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

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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 $M_{2\text{-}3}$ 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 and appears unlikely. 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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Abstract

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 $M_{2\text{-}3}$ 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 and appears unlikely. 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.

Introduction

Hyaenodonts are a significant component of Eocene carnivorous guilds across the Holarctic and Africa (Gunnell, 1998; Rose, 2006; Lewis and Morlo, 2010). Along with other “creodonts” (e.g., Oxyaenidae), hyaenodonts are distinguished from modern carnivorans and their fossil relatives (Carnivoraformes) by the presence of multiple carnassial pairs in the dentition, which results in alternating shearing and crushing/grinding areas in the dentition, rather than regional separation of the molar series into mesial shearing and distal crushing/grinding areas. The latter innovation in Carnivoraformes (and convergently in Viverravidae: Zack, 2019) may have facilitated the ecological diversification of carnivorans (Friscia and Van Valkenburgh, 2010), ultimately allowing carnivorans to displace hyaenodonts over the course of the Paleogene in the northern continents and Miocene in Africa (Wesley-Hunt, 2005; Friscia and Van Valkenburgh, 2010; Borths and Stevens, 2017).

In North America, hyaenodont diversity is greatest in the earlier half of the Eocene, particularly the Wasatchian and Bridgerian Land Mammal Ages (NALMAs) (Gunnell, 1998; Van Valkenburgh, 1999; Wesley-Hunt, 2005; Friscia and Van Valkenburgh, 2010). In the subsequent Uintan NALMA, hyaenodont diversity declines dramatically. Only three genera, *Limnocyon*, *Oxyaenoides*, and *Sinopa* have been described from Uintan faunas (Matthew, 1899, 1909; Peterson, 1919; Gustafson, 1986), although an additional, small hyaenodont taxon is known but undescribed (Rasmussen et al., 1999; pers. obs.). This mid-Eocene decline of hyaenodont and other “creodont” diversity corresponds with an increase in the diversity of carnivorans and their immediate relatives (Carnivoraformes) (Van Valkenburgh, 1999; Wesley-Hunt, 2005; Friscia and Van Valkenburgh, 2010), a pattern suggesting some form of replacement of hyaenodonts by carnivoraform taxa. Understanding the nature of that replacement requires a detailed record of the diversity of both groups.

Reexamination of existing collections is one key to refining the record of carnivorous mammals across this critical period, as overlooked or misidentified specimens can shift the temporal and geographic ranges of known taxa as well as allow recognition of new forms. MCZ VPM 19874, the specimen that forms the focus of the present study is an example of significant discoveries that can be made in existing collections. The specimen, a dentary with M_{2-3} was collected by a Harvard University expedition to the Uinta Basin, Utah in 1940 (Fig. 1) and has not been described or mentioned in the literature in almost 80 subsequent years. It documents a new hyaenodont taxon from the late Uintan that differs substantially from known Uintan hyaenodonts, particularly in its possession of a strongly hypercarnivorous morphology, greater than previously known in Wasatchian through Uintan North American hyaenodonts. In fact, the affinities of the new taxon appear to lie with *Propterodon*, a genus previously known only from eastern Asian faunas correlated with the Chinese middle Eocene Irdinmanhan and Sharamurunian stages (*sensu* Wang et al., 2019). The new taxon increases Uintan hyaenodont diversity and disparity while providing evidence for interchange of Asian and North American carnivores during this critical interval in the divergent histories of Hyaenodonta and Carnivoraformes.

Materials & Methods

Dental terminology follows Rana et al. (2015), with two exceptions. Mesiobuccal cingulid is used following Zack (2011) instead of buccal cingulid, as this structure is mesially restricted in the new species. Following Kay (1977), hypocristid is used rather than postcristid for the crest connecting the hypoconid and hypoconulid. Measurements follow Gingerich and Deutsch (1989, fig. 1) and Borths and Seiffert (2017, fig. 1e), with the addition of a measurement of maximum talonid height. Dental measurements taken are illustrated in Fig. 2. Mandibular depth was measured lingually below M_3. All measurements were taken to the nearest tenth of a millimeter with Neiko digital calipers. MCZ VPM 19874 was whitened using ammonium chloride prior to being photographed.

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Phylogenetic Methods—To test the affinities of the new species, it was added to a substantially modified version of the character taxon matrix used by Rana et al. (2015). While many recent phylogenetic assessments of hyaenodont relationships have used versions of the matrix introduced by Borths et al. (2016) (Borths and Seiffert, 2017; Solé and Mennecart, 2019; Borths and Stevens, 2019, *in press*), the Rana et al dental character sample is preferable as it includes fewer suites of characters that are likely to be non-independent (e.g., four characters describing metaconid size/presence on different loci). Sansom et al. (2017) have recently called attention to the potentially misleading phylogenetic signal of mammalian dental morphology, with character non-independence postulated as a leading driver of this problem (*see also* Kangas et al., 2004; Harjunmaa et al., 2014; Billet and Bardin, 2019). The Rana et al. (2015) dental sample was used to minimize this problem and additional changes have been made for the current study (e.g., removing a character describing the number of P^3 roots, which reflects development of a P^3 protocone lobe) to further minimize problems associated with character independence. Overall, several dental characters were revised, replaced, combined, or deleted, and one additional character describing the number of upper incisors was added from Borths and Stevens (2019). Numerous individual scorings were modified to improve scoring consistency, with particular emphasis was placed on ensure scoring consistency across geographic regions.

While the dental character sample from Rana et al. (2015) was used, the non-dental character sample used by Rana et al. (2015) which, in turn was derived from Polly (1996), was largely replaced by the cranial, mandibular, and postcranial character sample used by Borths and Stevens (2019), and Borths and Stevens' scorings were used with some additions (e.g., postcranial scorings were added for *Galecyon chronius* and *Prototomus martis*). One character from Rana et al. (2015) describing mandibular symphysis depth was retained, as this variation was not captured by Borths and Stevens' characters.

In addition to the inclusion of the new species, several changes were made to the taxonomic composition of the matrix. First, the composite *Propterodon* spp. OTU used by Rana et al. (2015) was replaced with separate OTUs for *P. morrisi* and *P. tongi*. Reflecting newly published material, the African *"Sinopa"* OTU included in Rana et al. (2015) was replaced by *Brychotherium ephalmos*, scored from descriptions in Borths et al. (2016) and accompanying models. Scorings of *Akhnatenavus* were updated to include *A. nefertiticyon* described in the same work, while scorings for *Masrasector* were updated to base on material of *M. nananubis* described by Borths and Seiffert (2017). The *Pterodon* spp. OTU was restricted to *P. dasyuroides* and rescored, given that new evidence indicates *Pterodon*, as traditionally used, is likely polyphyletic (Solé et al., 2015a; Borths and Stevens, 2019, *in press*). Three additional taxa were added to the matrix, *Boritia duffaudi*, *Preregidens langebadrae*, and *Matthodon menui*. These three taxa are either newly described or newly identified as hyaenodonts, and they significantly enhance the documentation of early European hyaenodonts (Solé et al., 2014a, 2015b).

In addition, six OTUs included in the Rana et al. (2015) matrix were excluded from the present analysis. As with *Pterodon*, monophyly of *Metapterodon*, as used by Rana et al. (2015), now appears dubious (Morales and Pickford, 2017; Borths and Stevens, *in press*), but, unlike the well-documented *Pterodon dasyuroides* individual species of *Metapterodon* are fragmentary and poorly known, contributing little to the broader structure of hyaenodont interrelationships. Until the composition of *Metapterodon* is better understood, the genus is better excluded. A second taxon, *Eoproviverra eisenmanni*, was removed over concerns about the successional status of the type and most informative specimen, MNHN.F.RI 400. Described as an M_2 (Godinot, 1981; Solé et al., 2015c), MNHN.F.RI 400 shows several features that suggest the tooth may instead represent dP_4, including a low paraconid, open trigonid, small talonid, and generally tall, delicate cusp construction. If this is the case, MNHN.F.RI 400 would likely represent a larger taxon than the remainder of the hypodigm.

Finally, *Tinerhodon disputatum* and the three representatives of Koholiinae (*Boualitomus marocanensis*, *Koholia atlasense*, *Lahimia selloumi*) were excluded. As briefly noted by Rana et al. (2015), the hyaenodont status of these taxa remains to be clearly demonstrated. Referral of all four taxa to Hyaenodonta appears to have been made based on the presence of multiple carnassial pairs and retention of three molars. As discussed by Zack (2019), this *de facto* definition of Hyaenodonta combines two eutherian symplesiomorphies (molar homodonty and three molars) with a trait found in all carnivorous clades (carnassials). Given this weak evidence, the possibility that some or all of these taxa are not hyaenodonts must be considered. In fact, *Tinerhodon disputatum* has not been consistently recovered as a hyaenodont in analyses that do not constrain the ingroup to monophyly (e.g., Borths and Stevens, *in press*). Members of Koholiinae have features that are unusual for Hyaenodonta but typical of members of Tenrecoidea including absence of P_1 (Gheerbrant et al., 2006; Solé et al., 2009) and an M^1 paracone that is distinctly lingual to the metacone (Crochet, 1988). Combined with the small size of the two earlier taxa, this raises the possibility that koholiines may actually represent an endemic African carnivorous radiation prior to an Eocene immigration of hyaenodonts to Africa.

The final matrix includes 48 ingroup taxa and two outgroups scored for 115 characters. The list of characters and specimens examined are available in the online Supplemental Information. The full matrix is also available on MorphoBank as project P3489 (http://morphobank.org/permalink/?P3489). The matrix was analyzed in TnT version 1.5 (Goloboff and Catalano, 2016). Initial analyses used the Sectorial Search algorithm under the New Technology search dialog. The matrix was analyzed until minimum length trees were recovered 100 times. Resulting trees were then submitted for branch swapping in the Traditional Search dialog to ensure that all minimum length trees were identified.

Institutional Abbreviations—AMNH FM, Fossil Mammal Collection, American Museum of Natural History, New York, New York, USA; **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; **HGL**, Hammada Gour Lazib, Algeria; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; **MCZ VPM**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **MNHN.F.ERH**, Muséum National d'Histoire Naturelle, Rhône Basin Collection, Paris, France; **MNHN.F.RI**, Muséum National d'Histoire Naturelle, Rians Collection, Paris, France; **ZIN**, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia.

Results

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758

EUTHERIA Huxley, 1880

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

HYAENODONTIDAE Leidy, 1869

HYAENODONTINAE (Leidy, 1869)

PROPTERODON Martin, 1906

Comments—*Propterodon* was named by Martin (1906) without designation of a type species. In 1925, Matthew and Granger named a new species that they referred to *Propterodon*, *P. irdinensis*. In the absence of any prior referral of a species to *Propterodon*, *P. irdinensis* became, by default, the type species, a situation that spawned considerable taxonomic confusion and was ultimately resolved by Polly and Lange-Badré (1993). Matthew and Granger (1925) named *Propterodon irdinensis* for a series of jaw fragments, not certainly associated, from Inner Mongolian exposures of the middle Eocene Irdin Manha Formation (Irdinmanhan stage) (Fig. 3). The previous year, Matthew and Granger (1924) had described *Paracynohyaenodon morrisi* from the same beds, and most recent workers have regarded the two species as conspecific, with *Propterodon morrisi* the appropriate name for this taxon (Dashzeveg, 1985; Polly and Lange-Badré, 1993; Morlo and Habersetzer, 1999). Dashzeveg (1985) named an additional hyaenodont taxon, *Pterodon rechetovi*, for two maxillae from the Irdin Manha-equivalent Khaichin Ula 2 fauna from the Khaichin Formation of Mongolia. This species was subsequently made the type species of a new genus, *Neoparapterodon*, by Lavrov (1996), but Morlo and Habersetzer (1999), noting that the upper dentition of *Propterodon morrisi* is essentially identical that of *N. rechetovi*, placed the latter genus and species in synonymy with the former. In addition to *P.*

morrisi, three other species of *Propterodon* have been named. *Propterodon pishigouensis* was named by Tong and Li (1986) for a dentary preserving P_4-M_1 from the Hetaoyuan Formation (Irdinmanhan), Henan Province, China (Fig. 3) (see Discussion). An additional Chinese species, *P. tongi* was named by Liu and Huang (2002) for a dentary with P_1-M_3 from the Huoshipo locality, Yuli Member of the Hedi Formation (Irdinmanhan), Shanxi Province. Most recently, Bonis et al. (2018) named *Propterodon panganensis* for a dentary preserving P_4-M_1 from the Sharamurunian equivalent Pondaung Formation of Myanmar (Fig. 3).

PROPTERODON WITTERI, sp. nov. urn:lsid:zoobank.org:act:4D88F815-E7BE-4997-890F-59BC65A06A28

(Fig. 4, Table 1)

Holotype—MCZ VPM 19874, left dentary preserving $M_{2\text{-}3}$, the back of the horizontal ramus and almost all of the ascending ramus.

Etymology—Named for R. V. Witter, whose party collected the type and only known specimen in 1940.

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

Stratigraphy and Age—Myton Member of the Uinta Formation (Uinta C), late Uintan (Ui_3) North American Land Mammal "Age" (NALMA), late middle Eocene (Prothero, 1996) (Fig. 3).

Diagnosis—Largest known species of *Propterodon*. Differs from *P. panganensis* in substantially larger size. Differs from *P. morrisi* in larger size, more reduced metaconids on $M_{2\text{-}}$

$_3$, and a relatively larger talonid on M_3. Differs from *P. tongi* in larger size, retention of rudimentary metaconids on $M_{2\text{-}3}$, larger talonids on $M_{2\text{-}3}$, and a less recumbent M_3 protoconid.

Description—The preserved portion of the horizontal ramus of the dentary is deep and transversely compressed beneath M_3 (Fig. 4A-B). Posterior to the toothrow, the coronoid process forms an approximately 60-degree angle with the alveolar margin. The process is elongate and extends well above the toothrow, although its dorsal extremity is lacking. The posterior margin of the coronoid process is concave, and the process appears to have overhung the mandibular condyle. On the ventral margin of the dentary, there is a slight concavity between the horizontal ramus and the angular process. The angular process itself is directed posteriorly, with no meaningful ventral or medial inflection. The process is relatively thick, with no medial excavation between the angular process and condyle. The tip of the process extends posterior to the mandibular condyle and has a slight dorsal curvature. The mandibular condyle is positioned at the level of the alveolar border. The condyle is flush with the ascending ramus, with no development of a neck. The visible portion of the condyle is deepest at its medial margin, tapering dorsally laterally. The bone of the ascending ramus is thickest in a low, broad ridge extending anteriorly and somewhat ventrally from the condyle. Just inferior to this ridge, near mid-length of the ascending ramus is the opening of the mandibular canal.

M_2 is complete, aside from slight damage to the apex of the paraconid and the buccal base of the talonid (Fig. 4A-C). The trigonid is much longer and more than twice the height of the talonid. It would likely have been taller, but a large, vertical wear facet on the buccal surface of the paracristid has removed the apex of the protoconid and likely the paraconid. The facet extends nearly to the base of the crown and, occlusally, has exposed dentine of both cusps.

The protoconid is the largest and tallest trigonid cusp. The paracristid descends relatively steeply and directly mesially from its apex to meet the paraconid portion of the paracristid in a deep carnassial notch that is continued lingually as a horizontal groove between the paraconid and protoconid. At the distolingual corner of the protoconid, the vertical protocristid is indistinct near the apex of the cusp, becoming better-defined basally and meeting the metaconid in a small carnassial notch.

Mesially, the paraconid is approximately two-thirds the height of the protoconid. The paraconid portion of the paracristid forms an angle of approximately 45 degrees to the long axis of the crown. From its junction with the protoconid portion, it rises slightly towards the paraconid apex. At the mesial margin of the tooth, the paraconid forms a mesial keel that helps define a flattened, diamond-shaped lingual surface. Lingually, the paraconid and protoconid are fused to a level close to three quarters the height of the former cusp. Buccally, the paraconid supports a strong, vertical mesiobuccal cingulid that extends to the level of the carnassial notch and projects further mesially than the mesial keel. Together, the cingulid and mesial keel form a well-defined embrasure for the back of the talonid of M_1.

The metaconid of M_2 is a tiny but distinct cusp positioned high on the protoconid, just below the level of the paraconid apex. The metaconid is fused with the protoconid to a level above the level of fusion of the paraconid and protoconid. The apex of the metaconid is directed slightly distally as well as lingually and bears a distinct crest that meets the protoconid portion of the protocristid.

The talonid is dominated by the hypoconid. The apex of the cusp is worn away but was likely flat topped, as in M_3. Buccally, the talonid falls away steeply from the apex of the hypoconid and a wear facet occupies most of the buccal surface of the talonid. Lingually, there is a gentler slope, forming a flat, inclined surface. The cristid obliqua is nearly longitudinal in orientation, meeting the base of the trigonid in a small carnassial notch. The contact is buccal to the level of the metaconid, but still well lingual of the buccal margin of the protoconid, resulting in a shallow hypoflexid.

Near the distal margin of the lingual side of the talonid is a shallow groove that appears to separate the hypoconid from a much smaller, lower hypoconulid. There is no entoconid or entocristid. Aside from the mesiobuccal cingulid, there is no development of cingulids. Buccal enamel extends slightly more basally than lingual enamel.

M_3 is larger than M_2 and almost unworn but is otherwise quite similar in gross morphology (Fig. 4A-C). The unworn protoconid of M_3 is slightly recumbent and the protoconid portion of the paracristid is modestly more elongate than the paraconid portion. The mesial keel of the paraconid is stronger than on M_2 and projects further than the mesiobuccal cingulid. The M_3 metaconid is even smaller than on M_2, reduced to a projection at the end of the almost vertical protocristid. Even in this rudimentary state, a tiny carnassial notch still separates the cusp from the protoconid, but there is no distal projection of the metaconid, unlike M_2.

The talonid is shorter than on M_2 and, unlike on the latter tooth, is noticeably narrower distally, with its lingual margin running distobuccally from the lingual base of the protoconid. As on M_2, the largest cusp on the M_3 talonid is the hypoconid. The unworn M_3 hypoconid is flat-topped, but the lingual enamel appears to be thickest near its distal margin, indicating a distal position for the hypoconid apex. As on M_2, the cristid obliqua meets the trigonid in a small carnassial notch buccal to the level of the metaconid. From that point, the cristid obliqua continues briefly as a vertical crest that ascends the trigonid, reaching approximately one third of the height of the protoconid. The hypoconulid of M_3 is small but better defined than on M_2, being separated from the hypoconid by a carnassial notch. At the lingual margin of the talonid, opposite the apex of the hypoconid, is a linear thickening of enamel that suggests the presence of a very weak entocristid.

Comparisons—The strongly hypercarnivorous morphology of *P. witteri* distinguishes the new species from known Uintan and older North American hyaenodonts. Among named Uintan hyaenodonts (Matthew, 1899, 1909; Hay, 1902; Peterson, 1919; Gustafson, 1986), *Sinopa longipes* and *S. major* differ dramatically from the new species, with relatively low, closed trigonids, unreduced metaconids, and large, deeply basined talonids. The limnocyonines *Limnocyon potens* and *Oxyaenodon dysodus* show greater carnivorous adaptation than species of *Sinopa*, but both have more closed trigonids, larger metaconids, and broader, better-developed talonids than *P. witteri*.

Wasatchian *Pyrocyon* and Bridgerian *Tritemnodon* (Fig. 3) more closely approach the morphology of the new species, but with less developed hypercarnivorous adaptation. $M_{2\text{-}3}$ in species of *Pyrocyon* (*P. dioctetus*, *P. strenuus*) and in *Tritemnodon agilis* resembles *Propterodon witteri* in having open trigonids with elongate prevallid shearing blades, reduced metaconids, strong mesiobuccal cingulids (particularly in *T. agilis*), small, narrow talonids, and reduced hypoconulids. However, in all of these features, the morphology of *P. witteri* is more extreme, with more open trigonids with more elongate prevallids, much more reduced metaconids, mesiobuccal cingulids that are stronger and more vertical, and more simplified talonids with a very weak to absent entoconid/entocristid complex, which is retained in both *Pyrocyon* and *Tritemnodon*. In addition, in both *Pyrocyon* and *Tritemnodon*, M_3 is subequal to M_2, while in *P. witteri*, it is substantially larger. *Tritemnodon agilis* further differs from *P. witteri* in having a shallower, more gracile dentary and a more inclined (less vertical) coronoid process.

The temporal gap between *Propterodon witteri* and species of *Pyrocyon* and *Tritemnodon* is also problematic (Fig. 3). *Pyrocyon* is well-known known from mid-Wasatchian faunas (Gingerich and Deutsch, 1989) but does not appear to persist until the end of the interval. In the Willwood Formation of the Bighorn Basin, *Pyrocyon* disappears from record during Wa_6, well below before the end of the densely sampled portion of the Willwood record (Chew, 2009), and the genus is unknown from Wa_7 through Uintan faunas. *Tritemnodon* is well-documented from the earlier portion of the Bridgerian, particularly Br_2, but has a limited record from Br_3 and no record from the earlier portions of the Uintan (Ui_{1-2}) (Eaton, 1982; Gunnell et al., 2009). Derivation of *P. witteri* from either genus would imply substantial gaps in the hyaenodont record.

Hypercarnivorous hyaenodonts are also present in mid-Eocene faunas from Africa (*Furodon*), Asia (*Propterodon*), and Europe (*Oxyaenoides*) (Matthew and Granger, 1924, 1925; Lange-Badré and Haubold, 1990; Lavrov, 1996; Liu and Huang, 2002; Solé et al., 2014b, 2015b, 2016; Godinot et al., 2018) (Fig. 3). Unlike *Pyrocyon* or *Tritemnodon*, and M_3 is distinctly larger than M_2 in these taxa, a similarity shared with *P. witteri*. A link to one or more of these taxa would have implications for the origins of the Uinta form and for intercontinental dispersals of hyaenodonts more generally.

Compared to *Propterodon witteri* the M_{2-3} trigonids of species of European *Oxyaenoides* (*O. bicuspidens*, *O. lindgreni*, *O. schlosseri*) are more closed, with a shorter paraconid portion of the paracristid (Lange-Badré and Haubold, 1990; Solé et al., 2014a, 2015b; Godinot et al., 2016) (Fig. 5B). *Oxyaenoides* has completely lost metaconids on all molars, while *P. witteri* retains small metaconids on M_{2-3}. In *Oxyaenoides*, the protoconid and paraconid are separated to a level close to the base of the crown, contrasting with *P. witteri*, where these cusps are fused to approximately mid-height. Both taxa have a distinct mesiobuccal cingulid, but it is much lower in *Oxyaenoides*. While both have reduced talonids, the hypoconulid is relatively larger in *Oxyaenoides* and a more distinct entoconid/entocristid complex is retained, even in the derived *O. schlosseri*. *Oxyaenoides* talonids are also much shorter relative to their width than in *P. witteri*. Overall, *Propterodon witteri* displays a mixture of more (open trigonids, trenchant talonids) and less (retained metaconids, elongate talonids) derived morphologies in comparison to *Oxyaenoides*. This pattern is suggestive of parallel developments in lineages assembling a hypercarnivorous morphology independently.

African *Furodon crocheti* has more closed trigonids than *Propterodon witteri* (Solé et al., 2014b) (Fig. 5C). However, the length of the paraconid portion of the prevallid blade is similar, resulting in the paraconid overhanging the lingual margin of the crown in *F. crocheti*. The metaconid is larger in *F. crocheti* than in *P. witteri*. However, whereas in *P. witteri*, the metaconid is positioned high on the protoconid, almost at the same height as the paraconid apex, it is positioned much lower in *F. crocheti*. As a result, despite its size, the metaconid apex is substantially lower than the paraconid apex. The talonids of *F. crocheti* are relatively larger than in *P. witteri*, particularly on M_2, and the M_2 talonid is much wider as well. The M_2 hypoconid has a mesial apex in *F. crocheti*, with a subequal cristid obliqua and hypocristid. In *P. witteri*, the apex of the hypoconid is distal and there is no hypocristid to speak of. While the hypoconulid appears to be small in *F. crocheti*, the entoconid/entocristid complex remains prominent, contrasting with the trenchant morphology present in *P. witteri*. Finally, on the dentary of *F. crocheti*, the ventral margin of the angular process grades smoothly into the horizontal ramus, lacking the distinct inflection that occurs in *P. witteri*.

Some of the features that distinguish *F. crocheti* from *P. witteri* are shared with other, less hypercarnivorous taxa from Africa and South Asia. The paraconid overhang is present in African *Brychotherium* and South Asian Indohyaenodontinae (Kumar, 1992; Egi et al., 2005; Rana et al., 2015; Borths et al., 2016), while the low placement of the metaconid is shared with these taxa as well as African *Glibzegdouia* and *Masrasector* (Solé et al., 2014b; Borths and Seiffert, 2017). A mesially positioned hypoconid apex occurs in *Glibzegdouia*, *Masrasector*, and the indohyaenodontines *Kyawdawia* and *Yarshea* (Egi et al., 2004, 2005; Solé et al., 2014b; Borths and Seiffert, 2017). These similarities are consistent with phylogenetic analyses that link *Furodon* to African and South Asian hyaenodonts (Rana et al., 2015; Borths et al., 2016; Borths and Seiffert, 2017; Borths and Stevens, 2019, *in press*). Their absence in *Propterodon witteri* indicate that its affinities lie elsewhere.

The morphology of the two best known species of Asian *Propterodon*, *P. morrisi* (senior synonym of the type species, *P. irdinensis*) (Fig. 5D) and *P. tongi* (Fig. 5E), is quite similar to that of *P. witteri* (Matthew and Granger, 1924, 1925; Liu and Huang, 2002). Trigonid proportions of $M_{2\text{-}3}$ in *P. morrisi* (e.g., AMNH FM 21553) are nearly identical to *P. witteri*, while *P. tongi* has slightly more open trigonids than either species. In *P. morrisi*, the metaconids of $M_{2\text{-}3}$ are reduced but remain slightly larger than in *P. witteri*. The opposite is true of *P. tongi*, with both M_2 and M_3 lacking defined metaconids. In *P. morrisi*, the metaconids are positioned high on the protoconid, comparable to *P. witteri*. Both Asian species have well-developed, vertical mesiobuccal cingulids that extend high up on the paraconid. Talonid structure is also closely comparable, at least on M_2. The Asian species have small talonids (smaller in *P. tongi*) with distal hypoconid apices, rudimentary hypoconulids positioned directly distal to the hypoconid, and no entoconid/entocristid complex, all identical to the morphology on M_2 of *P.*

witteri. The M_3 talonid is more reduced in the Asian forms than in the North American taxon. In the case of *P. tongi*, it is reduced to a cuspule on the distal end of the trigonid. The talonid is larger in *P. morrisi*, but still smaller than in *P. witteri*. As in the North American form, there does appear to be a trace of an entocristid on the M_3's of AMNH FM 20128 and 21553. Taken together, the morphology of *Propterodon witteri* is closely comparable to *P. morrisi* and *P. tongi*, particularly the former. The most significant morphological distinction is the relative size of the M_3 talonid, which is relatively larger in *P. witteri* than in either Asian species. Despite this contrast, Asian *Propterodon* species are clearly the closest matches to *P. witteri* among relevant taxa, and referral of the new species to *Propterodon* can be made with confidence.

Phylogenetic Results—Analysis of the matrix described in Materials & Methods produced 145 most parsimonious trees (L=510, CI=0.294, RI=0.615), the majority rules consensus of which is shown in Fig. 6. Resolution is poor, even using the majority rules rather than a strict consensus. The largest clade unites a paraphyletic Indohyaenodontinae with the three primary African subfamilies (Hyainailourinae, Apterodontinae, Teratodontinae). A second major clade comprises most members of Proviverrinae along with *Arfia*, which is unexpectedly deeply nested within Proviverrinae as the sister taxon of *Proviverra* and *Leonhardtina*. Smaller groupings include Limnocyoninae, Hyaenodontinae, and groupings of the North American *Sinopa* and *Gazinocyon* and the European hypercarnivorous genera *Oxyaenoides* and *Matthodon* and. All of these clades form a massive polytomy at the base of the ingroup, along with numerous genera and species of early and middle Eocene hyaenodont.

While disappointing, the poor resolution of the consensus tree is consistent with a lack of clarity in other recent analyses of hyaenodont phylogeny. While the consensus topology is better resolved, most clades recovered by Rana et al. (2015) have poor bootstrap support. Most nodes in Bayesian trees recovered by Borths and colleagues (Borths et al., 2016; Borths and Seiffert, 2017; Borths and Stevens, 2017, 2019, *in press*) have similarly low posterior probabilities, and there are substantial topological differences between analyses with different assumptions concerning character evolution (e.g., Prionogalidae in Borths and Stevens, 2019, supplementary fig. 1 versus 2). Simply put, many relationships within Hyaenodonta are neither stable nor well-resolved.

With regard to *Propterodon witteri*, two conclusions can be made. First, all trees recover a clade linking the new species to *Propterodon morrisi*, *P. tongi*, and *Hyaenodon*. Monophyly of *Propterodon* is not recovered, with a majority of trees linking *P. tongi* and *P. witteri* more closely to *Hyaenodon* than to *P. morrisi* on the basis of greater metaconid and entoconid reduction in the former species. These results indicate that *Propterodon* is paraphyletic and is likely to be directly ancestral to *Hyaenodon*, although further support would be desirable, particularly as metaconid and entoconid reduction have occurred convergently in many different lineages of carnivorous mammal (e.g., Muizon and Lange-Badré, 1997).

In addition, the position of Hyaenodontinae within Hyaenodonta is not well-resolved. While hyaenodontine monophyly is supported in all shortest trees, the subfamily is recovered in the large polytomy at the base of the ingroup. This contrasts with recent analyses that have consistently supported some form of a link to European hyaenodonts (Rana et al., 2015; Borths et al., 2016; Borths and Seiffert, 2017; Solé and Mennecart, 2019; Borths and Stevens, 2019, *in press*), particularly the hypercarnivorous *Oxyaenoides*. The implications of this aspect of the topology are discussed below

One other result that warrants brief comment is that the two recently described European hyaenodont genera, both described as potential proviverrines (Solé et al., 2014a, 2015b), *Boritia* and *Preregidens*, are not recovered in proximity to Proviverrinae. Consistent with this result, both genera lack the distinctive enlarged, bulbous entoconid typical of proviverrine molar talonids (e.g., Solé, 2013). Of the two, *Boritia* is very similar to several early Eocene North American hyaenodonts (*Prototomus martis*, *Pyrocyon* spp.), and it may represent a parallel development from an early European species of *Prototomus* (e.g., *P. girardoti*). Alternatively, it may document evidence of faunal exchange between North America and Europe after the PETM, consistent with evidence from the Abbey Wood fauna (Hooker, 2010).

Discussion

Hyaenodontine Origins—While the results of the phylogenetic analysis support monophyly of Hyaenodontinae, including *Propterodon witteri*, the broader relationships of hyaenodontines are not resolved. A number of recent phylogenetic assessments have broadly supported a link between hyaenodontines and European Eocene hyaenodonts (Rana et al., 2015; Borths et al., 2016; Borths and Seiffert, 2017; Borths and Stevens, 2017, 2019, *in press*; Solé and Mennecart, 2019). A particular recurring pattern has been a link between Hyaenodontinae and *Oxyaenoides*, supported by all of these studies except Rana et al. (2015). However, comparisons between species of *Oxyaenoides* and early hyaenodontines call such a link into question. As discussed above, *Propterodon witteri* has more open trigonids and more simplified talonids than species of *Oxyaenoides*, while retaining distinct metaconids and larger talonids, contrasts that also distinguish *P. morrisi* from *Oxyaenoides*.

Further comparisons between *Oxyaenoides* and *Propterodon* of aspects of dental and mandibular morphology that are unknown in *P. witteri* reveal additional contrasts. *Propterodon* has a low, elongate mandibular symphysis (e.g., Li and Huang, 2002), contrasting with the shorter but deeper symphysis in species of *Oxyaenoides* (e.g., Solé et al., 2015b). Despite having a relatively large P_1, the tooth remains single-rooted in *Propterodon*. In contrast, the comparatively smaller P_1 of *Oxyaenoides* is double-rooted. P_2 is a relatively large, elongate tooth in *Propterodon*, while in *Oxyaenoides*, this tooth is unusually small for a hyaenodont. P_4 morphology is superficially similar. Both genera have a tall protoconid and a trenchant hypoconid, the latter a typical feature of hypercarnivorous hyaenodonts. However, while *Propterodon* lacks a paraconid on P_4 (Li and Huang, 2002) it does not have the distinctive low shelf at the mesial base of the protoconid that is characteristic of *Oxyaenoides* (Lange-Badré and Haubold, 1990; Solé et al., 2014a, 2015b).

Upper molar morphology shows further distinctions. In *Propterodon morrisi* (the upper dentition is unknown in other *Propterodon* species), the metastylar blade is longer and more longitudinally oriented than in *Oxyaenoides* (Lange-Badré and Haubold, 1990; Lavrov, 1996). On both M^1 and M^2 of *P. morrisi*, parastylar development is limited to a weak cingular thickening. In contrast, in *Oxyaenoides* the parastyles are large and buccally projecting, especially on M^2. Fusion of the paracone and metacone is more extensive in *P. morrisi* than in *Oxyaenoides*. In *P. morrisi*, the paracone remains taller than the metacone (e.g., AMNH FM 21555), while the metacone is taller in *O. bicuspidens* (Lange-Badré and Haubold, 1990). However, this is not the case in an M^1 referred to *O. lindgreni* (Solé et al., 2014a), which has a taller paracone. In both genera, the protocone is reduced and does not project far lingual of the buccal cusps. In *P. morrisi*, the protocone is also strongly compressed mesiodistally, but it is distinctly more elongate in *Oxyaenoides*.

Taken together, the contrasts between *Oxyaenoides* and *Propterodon* are substantial. Aside from features that are widespread among hypercarnivorous hyaenodonts generally, there is little to suggest a close relationship. Some of the features that distinguish *Oxyaenoides* from *Propterodon* may link the former genus to other European hyaenodonts. The morphology of the talonid in *Oxyaenoides*, with three, more or less equally developed and equidistantly spaced cusps, is present in a variety of European Eocene hyaenodonts. Similarly, a double-rooted P_1 is widespread among European forms. Both features have been cited in support of monophyly of a broadly conceived Proviverrinae (e.g., Solé, 2013). The lack of comparable morphology in *Propterodon*, on the other hand, suggests that the origin of hyaenodontines should be sought elsewhere. The ?Arshantan fauna from Andarak-2, Khaichin Formation, Kyrgyzstan, includes a fragmentary hyaenodont dentition (ZIN 34494) described by Lavrov and Averianov (1998) as similar to *Neoparapterodon rechetovi*, the latter a likely synonym of *Propterodon morrisi* according to Morlo and Habersetzer (1999). If correctly identified, this would extend the Asian record of Hyaenodontinae back to the early part of the middle Eocene and would support an Asian origin for the subfamily. Unfortunately, the hyaenodont record from the Arshantan and the preceding Lingchan (equivalent to the Bumbanian) is very poor. Aside from ZIN 34494, the published hyaenodont record from the Arshantan is limited to the type specimen of *Isphanatherium ferganensis* (Lavrov and Averianov, 1998), which may not be a hyaenodont (see below). Lingchan hyaenodont records comprise two specimens referred to distinct species of *Arfia* and two specimens referred to *?Prototomus* sp. (Lavrov and Lopatin, 2004; Tong and Wang, 2006; Morlo et al., 2014; Solé et al., 2013). Until early and early middle Eocene hyaenodonts from Asia are better documented, it is difficult to determine what role, if any, Asia played in the origin of Hyaenodontinae.

"Propterodon" pishigouensis—In addition to *P. morrisi* and *P. tongi*, the most recent review of the genus (Bonis et al., 2018) recognized two additional Asian species of *Propterodon*, *P. pishigouensis* and *P. panganensis*. Each of these species is known only from a partial dentary preserving P_4 and M_1, precluding direct comparisons with *P. witteri*. Of the two, *P. panganensis* has some unusual features (symmetric P_4 protoconid, P_4 and M_1 similar in size, very reduced M_1 talonid) that suggest its relationship to other *Propterodon* requires confirmation, but it is clearly a hypercarnivorous hyaenodont. *Propterodon pishigouensis*, on the other hand, appears to represent a different clade entirely.

The most distinctive feature of *Propterodon pishigouensis* is the shape of the dentary, which is ventrally deflected anteriorly, beginning below the anterior root of P_4 (Tong and Li, 1986), indicating the presence of an anterior flange. In contrast, the symphysial region is shallow in *P. morrisi* and *P. tongi* and tapers anteriorly. In fact, an anterior dentary flange has not been documented in any hyaenodont. The only middle Eocene carnivorous mammals known to possess such a flange are machaeroidines (Scott, 1938; Matthew, 1909; Gazin, 1946; Dawson et al., 1986), a small clade of North American Wasatchian through Uintan carnivores recently supported as oxyaenids (Zack, 2019).

Machaeroidines, particularly the Uintan *Apataelurus kayi*, share substantial similarities with the type specimen of *Propterodon pishigouensis*, including features that distinguish the latter species from other *Propterodon*. On P_4, both *A. kayi* and *P. pishigouensis* have a well-developed paraconid that is nearly as tall as the talonid (Scott, 1938; Tong and Li, 1986). The paraconid is absent on P_4 in *P. tongi* (Liu and Huang, 2002). In *P. panganensis* it is low and weakly developed (Bonis et al., 2018). While all relevant species have simple P_4 talonids dominated by a tall hypoconid, in *P. pishigouensis* and *A. kayi*, the talonid is distinctly broader than the remainder of the crown (Scott, 1938; Tong and Li, 1986). In contrast, P_4 width is uniformly narrow in *P. panganensis* and *P. tongi* (Liu and Huang, 2002; Bonis et al., 2018). In *Propterodon tongi* and, to judge the roots of P_4, *P. morrisi*, P_4 is enlarged relative to M_1 (Matthew and Granger, 1925; Liu and Huang, 2002). In *P. pishigouensis* and *A. kayi*, along with *P. panganensis*, the two teeth are subequal in size (Scott, 1938; Tong and Li, 1986; Bonis et al., 2018).

On M_1, a defined metaconid is lacking in *P. pishigouensis* and *A. kayi* (Scott, 1938; Tong and Li, 1986), again along with *P. panganensis* (Bonis et al., 2018), but retained in *P. morrisi* (e.g., AMNH FM 21553), with M_1 of *P. tongi* too worn to assess. The primary difference in M_1 morphology is in the talonid. The talonids of *P. morrisi*, *P. tongi*, and *P. panganensis* are short and much lower than the paraconid (Matthew and Granger, 1925; Liu and Huang, 2002; Bonis et al., 2018; pers. obs. of AMNH FM 21553). In *P. pishigouensis* and *A. kayi*, the talonid is relatively elongate and nearly as tall as the paraconid (Scott, 1938; Tong and Li, 1986). Talonid morphology is simplified in both *P. pishigouensis* and *A. kayi*, with both taxa only retaining a hypoconid. In *P. morrisi* and *P. tongi*, some lingual structure is retained, although the extremely reduced talonid of *P. panganensis* is also simplified.

Taken together, the mandibular and dental morphology of *Propterodon pishigouensis* differs substantially from other species of *Propterodon*, particularly *P. morrisi* and *P. tongi*, but closely matches the morphology of the North American machaeroidine *Apataelurus kayi*. Accordingly, *Propterodon pishigouensis* is recombined as *Apataelurus pishigouensis* **new**

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

There may be an additional, older Asian machaeroidine, also initially described as a hyaenodont. *Isphanatherium ferganensis* was named for an isolated upper molar from the Andarak-2 fauna (Lavrov and Averianov, 1998). The morphology of *I. ferganensis* is strikingly derived for an early hyaenodont, with an extremely elongate, longitudinally oriented postvallum blade and a strongly reduced protocone. Both of these features would be consistent with a machaeroidine identity. The overall morphology of the type of *I. ferganensis* is closely comparable to M^1 of *Machaeroides* spp. from the early and middle Eocene of North America (Gazin, 1946; Dawson et al., 1986). They share development and orientation of the metastylar blade, protocone reduction without mesiodistal compression, fusion of the paracone and metacone to a point close to their apices, with the metacone taller than the paracone, and the presence of a low but distinct parastyle that is continuous with a buccal cingulum that is restricted to the mesial portion of the crown. A specific similarity shared by *I. ferganensis* and *M. simpsoni* (pers. obs. of CM 45115) is the presence of contrasting compression of the paracone and metacone, with the former compressed mesiodistally while the latter is compressed transversely. More material is needed to be certain, but the age and morphology of *Isphanatherium ferganensis* supports the tentative reidentification of the species as a machaeroidine and of the holotype as an M^1 rather than an M^2.

Late Uintan Carnivore Dispersals—In addition to *Propterodon*, several other carnivorous taxa appear in the late Uintan ($Ui_{2\text{-}3}$) without obvious antecedents in early Uintan (Ui_1) faunas. Among hyaenodonts, *Oxyaenodon dysodus* does not appear to be derivable from *Limnocyon potens* (*contra* Morlo and Gunnell, 2005), the only limnocyonine known from the early Uintan. Compared to *L. potens*, *O. dysodus* is smaller and more hypercarnivorously adapted, with smaller, less basined talonids and a longer M_2 prevallid blade. *Oxyaenodon dysodus* also retains a full complement of relatively uniform incisors, while *L. potens* has enlarged I^2 and lost I^3 (Denison, 1938). The affinities of another late Uintan hyaenodont, the small undescribed taxon or taxa referenced above are unclear at present, but small hyaenodontid material from the Mission Valley Formation appear to document a non-limnocyonine with a narrow M_1 talonid (pers. obs.), inconsistent with derivation from either *Limnocyon* or *Sinopa*, the only hyaenodont genera known from the early Uintan.

Other carnivorous groups show a similar pattern. At least two machaeroidine taxa are present in late Uintan faunas (Scott, 1937, 1938; Rasmussen et al., 1999; Wagner, 1999; Zack, 2019), but none is known from Ui_1. Among miacids, several taxa appear in the late Uintan without obvious Ui_1 antecedents, including *Tapocyon* spp., *"Miacis" uintensis*, and *"M." hookwayi* (Wesley and Flynn, 2003; Spaulding and Flynn, 2009; Tomiya, 2013). Finally, the enigmatic carnivorous mammal *Simidectes* first appears in the late Uintan, again without obvious early Uintan relatives (Coombs, 1971).

The lack of an early Uintan ancestry for some taxa may reflect limited data from the Ui_1 interval, which remains relatively poorly sampled. With this caveat, the discovery of *Propterodon witteri* is evidence of a potential Asian origin for many of the carnivorous taxa that first appear in the late Uintan. Referral of *Propterodon pishigouensis* to *Apataelurus* documents an additional tie between the carnivorous faunas of the Irdinmanhan and Uintan. In addition, both the hyaenodont *Sinopa* and the mesonychid *Harpagolestes* are shared by Irdinmanhan and Uintan faunas (Jin, 2005, 2012; Morlo et al., 2014; Robson et al., 2019). The Huadian Formation fauna containing *S. jilinia* was considered post-Irdinmanhan in age by Morlo et al.

(2014) based on the stage of evolution of the omomyid *Asiomomys*, but the presence of *Zelomys*, a genus otherwise known from the Irdinmanhan Yuli Member of the Hedi Formation (Dawson et al., 2003) suggests an older age.

A complicating factor is the poor quality of the Asian middle Eocene carnivore record. As discussed above, the Lingchan and Arshantan record of hyaenodonts is extremely poor, and other carnivorous clades are also poorly sampled in both intervals. The Irdinmanhan record is somewhat better but remains inadequate. Among non-mesonychians, Irdinmanhan hyaenodonts include two species of *Propterodon*, *P. morrisi* and *P. tongi*, the sinopanine *Sinopa jilinia*, and the limnocyonine *Prolaena parva* (Matthew and Granger, 1924, 1925; Xu et al., 1979; Tong and Li, 1986; Lavrov, 1996; Liu and Huang, 2002; Morlo et al., 2014). In addition to the machaeroidine *Apataelurus pishigouensis*, the last recorded oxyaenine, *Sarkastodon hetangensis* occurs in the Irdinmanhan (Tong and Li, 1986). Finally, Irdinmanhan miacoids are represented by three species, all questionably referred to *Miacis*: *M. boqinghensis*, *M. invictus*, and *M. lushiensis* (Matthew and Granger, 1925; Chow, 1975; Tong and Li, 1986; Qi et al., 1991; Huang et al., 1999). Of these, only *Propterodon morrisi* and *Miacis lushiensis* are represented by multiple specimens (this may be in error for *M. lushiensis* as the size and morphology of referred material suggests the presence of multiple species).

Considering the limited nature of the Asian record, the presence of four genera shared between Uintan and Irdinmanhan faunas (*Harpagolestes*, *Apataelurus*, *Sinopa*, *Propterodon*) constitutes clear evidence for substantial exchange of carnivorous mammals during this interval. To this list can potentially be added *Prolaena*, which has been considered a potential relative of North American *Oxyaenoides* (Tong and Li, 1986), although this hypothesis was regarded skeptically by Morlo and Gunnell (2003). Despite the assignment of species on both continents to a wastebasket *"Miacis"*, there is less obvious overlap between miacoids, although *"Miacis" lushiensis* has been compared with Bridgerian *"M." hargeri* (Tong and Li, 1986). Further study will be required to confirm this possibility and assess the potential for North American connections for other Irdinmanhan *"Miacis"*. For the present, it is clear that investigations into the decline in North American hyaenodont diversity and coincident rise in carnivoraform diversity must consider the role of immigration in shaping the North American carnivore guild during the Uintan.

Conclusions

The new species described in this work, *Propterodon witteri*, is the first known North American representative of the genus *Propterodon*. Comparisons of the new species with other early and middle Eocene hypercarnivorous hyaenodonts support a link to Asian *Propterodon* and Hyaenodontinae more generally, a conclusion supported by the results of the phylogenetic analysis. The broader relationships of Hyaenodontinae are not well-resolved. Despite being supported by several phylogenetic assessments, a link to European *Oxyaenoides* is unlikely. An Asian origin for Hyaenodontinae is more likely, but better material of poorly known Linchan and Arshantan hyaenodonts is needed to test this hypothesis. Recognition of a Uintan hyaenodontine and an Irdinmanhan machaeroidine increases the evidence for dispersal of carnivorous mammals between Asia and North America during the late middle Eocene. Much of the apparent shift from "creodont" to carnivoramorphan dominated North American carnivorous guilds may ultimately reflect the effects of this immigration rather than intrinsic processes within North American faunas.

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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
	Mandibular depth	24.7						

Note: Abbreviations as in Fig. 2.

Figure 1

Map of Utah, United States showing the location of Uintah County and Leota Quarry.

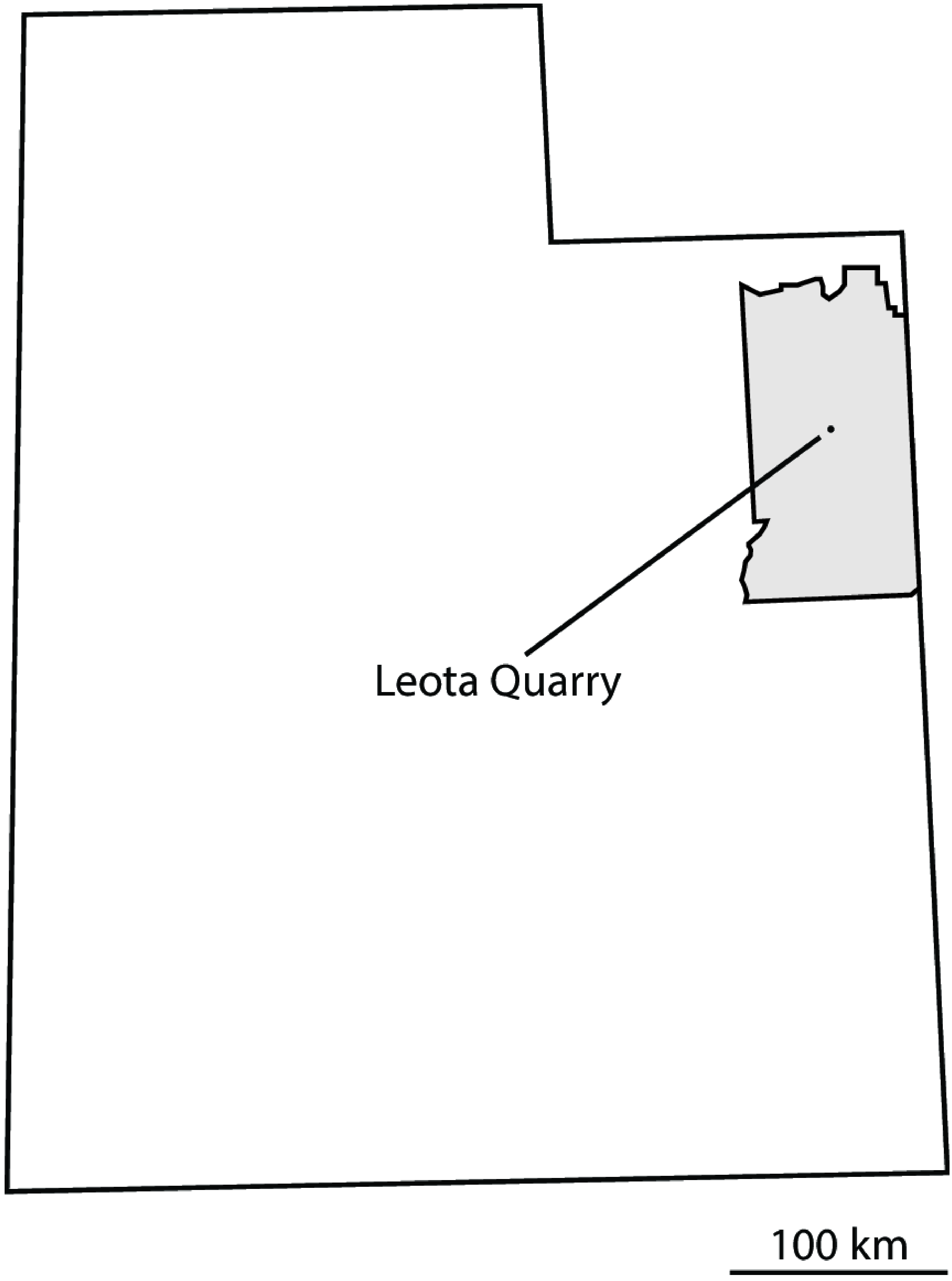
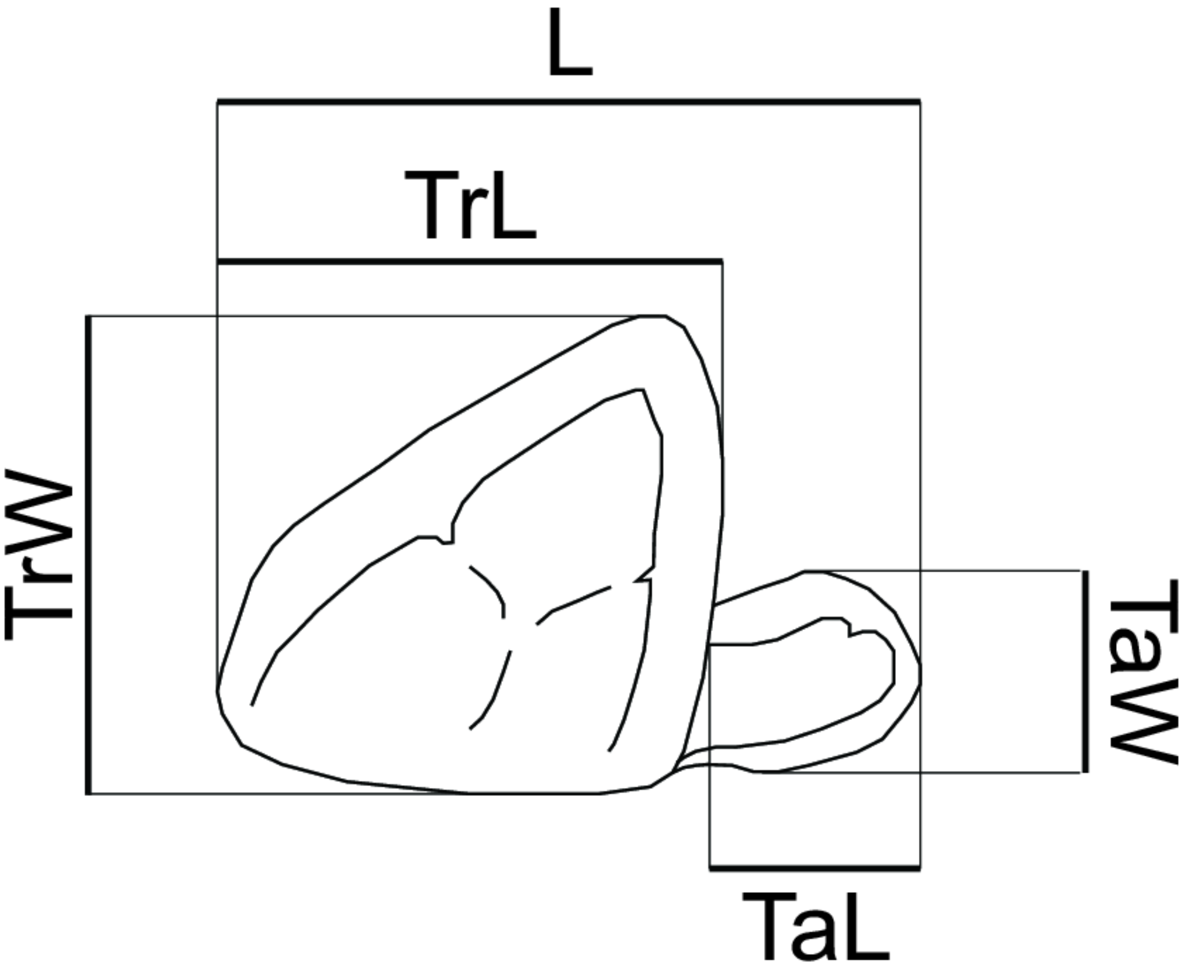

Leota Quarry
100 km

Figure 2

Measurements of hyaenodont lower molars.

Schematic drawing of a hyaenodont lower molar in occlusal (top) and buccal (bottom) 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.


L
TrL
TrW
TaW
TaL

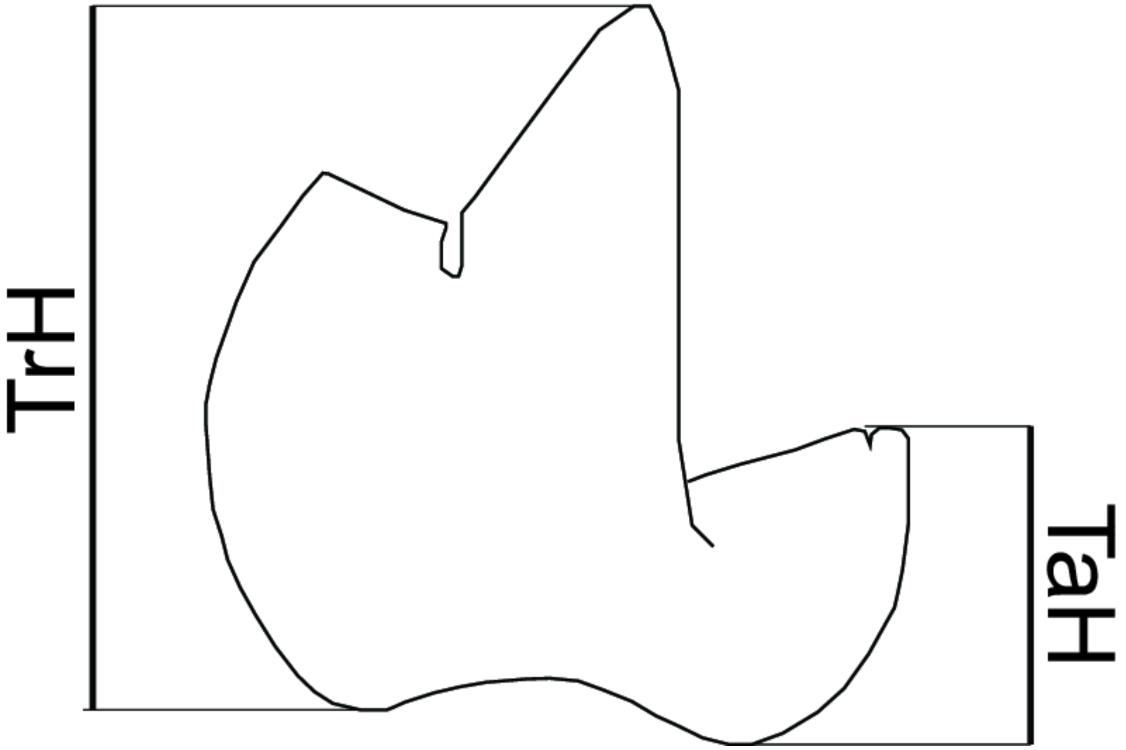

TrH
TaH

Figure 3

Temporal distribution of significant taxa discussed in this work.

Geomagnetic 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 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.

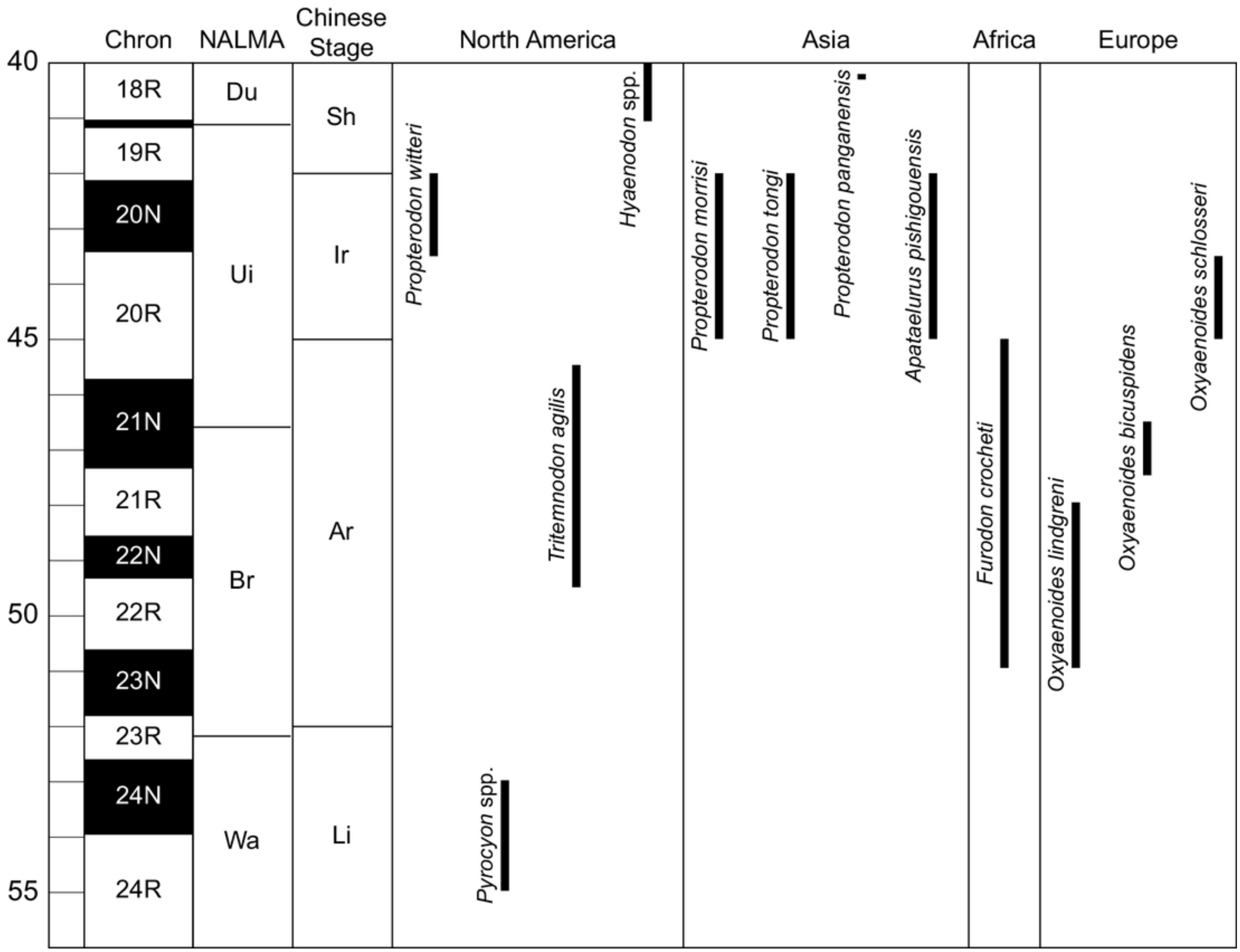

Chron
NALMA
Chinese Stage
North America
Asia
Africa
Europe
40
45
50
55
18R
19R
20N
20R
21N
21R
22N
22R
23N
23R
24N
24R
Du
Ui
Br
Wa
Sh
Ir
Ar
Li
Propterodon witteri
Hyaenodon spp.
Tritemnodon agilis
Pyrocyon spp.
Propterodon morrisi
Propterodon tongi
Propterodon panganensis
Apataelurus pishigouensis
Furodon crocheti
Oxyaenoides lindgreni
Oxyaenoides bicuspidens
Oxyaenoides schlosseri

Figure 4

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

Right dentary with $M_{2\text{-}3}$ in (**A**) buccal, (**B**) lingual, and (**C**) occlusal views. Scale is 10 mm.

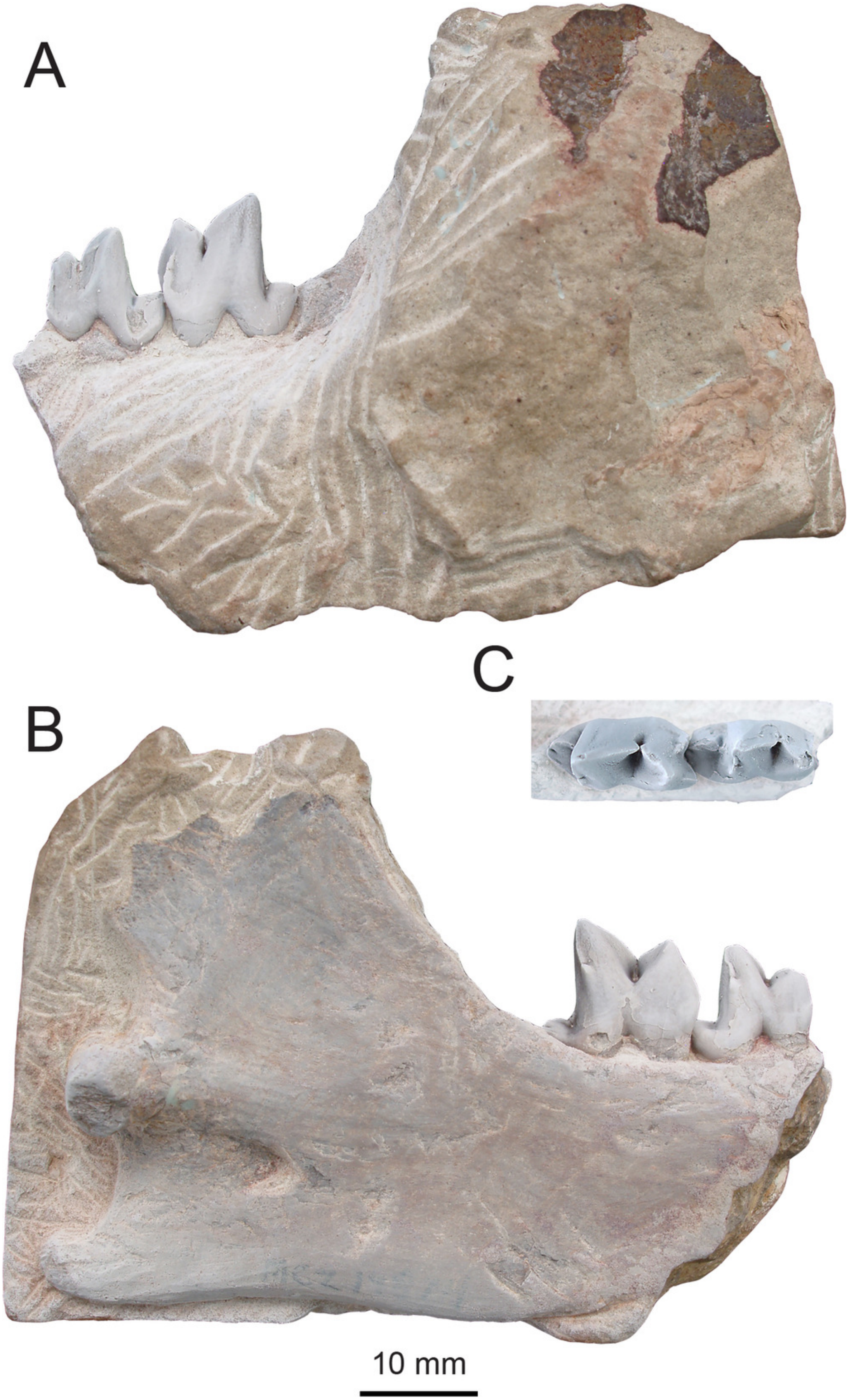

A
B
C
10 mm

Figure 5

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

(**A**) *Propterodon witteri*, MCZ VPM 19874; (**B**) *Oxyaenoides schlosseri*, MNHN.F.ERH 429 (reversed); (**C**) *Furodon crocheti*, HGL 50bis-56; (**D**) *Propterodon morrisi*, AMNH FM 21553 (reversed); (**E**) *Propterodon tongi*, IVPP V12612. Each image shows left M_{2-3} in lingual (top) and occlusal (bottom) views. All scale bars are 10mm. **B** after Solé et al. (2015b, fig. 4); **C** after Solé et al. (2014, fig. 2).

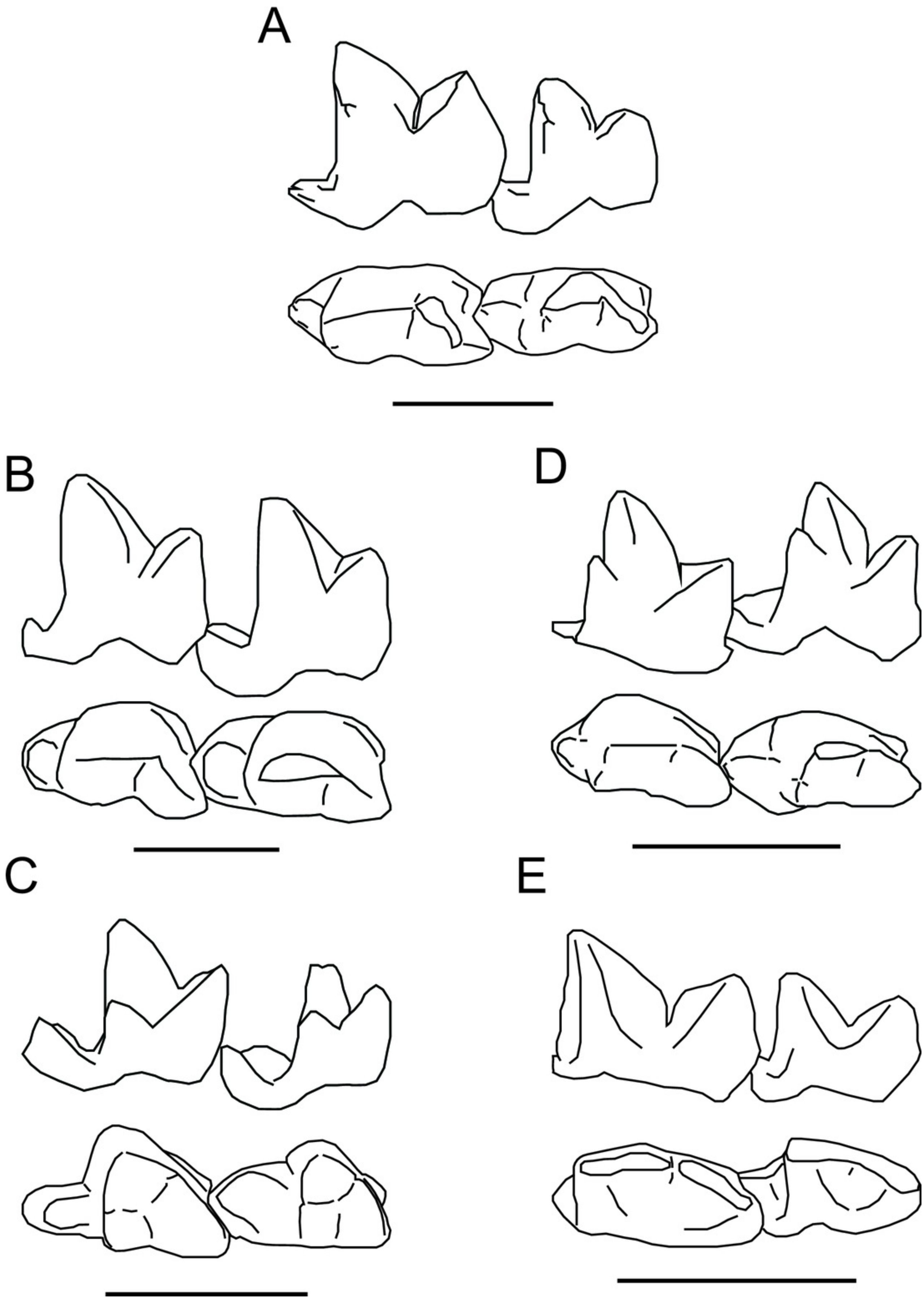
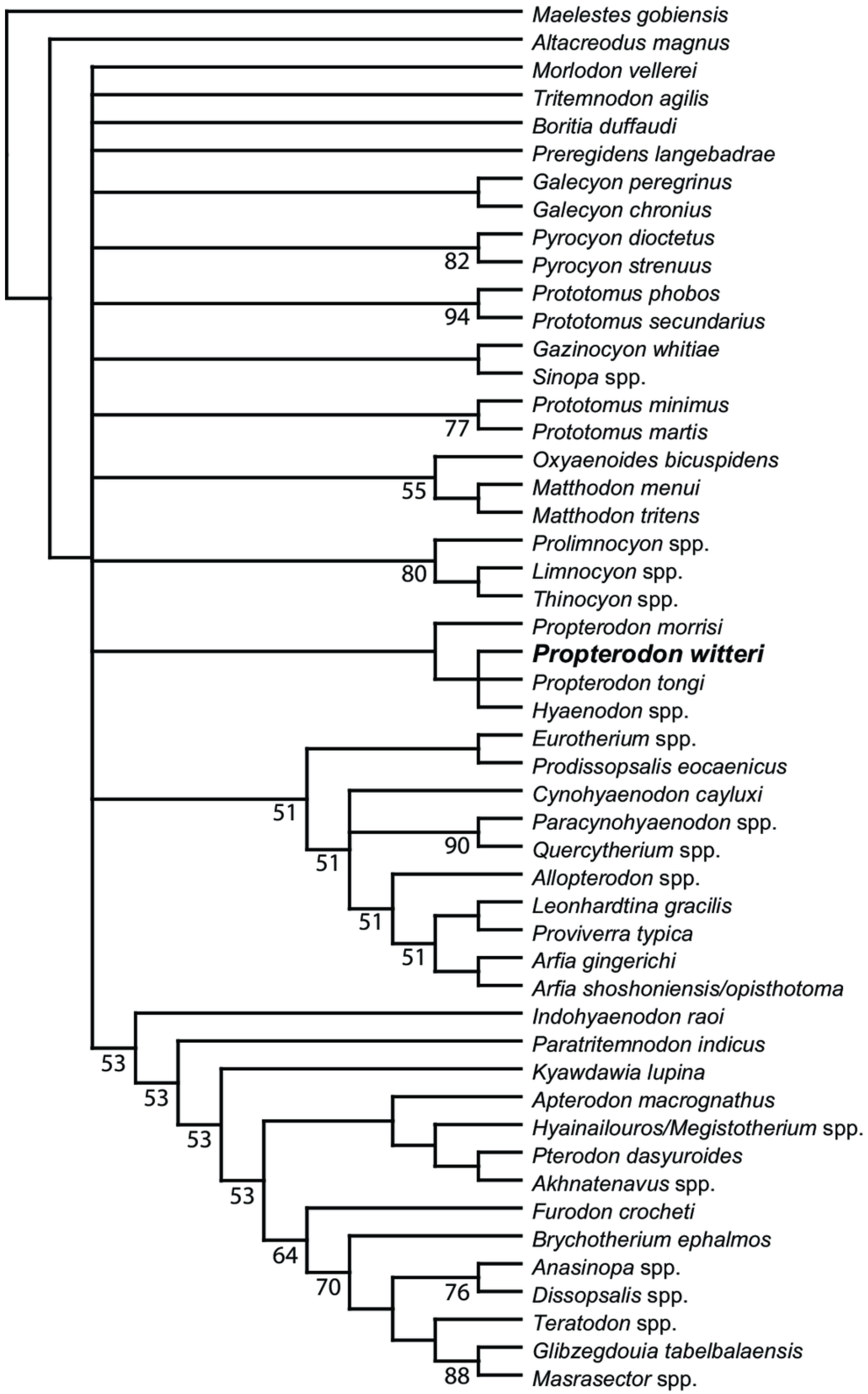

A
B
D
C
E

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.


Maelestes gobiensis
Altacreodus magnus
Morlodon vellerei
Tritemnodon agilis
Boritia duffaudi
Preregidens langebadrae
Galecyon peregrinus
Galecyon chronius
Pyrocyon dioctetus
Pyrocyon strenuus
82
Prototomus phobos
Prototomus secundarius
94
Gazinocyon whitiae
Sinopa spp.
Prototomus minimus
Prototomus martis
77
Oxyaenoides bicuspidens
Matthodon menui
Matthodon tritens
55
Prolimnocyon spp.
Limnocyon spp.
Thinocyon spp.
80
Propterodon morrisi
Propterodon witteri
Propterodon tongi
Hyaenodon spp.
Eurotherium spp.
Prodissopsalis eocaenicus
Cynohyaenodon cayluxi
Paracynohyaenodon spp.
Quercytherium spp.
90
51
51
Allopterodon spp.
Leonhardtina gracilis
Proviverra typica
Arfia gingerichi
Arfia shoshoniensis/opisthotoma
51
51
Indohyaenodon raoi
Paratritemnodon indicus
Kyawdawia lupina
Apterodon macrognathus
Hyainailouros/Megistotherium spp.
Pterodon dasyuroides
Akhnatenavus spp.
53
53
53
53
Furodon crocheti
Brychotherium ephalmos
Anasinopa spp.
Dissopsalis spp.
76
64
70
Teratodon spp.
Glibzegdouia tabelbalaensis
Masrasector spp.
88