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A new, ‘dwarfed’ species of the phenacodontid ‘condylarth’ *Ectocion* Cope from the late Paleocene of Alberta, Canada, and its implications

Marisol Montellano-Ballesteros, Richard C. Fox, and Craig S. Scott

Abstract: A large collection of dentigerous jaws quarried from the Gao Mine locality, late Paleocene, Paskapoo Formation, central Alberta, Canada, documents a new species of the early Paleogene phenacodontid ‘condylarth’ *Ectocion* Cope. The new species, *E. stockeyae*, the smallest of the genus, occurs well before the abrupt global warming at the Paleocene–Eocene Thermal Maximum, an event purportedly causing the rapid evolution of ‘dwarfed’ mammals, including a species of *Ectocion*; however, there is no evidence of increased temperatures at Gao Mine to account for the small size of *E. stockeyae*, raising questions of the relationship between temperature and body size in *Ectocion*. *E. stockeyae* also exhibits sexual dimorphism of the canines, a pattern in mammals often associated with a population structure in which the males are relatively few and polygynous, resulting in intense male rivalry for mating success. The sample of *E. stockeyae* from Gao Mine includes a substantial majority of ‘juvenile’ individuals retaining deciduous posterior premolars, many even after eruption of the molars had been completed, suggesting short life spans, accelerated growth, and rapid dental development in this species as expressed in Schultz’s Rule.

Key words: Mammalia, Paleocene, phenacodontid, *Ectocion* n. sp., paleobiology.

Introduction

Paleocene mammals from western Canada are presently known from over 50 localities, most of which occur in deposits of the Alberta Syncline, north from the Porcupine Hills (Fox 1990; Scott et al. 2013). In the biochronological framework of North American Land Mammal Ages (Lofgren et al. 2004), these occurrences range in age from Puercan (early Paleocene) to late Tiffanian (late Paleocene). In the context of the Paleocene of western Canada, one site, Gao Mine, is particularly notable for its yield of well-preserved mammalian and plant fossils (e.g., Fox 1988, 1990, 2005; in progress; Stockey et al. 2013) (Fig. 1). Gao Mine is at a roadcut exposing the Paskapoo Formation near the city of Red Deer, south central Alberta; it is of late Tiffanian (Ti5) age (Scott 2010).

The most abundant mammal at Gao Mine is one species of *Ectocion* Cope 1882, the subject of the present paper. *Ectocion* is a late Paleocene–early Eocene North American phenacodontid ‘condylarth’, long known from rich deposits in the western United States, which have yielded the remains of seven species of the genus (Thewissen 1990). At present, ‘condylarths’ are widely considered to be a paraphyletic or possibly polyphyletic group of ancestral ‘hoofed’ mammals, of uncertain relationship to modern ungulate orders (Rose, 2006). Nonetheless, even within these uncertainties, phenacodontids are often thought to be closely related to Perissodactyla (tapirs, rhinoceroses, horses; Radinsky 1966; Rose 2006), and have thus been of special interest to researchers. *Ectocion* differs dentally from other phenacodontids mostly by greater lophodonty of the molars; in addition, the upper molars have a relatively large parastyle and labially bulging

mesostyle, and a U-shaped protocristid marks the lower molars (Thewissen 1990). The Gao Mine specimens identified as *Ectocion* in this study share these diagnostic characters, and are readily distinguished from the other, more bunodont, members of the family (*Tetraclaenodon* Scott 1893, *Phenacodus* Cope 1873, and *Copecion* Gingerich 1989).

In the collections from Gao Mine, *Ectocion* is represented by numerous (101) well-preserved, dentigerous upper and lower jaws, plus a small number of isolated teeth. These fossils document a new species of *Ectocion*, which, besides being new, raises issues concerning: (1) the occurrence of small size during the evolution of *Ectocion*; (2) presumed sexual dimorphism of the canines, a feature previously recognized in *Ectocion osbornianus* (Cope 1882) (Thewissen 1990: 38, fig. 21, the only other phenacodontid in which this difference has been reported; (3) the large number of ‘juvenile’ individuals as indicated by possession of the deciduous penultimate and ultimate upper and lower premolars, even after the molars had erupted. While postcrania of *E. stockeyae* might well have been present in the deposit, no ‘dental specimens’ of this species were accompanied by associated postcranial bones.

Geographical and geological occurrence

Gao Mine is an exposure of the continental Paskapoo Formation on the north side of Provincial Highway 595, approximately 14 km east of Red Deer, Alberta (Fig. 1). The Paskapoo Formation is widespread at or near the surface in Alberta as bedrock along an axis east of the Rocky Mountains from Calgary north to the Swan Hills. It consists of somber brownish to grayish clastics—siltstones, sandstones, and mudstones—plus coals,

some of which are of commercial importance as a thermal source for electrical power generation. Paskapoo deposits were eroded during the Laramide rise of the Rocky Mountains, with sediments carried eastward by slow-moving rivers and streams; final deposition was in channels, floodplains, swamps, and ponds, in a climate that appears to have been warm temperate overall (Gibson 1977; Jerzykiewicz 1997). Stockey et al. (2013) has provided a detailed stratigraphy of the Gao Mine locality, showing the relationships of important floral remains to the vertebrate horizon and the correlation of the locality with others in the region from mammalian, floral, and paleomagnetic evidence.

Ectocion material is accompanied by the remains of other mammals, including multituberculates (*Ectypodus* sp., *Microcosmodon conus*, and *Pentacosmodon pronus*), marsupials, ‘insectivoran-grade’ eutherians (e.g., mixodectids, palaeoryctids such as *Lainoryctes youzwysnyi*), lipotyphlans (*Diachocherus minutus*, and *D. meizon*), primates (*Plesiadapis churchilli*, *Carpodaptus* sp., and *Phenacolemus* sp.), carnivorans, and other ‘condylarths’, some of which have been described (e.g., Fox 2004, 2005; Scott 2004, 2010); peculiarly, non-mammalian vertebrate remains are uncommon and consist mostly of isolated bones and teeth.

Materials and methods

The fossils of *Ectocion* from Gao Mine occur in a thin seam 0.5 m or less in variable thickness and hence are considered synchronous geochronologically. All specimens were quarried manually, using chisels, awls, rock hammers, and small sledge-hammers, a method for recovery of fossils intended to minimize breakage of the specimens.

Underwater screen washing was not undertaken as a collecting method at Gao Mine: the fossiliferous siltstones exposed there disaggregate poorly in water or water plus wetting agents; moreover, screen washing unavoidably results in breakage of specimens, which would have defeated the purpose of securing anatomically well- preserved materials from this site.

Once fossils were exposed by splitting of the host siltstone, glue or resin was applied to stabilize them as necessary; they were then wrapped in soft tissue paper and collector's initials, date, and locality recorded. In the laboratory, each fossil was carefully prepared manually, using insect pins held by pin vices, under 10–40 magnifications of a binocular zoom microscope manufactured by Bausch and LombTM. Measurements were made with an eyepiece millimeter scale, calibrated with a StarrettTM beam caliper. Photographs were taken with a Nikon Camara D90, lens AF-S DX NIKKOR 18-140mm f/3.5-5.6G ED VR. Permanent storage of specimens is in small cardboard trays or in glass vials, depending on size. All specimens are catalogued and housed in the collections of either the Laboratory for Vertebrate Paleontology, University of Alberta, or the Royal Tyrrell Museum of Palaeontology.

Abbreviations and other conventions

TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UALVP, Laboratory for Vertebrate Paleontology, Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada; UM, Museum of Paleontology, The University of Michigan, Ann Arbor, Michigan, U. S. A. NALMA, North American Land Mammal Age: Ti, Tiffanian. PETM, Paleocene–Eocene Thermal Maximum. i/I, c/C, p/P,

126 m/M signify teeth at incisor, canine, premolar, and molar positions, with lower case
127 abbreviation indicating lower teeth and upper case, uppers. Lacking evidence to the
128 contrary and in keeping with Thewissen (1990), we consider teeth at the anteriormost
129 premolar locus in the specimens at hand to be part of the replacement series (i.e., p1/P1).
130 With no knowledge of the reproductive status of the individuals concerned, we use the
131 terms 'juvenile' and 'adult' only informally.

132 **Systematic paleontology**

133 Class Mammalia Linnaeus, 1758

134 Infraclass Placentalia Owen, 1837

135 Family Phenacodontidae Cope, 1881

136 Genus *Ectocion* Cope, 1882

137 *Ectocion stockeyae* n. sp.

138 (Figs. 2–5; Table 1, Fig. A1, Table A1)

139 ZOOBANK [1SID:zoobank.org:pub:3758AED2-CBF4-4900-9ADF-A942E1F2F495](https://zoobank.org/pub:3758AED2-CBF4-4900-9ADF-A942E1F2F495)

140 HOLOTYPE: UALVP 55562, incomplete right dentary containing i1–3, premolariform c1,
141 p1–4, m1–3.

142 TYPE LOCALITY: Gao Mine (Fox 1988; Stockey et al. 2013).

143 KNOWN OCCURRENCE: Type locality only, Paskapoo Formation, late Tiffanian, Ti5 (Scott
144 2010), magnetostratigraphic chron 25R (Lerbekmo et al. 1992).

145 REFERRRED SPECIMENS: ***Lower dentitions***—UALVP 55556, incomplete right dentary,
146 containing caniniform c1, dp3–4, m1–3, and alveoli for i3, p1–2; UALVP 55559,
147 incomplete right dentary containing premolariform c1, dp3–4, m1–2, alveoli for p1–2;
148 UALVP 55820, incomplete left dentary containing i3, premolariform c1, dp3; UALVP
149 35570, incomplete right dentary containing dp4, m1–3; UALVP 55821, incomplete right
150 dentary containing dp4, m1–2; UALVP 35567, incomplete left dentary containing dp3
151 [broken]–4, m1; UALVP 35825, incomplete right dentary containing dp3–4, m1;
152 UALVP 35569, incomplete right dentary containing dp3 [broken]–4, and unassociated
153 incomplete left dentary containing dp3–4; UALVP 35571, incomplete left dentary
154 containing p2, dp4, m1–2, and alveoli for p1, dp3, and m3; incomplete left dentary
155 containing erupting caniniform c1, dp3; UALVP 55568, incomplete right dentary
156 containing p2 (broken), dp3 (broken), dp4, partly formed replacement p4, m1–3, alveoli
157 for c1, p1; UALVP 35584, incomplete left dentary containing dp4, m1–2; UALVP
158 55829, incomplete left dentary containing i3 (root only), p2, dp3–4, m1–3, alveoli for c1
159 and p1; UALVP 35558, incomplete left dentary containing dp3–4, m1; UALVP 33575,
160 incomplete right dentary containing dp3–4, m1; UALVP 55560, incomplete right dentary
161 containing p2, dp3–4, m1–2; UALVP 55828, incomplete left dentary containing dp3–4,
162 m1–3; UALVP 35557, incomplete left dentary containing dp3–4, m1; UALVP 35556,
163 incomplete right dentary containing p2, dp3–4, m1–3, alveolus for p1; UALVP 55557,
164 incomplete left dentary containing p2, dp3–4, m1–3; UALVP 55558, incomplete right
165 dentary containing dp3, dp4 (roots only), m1–3 (m3 erupting); UALVP 55827,
166 incomplete right dentary containing dp3–4, m1–3; UALVP 35574, incomplete right
167 dentary containing dp4, m1 (erupting); UALVP 35559, incomplete right dentary

168 containing dp3–4; UALVP 35582, incomplete left dentary containing dp4 (broken), m1–
 169 3; UALVP 35565, incomplete right dentary containing dp3, dp4 (talonid only), m1, m2
 170 (erupting); UALVP 35566, incomplete right dentary containing dp4 (talonid only), m1–3
 171 (m3 erupting); UALVP 55825, incomplete right dentary containing dp3–4, m1; UALVP
 172 35577, incomplete left dentary containing dp3–4; TMP 2009.161.0106, incomplete right
 173 dentary containing dp3–4; TMP 2010.114.0037, incomplete right dentary containing dp4;
 174 TMP 2011.106.0483, incomplete right dentary containing dp3, m1, m2 (erupting) [very
 175 shallow, young jaw]; TMP 2011.106.0722, incomplete right dentary containing dp4, m1;
 176 TMP 2009.161.0643, incomplete left dentary containing dp3–4 (worn); TMP
 177 2009.161.0644, isolated dp4; UALVP 35581, incomplete left dentary containing m1–3
 178 unworn; UALVP 35562, incomplete left dentary containing m1–2 unworn.

179 UALVP 55561, incomplete right dentary containing p1–4, m1–3; UALVP 35564,
 180 incomplete left dentary containing p4, m1–2; UALVP 55567, incomplete left dentary
 181 containing p4, m1–3; UALVP 55563, incomplete left dentary containing p2–4, m1–3,
 182 alveoli for c1, p1; UALVP 55564, incomplete left dentary containing p3–4, m1–3;
 183 UALVP 55569, incomplete left dentary containing p4, m1–3; UALVP 35580, incomplete
 184 left dentary containing i2, p2–4, m1, alveoli for c1, p1; and incomplete left dentary
 185 containing m2–3 from a different individual; UALVP 55565, incomplete right dentary
 186 containing p3–4, m1–3; UALVP 35583, incomplete right dentary containing p3–4, m1–2
 187 (deeply worn, flat); UALVP 55566, incomplete right dentary containing p3–4, m1–3,
 188 alveoli for p1–2; UALVP 35563, incomplete right dentary containing p3–4; UALVP
 189 35568, incomplete right dentary containing p2–4, m1–2, m3 (trigonid only); UALVP
 190 55823, incomplete right dentary containing p3–4, m1, alveoli for c, p1–2; UALVP

191 35573, incomplete right dentary containing i1–3, caniniform c1 (incompletely erupted),
 192 p1–3, p4 (trigonid only); UALVP 55822, incomplete right dentary containing p4, m1–3;
 193 UALVP 55824, incomplete right dentary containing p3–4, m1–2; UALVP 55826,
 194 incomplete right dentary containing p3–4, m1–2, m3 (broken), and alveoli for c1, p1–2;
 195 UALVP 35576, incomplete right dentary containing p3–4; UALVP 35560, incomplete
 196 left dentary containing p1–3; TMP 2011.106.0143 incomplete left dentary containing i1–
 197 3, caniniform c1, p3–4, m1, alveoli for p1–2; UALVP 55570, incomplete right dentary
 198 containing p4, m1–3, alveoli for p3; TMP 2011.106.0755, incomplete right dentary
 199 containing p2 (roots only), p3–4, m1–3; TMP 2011.106.0143, incomplete left dentary
 200 containing i1 broken, i2–3, c, alveoli for p1–2, p3–4, m1; TMP 2009.161.0035, incomplete
 201 left dentary containing m1–2; UALVP 35578, incomplete left dentary containing m1–3
 202 unworn; UALVP 35561, incomplete left dentary containing m1–2 unworn; UALVP
 203 55819 incomplete right dentary containing c, roots p1, ?dp2, dp3.

204 ***Upper dentitions***—UALVP 55554, incomplete right maxilla containing P2, dP3–4, M1–
 205 3; UALVP 55833, incomplete left maxilla containing P1, dP3–4, M1; UALVP 35541,
 206 incomplete right maxilla containing dP3–4, M1–2; ; UALVP 35540, incomplete left
 207 maxilla containing P2, dP3–4, M1–3 (M3 erupting); UALVP 55549, incomplete left
 208 maxilla containing dP3–4, M1–3, incomplete right maxilla containing P2, dP3–4, M1–3,
 209 alveoli for two-rooted P1, incomplete right dentary (different individual than maxillae in
 210 this entry) containing p3–4, m1–3, alveolus for p1; UALVP 55552, incomplete right
 211 maxilla containing P2, dP3–4, M1–3 (good eruption sequence); UALVP 55551,
 212 incomplete right maxilla containing dP3–4, M1–3; UALVP 55834, incomplete right
 213 maxilla containing dP4, M1–3; UALVP 55836, incomplete right maxilla containing dP3–

214 4, M1–2; UALVP 55838, incomplete left maxilla containing dP3–4, M1–2; UALVP
215 55840, incomplete right maxilla containing dP3–4, M1–2; UALVP 35553, incomplete
216 right maxilla containing P2. dP4, M1–3; UALVP 35549, incomplete left maxilla
217 containing dP4, M1; left M2 (different individual); UALVP 35548, incomplete left
218 maxilla containing dP3–4; UALVP 55839, incomplete left maxilla containing dP3–4, M1
219 (broken); UALVP 35552, incomplete left maxilla containing dP3–4, M1–2; UALVP
220 35555, incomplete left maxilla containing ?dP2–dP3; TMP 2011.106.0373, incomplete
221 left maxilla containing dP4, M1–2. UALVP 35544, incomplete left maxilla containing
222 P2, dP3–4, M1–2, M3 broken.

223 UALVP 55548, incomplete left maxilla containing P2–4, M1–3; UALVP 55832,
224 incomplete left maxilla containing P2, broken P3–4, M1–3; UALVP 55831, incomplete
225 left maxilla containing P4, M1–2; UALVP 55830, incomplete right maxilla containing
226 P2–4; UALVP 55835, incomplete right maxilla containing P3–4, M1–3 (M3 broken), and
227 isolated right dP3 in this entry; UALVP 55553, incomplete right maxilla containing P3–
228 4, M1–3; UALVP 35550, incomplete right maxilla containing P2–4 (P4 protocone only);
229 UALVP 35579, incomplete left maxilla containing P2–3; TMP 2009.161.0095,
230 incomplete left maxilla containing P3–4, M1–3; UALVP 35545, incomplete left maxilla
231 containing M1–3 unworn; UALVP 35542, incomplete right maxilla containing M1–2
232 unworn; UALVP 35551, incomplete right maxilla containing M1–3; UALVP 35547,
233 incomplete right maxilla containing M1–2; UALVP 35546, incomplete left maxilla
234 containing M1–3; UALVP 55550, incomplete left maxilla containing M1–3; TMP
235 2011.106.0434, incomplete left maxilla containing M1–2; UALVP 35554, incomplete

right maxilla containing M1–3 (M3 just erupting); UALVP 35543, incomplete right maxilla containing M1–3; UALVP 55555, incomplete left maxilla containing P4, M1-3.

SPECIFIC ETYMOLOGY: Named in honor of Dr. Ruth A. Stockey, Oregon State University, Corvallis, in recognition of her collection, research, and publication of the megaf flora and stratigraphy of Gao Mine (Stockey et al. 2013) and her important contributions to paleobotany more generally.

DIAGNOSIS: Differs from all known species of *Ectocion* except *E. parvus* in substantially smaller size; differs from *E. parvus* in shorter, narrower p3 with prominent, anteriorly positioned paraconid. Differs from similar phenacodontid *Copecion* spp. in smaller size, less bunodont molar crowns having stronger parastyle and mesostyle, and stronger hypoconid in p3.

Description and comparisons

Lower incisors

The lower incisors of *E. stockeyae* are known from four jaws, UALVP 55562 (holotype), TMP 2011.106.0143, UALVP 35580 (i2 only), UALVP 55820 (i3 only), and several uncatalogued, isolated teeth. In the holotype, i1–3 are virtually in their original positions: each is procumbent, with labiolingually flattened, spatulate crowns that are weakly convex on their anterior sides and shallowly concave over much of their lingual sides; they are slightly imbricated, labially overlapping the anteriormost part of the crown of the next posterior incisor. The crowns are narrowest at the base and widest at their cutting edges, which are horizontal or gently sloping, elongated, and lightly worn. The first incisor is the smallest but labiolingually most robust, especially medially, where an

interdental wear facet along the widened medial edge marks its contact in life with its counterpart in the opposite (left) dentary. The root of i1 is exposed: it is long, anterodorsally/posteroventrally oblique in keeping with the procumbent crown, with no evidence of a replacing tooth. The i2 is posterior and slightly lateral to i1 (i.e., the lower incisor row trends weakly from anteromedial to posterolateral), and has a longer cutting edge; the lingual side of the crown is weakly swollen at its base. The i3 is slightly smaller than i2, with a shorter crown; it displays, however, a distinct cusp arising posteriorly from its cutting edge, a feature absent from i1 and i2. As in i2, the crown is slightly swollen posterobasally on its lingual side. There is no diastema between i3 and c1. In TMP 2011.106.0143, only i3 is well preserved, closely resembling i3 in UALVP 55562, including having a distinct posterior cusp offset from the main cutting edge. In TMP 2011.106.0143, i1 has been severely damaged and i2 heavily worn, with neither tooth adding to the information from UALVP 55562; all three incisors appear somewhat displaced from their original positions, not showing the imbrication or other contacts as seen in UALVP 55562. The i2 of UALVP 35580 and i3 of 35582 furnish no additional information than the above. Upper incisors of *E. stockeyae* have yet to be discovered.

Canine

Ectocion stockeyae clearly exhibits dimorphism of c1 (C1 is known only from one specimen; see below). In one morph, represented by UALVP 55562 (the holotype, Fig. 2A–C), 55559, and 55819, c1 is low, premolariform, slightly procumbent, in cross section having a narrow, flange-like anterior margin (sometimes faintly crenulated: UALVP 55559), a wider, rounded posterior margin, convex labial surface and slightly hollowed lingual side of the anterior flange, and a miniscule posterobasal cusp. In the

other morph (Fig. 2 D-F), c1 is elongate, caniniform, subcircular in cross section, and gently recurved; weak anterior and posterior ridges extend along the height of the crown; there is no posterobasal cusp. In both morphs, c1 is supported by a single stout root. In UALVP 55559, the root is fully exposed at the broken anterior end of the dentary: its length is about 3X the height of the crown, with no evidence of a replacing tooth. For lack of credible alternatives as elaborated below, we interpret these morphs as sexual in origin, with the caniniform canines representing males, the premolariform canines representing females by analogy with similar patterns of canine dimorphism across a diversity of extinct and extant placental mammal orders (Rose, 2006). Because lower canine dimorphism in *E. stockeyae* occurs both in specimens in which the posterior premolars are deciduous (and the molars are little worn) and in those in which the posterior premolars are replacement teeth (and the molars are more deeply worn), we reject the alternative that these differences are ontogenetic, i.e., that the premolariform teeth are deciduous canines that are replaced by caniniform successors. We also reject the alternative that the canine dimorphism is taxonomic, i.e., that these two groups represent separate species of *Ectocion*: we have found no other dental features in the specimens at hand, including size that would favor this alternative. An incompletely erupted caniniform c1 occurs in UALVP 35571, a 'juvenile' individual, and in UALVP 35573, an 'adult' individual, but no specimens show an incompletely erupted premolariform canine, which seems likely a function of the few individuals at hand in which this tooth is preserved.

UALVP 55555 is an incomplete maxilla that contains the upper canine, P1, P4, and the molars, the only maxilla of *E. stockeyae* in the collection in which C1 is preserved. It

is long and caniniform (although its tip is missing), weakly recurved, and slightly swollen posteriorly at its base. This tooth is shorter than the caniniform c1s described above, but longer and more slender than the premolariform c1s of this species. Its overall caniniform shape and its length suggest that this individual was a male. Canine dimorphism in *E. stockeyae* allows for novel, but credible insight about comparative aspects of the behavior and ecology of this species, as discussed below.

p1–2, P1–2

The p1 of *E. stockeyae* is present in UALVP 35573, 55561, and 55562. Its crown is supported by a stout root and is small, premolariform, with a single cusp (protoconid). The anterior edge of the cusp is thin and anteriorly convex; the longer, thicker posterior edge is weakly concave anteriorly; posterobasally the crown is weakly hollowed to form—from comparison to p2—an incipient talonid; a posterior crest extends from the apex of the protoconid to a tiny hypoconid. Short diastemata separate p1 from c1 and from p2 as seen in, e.g., UALVP 35573.

The p2, present in several specimens, can be single rooted (UALVP 35556) or, more commonly, two-rooted (e.g., UALVP 55549, 55819); in the latter, the roots are strong and diverging, but we have found no evidence of a replacing tooth at the crypt at this locus. Photographs and x-rays of 31 specimens (juvenile and adult) have a double-rooted p2. (See Fig A1). Although p2 is somewhat larger than p1, it is nonetheless small, premolariform—having a single main cusp, the protoconid—with its anterior margin thin, flange-like, and anteriorly convex, but posteriorly widening into a broad talonid bearing in some individuals a comparatively robust hypoconid, whereas in others (e.g., UALVP

55561), this cusp is absent. A weak posterior ridge extends between the protoconid and talonid cusp. West (1971) provided no clear distinction between dp2 and p2 in *Ectocion* or other phenacodontids; lacking evidence of alternatives, premolars at this locus are considered to be replacement teeth.

P1 of *E. stockeyae* is known from an incomplete maxilla that also contains dP3–4, M1 (UALVP 55833). It is small, single-rooted, with a premolariform crown having but one major cusp, the paracone. In cross section the crown is asymmetrically tear drop-shaped, more swollen lingually than labially, and wider posteriorly than anteriorly. Anteriorly, a crest extends from the apex of the paracone to its base, where a small, parastylar cuspule is developed. Posteriorly, a sharper, longer, and less steep crest connects the apex of the paracone to the base of the crown; this crest terminates in a small swelling, but a metastylar cusp is not present. Diastemata intervene between P1 and C1 and between P1 and P2, respectively. UALVP 55549, consisting of left and right maxillae, is missing the crown of P1 bilaterally, but the remnants of the tooth in its alveoli show that P1 can be two-rooted in some individuals.

P2 of *E. stockeyae* occurs in several specimens in which it is well preserved. It is a premolariform tooth, much like P1, but with the following differences: (1) it is larger and taller; (2) it is invariably two-rooted; (3) it is wider posteriorly and proportionally more swollen posterolingually, but a protocone is not developed; (4) an anterior cingulum meets the preparacrista at a diminutive basal parastyle; (5) in some specimens, the anterior cingulum is lingually continuous with a posterolingual cingulum, whereas in others (e.g., UALVP 35544), it is not; (5) the posterior crest and the posterior cingulum meet at a slight elevation, where a miniscule metastylar cusp can be developed. The

349 metastylar corner of P2 contacts the anterior parastylar process of dP3/P3, i.e., a diastema
350 is not developed there.

351 According to West (1971), dP2 is unknown in phenacodontids, making it impossible
352 to determine whether the tooth at the P2 position in *E. stockeyae* is a deciduous premolar,
353 corresponding with dP3–4 in that species, or its ‘permanent’ successor. We have detected
354 no consistent differences in teeth at the P2 position between individuals having deciduous
355 posterior upper premolars and those having their successors and hence, as with their
356 lower counterparts, we consider these to be replacement teeth.

357 *dp3–4, dP3–4*

358 Two-thirds of the specimens of *E. stockeyae* from Gao Mine retain deciduous teeth at
359 the penultimate and ultimate premolar loci, in both lower and upper jaws. These teeth
360 display many, but not all, of the criteria of West (1971) for deciduous teeth at the
361 posterior premolar positions in *Ectocion* and other phenacodontids: he cited crowns lower
362 than their successors, roots weak and splayed for receipt of the replacing tooth, deeper
363 wear than the molars in place with them, paler color than replacement teeth because of
364 weaker mineralization, and thinner enamel than in their successors. In regards dp3–4 of
365 *E. stockeyae* and West’s (1971) criteria: (1) there is no consistent difference in color
366 versus molars in the same jaw; (2) in all specimens, dp3–4 are more heavily worn than
367 the molars occurring with them; (3) the roots of dp3–4 are stout and diverge only slightly
368 (are not weak and widely splayed); (4) the enamel is slightly thinner than in the molars.

369 In *E. stockeyae*, the crown of dp3 is relatively small and narrow (Fig. 3 A, a, B, b).

370 The paraconid is conical, strongly developed but bluntly rounded apically, is in an

anterior position, and arises half the height of the protoconid on the anterior margin. A sharp crest extends from the apex of the protoconid to the base of the paraconid. The protoconid is the largest cusp, subtriangular in cross section, and is aligned directly posterior to the paraconid. The metaconid is variably present, arising from the posterolingual shoulder of the protoconid as a miniscule cusp in at least 80% of the cases, a minor crest, or it can be absent altogether. The talonid is strongly developed, unbasined, and has a high, trenchant cristid obliqua extending from the posterolingual side of the postvallid wall (and metaconid, if present) to the robust hypoconid. Short, weak pre- and postcingulids are present in some dp3s absent in others.

The dp4 of *E. stockeyae* is larger than dp3; the crown is elongate and tapers anteriorly, but is fully molariform, with a tricuspid trigonid and a tricuspid, basined talonid. The paraconid is robust, in an anterolingual position, spaced relatively far anteriorly from the metaconid, and in some specimens, is twinned, producing a squared-up trigonid (Fig. 3A, a, B, b). The apex of the cusp rises little above the height of the paracristid, which forms a tall crest that is directed labially and then flexed posteriorly to begin an ascent on the protoconid. The protoconid is slightly taller than the paraconid, is subtriangular in cross section, and located at the posterolabial corner of the trigonid. The metaconid is positioned almost directly lingual to the protoconid, with the postvallid wall weakly oblique from posterolingual to anterolabial. The talonid is broader than the trigonid, with well-developed hypoconid, hypoconulid, and entoconid; the hypoconulid is lingual to the midline of the crown, closer to the entoconid but not twinned with it. The cristid obliqua is high and meets the postvallid wall slightly lingual to the deepest part of the protocristid notch. Some specimens show an accessory cusp on the lingual edge of the postvallid

394 wall, below the metaconid. The pre- and postcingulids are longer and more prominent
395 than in dp3. These premolars of *E. stockeyae* closely resemble dp3–4 of *E. osbornianus*
396 as illustrated by West (1971: fig. 18), confirming that they are deciduous teeth.

397 In dP3 of *E. stockeyae*, the crown is relatively small, subtriangular in occlusal outline,
398 with a robust anterior parastylar process, a long, strongly oblique (anterolabial to
399 posterolingual) anterior margin, is wider posteriorly than anteriorly, and is three-rooted.
400 The protocone is shorter than paracone and metacone, and is in a posterior position,
401 lingually opposite the metacone. The paracone and metacone are joined through most of
402 their height; there is no mesostyle or hypocone. The conules are small and variably
403 developed: among nine specimens examined, a well-developed paraconule but no
404 metaconule occurred in six, both conules were present in three, but with the metaconule
405 small and irregular in form; no dP3s had a metaconule but no paraconule.

406 In dP4, the crown is larger than in dP3 (Fig. 4), is subquadrate in occlusal outline
407 (subequal in length and width) with rounded corners, and is three-rooted; a parastyle is
408 present, but not projecting anteriorly as in dP3. The paracone and metacone are well
409 separated by a prominent, labially bulging mesostyle, and with their accompanying
410 crests, form a W-shaped ectoloph. A strong protocone (lingually opposite the paracone),
411 plus robust conules and hypocone (lingually opposite the metacone) are developed, with
412 the whole comprising a fully molariform occlusal morphology, differing from M1
413 primarily in its smaller size and less transverse dimensions.

414 *p3–4, P3–4*

415 In comparison to dp3, p3 of *E. stockeyae* is: (1) wider and stouter overall; (2) the

paraconid is usually smaller and can be represented only by the paracristid without a cusp at the end of the crest; (3) the protoconid is subequal in height to that in dp3 but is more robust; (4) the talonid is better developed and in some specimens, an incomplete basin is formed, accompanied by an entoconid (e.g., UALVP 35580) or an entoconid and incipient hypoconulid (e.g., UALVP 35568, 55563), but open lingually at a deep, narrow talonid notch; (5) pre- and postcingulids are longer and more conspicuous than in dp3 (Fig. 3C, c, D, d).

The p4 of *E. stockeyae* is readily distinguished from dp4: (1) it is wider relative to its length; (2) the paraconid is usually more labial in position, inset somewhat from the lingual margin of the trigonid and more in line with the protoconid, not the metaconid; (3) the paraconid is closer to the metaconid, with paracristid and trigonid overall proportionally shorter anteroposteriorly; (4) the talonid is shorter and wider relative to its length, but its basin is smaller and shallower; (5) the talonid cusps are variable, not always well developed, but when present are usually lower and more swollen than in dp4. In the ‘juveniles’ of *E. stockeyae* at hand, occlusal wear is always greater on dp3–4/dP3–4 than on the molars, which show little or any wear at all, whereas in ‘adult’ specimens, p3–4 show little wear, whereas the molars are more deeply worn, in some specimens the occlusal surface having been worn flat. Thewissen (1990: 29) stated that in ‘typical’ *Ectocion*, the stage of wear is similar in p4 and m1, which is not the case in either the ‘juvenile’ or ‘adult’ specimens of *E. stockeyae* from Gao Mine.

Of previously known species of *Ectocion*, *E. parvus* is closest to *E. stockeyae* in size (*E. nanabiensis* Beard and Dawson, 2009, from the early Wasatchian of Mississippi, may be smaller than *E. parvus* but is only known from P4 and an incomplete M1 and is

considered no further here). Indeed, the most distinctive feature of the lower dentition of *E. stockeyae* compared to that of *E. parvus* is the relatively small size of p3 (mean L = 4.14, mean W = 2.35, n = 23), about 30% shorter than that of *E. parvus* (e.g., from the earliest Wasatchian of the Bighorn Basin, northwestern Wyoming (mean L = 5.62, mean W = 3.16, n = 6/7: Gingerich 1989: table 20; see also Thewissen 1990: table A13; Rose et al. 2012: table 9). In *E. parvus*, p3 is relatively large compared to the lower molars (Thewissen 1990: 42), which are subequal in size to those of *E. stockeyae* (Table 1). Moreover, in *E. stockeyae*, the paraconid of p3 is well developed and in an anterior position; this cusp is weak or absent in p3 of *E. parvus* (Gingerich 1989: 50; Thewissen 1990: fig. 26; Rose et al. 2012: fig. 46). An additional difference is seen in the coronal morphology of p4: in *E. parvus*, the paraconid has been recorded as absent (Thewissen 1990: 42), but it is present and often well developed (sometimes 'twinned') in *E. stockeyae*, as noted above.

P3 of *E. stockeyae* differs from dP3 in several respects, including: (1) larger size with proportionally larger coronal features; (2) a weakly projecting anterior parastylar process and smaller parastyle; (3) a more nearly transverse anterior margin of the crown, closer in length to the posterior margin; (4) the protocone more anteriorly positioned relative to the metacone, opposite the centrocrista notch or, in some individuals, opposite the paracone (e.g., UALVP 55548, Fig. 4); (5) robust paraconule, lingually positioned away from the paracone (but no metaconule in the few specimens at hand); and (6) a well developed, anteroposteriorly continuous ectocingulum.

In comparison to dP4, P4 of *E. stockeyae*: (1) is larger; (2) has a less projecting anterior parastylar process and a less oblique (i.e., more nearly transverse) anterior

margin; (3) the anterior and posterior margins are subequal in length; (4) the crown is shorter anteroposteriorly and more transverse; (5) a mesostyle is absent; (6) has a larger, more robust paraconule; and (7) a small hypocone in some (e.g., UALVP 55548, 55835). The features of P3–4 in *E. stockeyae* clearly agree with those of replacement teeth at these loci in other species of *Ectocion* (see West, 1971; Thewissen, 1990). The eruption sequence of the penultimate and ultimate replacement premolars relative to one another in either the lower or upper jaws cannot be determined from the specimens of *E. stockeyae* at hand.

Molars

As shown in the specimen lists above, the molars of *E. stockeyae* are abundantly represented in the collections from Gao Mine. They share the characteristic features of *Ectocion* as elaborated by Thewissen (1990: 25): bunolophodonty, a U-shaped protocristid (metacristid of Thewissen) in the lower molars, a low paracristid, and usually no paraconid, upper molars with large parastyle and mesostyle connected by a W-shaped ectoloph, and no hypocone in M3. The molars of some specimens are exceptionally well preserved (e.g., UALVP 35546), while other specimens record aspects of the replacement sequence, showing, e.g., graduated, decreasing wear from M1 to M3 (UALVP 55836), and, hence relative timing of eruption: collectively, these specimens indicate that m1/M1 erupted first, followed successively by m2/M2 and then m3/M3. In this context, perhaps the youngest specimen among those at hand is UALVP 35574, an incomplete dentary in which dp4 is in place but m1 had only partly erupted (the other teeth of this individual are not preserved). Numerous specimens of *E. stockeyae*, however, demonstrate that dp3–4/dP3–4 were still functional after the molars in the same jaw had fully erupted (e.g.,

UALVP 55556, 55568, 55829 [dentaries]; UALVP 5554, 55549, 55552 [maxillae])—
although these teeth were perhaps replaced soon after, as in no specimens containing
deciduous posterior premolars are the molars more than slightly worn, which is near
universally the case in those in which p3–4/P3–4 are in place.

Some comparisons with other species of Ectocion

According to Thewissen (1990: 25): “Overall size and shape characters of the
premolars distinguish best between different *Ectocion*”; in our opinion, these features are
most clearly seen in p3–4/P3–4. Whereas the p3 of *E. stockeyae* is substantially smaller
than p3 in all other species of *Ectocion*, it exhibits distinctive morphological features, as
well. It has a small, but well-developed, subconical paraconid, in contrast to *E. parvus*, in
which a paraconid is absent (Gingerich 1989), and *E. osbornianus*, in which is variable in
occurrence (Thewissen 1990: 37, figs. 18, 19); the paraconid in *E. cedrus* is “high”
relative to other trigonid cusps (Thewissen 1990: 29). In *E. stockeyae*, p3 lacks a
metaconid, resembling *E. collinus*, *E. superstes* and *E. parvus* in that regard, but unlike *E.*
cedrus and *E. major*, in which a metaconid is present or *E. mediotuber* and *E.*
osbornianus, in which this cusp can be present or absent (Thewissen 1990). The
hypoconid in p3 of *E. stockeyae* is high relative to other talonid cusps and often robust,
resembling that in *E. osbornianus*, *E. parvus*, and *E. superstes*, but contrasting with *E.*
collinus, *E. cedrus*, *E. mediotuber*, and *E. major*, in which the p3 hypoconid is small
(Thewissen 1990).

Like p3, the p4 of *E. stockeyae* is smaller than its counterpart in other *Ectocion*
species. The paraconid is always present, small in some individuals (e.g., UALVP

55568), but large in others, in which it may be accompanied by accessory cuspules (UALVP 55566), unlike in *E. mediotuber*, in which the paraconid on p4 is small or absent, or in *E. parvus*, in which the p4 paraconid is absent altogether (Thewissen 1990).

Although the morphology of the posterior premolars may be the best means of distinguishing the species of *Ectocion*, the interspecific distribution of coronal features reveals no clearly compelling patterns on which to base a hypothesis of relationships.

Comparison with *Copecion*

Ectocion stockeyae is notable for its small size, slightly less than *E. parvus* from the late Clarkforkian and early Wasatchian of Wyoming and Colorado (Thewissen 1990; Burger 2012). *E. parvus*, in turn, resembles in many respects the small phenacodontid *Copecion* Gingerich 1989, from the Clarkforkian and Wasatchian of the Western Interior (Gingerich 1989; Thewissen 1990; Rose et al. 2012). Of particular interest here, however, is the resemblance of the presumed replacement p4 in *Copecion* (as illustrated in, e.g., Thewissen 1990: fig. 43) to the dp4s of *Ectocion*. Might, then, *E. stockeyae* be instead a species of *Copecion*? A clearly diagnostic difference between *Copecion* and *Ectocion*, however, is present in p3: in *Copecion*, the hypoconid is weak, whereas in p3 of *Ectocion* the hypoconid is strong (Thewissen 1990), proportions seen in p3 of *E. stockeyae*, as well (e.g., UALVP 55561, 55563). In addition, the dental dimensions of the species of *Copecion* are significantly greater than those of *E. stockeyae* (see Thewissen 1990)—all features that remove *Copecion* from consideration in determining the identification of the new species of *Ectocion* from Gao Mine.

Aspects of the paleobiology of *Ectocion stockeyae*

The large collection of well-preserved dental specimens from Gao Mine allows for several insights into the paleobiology of *E. stockeyae*. As noted, an unusual feature of this collection is the large number of ‘juveniles’ that retain dp3–4/dP3–4, occurring in a ratio of about 3:2 to ‘adults’ in which these teeth have been replaced. Moreover, the molars of the ‘juveniles’ are little worn or not worn at all (e.g., UALVP 35546), whereas those of the ‘adults’ are always worn, sometimes deeply so with complete loss of occlusal features (see, e.g., UALVP 35571)—all in keeping with the relative ontogenetic age of the two groups as implied initially by their premolar morphology. ‘Juveniles’ in which deciduous premolars are in place and functional are quite uncommon at other, large Paleocene mammal assemblages from the Alberta Basin (e.g., Youzwysyn 1988; Scott 2003, 2008; Scott et al. 2015; Fox in progress), and are often not represented at all in collections from these sites. The different numbers in the two age classes of *E. stockeyae* at Gao Mine cannot be explained by physical factors, e.g., sedimentologic sorting or other taphonomic effects on these specimens, which are unimodal in molar size, or by biased choice of specimens in collecting. Instead, the large numbers of the ‘juvenile’ individuals from the site must reflect post-mortem sampling from a population or populations in which ‘juveniles’ predominated originally, a structure that has not been reported in other phenacodontids, including *Ectocion* (Thewissen 1990; Rose et al. 2012).

During this study, we X-rayed 21 dentaries containing the deciduous posterior premolars to determine if replacement teeth were forming at these loci, but none were discovered using this technique. In addition, several dentaries were dissected for the same purpose; of these, only one (UALVP 55568) contained a partially formed premolar, directly beneath dp4, in a dentary that also contains dp3. This and the large number of

552 individuals in which the deciduous posterior premolars and the molars are in place
553 suggest a delay in the timing of replacement of the posterior premolars or acceleration in
554 the emergence of the molars (Fig. 5 and Fig. A1). West (1971: 35–36) recorded 28
555 specimens from three species of *Ectocion* at nine ‘localities’ (spanning mid-Tiffanian to
556 Wasatchian in age) in which deciduous posterior premolars were preserved in jaws in
557 which one or more molars had erupted. This small number of specimens and their wide
558 distribution geographically and temporally (no more than 11 specimens at any one
559 ‘locality’) give no clear signal concerning the biological meaning of a pattern if one is,
560 indeed, present. By contrast, the sample of *E. stockeyae*, from a single horizon in a single
561 quarry, provides insight into the original population structure not yet recorded for
562 phenacodontids (see, e.g., Domingo et al. 2018 for the importance of such occurrences).
563 From the size of the jaws concerned and the dimensions of the molars, it appears that
564 these ‘juveniles’ of *E. stockeyae* were relatively large at this stage in their lives, many
565 equal in body size to those possessing a fully ‘adult’ dentition as well as being more
566 numerous. In marked contrast, however, the sample from Gao Mine includes no
567 individuals in which dp3–4, dP3–4 are erupting, leaving earlier stages in the ontogeny of
568 *E. stockeyae* entirely unrepresented in the collection—even though during life this age
569 cohort must have been the most numerous of all. This pattern of replacement, in which
570 deciduous premolars were retained until the molars had erupted and were functional,
571 suggests that the life span of *E. stockeyae* was short, and growth and dental development
572 rapid as expressed in Schultz’s Rule: in such species, the molars have erupted before the
573 premolars are replaced, contrasting with species having long life spans, and slow growth

574 and dental replacement (Schultz 1960; Smith 2000; Sánchez-Villagra 2010; Domingo et
575 al. 2018).

576 A second aspect of the paleobiology of *E. stockeyae* of interest stems from the
577 dimorphism of the lower canines, with the caniniform teeth representing males and the
578 premolariform teeth, females (we assume that dimorphism also characterizes C1, but as
579 described above, only one specimen containing C1 is presently known). This pattern
580 departs somewhat from canine dimorphism in many other mammals, both extinct and
581 extant, in which the upper and lower canines are caniniform but differ in size, with c1
582 being somewhat smaller in females than in males. Gingerich (1981) described this latter
583 pattern in the early Eocene horse *Hyracotherium*, Krishtalka et al. (1990) in the Eocene
584 primate *Notharctus*, and O’Leary et al. (2000) in the early Paleocene mesonychid
585 *Ankalagon* (Matthew, 1897). Gingerich (1981) cited several other examples of probable
586 canine sexual dimorphism in uinatheres, tapiroids, primates, and other equids. We,
587 however, know of no other published example of a species in which c1 can be caniniform
588 or premolariform, as in *E. stockeyae*: by contrast, in *E. osbornianus* the lower canine in
589 ostensible females is smaller than the upper but is nonetheless caniniform in shape
590 (Thewissen 1990: fig. 18). The specimen of *E. parvus* illustrated by Gingerich (1989) and
591 Thewissen (1990: fig. 26) (UM 77202, from the Clarks Fork Basin, Wyoming) has a
592 small canine and on that account was perhaps from a female individual.

593 Two implications from this pattern in *E. stockeyae* suggest themselves. First, sexual
594 dimorphism of the canines in mammals is often related to a distinctive population
595 structure in which males are significantly outnumbered by females in social groups and
596 are polygynous, with intense competition among the fewer males for mates. Again, while

the specimens of *E. stockeyae* that preserve canines are too few at present to yield meaningful numbers of ostensible males versus females, the clear dimorphism in the canines that these specimens do exhibit is consistent with the hypothesis of polygyny in *E. stockeyae*, as in, e.g., *Hyracotherium*, *Notharctus* (Gingerich 1981; Krishtalka et al. 1990), and other species having a similar canine pattern.

Second, dimorphic canines could reflect different food niches of the sexes, perhaps a difference greater than in species in which the female canines are smaller than in males but are nonetheless caniniform, piercing teeth. On the other hand, we have found no other consistent morphological differences between the sexes in teeth at other loci that would indicate dietary differences, a general pattern as reported by Gingerich (1981: 447): “Even in highly dimorphic species of mammals, the sizes of central cheek teeth in males and females are too similar to appear bimodal and permit recognition of the sex of individuals.” There is no evidence of bimodality in p1/P1–p2/P2 or the molars of *E. stockeyae*, only in the posterior premolars, reflecting difference in ontogenetic age, not sex. Moreover, specimens of *E. stockeyae* that retain canines are at present too few to determine whether males or females had higher mortalities, either as ‘juveniles’ or as ‘adult’ animals.

A final issue raised by *E. stockeyae* from Gao Mine concerns the pattern of species evolution within the genus. In Thewissen’s (1990) review of *Ectocion*, seven species were recognized as valid, ranging in age from early Tiffanian to early Bridgerian (Thewissen 1990: fig. 59). Thewissen did not undertake an explicit analysis of relationships among these species, but plotted their stratigraphic distributions in the sedimentary basins in which they occur. Three of these species are closest in age to *E.*

620 *stockeyae*: *E. collinus* Russell 1929, from earliest to middle Tiffanian; *E. cedrus*
621 Thewissen 1990, from middle to late Tiffanian; and *E. mediotuber* Thewissen 1990, late
622 Tiffanian, to the Tiffanian–Clarkforkian boundary. The Gao Mine species, however, is
623 closest in size to *E. parvus* Granger 1915, which is substantially younger than Gao Mine,
624 first appearing in the late Clarkforkian and ranging into the early Wasatchian (Gingerich
625 1989; Thewissen 1990; Burger 2012). *E. parvus* was previously the smallest known
626 species of *Ectocion*, an aspect given special interest owing to its occurrence at the
627 Paleocene/Eocene Thermal Maximum and reports of mammalian ‘dwarfing’ during that
628 interval (e.g., Gingerich 1989; Gingerich and Smith 2006; Yans et al. 2006; Burger 2012;
629 Rose et al. 2012; Secord et al. 2012; D’Ambrosia et al. 2017). Indeed, *E. parvus* has been
630 considered to possibly be a “dwarfed version of *E. osbornianus* coincident with the
631 PETM” (Wood et al. 2007: 249), and, more broadly, distinguished morphologically only
632 from co-eval *E. osbornianus* by its smaller size (about 18% smaller: Gingerich 1989: 51,
633 fig. 32; Burger 2012).

634 *E. stockeyae* is significantly smaller in dental dimensions than those species nearest to
635 it in age—*E. collinus*, *E. cedrus*, and *E. mediotuber*—and is smaller than *E. parvus* from
636 Wyoming and Colorado in most dental dimensions (Table 1), a species already widely
637 characterized as ‘dwarfed’ (Gingerich 1989; Thewissen 1990; Burger 2012; Rose et al.
638 2012). From the evidence presented here, it is clear that ‘dwarfing’ in *E. stockeyae* was
639 independent of that in the similar-sized *E. parvus* and did not stem from a sharp
640 temperature rise like that of the PETM: no evidence of a similar temperature excursion
641 can be inferred from the paleobotanical record at Gao Mine (Stockey et al. 2013 and
642 references there), nor from marine benthic temperatures and correlative North American

Ti5a mammal localities more generally (Secord 2008: fig. 65); on that account, it also seems clear that *E. stockeyae* was not a northward migrant responding to warming temperatures, as Burger (2012) has hypothesized for *E. parvus* in Colorado and Wyoming. Hence, it is evident that some other factor(s) than temperature change must be invoked to explain ‘dwarfing’ in *E. stockeyae* at Gao Mine. What these factors might have been, however, is probably beyond the capacity of the fossil record to reveal.

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Figure captions:

Fig. 1. Map of Alberta, Canada, showing the location of Gao Mine (Modified from Stockey et al. 2013). Solid black lines represent numbered highways; dotted lines show township boundaries.

Fig. 2. *Ectocion stockeyae* sp. nov. from the late Tiffanian Gao Mine locality, Paskapoo Formation, Alberta. UALVP 55562 (holotype), incomplete right dentary containing i3, c1, p1–4, m1–3, (A) lingual, (B), occlusal, and (C), labial views. UALVP 55556, incomplete right dentary containing caniniform c1, dp3–4, m1–3, and alveoli for i3, p1–2, in (D) lingual, (E) occlusal, and (F) labial views.

Fig. 3. *Ectocion stockeyae* sp. nov. from the late Tiffanian Gao Mine locality, Paskapoo Formation, Alberta. Occlusal views of dentaries of juvenile and adult specimens and close ups of p3–4 and dp3–4. (A, a) UALVP 55828 and (B, b) UALVP 55556 correspond to juveniles, observe the shapes of dp3 and dp4. (C, c) UALVP 55562 and (D, d) 55561 correspond to adults, compared the shape of p3 and p4.

Fig. 4. *Ectocion stockeyae* sp. nov. from the late Tiffanian Gao Mine locality, Paskapoo Formation, Alberta. Occlusal views of (A) UALVP 55549, incomplete right maxilla containing P1–4, M1–3; (B) UALVP 55548, incomplete left maxilla, containing P2–4, M1–3; and (C) UALVP 55554, incomplete right maxilla containing P2, dp3–4, M1–3.

Fig. 5. *Ectocion stockeyae* sp. nov. from the late Tiffanian Gao Mine locality, Paskapoo Formation, Alberta: wear stages in the lower dentition. (A) UALVP 55556, incomplete right dentary, containing caniniform c1, dp3–4, m1–3, and alveoli for i3, p1–2. (B) UALVP 55559, incomplete right dentary containing premolariform c1, dp3–4, m1–2, alveoli for p1–2. (C) UALVP 55549, incomplete right dentary (different individual than maxillae in this entry) containing p3–4, m1–3, alveolus for p1. (D) UALVP 55562, incomplete right dentary containing i1–3, premolariform c1, p1–4, m1–3. (E) UALVP 55564, incomplete left dentary containing p3–4, m1–3. (F) UALVP 55826, incomplete right dentary containing p3–4, m1–2, m3 (broken), and alveoli for c1, p1–2.

Fig.A1. *Ectocion stockeyae* sp. nov. from the late Tiffanian Gao Mine locality, Paskapoo Formation, Alberta. X-rays of lower jaws. (A) UALVP 55556, incomplete right dentary containing caniniform c1, dp3–4, m1–3, and alveoli for i3, p1–2, in. (B) UALVP 55827, incomplete right dentary containing dp3–4, m1–3. (C) UALVP 55568, incomplete right dentary containing p2 (broken), dp3 (broken), dp4, partly formed replacement p4, m1–3, alveoli for c1, p1. (D) UALVP 55562 (holotype), incomplete right dentary containing i3, c1, p1–4, m1–3.

Table 1.- Summary statistics of *Ectocion stockeyae* (in mm.) and mean values of *E. parvus* (in mm. Taken from Thewissen, 1990). N, number of specimens; σ , standard deviation; c.v., coefficient of variation.

	p3	p4	m1	m2	m3	P3	P4	M1	M2	M3
Mean length	4.24	5.52	5.64	5.90	6.12	4.55	5.34	5.96	6.21	5.11
<i>E. parvus</i> mean length	5.77	6.3	5.47	5.48	5.88	5.20	5.60	5.67	6.33	5.2
Observed range	3.7- 4.7	4.7- 6.2	5.0- 7.0	5.4- 6.7	5.6- 6.9	4.0- 5.1	4.6- 6.0	5.2- 6.6	5.4- 7.3	4.5- 6.1
σ	0.25	0.30	0.36	0.29	0.44	0.304	0.36	0.36	0.425	0.54 2
c.v.	5.86	5.57	6.37	5.06	5.52	6.67	6.77	6.16	6.8	10.6
Mean width	2.61	3.57	4.31	4.43	3.9	4.38	5.9	7.48	8.11	6.0
<i>E. parvus</i> mean width	2.8	4.2	4.36	4.64	3.83	5.15	6.55	7.37	7.3	6.0
Observed range	1.9- 3.9	3.0- 4.5	3.5- 5.4	3.8- 5.5	3.3- 4.9	3.8- 5.4	5.0- 7.1	6.5- 8.5	7.2- 9.4	5.1- 7.9
σ	0.40	0.31	0.32	0.34	0.44	0.46	0.60	0.39	0.50	0.68
c.v.	15.4 5	8.88	7.59	7.77	11.2 9	10.6	10.3	5.24	6.24	11.3
N	42	52	51	41	31	23	27	30	29	18

Fig. 2. *Ectocion stockeyae* sp. nov. from the late Tiffanian Gao Mine locality, Paskapoo Formation, Alberta. UALVP 55562 (holotype), incomplete right dentary containing i3, c1, p1–4, m1–3, (A) lingual, (B), occlusal, and (C), labial views. UALVP 55556, incomplete right dentary containing caniniform c1, dp3–4, m1–3, and alveoli for i3, p1–2, in (D) lingual, (E) occlusal, and (F) labial views.

Fig. 3. *Ectocion stockeyae* sp. nov. from the late Tiffanian Gao Mine locality, Paskapoo Formation, Alberta. Occlusal views of dentaries of juvenile and adult specimens and close ups of p3-4 and dp3-4. (A, a) UALVP 55828 and (B, b) UALVP 55556 correspond to juveniles, observe the shapes of dp3 and dp4. (C, c) UALVP 55562 and (D, d) 55561 correspond to adults, compared the shape of p3 and p4.

Fig. 4. *Ectocion stockeyae* sp. nov. from the late Tiffanian Gao Mine locality, Paskapoo Formation, Alberta. Occlusal views of (A) UALVP 55549, incomplete right maxilla containing P1–4, M1–3; (B) UALVP 55548, incomplete left maxilla, containing P2–4, M1–3; and (C) UALVP 55554, incomplete right maxilla containing P2, dP3–4, M1–

Fig. 5. *Ectocion stockeyae* sp. nov. from the late Tiffanian Gao Mine locality, Paskapoo Formation, Alberta: wear stages in the lower dentition. (A) UALVP 55556, incomplete right dentary, containing caniniform c1, dp3-4, m1-3, and alveoli for i3, p1-2. (B) UALVP 55559, incomplete right dentary containing premolariform c1, dp3-4, m1-2, alveoli for p1-2. (C) UALVP 55549, incomplete right dentary (different individual than maxillae in this entry) containing p3-4, m1-3, alveolus for p1. (D) UALVP 55562, incomplete right dentary containing i1-3, premolariform c1, p1-4, m1-3. (E) UALVP 55564, incomplete left dentary containing p3-4, m1-3. (F) UALVP 55826, incomplete right dentary containing p3-4, m1-2, m3 (broken), and alveoli for c1, p1-2.

Table 1S. Measurements in millimeters of the specimens mentioned or figured in the manuscript. L, length; W, width. *Figured

Lower dentition

Specimen	p3	p3	p4	p4	m1	m1	m2	m2	m3	m3
UALVP	L	W	L	W	L	W	L	W	L	W
35556	3.7	2	5.5	3.1	5.4	3.9	5.7	4		
35568	4.3	2.8	4.7	3.6	5.4	4.1	5.6	4.2	5.6	4.2
35571			5.5	3.6	5	4.6	5.8	4.8	5.8	4.8
35573	4.5	2.8								
35574			5.4	3.2						
35580	4.3	3	5	3	5.5	4.5				
35582					5.2	4.2	5.5	4.5	5.8	3.3
55549*	4.7	3.1	5.3	3.8	5.4	4.3	5.7	4.4	6.2	3.5
55556*	4.1	2.5	5.7	3.2	5.7	4	6.1	4.1	6.5	3.6
55559*	4	2.4	5.5	3	5.4	4.2	5.8	3.9		
55561foto	4.5	2.7	5.5	3.8	5.9	4.4	6	4.7	6.9	3.6
55562 (holotype)*	4.7	3.1	5.3	3.8	5.4	4.3	5.7	4.4	6.2	3.5
55563	4.4	3.1	5.2	3.9	5.9	4.3	6	4.4	6.1	3.5
55564*	4.5	2.9	5.5	4	5.7	5.1	5.9	4.9	6	3.8
55565	4.2	2.7	5.4	3.6	5.5	4.1	6	4.3	6	3.6
55566	4.4	2.8	5.6	3.6	5.4	4	5.7	4.5	6.5	3.5
55567			5.7	3.9	6	5.4	5.6	4.5	6.3	4
55568			5.7	3.5	5.8	4.3	6.2	4.3	6.1	3.5

55819	4,1	2.3								
55820	4	1.9								
55826	4.5	2.9	5.7	3.8	6	4.5	6.2	4.5		
55829*	4.2	2.4	5.9	3.4	5.4	4.3	5.7	4.5	6.2	3.9
Tyrrell specimen										
TMP 2011.106.0143	4.2	3	5.1	3.8	5.6	4.6				

Upper dentition

Specimen	P3	P3	P4	P4	M1	M1	M2	M2	M3	M3
UALVP	L	W	L	W	L	W	L	W	L	W
35544	4.2	4.3	5.5	5.6	5.9	7.5	6.3	8		
35546					6.1	7.9	6.3	8.5	5	6
55554	4.4	4.1	5.7	5.5	5.6	7.5	5.8	8		
55548*	5.1	5.4	5.7	7.1	6.1	8.5	7.3	9.4	6	7.9
55549*	4.4	3.9	5	5.5	5.4	7.1	5.5	7.5	4.5	5.5
55552	4.9	4.4	6	5.9	6.6	7.2	6.7	8.3	5.8	6.3
55555			5	6.4	5.9	7.6	6	8.3	4.7	6.2
55833	4.5	4.1	5.2	5.7	6					
55835	5	5.1	5.5	7.1	6.6	8	6.9	9.2	5.8	
55836	4.2	4.3	5.6	6	6	7.9	6.9	8.3