Journal of Vertebrate Paleontology

ISSN: 0272-4634 (Print) 1937-2809 (Online) Journal homepage: www.tandfonline.com/journals/ujvp20

New material of *Adelphailurus kansensis* sheds light on the cranial anatomy of an early-diverging machairodontine felid

Narimane Chatar & Z. Jack Tseng

To cite this article: Narimane Chatar & Z. Jack Tseng (19 Jun 2026): New material of *Adelphailurus kansensis* sheds light on the cranial anatomy of an early-diverging machairodontine felid, Journal of Vertebrate Paleontology, DOI: 10.1080/02724634.2026.2667939

To link to this article: https://doi.org/10.1080/02724634.2026.2667939

© 2026 Narimane Chatar, Z. Jack Tseng

View supplementary material

Published online: 19 Jun 2026.

Submit your article to this journal

View related articles

View Crossmark data

Full Terms & Conditions of access and use can be found at
https://www.tandfonline.com/action/journalInformation?journalCode=ujvp20

Journal of Vertebrate Paleontology e2667939 (19 pages)
Published with license by the Society of Vertebrate Paleontology
DOI: 10.1080/02724634.2026.2667939

Check for updates

ARTICLE

NEW MATERIAL OF *ADELPHAILURUS KANSENSIS* SHEDS LIGHT ON THE CRANIAL ANATOMY OF AN EARLY-DIVERGING MACHAIRODONTINE FELID

NARIMANE CHATAR, [1,2]* and Z. JACK TSENG [1]
[1]Functional Anatomy and Vertebrate Evolution Laboratory, Department of Integrative Biology, University of California, Berkeley, CA, U.S.A., Narimane.chatar@berkeley.edu;
[2]Departamento de Ecología y Geología, Facultad de Ciencias, Universidad de Málaga, Spain

ABSTRACT—*Adelphailurus kansensis* is a puma-sized felid, originally described from fragmentary material in the Edson Quarry (Kansas, Mio-Pliocene). Here, we describe a nearly complete cranium from the Wikieup local fauna of the Big Sandy Formation, along with associated dental remains, and refer it to *A. kansensis*. Comparative analysis with *Metailurus major*, *Yoshi minor*, *Y. garevskii*, and *Y. yongdengensis* reveals a unique combination of features. *A. kansensis* shares certain traits with *Metailurus* (narrow snout, M1 orientation) and *Yoshi* (rounded cranial profile) but differs from both in having thinner zygomatic arches of nearly constant width, a more pronounced postglenoid process, and specific dental characteristics, including a P3 lacking an anterior accessory cusp and upper canines with serrations on both margins. Geometric morphometric analyses place *A. kansensis* morphologically between *Metailurus* and *Yoshi*, illustrating its intermediate cranial proportions yet confirming its distinctiveness. Several elements, including this cranium and previously misattributed specimens, were originally referred to *Pseudaelurus*, highlighting the persistent taxonomic issues surrounding early diverging felids. This study refines the diagnosis of *A. kansensis*, and clarifies its relationships within "metailurins."

SUPPLEMENTARY FILES—Supplementary files are available for this article for free at www.tandfonline.com/UJVP.

Citation for this article: Chatar, N., & Tseng, Z. J. (2026) New material of *Adelphailurus kansensis* sheds light on the cranial anatomy of an early-diverging machairodontine felid. *Journal of Vertebrate Paleontology*. https://doi.org/10.1080/02724634.2026.2667939

Submitted: October 21, 2025
Revisions received: April 15, 2026
Accepted: April 15, 2026

INTRODUCTION

The machairodontine felid *Adelphailurus kansensis* was a puma-sized felid, originally described from the late Hemphillian (latest Miocene) deposits of the Edson Quarry, Kansas. The holotype (KUVP 3462) consists of left and right maxillae with a nearly complete dentition (lacking only the right M1) (Hibbard, 1934). Since then, additional material has been referred to this species. Harrison (1983) identified postcranial remains from the Wikieup local fauna (Mohave County, Arizona), housed at the American Museum of Natural History, but did not describe the full set of fossil remains from the locality, which includes a virtually complete cranium with associated canines and mandibular fragments. Other referred material includes a maxilla (IGM 6674) and an isolated P4 from Mexico (Lindsay, 1984) and a partial cranium with associated lower jaw (MSM P7628) from Wikieup (Hodnett, 2010), although only the jaw was figured. Therefore, the cranial anatomy of *A. kansensis* remains poorly known.

Various authors have placed *A. kansensis* within Metailurini, a tribe of machairodontine felids with relatively short upper canines, including genera such as *Metailurus* and *Dinofelis* (e.g., Salesa et al., 2010; Turner & Antón, 1997). They are considered by some authors to exhibit intermediate morphology between other machairodontine felids and members of the genus *Panthera* (Madurell-Malapeira et al., 2021). However, multiple authors have expressed concern regarding the grouping of those taxa (see Spassov & Geraads, 2015; Li & Spassov, 2017). Metailurini was originally characterized as the least specialized tribe of Machairodontinae (Harrison, 1983), with some authors even proposing a distinct subfamily status, somewhere in between machairodontines and non-machairodontine felids (Crusafont & Aguirre, 1972). Suggested diagnostic traits of this group include a reduced occipital region compared to machairodontines and the presence of an antero-internal groove on the upper canines (Harrison, 1983). However, the validity of the group remains questionable and it has often served as a repository for taxa lacking extreme sabertooth specializations.

A paucity of more complete material of *Adalphailurus* has prevented the taxon from being incorporated into ongoing studies of metailurine-grade felids. A recent study described new remains

*Corresponding author.
© 2026 Narimane Chatar, Z. Jack Tseng. This is an Open Access article distributed under the terms of the Creative Commons Attribution-Non-Commercial-NoDerivatives License (http://creativecommons.org/licenses/by-nc-nd/4.0/), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited, and is not altered, transformed, or built upon in any way. The terms on which this article has been published allow the posting of the Accepted Manuscript in a repository by the author(s) or with their consent.

Color versions of one or more of the figures in the article can be found online at www.tandfonline.com/ujvp.

Published online 19 Jun 2026

from the Upper Miocene deposits of northwestern China, the basis for naming two new species: *Yoshi yongdengensis* and *Yoshi faie*, and also introduced a remarkably complete skull of an established species, *Paramachaerodus schlosseri* (Jiangzuo et al., 2022a). This new material allowed to revise the phylogenetic relationships among 'Metailurini' including most of the known species, notably highlighting some previously suggested issues such as the paraphyly of the genus *Paramachaerodus*, but also a quite low support for most internal nodes within metailurini (Jiangzuo et al., 2022a). *Adelphailurus kansensis* was excluded from that study due to the incompleteness of the holotype, and is usually excluded from any phylogenetic analyses (Christiansen, 2012; Jiangzuo et al., 2022a; Jiangzuo, Werdelin, et al., 2022). This omission is associated with challenges in resolving relationships among Late Miocene taxa, underscored by recent studies that highlight the taxonomic complexity within late Miocene metailurine in the debate surrounding the genera *Yoshi* and *Metailurus*. The genus *Metailurus* was erected by Zdansky (1924) based on material from the upper Miocene of China (*M. major*). Later, *Yoshi* was erected by Spassov & Geraads (2015), arguing that the skull referred to *M. minor* (Zdansky 1924:pl. 30, figs. 1–3) differs markedly from *M. major* in its smaller size, shorter rostrum, wider forehead, and overall cranial proportions, and therefore should not be retained within the same genus. The species originally described as "*Machairodus parvulus*" by Hensel (1862), based on a fragment of mandible from the Late Miocene (MN12) in Pikermi (Greece), was subsequently reported from several Eurasian localities, although its type material remains taxonomically uninformative. As noted by Koufos (2022), much of the European material historically attributed to *Metailurus* is incomplete and problematic, and "*Metailurus parvulus*" has therefore been treated with caution in recent literature.

The potential continuum of cranial morphological characteristics in metailurine-grade felids has reinforced disagreements in taxonomic interpretations among systematics workers. While some authors have suggested that *Yoshi* may represent a junior subjective synonym of "*Metailurus parvulus*" (see Madurell-Malapeira et al., 2021), others maintain *Yoshi* as a valid genus based on refined craniodental distinctions (e.g., Jiangzuo et al., 2022a), arguing that while some traits used by Spassov & Geraads (2015) to separate *Yoshi* from *Metailurus* are no longer diagnostic because they also apply to the type of *Metailurus major*, *Yoshi* remains a different genus due to its shorter rostrum, higher crowned premolars, straighter canine and P4 morphology. However, Jiangzuo et al. (2022a) still noted that *Yoshi* and *Metailurus* appear closer than originally thought. The taxonomic debate also expands to the genus *Paramachaerodus*, with some authors (e.g., Jiangzuo et al., 2022a) considering it within metailurine 'tribe,' while others suggest it could include *Promegantereon* (see Madurell-Malapeira et al., 2021). Given the limited number of well-preserved specimens attributed to this group, any new cranial material has the potential to significantly refine our understanding of their anatomy, ecology, and evolutionary relationships. Here, we describe the first complete skull of *A. kansensis*, providing a detailed comparative analysis with similarly sized felids. Our results show that *A. kansensis* exhibits cranial morphology intermediate between the genera *Yoshi* and *Metailurus*, offering new insights into the morphology and systematics of this enigmatic machairodontine.

MATERIAL AND METHODS

Material for Comparative Descriptions

Comparative descriptions were based on well-preserved other machairodontine felid crania. In this study, *Yoshi minor* is considered a valid species following Jiangzuo et al. (2022a) although some authors regard the genus *Yoshi* as a junior subjective synonym of *Metailurus parvulus* (see Madurell-Malapeira et al., 2021). The comparative sample includes:

Yoshi minor (two skulls: PMU 21766/1 and PMU 21767/1). Initially described by Zdansky (1924) as '*Metailurus minor*' (labeled M3836 and M71, respectively) and later reassigned to *Yoshi* by Spassov and Geraads (2015).

Yoshi garevskii (MMNH-Sk KAR 69). Based on 3D models of the type specimen described by Spassov and Geraads (2015) from the upper Miocene (Turolian) of Macedonia (Karaslari, Vardar Basin).

Metailurus major (PMU 21771-1). The type skull described by Zdansky (1924) from the Upper Miocene deposits in the Baode area in Shanxi Province, north China (Loc. 30: 'Tay-Chia-Kou' in Zdansky, 1924 or Daijiagou in modern Chinese pinyin), and a cast (AMNH F:M 131854, cast of IVPP 5679) labeled "*Metailurus* sp." from the Hounao Quarry (Yushe Basin, Shanxi Province, China). While most of the basin is Pliocene in age, Hounao Quarry was assigned to the Late Miocene (Z.-X. Qiu & Tedford, 2013; Wei & Hu, 1994). However, the AMNH cast is dorsoventrally compressed, and was therefore given limited weight in the comparison but it preserves the basicranium (missing in the holotype), allowing additional comparison, particularly in ventral and posterior views.

Yoshi yongdengensis (YLSNHM 01795). The type skull described by Jiangzuo et al. (2022b) from the upper Miocene of Yongdeng, China.

Yoshi faie (IVPP V31254). The type specimen (a rostrum) described by Jiangzuo, Niu, et al. (2022) from the upper Miocene of Yongdeng, China.

Scans of all the comparative specimens were obtained using a Creaform Handyscan laser scanner, with a resolution of 0.2–0.5 mm. The holotype of *Adelphailurus kansensis* was not examined directly as we did not have an opportunity to visit its repository, but a cast housed at the Yale Peabody Museum (YPM VP 014162) was scanned for comparison. High resolution surface scans of the cranium AMNH F:AM 62192 and the upper canine AMNH F:AM 62249 are available on MorphoSource (project ID 000770658): https://www.morphosource.org/projects/000770658. Other remains were photographed but not scanned.

Morphological variation among taxa was assessed by capturing screenshots of 3D models in dorsal, ventral, lateral, anterior, and posterior views using the snapshot tool in Meshlab (Cigoni et al., 2008) using the orthographic camera enabled to maintain parallel lines and avoid distortion. Linear measurements were taken directly on the 3D models in GeoMagic Wrap (Artec 3D, 2021), and angular measurements were taken from lateral-view screenshots in ImageJ (Rasband, 2012). For comparative purposes, diastema length, mandible length, and the angle between the mandibular symphysis were measured on *Yoshi* and *Metailurus major* specimens, as well as on the newly described *A. kansensis* mandibular.

To quantify the cranial shape of the newly referred specimen AMNH F:AM 62192 we placed a series of points and curves in Stratovan Checkpoint (Stratovan Corporation, 2023), using the same landmark scheme as in Chatar et al. (2024). We then extracted a subset of machairodontine felids landmarks from the same publication and performed Procrustes superimposition and a principal component analysis (PCA) using the geomorph package (Adams & Otárola-Castillo, 2013) in the R statistical environment (R Core Team, 2021). The R script used to perform the analyses is available as Supplemental File 1 and the landmark coordinates for AMNH F:AM 62192 are available as Supplemental File 2. The 3D models used for comparison were available on MorphoSource: https://www.morphosource.org/projects/000548886. As 3DGM analyses require high-resolution 3D surface models, it was not possible to include all taxa

mentioned in the comparative description in the morphospace and/or the phylogenetic analysis (e.g., *Yoshi yongdengensis*). Conversely, anatomical description and detailed phylogenetic scoring may be limited when based solely on 3D models lacking texture or firsthand observations. For these reasons, OTUs differ in each section. All specimen numbers included in each analysis are listed in Table S1 (Supplementary File 3).

Institutional Abbreviations—**AMNH**, Division of Paleontology, American Museum of Natural History, New York, NY, U.S.A.; **F:AM**, Frick fossil mammal collection, Division of Paleontology, American Museum of Natural History, New York, NY, U.S.A.; **KUVP**, Vertebrate Paleontology Collections, Biodiversity Institute and Natural History Museum, Kansas University, Lawrence, KS, U.S.A.; **MMNH-Sk**, Macedonian Museum of Natural History, Skopje, Republic of Macedonia (FYROM); **PMU**, Evolutionsmuseet, Paleontological Museum Uppsala Universitet, Uppsala, Sweden; **YPM**, Peabody Museum, Yale University, New Haven, CT, U.S.A.

Phylogenetic Analysis

Our phylogenetic analysis is based on the morphological character matrix published by Barrett and Hopkins (2024) which includes 124 species of fossil and extant feliform carnivorans, five caniform outgroups, and 324 characters. That study is the most complete phylogenetic work published including machairodontine felids, combining morphological and molecular data, notably characters based or modified from multiple previous studies (Barrett, 2016, 2021; Barrett et al., 2021; Barrett & Hopkins, 2024; Christiansen, 2008, 2012; Morales et al., 2019; Peigné, 2003; Robles et al., 2013; Rothwell, 2003; Sakamoto & Ruta, 2012; Salesa et al., 2010, 2012; Salles, 1992; Spaulding & Flynn, 2012; Tseng & Wang, 2007; Van Valkenburgh et al., 1990; Werdelin & Solounias, 1991; Wesley-Hunt & Flynn, 2005). However, one character (character 175) was missing from the 2024 character list and was added following personal communication with the first author (Paul Z. Barett pers. comm.). First, we opened the Nexus file in Mesquite (Maddison & Maddison, 2019), reduced the list of taxa to Felidae (32 species) and only kept *Canis latrans frustror* as outgroup. Then we added *Adelphailurus kansensis* as a new operational taxonomic unit (OTU) and coded the characters for this new OTU using 3D scans and pictures of the material mentioned above. After careful evaluation, we chose to use Barrett and Hopkins (2024) over Jiangzuo et al. (2022b) despite the latter incorporating more machairodontine felids for the following three methodological reasons:

(1) Character sampling, Barrett and Hopkins (2024) include 324 characters, compared to only 72 in Jiangzuo et al. (2022b). Empirical studies have shown that increasing character sampling generally improves phylogenetic resolution and stability (see Scotland et al. (2003) and references therein) and a more recent study suggested that between 100 and 500 variable characters are necessary to achieve robust Bayesian topologies (Capobianco, 2025), therefore suggesting that Jiangzuo et al. (2022b) might not contain enough characters to fully resolve the relationship between machairodontine felids.
(2) Character composition, the Jiangzuo et al. (2022b) matrix is strongly dominated by dental characters (>65%): 47 dental, 21 cranial, and 4 mandibular characters, whereas Barrett and Hopkins (2024) contains 92 dental, 103 cranial + mandibular and 130 postcranial characters. Previous studies have repeatedly shown that dental characters tend to exhibit higher rates of morphological evolution and that dietary pressure increases convergence, making them less reliable for the reconstruction of fossil mammal phylogenies (e.g., Billet & Bardin, 2019; Brocklehurst & Benevento, 2020; Harjunmaa et al., 2014; Kavanagh et al., 2007) and that the inclusion of morphological characters other than dental tend to provide results that align more with molecular data.
(3) Character documentation, Barrett and Hopkins (2024), provide an extensive character description document (40 pages), including measurements and explicit state definitions. In Jiangzuo et al. (2022b), character descriptions are more condensed, summarizing all the characters in a one page Excel file with the delimitation between character states also being less clear, which makes consistent rescoring without firsthand material more challenging.

For these reasons, we consider Barrett and Hopkins (2024) to provide a more suitable framework for the specific objectives of this study. Our aim is not to produce a comprehensive revision of the machairodontine phylogeny, but to document new cranial material of *Adelphailurus kansensis*, and make a high-resolution 3D model available. A full-scale phylogenetic reassessment of all early diverging machairodontines would require extensive firsthand study of numerous taxa and is beyond the scope of the present contribution.

We updated the character list in the following ways: we removed character 1 [lacrimal facial process: [0], broad rostral flange; [1], small, present on face; [2], not present on face; [3], orbital flange reduced to area around lacrimal foramen [Wesley-Hunt & Flynn, 2005]: character 1]. The limit between state 2 and 3 was too subtle in our assessment and introduced uncertainty. We modified character 46: P4 protocone: (0) large, well-developed; (1) reduced or absent (Wesley-Hunt & Flynn, 2005): character 56) as the size of the P4 protocone compared to the parastyle to better define the character. We deleted character 324 (petrobasilar foramen) as it was not coded for any single taxon (including outgroups) in our trimmed matrix and was therefore uninformative. This resulted in a matrix comprising 322 characters and 34 taxa. The updated matrix, character lists, and various output files are also available on Morphobank: https://www.morphobank.org/permalink/?P6080.

We used TNT v1.5 (Goloboff & Catalano, 2016) to perform parsimony cladistic analysis under implied weighting using the same scripts as in Chatar et al. (2022b) (script provided in Supplementary File 4). We expanded the memory of TNT to a maximum of 100,000 trees. We set the search parameters to: new technology search; 200 ratchet iterations; 10 cycles of drifting; five hits; and five replications for each hit. We then used the tree branch bisection and reconnection (TBR) algorithm to fully explore the tree islands identified by the ratchet. Nodal support was measured using symmetric resampling with 1000 replications, each replication involving a new technology search with a change probability of 33%. We choose symmetric resampling over bootstrapping or jack-knifing because this measure is not affected by character weighting and is thus more appropriate to deal with implied weights (Goloboff et al., 2003). As the analysis published by Barrett and Hopkins (2024) comprised molecular data for extant taxa which was not available in our implied weighting analyses, we applied constraints in TNT to fix the topology of extant species as a scaffold (see script in Supplementary File 4). We employed a single concavity value ($k = 8$) following (Ezcurra, 2024) (see Table S2 in Supplementary File 3 for more details such as tree length, best score). To do so, we used the maximum branch length method of the timePaleoPhy function from the strap v1.4 package in R with vartime=3 (Bell & Lloyd, 2015) and a dataset describing the temporal biozones of each OTU.

We then generated the time tree using the geoscalePhylo function from the paleotree v3.3.25 package (Bapst, 2012).

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821
Family FELIDAE Fischer, 1821
Subfamily MACHAIRODONTINAE Gill, 1872
ADELPHAILURUS KANSENSIS, Hibbard, 1934

Included Taxa—*Pseudaelurus hibbardi* (junior synonym, according to Hodnett (2014)).

Etymology—From *Adelphos* (brother) and *ailurus* (cat).

Holotype—KUVP 346, a left and right maxillae bearing a very well-preserved dentition only lacking the right m1.

Type Locality—Edson Quarry, Sherman County, Kansas.

Age—late Hemphillian North American Land Mammal Age (NALMA), 6.8–4.75 Ma.

Newly Referred Specimens—AMNH F:AM 62192, a virtually complete cranium (Fig. 1) and a fragment of right hemimandible AMNH F:AM 62195 (Fig. 2) from Clay Bank Quarry, Mohave Co, Arizona, Big Sandy Fm (late Hemphillian) (Fig. 3A, B). Three isolated upper canines, AMNH F:AM 62249, AMNH F:AM 62249A, AMNH F:AM 62216A (Fig. 2) from Bird Bone Quarry, Mohave Co, Arizona, Big Sandy Fm (late Hemphillian) (Fig. 3A, B). Note that Bird Bone Quarry is situated 125 m west of Clay Bank Quarry (MacFadden & Skinner, 1979) and the two are considered nearly contemporaneous (Bickart, 1990; Macfadden et al., 1979).

Additional Material—See Fig. 3C for a map showing the different fossil localities. AMNH F:AM 62224 (partial humerus with associated radius and ulna), AMNH F:AM 104740 (first phalanx), AMNH F:AM 104741 (first phalanx) from the Edson Quarry (Kansas, U.S.A.); AMNH F:AM 62225, (radius), AMNH F:AM 62230 (partial radius) from Marshall Ranch (Nebraska, U.S.A.); TMM 41261-3 (Fragment of left dentary) from Coffee Ranch (Texas U.S.A.); MSM P7628 (Fragment of skull associated with complete lower jaws) from Big Sandy Fm, Mohave Co (Arizona, U.S.A.); IGM 6674 (maxilla with P3—P4) and IGM 6673 (isolated P4) from Guanajuato, Mexico.

Diagnosis—Prominent P4 parastyle; P4 paracone, and metacone strongly developed and separated by a deep carnassial notch. Vestigial P2 located at an oblique angle to the dentition line. Small diastema between P2 and P3. Greatly reduced diastema between P2 and the upper canine. Upper canines bearing an anterior and posterior cutting edge, the anterior one being less pronounced distally than in the proximal half. Upper canines slightly serrated near the base. Deep groove present behind the anterointernal edge, extending nearly to the tip of the canines. Broad nasomaxillary processes, rounded at the end and almost parallel.

Emended Diagnosis—Average-sized machairodontine felid with a wide frontal region, relatively narrow and elongate snout slightly constricted at the level of the infraorbital foramen, very thin zygomatic arches of nearly constant width in dorsal view, palate short and wide, major posterior palatine foramen positioned near the level of the P4 paracone, and M1 oriented almost perpendicular to P4. Palatine process medial to M1 absent. Postglenoid process pronounced; glenoid fossa relatively narrow. Upper canines laterally flattened with serrations on both anterior and posterior margins, the posterior edge more strongly developed than the anterior one; anterolingual surface bearing a slight groove.

TABLE 1. Dental measurements (in mm) in AMNH F:AM 62192 and YPM VP 014162.

	YPM VP 014162	AMNH F:AM 62192	Size difference
Right P4	23.54	21.67	7.94%
Right P3	15.49	14.49	6.49%
Left P4	24.05	21.11	12.22%
Left P3	15.65	14.47	7.54%
		AVERAGE:	8.54%

Differential Diagnosis—Differs from both *Yoshi* spp. and *Metailurus major* in exhibiting thinner zygomatic arches of constant width rather than anteriorly thickened, a more pronounced postglenoid process, absence of a posterior palatine process medial to M1, and an upper canine morphology with both anterior and posterior serrations (anterior less pronounced distally). Differs from *Yoshi* spp. in having a smaller braincase; relatively narrower and longer snout; infraorbital foramen opening slightly dorsally rather than entirely anteriorly; narrower glenoid fossa; mastoid process more developed than in *Yoshi* spp., being more similar to *M. major*; upper P3 lacking anterior accessory cusp; diastema between lower canine and p3 proportionally longer; ventral border of mandible flatter. Differs from *Metailurus major* in having zygomatic arches more rounded and wider in dorsal view; upper P3 lacking anterior accessory cusp; M1 smaller and oriented at ~90° to P4 rather than oblique; infraorbital foramen opening less dorsally; postglenoid process less developed than in *M. major*.

DESCRIPTION AND COMPARISON

The newly referred cranium is approximately 8.5% smaller than the holotype based on dental measurements (Table 1). However, once scaled to 91.5%, the two maxillae of KUVP 346 are very comparable to AMNH F:AM 62192 as shown in Fig. 4.

Cranium

The specimen AMNH FAM 62192 is a virtually complete, three-dimensionally preserved cranium (Fig. 1). The dentition is relatively well preserved, although all incisors, both upper canines, and the second premolars are missing. The left auditory bulla is broken, and plaster covering the nasal region prevents a detailed description of the nasal bones.

Dorsal View—In dorsal view, the cranium is short, wide, and strongly rounded, with broadly flared zygomatic arches. These arches are thinner than in *Yoshi minor* and *Metailurus major*, and strikingly thinner than in *Y. yongdengensis*. In outline, the arches are wide and rounded, resembling *Y. yongdengensis*, whereas *M. major* exhibits narrower, more triangular arches (Fig. 5).

The snout is narrow, resembling *M. major*, whereas both *Yoshi* species have a proportionally shorter and wider snout. In *A. kansensis*, the snout is slightly constricted at the level of the infraorbital foramen, a condition also seen in *M. major* (Fig. 5). In both *A. kansensis* and *M. major*, the infraorbital foramen is clearly visible in dorsal view, in contrast to *Yoshi* spp. where it opens more anteriorly. Although the skull of AMNH F:AM 62192 superficially resembles the holotype of *Y. yongdengensis* in dorsal view (Jiangzuo et al., 2022a:fig. 3a) the striking difference is the snout that appear closer to that of *M. major*.

A slight depression is present in the glabellar region, weaker than in *Y. garevskii* or *M. major*, but more pronounced than in *Y. minor* (Fig. 5). All specimens except *Y. minor* display a depression between the nasal bones, although this may be taphonomic. The postorbital processes are short and blunt, closely resembling those of *Y. minor*.

The braincase is relatively narrow compared to *Y. minor* and *Y. garevskii*, similar in size to *M. major*, but lacking the postorbital constriction seen in the latter (Fig. 5). The frontal region is broad and most closely resembles *Y. minor*. The sagittal crest is smallest in *Y. garevskii*; in *A. kansensis*, it is similar in development to *Y. minor*. The nuchal crest is well developed and comparable to that of *Y. minor*, though it is partially broken in *Y. garevskii* and completely absent in the preserved material of *M. major*, precluding comparison with those taxa.

Ventral View—The palate of *A. kansensis* is relatively short and wide compared to *M. major*, and closely resembles that of *Y. garevskii* and *Y. minor* (Fig. 6), maybe somewhat wider than

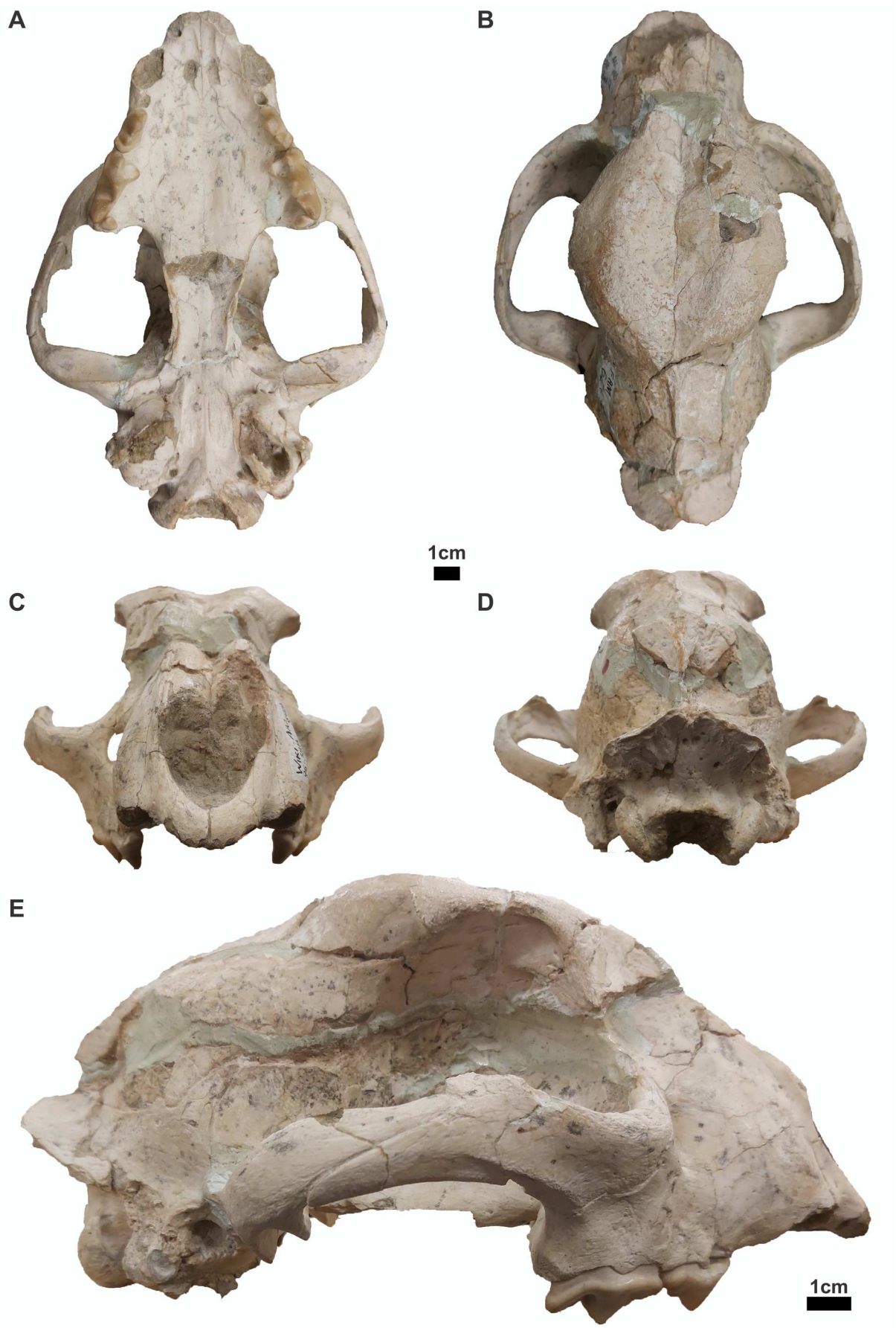

FIGURE 1. Cranium of *Adelphailurus kansensis* AMNH F:AM 62192 in **A**, ventral; **B**, dorsal; **C**, anterior; **D**, posterior; and **E**, lateral view.

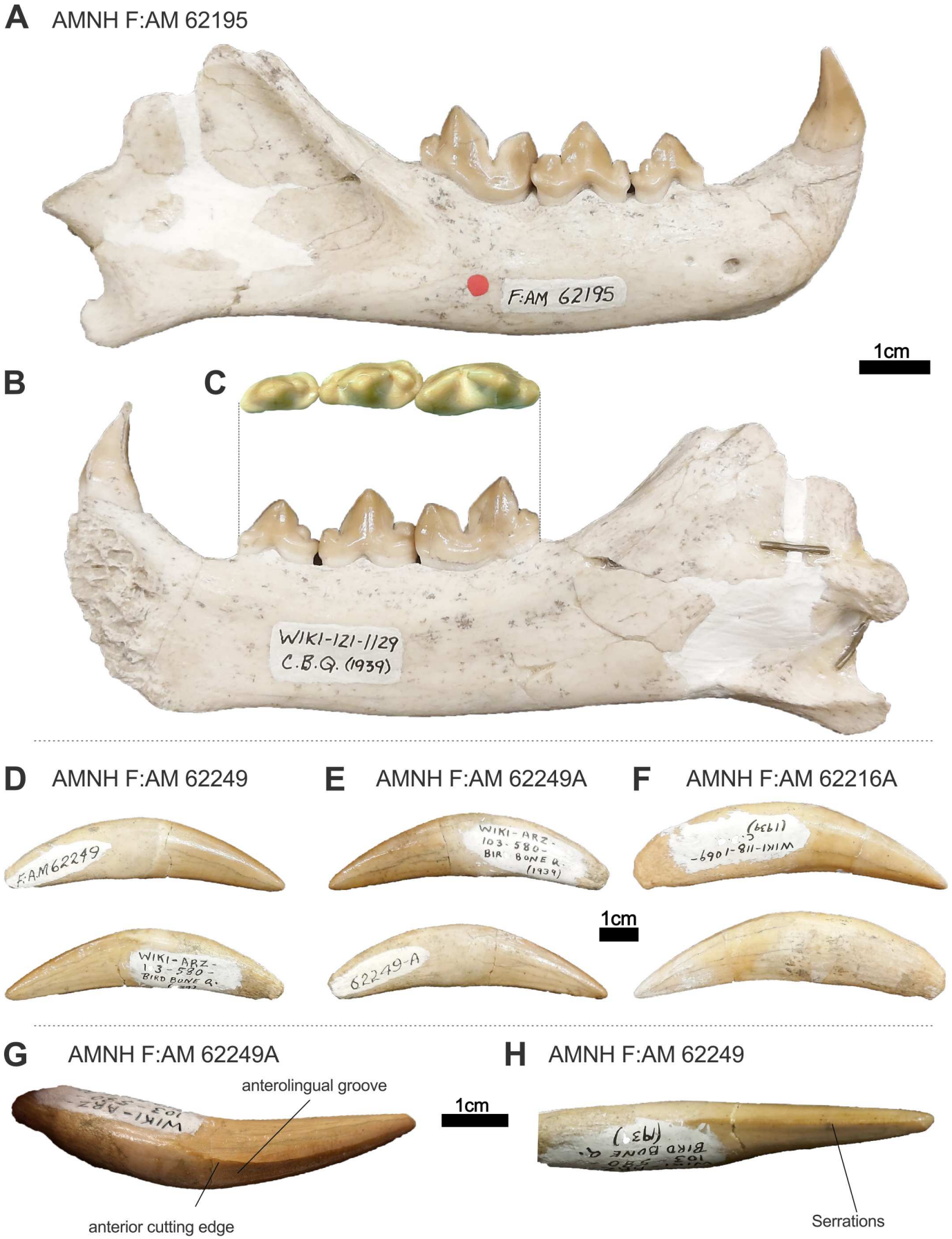

FIGURE 2. Right hemimandible (**A**–**C**, AMNH F:AM 62195) and upper canines (**D**–**H**, AMNH F:AM 62249, AMNH F:AM 62249A, AMNH F:AM 62216A), hereby referred to *A. kansensis*, in different views.

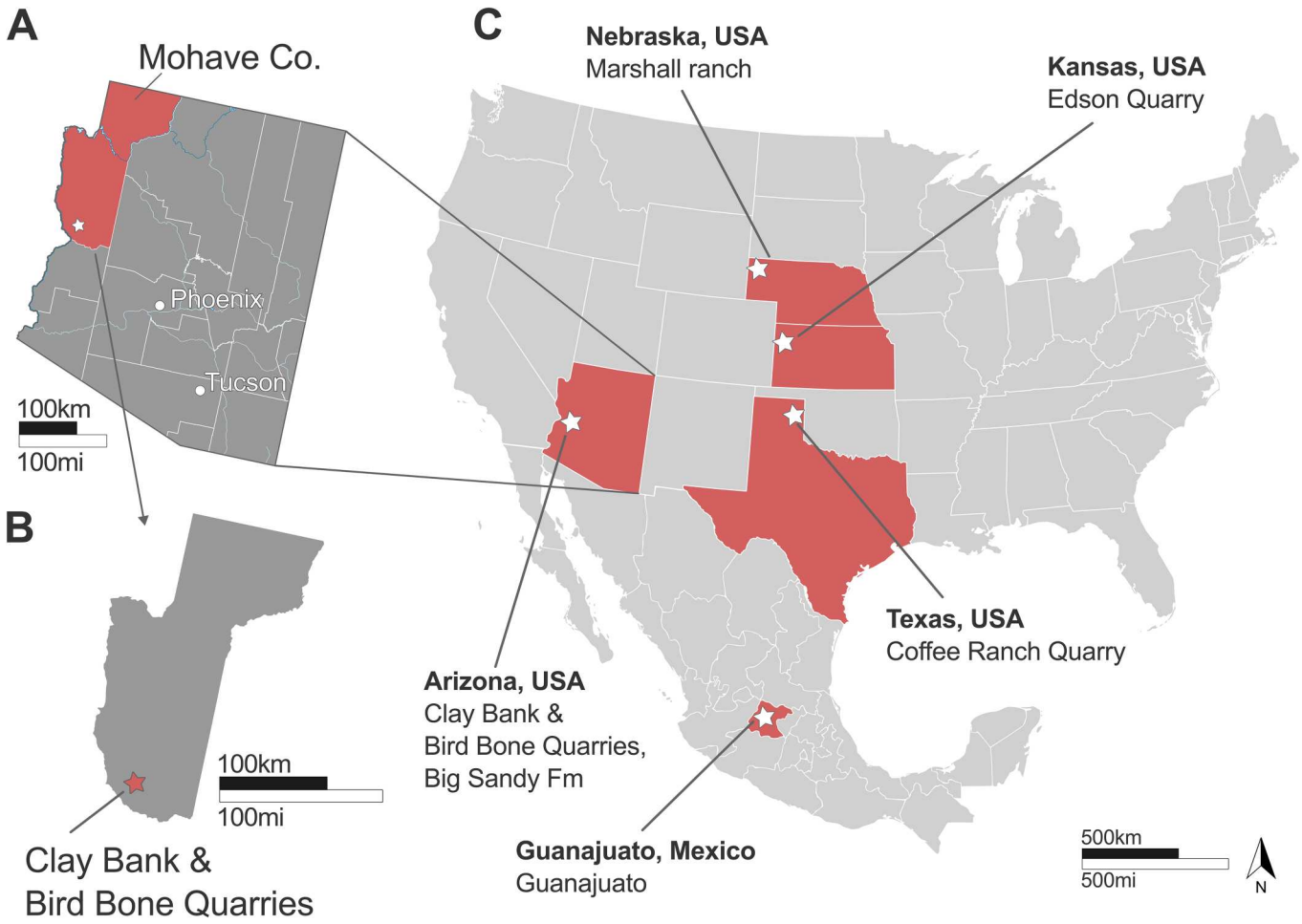

FIGURE 3. Location of the fossil site where the newly referred specimens were discovered. Base vector maps obtained from Wikipedia.

Y. faie and *Y. yongdengensis*. The incisor row is only slightly curved, intermediate between the condition in *Yoshi* spp. and *M. major*. The alveolus for P2 is present, although the tooth itself is missing, indicating the presence of a vestigial P2 in *A. kansensis*, while it is absent in *M. major*, *Y. garevskii*, *Yoshi faie*, and *Yoshi minor*. All incisors are absent, but alveolar evidence shows that I3 was much larger than I2 and I1, the latter two being similar in size. The choana region is poorly preserved, but appears to open well behind M1, in a position more posterior than in *Y. minor* and comparable to that of *Y. garevskii*, *M. major*, and *Y. yongdengensis* (Fig. 6). Jiangzuo et al. (2022b) noted the presence of a distinct posterior process of the palatine medial to M1 in *Y. yongdengensis*. This process is present in *Y. minor* and on the left side of *M. major*, but is absent in both *Y. garevskii* and *A. kansensis* (Fig. 6).

The major posterior palatine foramen lies much farther anteriorly than in *Y. minor*, *Y. garevskii*, or *M. major*, positioned near the level of the P4 paracone: an arrangement extremely similar to that in *Y. yongdengensis* (Jiangzuo et al., 2022a). The glenoid fossa is relatively narrow, narrower than in *M. major*. In ventral view, the postglenoid process is more developed than in *Y. minor*, but less so than in *M. major* (Fig. 6).

In ventral view, the postglenoid process appears more developed than in *Y. minor*, but less than in *M. major*. The foramen ovale is not well visible in ventral view; it is most clearly seen in *Y. minor*, followed by *M. major*, but is barely discernible in *Y. garevskii*, *A. kansensis* (Fig. 6) or *Y. yongdengensis* (Jiangzuo et al., 2022a). The auditory bullae are damaged but most closely resemble those of *Y. garevskii* (Fig. 6), and the spacing between the bullae appears similar across all compared species. The mastoid process is expanding laterally enough to be slightly visible in dorsal view. Occipital condyles appear somewhat smaller than in *Y. minor* or *Y. garevskii*. The occipital condyles are somewhat smaller than in *Y. minor* or *Y. garevskii*. The condylar foramen lies slightly closer to the auditory bulla than in *Y. minor*. Although this feature is not preserved in PMU 21771-1, Roussiakis (2001) noted a similar proximity in the *M. major* specimen from Pikermi, in Greece.

Finally, the zygomatic arches are wide and rounded in both ventral and dorsal views (Figs. 5, 6), more so than in *Yoshi* spp. or *M. major*, and somewhat comparable to the condition in the extant snow leopard (*Panthera uncia*).

Lateral View—In lateral view, the postglenoid process is more pronounced than in *Yoshi* spp. or *M. major* (Fig. 7). All compared specimens display a rounded dorsal cranial profile. In *Yoshi* and *Metailurus major*, the mastoid process is relatively small compared to taxa with extreme sabertooth adaptations; it is vertically oriented and does not extend ventrally beyond the lower margin of the auditory bulla, although in *M. major* it reaches approximately the same level.

In *A. kansensis* the region surrounding the auditory bullae is damaged (see Fig. 1A) but the preserved portion of the mastoid process appears more similar to *M. major* than to *Yoshi* spp. In all taxa compared, the infraorbital foramen opens just anterior to the P4. In *Y. minor* and *Y. garevskii*, the opening faces entirely anteriorly, whereas in *M. major* it is

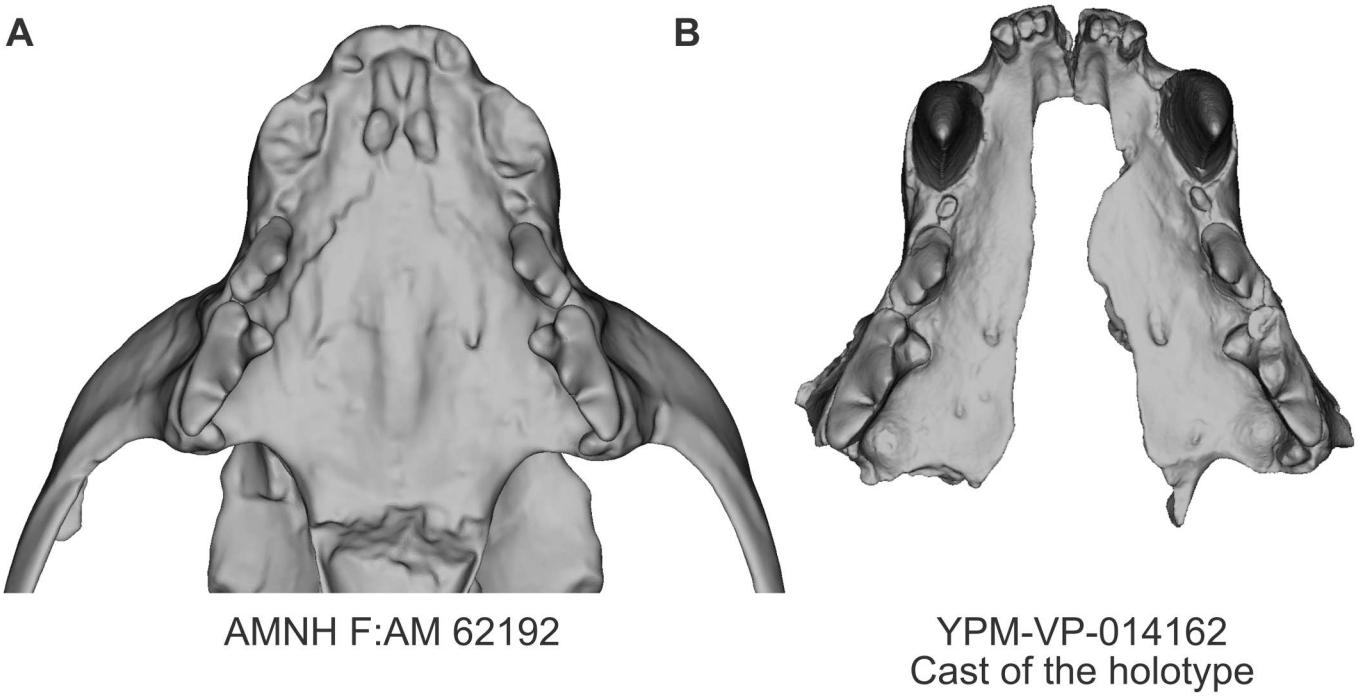

FIGURE 4. Comparison of **A**, the newly referred specimen of *A. kansensis* described in this contribution; and **B**, a cast of the holotype. AMNH F:AM 62192 scan © American Museum of Natural History.

directed slightly dorsally. *A. kansensis* shows a predominantly anterior orientation with a slight dorsal inclination. The orbit is proportionally wide for a felid of this size, though missing portions of the jugal prevent a complete assessment of its size.

Anterior View—The nasal cavity of *A. kansensis* is narrower than in *Yoshi* spp., closely resembling *M. major* (Fig. 8). The rostral opening of the infraorbital foramen is smaller than in *Yoshi* spp., but somewhat larger than in *M. major*.

Posterior View—In posterior view, the nuchal ridge of *A. kansensis* is rounded, in contrast to the triangular shape seen in *Yoshi* spp. (Fig. 8). Although the nuchal crest is not preserved in the *M. major* holotype from Baode, it is triangular in posterior view in *Metailurus* sp. AMNH F:M 131854.

The posterior section of the zygomatic arches in *A. kansensis* is thin and comparable to *Yoshi* spp., whereas in *M. major* it is even thinner. In *Yoshi* spp. and *M. major*, the arches are very thin posteriorly and thicken anteriorly, whereas in *A. kansensis* they maintain a consistent thickness along their length (Figs. 7, 8). The braincase closely resembles that of *M. major* in posterior view.

Upper Dentition

The upper P4 of *A. kansensis* has a well-developed protocone, with a cingulum larger than in *Y. minor* but less developed than in *M. major*. As noted by Spassov and Geraads (2015) the P3 of *Yoshi* lacks a distinct mesial accessory cusp. In *A. kansensis*, the P3 has no anterior cusp, resembling *Y. minor*, whereas *M. major* bears a well-developed one.

The M1 is present, but reduced to a single cusp contrary to *Y. minor* which exhibits a more developed M1 with a main cusp and a small accessory cusp, and *M. major* which exhibits a single cusped M1 that is nearly twice as large as in *A. kansensis*. In *A. kansensis*, the M1 is positioned almost perpendicular to the P4, as in *Yoshi* spp. In contrast, *M. major* possesses a larger M1 that forms a ~60° angle with the P4.

The specimen AMNH FAM 62192 is associated with several other remains, including a mandible (Fig. 2A, B) and isolated upper canines (Fig. 2C, G). Although there is no definitive evidence that these elements belong to the same individual, the upper canines closely match those of the *A. kansensis* holotype (KUVP 346). These canines are laterally flattened and bear two cutting edges, with the posterior one well marked. Hibbard (1934) distinguished *A. kansensis* from *Metailurus major* by the presence of a primary cutting edge mainly along the posterior margin of the upper canine, which is slightly serrated (Fig. 2G). Harrison (1983) contested this, noting that *A. kansensis* also has an anterior cutting edge, although less pronounced distally than proximally. The upper canines associated with AMNH F:AM 62192 exhibit serrations on both margins, weaker on the anterior side and fading distally. The anterolingual surface bears a slight groove. Hibbard (1934) also described a unique medial groove along the anterior edge of the upper canines; the morphology on the isolate canines matches Harrison's description (Harrison, 1983), and they are hitherto referred to *A. kansensis*.

By contrast, species of *Yoshi* possess upper canines without crenulations, with an anterior keel positioned mesially rather than mesio-lingually. In *Yoshi*, the lingual surface is flat to slightly convex, while the buccal surface is slightly flattened to convex (Spassov & Geraads, 2015).

Mandible and Lower Dentition

The mandibular fragment AMNH F:AM 62195 bears strong wear facets on both the lower canine and m1 (Fig. 2A, B). It lacks a mandibular flange and has a single mental foramen located slightly anterior to the mesial tip of p3. The mandibular corpus is relatively slender. The ventral border of the mandible is relatively flat and less convex than in *Y. garevskii*, but not as straight as in *M. major*. The angular process is well developed. The anterior accessory cusp is small, smaller than the posterior one, which is similar to the condition observed in *Yoshi minor* and not very common in felids.

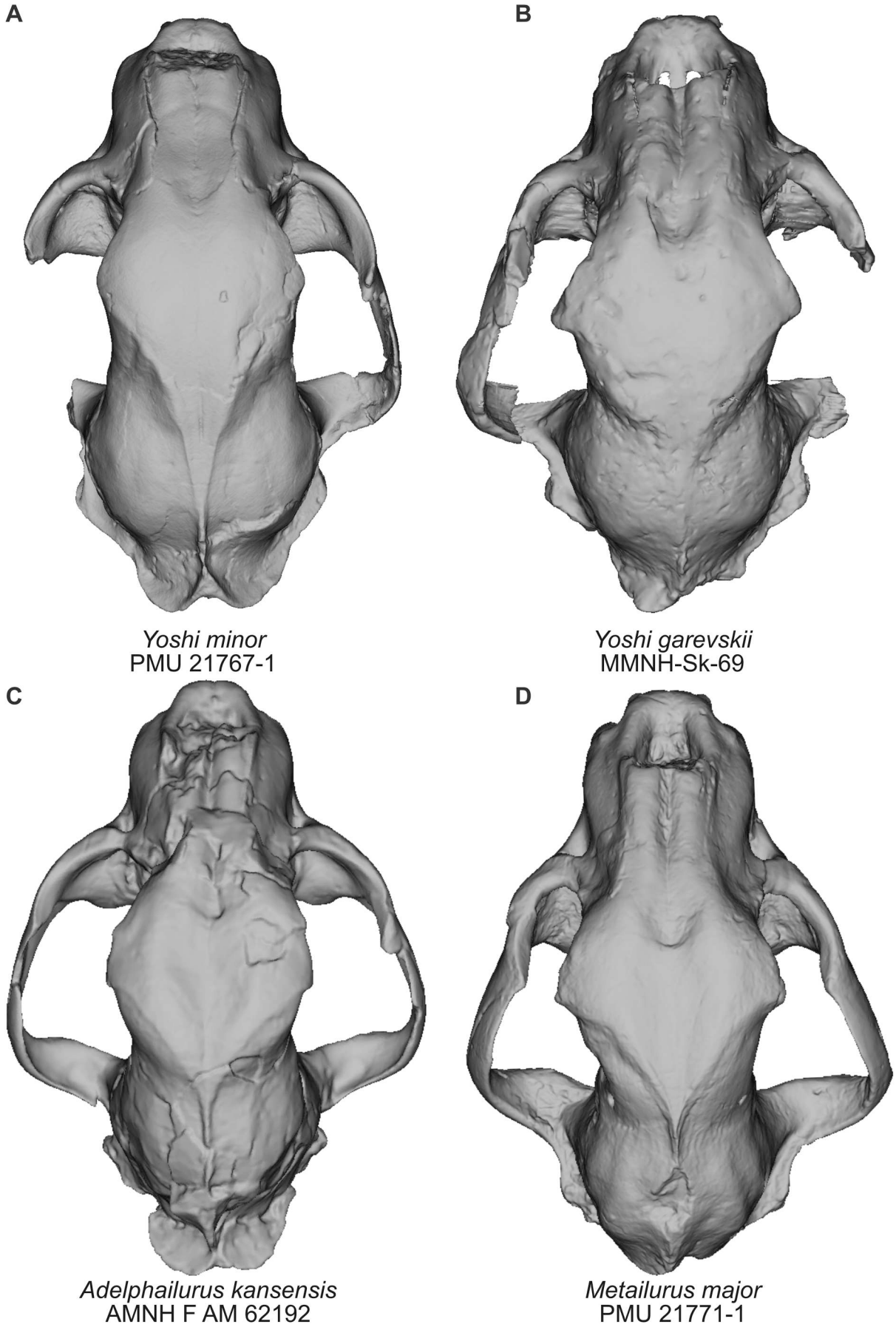

FIGURE 5. 3D models of crania in dorsal view scaled to the same length for comparison. **A**, *Yoshi minor*; **B**, *Yoshi garevskii*; **C**, *Adelphailurus kansensis*; and **D**, *Metailurus major*. AMNH F:AM 62192 scan © American Museum of Natural History.

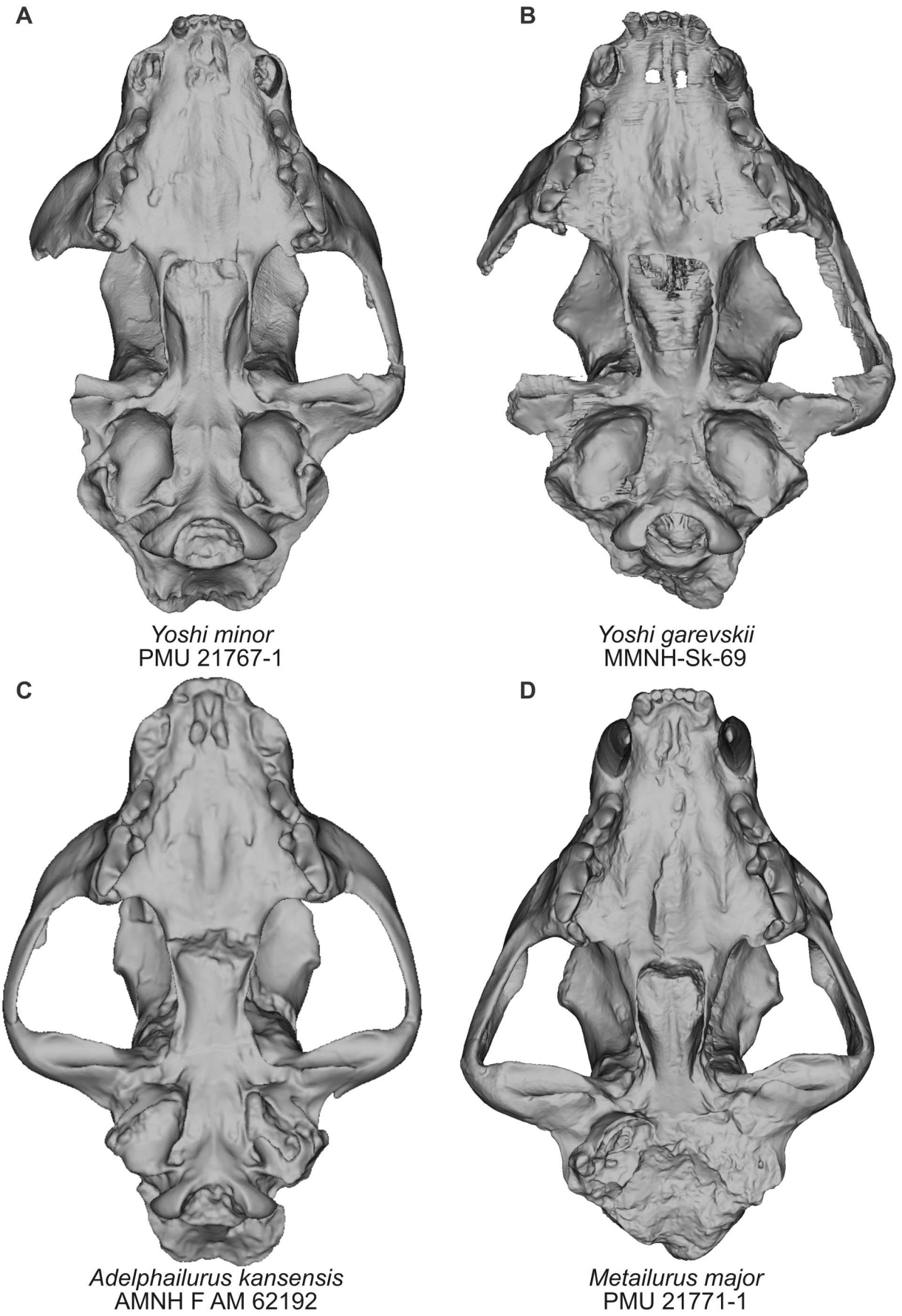

FIGURE 6. 3D models of crania in ventral view scaled to the same length for comparison. **A**, *Yoshi minor*; **B**, *Yoshi garevskii*; **C**, *Adelphailurus kansensis*; and **D**, *Metailurus major*. AMNH F:AM 62192 scan © American Museum of Natural History.

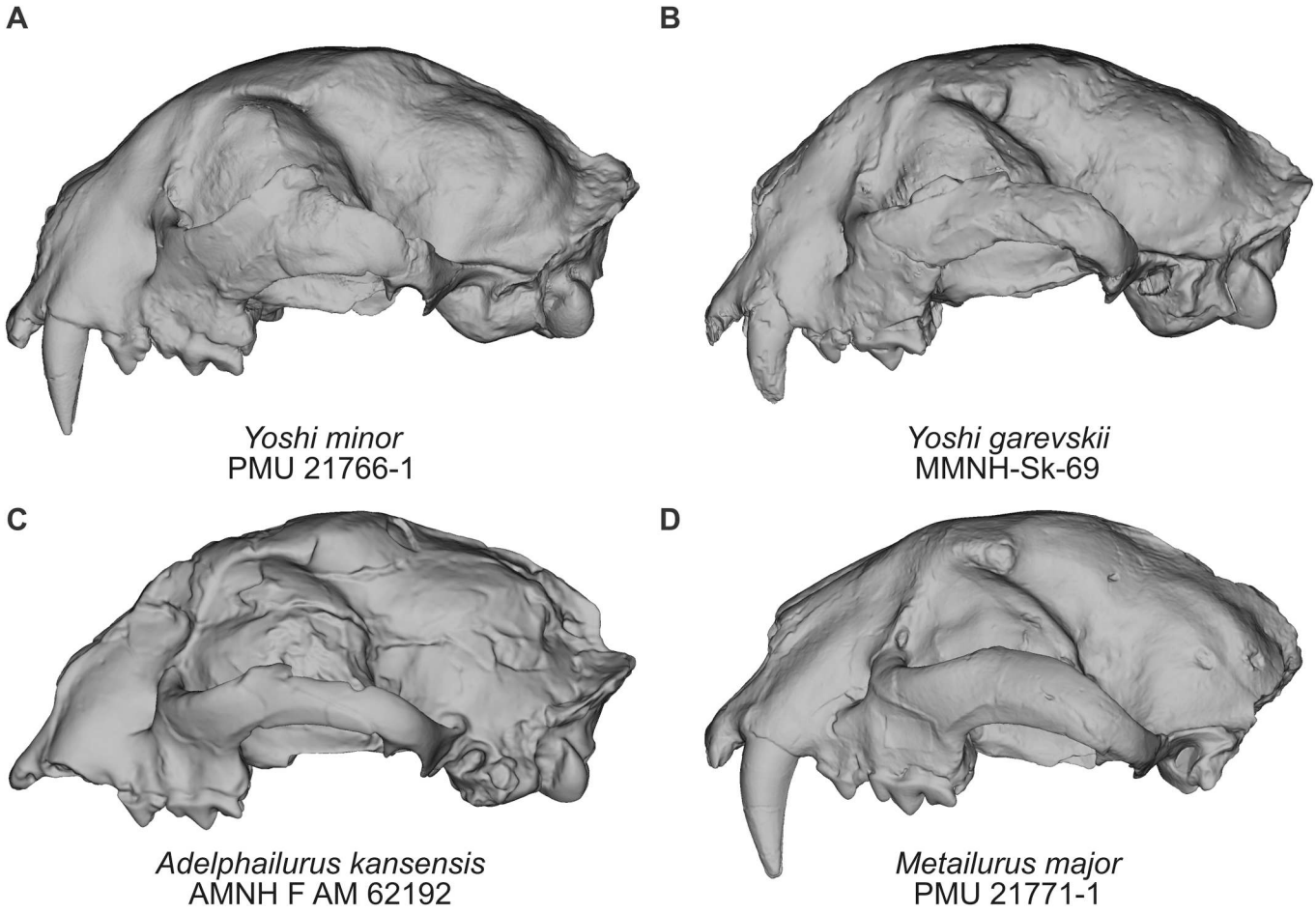

FIGURE 7. 3D models of crania in lateral view scaled to the same length for comparison. **A**, *Yoshi minor*; **B**, *Yoshi garevskii*; **C**, *Adelphailurus kansensis*; and **D**, *Metailurus major*. AMNH F:AM 62192 scan © American Museum of Natural History.

The diastema *of Y. minor* and *Y. garesvkii* appear of similar proportion relative to the mandible length (see Table 2, *Y. minor* = 6.5%, *Y. garevski* = 7.9%) whereas that of *A. kansensis* is proportionally longer (12.9%), almost as long as in *M. major* (13.3%) (Table 2). The masseteric fossa extends anteriorly to the level of m1. The m1 bears a distinct talonid. The p4 has a small but distinct anterior accessory cusp, a large posterior accessory cusp, and a well-defined cingulum. The p3 shows two distinct posterior accessory cusps. The angular process is well-developed.

Within compared taxa (Y. *minor*, *Y. garesvkii*, *M. major*, and *A. kansensis*), the most vertical mandibular symphysis (closest to 90°) is seen in *Y. garevskii* (76.2°), though this may be taphonomic. *M. major* follows (69.5°), while *Y. minor* has the lowest value (65.4°). *A. kansensis* (66.5°) is closer to *Y. minor* in this regard.

Adelphailurus kansensis in the Machairodontine Felids Morphospace

Our PCA on a subset of felids from Chatar et al. (2024) retrieved 22 axes, the first two explaining respectively 39.01 and 14.88% of variance (Fig. 9). The first axis mainly discriminates between taxa with longer or shorter upper canines with higher PC1 values occupied by taxa bearing the most elongated upper canines, which are associated with notable shape differences such as the development of a stronger sagittal crest, a protruding premaxilla, shortened and thickened zygomatic arches, less developed temporal fossa, an enlarged mastoid process, among others. All of those traits are considered typical 'saber-tooth traits' (see Anton et al., 2004). The species exhibiting the highest PC1 value being *Smilodon populator.*

On the other hand, in the lowest PC1 values we find taxa with the shortest upper canines such as *Yoshi* spp., *Metailurus* spp., or *Dinofelis* spp. (Fig. 9), which still differ from non-machairodontine felids in terms of cranial shape but do not exhibit the extreme morphological specialization seen in taxa bearing longer upper canines occupying high PC1 values. The specimen exhibiting the lowest values on PC1 belongs to the specimen AMNH F:M 131854 labeled as *Metailurus* sp., followed by the newly described specimen of *A. kansensis.* Shape variations on PC2 are more subtle, involving rotation of various parts of the cranium.

Our morphometric analysis confirms the results of the morphological comparison: the newly referred specimen of *A. kansensis* has a morphology somewhat in between of the genera *Yoshi* and *Metailurus*. *Adelphailurus kansensis* falls in the range of *Metailurus* spp. on PC1 but is halfway in between *Metailurus* and *Yoshi* on the second axis.

Phylogenetic Analyses

Our analysis retrieved three equally parsimonious trees (length = 895), the only variation was the position of *Adelphailurus kansensis* and *Promegantereon ogygia*. *Adelphailurus kansensis* was either retrieved as: (1) an early diverging lineage nested in between *Pseudaelurus validus* and all the other felids with a resampling probability of 67, (2) an early diverging

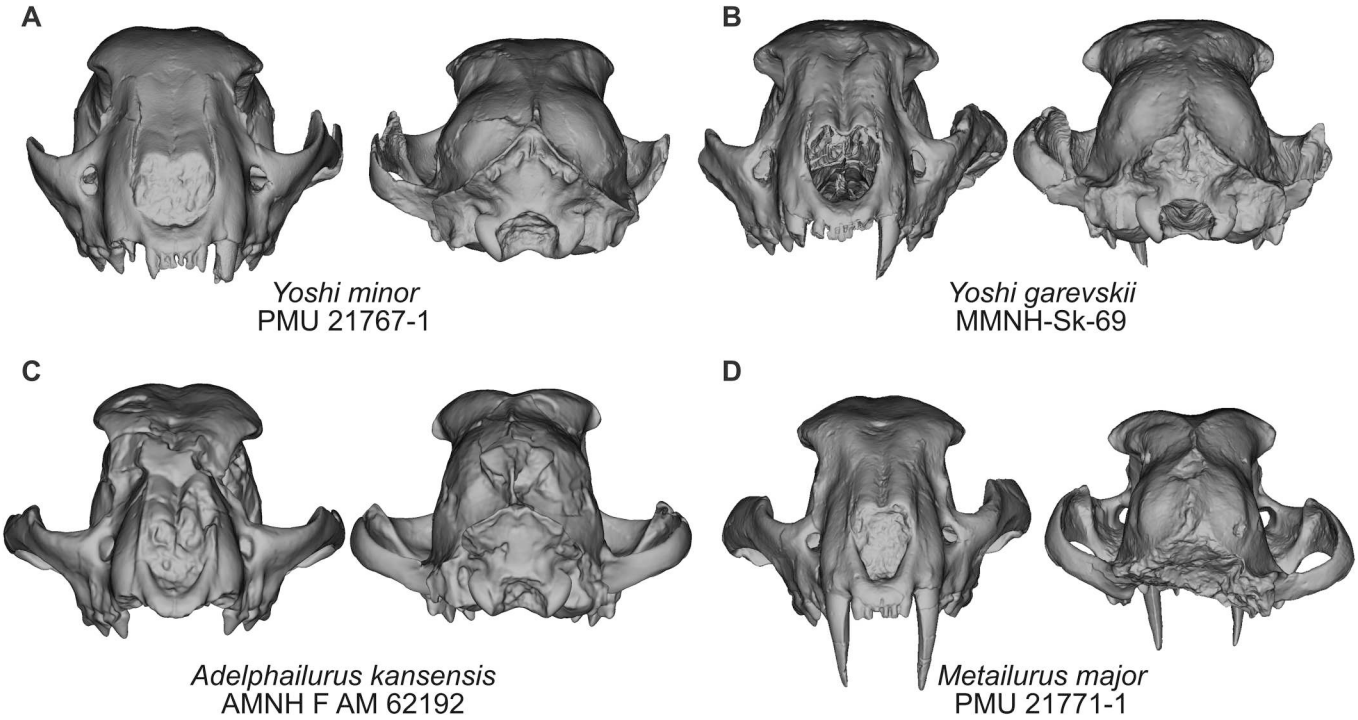

FIGURE 8. 3D models of crania in anterior and posterior view scaled to the same width for comparison. **A**, *Yoshi minor*; **B**, *Yoshi garevskii*; **C**, *Adelphailurus kansensis*; and **D**, *Metailurus major*. AMNH F:AM 62192 scan © American Museum of Natural History.

branch at the base of machairodontine felids with a resampling probability of 78, or (3) a sister taxon to *Pr. ogygia* forming a clade at the base of machairodontine felids with a resampling probability of 82. A screenshot of each tree is available in Supplementary File 4, alongside the log file from TNT and a MPT file containing the three trees. The strict consensus tree therefore creates a polytomy at the base of felids with *Pr. ogygia* and *A. kansensis* (Fig. 10). We were not able to score a majority of characters for *A. kansensis*, which could partially explain its uncertain position. However, TNT highlighted a Consistency Index (CI) of 0.349, and a Retention Index (RI) of 0.429. Both those metrics are measures of homoplasy; CI being obtained by dividing the number of steps expected given the number of character states in the data by the actual number of steps whereas the retention index measures the amount of synapomorphy expected from a data set that is retained as synapomorphy on a cladogram. A low CI (0.349) indicates a dataset with substantial homoplasy. The average RI (0.5) highlights only moderate retention of phylogenetic signal, meaning that many characters are either convergent/reversed or only partly consistent with the inferred tree. These metrics suggest that there is room for character list improvement in future studies.

DISCUSSION

Adelphailurus within Machairodontinae

The relationships within "metailurins," and between "metailurins" and other felids, remain poorly resolved. Some authors have suggested grouping multiple genera (*Stenailurus*, *Fortunictis*, and *Adelphailurus*) under the genus *Metailurus* (see Andersson & Werdelin, 2005), which was later refuted by multiple authors (Jiangzuo et al., 2021a; Jiangzuo et al., 2022a; Spassov & Geraads, 2015; Yu, 2014). Our description and morphometric analyses support considering *Adelphailurus* as a genus distinct from *Metailurus*.

Spassov and Geraads (2015) erected *Yoshi* based on several cranial and dental differences from *M. major*, including a wide forehead, rounded dorsal cranial profile, very short rostrum, high-crowned premolars, and a very low second lobe

TABLE 2. Measurements on the lower mandible of selected specimens. Lengths are given in mm and angles are given in degrees.

Taxon	Specimen ID	Diastema length	Mandible length	Ratio diastema mandible	Symphysis angle
Yoshi minor	PMU-21766/2 (left)	6.568	101.189	0.065	66.214
	PMU-21766/2 (right)	5.477	102.011	0.054	68.422
	PMU 21767/2	7.846	102.084	0.077	61.500
	AVERAGE	6.630	101.761	0.065	65.379
Yoshi garevskii	MMNH-Sk KAR 69 (left)	8.424	108.420	0.078	73.312
	MMNH-Sk KAR 69 (right)	8.850	109.400	0.081	78.995
	AVERAGE	8.637	108.910	0.079	76.154
Metailurus major	PMU 21771/2 (left)	18.074	137.534	0.131	70.304
	PMU 21771/2 (right)	18.547	138.224	0.134	68.511
	AVERAGE	18.311	137.879	0.133	69.408
Adelphailurus kansensis	AMNH F:AM 62195	15.654	121.796	0.129	66.525

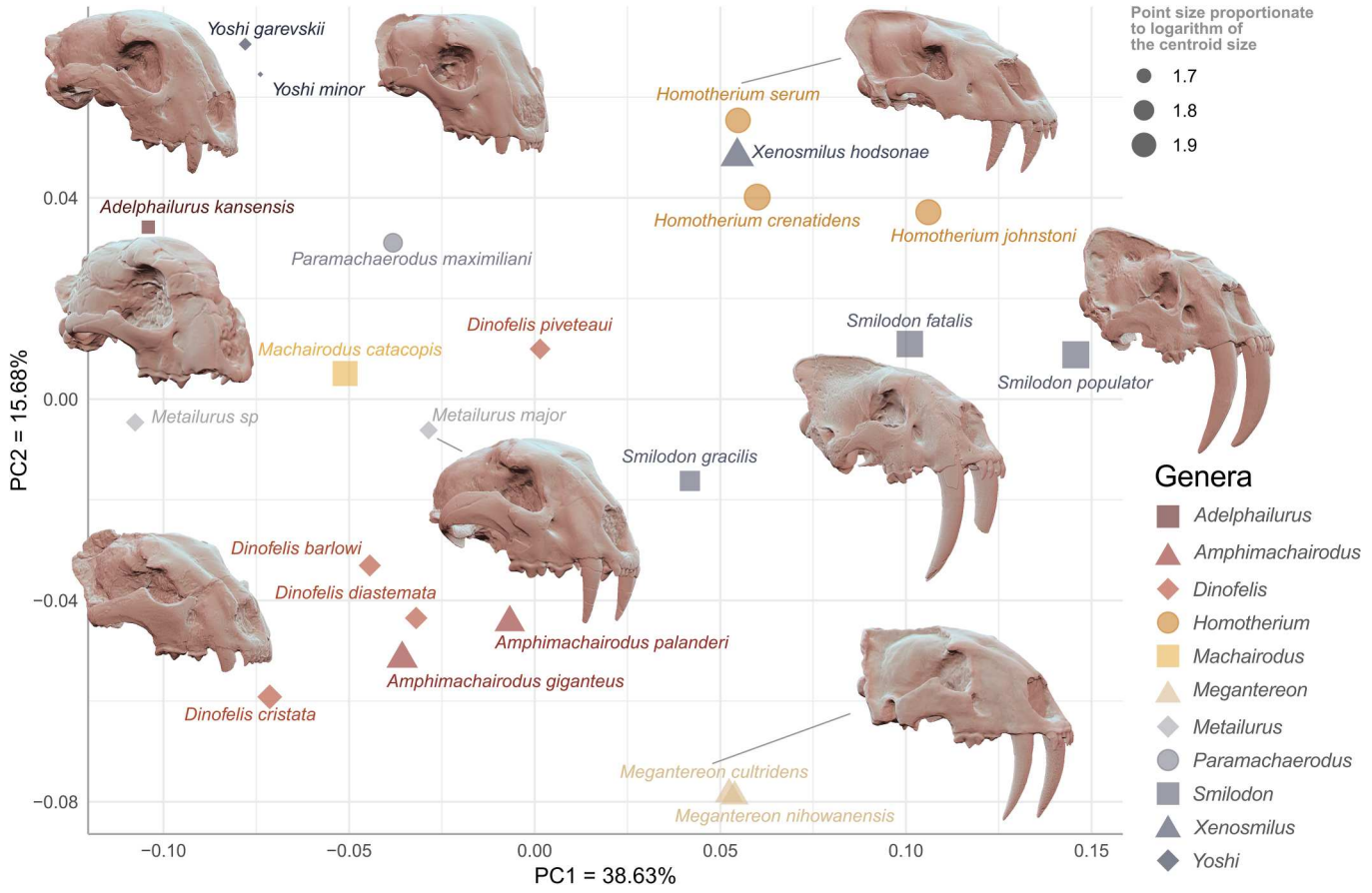

FIGURE 9. Morphospace obtained from a PCA performed on landmark coordinates on a subset of machairodontine felids. *Adelphailurus kansensis* AMNH F:AM 62192 scan © American Museum of Natural History.

of the P4 metacone/metastyle. Jiangzuo et al. (2022b) later disputed some of these characters, specifically the wide forehead and rounded dorsal profile, arguing that they also occur in *M. major*. Our re-examination of the *M. major* holotype and several *Y. minor* specimens suggests that *Yoshi* generally exhibits a larger forehead and more rounded cranial profile than *Metailurus*, consistent with Spassov and Geraads (2015). However, as noted by Jiangzuo et al. (2022b), the distinction between these two genera is not always clear-cut. The rising realization that machairodontine felids exhibit a continuum of morphological disparity, often challenging our preexisting well-defined categories, parallels recent studies highlighting a continuum of cranial shape and mechanical behavior within the group (e.g., Chatar et al., 2021, 2022a, 2024; Figueirido et al., 2018; Lautenschlager et al., 2020; Pollock et al., 2025; Shelbourne & Lautenschlager, 2025). Interestingly, our description of new *A. kansensis* material reveals a morphology intermediate between *Yoshi* and *Metailurus*. This observation is supported by our geometric morphometric analyses: *A. kansensis* plots in morphospace midway between *Metailurus* sp. AMNH 131854 and *Yoshi* spp. on PC2, but closer to *Metailurus* sp. on PC1. Nevertheless, *A. kansensis* differs from *Metailurus* in several features, including the overall shape of the zygomatic arches, a more rounded and wider cranium, and a P3 lacking a distinct anterior accessory cusp. It also differs from both *Yoshi* and *Metailurus* in having thinner zygomatic arches of nearly constant width.

Although "metailurin" relationships remain debated, our new material confirms that *Adelphailurus* is morphologically distinct from the genera *Yoshi* and *Metailurus*, a conclusion reinforced by geometric morphometric. Our phylogenetic analyses did not resolve those relationships, in part due to the high proportion of missing data or the strong presence of homoplastic characters in the matrix employed (see our RI and CI values). The unresolved position of *Adelphailurus* is consistent with the prevailing interpretation of some metailurines as having fewer derived sabertooth characteristics and most other machairondontines, and thus belong in a more stemward position on the phylogeny. The inclusion of other 'metailurins' (e.g., *Y. minor*, Y. *garevskii*, etc.) in the analysis could help shed light on the early stages of machairodontine cladogenesis in the future. Recent work has questioned the monophyly of "Metailurini" and emphasized the close but ambiguous relationships among *Yoshi*, *Metailurus*, and *Paramachaerodus* (e.g., Jiangzuo et al. 2022a; Madurell-Malapeira et al., 2021). Expanding the taxonomic sampling of early-diverging forms (particularly additional species traditionally referred to "metailurines" such as *Y. minor* or *Y. garevskii*) in the present matrix may help clarify the early stages of machairodontine cladogenesis. While our study does not resolve these broader taxonomic uncertainties, it reinforces the notion that early machairodontine evolution was characterized by substantial morphological convergence and phylogenetic instability and highlight the need to find better European and North American specimens.

Late Miocene Felid Dispersion in North America

Extensive faunal interchange occurred between Eurasia and North America during the Neogene, and for carnivorans

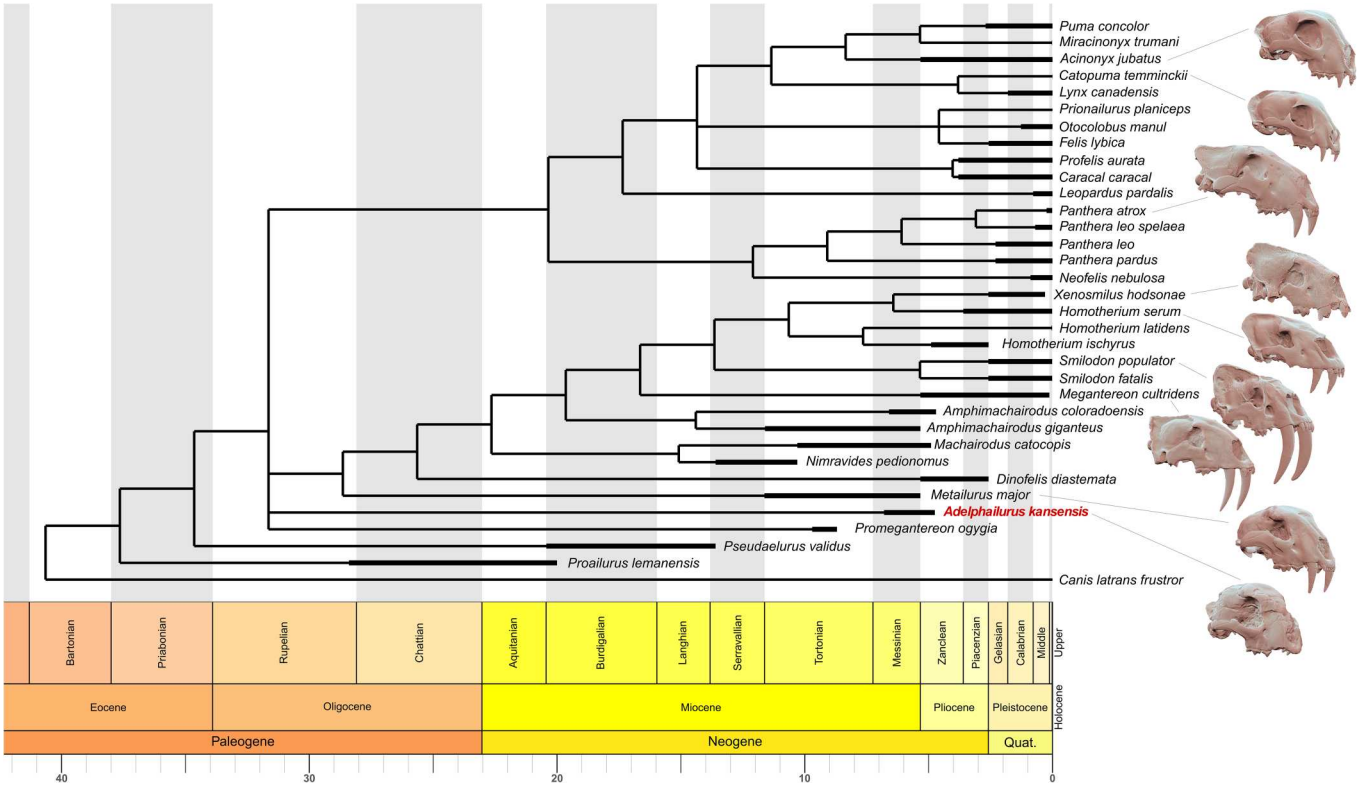

FIGURE 10. Topology obtained from the implied weighting analyses. Note that the tree was time scaled using a basic minimum branch length approximation in R and is displayed for graphical purposes only. *Adelphailurus kansensis* AMNH F:AM 62192 scan © American Museum of Natural History.

particularly during three major dispersal waves: ca. 21–18 Ma, ca. 7–8 Ma, and in the Early Pliocene (around 4 Ma) (Qiu, 2003). Several carnivoran genera are considered likely Eurasian immigrants to North America, including *Lynx*, *Trigonictis*, *Canimartes*, *Enhydra*, *Enhydriodon*, *Ursus*, and *Chasmaporthetes* (Repenning, 1967). It has been proposed that the first felid migration into North America occurred between 18 and 7 Ma (Repenning, 1967), outside the main dispersal waves, and involved early-diverging felids traditionally labeled as *Pseudaelurus* (Polly, 2020) marking the end of the 'cat gap' (Van Valkenburgh, 1989), a period during which no fossils of cat-like taxa are known from North America following the extinction of the last non-barbourofeline nimravid around 23 Ma (Van Valkenburgh, 1999). In this context, *Adelphailurus* specimens have been described from several Hemphillian (latest Miocene–earliest Pliocene) localities in the U.S.A. and Mexico (Fig. 3C), possibly representing a separate trans-Beringian dispersal event from the *Pseudaelurus* event. Numerous 'metailurin' taxa are recorded from the Middle Miocene to Early Pleistocene across Europe, Asia, Africa, and North America (see Jiangzuo et al., 2022a; Madurell-Malapeira et al., 2021; Spassov et al., 2018; Werdelin & Lewis, 2001), some potentially representing sister taxa to *Adelphailurus*. The earliest well-established occurrences of *Metailurus* date to the Middle Miocene of China (Tunggur Fm) (Yu, 2014), supporting an Asian center of origin. Recent examination of material from Tatrot (Siwaliks) (Jiangzuo et al., 2021b) extends the temporal range of *Metailurus* into the Late Pliocene in southern Asia, reinforcing Asia as both a likely center of origin and long-term refuge for early-diverging machairodontine lineages. Those early diverging machairodontine felids lineage quickly dispersed in Europe, where they became abundant already in the Late Miocene. The progressive uplift of the Tibetan Plateau likely restricted north/south exchanges within Asia (Deng et al., 2015), leaving westward (into Europe) and eastward (into North America via the Bering Land Bridge) routes as the primary dispersal corridors, with climatic cooling and expansion of open habitats facilitating large carnivoran dispersal. Climatic cooling and the expansion of more open habitats during the late Miocene may have further facilitated large carnivoran dispersal across northern Eurasia. Although the North American fossil record does not yet permit a full resolution of the number and timing of dispersal events, our reexamination of *Adelphailurus* cranial material highlights its mosaic morphology (as per Salesa et al., 2005; Antón et al., 2013) somewhat in between *Yoshi* and *Metailurus*, consistent with its placement near the base of machairodontine diversification.

The '*Pseudaelurus*' Problem

Rothwell (2003) recognized five North American *Pseudaelurus* species: *P. validus*, *P. skinneri*, *P. intrepidus*, *P. marshi*, *P. stouti*, appearing in the late Hemingfordian and disappearing by the late Barstovian. Other authors have noted distinct features in North American '*Pseudaelurus*' leading to the proposal of a new genus, *Hyperailurictis*, for these early felids, considered more similar to *Nimravides* than to Old World *Pseudaelurus* (Beaumont, 1978; Jiangzuo et al., 2021a; Werdelin et al., 2010). However, some recent studies still refer to North American specimens as '*Pseudaelurus*' (e.g., Polly, 2020) and there no clear consensus has been reached regarding the final taxonomy of North American pseudaelurines. This is in part a reflection of both *Pseudaelurus* and 'metailurins' being used as wastebasket taxa for early diverging Miocene felids.

Our re-examination of new *Adelphailurus* material originally attributed to *Pseudaelurus* underscores two key points: (1) the enduring value of museum-based projects for uncovering

FIGURE 11. Reconstruction of the skull and life appearance of *Adelphailurus kansensis* based on the newly described material, by Jesús Gamarra.

important, overlooked specimens, and (2) the long-standing taxonomic problems with *Pseudaelurus*. The genus name derived from the Greek 'pseudo' (ψευδής) meaning 'false' and 'aelurus' (αἴλουρος) meaning 'cat' was erected by Gervais (1850) initially attributing the Sansan '*Felis quadritentatus*' to a new species: *P. quadridentatus*, for which he noted strong resemblances with what he called the '*Felis*' group (= non-machairodontine felids) but differentiating from them by the presence of a vestigial p2 and a more developed talonid on the m1. Considered 'primitive', these traits led to the inclusion of many average-sized Miocene felids in *Pseudaelurus* simply because they lacked the 'derived' features of later lineages, making the genus a catch-all for early diverging taxa.

Because of this history, *Pseudaelurus* has been referred to as a wastebasket genus for average-sized Miocene felids (Rothwell, 2001), leading several authors to re-attribute specimens initially described as '*Pseudaelurus*' to different taxa after careful reexamination. For example, *Pseudaelurus hibbardi*, described by Dalquest (1996) based on a fragmentary left hemimandible from Coffee Ranch (TMM 41261-3), was reassigned to *A. kansensis* by Hodnett (2014). Similarly, a maxilla (IGM 6674) and an isolated P4 (IGM 6673) from Guanajuato, Mexico, originally identified as *P. intrepidus* by Carranza-Castañeda and Miller (1996) was later referred to *A. kansensis* (Hodnett, 2014). Our study reinforces the need to revisit historic *Pseudaelurus* material, particularly in North America, where almost every Early to Middle Miocene felid was initially assigned to this genus (Rothwell, 2001). Many of these specimens may represent early diverging members of established felid clades (machairodont or non-machairodontine felids) and could provide crucial insights into their evolutionary history. Indeed, our study allowed for a better comprehension of this enigmatic taxon previously known from very fragmentary material (Fig. 11). Nevertheless, our phylogenetic analysis indicates that the paucity of apomorphies in early diverging machairodontine felids remains a challenge to fully resolving this part of felid evolutionary history.

CONCLUSION

We described new material of *Adelphailurus kansensis*, a poorly known Late Miocene felid. Our observations highlight the morphological disparity within 'metailurin' felids, placing *Adelphailurus* morphologically between *Metailurus* and *Yoshi*, a position also supported by geometric morphometric analyses. Nevertheless, *A. kansensis* exhibits distinctive features, most notably zygomatic arches that are markedly thinner than in *Metailurus major* or *Yoshi* spp. It further differs from *Yoshi* in having a smaller braincase and a relatively narrower, longer snout, and from *Metailurus* in possessing more rounded and wider zygomatic arches in dorsal view and a P3 lacking a distinct anterior accessory cusp. This material, previously assigned to *Pseudaelurus*, underscores the unresolved nature of relationships among early-diverging felids, as highlighted by our phylogenetic analyses.

ACKNOWLEDGMENTS

We are infinitely grateful to the curators who allowed us to complete this project, notably to: J. Meng, J. Galkin, and K. Clark (AMNH, New York, U.S.A.), D. Brinkman and Vanessa R. Rhue (YPM, New Haven, U.S.A.), and B. Kear (PMU, Uppsala, Sweden). We also would like to thank D. Geraads for sharing the 3D model of *Yoshi garevskii*. JVP editor D. Ehret, as well as two reviewers, provided detailed suggestions that improved the flow and framing of the paper. We are particularly grateful to our phylogenetics editor, P. Godoy, for his precious time helping us build a stronger manuscript. This work was supported by a grant from the National Science Foundation (NSF DBI-2128146) to ZJT, as well as grants from the Fonds de la Recherche Scientifique F.R.S.–FNRS (FRIA grant number FRIA FC 36251), the Belgian American Educational Foundation (BAEF) and a European Union's Marie Skłodowska-Curie Actions (MSCA) Postdoctoral Fellowships 2024 (HORIZON-MSCA-2024-PF-01) grant agreement no. 101207039 to NC.

AUTHOR CONTRIBUTIONS

CRediT: NC: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Validation, Visualization, Writing – original draft, Writing – review & editing; ZJT: Formal analysis, Funding acquisition, Investigation, Methodology, Supervision, Writing – original draft, Writing – review & editing. NC and ZJT designed the study. NC examined the original material, scanned the specimen, and gathered the systematics and morphometric data. All authors drafted and edited the manuscript.

DATA AVAILABILITY STATEMENT

Surface scans of the newly referred specimens are available on MorphoSource: MorphoSource (project ID 000770658): https://www.morphosource.org/projects/000770658. Landmarks and script used to create the morphospace from Fig. 9 are provided as supplementary material.

Other 3D models used in this study were either already available on MorphoSource (Project 000548886, https://www.morphosource.org/projects/000548886) or were kindly shared by colleagues (e.g., *Yoshi garevskii*). The modified matrix, along with a zip file containing all the TNT scripts, outputs resulting from the analyses as well as the consensus tree are available on MorphoBank: https://www.morphobank.org/permalink/?P6080

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

ORCID

Narimane Chatar http://orcid.org/0000-0003-0449-8574
Z. Jack Tseng http://orcid.org/0000-0001-5335-4230

SUPPLEMENTARY FILES

Supplemental File 1: R script used to create the morphospace and timescaled tree.

Supplemental File 2.pts: landmarks placed on the AMNH 62192 cranium, others were obtained from Chatar et al. (2024).

Supplemental File 3.docx: Table S1–S2 and character list modified from Barrett & Hopkins (2024).

Supplemental File 4.zip: compressed folder containing various file resulting from the phylogenetic analyses, as well as the matrix.

LITERATURE CITED

Adams, D. C., & Otárola-Castillo, E. (2013). geomorph: an R package for the collection and analysis of geometric morphometric shape data. *Methods in Ecology and Evolution*, *4*(4), 393–399. https://doi.org/10.1111/2041-210X.12035

Andersson, K., & Werdelin, L. (2005). Carnivora from the late miocene of Lantian, China. *Vertebrata PalAsiatica*, *43*(4), 256–271.

Anton, M., Salesa, M. J., Morales, J., & Turner, A. (2004). First known complete skulls of the scimitar-toothed cat *Machairodus aphanistus*

(Felidae, Carnivora) from the Spanish late Miocene site of Batallones-1. *Journal of Vertebrate Paleontology*, *24*(4), 957–969. doi:10.1671/0272-4634(2004)024[0957:FKCSOT]2.0.CO;2

Antón, M., Salesa, M. J., & Siliceo, G. (2013). Machairodont adaptations and affinities of the Holarctic late Miocene homotherin *Machairodus* (Mammalia, Carnivora, Felidae): the case of *Machairodus catocopis* Cope, 1887. *Journal of Vertebrate Paleontology*, *33*(5), 1202–1213. https://doi.org/10.1080/02724634.2013.760468

Artec 3D. (2021). *Geomagic Wrap* [Logiciel].

Bapst, D. W. (2012). paleotree: an R package for paleontological and phylogenetic analyses of evolution. *Methods in Ecology and Evolution*, *3*(5), 803–807. https://doi.org/10.1111/j.2041-210X.2012.00223.x

Barrett, P. Z. (2016). Taxonomic and systematic revisions to the North American Nimravidae (Mammalia, Carnivora). *PeerJ*, e1658. https://doi.org/10.7717/peerj.1658

Barrett, P. Z. (2021). The largest hoplophonine and a complex new hypothesis of nimravid evolution. *Scientific Reports*, *11*(1), 1–9. https://doi.org/10.1038/s41598-021-00521-1

Barrett, P. Z., & Hopkins, S. S. B. (2024). Mosaic evolution underlies feliform morphological disparity. *Proceedings of the Royal Society B: Biological Sciences*, *291*(2028), 20240756. https://doi.org/10.1098/rspb.2024.0756

Barrett, P. Z., Hopkins, S. S. B., & Price, S. A. (2021). How many sabertooths? Reevaluating the number of carnivoran sabretooth lineages with total-evidence Bayesian techniques and a novel origin of the Miocene Nimravidae. *Journal of Vertebrate Paleontology*, *41*(1), 1–15. https://doi.org/10.1080/02724634.2021.1923523

Beaumont, G. d. (1978). Notes complementaires sur quelques féidés (Carnivores). *Archives des Sciences, Genève*, *31*, 219–227.

Bell, M. A., & Lloyd, G. T. (2015). strap: an R package for plotting phylogenies against stratigraphy and assessing their stratigraphic congruence. *Palaeontology*, *58*(2), 379–389. https://doi.org/10.1111/PALA.12142

Bickart, K. J. (1990). Part I: The Birds of the Late Miocene-Early Pliocene Big Sandy Formation, Mohave County, Arizona. *Ornithological Monographs*, (44), 1–72. https://doi.org/10.2307/40166673

Billet, G., & Bardin, J. (2019). Serial homology and correlated characters in morphological phylogenetics: Modeling the evolution of dental crests in placentals. *Systematic Biology*, *68*(2), 267–280. https://doi.org/10.1093/SYSBIO/SYY071

Bowdich, T. E. (1821). *An analysis of the natural classifications of Mammalia, for the use of students and travellers.* J. Smith.

Brocklehurst, N., & Benevento, G. L. (2020). Dental characters used in phylogenetic analyses of mammals show higher rates of evolution, but not reduced independence. *PeerJ*, *8*, e8744. https://doi.org/10.7717/peerj.8744

Capobianco, A. (2025). How many characters are needed to reconstruct a phylogeny? *Biology Letters*, *21*(10), 20250288. https://doi.org/10.1098/rsbl.2025.0288

Carranza-Castañeda, O., & Miller, W. E. (1996). Hemphillian and Blancan Felids from central Mexico. *Journal of Paleontology*, *70*(3), 509–518. https://doi.org/10.1017/S0022336000038439

Chatar, N., Fischer, V., Siliceo, G., Antón, M., Morales, J., & Salesa, M. J. (2021). Morphometric analysis of the mandible of primitive sabertoothed felids from the late Miocene of Spain. *Journal of Mammalian Evolution*, *28*(3), 753–771. https://doi.org/10.1007/s10914-021-09541-0

Chatar, N., Fischer, V., & Tseng, Z. J. (2022a). Many-to-one function of cat-like mandibles highlights a continuum of sabre-tooth adaptations. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1988), https://doi.org/10.1098/rspb.2022.1627

Chatar, N., Michaud, M., & Fischer, V. (2022b). Not a jaguar after all? Phylogenetic affinities and morphology of the Pleistocene felid *Panthera gombaszoegensis*. *Papers in Palaeontology*, *8*(5), e1464. https://doi.org/10.1002/spp2.1464

Chatar, N., Michaud, M., Tamagnini, D., & Fischer, V. (2024). Evolutionary patterns of cat-like carnivorans unveil drivers of the sabertooth morphology. *Current biology*, *34*(11), 2460–2473.e4. https://doi.org/10.1016/j.cub.2024.04.055

Christiansen, P. (2008). *Phylogeny of the great cats (Felidae : Pantherinae), and the influence of fossil taxa and missing characters*, *24*, 977–992.

Christiansen, P. (2012). Phylogeny of the sabertoothed felids (Carnivora : Felidae : Machairodontinae). *Cladistics*, 1–17.

Cigoni, P., Callieri, M., & Corsini, M. (2008). Meshlab : An open-source mesh processing tool. *ERCIM NEWS*, *73*, 47–48.

Crusafont, M., & Aguirre, E. (1972). *Stenailurus*, Félidé nouveau du Turolien d'Éspagne. *Annales de Paléontologie*, *58*(2), 211–223.

Dalquest, W. W. (1996). Pliocene Carnivores of The Coffee Ranch (Type Hemphill) Local Fauna. *The Bulletin of the Texas Memorial Museum*, *15*, 1–44.

Deng, T., Wang, X., Wang, S., Li, Q., & Hou, S. (2015). Evolution of the Chinese Neogene mammalian faunas and its relationship to uplift of the Tibetan Plateau. *Advances in Earth Science*, *30*(4), https://doi.org/10.1167/j.issn.1001-8166.2015.04.0407

Ezcurra, M. D. (2024). Exploring the effects of weighting against homoplasy in genealogies of palaeontological phylogenetic matrices. *Cladistics*, *40*(3), 242–281. https://doi.org/10.1111/cla.12581

Figueirido, B., Lautenschlager, S., Pérez-Ramos, A., & Van Valkenburgh, B. (2018). Distinct predatory behaviors in Scimitar- and Dirk-Toothed sabertooth cats. *Current Biology*, *28*(20), 3260-3266.e3.e3. https://doi.org/10.1016/j.cub.2018.08.012

Fischer, G. (1821). Adversaria zoologica. *Mémoires de la Société impériale des naturalistes de Moscou*, *5*, 357–428.

Gervais, P. (1850). *Zoologie et paléontologie françaises (animaux vertébrés) ou nouvelles recherches sur les animaux vivants et fossiles de la France.* Arthus Bertrand, Librairie-Editeur.

Gill, T. (1872). Arrangement of the families of mammals with analytical tables. *Smithsonian miscellaneous collections*, *11*(1): 2–98.

Goloboff, P. A., & Catalano, S. A. (2016). TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics*, *32*(3), 221–238. https://doi.org/10.1111/cla.12160

Goloboff, P. A., Farris, J. S., Källersjö, M., Oxelman, B., Ramıacute;rez, M. J., & Szumik, C. A. (2003). Improvements to resampling measures of group support. *Cladistics*, *19*(4), 324–332. https://doi.org/10.1111/J.1096-0031.2003.TB00376.X

Harjunmaa, E., Seidel, K., Häkkinen, T., Renvoisé, E., Corfe, I. J., Kallonen, A., Zhang, Z.-Q., Evans, A. R., Mikkola, M. L., Salazar-Ciudad, I., Klein, O. D., & Jernvall, J. (2014). Replaying evolutionary transitions from the dental fossil record. *Nature*, *512*(7512), 44–48. https://doi.org/10.1038/nature13613

Harrison, J. A. (1983). Carnivora of the Edson Local Fauna (Late Hemphillian), Kansas. *Smithsonian Contributions to Paleobiology*, (54), 1–42. https://doi.org/10.5479/si.00810266.54.1

Hensel, R. F. (1862). Über die Reste einiger Säugetierarten von Pikermi in der Münchener Sammlung. *Monatsberichte Akad Wiss*, *27*, 560–569.

Hibbard, C. W. (1934). Two new genera of Felidae from the Middle Pliocene of Kansas. *Transactions of the Kansas Academy of Science (1903-)*, *37*, 239–255. doi:10.2307/3625308

Hodnett, J.-P. (2010). A Machairodont felid (Mammalia; Carnivora; Felidae) from the latest Hemphillian (Late Miocene/Early Pliocene) Bidahochi Formation, northeastern Arizona. *PaleoBios*, *29*(3), https://doi.org/10.5070/P9293021800

Jiangzuo, Q., Sun, D., & Flynn, J. J. (2021a). Paleobiogeographic implications of additional Felidae (Carnivora, Mammalia) specimens from the Siwaliks. *Historical Biology*, *33*(9), 1767–1780. https://doi.org/10.1080/08912963.2020.1737683

Jiangzuo, Q., Sun, D., & Flynn, J. J. (2021b). Paleobiogeographic implications of additional Felidae (Carnivora, Mammalia) specimens from the Siwaliks. *Historical Biology*, *33*(9), 1767–1780. https://doi.org/10.1080/08912963.2020.1737683

Jiangzuo, Q., Niu, K., Li, S., Fu, J., & Wang, S. (2022). A diverse metailurine guild from the Latest Miocene Xingjiawan Fauna, Yongdeng, Northwestern China, and generic differentiation of metailurine Felids. *Journal of Mammalian Evolution*, *29*(4), 845–862. https://doi.org/10.1007/s10914-022-09622-8

Jiangzuo, Q., Werdelin, L., & Sun, Y. (2022). A dwarf sabertooth cat (Felidae: Machairodontinae) from Shanxi, China, and the phylogeny of the sabertooth tribe Machairodontini. *Quaternary Science Reviews*, *284*, 107517. https://doi.org/10.1016/j.quascirev.2022.107517

Kavanagh, K. D., Evans, A. R., & Jernvall, J. (2007). Predicting evolutionary patterns of mammalian teeth from development. *Nature*, *449*(7161), 427–432. https://doi.org/10.1038/nature06153

Koufos, G. D. (2022). The fossil record of felids (Mammalia: Carnivora: Felidae) in Greece. In E. Vlachos (Éd.), *Fossil Vertebrates of Greece Vol. 2* (p. 519–539). Springer International Publishing. https://doi.org/10.1007/978-3-030-68442-6_16

Lautenschlager, S., Figueirido, B., Cashmore, D. D., Bendel, E. M., & Stubbs, T. L. (2020). Morphological convergence obscures functional diversity in sabre-toothed carnivores. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1935), https://doi.org/10.1098/rspb.2020.1818

Li, Y., & Spassov, N. (2017). A new species of *Paramachaerodus* (Mammalia, Carnivora, Felidae) from the late Miocene of China and Bulgaria, and revision of *Promegantereon* Kretzoi, 1938 and *Paramachaerodus* Pilgrim, 1913. *PalZ*, *91*(3), 409–426. https://doi.org/10.1007/s12542-017-0371-7

Lindsay, E. H. (1984). Windows to the past : Fossils of the San Pedro Valley. *rizona Bureau of Geology and Mineral Technology Fieldnotes*, *14*(12), 1–9.

Macfadden, B. J., Johnson, N. M., & Opdyke, N. D. (1979). Magnetic polarity stratigraphy of the Mio-Pliocene mammal-bearing Big Sandy Formation of western Arizona. *Earth and Planetary Science Letters*, *44*(3), 349–364. https://doi.org/10.1016/0012-821X(79)90074-8

MacFadden, B. J., & Skinner, M. F. (1979). Diversification and biogeography of the one-toed horses *Onohippidium* and *Hippidion*. *Postilla*, *175*, 1–10.

Maddison, W. P., & Maddison, D. R. (2019). Mesquite: A modular system for evolutionary analysis, ver. 2.72. In Ci.nii.ac.jp [Logiciel]. http://www.mesquiteproject.org.

Madurell-Malapeira, J., Rodríguez-Hidalgo, A., Aouraghe, H., Haddoumi, H., Lucenti, S. B., Oujaa, A., Saladié, P., Bengamra, S., Marín, J., Souhir, M., Farkouch, M., Mhamdi, H., Aissa, A. M., Werdelin, L., Chacón, M. G., & Sala-Ramos, R. (2021). First small-sized *Dinofelis*: Evidence from the Plio-Pleistocene of North Africa. *Quaternary Science Reviews*, *265*(107028). https://doi.org/10.1016/J.QUASCIREV.2021.107028

Morales, J., Mayda, S., Valenciano, A., DeMiguel, D., & Kaya, T. (2019). A new lophocyonid, *Izmirictis cani* gen. et sp. nov. (Carnivora: Mammalia), from the lower Miocene of Turkey. *Journal of Systematic Palaeontology*, *17*(16), 1347–1358. https://doi.org/10.1080/14772019.2018.1529000

Peigné, S. (2003). Systematic review of European Nimravinae (Mammalia, Carnivora, Nimravidae) and the phylogenetic relationships of Palaeogene Nimravidae. *Zoologica Scripta*, *32*(3), 199–229. doi:10.1046/j.1463-6409.2003.00116.x

Pollock, T. I., Deaking, W. J., Chatar, N., Milla Carmona, P., Rovinsky, D. S., Panagiotopoulou, O., Parker, W. M. G., Adams, J. W., Hocking, D. P., Donoghue, P. C. J., Rayfield, E. J., & Evans, A. R. (2025). Functional optimality underpins the repeated evolution of the extreme "saber-tooth" morphology. *Current Biology*, *35*(3), 455–467.e6. https://doi.org/10.1016/j.cub.2024.11.059

Polly, P. D. (2020). Ecometrics and Neogene faunal turnover: The roles of cats and hindlimb morphology in the assembly of carnivoran communities in the New World. *Geodiversitas*, *42*(17), 257. https://doi.org/10.5252/geodiversitas2020v42a17

Qiu, Z. (2003). Chapter 2. *Bulletin of the American Museum of Natural History*, *279*, 18–31. https://doi.org/10.1206/0003-0090(2003)279%253C0018:C%253E2.0.CO;2

Qiu, Z.-X., & Tedford, R. H. (2013). History of Scientific Exploration of Yushe Basin. In R. H. Tedford, Z.-X. Qiu, & L. J. Flynn (Éds.), *Late Cenozoic Yushe Basin, Shanxi Province, China : Geology and Fossil Mammals* (p. 7–34). Springer Netherlands. https://doi.org/10.1007/978-90-481-8714-0_2

R Core Team. (2021). *R: A language and environment for statistical computing*. [Logiciel]. R Foundation for Statistical Computing.

Rasband, W. S. (2012). ImageJ: Image processing and analysis in Java. *Astrophysics Source Code Library*, ascl:1206.013.

Repenning, C. A. (1967). Palearctic-Nearctic mammalian dispersals in the late Cenozoic. In *The Bering land bridge* (pp. 288–311). Stanford University Press.

Robles, J. M., Alba, D. M., Fortuny, J., Esteban-Trivigno, S. D., Rotgers, C., Balaguer, J., Carmona, R., Galindo, J., Almécija, S., Bertó, J. V., Moyà-Solà, S., De Esteban-Trivigno, S., Rotgers, C., Balaguer, J., Carmona, R., Galindo, J., Almécija, S., Bertó, J. V., Moyà-Solà, S., & Soì, S. M. (2013). New craniodental remains of the barbourofelid *Albanosmilus jourdani* (Filhol, 1883) from the Miocene of the Vallès-Penedès Basin (NE Iberian Peninsula) and the phylogeny of the Barbourofelini. *Journal of Systematic Palaeontology*, *11*(8), 993–1022. https://doi.org/10.1080/14772019.2012.724090

Rothwell, T. (2001). A Partial Skeleton of *Pseudaelurus* (Carnivora: Felidae) from the Nambé Member of the Tesuque Formation, Española Basin, New Mexico. *American Museum Novitates*, *3342*(3342), 1–31. doi:10.1206/0003-0082(2001)342<0001:APSOPC>2.0.CO;2

Rothwell, T. (2003). Phylogenetic systematics of North American *Pseudaelurus* (Carnivora: Felidae). *American Museum Novitates*, *3403*(3403), 1–64. doi:10.1206/0003-0082(2003)403<0001:PSONAP>2.0.CO;2

Roussiakis, S. J. (2001). Metailurus major Zdansky, 1924 (Carnivora, Mammalia) from the classical locality of Pikermi (Attica, Greece). *Annales de Paléontologie*, *87*(2), 119–132. https://doi.org/10.1016/S0753-3969(01)80006-9

Sakamoto, M., & Ruta, M. (2012). Convergence and Divergence in the Evolution of Cat Skulls: Temporal and Spatial Patterns of Morphological Diversity. *PLoS ONE*, *7*(7), e39752. https://doi.org/10.1371/journal.pone.0039752

Salesa, M. J., Antón, M., Turner, A., Alcalá, L., Montoya, P., & Morales, J. (2010). Systematic revision of the Late Miocene sabre-toothed felid Paramachaerodus in Spain. *Palaeontology*, *53*(6), 1369–1391. https://doi.org/10.1111/j.1475-4983.2010.01013.x

Salesa, M. J., Antón, M., Turner, A., & Morales, J. (2005). Aspects of the functional morphology in the cranial and cervical skeleton of the sabre-toothed cat *Paramachairodus ogygia* (Kaup, 1832) (Felidae, Machairodontinae) from the Late Miocene of Spain: Implications for the origins of the machairodont killing bite. *Zoological Journal of the Linnean Society*, *144*(3), 363–377. https://doi.org/10.1111/j.1096-3642.2005.00174.x

Salesa, M. J., Pesquero, M. D., Siliceo, G., Antón, M., Alcalá, L., & Morales, J. (2012). A rich community of Felidae (Mammalia, Carnivora) from the late Miocene (Turolian, MN 13) site of Las Casiones (Villalba Baja, Teruel, Spain). *Journal of Vertebrate Paleontology*, *32*(3), 658–676. https://doi.org/10.1080/02724634.2012.649816

Salles, L. O. (1992). Felid phylogenetics: extant taxa and skull morphology (Felidae, Aeluroidea). *American Museum Novltates*, *3047*, 1–67.

Scotland, R. W., Olmstead, R. G., & Bennett, J. R. (2003). Phylogeny Reconstruction: The Role of Morphology. *Systematic Biology*, *52*(4), 539–548. https://doi.org/10.1080/10635150309309

Shelbourne, C. D., & Lautenschlager, S. (2025). Morphological diversity of saber-tooth upper canines and its functional implications. *The Anatomical Record*, *38*(11), 3007–3021. ar.25458. https://doi.org/10.1002/ar.25458

Spassov, N., & Geraads, D. (2015). A new felid from the Late Miocene of the Balkans and the contents of the genus *Metailurus* Zdansky, 1924 (Carnivora, Felidae). *Journal of Mammalian Evolution*, *22*(1), 45–56. https://doi.org/10.1007/s10914-014-9266-5

Spassov, N., Geraads, D., Hristova, L., Markov, G. N., Garevska, B., & Garevski, R. (2018). The late Miocene mammal faunas of the Republic of Macedonia (FYROM). *Palaeontographica Abteilung A*, *311*(1-6), 1–85. https://doi.org/10.1127/pala/2018/0073

Spaulding, M., & Flynn, J. J. (2012). Phylogeny of the Carnivoramorpha: The impact of postcranial characters. *Journal of Systematic Palaeontology*, *10*(4), 653–677. https://doi.org/10.1080/14772019.2011.630681

Stratovan Corporation. (2023). *Stratovan Checkpoint* [Logiciel]. https://www.stratovan.com/products/checkpoint

Tseng, Z. J., & Wang, X. (2007). The first record of the late Miocene *Hyaenictitherium hyaenoides* Zdansky (Carnivora: Hyaenidae) in Inner Mongolia and an evaluation of the genus. *Journal of Vertebrate Paleontology*, *27*(3), 699–708. doi:10.1671/0272-4634(2007)27[699:TFROTL]2.0.CO;2

Turner, A., & Antón, M. (1997). *The big cats and their fossil relatives: An illustrated guide to their evolution and natural history*. Columbia University Press.

Van Valkenburgh, B. (1989). Carnivore Dental Adaptations and Diet: A Study of Trophic Diversity within Guilds. In J. L. Gittleman (Éd.), *Carnivore Behavior, Ecology, and Evolution* (p. 410–436). Springer.

Van Valkenburgh, B. (1999). Major patterns in the history of carnivorous mammals. *Annual Review of Earth and Planetary Sciences*, *27*(1), 463–493. https://doi.org/10.1146/annurev.earth.27.1.463

Van Valkenburgh, B., Grady, F., & Kurtén, B. (1990). The Plio-Pleistocene cheetah-like cat *Miracinonyx inexpectatus* of North America. *Journal of Vertebrate Paleontology*, *10*(4), 434–454. https://doi.org/10.1080/02724634.1990.10011827

Wei, D., & Hu, C. (1994). The Late Miocene cervidae from Hounao, Yushe Basin, Shanxi. *Vertebrata PalAsiatica*. *32*(3), 209–227.

Werdelin, L., & Lewis, M. E. (2001). A revision of the genus *Dinofelis* (Mammalia, Felidae). *Zoological Journal of the Linnean Society*, *132*(2), 147–258. doi:10.1111/j.1096-3642.2001.tb02465.x

Werdelin, L., & Solounias, N. (1991). *The Hyaenidae: Taxonomy, systematics and evolution* (Vol. 30). Universitetsforlaget. https://doi.org/10.18261/8200374815-1991

Werdelin, L., Yamaguchi, N., Johnson, E., & Brien, S. J. O. (2010). Phylogeny and evolution of cats (Felidae). In D. Macdonald & A. Loveridge (Éds.), *Biology and Conservation of Wild Felids* (Vol. 12, Numéro October, p. 59–82). Oxford University Press.

Wesley-Hunt, G. D., & Flynn, J. J. (2005). Phylogeny of the Carnivora: Basal relationships among the carnivoramorphans, and assessment of the position of 'Miacoidea' relative to Carnivora. *Journal of Systematic Palaeontology*, *3*(1), 1–28. https://doi.org/10.1017/S1477201904001518

Yu, L. (2014). Restudy of *Metailurus major* from Yushe Basin, Shanxi Province reported by Teilhard de Chardin and Leroy. *Vertebrata PalAsiatica*, *52*(4), 467–485.

Zdansky, O. (1924). Jungtertiäre Carnivoren Chinas. *Palaeontologia Sinica*, *2*(1), 1–149.

Handling Editor: Matthew Borths.
Phylogenetics Editor: Pedro Godoy.