

Biochronology and biogeography of *Paradaphoenus* (Carnivora: Amphicyonidae) within the Great Plains Region of North America

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The amphicyonid, or “bear-dog,” *Paradaphoenus* was a small-bodied, hypercarnivorous carnivoran that lived in North America during the Oligocene. Specimens of *Paradaphoenus* are rare, in part owing to the common inaccurate referral of specimens to the abundant canid *Hesperocyon*, which was similar in size and morphology. Four new specimens of *Paradaphoenus* are noted from North Dakota and South Dakota that expand the geographic range of this taxon within the Great Plains region of North America and expand our knowledge of its anatomy. A single specimen from either a transitional Orellan/Whitneyan or early Whitneyan fauna in the Little Badlands area of North Dakota is referred to *Paradaphoenus minimus*. That taxon is elsewhere restricted to Orellan faunae, making that specimen the youngest occurrence of *P. minimus* yet recognized. The remaining specimens are from two early Whitneyan faunas, the Cedar Pass local fauna in South Dakota and a new locality within the Little Badlands area of North Dakota, and are referred to *Paradaphoenus tooheyi*. These discoveries highlight the difficulties of elucidating the biostratigraphic and biogeographic distributions of relatively rare taxa within the White River Chronofauna given the propensity for many specimen identifications to be biased in favor of more abundant, well-known taxa.

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12 ABSTRACT

13 The amphicyonid, or “bear-dog,” *Paradaphoenus* was a small-bodied, hypercarnivorous
14 carnivoran that lived in North America during the Oligocene. Specimens of *Paradaphoenus* are
15 rare, in part owing to the common inaccurate referral of specimens to the abundant canid
16 *Hesperocyon*, which was similar in size and morphology. Four new specimens of
17 *Paradaphoenus* are noted from North Dakota and South Dakota that expand the geographic
18 range of this taxon within the Great Plains region of North America and expand our knowledge
19 of its anatomy. A single specimen from either a transitional Orellan/Whitneyan or early
20 Whitneyan fauna in the Little Badlands area of North Dakota is referred to *Paradaphoenus*
21 *minimus*. That taxon is elsewhere restricted to Orellan faunae, making that specimen the
22 youngest occurrence of *P. minimus* yet recognized. The remaining specimens are from two early
23 Whitneyan faunae, the Cedar Pass local fauna in South Dakota and a new locality within the
24 Little Badlands area of North Dakota, and are referred to *Paradaphoenus tooheyi*. These
25 discoveries highlight the difficulties of elucidating the biostratigraphic and biogeographic
26 distributions of relatively rare taxa within the White River Chronofauna given the propensity for
27 many specimen identifications to be biased in favor of more abundant, well-known taxa.

28

29 INTRODUCTION

30 Amphicyonids, informally known as “bear dogs,” were typically large carnivorans that
31 dominated the mammalian carnivore niches of Holarctic regions through the Miocene. Their
32 oldest occurrences suggest emergence and immediate radiation throughout the Holarctic during
33 the Eocene-Oligocene Transition (Hunt, 1996). The earliest representatives of Amphicyonidae
34 have been taxonomically enigmatic, with seemingly sudden widespread geographic ranges and

35 diverse morphologies across five taxa (*Cynodictis*, *Gustafsonia*, *Angelarctocyon*, *Daphoenictis*,
36 and *Daphoenus*) at the end of the middle Eocene (Tomiya and Tseng, 2016). In North America,
37 the late Eocene and early Oligocene amphicyonid record is dominated by taxa within the
38 subfamily Daphoeninae. The first report of North American daphoenine amphicyonids is
39 *Daphoenus lambei* in the Duchesnean North American Land Mammal Age (NALMA) (Bryant,
40 1992; Dawson, 1980; Hunt, 1996). Immediately after its first appearance that taxon is
41 geographically widespread, ranging from the Cypress Hills, Shirley Basin, and Beaver Divide in
42 Saskatchewan, the Badwater Locality in Wyoming, and the Porvenir local fauna in Texas
43 (Bryant, 1992; Dawson, 1980; Hunt, 1996).

44 The daphoenine amphicyonids *Daphoenictis* and *Brachyrhynchocyon* appear soon
45 afterwards in the Chadronian faunae at Flagstaff Rim in Wyoming and the Little Egypt faunae of
46 Texas (Hunt, 1996), though the former taxon may also be present in the Duchesnean Porvenir
47 fauna of Texas (Gustafson, 1986; Hunt, 1996). *Daphoenictis tedfordi* was a small, ‘cat-like’
48 amphicyonid, representing the most hypercarnivorous early amphicyonid (Hunt, 1974; Emry and
49 Hunt, 1980; Boardman and Hunt, 2015). *Brachyrhynchocyon* was a larger-bodied, relatively
50 common taxon, with all but a single lower jaw from the Pipestone Springs fauna in Montana (the
51 holotype of *Brachyrhynchocyon montanus*) referred to the species *Brachyrhynchocyon dodgei*
52 (Fig. 1). Some occurrences of *Brachyrhynchocyon* are reported as close to or slightly above the
53 “purplish-white” layer in Nebraska, which approaches the Chadronian-Orellan transition (Hunt,
54 1996). However, *Brachyrhynchocyon* has never been definitively confirmed in any Orellan
55 faunae (Hunt, 1996), likely restricting the last appearance of both *Daphoenictis* and the much
56 larger *Brachyrhynchocyon* to the Chadronian NALMA.

57 During the Chadronian NALMA, specimens of *Daphoenus* are known (Hunt, 1998), but
58 at the current time have not been referred to a known species (Fig. 1). Differences in size and
59 morphology noted in those specimens indicate the likely presence of two species that may be the
60 precursors of the Orellan species (Hunt, 1996). *Daphoenus* is the only Eocene amphicyonid that
61 persists across the Eocene-Oligocene transition, generally increasing in size in cline with its
62 biochronology. In the Orellan (early Oligocene) two species of *Daphoenus* are recognized that
63 are distinguished by both size and morphology: the larger *Daphoenus vetus* and the smaller
64 *Daphoenus hartshornianus*. There is some evidence that the *D. vetus* lineage persisted into the
65 Whitneyan in South Dakota (Hunt, 1998), but those occurrences are also currently identified
66 only as *Daphoenus* sp. In the Pacific Northwest region, multiple species of *Daphoenus* are
67 present beginning in the early Arikareean.

68 A second daphoenine taxon, *Paradaphoenus*, co-occurs with *Daphoenus* in the Oligocene
69 and ranges from the Orellan to the early Arikareean (Hunt, 2001). *Paradaphoenus* is the smallest
70 of the daphoenine amphicyonids (Hunt, 1998; Hunt, 2001), and is known from three species. The
71 earliest records are from Orellan faunae (early Oligocene) in the Great Plains region, all
72 attributed to *Paradaphoenus minimus* (Fig. 2). A second taxon, *Paradaphoenus tooheyi*, is
73 reported from Whitneyan and early Arikareean faunae in the Great Plains region. Thus far, those
74 two species have not been recorded together in a single fauna. It is possible that those two
75 species represent morphologically distinct forms that arose from anagenetic change within a
76 single lineage sequestered within the Great Plains region of North America, but those two taxa
77 are currently too poorly sampled to properly test that hypothesis at this time. A third species,
78 *Paradaphoenus cuspidigerus*, is found in the Pacific Northwest during the Arikareean. At this time

79 there is no evidence that *Paradaphoenus* survived into the Miocene, as is the case for all
80 daphoenines aside from *Daphoenodon* (Hunt, 1998).

81 While *Paradaphoenus* does appear to be a rare component of the White River
82 Chronofauna, its similarity in size and appearance to the contemporaneous and abundant canid
83 *Hesperocyon gregarius* commonly results in specimens of the former being misidentified as the
84 latter (Hunt, 2001). Confusion of early amphicyonids with *H. gregarius* (and vice versa) is
85 common and is also reflected in the fact that *H. gregarius* was previously classified within the
86 early amphicyonid taxon *Cynodictis* (Scott and Osborn, 1887; Scott, 1898) until additional study
87 revealed its identity as a canid. New material attributed to *Paradaphoenus tooheyi* was
88 discovered while examining canid material from the Cedar Pass local fauna (Fig. 3: Poleslide
89 Member, Brule Formation, Jackson County, South Dakota) repositated at the South Dakota School
90 of Mines Museum of Geology. All of those specimens were previously identified and catalogued
91 as the canid *Hesperocyon*. Additionally, examination of specimens recently collected by the
92 North Dakota Geological Survey from two localities in Brule Formation in the Little Badlands
93 area of Stark County, North Dakota (Fig. 4) revealed two additional *Paradaphoenus* specimens,
94 one referable to *P. tooheyi* and another to *P. minimus*. All of these new specimens provide
95 important new insights into the biostratigraphic and biogeographic distribution of
96 *Paradaphoenus* within the Great Plains region. This study serves as a supplement to prior work
97 on *Paradaphoenus* (e.g., Hunt, 1996, 1998, 2001), focusing on new information gleaned from
98 these specimens rather than providing a thorough review or revision of the taxon.

99 **Institutional Abbreviations:**

100 AMNH, American Museum of Natural History, New York, NY; BADL, Badlands National Park,
101 Interior, SD; NDGS, North Dakota Geological Survey, Bismarck, ND; SDSM, South Dakota

102 School of Mines and Technology Museum of Geology, Rapid City, SD; SMM, Science Museum
103 of Minnesota, Saint Paul, MN; UNSM; University of Nebraska State Museum, Lincoln, NE.

104

105 **METHODS**

106 Specimens were measured with a digital caliper (various models) to the hundredth of a
107 millimeter, and rounded to the nearest tenth of a millimeter for reporting. In the text below tooth
108 positions with uppercase letters refer to teeth from the upper dentition, while tooth positions with
109 lowercase letters refer to teeth from the lower dentition. Dental terminology follows that of Hunt
110 (2001). All specimens included in this study were studied first hand by at least one of the authors
111 and all are permanently housed in public collections facilities.

112

113 **SYSTEMATIC PALEONTOLOGY**

114 CARNIVORA Bowdich, 1821

115 ARCTOIDEA Flower, 1869

116 AMPHICYONIDAE Trouessart, 1885

117 *PARADAPHOENUS* Wortman and Matthew, 1899

118 **Name Bearing Species:**

119 *Paradaphoenus cuspigerus* (Cope, 1878)

120 **Other Included Species:**

121 *Paradaphoenus minimus* (Hough, 1948) and *Paradaphoenus tooheyi* Hunt, 2001

122 **Diagnosis:**

123 This diagnosis is taken from Hunt (2001:p. 3-4): “Smallest (<3-4 kg) North American
124 amphicyonid carnivorans with m1 lengths of 8.3-9.4 mm; rudimentary auditory bulla formed by

125 a slightly inflated ossified ectotympanic that does not fully enclose the middle ear; dental
126 formula 3-1-4-3/3-1-4-3; P4 length short relative to combined lengths of M1-2 (P4L/M1-2L:
127 Orellan, 80.8%; early Arikareean, Great Plains, 77.6%; early or mid-Arikareean, Oregon, 67.7-
128 73.2%); P4 with abbreviated protocone relative to *Daphoenus*, *Hesperocyon*, and *Cynodictis*; M1
129 with well-developed meta- and paraconules as in *Cynodictis*; M2 prominent and the central
130 member of an upper molar row that gradually diminishes in size from M1-2; m1 with basined
131 talonid, m1 paraconid blade not anteriorly expanded (it is extended in *Hesperocyon*); prominent
132 rectangular m2 with basined talonid and anterolabial swelling of the cingulum (m1-2 talonids are
133 markedly enlarged with prominent basins in Whitneyan and Arikareean species, less so in
134 Orellan); postorbital/preorbital length ratio ~2:1.”

135 *PARADAPHOENUS MINIMUS* (Hough, 1948)

136 *Daphoenus minimus* Hough, 1948

137 *Paradaphoenus minimus* Hunt, 1996

138 *Paradaphoenus minimus* Hunt, 2001

139 Figs. 5A-B. Table 1.

140 **Holotype:**

141 AMNH 39099: Partial skull with right P2-M2 and left P3-M1.

142 **Type Locality:**

143 Orellan NALMA (CP84A: Janis et al., 2008), likely Scenic Member [lower Oreodon
144 beds], Brule Formation, White River Group, southwest of Sheep Mountain Table near Scenic,
145 Oglala Lakota County, South Dakota, USA (Hough, 1948).

146 **Referred Specimens:**

147 UNSM 25030: partial dentary with m1-m3; UNSM 25305: partial dentary with partial p4,
148 m1-2; UNSM 26139: partial dentary with m1-2; UNSM 25148: partial dentary with m1-2;
149 NDGS 2735: associated right M2, right dentary fragment with m2 and alveoli for m1 and m3,
150 and miscellaneous postcrania.

151 **Distribution:**

152 Orellan NALMA (CP99A: Janis et al., 2008), Orella “A” and Orella Member of Brule
153 Formation, White River Group, northwest of Crawford, Dawes County, Nebraska, USA; Orellan
154 NALMA (CP99A: Hunt, 2001; Janis et al., 2008), Brule Formation, White River Group,
155 Scottsbluff County, Nebraska, USA; Transitional Orellan/Whitneyan NALMAs (NP50B: Janis et
156 al., 2008; Korth et al., in review), Fitterer Ranch fauna (sublocality NDGS L238), Brule
157 Formation, White River Group, southwest of Dickinson, Stark County, North Dakota, USA.

158 **Diagnosis:**

159 The following differential diagnosis is modified from that provided by Hunt (2001:p. 20)
160 for *Paradaphoenus tooheyi*: P4 length/ M1-2 length, 80-81% relative to 77-78% for *P. tooheyi*
161 and 67-74% for *P. cuspidigerus*; m1-2 talonids not transversely broadened (talonid equal or
162 slightly narrower than trigonid) relative to *P. tooheyi*, which bears more broadly basined
163 talonids; crowding of m2 trigonid to the front of the tooth less well-developed relative to *P.*
164 *tooheyi*, in which the length of the trigonid is reduced relative to the length of the talonid; m2
165 paraconid less diminished, relative to *P. tooheyi*; m2 width 3.6-3.9 mm relative to 4.3 mm in *P.*
166 *minimus*; m1-2 talonids much less expanded than in *P. cuspidigerus*; m1 width 4.2-4.3 mm relative
167 to 5.2 mm in *P. cuspidigerus*; M1-2 much less enlarged and transversely broadened than M1-2 of
168 *P. cuspidigerus*. Additionally, the upper molars of *P. minimus* have a larger parastyle and a less
169 prominent metastyle when compared to *P. tooheyi*.

170 **Comments:**

171 Examination of the SMM paleontological collections revealed the presence of a skull
172 labeled *Cynodictis* sp. (SMM P64.12.1) that was collected near Scenic, South Dakota. That
173 specimen preserves the left P2-M3 and the right P3-M2 (Fig. 7). The distinct parastyle present on
174 the upper molars of that specimen suggest that it is actually referable to *P. minimus*. The locality
175 (Scenic, South Dakota) places the geologic provenance in either the Chadron Formation or the
176 Scenic Member of the Brule Formation, with the latter option more likely considering the brown
177 mudstone matrix affixed to the specimen. The type specimen of *P. minimus* was also collected in
178 that same geographic area from the Scenic Member of the Brule Formation.

179 Though all species of *Paradaphoenus* retained the M3, that tooth position is not
180 preserved in any of the specimens previously reported from the Great Plains region. The
181 presence of the M3 in the holotype of *P. minimus* (AMNH 39099) is indicated solely by an
182 indentation at the posterior border of the left maxilla (Wortman and Matthew, 1899; Hunt, 2001).
183 Hough (1948) was less confident of the presence of M3 in *P. minimus*, but did not exclude the
184 possibility of a reduced M3. The M3 of SMM P64.12.1 is significantly reduced compared to the
185 M1 and M2 and bears only a paracone and protocone, giving the tooth an ovate outline (Fig. 6).
186 The preprotocrista and postprotocrista accentuate the ovate trigon. This reduction of the M3
187 contrasts with the holotype of *P. cuspidigerus* (AMNH 6853) and the 3-rooted alveoli for *P.*
188 *tooheyi* (LACM 21649), where the M3 is more transversely widened and retains the tribosphenic
189 morphology. The M3 reduction in SMM P64.12.1 is intermediate between the larger and more
190 developed M3 of *P. cuspidigerus* and the often absent M3 in European taxon *Cynodictis* (Teilhard,
191 1915; Hunt, 2001). Variable M3 reduction or loss is also observed in *Daphoenus hartshornianus*
192 and *Protamnocyon inflatus* (Hough, 1948), which would infer homologous M3 variation if

193 Hunt's (1996) suggested phylogeny is accurate. Of course, it is currently impossible to assess the
194 range of tokogenetic variation *Paradaphoenus* displayed in the size and morphology of M3
195 given how few specimens are currently known and Hough (1948) demonstrated the wide
196 variation of the M3 within the Amphicyonidae (i.e., possessing one-, two-, or three-rooted M3,
197 or none at all). This newly recognized skull of *P. minimus* is undergoing more detailed
198 examination and will be the focus of a forthcoming study.

199

200 *PARADAPHOENUS TOOHEYI* Hunt, 2001

201 Figs. 5C-D, 7. Table 1.

202 **Holotype:**

203 UNSM 6002-92: left dentary with p4-m2 and alveoli for p1-3 and canine root.

204 **Type Locality:**

205 Early Arikareean NALMA, Wagner Quarry, basal Arikaree Group, southwest of
206 Chadron, Dawes County, Nebraska, USA (Hunt, 2001; Hayes, 2005).

207 **Referred Specimens:**

208 BADL 10998: right M1; BADL 20233: right dentary with p3-m1; LACM 21649: partial
209 right maxilla with broken P4, complete M1-2, and alveoli for P3 and M3; NDGS 2736: left M2;
210 UNSM 26130: dentary with p2-m1.

211 **Distribution:**

212 Whitneyan NALMA (CP84B: Janis et al., 2008; Korth, 2014), Cedar Pass local fauna,
213 Poleslide Member, Brule Formation, White River Group, northeast of Interior, Jackson County,
214 South Dakota, USA; Whitneyan NALMA (CP99B: Hunt, 2001; Janis et al., 2008), 30 feet below
215 contact between the Brule and Gering Formations, White River Group, Banner County,

216 Nebraska, USA; Arikareean NALMA (CP85C: Janis et al., 2008), Wounded Knee area (LACM
217 Loc. 1981 = SDSM V5359 of Macdonald [1970]), Sharps Formation, Arikaree Group, Oglala
218 Lakota County, South Dakota, USA; Whitneyan? NALMA (NP50C: Janis et al., 2008), Obritsch
219 Ranch fauna (sublocality NDGS L235), Brule Formation, White River Group, southwest of
220 Dickinson, Stark County, North Dakota, USA.

221 **Diagnosis:**

222 The following differential diagnosis was provided by Hunt (2001:p. 20): “P4 length/ M1-
223 2 length, 77-78% relative to 80-81% for *P. minimus* and 67-74% for *P. cuspidigerus*; m1-2
224 talonids transversely broadened with prominent basins relative to *P. minimus* which lacks
225 broadly basined talonids; m2 trigonid reduced and crowded to the front of the tooth relative to *P.*
226 *minimus* in which crowding does not occur; m2 proto- and metaconids accentuated, and
227 paraconid diminished, relative to *P. minimus*; m2 width 4.3 mm relative to 3.6-3.9 mm in *P.*
228 *minimus*; m1-2 talonids not as expanded as in *P. cuspidigerus*; m1 width 4.4-4.5 mm relative to 5.2
229 mm in *P. cuspidigerus*; M1-2 not as enlarged and transversely broadened as M1-2 of *P.*
230 *cuspidigerus*.” Additionally, the upper molars of *P. tooheyi* have a reduced parastyle and a more
231 prominent metastyle when compared to *P. minimus*. The prominence of a metastyle is not
232 present in any other contemporaneous caniforms.

233 **Comments:**

234 *Paradaphoenus tooheyi* is previously known from maxillary teeth from the Sharps
235 Formation in South Dakota and dentary teeth from the Whitney Member of the Brule Formation
236 of Nebraska (Hunt, 2001). That assignment of upper and lower dentigerous material from
237 geographically and biochronologically disparate sites to *P. tooheyi* was based on inferred

238 occlusion (Hunt, 2001). At this time no specimen referred to *P. tooheyi* preserves portions of
239 both the lower and upper dentition, including those specimens referred in this study.

240

241 **DISCUSSION**

242 *Biostratigraphic Age of the Cedar Pass Local Fauna*

243 The latter portion of the Orellan NALMA and the entirety of the Whitneyan NALMA are
244 subdivided based primarily upon the oreodont fauna (e.g., Prothero and Whittlesley, 1998;
245 Prothero and Emry, 2004). Specifically, the latest Orellan (Or4) is the *Merycoiododon bullatus*
246 Interval Zone, the early Whitneyan (Wh1) is the *Leptauchenia major* Interval Zone, and the late
247 Whitneyan (Wh2) is the *Merycoiododon major* Interval Zone. The Schultz and Falkenbach (1968)
248 collection data of merycoiododontid oreodonts from the Cedar Pass area indicate the presence of a
249 Whitneyan fauna at that site. Though the work of Shultz and Falkenbach (1968) has been
250 considered dubiously over split, the more recent taxonomic revisions of Stevens and Stevens
251 (1996) has helped clarify the taxonomy of known merycoiododontids present at Cedar Pass. Taxa
252 listed at Cedar Pass by the latter study include *Merycoiododon bullatus* (including *Merycoiododon*
253 *galushai* and *Genetochoerus geygani*), *Merycoiododon major* (including *M. major*,
254 *Paramerycoiododon wanlessi*, *Otionohyus hybridus*, and *Otionohyus alexi*), *Leptauchenia decora*
255 (including *L. decora*, *Leptauchenia martini*, and *Hadroleptauchenia eiseleyi*), and *Leptauchenia*
256 *major* (including formerly known *Hadroleptauchenia shanafeltae*, *Pseudocyclopidius*
257 *frankforteri*, and *Pseudocyclopidius major*) (Schultz and Falkenbach, 1968; Stevens and Stevens,
258 1996). The co-presence of *M. bullatus* and *M. major* is atypical, as *M. bullatus* is elsewhere
259 restricted to the latest Orellan or early Whitneyan (Prothero and Emry, 2004). Thus, the oreodont

260 portion of the fauna alone does resolve the question of whether the Cedar Pass local fauna is an
261 early or late Whitneyan fauna.

262 Korth (2014) utilized the rodent fauna from Cedar Pass to verify an early Whitneyan
263 (Wh1) NALMA for the Cedar Pass local fauna. Thus, the presence of *M. major* at Cedar Pass is
264 an atypical early occurrence of that taxon within an otherwise typical early Whitneyan (Wh1)
265 fauna. Similarly, Korth (2014) identified four specimens of *Ischyromys typus* from the Cedar
266 Pass fauna, a taxon that is typically considered to have a last appearance in the latest Orellan
267 (Or4: Prothero and Emry, 2004). Prior to that study, only five specimens of *Ischyromys* were
268 previously reported from the lower Poleslide Member in South Dakota and the Whitney Member
269 in Nebraska (Heaton, 1993; Simpson, 1985), both of which contain characteristic Whitneyan
270 faunae. Together, these findings indicate that the presence of *Ischyromys* does not necessarily
271 dictate the presence of an Orellan fauna, nor does the first appearance of *Merycoiododon major*
272 alone necessitate the presence of a late Whitneyan (Wh2) fauna. Instead, these observations
273 make it clear that our understanding of the taxonomic compositions of late Orellan through late
274 Whitneyan faunae remains incomplete.

275 *Biostratigraphic Age of the Fitterer Ranch Specimen*

276 The Fitterer Ranch paleontological locality is positioned along the southern margin of the
277 area generally termed the Little Badlands in Stark County, North Dakota. The traditional
278 interpretation of the fauna preserved at Fitterer Ranch is that the lower portion of the Brule
279 Formation (below unit 6 of Skinner [1951]) contains an Orellan fauna, while the upper portion
280 (the entirety of unit 6) contains a Whitneyan fauna. Kihm (1990) challenged that interpretation,
281 noting that within the Little Badlands area of North Dakota the cricetid rodent *Eumys brachyodus*
282 was present within the basal portion of the Brule Formation while *Eumys elegans* was

283 completely absent. Those two taxa are typically restricted to Whitneyan and Orellan faunae,
284 respectively, suggesting the whole of the Brule Formation preserved in the Little Badlands area,
285 including Fitterer Ranch, contains a Whitneyan fauna. A detailed review of the stratigraphically
286 correlated rodent specimens from Fitterer Ranch confirmed the presence of *E. brachyodus*
287 throughout the lower Brule Formation and the absence of *E. elegans* (Korth et al., in review).
288 That study also noted the co-presence of taxa previously restricted to either Orellan (e.g.,
289 *Adjidaumo minutus*) or Whitneyan (e.g., *E. brachyodus*) in all well-sampled stratigraphic units.
290 As noted in that study, the oreodonts *Miniochoerus starkensis* and *Merycoidodon bullatus* are
291 also present beginning in the basal-most beds of the Brule Formation. Those taxa are elsewhere
292 restricted to latest Orellan (Or4) and early Whitneyan (Wh1) faunae (Prothero and Whittlesey,
293 1998; Prothero and Emry, 2004). Taken together, the faunal evidence suggests that the oldest
294 rocks of the Brule Formation at Fitterer Ranch preserve either a latest Orellan (Or4) or
295 transitional Orellan/Whitneyan fauna. Additionally, the local first appearance within the “Fitterer
296 Channel” (unit 5B: see Fig. 4) of the castorid rodent *Agnotocastor praetereadens*, which is
297 elsewhere restricted to early Whitneyan (Wh1) faunae, was cited as possible evidence of the
298 beginning of the Whitneyan at Fitterer Ranch (Korth et al., in review). However, it is also
299 possible that the first appearance of *A. praetereadens* within the “Fitterer Channel” may be
300 paleoenvironmentally controlled (presence of prominent channel sandstone facies) rather than
301 indicative of faunal turnover.

302 The specimen of *Paradaphoenus minimus* reported in this study was collected within unit
303 5B (=“Fitterer Channel” of Skinner [1951]; level 5 of Korth et al. [in review]) from a muddy
304 siltstone above the prominent channel sandstone facies of the “Fitterer Bed,” and immediately
305 below the “Local Channel” (Fig. 4). That is the same interval that contains the local first

306 appearance of *A. praetereadens*; thus, that specimen of *P. minimus* could be the first occurrence
307 of that taxon in a Whitneyan fauna. However, given the atypical mix of Orellan and Whitneyan
308 rodent taxa reported from that interval (Korth et al., in review), we provisionally consider those
309 specimens collected from the “Fitterer Channel” to be part of a transitional Orellan/Whitneyan
310 fauna. Regardless, that specimen is the youngest report of *P. minimus* yet noted.

311 *Biostratigraphic Age of the Obritsch Ranch Specimen*

312 The stratigraphy of the Brule Formation at Obritsch Ranch is very similar to that
313 observed at Fitterer Ranch, which is located only three miles southwest of Obritsch Ranch. There
314 is no local equivalent of the “Fitterer Channel” (subunit 5B of Skinner [1951]) at Obritsch
315 Ranch; however, there are channel sandstones that are similar in appearance to the “Fitterer Bed”
316 situated at a higher stratigraphic level within what Skinner (1951) identified as the “1st banded
317 layer” (subunit 6A: Fig. 4). Skinner (1951) considered the whole of his unit 6 to contain a
318 Whitneyan fauna, though he did not provide specific evidence to support that conclusion. A
319 diverse fauna has been collected by the NDGS from the local channel sandstone within subunit
320 6A at Obritsch Ranch (NDGS L234), but it has not been studied in detail to determine the
321 biostratigraphic age. The base of subunit 6B at Obritsch Ranch is composed of a buff, nodular
322 siltstone overlain by a pink mudstone. The nodular siltstone tends to form a resistant ledge in the
323 local area, and is fossiliferous. The referred specimen of *P. tooheyi* (NDGS 2736) was collected
324 as float on the ledge formed by that siltstone, with only a few meters of overlying pink mudstone
325 present at that location. Thus, that specimen was derived from either the nodular siltstone, which
326 produces most of the fossils at that site, or the pink mudstones. Either way, it comes from subunit
327 6B (Fig. 4). This locality is tentatively referred to the Whitneyan based on the previous
328 comments by Skinner (1951) and its stratigraphic position above unit 5, which contains either a

329 transitional Orellan Whitneyan or early Whitneyan (Wh1) fauna. A Whitneyan age is also
330 consistent with the previously known biostratigraphic range of *P. tooheyi*, and the observed
331 stratigraphic succession of *P. minimus* and *P. tooheyi* in the Brule Formation of North Dakota
332 also matches the pattern observed elsewhere in the Great Plains region.

333

334 CONCLUSIONS

335 Several of the specimens Hunt (2001) referred to *Paradaphoenus* were previously
336 misidentified as the hesperocyonine canid *Hesperocyon*. Those erroneous referrals are most
337 likely a result of the fact that *Paradaphoenus* shares a basic hypercarnivorous caniform structure
338 of the dentition with the contemporaneous and much more abundant *Hesperocyon*. Similar
339 innocuous misidentifications were also echoed through the discovery of the specimens referred
340 to *Paradaphoenus* in this study from the Cedar Pass local fauna. Overall, those specimens
341 referred in this study to *Paradaphoenus* expand our biogeographical information about that
342 taxon, but are less impactful on the biochronologic distribution and do not significantly impact
343 the relative abundance of *Paradaphoenus* within the carnivore niches of the White River
344 Chronofauna.

345 The declining diversity, relative scarcity, and short longevity of small-bodied
346 amphicyonids may have contributed to the increase in canid diversity following the Eocene-
347 Oligocene thermal decline. The small canid *Hesperocyon* becomes increasingly more abundant
348 in Chadronian through Orellan paleontological localities in the Great Plains region. *Hesperocyon*
349 is by far the most abundant carnivore in that region during the early Oligocene, with nearly 500
350 referred specimens from Orellan localities (Wang, 1994). By contrast, Whitneyan specimens of
351 *Hesperocyon* are less abundant, with only 12 referred specimens in the most comprehensive

352 study to date (Wang, 1994). At the same time, several hypercarnivorous hesperocyonine lineages
353 display increases in body size in the Whitneyan (i.e., *Osbornodon*, *Parenhydrocyon*,
354 *Ectopocynus*, *Mesocyon*, and *Cynodesmus*). Given those trends, other contemporaneous, small-
355 bodied carnivoran taxa could have avoided competition with those larger-bodied
356 hypercarnivorous hesperocyonines by adapting to omnivorous or hypocarnivorous niches in the
357 middle of the Oligocene. The early radiation of borophagine canids (i.e., *Archaeocyon*,
358 *Otarocyon*, *Oxetocyon*, and *Cynarctoides*) demonstrates the viability of that strategy, given that
359 they retained small body size, akin to their hypercarnivorous predecessors, but developed
360 dentition better suited for omnivory or hypocarnivory (Wang et al., 1999). Alternatively,
361 *Paradaphoenus* maintained a small-bodied hypercarnivore niche during the ecological
362 evacuation of *Hesperocyon* in most of the Great Plains region in the Whitneyan.

363 As noted above, the oldest fauna recovered from the base of the Brule Formation at
364 Fitterer Ranch is either latest Orellan (Or4) or transitional Orellan/Whitneyan (Or4/Wh1) (Korth
365 et al., in review). Among the rodent portion of the fauna, there is some evidence to suggest that
366 the fauna present within the whole of the “Fitterer Channel” (sensu Skinner, 1951) and the
367 overlying rocks are Whitneyan (i.e., local first appearance of *Agnotocastor praetereadens*: Korth
368 et al., in review). If those rocks do contain a Whitneyan fauna, 37 specimens of *Hesperocyon*
369 collected within or above the “Fitterer Channel” that Wang (1994) identified as Orellan would
370 actually be Whitneyan, along with several dozen previously unreported specimens of
371 *Hesperocyon* that were collected from that same stratigraphic interval by the NDGS. Those
372 specimens would indicate a unique abundance of *Hesperocyon* in North Dakota during the
373 Whitneyan, far exceeding occurrences observed in other Whitneyan faunae in the Great Plains
374 region. The paleoecological aspects of *Hesperocyon* were briefly summarized by several authors

375 and synthesized by Wang (1994). The limb morphology of *Hesperocyon* reflects a scansorial
376 lifestyle (Wang, 1993), supporting prior interpretations that *Hesperocyon* likely preferred to
377 inhabit a “river-border forest” environment (e.g., Clark et al., 1967). That interpretation also
378 coincides with the relative abundance of *Hesperocyon* in Orellan faunae, particularly within the
379 Orella and Scenic Members of the Brule Formation (Wang, 1994), and the paleoenvironmental
380 interpretations of the Gleska Series paleosols of the Scenic Member by Retallack (1983). The
381 depositional setting within the “Fitterer Channel” at Fitterer Ranch closely resembles that of the
382 “Toadstool Park channel complex” within the Orella Member in Nebraska (LaGarry, 1998). It is
383 possible that the Whitneyan Fitterer channel deposits represent a paleoecologically isolated
384 refuge of Orellan river-border macrofauna, including the scarce individuals of *P. minimus* and
385 abnormally high numbers of *Hesperocyon*. Such a scenario could also help explain the unique
386 mixing at Fitterer Ranch of rodent taxa that are elsewhere reported exclusively from Orellan or
387 Whitneyan faunae (Korth et al., in review).

388

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399 necessarily reflect the opinions of the National Park Service.

400

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Table 1 (on next page)

Measurements of specimens referred to *Paradaphoenus* in this study.

Specimen		NDGS 2735	NDGS 2736	BADL 20233	BADL 10998
Taxon		<i>P. minimus</i>	<i>P. tooheyi</i>	<i>P. tooheyi</i>	<i>P. tooheyi</i>
p3	Length (mm)			5.9	
	Width (mm)			2.5	
p4	Length (mm)			6.9	
	Width (mm)			2.9	
m1	Length (mm)			8.7	
	Width (mm)			4.3	
m2	Length (mm)	5.2			
	Width (mm)	3.3			
M1	Length (mm)				6.4
	Width (mm)				8.7
M2	Length (mm)	4.6	4.4		
	Width (mm)	6.5	7.1		

1 Abbreviations: M, upper molar; m, lower molar; p, lower premolar.

2

3

Figure 1(on next page)

Biostratigraphic distribution of daphoenine amphicyonids in North America from the Duchesnean through the early Arikareean NALMAs.

Ages for NALMA boundaries are taken from Janis et al. (2008) and taxon distributions are compiled from the new reports in this study and the work of Hunt (1996, 1998, 2001).

Oligocene

Ar

2

1

Wh

2

1

Or

3

4

1

2

Eocene

Du

Du

Ch

1

2

3

4

30.0

32.0

33.7

36.9

40.1

*Daphoenus lambei**Daphoenus* sp.*Daphoenus vetus**Daphoenus hartshornianus**Daphoenus transversus**Daphoenus ruber**Daphoenictis tedfordi**Brachyrhynchocyon dodgei**Brachyrhynchocyon montanus**Paradaphoenus minimus**Paradaphoenus tooheyi**Paradaphoenus cuspidatus*

Figure 2(on next page)

Geographic distribution of *Paradaphoenus*.

Yellow symbols indicate the presence of *Paradaphoenus minimus*, blue indicates *Paradaphoenus tooheyi*, and red indicates *Paradaphoenus cuspigerus*. Modified from Hunt (2001:fig. 1).

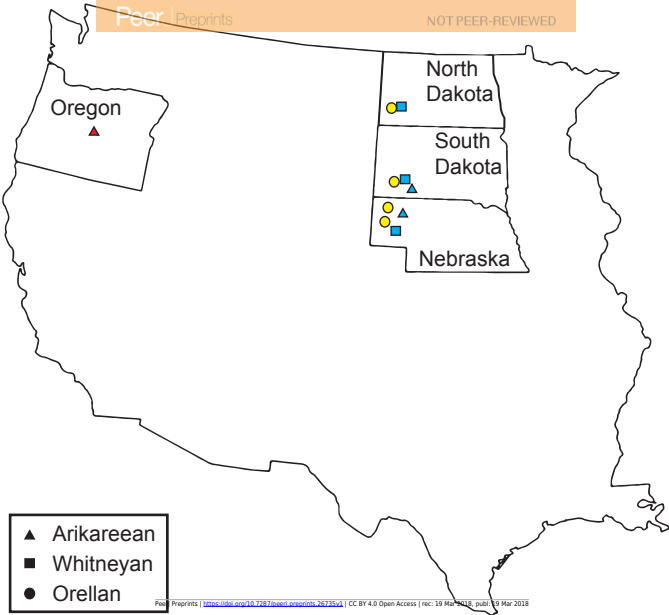


Figure 3(on next page)

Stratigraphic section of the Cedar Pass area of Badlands National Park, South Dakota showing the position of the Cedar Pass local fauna.

Unit numbers and informal names follow that of Evanoff et al. (2010). Lithologic patterns follow the FGDC Digital Cartographic Standard for Geologic Map Symbolization (U.S. Geological Survey, 2006). Vertical scale on the left is in meters.

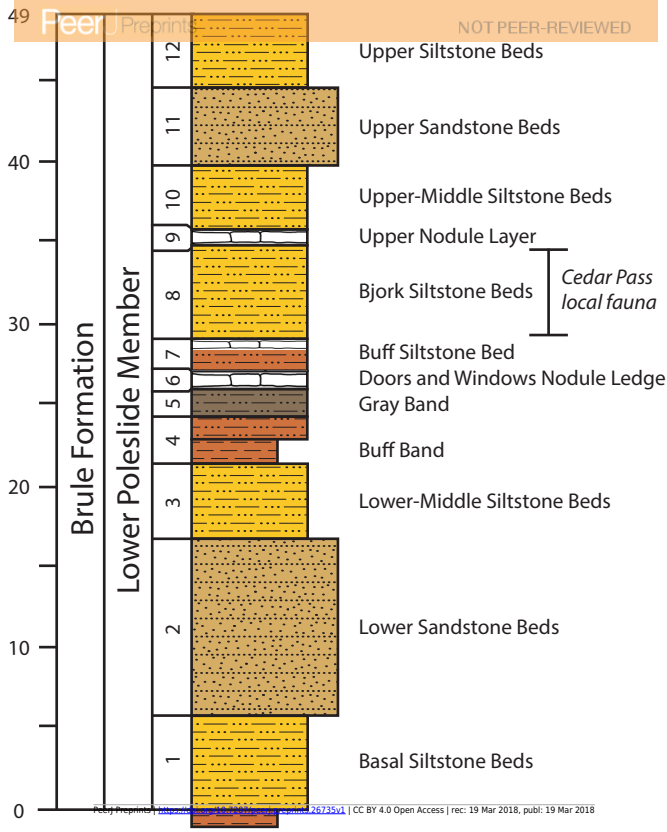


Figure 4

Generalized stratigraphic column for the Little Badlands area of Stark County, North Dakota.

Colored symbols indicate the positions of specimens discussed in this study. See Figure 2 for key to symbol colors and shapes. Stratigraphic data derived from personal observations of the authors, unpublished field notes of Dr. Richard Tedford (provided courtesy of the American Museum of Natural History), and published stratigraphic data (Skinner, 1951; Stone, 1973; Murphy et al., 1993). Unit and sub-unit numbers in the left-hand column refer to the units described by Skinner (1951). Lithologic patterns follow the FGDC Digital Cartographic Standard for Geologic Map Symbolization (U.S. Geological Survey, 2006). Abbreviations: AF, Arikaree Formation; CF, Chadron Formation.

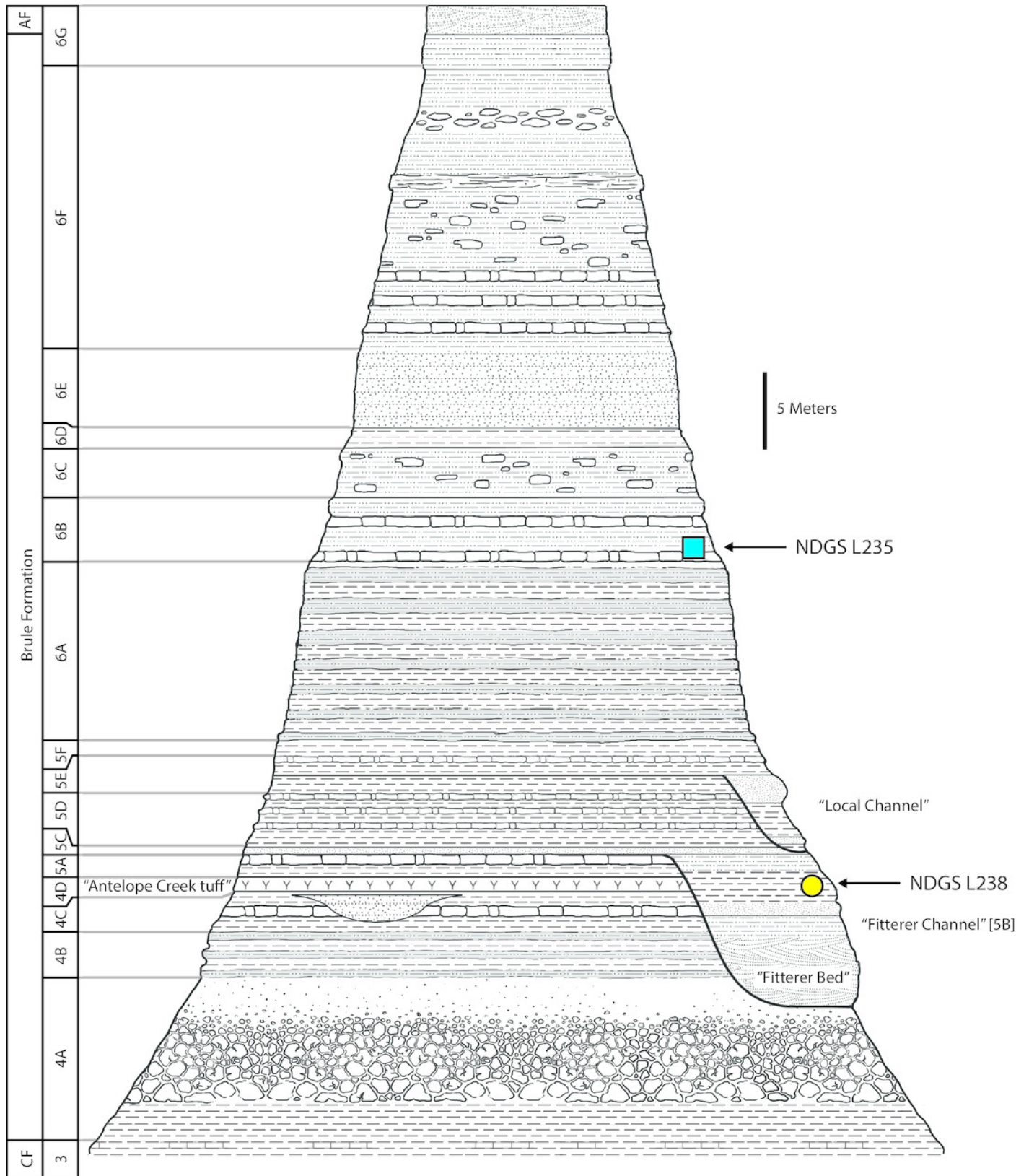


Figure 5(on next page)

Photographs of specimens here referred to *Paradaphoenus*.

(A) NDGS 2735: occlusal view of *Paradaphoenus minimus* right M2. (B) NDGS 2735: occlusal view of *Paradaphoenus minimus* right m2. (C) NDGS 2736: occlusal view of *Paradaphoenus tooheyi* left M2. (D) BADL 10998: occlusal view of *Paradaphoenus tooheyi* right M1. Scale bar equals 5 mm. Abbreviations: ant, anterior; lab, labial; lin, lingual, post, posterior.

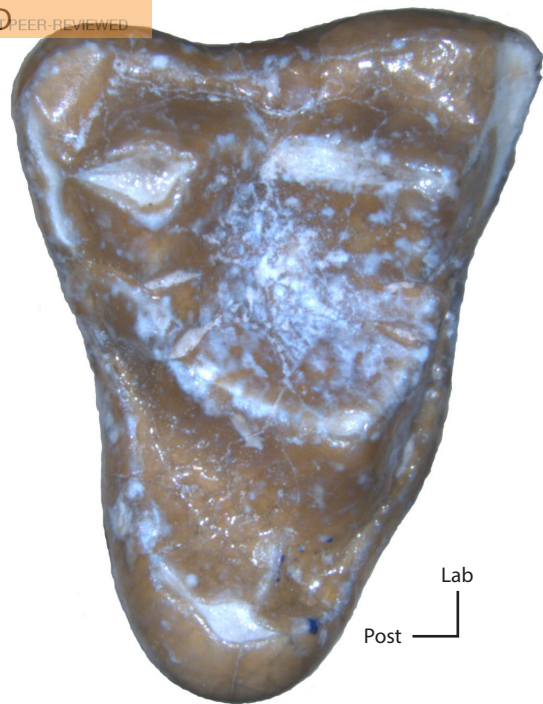
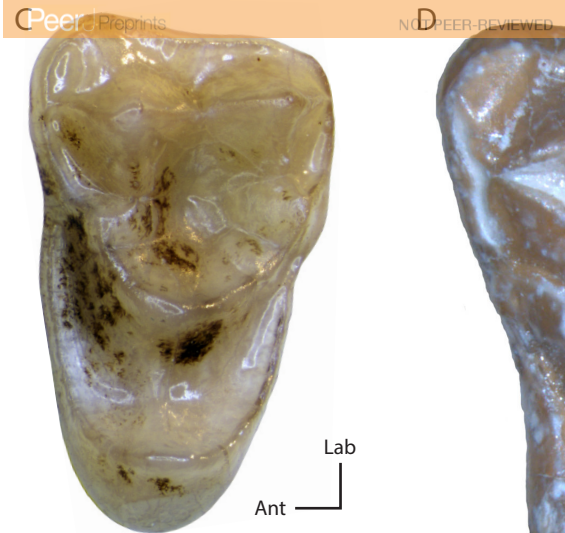


Figure 6(on next page)

Photograph of the left upper dentition (P3-M3) of SMM P64.12.1, referred to *Paradaphoenus minimus*.

Specimen was largely unprepared at the time of photography, but the full outlines of the teeth are exposed, showing the highly reduced M3. Scale bar equals 5 mm. Abbreviations: ant, anterior; lab, labial.



Figure 7 (on next page)

Photographs of BADL 20233, referred to *Paradaphoenus tooheyi*. lab, labial.

(A) Labial view of dentition. (B) Occlusal view of dentition. Scale bar equals 5 mm.

Abbreviations: lin, lingual; occ, occlusal; post, posterior. lab, labial.

A



B

