

An Early Nimravid from California and the Rise of Hypercarnivorous Mammals after the Middle Eocene Climatic Optimum

ASHLEY W. POUST^{1,2}, PAUL Z. BARRETT³, and SUSUMU TOMIYA^{2,4,5,6}

¹Department of Paleontology, San Diego Natural History Museum, San Diego, California, 92101, USA

²University of California Museum of Paleontology, Berkeley, California, 94720, USA

³Department of Earth Sciences, University of Oregon, Eugene, OR, 97403, USA

⁴Center for International Collaboration and Advanced Studies in Primatology, Kyoto University Primate Research Institute, Inuyama, Aichi, 484-8506, Japan

⁵Center for the Evolutionary Origins of Human Behavior, Kyoto University, Inuyama, Aichi, 484-8506, Japan

⁶Negaunee Integrative Research Center, Field Museum of Natural History, Chicago, Illinois, 60605, USA

OrcIDs: AWP 0000-0001-7955-613X; PZB 0000-0001-5717-9193; ST 0000-0001-6038-899X

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Carnivoraforms (crown carnivorans and their closest relatives) first occupied hypercarnivorous niches near the dawn of the late Eocene, 40–37 million years ago. This followed the decline or extinction of earlier carnivorous groups, Mesonychia and Oxyaenodonta, leaving carnivoraforms and hyaenodontan meat-eaters as high trophic level consumers. The pattern of this change and the relative contributions of the taxonomic groups has hitherto been unclear. We report a new genus and species of the sabretoothed mammalian carnivore family Nimravidae, *Pangurban egiae*, from the Eocene Pomerado Conglomerate of southern California, with strongly derived hypercarnivorous features. While geochronologically the oldest named nimravid in North America, *Pangurban egiae* is recovered as phylogenetically derived, with affinities to *Hoplophoneus*. This provides unequivocal evidence for rapid radiation and spread of nimravid carnivores across Asia and North America and constrains the timing of early divergences within the family. *Pangurban egiae* narrows the gap between convergent iterations of sabretoothed mammalian carnivores and demonstrates swift diversification of the hypercarnivorous nimravids during a period of global climatic instability. Furthermore, it highlights the top-to-bottom restructuring North American ecosystems underwent during the Eocene–Oligocene transition, resulting in carnivoraforms taking positions as trophic specialists for the first time, a niche they still occupy today.

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1. Introduction

The climatically dynamic period from the late middle Eocene to the early Oligocene (ca. 41–30 Ma) saw not only the reorganisation of biotas worldwide that is known as the Eocene–Oligocene biotic transition [1] but also the initial rise of members of crown Carnivora and their closest relatives as hypercarnivores [2,3]. The early nimravids joined the Hyaenodonta in this specialised niche, which carnivorans would later occupy alone until the present day. Due to the eventual extinction of these groups and the resulting lack of genetic data, fossils provide the only window into an important period of faunal change presaging the organisation of modern trophic structure.

However, the lack of early data from this critical period has presented a challenge to interpreting this transition. In particular, a general paucity of mammalian fossils from the Duchesnean North American Land Mammal ‘Age’ (NALMA; 41–37 Ma) has long obscured an early phase of the Eocene–Oligocene faunal transition in North America, particularly with respect to mammalian carnivores [4]. Recent taxonomic and biostratigraphic studies, however, have unveiled the late-middle-Eocene diversity of carnivores in southwestern North America sufficiently to permit its reassessment [5–9]. The turnover of mammalian carnivores during this period is noteworthy for the replacement of early meat-eating lineages by crown-clade carnivorans and their close carnivoraform relatives—an episode that broadly coincided with the global climatic fluctuations surrounding the Middle Eocene Climatic Optimum (MECO; [9]).

We report a new genus and species of nimravid, *Pangurban egiae*, on the basis of a partial maxilla with the upper 3rd and 4th premolars (P3–4) (Figure 1) from the likely upper middle Eocene portion of the Pomerado Conglomerate of San Diego County, California. *Pangurban* is one of the earliest diagnosable nimravids in the world, and preserves the earliest nimravid cheek teeth from North America, allowing its inclusion in phylogenetic analysis. Bearing similarities to the derived later nimravid *Hoplophoneus*, its early occurrence and hypercarnivorous adaptations demonstrate the rapid diversification of the group.

2. Methods

The new fossil is housed at the San Diego Natural History Museum (San Diego Society of Natural History collections, SDSNH). We scored the holotype specimen (SDSNH 60554) into the Bayesian tip-dating analysis of Barrett (2021) [10], with a uniform tip-date of 40.0–37.0 Ma based on the likely middle- to late-Duchesnean age of the specimen. The age of the holotype (and the only known specimen) of *Maofelis cantonensis* was updated to the late Eocene, following [11]. The Bayesian analysis utilized a fossilized birth-death process [12–14] with complex models of morphological evolution (e.g. ordered, multipath, Dollo) best supported for the nimravid character matrix of [10]. Additional details can be found in the electronic supplementary material. Markov Chain Monte Carlo runs were sampled every 1,000 generations in Beast 2 v. 2.6.3 ([15]), while trees were logged every 10,000 generations until Effective Sample Sizes were > 200, as determined in Tracer version 1.7.1 [16]. From the output of Tracer, sampling and timing (generation number) of the stability of the run was assessed. Thus, the first 10% of the generations were discarded (burn-in), and topology and posterior probabilities were

estimated from the remaining generations. The maximum clade credibility (MCC) tree of this analysis is presented in Figure 2a (barbourofelins and most outgroups not shown; see Fig. S2 for complete tree) and the electronic supplementary material, along with the XML run file. We reconstructed synapomorphies in TNT version 1.5, which only reports synapomorphies supported by both accelerated and delayed transformations. Body mass of the new taxon was estimated through linear regression analysis of P4 lengths and corresponding nimravid body masses (based originally on lower first molar [m1] lengths) in [10]. We estimated ancestral body masses along the branches of the MCC tree using the ‘fastANC’ function found in the ‘phytools’ [17] package for the R programming environment, v. 4.1.2 (R Development Core Team, 2021).

3. Results

3.1. Systematic Palaeontology

Class MAMMALIA sensu Rowe [18]

unranked clade CARNIVORAMORPHA sensu Bryant [19] (amended from Wyss and Flynn [20])

unranked clade CARNIVORAFORMES Flynn, Finarelli, and Spaulding [21]

Family NIMRAVIDAE sensu Bryant [22]

Pangurban egiae gen. et sp. nov.

Fig. 1

ZooBank LSID: XXXXXXXXXXXX (to be added upon acceptance)

Holotype. SDSNH 60554, right maxillary fragment with P3–P4; collected in 1997 by Stephen L. Walsh and Robert Gutzler, who also prepared the specimen, and housed at the San Diego Natural History Museum (San Diego, U.S.A.).

Type locality and horizon. SDSNH Locality 4042 (“Spring Canyon Site 2”). Upper member of Pomerado Conglomerate, San Diego, California, U.S.A., here considered middle to late Duchesnean in age (ca. 40–37 Ma; see SI Text).

Diagnosis. Anterior cutting edge of P4 expressed as sharp and distinct preparacristal blade, not reaching apex of paracone; anterior face of P4 flattened and nearly vertical giving the paracone a steep angle. Differs from: *Maofelis* and MA-PHQ 348 (undet. nimravid specimen housed at Museum d'Histoire Naturelle Victor Brun, Montauban, France [23]) in infraorbital foramen posterior to P3, double rooted P3, P3 width to length ratio 0.4–0.65; *Maofelis*, MA-PHQ 348, and “nimravines” of [10] which includes barbourofelins, in reduced or absent P4 protocone, P4 metastylar blade length to paracone length ratio of 1.0–1.3, P3 crown height 48–70% that of P4; hoplophoneins (*Hoplophoneus*, *Eusmilus*, and *Nanosmilus*) in absence of parastyle on P4.

Etymology. The generic name is from the Old Irish, in reference to the cat in the 9th century CE poem of the same name, whose hunting is likened to academic pursuit of truth. The species name honours the contribution of palaeontologist Naoko Egi to the study of terrestrial carnivore evolution on both sides of the northern Pacific Ocean, mirroring the nimravid distribution.

Remarks. SDSNH 60554 was previously identified as “cf. *Hyaenodon* sp.” in the collection, and was apparently the basis for the previously reported occurrence of that hyaenodontid genus in the upper Pomerado Conglomerate [24]. We re-identify this specimen as a nimravid based on the

combination of: low height of P3; presence of serration on P3; elongate posterior basal cusp of P3; absence of cuspidate protocone on P4; absence of parastyle from the anterolabial base of P4 (cf. [25,26]); presence of prominent P4 preparacrista; and absence of deep incision associated with carnassial notch on P4 (cf. [25]).

3.2. Morphology and Phylogeny

The double-rooted P3 measures 11.2 mm in length and 4.6 mm in width. It is labiolingually compressed, and its concave lingual wall descends steeply to its base without forming an appreciable lingual bulge (Fig. 1; SI Fig. 2). The anterior slope of the paracone forms a shallow angle with the palate near its base, but steepens toward the tip of the cusp. The anterior ridge is finely serrated (~3 slightly dorsally-inclined incisions per mm on preserved portion) except for ~1 mm at the base of the crown. No anterior cuspule is present. The presence of a prominent and likely trenchant posterior basal cusp, separated from the main cusp by a notch, is indicated by a groove on the labial wall and the outlines of the breakages.

The largely intact P4 measures 16.8 mm in length and 12.6 mm in width, which yielded an estimated body mass of 28 kg. Its anterolingual projection lacks a distinct protocone. The parastyle, cingular or otherwise in origin (cf. [27]), is absent. The preparacrista is notably trenchant. The carnassial notch lacks a deep incision. The metastylar blade is posterolabially deflected. There is no appreciable development of a cingulum. A very light facet of attritional wear is visible in inclined light on the lingual side of the P4. It surrounds the carnassial notch and rises onto the postparacrista, generally resembling wear found in *Dinictis* in both extent and severity.

The posteroventral curvature of the infraorbital foramen is preserved above the anterior edge of the P4. This differs from most “nimravines” of [10] and *Eusmilus*, in which it is located more anteriorly. A deep embrasure pit for the occlusion of the m1 protoconid is partially preserved lingual to the metastylar blade of P4.

In the MCC tree (Fig. 2a), we recovered *Pangurban egiae* as the sister taxon to the node-based tribe Hoplophoneini sensu Barrett [28], with which it was united by three synapomorphies: reduced or absent P4 protocone; P4 metastylar blade 1.0–1.3 times the length of paracone; and P3 crown height 48–70% of that of P4. All of these features would appear again in Miocene barbourofelins, and are thus not unambiguous synapomorphies, but they do indicate comparably derived hypercarnivory within this clade in the late middle Eocene.

The remaining topology of the MCC tree differed minimally from [10]. The hoplophoneins were recovered in largely the same arrangement, with successive divergences of *Hoplophoneus* (here recovered as a paraphyletic taxon), *Nanosmilus*, and *Eusmilus*.

4. Discussion

Published occurrences of sabretooth material have generally suggested a middle Eocene origin of nimravids within East Asia [11,29]. Subsequent dispersal(s) to North America later in the Eocene generated a cradle of diversification in disparate ecologies, from which additional immigrations into Asia and Europe seem to have occurred [10,11]. The holotype of *Pangurban*

egiae, SDSNH 60554, is significant as one of the oldest securely-identified nimravid fossils globally (Fig. 2b; see SI Text for further discussion). Although a few likely-older (ca. 40 Ma) specimens are known from the Pondaung Formation of Myanmar [30,31] and the Clarno Formation of Oregon, USA [32,33], it is the oldest nimravid fossil that preserves enough of the upper dentition to be meaningfully incorporated into a phylogenetic analysis. While not falsifying the hypothesis of East Asian origin for nimravids, the presence of a derived member in North America at such an early time demonstrates not only swift circum-Pacific dispersal for the group (in whatever direction), but also rapid evolution of the earliest nimravids. As such, it provides key information on the early evolution and distribution of the family.

On the MCC tree, *Pangurban egiae* displays a zero-length branch, indicating that it is a sampled ancestor. This status relates to *P. egiae* preserving derived character states that support its affinity with Hoplophoneini, while not preserving distinct apomorphies in this matrix. However, ~42% of sampled posterior trees have a tip-length greater than zero for *P. egiae*, indicating that its status as a true sampled ancestor should be treated with some hesitancy—a status that will require additional specimens to properly assess. In view of the unique combination of traits in SDSNH 60554, we prefer to assign it to a new genus.

The discovery of *Pangurban egiae* accentuates the Eocene–Oligocene taxic turnover across all trophic levels and highlights the late-middle-Eocene rise of hypercarnivorous mammals in southwestern North America. Taking pronounced reduction of the carnassial metaconid(s)—which is associated with a predominantly anteroposterior orientation of the prevallid—and its correlates as taxon-independent proxies for hypercarnivory [4,34,35], hypercarnivores are greatly outnumbered (both in species richness and abundance) by hypo- and mesocarnivores in the late Uintan of southern California and western Texas combined (age groups 1 & 2 in Fig. 2c; Table S1). The beginning of the Duchesnean NALMA is marked by the immigration from Asia of the hypercarnivorous/durophagous *Hyaenodon* ([36–38]; age group 3 in Fig. 2c); interestingly, the earliest Duchesnean deposits of southern California have yielded abundant fossils of *Hyaenodon*, whereas remains of carnivoraforms (none of whom are hypercarnivores) are rare [6,36,39]. Middle to late Duchesnean assemblages from southwestern North America contain more hypercarnivorous taxa (including *P. egiae*) than hypo- to mesocarnivorous taxa (age group 4 in Fig. 2c).

The shifting balance within the carnivore guild cannot be readily explained as a taphonomic artefact, and it seems likely to reflect ecological restructuring of the carnivore guild across the climatically unstable earlier Duchesnean. Notably, the same time period saw a marked decline in primate diversity in the region ([40]; Fig. 2c) and, in southern California, a ~40% loss of primarily woody angiosperm taxa [41]. Substantial disassembly and reassembly of a regional carnivore community concomitant with a major loss of primate diversity also characterises the late Bridgerian–early Uintan (ca. 48–44 Ma) faunal succession in the central Rocky Mountain region [42]. These events may reveal common faunal dynamics over evolutionary time in response to reduced forest canopies and spatial redistribution of biomass, within the context of the middle-to-late Eocene trend of declining precipitation in North America [43]. Perhaps the rise of carnivoraform hypercarnivores relates to the development of seasonally open canopies or mosaic forested landscapes. Following the loss of sabretooth machaeroidines prior to the Middle Eocene Climatic Optimum [44], a contingent opportunity may have occurred for circum-Pacific immigration of nimravids into North America. Concerted declines in relatively small, arboreal vertebrate prey such as primates (resulting in an upward shift in the body size distribution of vertebrate prey) and other food resources that are abundant in tropical/subtropical forests (e.g.,

fruits and insects) may have prompted evolution of, or invasion by, larger carnivoraforms with more specialised adaptations for carnivory, as dictated by feeding energetics (cf.[45,46]). In view of the relative stability of the morphological composition of terrestrial mammals [47] and carnivores in particular [48] across the Eocene–Oligocene boundary in North America, *Pangurban egiae* points to the late-middle to early-late Eocene as a dynamic period of key importance in the Eocene–Oligocene biotic transition and the origin of phylogenetically-modern terrestrial carnivore guilds.

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FIGURE CAPTIONS

Fig 1. Holotype SDSNH 60554 of *Pangurban egiae* gen. et sp. nov.

Right maxillary fragment with P3–P4 in lateral (a) and ventral (b) views. Approximate position on cranium marked on (c).

Fig. 2. Phylogenetic, geographic, and faunal context of *Pangurban egiae*.

(a) Tip-dated Bayesian MCC tree of nimravids. Node values indicate posterior probabilities of clades. Nimravid basal node marked by open circle (median age) and bar (95-percent credible interval). (b) Geographic distribution of Eocene nimravids (in part after [11,29]). Coloured (by land mammal ‘ages’ as in (a)) portions of icons indicate known dental elements. Taxonomically-questionable occurrences marked as “?”; nimravid material from Gongkang Formation apparently has never been described (cf. [49]). (c) Late-middle-Eocene carnivore (tooth icons) and primate (silhouettes) diversity in southern California and western Texas, divided into four age groups (data in Table S1; tooth icons modelled after *Lycophocyon hutchisoni* and *Diegoaelurus vanvalkenburghae*) and based primarily on [5,6,8,36,39,40,44,50–53]). Time scales for magnetochrons and NALMAs follow [33,54], and that for Asian Land Mammal ‘Ages’ (ALMAs) after [55]. NALMA/ALMA abbreviations: Ch, Chadronian; Du, Duchesnean; Er, Ergilian; Ir, Irдинmanhan; Sh, Sharamurunian; Ui, Uintan; Ul, Ulangochuian. Timings of middle Eocene global climatic anomalies and angiosperm diversity loss in southern California from [56] and [41].

1. Prothero DR, Berggren WA, editors. 1992 *Eocene-Oligocene climatic and biotic evolution*. Princeton University Press.
2. Van Valkenburgh B. 1999 Major patterns in the history of carnivorous mammals. *Annu. Rev. Earth Planet. Sci.* **27**, 463–493. (doi:10.1146/annurev.earth.27.1.463)

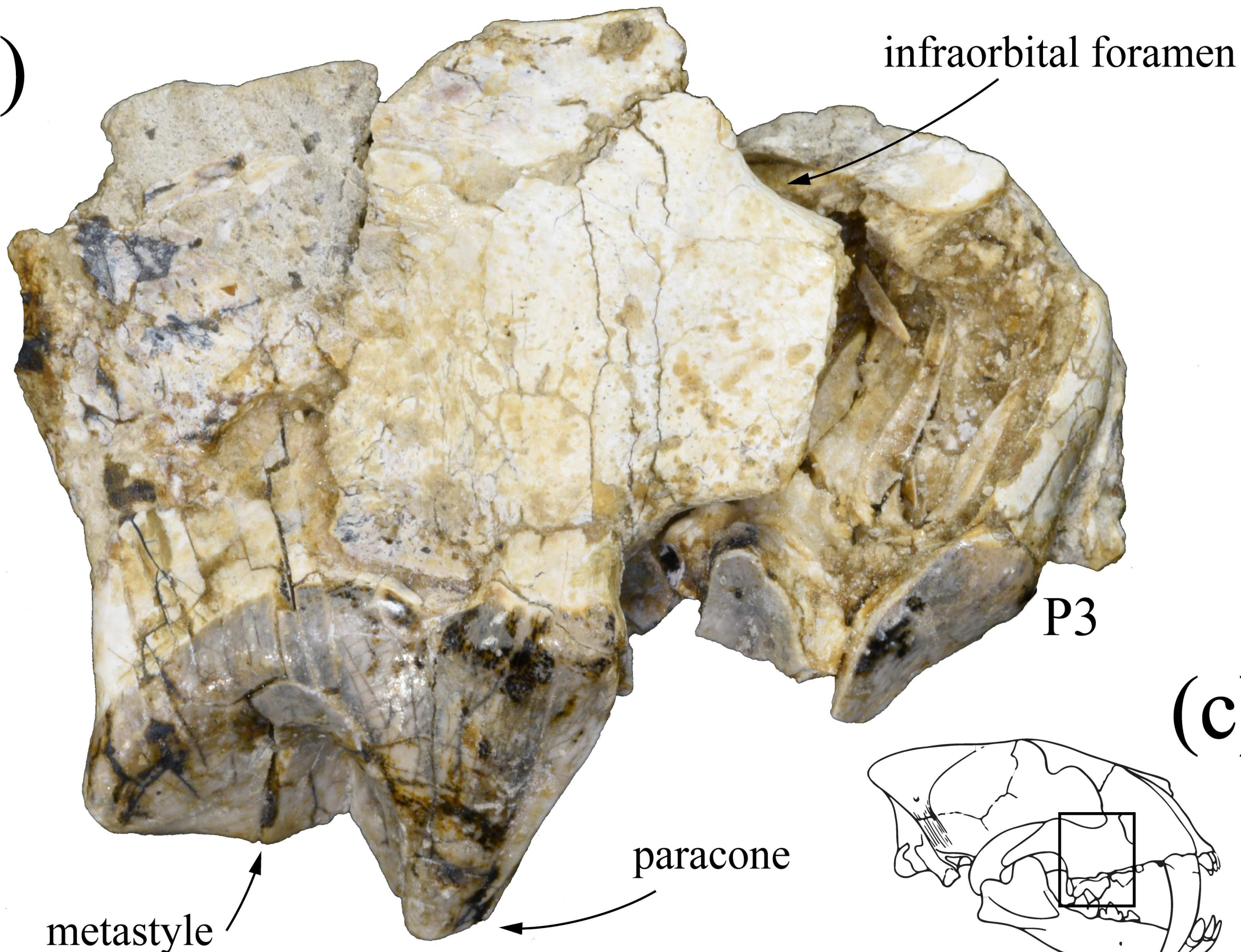
- 262 3. Sole F, Fischer V, Le Verger K, Mennecart B, Speijer RP, Peigne S, Smith T. 2022
263 Evolution of European carnivorous mammal assemblages through the Palaeogene. *Biol. J.*
264 *Linn. Soc.* **135**, 734–753. (doi:10.1093/biolinnean/blac002)
- 265 4. Wesley-Hunt GD. 2005 The morphological diversification of carnivores in North
266 America. *Paleobiology* **31**, 35–55. (doi:10.1666/0094-
267 8373(2005)031<0035:tmdoci>2.0.co;2)
- 268 5. Tomiya S. 2011 A new basal caniform (Mammalia: Carnivora) from the middle Eocene of
269 North America and remarks on the phylogeny of early carnivorans. *PLoS One* **6**.
270 (doi:10.1371/journal.pone.0024146)
- 271 6. Tomiya S. 2013 New carnivoraforms (Mammalia) from the middle Eocene of California,
272 USA, and comments on the taxonomic status of ‘Miacyis’ gracilis. *Palaeontol. Electron.*
273 **16**. (doi:10.26879/364)
- 274 7. Tomiya S, Tseng ZJ. 2016 Whence the beardogs? Reappraisal of the middle to late eocene
275 ‘miacyis’ from Texas, USA, and the origin of amphicyonidae (mammalia, carnivora). *R.*
276 *Soc. Open Sci.* **3**. (doi:10.1098/rsos.160518)
- 277 8. Lander EB. 2019 Early late Duchesnean (late middle Eocene) Titus Canyon fauna, Titus
278 Canyon Formation, Death Valley National Park, Inyo County, southeastern California. In
279 *Exploring Ends of Eras in the Eastern Mojave Desert, Desert Symposium Field Guide and*
280 *Proceedings: Desert Hot Springs, California, Desert Symposium Inc*, pp. 141–153.
- 281 9. Tomiya S, Morris ZS. 2020 Reidentification of Late Middle Eocene “Uinacyon” From
282 the Galisteo Formation (New Mexico, U.S.a.) As an Early Beardog (Mammalia,
283 Carnivora, Amphicyonidae). *Breviora* **567**, 1. (doi:10.3099/0006-9698-567.1.1)
- 284 10. Barrett PZ. 2021 The largest hoplophontine and a complex new hypothesis of nimravid
285 evolution. *Sci. Rep.* **11**, 1–9. (doi:10.1038/s41598-021-00521-1)
- 286 11. Averianov A, Obraztsova E, Danilov I, Skutschas P, Jin J. 2016 First nimravid skull from
287 Asia. *Sci. Rep.* **6**. (doi:10.1038/srep25812)
- 288 12. Stadler T. 2010 Sampling-through-time in birth-death trees. *J. Theor. Biol.* **267**, 396–404.
289 (doi:10.1016/j.jtbi.2010.09.010)
- 290 13. Didier G, Royer-Carenzi M, Laurin M. 2012 The reconstructed evolutionary process with
291 the fossil record. *J. Theor. Biol.* **315**, 26–37. (doi:10.1016/j.jtbi.2012.08.046)
- 292 14. Stadler T, Kühnert D, Bonhoeffer S, Drummond AJ. 2013 Birth-death skyline plot reveals
293 temporal changes of epidemic spread in HIV and hepatitis C virus (HCV). *Proc. Natl.*
294 *Acad. Sci. U. S. A.* **110**, 228–233. (doi:10.1073/pnas.1207965110)
- 295 15. Bouckaert R, Heled J, Kühnert D, Vaughan T, Wu CH, Xie D, Suchard MA, Rambaut A,
296 Drummond AJ. 2014 BEAST 2: A Software Platform for Bayesian Evolutionary Analysis.
297 *PLoS Comput. Biol.* **10**, 1–6. (doi:10.1371/journal.pcbi.1003537)
- 298 16. Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA. 2018 Posterior summarization
299 in Bayesian phylogenetics using Tracer 1.7. *Syst. Biol.* **67**, 901–904.
300 (doi:10.1093/sysbio/syy032)
- 301 17. Revell LJ. 2012 phytools: An R package for phylogenetic comparative biology (and other
302 things). *Methods Ecol. Evol.* **3**, 217–223. (doi:10.1111/j.2041-210X.2011.00169.x)
- 303 18. Rowe T. 1988 Definition, diagnosis, and origin of mammalia. *J. Vertebr. Paleontol.* **8**,
304 241–264. (doi:10.1080/02724634.1988.10011708)
- 305 19. Bryant HN. 1996 Explicitness, stability, and universality in the phylogenetic definition
306 and usage of taxon names: A case study of the phylogenetic taxonomy of the Carnivora
307 (mammalia). *Syst. Biol.* **45**, 174–189. (doi:10.1093/sysbio/45.2.174)

- 308 20. Wyss AR, Flynn JJ. 1993 A Phylogenetic Analysis and Definition of the Carnivora.
309 *Mammal Phylogeny* , 32–52. (doi:10.1007/978-1-4613-9246-0_4)
- 310 21. Flynn J, Finarelli J, Spaulding M. 2010 Phylogeny of the Carnivoramorpha, and the use of
311 the fossil record to enhance understanding of evolutionary transformations. In *Carnivoran*
312 *Evolution: New Views on Phylogeny, Form and Function* (eds A Goswami, A. Friscia),
313 pp. 25–63. Cambridge University Press.
- 314 22. Bryant HN. 1996 Nimravidae. In *The Terrestrial Eocene-Oligocene Transition in North*
315 *America* (eds DR Prothero, JR Emry), pp. 453–475. Cambridge University Press.
- 316 23. Peigné S. 2001 A primitive nimravine skull from the quercy fissures, France: Implications
317 for the origin and evolution of nimravidae (Carnivora). *Zool. J. Linn. Soc.* **132**, 401–410.
318 (doi:10.1111/j.1096-3642.2001.tb02467.x)
- 319 24. Walsh SL, Gutzler RQ. 1999 Late Duchesnean-early Chadronian mammals from the
320 upper member of the Pomerado Conglomerate, San Diego, California. *J. Vertebr.*
321 *Paleontol.* **19**(3), 82A.
- 322 25. Flynn JJ, Galiano H. 1982 Phylogeny of Early Tertiary Carnivora, With Description of a
323 New Species of Protictis From the Middle Eocene of Northwestern Wyoming. *Am.*
324 *Museum Novit.* , 1–64.
- 325 26. Bryant HN. 1991 Phylogenetic Relationships and Systematics of the Nimravidae
326 (Carnivora). *J. Mammal.* **72**, 56–78.
- 327 27. Peigné S. 2003 Systematic review of European Nimravinae (Mammalia, Carnivora,
328 Nimravidae) and the phylogenetic relationships of Palaeogene Nimravidae. *Zool. Scr.* **32**,
329 199–229. (doi:10.1046/j.1463-6409.2003.00116.x)
- 330 28. Barrett PZ. 2016 Taxonomic and systematic revisions to the North American Nimravidae
331 (Mammalia, Carnivora). *PeerJ* **2016**. (doi:10.7717/peerj.1658)
- 332 29. Egi N, Tsubamoto T, Saneyoshi M, Tsogtbaatar K, Watabe M, Mainbayar B, Chinzorig T,
333 Khatanbaatar P. 2016 Taxonomic revisions on nimravids and small feliforms (Mammalia,
334 Carnivora) from the Upper Eocene of Mongolia. *Hist. Biol.* **28**, 105–119.
335 (doi:10.1080/08912963.2015.1012508)
- 336 30. Tsubamoto T *et al.* 2006 A summary of the Pondaung fossil expeditions. *Asian*
337 *Paleoprimatology* **4**, 1–66.
- 338 31. Zaw K *et al.* 2014 The oldest anthropoid primates in SE Asia: Evidence from LA-ICP-MS
339 U-Pb zircon age in the Late Middle Eocene Pondaung Formation, Myanmar. *Gondwana*
340 *Res.* **26**, 122–131. (doi:10.1016/j.gr.2013.04.007)
- 341 32. Hanson CB. 2010 Stratigraphy and vertebrate faunas of the Bridgerian-Duchesnean
342 Clarno Formation, north-central Oregon. In *The Terrestrial Eocene-Oligocene Transition*
343 *in North America* (eds D Prothero, J Emry), pp. 206–239. Cambridge University Press.
344 (doi:10.1017/cbo9780511665431.012)
- 345 33. Kelly TS, Murphey PC, Walsh SL. 2012 New Records of Small Mammals From the
346 Middle Eocene Duchesne River. *Paludicola* **8**, 208–251.
- 347 34. Butler BPM. 1946 The evolution of carnassial dentitions in the Mammalia. *Proc. Zool.*
348 *Soc. London* **116**, 198–220.
- 349 35. Van Valen L. 1969 Evolution of Dental Growth and Adaptation in Mammalian
350 Carnivores. *Evolution (N. Y.)*. **23**, 96–117.
- 351 36. Mellett JS. 1977 *Paleobiology of North American Hyaenodon*. Karger Publishers.
- 352 37. Bastl K, Morlo M, Nagel D, Heizmann E. 2011 Differences in the tooth eruption sequence
353 in Hyaenodon ('Creodonta': Mammalia) and implications for the systematics of the genus.

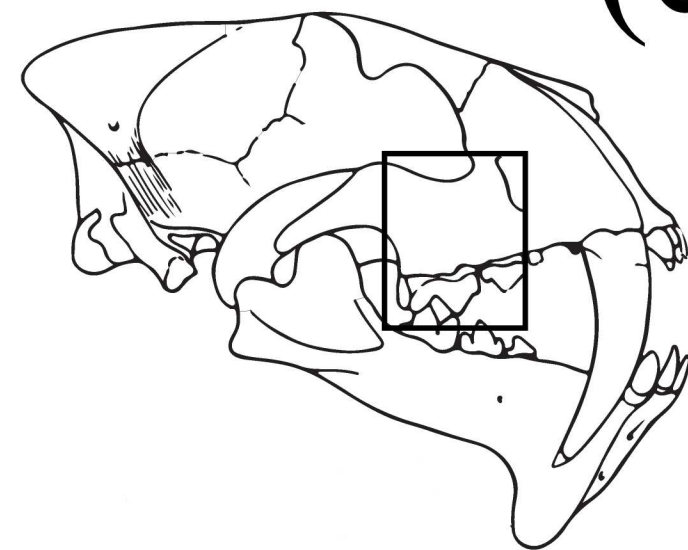
- J. Vertebr. Paleontol.* **31**, 181–192. (doi:10.1080/02724634.2011.540052)
38. Bastl K, Semprebon G, Nagel D. 2012 Low-magnification microwear in Carnivora and dietary diversity in Hyaenodon (Mammalia: Hyaenodontidae) with additional information on its enamel microstructure. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **348–349**, 13–20. (doi:10.1016/j.palaeo.2012.05.026)
39. Tomiya S. 2012 Ecological Aspects of the Diversity Dynamics of North American Fossil Mammals. University of California, Berkeley.
40. Williams BA, Kirk EC. 2008 New Uintan primates from Texas and their implications for North American patterns of species richness during the Eocene. *J. Hum. Evol.* **55**, 927–941. (doi:10.1016/j.jhevol.2008.07.007)
41. Frederiksen NO. 1991 Pulses of middle Eocene to earliest Oligocene climatic deterioration in southern California and the Gulf Coast. *Palaios* **6**, 564–571. (doi:10.2307/3514919)
42. Tomiya S, Zack SP, Spaulding M, Flynn JJ. 2021 Carnivorous mammals from the middle Eocene Washakie Formation, Wyoming, USA, and their diversity trajectory in a post-warming world. *J. Paleontol.* **95**, 1–115. (doi:10.1017/jpa.2020.74)
43. Eronen JT, Janis CM, Chamberlain CP, Mulch A. 2015 Mountain uplift explains differences in palaeogene patterns of mammalian evolution and extinction between north America and Europe. *Proc. R. Soc. B Biol. Sci.* **282**. (doi:10.1098/rspb.2015.0136)
44. Zack SP, Poust AW, Wagner H. 2022 Diegoaelurus, a new machaeroidine (Oxyaenidae) from the Santiago Formation (late Uintan) of southern California and the relationships of Machaeroidinae, the oldest group of sabertooth mammals. *PeerJ* **10**, e13032. (doi:10.7717/peerj.13032)
45. Carbone C, Mace GM, Roberts CR, Macdonald DW. 1999 Energetic constraints on the diet of terrestrial carnivores. *Nature* **402**, 286–288.
46. Van Valkenburgh B, Wang X, Damuth J. 2004 Cope's rule, hypercarnivory, and extinction in North American canids. *Science* (80-.). **306**, 101–104. (doi:10.1126/science.1102417)
47. Prothero DR, Heaton TH. 1996 Faunal stability during the early oligocene climatic crash. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **127**, 257–283. (doi:10.1016/S0031-0182(96)00099-5)
48. Valkenburgh B Van. 1994 Extinction and Replacement Among Predatory Mammals in the North American Late Eocene and Oligocene: Tracking a Paleoguild Over Twelve Million Years. *Hist. Biol.* **8**, 129–150. (doi:10.1080/10292389409380474)
49. Tang Y, Qui Z. 1979 Vertebrate faunas of Baise, Guangxi. In *Mesozoic and Cenozoic Red Beds of South China* (ed Academia Sinica Institute of Vertebrate Paleontology and Paleanthropology and Nanking Institute of Geology and Paleontology), pp. 407–415. Science Press.
50. López-Torres S, Silcox MT, Holroyd PA. 2018 New omomyoids (Euprimates, Mammalia) from the late Uintan of southern California, USA, and the question of the extinction of the paromomyidae (plesiadapiformes, primates). *Palaeontol. Electron.* **21**. (doi:10.26879/756)
51. Gustafson EP. 1986 Carnivorous mammals of the late Eocene and early Oligocene of Trans-Pecos Texas. *Texas Meml. Museum Bull.* **33**, 1–66.
52. Wesley GD, Flynn JJ. 2003 a Revision of Tapocyon (Carnivoramorpha), Including Analysis of the First Cranial Specimens and Identification of a New Species. *J. Paleontol.* **77**, 769–783. (doi:10.1666/0022-3360(2003)077<0769:arotci>2.0.co;2)

53. Kirk EC, Williams BA. 2011 New adapiform primate of Old World affinities from the Devil's Graveyard Formation of Texas. *J. Hum. Evol.* **61**, 156–168. (doi:10.1016/j.jhevol.2011.02.014)
54. Speijer RP, Pălike H, Hollis CJ, Hooker JJ, Ogg JG. 2020 *The Paleogene Period*. (doi:10.1016/b978-0-12-824360-2.00028-0)
55. Bai B, Wang YQ, Mao FY, Meng J. 2017 New Material of Eocene Helaeidae (Perissodactyla, Tapiroidea) from the Irind Manha Formation of the Erlian Basin, Inner Mongolia, China and Comments on Related Localities of the Huheboerhe Area. *Am. Museum Novit.* , 1–44. (doi:10.1206/3878.1)
56. Doria G, Royer DL, Wolfe AP, Fox A, Westgate JA, Beerling DJ. 2011 Declining atmospheric CO₂ during the late Middle Eocene climate transition. *Am. J. Sci.* **311**, 63–75. (doi:10.2475/01.2011.03)
57. Averianov A, Obraztsova E, Danilov I, Jin J. 2019 Anthracotheriid artiodactyl Anthracokeryx and an upper Eocene age for the Youganwo Formation of southern China. *Hist. Biol.* **31**, 1115–1122. (doi:10.1080/08912963.2017.1421639)
58. Barrett PZ, Hopkins SSB, Price SA. 2021 How many sabertooths? Reevaluating the number of carnivoran sabretooth lineages with total-evidence Bayesian techniques and a novel origin of the Miocene Nimravidae. *J. Vertebr. Paleontol.* **41**, 1–15. (doi:10.1080/02724634.2021.1923523)
59. Chow M. 1958 A record of the earliest sabre-tooth cats from the Eocene of Lushih, Honan. *Sci. Rec.* **N.S. 2**, 347–349.
60. Ding S, Zhen J, Zhang Y, Tong Y. 1977 The age and characteristic of the Liuniu and the Dongjun faunas, Bose Basin of Guangxi. *Vertebr. Palasiat.* **XV**, 35–45.
61. R Core Team. 2021 R: A language and environment for statistical computing.
62. Zack SP. 2019 The first North American propterodon (Hyaenodonta: Hyaenodontidae), a new species from the late Uintan of Utah. *PeerJ* **2019**. (doi:10.7717/peerj.8136)
63. Zheng J, Tang Y, Zhai R, Ding S, Huang X. 1978 Early Tertiary strata of Lunan Basin, Yunnan. *Prof. Pap. Stratigr. Paleontol. Beijing* , 22–29.

(a)



(c)



(b)

