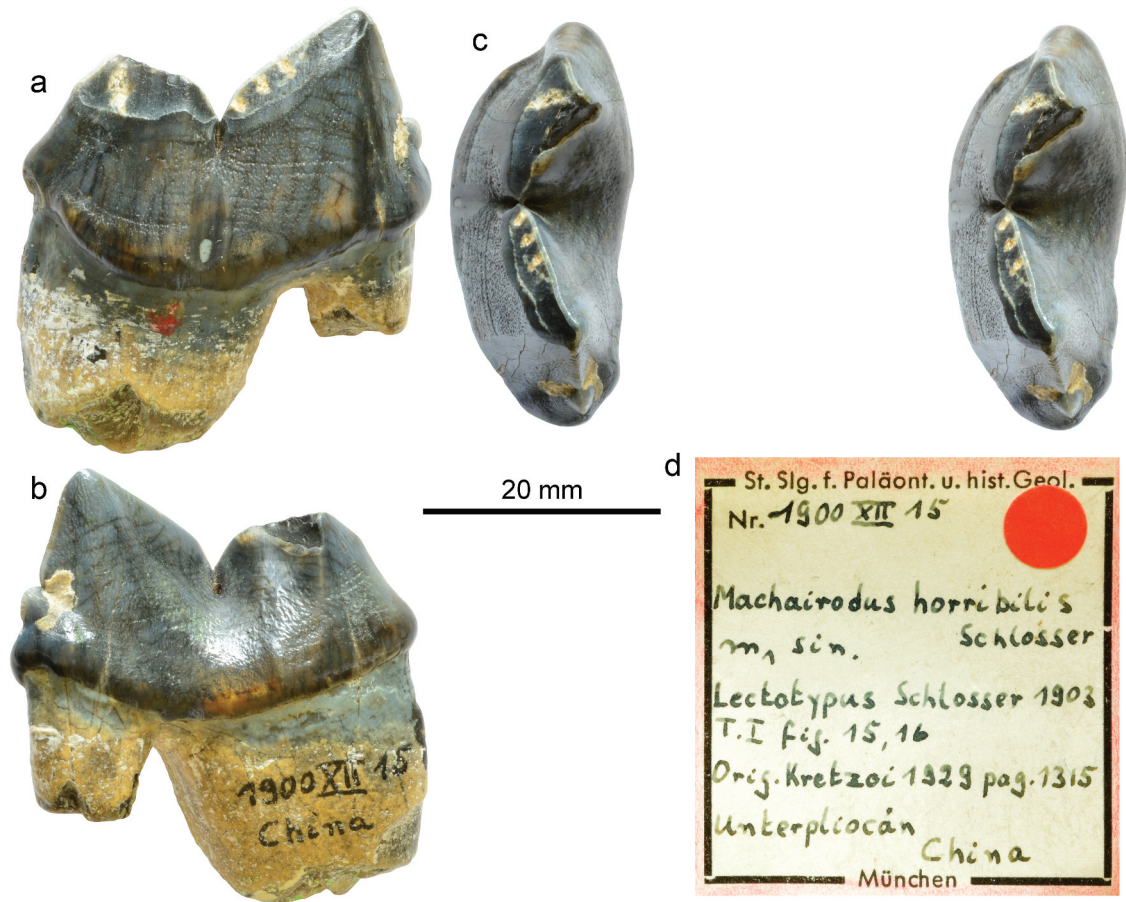
Figure 9. *Amphimachairodus horribilis* (Schlosser, 1903), SNSB-BSPG 1900 XII 15, left m1, lectotype, purchased from a drugstore in Tianjin by K. A. Haberer in 1899–1901. a, labial; b, lingual; c, occlusal (in stereo) views and d, SNSB-BSPG specimen label (note the same ink number on the specimen). Photograph by X. Wang with permission from Gertrud Rössner of SNSB-BSPG.
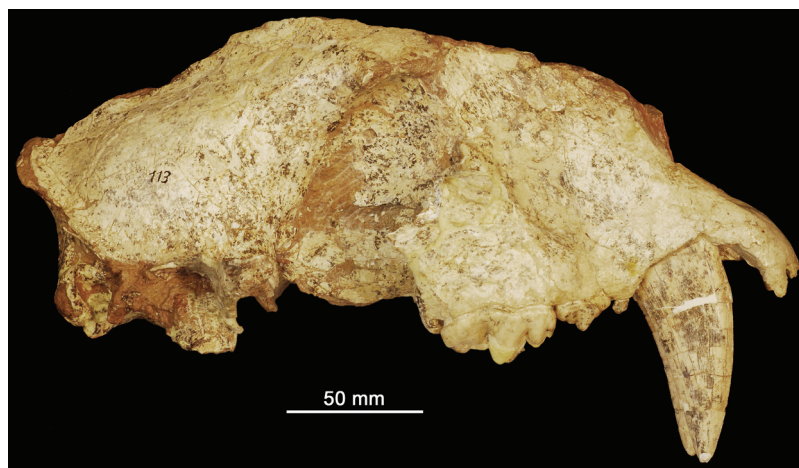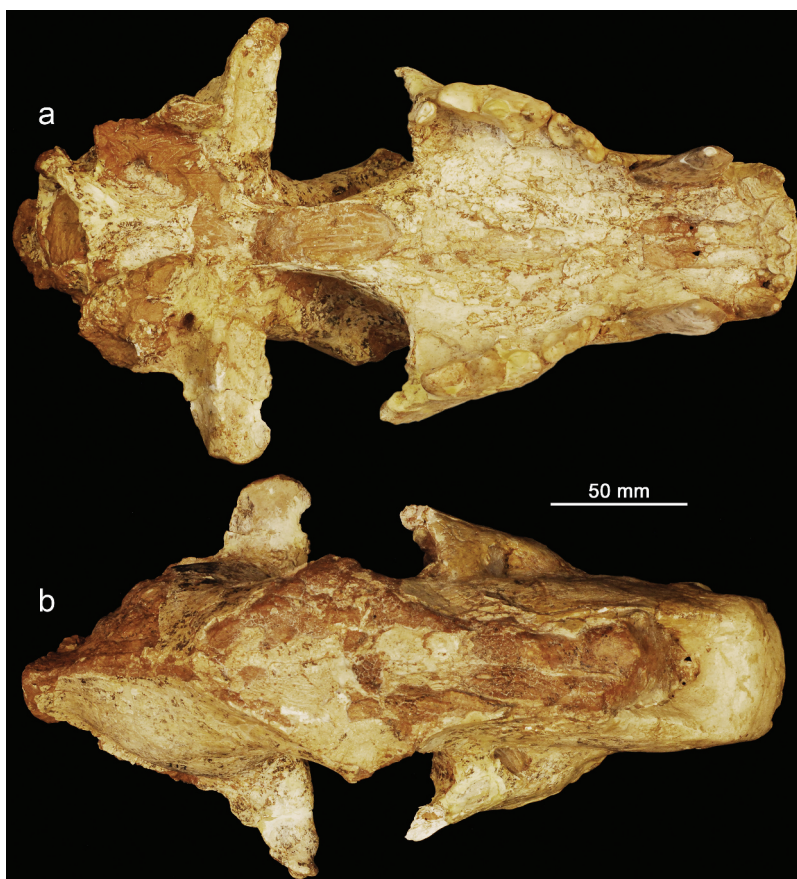

Figure 10. *Amphimachairodus palanderi* (Zdansky, 1924), skull, PMU 3850, lectotype, right lateral view. Photograph by X. Wang.

fairly accurate by modern standard, Zhaoqun Zhang pers. comm., September 2021). We thus treat Loc. 113 as stratigraphically equivalent to Loc. 108, i.e. middle Baode Formation, ~6.5 Ma.

The above stratigraphic context allows a sense of evolution through time for *Amphimachairodus* that no other record in the world could offer (Figure 12). Of the five specimens referred to *A. palanderi* by Zdansky (1924), Qiu et al. (2008) referred one Loc.

30 specimen (Ex 1) to *A. palanderi* and relegated the other Loc. 30 specimen (Ex 3) to *A. horribilis*, implying coexistence of *A. palanderi* and *A. horribilis* in the same horizon. We note, however, that Zdansky's Ex 1 (C-P4 length ~125 mm by Zdansky's measurements) is almost identical to Ex 3 (C-P4 length = 124 mm) in overall size and could well belong to the same taxon (i.e. *A. horribilis*).

Figure 11. *Amphimachairodus palanderi* (Zdansky, 1924), skull, PMU 3850, lectotype. a, ventral, and b, dorsal views. Photograph by X. Wang.

The above analysis suggests that all specimens at the top of the section (Loc. 30) likely belong to a single large-sized *A. horribilis* (including *A. tingii*, which was synonymised with *A. horribilis* by Qiu et al. 2008), whereas the rest of the middle and lower horizons (Localities 49, 108, 113) contain only *A. palanderi* (Figure 12). When viewed in this stratigraphic context, much of the size and morphological changes may be seen as anagenetic evolution, i.e. chronospecies succession without apparent cladogenetic divergence. Under our chronospecies interpretation, size increase from *A. palanderi* to *A. horribilis* amounts to 13% (based on the average length of m1s) during a little more than a million years (Figure 13; Table 1). The ratio of p3 length relative to p4 length, however, remains unchanged during this time.

Another recent record of *Amphimachairodus* was recovered from Hanjiaying Village of Wulanchabu, Inner Mongolia (Wang et al. 2021). This left maxillary fragment is tightly bracketed by two layers of basalts dated to 7.24 ± 0.19 and 6.85 ± 0.21 Ma. Wang et al. referred this specimen to *A. giganteus*, which is consistent with the present chronospecies theme. This specimen is similar to the age of Loc. 49 at Baode and probably represents one of the earliest records in East Asia.

Our chronospecies interpretation seems also applicable to the relationship of *A. giganteus* and *A. palanderi*. We plotted select European and western Asian records from Kemiklitepe of Turkey (Sen et al. 1994; Geraads et al. 2004), Samos and Halmyropotamos of Greece (Koufos 2013) and Las Casiones and Venta del Moro of Spain (Opdyke et al. 1997; van Dam et al. 2006; Salesa et al. 2012). Under our theme, the Spanish Las Casiones (6.33 Ma) form is rather large (m1 length

32.92 mm) (Alcalá 1994; Salesa et al. 2012) and falls at the lower end of *A. horribilis* grade. Specimens from Venta del Moro, however, are well within *A. horribilis* (m1 length = 35.80 mm; Table 1) (Salesa et al. 2012; Antón et al. 2013). Among the remaining records plotted in our chronological chart (Figure 12), the associated partial skull and jaw of *A. giganteus* from the Kemiklitepe, Turkey, have relatively small p4 (length 27.2 mm) (Geraads et al. 2004) as is the Kalmakpay record, falling in the range of *A. giganteus-palanderi* grade. The more restricted European and western Asian *A. giganteus* are slightly older than the Asian *A. palanderi*, although this could be an artefact of an ~ 0.5 (6.5–7.0 Ma) million-year gap in fossil records in Europe. Our stratigraphic plot (Figure 12) demonstrates that European *A. giganteus* is roughly contemporaneous with Asian *A. palanderi*, and as implied by most previous authors, the European and Chinese forms represent either ends of a wide geographic continuum, within which intra-continental introgression might have been the dominant process. Nevertheless, there is still utility in retaining *A. palanderi* in our discussions about anagenetic evolutions within East Asia in general and local successions within Baode Basin in particular.

As a charismatic apex predator, numerous species of *Amphimachairodus* have been named (see Morlo and Semenov 2004 for a partial list). Here, we evaluate a few to allow some appreciation of geographic and chronologic variations. Qi (1983) described an *Epimachairodus fires*, following Teilhard de Chardin and Leroy (1945) on their generic assignment, based on a few isolated teeth from Lufeng Basin, Yunnan Province. This South

China species is too poorly preserved to be treated here. However, its dental measurements generally fall in the range of *Amphimachairodus palanderi* and if confirmed in the future, offers a sense of geographic and environmental range of this species.

As remarked above, *Amphimachairodus irtyschensis* (Orlov 1936) from Pavlodar in Irtysh Basin of Kazakhstan can probably be synonymised with *A. horribilis*. The Pavlodar magnetostratigraphy features a short reversed chron followed by a longer normal chron below, which were correlated with C3An.1 r to C3An.2 n (Zykin et al. 2007), placing the Pavlodar form in the *A. palanderi-horribilis* transitional period. By our chronospecies scheme, it seems more likely that the Pavlodar *Amphimachairodus* occurs in the reversed zone (C3An.1 r). If so, *A. horribilis* would be the appropriate name.

Amphimachairodus kurteni (Sotnikova 1991) from Kalmakpai in Zaysan Basin of eastern Kazakhstan is relatively small, comparable in size to *A. palanderi*. Vislobokova et al. (2001) correlated the 'alternated' magnetostratigraphy of the Kalmakpai section with the C3An.2 n, which is consistent with the age range of *A. palanderi*. Based on the presence of a prominent mandibular flange, Sotnikova (1991) proposed that *A. kurteni* gave rise to *Homotherium*, but her proposal did not seem to gain currency. Existing evidence suggests that *A. kurteni* may not represent a cladogenetic event (towards *Homotherium*), as the North American *A. alvarezi* also has a distinct flange, and we treat *A. kurteni* as a junior synonym of *A. palanderi*. As Werdelin and Sardella (2006) remarked, morphological and to a lesser extent, chronological gaps between *Amphimachairodus* and *Homotherium* remain large.

We did not extend our analysis to African forms, which have fewer records. If our chronological reconstruction in Eurasia and North America is accurate, then *Amphimachairodus kabir* (Peigné et al. 2005) from Chad is likely comparable to the European *A. giganteus*. Its median size (m1 length 34.70 mm) and earlier occurrence (~7 Ma, as estimated by Peigné et al.) are consistent with this view. The Libyan records, referred to *A.* cf. *A. kabir*, are larger (m1 length 36.4 mm) and more advanced, converging on smilodontines (Sardella and Werdelin 2007).

Our chronological approach to species division within *Amphimachairodus* suggests two lineages of apex predators within both Eurasia and North America, each lasting about two million years. Although we do not fundamentally disagree with previous usage of a single Eurasian species of *A. giganteus* spanning two million years, our chronospecies division by using existing names helps to capture a sense of changes through time as successive morphological grades, especially since these changes are captured by a continuous sample from Baode Formation. As size and morphological changes accumulate through time, people often begin to name species, as in the case of *A. alvarezi* (Ruiz-Ramoni et al. 2019). Size increase in Eurasia and reduction in North America is the dominant mode of evolution as well as convergent trends towards reduction of premolars and increased hypercarnivory of carnassials. The appearance of the European *A. giganteus* seems to be a cladogenetic event, deriving from an ancestor close to *Machairodus aphanistus* (Figure 12).

Under such scenarios, what was previously characterised as mosaic evolution in machairodontines (Antón et al. 2013; Deng et al. 2016) may in part be attributed to morphological drift within

Figure 12. *Amphimachairodus palanderi* (Zdansky, 1924), left and right jaws, PMU 3851, lectotype. a, occlusal and b, right lateral view. Photograph by X. Wang.
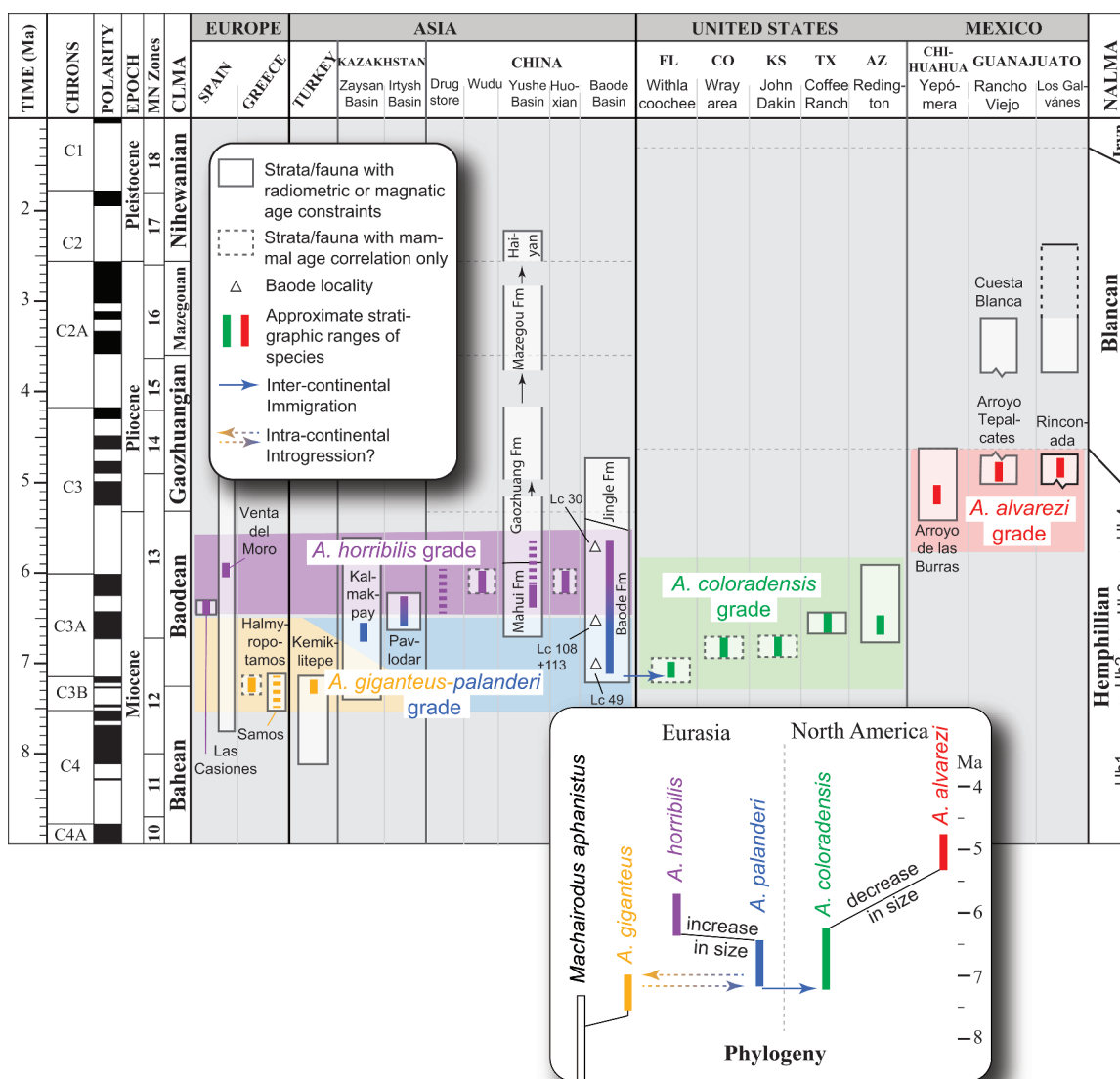
Figure 13. Holarctic chronologic and geographic distributions of *Amphimachairodus* and a postulated species phylogram (inset). Chronology for Eurasian forms is based on specimens from Pavlodar of Kazakhstan (Zykin et al. 2007), Kalmakpay of Kazakhstan (Sotnikova 1991), Kemiklitepe (level KTA-KTB) of Turkey (Sen et al. 1994; Geraads et al. 2004), Samos and Halmyropotamos of Greece (Koufos 2013), Las Casiones (6.33 Ma) and Venta del Moro (6.0 Ma) of Spain (Opdyke et al. 1997; van Dam et al. 2006; Salesa et al. 2012), Yushe Basin of China (Flynn and Qiu 2013) and Baode Basin of China (Kaakinen et al. 2013). Our selection of European records is not exhaustive, and the apparent gaps do not necessarily indicate the absence of *Amphimachairodus*. Chronological relationships of central Mexican localities and subdivision of Hemphillian NALMa are based on Carranza-Castañeda et al. (2013). Magnetic correlation of the Arroyo de las Burras section in Yepómera Basin is based on Lindsay et al. (2006). Chinese Land Mammal ages follow Qiu et al. (2013), and North American Land Mammal ages follow Tedford et al. (2004). Neogene Geomagnetic Polarity Time Scale (GPTS) is based on ATNTS2012 (Hilgen et al. 2012) .

a predominant theme of chronospecies replacements. The taxonomic consequence of such a chronospecies concept is that species partitioning is arbitrary and largely drawn on convenient gaps in fossil records, i.e. on our ability to discern morphological and/or stratigraphic gaps. As such, the existing species names do serve a purpose of discussions about changes in morphological grades within an evolutionary continuum. For this reason, we suggest conserving the Chinese *A. palanderi-horribilis* succession as a tangible example of anagenetic evolution even if the conceptual boundary of these two species remains arbitrarily drawn slightly above 6.5 Ma. Such a treatment has the advantage of resolving salient morphological changes through time (such as size), as opposed to lumping all morphological difference as geographic variations.

Immigration and chronospecies succession of *Amphimachairodus* spp. in North America

Antón et al. (2013) were the first to point out that some large North American late Miocene forms were an immigrant from Eurasian *Amphimachairodus*. The best representative of this immigration event is *A. coloradensis*, which was previously placed under *Machairodus* (Cook 1922; Dalquest 1969; Martin and Schultz 1975; Harrison 1983; Hodnett 2010). Such an *Amphimachairodus* linkage was adopted by more recent authors (Ruiz-Ramoni et al. 2019). Jiangzuo and Hulbert (2021) took a step further by directly referring their Withlacoochee form to the Chinese '*A*. cf. *A. horribilis*'. Antón et al. (2013 Fig. 8) made an attempt at summarising the chronological relationships of Eurasian and North American species. While this was a good idea, it was done at too

coarse a scale to be useful for a clear idea about the precise timing and sources of the immigration event. We synthesise the latest records in light of a chronospecies framework across the entire northern hemisphere (Figure 12).

From Figure 12, it is evident that the source of North American *Amphimachairodus* should be sought among the Eurasian stock of *A. giganteus-palanderi* grade, not the more derived *A. horribilis* used by Jiangzuo and Hulbert (2021). Jiangzuo and Hulbert, however, were right that the Withlacoochee records are the earliest known records of North American *Amphimachairodus*, i.e. the Florida materials represent the first arrival of an immigrant from East Asia. In fact, the density and chronologic precision of existing records are such that they suggest a rapid spread of the *Amphimachairodus* throughout the northern hemisphere, within 100,000–200,000 years, from the time of the first appearance of *A. giganteus* to *A. coloradensis*. Such a rapid geographic expansion and inter-continental dispersal, including crossing a high-latitude Beringia, is further evidence of a highly adaptive apex predator quickly occupying most available niches.

Although Jiangzuo and Hulbert (2021) correctly recognised the connection between their Withlacoochee materials and Old World forms, their taxonomic usage of *Amphimachairodus* cf. *A. horribilis* is unconventional. They justified this choice by speculating that the North American *A. coloradensis* represents a speciation event, warranting a separate species status from that of the Withlacoochee form. They envisioned that the Florida 'A. cf. *A. horribilis*' includes a mixture of features in *A. horribilis* from East Asia and *A. coloradensis* from North America. They further noted that the Withlacoochee form has a robust P4 with relatively large protocone and a large lower canine as primitive features compared to *A. coloradensis*. However, the above characteristics seem a weak justification for species distinction, let alone a cladogenetic

speciation, and the intermediate conditions of the Withlacoochee form with derived characteristics relative to the Chinese forms and primitive features compared to *A. coloradensis* are just as easily explained by anagenetic evolution, warranting no species distinction from *A. coloradensis*.

The evolutionary trajectory within North America, however, is different from those in Eurasia. In contrast to size increase in Eurasia, the North American *Amphimachairodus* saw a size reduction from *A. coloradensis* to *A. alvarezi*, representing an average decrease of 15% (measured by m1 length) (Figure 14; Table 1). Such a reduction, however, may also be accounted for in terms of latitudinal changes, i.e. Bergmann's rule, although carnivorans that follow Bergmann's rule may be shifting their body size in response to prey size reductions rather than the physics and physiology of heat exchange (McNab 1971). There is an apparent gap of about one million years in fossil records between *A. coloradensis* and *A. alvarezi*. Based on existing records, it seems clear that *A. coloradensis* was largely confined to the mid latitudes of North America, and by the latest Hemphillian, *Amphimachairodus* was surviving only in Mexico. To what extent this pattern is due to sampling bias or possible ecological interaction with other sabretooths can only be answered by more continuous records in the future from both mid and southern latitudes.

In addition to the above size reduction, the North American *Amphimachairodus* seems to follow a similar trajectory of morphological specialisation as their Old-World counterparts, such as reduction and loss of m1 talonid and high-crowned i3 relative to the lower canines. These features parallel similar trends seen in Eurasian *Amphimachairodus*. However, unlike in Eurasia, the North American *A. alvarezi* does have a significant reduction of the p3 relative to p4 (average ratio of p3 length/p4 length = 0.611) when compared to that of *A. coloradensis* (0.804 for the same ratio).
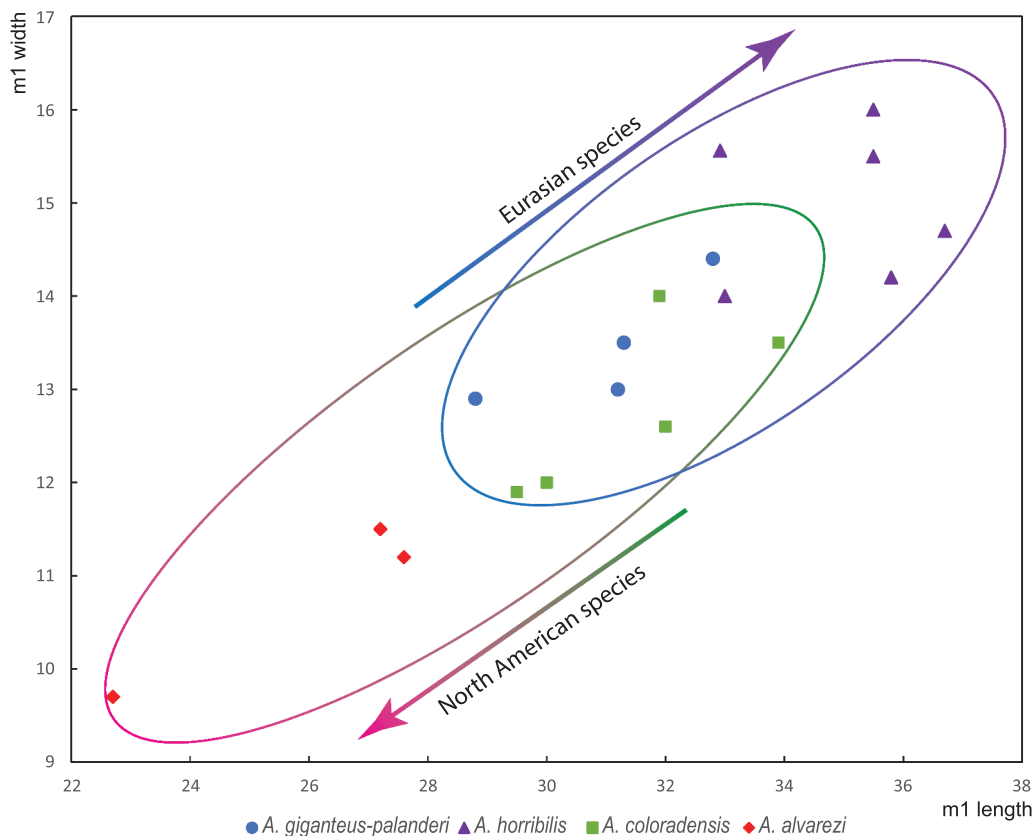

Figure 14. Bivariate plot of m1 length and width of *Amphimachairodus* spp. based on data in Table 1.

In addition, the holotype of *A. alvarezi* has the deepest mandibular flange of all *Amphimachairodus*. It may be tantalising to make the connection of *A. alvarezi* to *Homotherium*; however, a large enough morphological gap exists between *Amphimachairodus* and *Homotherium* that makes the question of where *Homotherium* came from difficult to answer (Werdelin and Sardella 2006; Antón et al. 2014).

Given the above size and morphological changes, a strong case of anagenetic evolution can be made in North America as well, although in opposite trend in body size compared to the Eurasian lineage. Evolution appears to proceed in a single lineage without cladogenesis, and current chronospecies succession of *A. coloradensis* to *A. alvarezi* is consistent with this pattern. The large gap in fossil records between these two species makes it a convenient and practical boundary, although such a boundary is by definition arbitrary, as is the *A. palanderi-horribilis* succession above.

Discussion

As carnivorans with the most hypercarnivorous dentitions, felids are easily recognisable in the fossil record and often some of the largest and presumably most ecologically dominant carnivorans in Neogene mammalian assemblages. Such success is reflected in their high taxonomic diversity through time, but felids' hypercarnivorous morphological tendencies also seem to impose a limit on their morphological disparity (Holliday and Steppan 2004; Holliday 2010). The stereotypical cranial and dental morphologies represent a challenge to traditional phylogenetic analysis – trees based on morphological characteristics alone (e.g. Salles 1992) bear little resemblance to modern understanding of relationships based on DNA sequences (Johnson et al. 2006; Li et al. 2016).

Such a limited morphological repertoire seems to operate equally well in the machairodontine sabretooths. Despite an early (>20 Ma) divergence from living felid clade (Paijmans et al. 2017; Barnett et al. 2020), their long evolutionary history seems to consist of repeated developments of convergent suites of 'mosaic' characteristics (Antón et al. 2004, 2013). As a result of this lack of consistent morphological patterns, machairodontine phylogenies are difficult to resolve despite their popularity as a subject of taxonomic and functional morphological research.

In this article, we follow the current consensus that *Amphimachairodus* represents a basal lineage in the homotheriine clade during the late Miocene. As a top sabretooth predator of their time, *Amphimachairodus* did not have much competition (*Paramachaerodus*, such as *P. maximiliani* from Shang-Yin-Kou, Xin'an County, Henan Province, is a substantially smaller cat, and the fact it did not occur in Baode Formation suggests that *Amphimachairodus* and *Paramachaerodus* did not overlap) in their ecological guild. Allowing some geographic and chronologic variations, a single Eurasian lineage dominating the apex predator position for about 2 million years before being replaced by *Homotherium* seems to be the prevailing view during the past 45 years since Beaumont (1975). Such a view has the benefit of simplicity, although it assumes unimpeded genetic exchange through much of Eurasia.

Our analysis substantiates this broader view, although we reintroduce *Amphimachairodus horribilis*, following Qiu et al. (2008), as chronospecies that highlights *in situ* evolution within a long sequence of Baode records. As defined by Stanley (1978, p. 26) as 'segments of evolutionary lineages subjectively designated as species', chronospecies, while often based on gaps of geologic records, do serve the purpose of documenting well-defined evolutionary changes. In the case of the Baode sequence, the *A. palanderi-horribilis* succession provides the best example in all of *Amphimachairodus* that allows a sense of anagenetic evolution through time. The main characteristic of this succession is a marked size increase through time throughout Eurasia (Figure 14; Table 1).

The North American records, on the other hand, are also consistent with a chronospecies succession of *Amphimachairodus coloradensis-alvarezi*. Unlike the Eurasian case, however, the North American succession is marked by size reduction (Figure 14; Table 1). This reduction is associated with a shift in distribution to more southern latitudes, i.e. *A. coloradensis* being from the United States in contrast to *A. alvarezi* being in Mexico. In their description of *A. alvarezi*, Ruiz-Ramoni et al. (2019) recognised that *A. coloradensis* and *A. alvarezi* belong to the same lineage, but they thought the relationship of these two species to be unclear. We propose that they have a direct ancestor-descendent relationship through time but with a shift in space towards lower latitudes.

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