The first North American *Propterodon* (Hyaenodonta: Hyaenodontidae), a new species from the late Uintan of Utah

Shawn P Zack Corresp. 1, 2

1 Department of Basic Medical Sciences, University of Arizona College of Medicine – Phoenix, Phoenix, AZ, United States

2 School of Human Evolution and Social Change, Arizona State University, Tempe, AZ, United States

Corresponding Author: Shawn P Zack
Email address: zack@email.arizona.edu

The carnivorous mammalian fauna from the Uintan (late middle Eocene) of North America remains relatively poorly documented. This is unfortunate, as this is a critical interval in the transition from "creodont" to carnivoran dominated carnivore guilds. This study reports a new species from the Uinta Formation of the Uinta Basin, Utah, the first North American species of the otherwise Asian hyaenodont genus *Propterodon*. The new species, *Propterodon witteri*, represented by a dentary with M_{2-3} from the late Uintan Leota Quarry, is larger than the well-known *P. morrisi* and *P. tongi* and has a larger M_3 talonid, but is otherwise very similar. A phylogenetic analysis of hyaenodont interrelationships recovers *P. witteri* as a hyaenodontine but is generally poorly resolved. A relationship between Hyaenodontinae and *Oxyaenoides*, recovered by many recent analyses, is not supported. Among the Asian species of *Propterodon*, *P. pishigouensis* is reidentified as a machaeroidine oxyaenid and recombined as *Apataelurus pishigouensis* new combination. *Isphanatherium ferganensis* may also represent an Asian machaeroidine. Identification of a North American species of *Propterodon* and an Asian *Apataelurus* increases the similarity of North American Uintan and Asian Irdinmanhan faunas and suggests that there was substantial exchange of carnivorous fauna during the late middle Eocene.

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6 Shawn P. Zack[1,2]

7

8 [1] Department of Basic Medical Sciences, University of Arizona College of Medicine-Phoenix,

9 Phoenix, Arizona, United States

10 [2] School of Human Evolution and Social Change, Arizona State University, Tempe, Arizona,

11 United States

12

13 Corresponding Author:

14 Shawn P. Zack[1]

15 435 N 5th Street, Phoenix, Arizona, 85004, United States

16 Email address: zack@email.arizona.edu

17

18 **Abstract**

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20 remains relatively poorly documented. This is unfortunate, as this is a critical interval in the

21 transition from "creodont" to carnivoran dominated carnivore guilds. This study reports a new

22 species from the Uinta Formation of the Uinta Basin, Utah, the first North American species of

23 the otherwise Asian hyaenodont genus *Propterodon*. The new species, *Propterodon witteri*,

24 represented by a dentary with M_{2-3} from the late Uintan Leota Quarry, is larger than the well-

25 known *P. morrisi* and *P. tongi* and has a larger M_3 talonid, but is otherwise very similar. A

26 phylogenetic analysis of hyaenodont interrelationships recovers *P. witteri* as a hyaenodontine but

27 is generally poorly resolved. A relationship between Hyaenodontinae and *Oxyaenoides*,

28 recovered by many recent analyses, is not supported. Among the Asian species of *Propterodon*,

29 *P. pishigouensis* is reidentified as a machaeroidine oxyaenid and recombined as *Apataelurus*

30 *pishigouensis* new combination. *Isphanatherium ferganensis* may also represent an Asian

31 machaeroidine. Identification of a North American species of *Propterodon* and an Asian

32 *Apataelurus* increases the similarity of North American Uintan and Asian Irdinmanhan faunas

33 and suggests that there was substantial exchange of carnivorous fauna during the late middle

34 Eocene.

35

Introduction

37 Hyaenodonts are a significant component of Eocene carnivorous guilds across the Holarctic and

38 Africa (Gunnell, 1998; Rose, 2006; Lewis and Morlo, 2010). Along with other "creodonts"

39 (e.g., Oxyaenidae), hyaenodonts are distinguished from modern carnivorans and their fossil

40 relatives (Carnivoraformes) by the presence of multiple carnassial pairs in the dentition, which

41 results in alternating shearing and crushing/grinding areas in the dentition, rather than regional

42 - - separation of the molar series into mesial shearing and distal crushing/grinding areas. The

43 latter innovation in Carnivoraformes (and convergently in Viverravidae: Zack, 2019) may have

44 facilitated the ecological diversification of carnivorans (Friscia and Van Valkenburgh, 2010),

45 ultimately allowing carnivorans to displace hyaenodonts over the course of the Paleogene in the

46 northern continents and Miocene in Africa (Wesley-Hunt, 2005; Friscia and Van Valkenburgh,

47 2010; Borths and Stevens, 2017).

48   In North America, hyaenodont diversity was greatest during the earlier half of the

49 Eocene, particularly the Wasatchian and Bridgerian North American Land Mammal Ages

50 (NALMAs) (Gunnell, 1998; Van Valkenburgh, 1999; Wesley-Hunt, 2005; Friscia and Van

51 Valkenburgh, 2010). In the subsequent Uintan NALMA, hyaenodont diversity declined

52 dramatically. Only four genera, *Limnocyon*, *Mimocyon*, *Oxyaenodon*, and *Sinopa* have been

53 described from Uintan faunas (Matthew, 1899, 1909; Peterson, 1919; Gustafson, 1986), although

54 an additional, small hyaenodont taxon is known but undescribed (Rasmussen et al., 1999; pers.

55 obs.). This mid-Eocene decline of hyaenodont and other "creodont" diversity corresponds with

56 an increase in the diversity of carnivorans and their immediate relatives (Carnivoraformes) (Van

57 Valkenburgh, 1999; Wesley-Hunt, 2005; Friscia and Van Valkenburgh, 2010), a pattern

58 suggesting some form of replacement of hyaenodonts by carnivoraform taxa. Understanding the

59 nature of that replacement requires a detailed record of the diversity of both groups.

60   Reexamination of existing collections is one key to refining the record of carnivorous

61 mammals across this critical period, as overlooked or misidentified specimens can shift the

62 temporal and geographic ranges of known taxa and allow recognition of new forms. MCZ VPM

63 19874, the specimen that forms the focus of the present study is an example of significant

64 discoveries that can be made in existing collections. The specimen, a dentary with M_{2-3}, was

65 collected by a Harvard University expedition to the Uinta Basin, Utah in 1940 (Fig. 1) and has

66 not been described or mentioned in the literature in almost 80 subsequent years. It documents a

67 new hyaenodont taxon from the late Uintan that differs substantially from known Uintan

68 hyaenodonts, particularly in its possession of a strongly hypercarnivorous morphology, greater

69   than previously known in Wasatchian through Uintan North American hyaenodonts. In fact, the

70   affinities of the new taxon appear to lie with *Propterodon*, a genus previously known only from

71   eastern Asian faunas correlated with the Chinese middle Eocene Irdinmanhan and

72   Sharamurunian stages (*sensu* Wang et al., 2019). The new taxon increases Uintan hyaenodont

73   diversity and disparity while providing evidence for interchange of Asian and North American

74   carnivores during this critical interval in the divergent histories of Hyaenodonta and

75   Carnivoraformes.

76

Materials & Methods

78   Dental terminology follows Rana et al. (2015), with two exceptions. "Mesiobuccal

79   cingulid" is used following Zack (2011) instead of "buccal cingulid", as this structure is mesially

80   restricted in the new species. Following Kay (1977), "hypocristid" is used rather than

81   "postcristid" for the crest connecting the hypoconid and hypoconulid. Measurements follow

82   Gingerich and Deutsch (1989, fig. 1) and Borths and Seiffert (2017, fig. 1e), with the addition of

83   a measurement of maximum talonid height. Dental measurements taken are illustrated in Fig. 2.

84   Mandibular depth was measured lingually below M_3. All measurements were taken to the

85   nearest tenth of a millimeter with Neiko digital calipers. MCZ VPM 19874 was whitened using

86   ammonium chloride prior to being photographed.

87   The electronic version of this article in Portable Document Format (PDF) will represent a

88   published work according to the International Commission on Zoological Nomenclature (ICZN),

89   and hence the new names contained in the electronic version are effectively published under that

90   Code from the electronic edition alone. This published work and the nomenclatural acts it

91   contains have been registered in ZooBank, the online registration system for the ICZN. The

92 ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed

93 through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The

94 LSID for this publication is: urn:lsid:zoobank.org:pub:CDA777EE-C052-4922-90DD-

95 AAFD41D3F345. The online version of this work is archived and available from the following

96 digital repositories: PeerJ, PubMed Central and CLOCKSS.

97   **Phylogenetic Methods**—To test the taxonomic affinities of the new species, it was

98 added to a substantially modified version of the character taxon matrix used by Rana et al.

99 (2015). The dental sample used by Rana et al. (2015) was modified to eliminate non-

100 independent characters (e.g., removing a character describing the number of P^3 roots, which

101 reflects development of a P^3 protocone lobe), following the recommendations of recent authors

102 who have argued that inclusion of non-independent characters can mislead phylogenetic analyses

103 that rely heavily on mammalian dental morphology (Sansom et al., 2017; Billet and Bardin,

104 2019). Overall, several dental characters were revised, replaced, combined, or deleted, and one

105 additional character describing the number of upper incisors was added from Borths and Stevens

106 (2019a). Numerous individual scorings were modified to improve scoring consistency, with

107 particular emphasis placed on ensuring scoring consistency across geographic regions.

108   While the dental character sample from Rana et al. (2015) was used, the non-dental

109 character sample used by Rana et al. (2015) which, in turn was derived from Polly (1996), was

110 largely replaced by the cranial, mandibular, and postcranial character sample used by Borths and

111 Stevens (2019a), and Borths and Stevens' scorings were used with some additions (e.g.,

112 postcranial scorings were added for *Galecyon chronius* and *Prototomus martis*). One character

113 from Rana et al. (2015) describing mandibular symphysis depth was retained because this

114 variation was not captured by Borths and Stevens' characters.

115   In addition to the inclusion of the new species, several changes were made to the

116   taxonomic composition of the matrix. First, the composite *Propterodon* spp. OTU used by Rana

117   et al. (2015) was replaced with separate OTUs for *P. morrisi* and *P. tongi*. Reflecting newly

118   published material, the African *"Sinopa"* OTU included in Rana et al. (2015) was replaced by

119   *Brychotherium ephalmos*, scored from descriptions in Borths et al. (2016) and accompanying 3D

120   models. Scorings of *Akhnatenavus* were updated to include *A. nefertiticyon* described in the

121   same work, while scorings for *Masrasector* were updated based on material of *M. nananubis*

122   described by Borths and Seiffert (2017). The *Pterodon* spp. OTU was restricted to *P.*

123   *dasyuroides* and rescored, given that new evidence indicates *Pterodon*, as traditionally defined,

124   is likely polyphyletic (Solé et al., 2015a; Borths and Stevens, 2019a, b). Three additional taxa

125   were added to the matrix, *Boritia duffaudi*, *Preregidens langebadrae*, and *Matthodon menui*.

126   These three taxa are either newly described or newly identified as hyaenodonts, and they

127   significantly enhance the documentation of early European hyaenodonts (Solé et al., 2014a,

128   2015b).

129   In addition, six OTUs included in the Rana et al. (2015) matrix were excluded from the

130   present analysis. As with *Pterodon*, monophyly of *Metapterodon*, as used by Rana et al. (2015),

131   now appears dubious (Morales and Pickford, 2017; Borths and Stevens, 2019b), but, unlike the

132   well-documented *Pterodon dasyuroides*, individual species of *Metapterodon* are fragmentary and

133   poorly known, contributing little to the broader structure of hyaenodont interrelationships. Until

134   the composition of *Metapterodon* is better understood, the genus is better excluded. A second

135   taxon, *Eoproviverra eisenmanni*, was removed over concerns about the permanent versus

136   deciduous status of the type and most informative specimen, MNHN.F.RI 400. Described as an

137   M_2 (Godinot, 1981; Solé et al., 2015c), MNHN.F.RI 400 shows several features that suggest the

138   tooth may instead represent dP$_4$, including a low paraconid, open trigonid, small talonid, and

139   generally tall, delicate cusp construction. If this is the case, MNHN.F.RI 400 would likely

140   represent a larger taxon than the remainder of the hypodigm.

141   Finally, *Tinerhodon disputatum* and the three species that have been referred to

142   Koholiinae (*Boualitomus marocanensis*, *Koholia atlasense*, *Lahimia selloumi*) were excluded.

143   As briefly noted by Rana et al. (2015), the hyaenodont status of these taxa remains to be clearly

144   demonstrated. Referral of all four taxa to Hyaenodonta appears to have been made based on the

145   presence of multiple carnassial pairs and retention of three molars. As discussed by Zack (2019),

146   this *de facto* definition of Hyaenodonta combines two eutherian symplesiomorphies (molar

147   homodonty and three molars) with a trait found in all carnivorous clades (carnassials). Given

148   this weak evidence, the possibility that some or all these taxa are not hyaenodonts must be

149   considered. In fact, *Tinerhodon disputatum* has not been consistently recovered as a hyaenodont

150   in analyses that do not constrain the ingroup to monophyly (e.g., Borths and Stevens, 2019b).

151   Among members of the potentially polyphyletic Koholiinae, two species known exclusively

152   from lower dentitions (*Boualitomus marocanensis* and *Lahimia selloumi*) lack P$_1$, a feature that

153   is unusual for Hyaenodonta but typical for members of Tenrecoidea (Gheerbrant et al., 2006;

154   Solé et al., 2009). Combined with the small size of both species, this raises the possibility that

155   koholiines may actually represent an endemic African carnivorous radiation prior to an Eocene

156   immigration of hyaenodonts to Africa.   The third koholiine, *Koholia atlasense*, is known only

157   from a fragmentary upper dentition, and recent phylogenetic analyses have not recovered it in a

158   clade with *B. marocanensis* and *L, selloumi* (Borths et al., 2016; Borths and Seiffert, 2017;

159   Borths and Stevens, 2017, 2019a, b).   The M^1 of *K. atlasense* has a paracone that is distinctly

160   lingual to the metacone, although this may be exaggerated by damage to the metacone (Crochet,

161   1988). This morphology is not characteristic of hyaenodonts but occurs in the early tenrecoids

162   *Sperrgale minutus* and *Arenagale calcareus* (Pickford, 2015). Other aspects of the morphology

163   of *K. atlasense* are also unusual for a hyaenodont including the elongate P^4 metastyle, strong M^1

164   prevallum shear, and massive M^1 parastyle connected to the preparacrista at its mesial margin.

165   The overall morphology of *K. atlasense* is distinctive enough to cast doubt on its hyaenodont

166   status.

167   The final matrix includes 48 ingroup taxa and two outgroups scored for 115 characters.

168   The list of characters and specimens examined are available in the online Supplemental

169   Information. The full matrix is also available on MorphoBank as project P3489

170   (http://morphobank.org/permalink/?P3489). The matrix was analyzed using parsimony in TnT

171   version 1.5 (Goloboff and Catalano, 2016). Initial analyses used the Sectorial Search algorithm

172   under the New Technology search dialog. The matrix was analyzed until trees of the same

173   minimum length were recovered by 100 replicates of the algorithm, each beginning from a

174   different starting topology. If a particular replicate identified a tree shorter than the existing

175   minimum length trees, the process restarted until 100 replicates had recovered trees of the new

176   minimum length. Novel minimum length trees from each replicate were retained, up to 10,000.

177   Once this process was completed, resulting trees were then submitted for branch swapping in the

178   Traditional Search dialog to ensure that all most parsimonious trees were identified, again with a

179   limit of 10,000 trees in total.

180   **Institutional Abbreviations—AMNH FM**, Fossil Mammal Collection, American

181   Museum of Natural History, New York, New York, USA; **CM**, Carnegie Museum of Natural

182   History, Pittsburgh, Pennsylvania, USA; **HGL**, Hammada Gour Lazib, Algeria; **IVPP**, Institute

183   of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing,

184   China; **MCZ VPM**, Museum of Comparative Zoology, Harvard University, Cambridge,

185   Massachusetts, USA; **MNHN.F.ERH**, Muséum National d'Histoire Naturelle, Rhône Basin

186   Collection, Paris, France; **MNHN.F.RI**, Muséum National d'Histoire Naturelle, Rians

187   Collection, Paris, France; **ZIN**, Zoological Institute, Russian Academy of Sciences, Saint

188   Petersburg, Russia.

189

190   **Results**

191   SYSTEMATIC PALEONTOLOGY

192

193   MAMMALIA Linnaeus, 1758

194   EUTHERIA Huxley, 1880

195   HYAENODONTA Van Valen, 1967 (*sensu* Solé, 2013)

196   HYAENODONTIDAE Leidy, 1869

197   HYAENODONTINAE (Leidy, 1869)

198   *PROPTERODON* Martin, 1906

199

200   **Comments**—*Propterodon* was named by Martin (1906) without designation of a type

201   species. In 1925, Matthew and Granger named a new species that they referred to *Propterodon*,

202   *P. irdinensis*. In the absence of any prior referral of a species to *Propterodon*, *P. irdinensis*

203   became, by default, the type species, a situation that spawned considerable taxonomic confusion

204   and was ultimately resolved by Polly and Lange-Badré (1993). Matthew and Granger (1925)

205   named *Propterodon irdinensis* based on jaw fragments, not certainly associated, from Inner

206   Mongolian exposures of the middle Eocene Irdin Manha Formation (Irdinmanhan stage) (Fig. 3).

207   The previous year, Matthew and Granger (1924) had described *Paracynohyaenodon morrisi*

208   from the same beds, and most recent workers have regarded the two species as conspecific, with

209   *Propterodon morrisi* the appropriate name for this taxon (Dashzeveg, 1985; Polly and Lange-

210   Badré, 1993; Morlo and Habersetzer, 1999). Dashzeveg (1985) named an additional hyaenodont

211   taxon, *Pterodon rechetovi*, for two maxillae from the Irdin Manha-equivalent Khaichin Ula 2

212   fauna from the Khaichin Formation of Mongolia. This species was subsequently made the type

213   species of a new genus, *Neoparapterodon*, by Lavrov (1996), but Morlo and Habersetzer (1999),

214   noting that the upper dentition of *Propterodon morrisi* is essentially identical to that of *N.*

215   *rechetovi*, placed the latter genus and species in synonymy with the former. In addition to *P.*

216   *morrisi*, three other species of *Propterodon* have been named. *Propterodon pishigouensis* was

217   named by Tong and Lei (1986) for a dentary preserving P_4-M_1 from the Hetaoyuan Formation

218   (Irdinmanhan), Henan Province, China (Fig. 3). As is discussed below, the affinities of *P.*

219   *pishigouensis*, do not appear to lie with either *Propterodon* or with Hyaenodonta generally. An

220   additional Chinese species, *P. tongi* was named by Liu and Huang (2002) for a dentary with P_1-

221   M_3 from the Huoshipo locality, Yuli Member of the Hedi Formation (Irdinmanhan), Shanxi

222   Province. This species differs from *P. morrisi* in being slightly smaller and in having a more

223   strongly hypercarnivorous morphology, with metaconids lacking at least on M_{2-3}, trigonids more

224   open, and talonids more reduced, especially on M_3. Most recently, Bonis et al. (2018) named

225   *Propterodon panganensis* for a dentary preserving P_4-M_1 from the Sharamurunian equivalent

226   Pondaung Formation of Myanmar (Fig. 3). This species has some unusual features (symmetric

227   P_4 protoconid, P_4 and M_1 similar in size, very reduced M_1 talonid) that suggest its relationship to

228   other *Propterodon* requires confirmation, but it is clearly a hypercarnivorous hyaenodont.

229

230   *PROPTERODON WITTERI*, sp. nov. urn:lsid:zoobank.org:act:4D88F815-E7BE-4997-890F-

231   59BC65A06A28

232   (Fig. 4, Table 1)

233

234   **Holotype**—MCZ VPM 19874, left dentary preserving M_{2-3}, the back of the horizontal

235   ramus and almost all of the ascending ramus.

236   **Etymology**—Named for R. V. Witter, whose party collected the type and only known

237   specimen in 1940.

238   **Type Locality**—Leota Quarry, Uinta Basin, Uintah County, Utah (Fig. 1B).

239   **Stratigraphy and Age**—Myton Member of the Uinta Formation (Uinta C, Fig. 1A), late

240   Uintan (Ui_3) North American Land Mammal Age (NALMA), late middle Eocene (Prothero,

241   1996) (Fig. 3).

242   **Diagnosis**—Largest known species of *Propterodon*, with M_2 and M_3 lengths

243   approximately 11 and 13 mm, respectively, and dentary depth approximately 25 mm beneath M_3.

244   Talonid on M_3 relatively large, comparable to M_2 talonid. Metaconids on M_{2-3} present but

245   extremely reduced.

246   **Differential Diagnosis**—Differs from *P. panganensis* in substantially larger size, with

247   dentary more than 100% deeper. Differs from *P. morrisi* in larger size, approximately 40%

248   longer M_{2-3}, more reduced metaconids on M_{2-3}, and a relatively larger talonid on M_3. Differs

249   from *P. tongi* in larger size, approximately 50% longer M_{2-3}, retention of rudimentary

250   metaconids on M_{2-3}, larger talonids on M_{2-3}, and a less recumbent M_3 protoconid.

251   **Description**—The preserved portion of the horizontal ramus of the dentary is deep and

252   transversely compressed beneath M_3 (Fig. 4A-B). Posterior to the tooth row, the coronoid

253   process forms an approximately 60-degree angle with the alveolar margin. The process is

254   elongate and extends well above the tooth row, although its dorsal extremity is lacking. The

255   posterior margin of the coronoid process is concave, and the process appears to have overhung

256   the mandibular condyle. On the ventral margin of the dentary, there is a slight concavity

257   between the horizontal ramus and the angular process. The angular process itself is directed

258   posteriorly, with no meaningful ventral or medial inflection. The process is relatively thick, with

259   no medial excavation between the angular process and condyle. The tip of the process extends

260   posterior to the mandibular condyle and has a slight dorsal curvature. The mandibular condyle is

261   positioned at the level of the alveolar border. The condyle is flush with the ascending ramus,

262   with no development of a neck. The visible portion of the condyle is deepest at its medial

263   margin, tapering dorsolaterally. The bone of the ascending ramus is thickest in a low, broad

264   ridge extending anteriorly and somewhat ventrally from the condyle. Just inferior to this ridge,

265   near mid-length of the ascending ramus is the opening of the mandibular canal.

266   M_2 is complete, aside from slight damage to the apex of the paraconid and the buccal

267   base of the talonid (Fig. 4A-C). The trigonid is much longer and more than twice the height of

268   the talonid. It would likely have been taller, but a large, vertical wear facet on the buccal surface

269   of the paracristid has removed the apex of the protoconid and likely the paraconid. The facet

270   extends nearly to the base of the crown and, occlusally, has exposed dentine of both cusps.

271   The protoconid is the largest and tallest trigonid cusp. The paracristid descends relatively

272   steeply and directly mesially from its apex to meet the paraconid portion of the paracristid in a

273   deep carnassial notch that is continued lingually as a horizontal groove between the paraconid

274   and protoconid. At the distolingual corner of the protoconid, the vertical protocristid is indistinct

275   near the apex of the cusp, becoming better-defined basally and meeting the metaconid in a small

276   carnassial notch.

277   Mesially, the paraconid is approximately two-thirds the height of the protoconid. The

278   paraconid portion of the paracristid forms an angle of approximately 45 degrees to the long axis

279   of the crown. From its junction with the protoconid portion, it rises slightly towards the

280   paraconid apex. At the mesial margin of the tooth, the paraconid forms a mesial keel that helps

281   define a flattened, diamond-shaped lingual surface. Lingually, the paraconid and protoconid are

282   fused to a level close to three quarters the height of the former cusp. Buccally, the paraconid

283   supports a strong, vertical mesiobuccal cingulid that extends distally, even with the carnassial

284   notch and projects further mesially than the mesial keel. Together, the cingulid and mesial keel

285   form a well-defined embrasure for the back of the talonid of M_1.

286   The metaconid of M_2 is a tiny but distinct cusp positioned high on the protoconid, just

287   below the level of the paraconid apex. The metaconid is fused with the protoconid to a level

288   above the level of fusion of the paraconid and protoconid. The apex of the metaconid is directed

289   slightly distally as well as lingually and bears a distinct crest that meets the protoconid portion of

290   the protocristid.

291   The talonid is dominated by the hypoconid. The apex of the cusp is worn away but was

292   likely flat topped, as in M_3. Buccally, the talonid falls away steeply from the apex of the

293   hypoconid and a wear facet occupies most of the buccal surface of the talonid. Lingually, there

294   is a gentler slope, forming a flat, inclined surface. The cristid obliqua is nearly longitudinal in

295   orientation, meeting the base of the trigonid in a small carnassial notch. The contact is buccal to

296   the level of the metaconid, but still well lingual of the buccal margin of the protoconid, resulting

297   in a shallow hypoflexid.

298   Near the distal margin of the lingual side of the talonid is a shallow groove that appears

299   to separate the hypoconid from a much smaller, lower hypoconulid. There is no entoconid or

300   entocristid. Aside from the mesiobuccal cingulid, there is no development of cingulids. Buccal

301   enamel extends slightly more basally than lingual enamel.

302   M_3 is larger than M_2 and almost unworn but is otherwise quite similar in gross

303   morphology (Fig. 4A-C). The unworn protoconid of M_3 is slightly recumbent and the protoconid

304   portion of the paracristid is modestly more elongate than the paraconid portion. The mesial keel

305   of the paraconid is stronger than on M_2 and projects further than the mesiobuccal cingulid. The

306   M_3 metaconid is even smaller than on M_2, reduced to a projection at the end of the almost

307   vertical protocristid. Even in this rudimentary state, a tiny carnassial notch still separates the

308   cusp from the protoconid, but there is no distal projection of the metaconid, unlike M_2.

309   The talonid is shorter than on M_2 and, unlike on the latter tooth, is noticeably narrower

310   distally, with its lingual margin running distobuccally from the lingual base of the protoconid.

311   As on M_2, the largest cusp on the M_3 talonid is the hypoconid. The unworn M_3 hypoconid is

312   flat-topped, but the lingual enamel appears to be thickest near its distal margin, indicating a distal

313   position for the hypoconid apex. As on M_2, the cristid obliqua meets the trigonid in a small

314   carnassial notch buccal to the level of the metaconid. From that point, the cristid obliqua

315   continues briefly as a vertical crest that ascends the trigonid, reaching approximately one third of

316   the height of the protoconid. The hypoconulid of M_3 is small but better defined than on M_2,

317   being separated from the hypoconid by a carnassial notch. At the lingual margin of the talonid,

318   opposite the apex of the hypoconid, is a linear thickening of enamel that suggests the presence of

319   a very weak entocristid.

320   **Comparisons**—The strongly hypercarnivorous morphology of *P. witteri* distinguishes

321   the new species from known Uintan and older North American hyaenodonts. Among named

322   Uintan hyaenodonts (Matthew, 1899, 1909; Hay, 1902; Peterson, 1919; Gustafson, 1986),

323   *Mimocyon longipes* and *Sinopa major* differ dramatically from the new species, with relatively

324   low, closed trigonids, unreduced metaconids, and large, deeply basined talonids. The

325   limnocyonines *Limnocyon potens* and *Oxyaenodon dysodus* show greater carnivorous adaptation

326   than *Mimocyon* or *Sinopa*, but both have more closed trigonids, larger metaconids, and broader,

327   better-developed talonids than *P. witteri*.

328   Wasatchian *Pyrocyon* and Bridgerian *Tritemnodon* (Fig. 3) more closely approach the

329   morphology of the new species, but with less developed hypercarnivorous adaptation. M_{2-3} in

330   species of *Pyrocyon* (*P. dioctetus*, *P. strenuus*) and in *Tritemnodon agilis* resembles *Propterodon*

331   *witteri* in having open trigonids (that is, with the paraconid apex well mesial to the apices of the

332   protoconid and, if present, metaconid) with elongate prevallid shearing blades, reduced

333   metaconids, strong mesiobuccal cingulids (particularly in *T. agilis*), small, narrow talonids, and

334   reduced hypoconulids. However, in all of these features, the morphology of *P. witteri* is more

335   extreme, with more open trigonids with more elongate prevallids, much more reduced

336   metaconids, mesiobuccal cingulids that are stronger and more vertical, and more simplified

337   talonids with a very weak to absent entoconid/entocristid complex, which is retained in both

338   *Pyrocyon* and *Tritemnodon*. In addition, in both *Pyrocyon* and *Tritemnodon*, M_3 is subequal to

339   M_2, while in *P. witteri*, it is substantially larger. *Tritemnodon agilis* further differs from *P.*

340   *witteri* in having a shallower, more gracile dentary and a more inclined (less vertical) coronoid

341   process.

342   The temporal gap between *Propterodon witteri* and species of *Pyrocyon* and *Tritemnodon*

343   is also problematic (Fig. 3). *Pyrocyon* is well-known known from mid-Wasatchian faunas

344   (Gingerich and Deutsch, 1989) but does not appear to persist until the end of the interval. In the

345   Willwood Formation of the Bighorn Basin, *Pyrocyon* disappears from the record during Wa_6,

346   well before the end of the densely sampled portion of the Willwood record (Chew, 2009), and

347   the genus is unknown from Wa_7 through Uintan faunas. *Tritemnodon* is well-documented from

348   the earlier portion of the Bridgerian, particularly Br_2, but has a limited record from Br_3 and no

349   record from the earlier portions of the Uintan (Ui_{1-2}) (Eaton, 1982; Gunnell et al., 2009). A close

350   relationship of *P. witteri* to either genus would imply substantial gaps in the hyaenodont record.

351   Hypercarnivorous hyaenodonts are also present in mid-Eocene faunas from Africa

352   (*Furodon*), Asia (*Propterodon*), and Europe (*Oxyaenoides*) (Matthew and Granger, 1924, 1925;

353   Lange-Badré and Haubold, 1990; Lavrov, 1996; Liu and Huang, 2002; Solé et al., 2014b, 2015b,

354   2016; Godinot et al., 2018) (Fig. 3). Unlike *Pyrocyon* or *Tritemnodon*, M_3 is distinctly larger

355   than M_2 in these taxa, a similarity shared with *P. witteri*. A link to one or more of these taxa

356   would have implications for the origins of the Uinta form and for intercontinental dispersals of

357   hyaenodonts more generally.

358   Compared to *Propterodon witteri* the M_{2-3} trigonids of species of European *Oxyaenoides*

359   (*O. bicuspidens*, *O. lindgreni*, *O. schlosseri*) are more closed, with a shorter paraconid portion of

360   the paracristid (Lange-Badré and Haubold, 1990; Solé et al., 2014a, 2015b; Godinot et al., 2018)

361   (Fig. 5C-D). *Oxyaenoides* has completely lost metaconids on all molars, while *P. witteri* retains

362   small metaconids on M_{2-3}. In *Oxyaenoides*, the protoconid and paraconid are separated to a level

363   close to the base of the crown, contrasting with *P. witteri*, where these cusps are fused to

364   approximately mid-height. Both taxa have a distinct mesiobuccal cingulid, but it is much lower

365 in *Oxyaenoides*. While both have reduced talonids, the hypoconulid is relatively larger in

366 *Oxyaenoides* and a more distinct entoconid/entocristid complex is retained, even in the derived

367 *O. schlosseri*. *Oxyaenoides* talonids are also much shorter relative to their width than in *P.*

368 *witteri*. Overall, *Propterodon witteri* displays a mixture of more derived morphologies (open

369 trigonids, trenchant talonids) and less derived morphologies (retained metaconids, elongate

370 talonids) in comparison to *Oxyaenoides*. This pattern is suggestive of parallel developments in

371 lineages assembling a hypercarnivorous morphology independently.

372   African *Furodon crocheti* has more closed trigonids than *Propterodon witteri* (Solé et al.,

373 2014b) (Fig. 5E-F). However, the length of the paraconid portion of the prevallid blade is

374 similar, resulting in the paraconid overhanging the lingual margin of the crown in *F. crocheti*.

375 The metaconid is larger in *F. crocheti* than in *P. witteri*. However, whereas in *P. witteri*, the

376 metaconid is positioned high on the protoconid, almost at the same height as the paraconid apex,

377 it is positioned much lower in *F. crocheti*. As a result, despite its size, the metaconid apex is

378 substantially lower than the paraconid apex. The talonids of *F. crocheti* are relatively larger than

379 in *P. witteri*, particularly on M_2, and the M_2 talonid is much wider as well. The M_2 hypoconid

380 has a mesial apex in *F. crocheti*, with a subequal cristid obliqua and hypocristid. In *P. witteri*,

381 the apex of the hypoconid is distal and there is no hypocristid to speak of. While the

382 hypoconulid appears to be small in *F. crocheti*, the entoconid/entocristid complex remains

383 prominent, contrasting with the trenchant morphology present in *P. witteri*. Finally, on the

384 dentary of *F. crocheti*, the ventral margin of the angular process grades smoothly into the

385 horizontal ramus, lacking the distinct inflection that occurs in *P. witteri*.

386   Some of the features that distinguish *F. crocheti* from *P. witteri* are shared with other,

387 less hypercarnivorous taxa from Africa and South Asia. The paraconid overhang is present in

388   African *Brychotherium* and South Asian Indohyaenodontinae (Kumar, 1992; Egi et al., 2005;

389   Rana et al., 2015; Borths et al., 2016), while the low placement of the metaconid is shared with

390   these taxa as well as African *Glibzegdouia* and *Masrasector* (Solé et al., 2014b; Borths and

391   Seiffert, 2017). A mesially positioned hypoconid apex occurs in *Glibzegdouia*, *Masrasector*, and

392   the indohyaenodontines *Kyawdawia* and *Yarshea* (Egi et al., 2004, 2005; Solé et al., 2014b;

393   Borths and Seiffert, 2017). These similarities are consistent with phylogenetic analyses that link

394   *Furodon* to African and South Asian hyaenodonts (Rana et al., 2015; Borths et al., 2016; Borths

395   and Seiffert, 2017; Borths and Stevens, 2019a, b). Their absence in *Propterodon witteri* indicate

396   that its affinities lie elsewhere.

397   The morphology of the two best known species of Asian *Propterodon*, *P. morrisi* (senior

398   synonym of the type species, *P. irdinensis*) (Fig. 5G-H) and *P. tongi* (Fig. 5I-J), is quite similar

399   to that of *P. witteri* (Matthew and Granger, 1924, 1925; Liu and Huang, 2002). Trigonid

400   proportions of M_{2-3} in *P. morrisi* (e.g., AMNH FM 21553) are nearly identical to *P. witteri*,

401   while *P. tongi* has slightly more open trigonids than either species. In *P. morrisi*, the metaconids

402   of M_{2-3} are reduced but remain slightly larger than in *P. witteri*. The opposite is true of *P. tongi*,

403   with both M_2 and M_3 lacking defined metaconids. In *P. morrisi*, the metaconids are positioned

404   high on the protoconid, comparable to *P. witteri*. Both Asian species have well-developed,

405   vertical mesiobuccal cingulids that extend high up on the paraconid. Talonid structure is also

406   closely comparable, at least on M_2. The Asian species have small talonids (smaller in *P. tongi*)

407   with distal hypoconid apices, rudimentary hypoconulids positioned directly distal to the

408   hypoconid, and no entoconid/entocristid complex, all identical to the morphology on M_2 of *P.*

409   *witteri*. The M_3 talonid is more reduced in the Asian forms than in the North American taxon.

410   In the case of *P. tongi*, it is reduced to a cuspule on the distal end of the trigonid. The talonid is

411   larger in *P. morrisi*, but still smaller than in *P. witteri*. As in the North American form, there

412   does appear to be a trace of an entocristid on the M$_3$'s of AMNH FM 20128 and 21553. Taken

413   together, the morphology of *Propterodon witteri* is closely comparable to *P. morrisi* and *P.*

414   *tongi,* particularly the former. The most significant morphological distinction is the relative size

415   of the M$_3$ talonid, which is relatively larger in *P. witteri* than in either Asian species. Despite

416   this contrast, Asian *Propterodon* species are clearly the closest matches to *P. witteri* among

417   relevant taxa, and referral of the new species to *Propterodon* can be made with confidence.

418   **Phylogenetic Results**—Analysis of the matrix described in Materials & Methods produced 145

419   most parsimonious trees (L=510, CI=0.294, RI=0.615), the majority rules consensus of which is

420   shown in Fig. 6. Resolution is poor, even using the majority rules rather than a strict consensus.

421   The largest clade unites a paraphyletic Indohyaenodontinae with the three primary African

422   subfamilies (Hyainailourinae, Apterodontinae, Teratodontinae). A second major clade comprises

423   most members of Proviverrinae along with *Arfia*, which is unexpectedly deeply nested within

424   Proviverrinae as the sister taxon of *Proviverra* and *Leonhardtina*. Smaller groupings include

425   Limnocyoninae, Hyaenodontinae, and groupings of the North American *Sinopa* and *Gazinocyon*

426   and the European hypercarnivorous genera *Oxyaenoides* and *Matthodon*. All of these clades

427   form a massive polytomy at the base of the ingroup, along with numerous genera and species of

428   early and middle Eocene hyaenodont.

429   While disappointing, the poor resolution of the consensus tree is consistent with a lack of

430   clarity in other recent analyses of hyaenodont phylogeny. While the consensus topology is better

431   resolved, most clades recovered by Rana et al. (2015) have poor bootstrap support. This is also

432   true in other recent analyses using parsimony (Borths et al., 2016; Borths and Seiffert, 2017).

433   Most nodes in Bayesian trees recovered by Borths and colleagues (Borths et al., 2016; Borths

434   and Seiffert, 2017; Borths and Stevens, 2017, 2019a, b) have similarly low posterior

435   probabilities, and there are substantial topological differences between analyses with different

436   assumptions concerning character evolution (e.g., Prionogalidae in Borths and Stevens, 2019a,

437   supplementary fig. 1 versus 2). Simply put, many relationships within Hyaenodonta are neither

438   stable nor well-resolved.

439   With regard to *Propterodon witteri*, two conclusions can be made. First, all trees recover

440   a clade linking the new species to *Propterodon morrisi*, *P. tongi*, and *Hyaenodon*. Monophyly of

441   *Propterodon* is not recovered, with a majority of trees linking *P. tongi* and *P. witteri* more

442   closely to *Hyaenodon* than to *P. morrisi* on the basis of greater metaconid and entoconid

443   reduction in the former species. These results indicate that *Propterodon* is paraphyletic and is

444   likely to be directly ancestral to *Hyaenodon*, although further support would be desirable,

445   particularly as metaconid and entoconid reduction have occurred convergently in many different

446   lineages of carnivorous mammal (e.g., Muizon and Lange-Badré, 1997).

447   In addition, the position of Hyaenodontinae within Hyaenodonta is not well-resolved.

448   While hyaenodontine monophyly is supported in all shortest trees, the subfamily is recovered in

449   the large polytomy at the base of the ingroup. This contrasts with recent analyses that have

450   consistently supported some form of a link to European hyaenodonts (Rana et al., 2015; Borths

451   et al., 2016; Borths and Seiffert, 2017; Solé and Mennecart, 2019; Borths and Stevens, 2019a, b),

452   particularly the hypercarnivorous *Oxyaenoides*. The implications of this aspect of the topology

453   are discussed below

454   One other result that warrants brief comment is that the two recently described European

455   hyaenodont genera, both described as potential proviverrines (Solé et al., 2014a, 2015b), *Boritia*

456   and *Preregidens*, are not recovered in proximity to Proviverrinae. Instead, many individual trees

457 recover these genera in positions proximate to species of *Prototomus* (specifically *P. martis* and

458 *P. minimus*) and *Pyrocyon*. This includes trees in which the European genera are successive

459 sister taxa to *Pyrocyon* and trees in which *Preregidens* is the sister taxon of *Prototomus minimus*

460 (with *P. martis* as sister taxon to this clade). Consistent with this result, both genera lack the

461 distinctive enlarged, bulbous entoconid typical of proviverrine molar talonids (e.g., Solé, 2013).

462 Of the two, *Boritia* is very similar to several early Eocene North American hyaenodonts

463 (*Prototomus martis*, *Pyrocyon* spp.), and it may represent a parallel development from an early

464 European species of *Prototomus* (e.g., *P. girardoti*). Alternatively, it may document evidence of

465 faunal exchange between North America and Europe after the Paleocene-Eocene Thermal

466 Maximum, consistent with evidence from the Abbey Wood fauna (Hooker, 2010).

467

468 OXYAENODONTA Van Valen, 1971

469 OXYAENIDAE Cope, 1877

470 MACHAEROIDINAE Matthew, 1909

471 *APATAELURUS* Scott, 1937

472 *APATAELURUS PISHIGOUENSIS* (Tong & Lei, 1986), comb. nov.

473 (Fig. 7)

474 *?Propterodon pishigouensis* Tong & Lei, 1986:212, fig. 2, pl. 1.3

475 *?Propterodon shipigouensis* Tong, 1997:6 (lapsus calami)

476

477 **Holotype**—IVPP V7997, left dentary preserving P_4-M_1.

478 **Type Locality**—Shipigou, Liguanqiao Basin, Xichuan County, Henan Province, China.

479 **Stratigraphy and Age**—Hetaoyuan Formation, Irdinmanhan stage (Wang et al., 2019).

480 **Revised Diagnosis**—Smallest known species of *Apataelurus*, with P_4 and M_1 lengths

481 approximately 10 and 9 mm, respectively.

482 **Comparisons and Discussion**—Tong and Lei (1986) described IVPP V7997 as a new

483 species of *Propterodon*, *P. pishigouensis*. Compared to other species referred to *Propterodon*,

484 the most distinctive feature of *"P." pishigouensis* is the shape of the dentary, which is ventrally

485 deflected anteriorly, beginning below the anterior root of P_4 (Tong and Lei, 1986), indicating the

486 presence of an anterior flange (Fig. 7A). In contrast, the symphysial region is shallow in *P.*

487 *morrisi* and *P. tongi* and tapers anteriorly. In fact, an anterior dentary flange has not been

488 documented in any hyaenodont. The only middle Eocene carnivorous mammals known to

489 possess such a flange are machaeroidines (Scott, 1938; Matthew, 1909; Gazin, 1946; Dawson et

490 al., 1986), a small clade of North American Wasatchian through Uintan carnivores recently

491 supported as oxyaenids (Zack, 2019).

492 Machaeroidines, particularly the Uintan *Apataelurus kayi*, share substantial similarities

493 with the type specimen of *"Propterodon" pishigouensis*, including features that distinguish the

494 latter species from other *Propterodon* (Fig. 7). On P_4, both *A. kayi* and *pishigouensis* have a

495 well-developed paraconid that is nearly as tall as the talonid (Scott, 1938; Tong and Lei, 1986).

496 The paraconid is absent on P_4 in *P. tongi* (Liu and Huang, 2002). In *P. panganensis* it is low and

497 weakly developed (Bonis et al., 2018). While all relevant species have simple P_4 talonids

498 dominated by a tall hypoconid, in *pishigouensis* and *A. kayi*, the talonid is distinctly broader than

499 the remainder of the crown (Scott, 1938; Tong and Lei, 1986). In contrast, P_4 width is uniformly

500 narrow in *P. panganensis* and *P. tongi* (Liu and Huang, 2002; Bonis et al., 2018). In

501 *Propterodon tongi* and, to judge the roots of P_4, *P. morrisi*, P_4 is enlarged relative to M_1

502 (Matthew and Granger, 1925; Liu and Huang, 2002). In *pishigouensis* and *A. kayi,* along with *P.*

503   *panganensis*, the two teeth are subequal in size (Scott, 1938; Tong and Lei, 1986; Bonis et al.,

504   2018).

505   On M_1, a defined metaconid is lacking in *pishigouensis* and *A. kayi* (Scott, 1938; Tong

506   and Lei, 1986), again along with *P. panganensis* (Bonis et al., 2018), but retained in *P. morrisi*

507   (e.g., AMNH FM 21553), with M_1 of *P. tongi* too worn to assess. The primary difference in M_1

508   morphology is in the talonid. The talonids of *P. morrisi*, *P. tongi*, and *P. panganensis* are short

509   and much lower than the paraconid (Matthew and Granger, 1925; Liu and Huang, 2002; Bonis et

510   al., 2018; pers. obs. of AMNH FM 21553). In *pishigouensis* and *A. kayi*, the talonid is relatively

511   elongate and nearly as tall as the paraconid (Scott, 1938; Tong and Lei, 1986). Talonid

512   morphology is simplified in both *pishigouensis* and *A. kayi*, with both taxa only retaining a

513   hypoconid. In *P. morrisi* and *P. tongi*, some lingual structure is retained, although the extremely

514   reduced talonid of *P. panganensis* is also simplified.

515   Taken together, the mandibular and dental morphology of *"Propterodon" pishigouensis*

516   differs substantially from other species of *Propterodon*, particularly *P. morrisi* and *P. tongi*, but

517   closely matches the morphology of the North American machaeroidine *Apataelurus kayi*.

518   Accordingly, *Propterodon pishigouensis* is recombined as *Apataelurus pishigouensis*. As a

519   species of *Apataelurus*, *A. pishigouensis* differs from *A. kayi* primarily in its somewhat smaller

520   size. The talonid of *A. pishigouensis* may be smaller than that of *A. kayi*, but this is complicated

521   by heavier wear in the type and only described specimen of the North American form. Referral

522   of *pishigouensis* to Machaeroidinae represents the first clear record of a machaeroidine in Asia.

523   There may be an additional, older Asian machaeroidine, also initially described as a

524   hyaenodont. *Isphanatherium ferganensis* was named for an isolated upper molar from the

525   Andarak-2 fauna (Lavrov and Averianov, 1998). The morphology of *I. ferganensis* is strikingly

526 derived for an early hyaenodont, with an extremely elongate, longitudinally oriented postvallum

527 blade and a strongly reduced protocone. Both of these features would be consistent with a

528 machaeroidine identity. The overall morphology of the type of *I. ferganensis* is closely

529 comparable to M^1 of *Machaeroides* spp. from the early and middle Eocene of North America

530 (Gazin, 1946; Dawson et al., 1986). They share development and orientation of the metastylar

531 blade, protocone reduction without mesiodistal compression, fusion of the paracone and

532 metacone to a point close to their apices, with the metacone taller than the paracone, and the

533 presence of a low but distinct parastyle that is continuous with a buccal cingulum that is

534 restricted to the mesial portion of the crown. A specific similarity shared by *I. ferganensis* and

535 *M. simpsoni* (pers. obs. of CM 45115) is the presence of contrasting compression of the paracone

536 and metacone, with the former compressed mesiodistally while the latter is compressed

537 transversely. More material is needed to be certain, but the age and morphology of

538 *Isphanatherium ferganensis* supports the tentative reidentification of the species as a

539 machaeroidine and of the holotype as an M^1 rather than an M^2.

540

541 **Discussion**

542 **Hyaenodontine Origins**— Recent assessments of hyaenodont biogeography (Borths et al.,

543 2016; Borths and Stevens, 2017) have supported a European divergence of Hyaenodontinae from

544 *Oxyaenoides*, which was recovered as the sister taxon of Hyaenodontinae in both analyses. This

545 grouping is nested within a broader assemblage of European hyaenodonts comprising taxa

546 referred to Proviverrinae by Solé (2013) and Solé et al. (2015b). More recent studies (Borths and

547 Stevens, 2019a, b; Solé and Mennecart, 2019) complicate this scenario slightly by recovering

548 Prionogalidae and *Thereutherium* within the clade defined by *Oxyaenoides* and Hyaenodontinae,

549   but the basic biogeographic scenario is unchanged, with Hyaenodontinae deeply nested within a

550   clade of European hyaenodonts. As was noted by Borths and Stevens (2019a) with regard to the

551   position of Prionogalidae, the character support uniting *Oxyaenoides*, *Thereutherium*,

552   Prionogalidae, and Hyaenodontinae consists primarily of features associated with

553   hypercarnivory, specifically reduction of the metaconids and talonids on lower molariform teeth.

554   Hypercarnivory has evolved iteratively in diverse carnivorous mammalian clades and homoplasy

555   in features associated with hypercarnivory is well-documented (Muizon and Lange-Badré, 1997;

556   Holliday and Steppan, 2004; Solé and Ladevèze, 2017). Accordingly, support for a close

557   relationship between *Oxyaenoides* and Hyaenodontinae should be regarded cautiously, despite its

558   recovery in several analyses.

559   In contrast to the analyses just discussed, results of the current phylogenetic analysis do

560   not place Hyaenodontinae phylogenetically proximate to *Oxyaenoides*, nor do the results of Rana

561   et al.'s (2015) analysis. While the position of Hyaenodontinae is not consistently resolved in the

562   present study, a sister taxon relationship to *Oxyaenoides* is not present in any most parsimonious

563   tree. Some most parsimonious trees (MPTs) do recover Hyaenodontinae as the sister taxon of

564   Proviverrinae, as used by Solé (2013) and Solé et al. (2015b). However, other MPTs recover

565   Hyaenodontinae as the sister taxon of North American and European *Galecyon* or to a clade

566   comprising *Galecyon* plus Holarctic *Arfia*. Still other MPTs place Hyaenodontinae at the base of

567   a diverse grouping that includes all sampled taxa excepting *Arfia* and Proviverrinae, with Asian

568   and North American Limnocyoninae the next diverging clade. There is no particular support in

569   this analysis for a European origin for Hyaenodontinae.

570   In fact, a European origin appears unlikely. Unlike *Oxyaenoides*, which shares some

571   distinctive dental features with other proviverrines, including a double-rooted P_1 and molar

572   talonids with three, more or less equally developed and equidistantly spaced cusps,

573   hyaenodontine dental morphology has little in common with proviverrines.   The relatively large

574   P_1 remains single-rooted in *P. morrisi* and *P. tongi* (Matthew and Granger, 1925; Liu and Huang,

575   2002), while the entoconid and hypoconulid are weakly developed in all species of *Propterodon*.

576   With the exception of a reduced metacingulum on M^{1-2}, other distinctive proviverrine dental

577   features enumerated by Solé (2013) (entoconids on P_{3-4}, prominent paraconids on P_{2-3} and

578   parastyle on P^4, M^{1-2} with metacones taller than paracones) are absent in *Propterodon* (Matthew

579   and Granger, 1925; Lavrov, 1996; Liu and Huang, 2002).

580   Biogeographic evidence also suggests that derivation of hyaenodontines from within the

581   European Eocene hyaenodont radiation is unlikely. From the late early Eocene through the

582   Eocene/Oligocene transition, Europe was an island isolated from the rest of Holarctica (e.g.,

583   Meulenkamp and Sissingh, 2003), resulting in the evolution of a diverse endemic mammalian

584   fauna (Hooker, 1989; Badiola et al., 2009; Danilo et al., 2013). This period encompasses the

585   radiation of proviverrine hyaenodonts (sensu Solé, 2013), which formed the dominant

586   carnivorous element of this endemic European fauna. There is little evidence of mammalian

587   dispersal from Europe to Asia during this interval.

588   In fact, there is some evidence from the fossil record consistent with an earlier Asian

589   record of Hyaenodontinae. The ?Arshantan fauna from Andarak-2, Khaichin Formation,

590   Kyrgyzstan, includes a fragmentary hyaenodont dentition (ZIN 34494) described by Lavrov and

591   Averianov (1998) as similar to *Neoparapterodon rechetovi*, the latter a likely synonym of

592   *Propterodon morrisi* according to Morlo and Habersetzer (1999). If correctly identified, this

593   would extend the Asian record of Hyaenodontinae back to the early part of the middle Eocene

594   and would support an Asian origin for the subfamily. Unfortunately, the hyaenodont record from

595   both the Arshantan and the preceding Lingchan (equivalent to the Bumbanian) is very poor.

596   Aside from ZIN 34494, the published hyaenodont record from the Arshantan is limited to the

597   type specimen of *Isphanatherium ferganensis* (Lavrov and Averianov, 1998), which may not be

598   a hyaenodont (see above). Lingchan hyaenodont records comprise two specimens referred to

599   distinct species of *Arfia* and two specimens referred to *?Prototomus* sp. (Lavrov and Lopatin,

600   2004; Tong and Wang, 2006; Morlo et al., 2014; Solé et al., 2013). Until early and early middle

601   Eocene hyaenodonts from Asia are better documented, it is difficult to determine what role, if

602   any, Asia played in the origin of Hyaenodontinae.

603   **Late Uintan Carnivore Dispersals**—In addition to *Propterodon*, several other

604   carnivorous taxa that first appear in the late Uintan (Ui_{2-3}) have a potential origin outside western

605   North America. Among hyaenodonts, the limnocyonine *Oxyaenodon dysodus* is quite distinct

606   from *Limnocyon potens*, the only limnocyonine known from the early Uintan. Compared to *L.*

607   *potens*, *O. dysodus* is smaller and more hypercarnivorously adapted, with smaller, less basined

608   talonids and a longer M_2 prevallid blade. *Oxyaenodon dysodus* also retains a full complement of

609   relatively uniform incisors, while *L. potens* has enlarged I^2 and lost I^3 (Denison, 1938). While

610   Morlo and Gunnell (2005) recovered *O. dysodus* and *L. potens* as sister taxa in a phylogenetic

611   analysis of limnocyonines, an earlier analysis of a nearly identical matrix (Morlo and Gunnell,

612   2003) recovered *O. dysodus* as the sister taxon of Bridgerian *Thinocyon medius*, outside of a

613   monophyletic *Limnocyon* (note that the consensus tree shown in Morlo and Gunnell [2005, fig.

614   1] is in error; all four shortest trees found by analyzing the published matrix without

615   modification recover *Thinocyon medius* rather than Bridgerian *Limnocyon* as the sister taxon of

616   *L. potens* plus *O. dysodus*). Both Morlo and Gunnell (2003) and Tong and Lei (1986) have noted

617   similarities to the Irdinmanhan Chinese taxon *Prolaena parva*. Taken together, it is plausible

618   that the appearance of *Oxyaenodon* in the late Uintan reflects immigration from Asia, similar to

619   the pattern hypothesized for *P. witteri*. A full assessment of the affinities of *Oxyaenodon* is

620   beyond the scope of this study. Published descriptions and illustrations of material of *O. dysodus*

621   are inadequate to confidently score the species, and substantial additional material remains

622   unpublished (Friscia and Dunn, 2016).

623   The affinities of another late Uintan hyaenodont, the small undescribed taxon or taxa

624   referenced above are unclear at present, but small hyaenodontid material from the Mission

625   Valley Formation appear to document a non-limnocyonine with a narrow M_1 talonid (pers. obs.),

626   very divergent from both *Limnocyon* or *Sinopa*, the only hyaenodont genera known from the

627   early Uintan.

628   Other carnivorous groups show a similar pattern. At least two machaeroidine taxa are

629   present in late Uintan faunas (Scott, 1937, 1938; Rasmussen et al., 1999; Wagner, 1999; Zack,

630   2019), but none is known from Ui_1. Among miacids, several taxa appear in the late Uintan

631   without obvious Ui_1 antecedents, including *Tapocyon* spp., *"Miacis" uintensis*, and *"M."*

632   *hookwayi* (Wesley and Flynn, 2003; Spaulding and Flynn, 2009; Tomiya, 2013). Finally, the

633   enigmatic carnivorous mammal *Simidectes* first appears in the late Uintan, again without obvious

634   early Uintan relatives (Coombs, 1971).

635   The lack of an early Uintan ancestry for some taxa may reflect limited data from the Ui_1

636   interval, which remains relatively poorly sampled. With this caveat, the discovery of

637   *Propterodon witteri* is evidence of a potential Asian origin for many of the carnivorous taxa that

638   first appear in the late Uintan. Referral of *Propterodon pishigouensis* to *Apataelurus* documents

639   an additional tie between the carnivorous faunas of the Irdinmanhan and Uintan. In addition,

640   both the hyaenodont *Sinopa* and the mesonychid *Harpagolestes* are shared by Irdinmanhan and

641   Uintan faunas (Jin, 2005, 2012; Morlo et al., 2014; Robson et al., 2019). The Huadian

642   Formation fauna containing *S. jilinia* was considered post-Irdinmanhan in age by Morlo et al.

643   (2014) based on the stage of evolution of the omomyid *Asiomomys*, but the presence of *Zelomys*,

644   a genus otherwise known from the Irdinmanhan Yuli Member of the Hedi Formation (Dawson et

645   al., 2003) suggests an older age. Carnivore dispersals from Asia to North America during the

646   later Uintan would be concordant with evidence for dispersal of other mammals from Asia to

647   North America during this interval, including the chalicotheroid perissodactyl *Grangeria* and the

648   omomyid primate *Macrotarsius* in Ui_2 (Woodburne, 2004). Ui_3 sees additional dispersals

649   including several brontotheriid perissodactyls, and *Mytonolagus*, the oldest known North

650   American lagomorph (Woodburne, 2004; Mihlbachler, 2008).

651   A complicating factor is the poor quality of the Asian middle Eocene carnivore record.

652   As discussed above, the Lingchan and Arshantan record of hyaenodonts is extremely poor, and

653   other carnivorous clades are also poorly sampled in both intervals. The Irdinmanhan record is

654   somewhat better but remains inadequate. Among non-mesonychians, Irdinmanhan hyaenodonts

655   include two species of *Propterodon*, *P. morrisi* and *P. tongi*, the sinopanine *Sinopa jilinia*, and

656   the limnocyonine *Prolaena parva* (Matthew and Granger, 1924, 1925; Xu et al., 1979; Tong and

657   Lei, 1986; Lavrov, 1996; Liu and Huang, 2002; Morlo et al., 2014). In addition to the

658   machaeroidine *Apataelurus pishigouensis*, the last recorded oxyaenine, *Sarkastodon hetangensis*,

659   occurs in the Irdinmanhan (Tong and Lei, 1986). Finally, Irdinmanhan miacoids are represented

660   by three species, all questionably referred to *Miacis*: *M. boqinghensis*, *M. invictus*, and *M.*

661   *lushiensis* (Matthew and Granger, 1925; Chow, 1975; Tong and Lei, 1986; Qi et al., 1991;

662   Huang et al., 1999). Of these, only *Propterodon morrisi* and *Miacis lushiensis* are represented

663   by multiple specimens (this may be in error for *M. lushiensis* as the size and morphology of

664   referred material suggests the presence of multiple species).

665   Considering the limited nature of the Asian record, the presence of four genera shared

666   between Uintan and Irdinmanhan faunas (*Harpagolestes*, *Apataelurus*, *Sinopa*, *Propterodon*)

667   constitutes clear evidence for substantial exchange of carnivorous mammals during this interval.

668   As noted above, *Prolaena* can be potentially added to this list although Morlo and Gunnell

669   (2003) were skeptical of a relationship between Asian *Prolaena* and North American

670   *Oxyaenodon*. Despite the assignment of species on both continents to a wastebasket *"Miacis"*,

671   there is less obvious overlap between miacoids, although *"Miacis" lushiensis* has been compared

672   with Bridgerian *"M." hargeri* (Tong and Lei, 1986). Further study will be required to confirm

673   this possibility and assess the potential for North American connections for other Irdinmanhan

674   *"Miacis"*. For the present, it is clear that investigations into the decline in North American

675   hyaenodont diversity and coincident rise in carnivoraform diversity must consider the role of

676   immigration in shaping the North American carnivore guild during the Uintan.

677

678

679   **Conclusions**

680   The new species described in this work, *Propterodon witteri*, is the first known North

681   American representative of the genus *Propterodon*. Comparisons of the new species with other

682   early and middle Eocene hypercarnivorous hyaenodonts support a link to Asian *Propterodon* and

683   Hyaenodontinae more generally, a conclusion supported by the results of the phylogenetic

684   analysis. The broader relationships of Hyaenodontinae are not well-resolved. Despite being

685   supported by several phylogenetic assessments, a link to European *Oxyaenoides* is unlikely. An

686 Asian origin for Hyaenodontinae is more likely, but better material of poorly known Linchan and

687 Arshantan hyaenodonts is needed to test this hypothesis. Recognition of a Uintan hyaenodontine

688 and an Irdinmanhan machaeroidine increases the evidence for dispersal of carnivorous mammals

689 between Asia and North America during the late middle Eocene. Much of the apparent shift in

690 North American carnivorous guilds, from "creodont" to carnivoramorphan dominated, may

691 ultimately reflect the effects of this immigration rather than intrinsic processes within North

692 American faunas.

693

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Table 1(on next page)

Measurements (mm) of the holotype of *Propterodon witteri*.

Specimen Number	Locus	L	TrL	TrW	TrH	TaL	TaW	TaH
MCZ VPM 19874	M_2	11.5	7.8	5.4	9.7	3.8	4.0	4.8
	M_3	13.5	10.3	6.2	12.2	3.2	3.7	4.8
Dentary depth	24.7							

1 **Note:** Abbreviations as in Fig. 2.

Figure 1

Stratigraphic and geographic position of Leota Quarry.

(**A**) Generalized stratigraphic section of middle Eocene Uinta Formation in the west-central Uinta Basin showing the position of Leota Quarry along with biochron boundaries (Prothero, 1996) and geomagnetic polarity chrons (Murphey et al., 2018). (**B**) Map of Utah, United States showing the location of Uintah County and map of Uintah County showing the position of Leota Quarry (as indicated by Peterson and Kay, 1931). Orange shading in **B** indicates outcrop of the Uinta Formation (after Hintze, 1980). **Abbreviations**: **BB Mbr**, Brennan Basin Member of the late middle Eocene Duchesne River Formation, **Gr Fm**, early middle Eocene Green River Formation. Drawings by Shawn P. Zack.

Figure 2

Measurements of hyaenodont lower molars.

Schematic drawing of a hyaenodont lower molar in (**A**) occlusal and (**B**) buccal views to show measurements taken for this study. **Abbreviations**: **L**, maximum length; **TrL**, maximum trigonid length; **TrW**, maximum trigonid width; **TrH**, maximum trigonid height; **TaL**, maximum talonid length; **TaW**, maximum talonid width; **TaH**, maximum talonid height. Drawings by Shawn P. Zack.
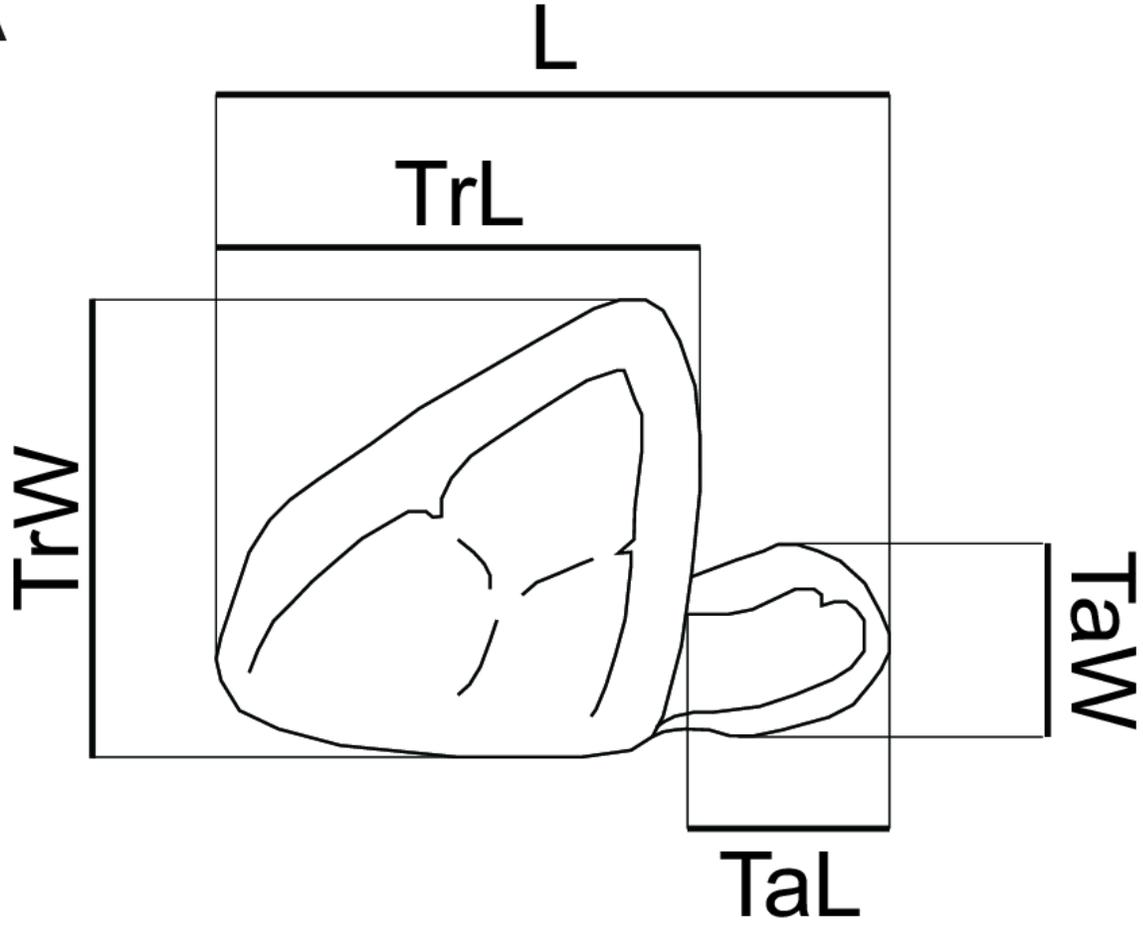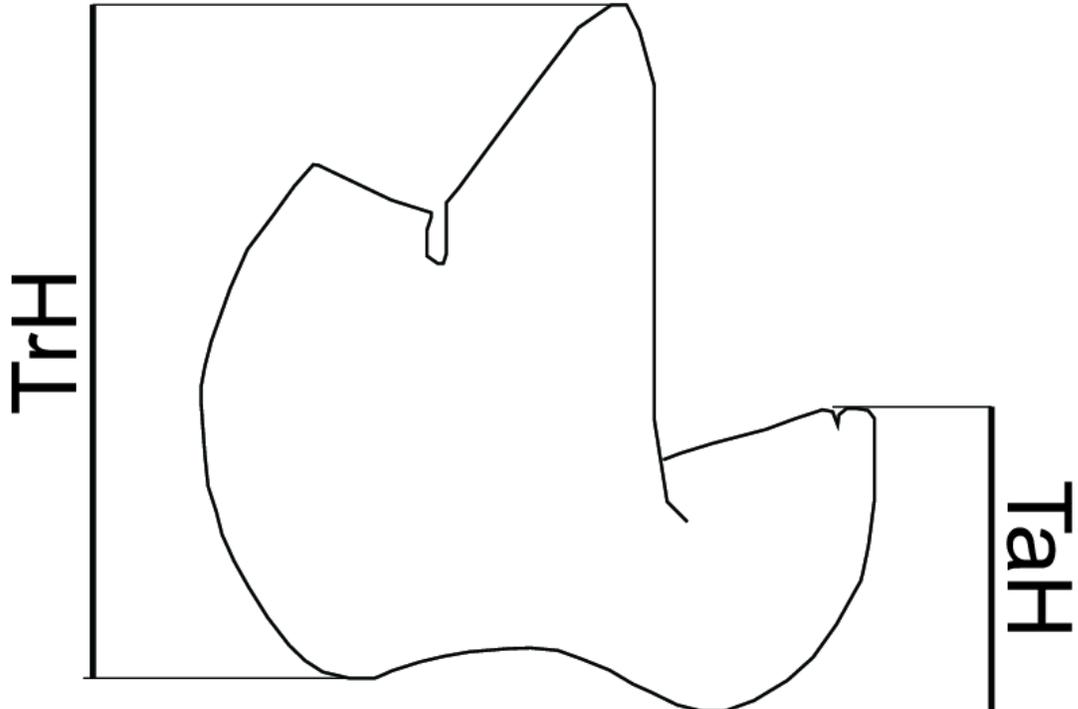
Figure 3

Temporal distribution of significant taxa discussed in this work.

Geomagnetic polarity chrons follow Ogg et al. (2016). North American Land Mammal Age (NALMA) boundaries follow Tsukui and Clyde (2012) and Murphey et al. (2018). Chinese stage boundaries follow Wang et al. (2019). Age ranges for hyaenodont and oxyaenodont taxa follow Prothero (1996), Gunnell et al. (2009), Liu and Huang (2002), Tomiya (2013), Zaw et al. (2014), Solé et al. (2015b, 2016), Wang et al. (2019), and personal observation of *Pyrocyon* spp. **Abbreviations**: **Ar**, Arshantan; **Br**, Bridgerian; **Du**, Duchesnean; **Ir**, Irdinmanhan; **Li**, Lingchan; **Sh**, Sharamurunian; **Ui**, Uintan; **Wa**, Wasatchian. Drawings by Shawn P. Zack.
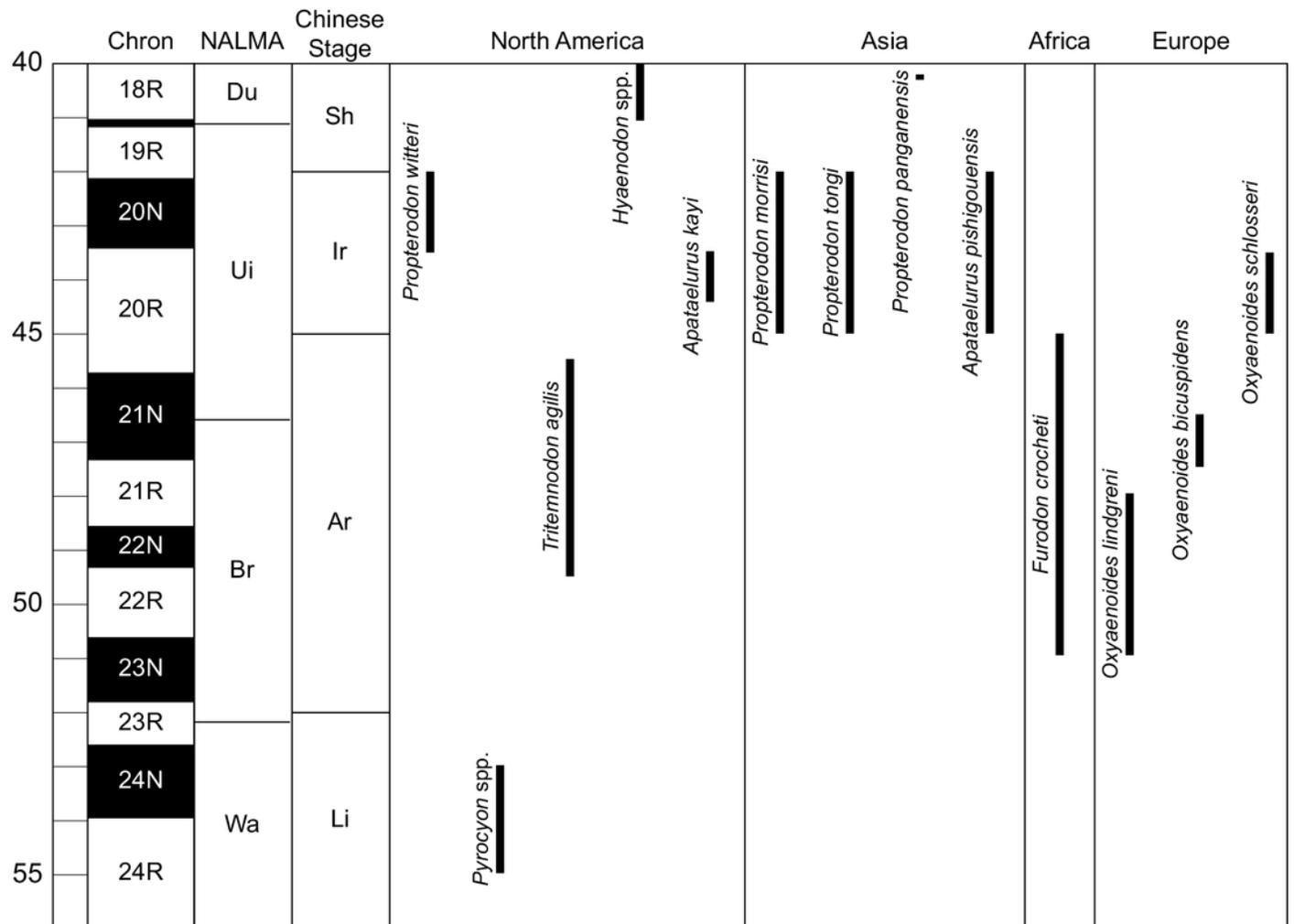
Figure 4

Holotype of *Propterodon witteri* sp. nov. (MCZ VPM 19874).

Right dentary with M_{2-3} in (**A**) buccal, (**B**) lingual, and (**C**) occlusal views. Scale bars are 10 mm. Photographs by Shawn P. Zack.

A

10 mm

B

C
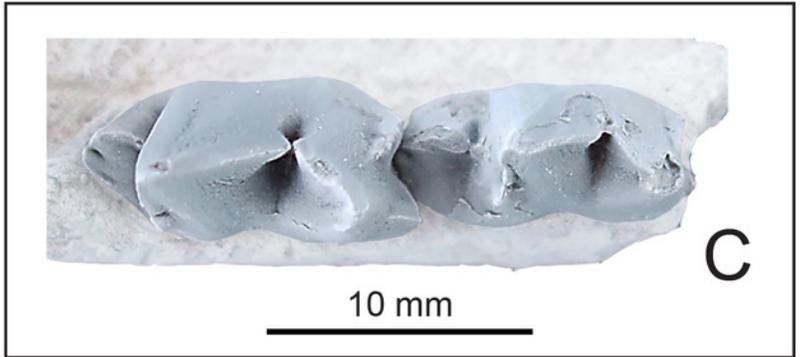
10 mm

Figure 5

Comparison of M_{2-3} of *Propterodon witteri* sp. nov. with other middle Eocene hypercarnivorous hyaenodonts.

Left M_{2-3} of *Propterodon witteri*, MCZ VPM 19874, in (**A**) lingual and (**B**) occlusal views. Right M_{2-3} (reversed) of *Oxyaenoides schlosseri*, MNHN.F.ERH 429, in (**C**) lingual and (**D**) occlusal views. Left M_{2-3} of *Furodon crocheti*, HGL 50bis-56, in (**E**) lingual and (**F**) occlusal views. Right M_{2-3} (reversed) of *Propterodon morrisi*, AMNH FM 21553, in (**G**) lingual and (**H**) occlusal views. Left M_{2-3} of *Propterodon tongi*, IVPP V12612, in (**I**) lingual and (**J**) occlusal views. All scale bars are 10mm. Drawings by Shawn P. Zack. **A**-**B** and **G**-**H** drawn from photographs by Shawn P. Zack. **C- D** drawn from Solé et al. (2015b, fig. 4). **E- F** drawn from Solé et al. (2014b, fig. 2). **I-J** drawn from photographs provided by M. Borths.
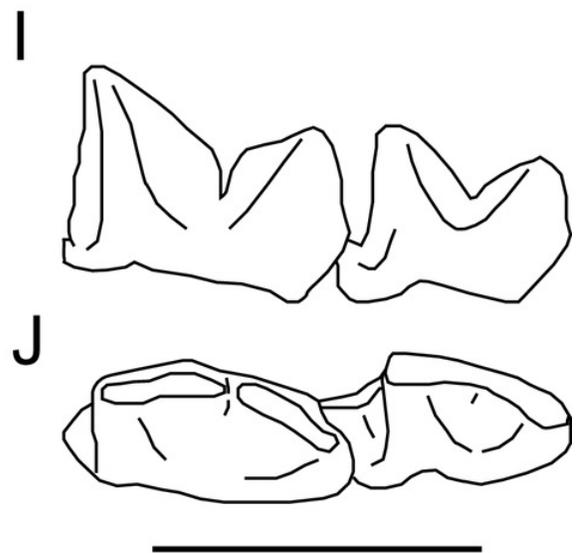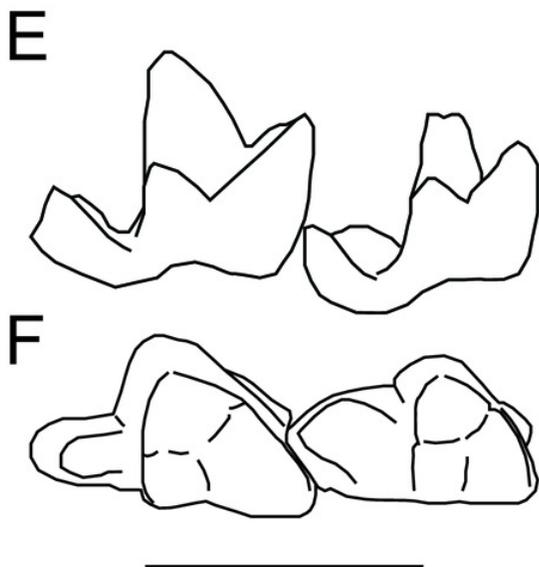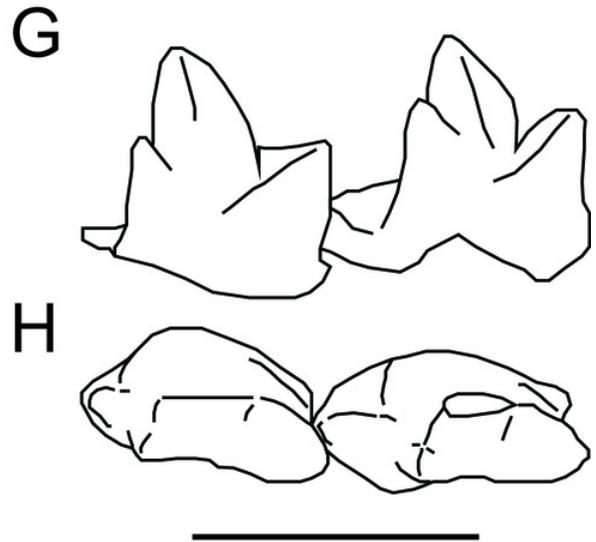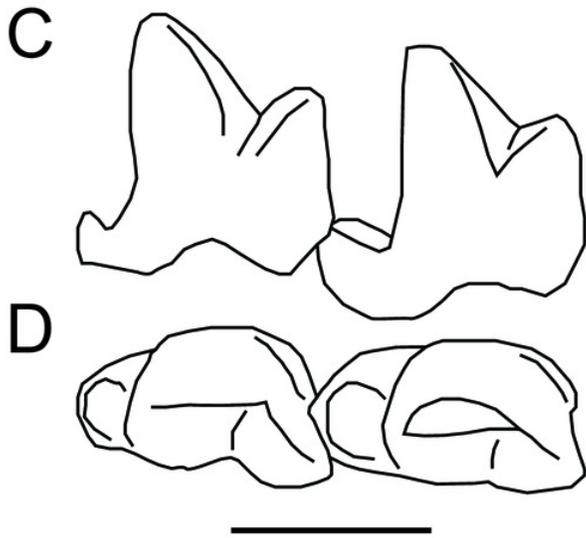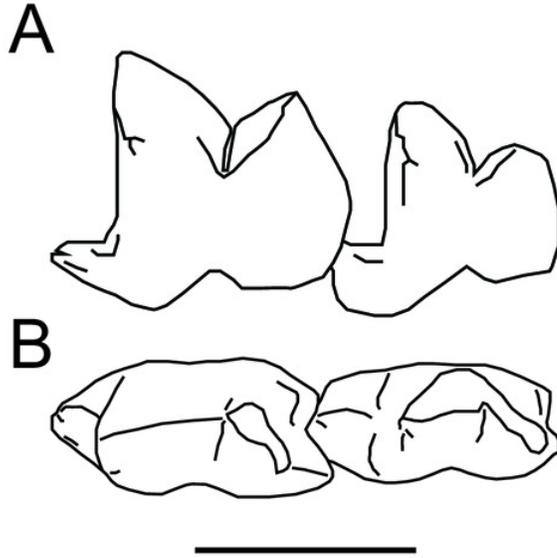
Figure 6

Phylogenetic position of *Propterodon witteri* sp. nov.

Majority rule consensus of 145 most parsimonious trees (L=510, CI=0.294, RI=0.615) showing the inferred phylogenetic position of *Propterodon witteri* sp. nov. Numbers below branches indicate percent support, where less than 100 percent. Subfamilies mentioned in the text are labelled. Taxa included in Proviverrinae follows Solé et al. (2015b).

Abbreviations: **Apt**, Apterodontinae; **Hyd**, Hyaenodontinae; **Hyl**, Hyainailourinae; **Ind**, Indohyaenodontinae; **Lim**, Limnocyoninae; **Prov**, Proviverrinae; **Ter**, Teratodontinae. Drawings by Shawn P. Zack.
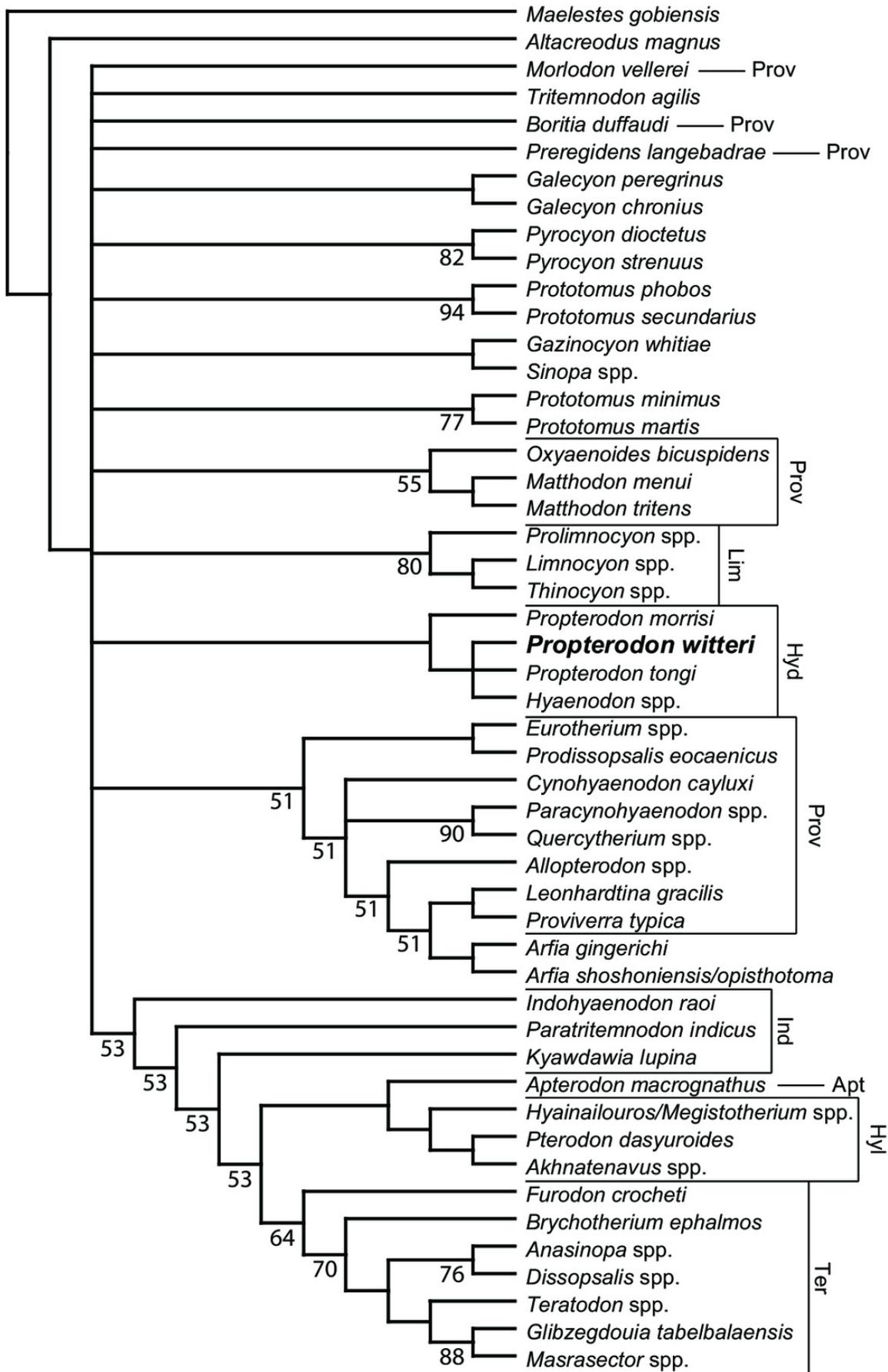
Figure 7

Comparison of *Apataelurus pishigouensis* comb. nov. with *A. kayi*

(**A**) *Apataelurus pishigouensis*, IVPP V7997, left dentary with P_4-M_1; (**B**) *Apataelurus kayi*, CM 11920, right dentary with P_3-M_2 (reversed). Both images show the dentary in buccal view. Arrows indicate the ventral deflection of the dentaries of both specimens. Note that the apparently greater height of the protoconids on P_4 and M_1 and paraconid on M_1 in *A. pishigouensis* reflects much heavier wear in *A. kayi*. All scale bars are 10mm. Drawings by Shawn P. Zack. **A** drawn from Tong and Lei (1986, pl. 1). **B** drawn from a photograph by Shawn P. Zack.

A

10 mm

B

10 mm