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

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25 RH: POUST et al.—EARLY NIMRAVID

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

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45 Electronic supplementary material is available at http://dx.doi.org/XXXXX or via
46 http://rsbl.royalsocietypublishing.org.
47

1. Introduction

49 The climatically dynamic period from the late middle Eocene to the early Oligocene (ca. 41–30
50 Ma) saw not only the reorganisation of biotas worldwide that is known as the Eocene–Oligocene
51 biotic transition [1] but also the initial rise of members of crown Carnivora and their closest
52 relatives as hypercarnivores[2,3]. The early nimravids joined the Hyaenodonta in this specialised
53 niche, which carnivorans would later occupy alone until the present day. Due to the eventual
54 extinction of these groups and the resulting lack of genetic data, fossils provide the only window
55 into an important period of faunal change presaging the organisation of modern trophic structure.
56   However, the lack of early data from this critical period has presented a challenge to
57 interpreting this transition. In particular, a general paucity of mammalian fossils from the
58 Duchesnean North American Land Mammal 'Age' (NALMA; 41–37 Ma) has long obscured an
59 early phase of the Eocene–Oligocene faunal transition in North America, particularly with
60 respect to mammalian carnivores [4]. Recent taxonomic and biostratigraphic studies, however,
61 have unveiled the late-middle-Eocene diversity of carnivores in southwestern North America
62 sufficiently to permit its reassessment [5–9]. The turnover of mammalian carnivores during this
63 period is noteworthy for the replacement of early meat-eating lineages by crown-clade
64 carnivorans and their close carnivoraform relatives—an episode that broadly coincided with the
65 global climatic fluctuations surrounding the Middle Eocene Climatic Optimum (MECO; [9]).
66   We report a new genus and species of nimravid, *Pangurban egiae,* on the basis of a
67 partial maxilla with the upper 3rd and 4th premolars (P3–4) (Figure 1) from the likely upper
68 middle Eocene portion of the Pomerado Conglomerate of San Diego County, California.
69 *Pangurban* is one of the earliest diagnosable nimravids in the world, and preserves the earliest
70 nimravid cheek teeth from North America, allowing its inclusion in phylogenetic analysis.
71 Bearing similarities to the derived later nimravid *Hoplophoneus*, its early occurrence and
72 hypercarnivorous adaptations demonstrate the rapid diversification of the group.

2. Methods

74   The new fossil is housed at the San Diego Natural History Museum (San Diego Society
75 of Natural History collections, SDSNH).We scored the holotype specimen (SDSNH 60554) into
76 the Bayesian tip-dating analysis of Barrett (2021) [10], with a uniform tip-date of 40.0–37.0 Ma
77 based on the likely middle- to late-Duchesnean age of the specimen. The age of the holotype
78 (and the only known specimen) of *Maofelis cantonensis* was updated to the late Eocene,
79 following [11]. The Bayesian analysis utilized a fossilized birth-death process [12–14] with
80 complex models of morphological evolution (e.g. ordered, multipath, Dollo) best supported for
81 the nimravid character matrix of [10]. Additional details can be found in the electronic
82 supplementary material. Markov Chain Monte Carlo runs were sampled every 1,000 generations
83 in Beast 2 v. 2.6.3 ([15]), while trees were logged every 10,000 generations until Effective
84 Sample Sizes were > 200, as determined in Tracer version 1.7.1 [16]. From the output of Tracer,
85 sampling and timing (generation number) of the stability of the run was assessed. Thus, the first
86 10% of the generations were discarded (burn-in), and topology and posterior probabilities were

87 estimated from the remaining generations. The maximum clade credibility (MCC) tree of this
88 analysis is presented in Figure 2a (barbourofelins and most outgroups not shown; see Fig. S2 for
89 complete tree) and the electronic supplementary material, along with the XML run file. We
90 reconstructed synapomorphies in TNT version 1.5, which only reports synapomorphies
91 supported by both accelerated and delayed transformations. Body mass of the new taxon was
92 estimated through linear regression analysis of P4 lengths and corresponding nimravid body
93 masses (based originally on lower first molar [m1] lengths) in [10]. We estimated ancestral body
94 masses along the branches of the MCC tree using the 'fastANC' function found in the 'phytools'
95 [17] package for the R programming environment, v. 4.1.2 (R Development Core Team, 2021).
96

3. Results

3.1. Systematic Palaeontology

99
100 Class MAMMALIA sensu Rowe [18]
101 unranked clade CARNIVORAMORPHA sensu Bryant [19] (amended from Wyss and Flynn
102 [20])
103 unranked clade CARNIVORAFORMES Flynn, Finarelli, and Spaulding [21]
104 Family NIMRAVIDAE sensu Bryant [22]
105 ***Pangurban egiae*** gen. et sp. nov.
106 Fig. 1
107 ZooBank LSID: XXXXXXXXXX (to be added upon acceptance)
108
109 **Holotype.** SDSNH 60554, right maxillary fragment with P3–P4; collected in 1997 by Stephen L.
110 Walsh and Robert Gutzler, who also prepared the specimen, and housed at the San Diego Natural
111 History Museum (San Diego, U.S.A.).
112 **Type locality and horizon.** SDSNH Locality 4042 ("Spring Canyon Site 2"). Upper member of
113 Pomerado Conglomerate, San Diego, California, U.S.A., here considered middle to late
114 Duchesnean in age (ca. 40–37 Ma; see SI Text).
115 **Diagnosis**. Anterior cutting edge of P4 expressed as sharp and distinct preparacristal blade, not
116 reaching apex of paracone; anterior face of P4 flattened and nearly vertical giving the paracone a
117 steep angle. Differs from: *Maofelis* and MA-PHQ 348 (undet. nimravid specimen housed at
118 Museum d'Histoire Naturelle Victor Brun, Montauban, France [23]) in infraorbital foramen
119 posterior to P3, double rooted P3, P3 width to length ratio 0.4–0.65; *Maofelis*, MA-PHQ 348,
120 and "nimravines" of [10]which includes barbourofelins, in reduced or absent P4 protocone, P4
121 metastylar blade length to paracone length ratio of 1.0–1.3, P3 crown height 48–70% that of P4;
122 hoplophoneins (*Hoplophoneus*, *Eusmilus*, and *Nanosmilus*) in absence of parastyle on P4.
123 **Etymology.** The generic name is from the Old Irish, in reference to the cat in the 9th century CE
124 poem of the same name, whose hunting is likened to academic pursuit of truth. The species name
125 honours the contribution of palaeontologist Naoko Egi to the study of terrestrial carnivore
126 evolution on both sides of the northern Pacific Ocean, mirroring the nimravid distribution.
127 **Remarks.** SDSNH 60554 was previously identified as "cf. *Hyaenodon* sp." in the collection, and
128 was apparently the basis for the previously reported occurrence of that hyaenodontid genus in the
129 upper Pomerado Conglomerate [24]. We re-identify this specimen as a nimravid based on the

130 combination of: low height of P3; presence of serration on P3; elongate posterior basal cusp of
131 P3; absence of cuspidate protocone on P4; absence of parastyle from the anterolabial base of P4
132 (cf. [25,26]); presence of prominent P4 preparacrista; and absence of deep incision associated
133 with carnassial notch on P4 (cf. [25]).
134

3.2. Morphology and Phylogeny

137   The double-rooted P3 measures 11.2 mm in length and 4.6 mm in width. It is
138 labiolingually compressed, and its concave lingual wall descends steeply to its base without
139 forming an appreciable lingual bulge (Fig. 1; SI Fig. 2). The anterior slope of the paracone forms
140 a shallow angle with the palate near its base, but steepens toward the tip of the cusp. The anterior
141 ridge is finely serrated (~3 slightly dorsally-inclined incisions per mm on preserved portion)
142 except for ~1 mm at the base of the crown. No anterior cuspule is present. The presence of a
143 prominent and likely trenchant posterior basal cusp, separated from the main cusp by a notch, is
144 indicated by a groove on the labial wall and the outlines of the breakages.
145   The largely intact P4 measures 16.8 mm in length and 12.6 mm in width, which yielded
146 an estimated body mass of 28 kg. Its anterolingual projection lacks a distinct protocone. The
147 parastyle, cingular or otherwise in origin (cf. [27]), is absent. The preparacrista is notably
148 trenchant. The carnassial notch lacks a deep incision. The metastylar blade is posterolabially
149 deflected. There is no appreciable development of a cingulum. A very light facet of attritional
150 wear is visible in inclined light on the lingual side of the P4. It surrounds the carnassial notch and
151 rises onto the postparacrista, generally resembling wear found in *Dinictis* in both extent and
152 severity.
153   The posteroventral curvature of the infraorbital foramen is preserved above the anterior
154 edge of the P4. This differs from most "nimravines" of [10] and *Eusmilus*, in which it is located
155 more anteriorly. A deep embrasure pit for the occlusion of the m1 protoconid is partially
156 preserved lingual to the metastylar blade of P4.
157   In the MCC tree (Fig. 2a), we recovered *Pangurban egiae* as the sister taxon to the node-
158 based tribe Hoplophoneini sensu Barrett [28], with which it was united by three
159 synapomorphies: reduced or absent P4 protocone; P4 metastylar blade 1.0–1.3 times the length
160 of paracone; and P3 crown height 48–70% of that of P4. All of these features would appear again
161 in Miocene barbourofelins, and are thus not unambiguous synapomorphies, but they do indicate
162 comparably derived hypercarnivory within this clade in the late middle Eocene.
163   The remaining topology of the MCC tree differed minimally from [10]. The
164 hoplophoneins were recovered in largely the same arrangement, with successive divergences of
165 *Hoplophoneus* (here recovered as a paraphyletic taxon), *Nanosmilus*, and *Eusmilus*.

4. Discussion

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

172 *egiae*, SDSNH 60554, is significant as one of the oldest securely-identified nimravid fossils
173 globally (Fig. 2*b*; see SI Text for further discussion). Although a few likely-older (ca. 40 Ma)
174 specimens are known from the Pondaung Formation of Myanmar [30,31] and the Clarno
175 Formation of Oregon, USA [32,33], it is the oldest nimravid fossil that preserves enough of the
176 upper dentition to be meaningfully incorporated into a phylogenetic analysis. While not
177 falsifying the hypothesis of East Asian origin for nimravids, the presence of a derived member in
178 North America at such an early time demonstrates not only swift circum-Pacific dispersal for the
179 group (in whatever direction), but also rapid evolution of the earliest nimravids. As such, it
180 provides key information on the early evolution and distribution of the family.
181 　　　On the MCC tree, *Pangurban egiae* displays a zero-length branch, indicating that it is a
182 sampled ancestor. This status relates to *P. egiae* preserving derived character states that support
183 its affinity with Hoplophoneini, while not preserving distinct apomorphies in this matrix.
184 However, ~42% of sampled posterior trees have a tip-length greater than zero for *P. egiae*,
185 indicating that its status as a true sampled ancestor should be treated with some hesitancy—a
186 status that will require additional specimens to properly assess. In view of the unique
187 combination of traits in SDSNH 60554, we prefer to assign it to a new genus.
188 　　　The discovery of *Pangurban egiae* accentuates the Eocene–Oligocene taxic turnover
189 across all trophic levels and highlights the late-middle-Eocene rise of hypercarnivorous
190 mammals in southwestern North America. Taking pronounced reduction of the carnassial
191 metaconid(s)—which is associated with a predominantly anteroposterior orientation of the
192 prevallid—and its correlates as taxon-independent proxies for hypercarnivory [4,34,35],
193 hypercarnivores are greatly outnumbered (both in species richness and abundance) by hypo- and
194 mesocarnivores in the late Uintan of southern California and western Texas combined (age
195 groups 1 & 2 in Fig. 2*c*; Table S1). The beginning of the Duchesnean NALMA is marked by the
196 immigration from Asia of the hypercarnivorous/durophagous *Hyaenodon* ([36–38]; age group 3
197 in Fig. 2*c*); interestingly, the earliest Duchesnean deposits of southern California have yielded
198 abundant fossils of *Hyaenodon*, whereas remains of carnivoraforms (none of whom are
199 hypercarnivores) are rare [6,36,39]. Middle to late Duchesnean assemblages from southwestern
200 North America contain more hypercarnivorous taxa (including *P. egiae*) than hypo- to
201 mesocarnivorous taxa (age group 4 in Fig. 2*c*).
202 　　　The shifting balance within the carnivore guild cannot be readily explained as a
203 taphonomic artefact, and it seems likely to reflect ecological restructuring of the carnivore guild
204 across the climatically unstable earlier Duchesnean. Notably, the same time period saw a marked
205 decline in primate diversity in the region ([40]; Fig. 2*c*) and, in southern California, a ~40% loss
206 of primarily woody angiosperm taxa [41]. Substantial disassembly and reassembly of a regional
207 carnivore community concomitant with a major loss of primate diversity also characterises the
208 late Bridgerian–early Uintan (ca. 48–44 Ma) faunal succession in the central Rocky Mountain
209 region [42]. These events may reveal common faunal dynamics over evolutionary time in
210 response to reduced forest canopies and spatial redistribution of biomass, within the context of
211 the middle-to-late Eocene trend of declining precipitation in North America [43]. Perhaps the
212 rise of carnivoraform hypercarnivores relates to the development of seasonally open canopies or
213 mosaic forested landscapes. Following the loss of sabretooth machaeroidines prior to the Middle
214 Eocene Climatic Optimum [44], a contingent opportunity may have occurred for circum-Pacific
215 immigration of nimravids into North America. Concerted declines in relatively small, arboreal
216 vertebrate prey such as primates (resulting in an upward shift in the body size distribution of
217 vertebrate prey) and other food resources that are abundant in tropical/subtropical forests (e.g.,

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

225

235

236 FIGURE CAPTIONS

237
238 Fig 1. Holotype SDSNH 60554 of *Pangurban egiae* gen. et sp. nov.
239 Right maxillary fragment with P3–P4 in lateral (*a*) and ventral (*b*) views. Approximate position
240 on cranium marked on (*c*).

241
242 Fig. 2. Phylogenetic, geographic, and faunal context of *Pangurban egiae*.
243 (*a*) Tip-dated Bayesian MCC tree of nimravids. Node values indicate posterior probabilities of
244 clades. Nimravid basal node marked by open circle (median age) and bar (95-percent credible
245 interval). (*b*) Geographic distribution of Eocene nimravids (in part after [11,29]). Coloured (by
246 land mammal 'ages' as in (*a*)) portions of icons indicate known dental elements. Taxonomically-
247 questionable occurrences marked as "?"; nimravid material from Gongkang Formation
248 apparently has never been described (cf. [49]). (*c*) Late-middle-Eocene carnivore (tooth icons)
249 and primate (silhouettes) diversity in southern California and western Texas, divided into four
250 age groups (data in Table S1; tooth icons modelled after *Lycophocyon hutchisoni* and
251 *Diegoaelurus vanvalkenburghae*) and based primarily on [5,6,8,36,39,40,44,50–53]). Time
252 scales for magnetochrons and NALMAs follow [33,54], and that for Asian Land Mammal
253 'Ages' (ALMAs) after [55]. NALMA/ALMA abbreviations: Ch, Chadronian; Du, Duchesnean;
254 Er, Ergilian; Ir, Irdinmanhan; Sh, Sharamurunian; Ui, Uintan; Ul, Ulangochuian. Timings of
255 middle Eocene global climatic anomalies and angiosperm diversity loss in southern California
256 from [56] and [41].

257

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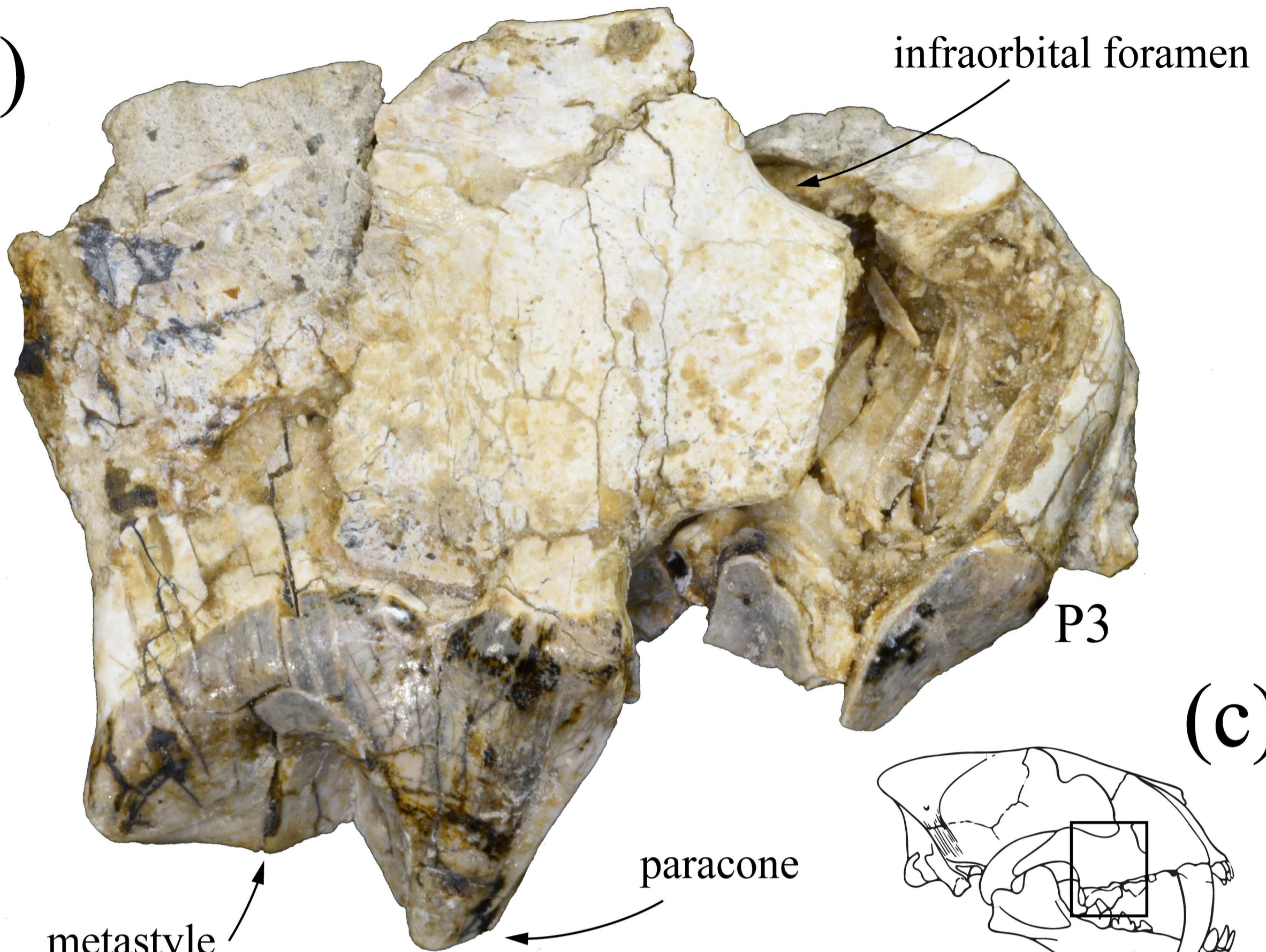261   Rev. Earth Planet. Sci.* **27**, 463–493. (doi:10.1146/annurev.earth.27.1.463)

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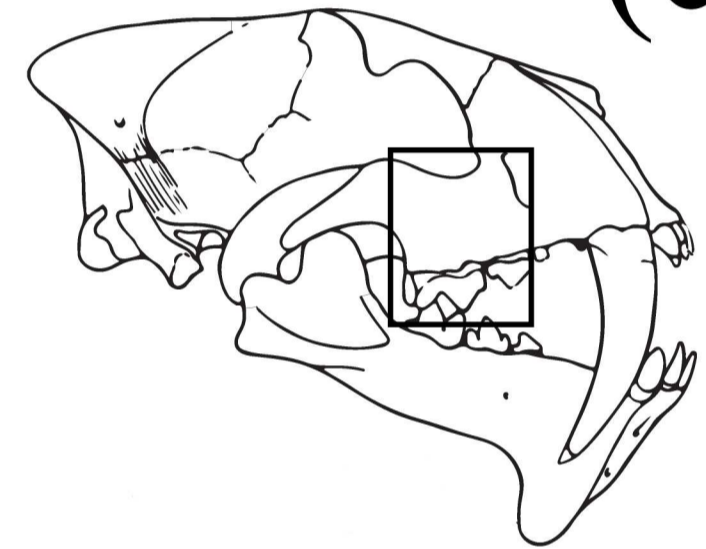
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428
429

(a)

infraorbital foramen

P3

metastyle

paracone

P4

(c)

(b)

preparacrista

posterior basal cusp

P3

serrations

carnassial
notch

Lorem ipsum

reduced protocone

15 mm