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

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

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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$_{2,3}$ 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.

**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 was greatest during the earlier half of the Eocene, particularly the Wasatchian and Bridgerian North American Land Mammal Ages (NALMAs) (Gunnell, 1998; Van Valkenburgh, 1999; Wesley-Hunt, 2005; Friscia and Van Valkenburgh, 2010). In the subsequent Uintan NALMA, hyaenodont diversity declined dramatically. Only four genera, *Limnocyon*, *Mimocyon*, *Oxyaenodon*, 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 carnivores 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 and 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 M2-3, 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 M₃. 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 taxonomic affinities of the new species, it was added to a substantially modified version of the character taxon matrix used by Rana et al. (2015). The dental sample used by Rana et al. (2015) was modified to eliminate non-independent characters (e.g., removing a character describing the number of P³ roots, which reflects development of a P³ protocone lobe), following the recommendations of recent authors who have argued that inclusion of non-independent characters can mislead phylogenetic analyses that rely heavily on mammalian dental morphology (Sansom et al., 2017; Billet and Bardin, 2019). 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 (2019a). Numerous individual scorings were modified to improve scoring consistency, with particular emphasis placed on ensuring 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 (2019a), 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 because 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 3D models. Scorings of *Akhnatenavus* were updated to include *A. nefertiticyon* described in the same work, while scorings for *Masrasector* were updated based 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 defined, is likely polyphyletic (Solé et al., 2015a; Borths and Stevens, 2019a, b). 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, 2019b), 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 permanent versus deciduous status of the type and most informative specimen, MNHN.F.RI 400. Described as an *M₂* (Godinot, 1981; Solé et al., 2015c), MNHN.F.RI 400 shows several features that suggest the
tooth may instead represent dP₄, 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 species that have been referred to *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 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, 2019b).

Among members of the potentially polyphyletic Koholiinae, two species known exclusively from lower dentitions (*Boualitomus marocanensis* and *Lahimia selloumi*) lack P₁, a feature that is unusual for Hyaenodonta but typical for members of Tenrecoidea (Gheerbrant et al., 2006; Solé et al., 2009). Combined with the small size of both species, this raises the possibility that kohlioniines may actually represent an endemic African carnivorous radiation prior to an Eocene immigration of hyaenodonts to Africa. The third koholiine, *Koholia atlasense*, is known only from a fragmentary upper dentition, and recent phylogenetic analyses have not recovered it in a clade with *B. marocanensis* and *L. selloumi* (Borths et al., 2016; Borths and Seiffert, 2017; Borths and Stevens, 2017, 2019a, b). The M₁ of *K. atlasense* has a paracone that is distinctly lingual to the metacone, although this may be exaggerated by damage to the metacone (Crochet, 2019).
This morphology is not characteristic of hyaenodonts but occurs in the early tenrecoids
Sperrgale minutus and Arenagale calcareus (Pickford, 2015). Other aspects of the morphology
of K. atlasense are also unusual for a hyaenodont including the elongate P4 metastyle, strong M1
prevallum shear, and massive M1 parastyle connected to the preparacrista at its mesial margin.
The overall morphology of K. atlasense is distinctive enough to cast doubt on its hyaenodont
status.

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 using parsimony 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 trees of the same
minimum length were recovered by 100 replicates of the algorithm, each beginning from a
different starting topology. If a particular replicate identified a tree shorter than the existing
minimum length trees, the process restarted until 100 replicates had recovered trees of the new
minimum length. Novel minimum length trees from each replicate were retained, up to 10,000.
Once this process was completed, resulting trees were then submitted for branch swapping in the
Traditional Search dialog to ensure that all most parsimonious trees were identified, again with a
limit of 10,000 trees in total.

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,
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 based on 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 to 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 Lei (1986) for a dentary preserving P₄-M₁ from the Hetaoyuan Formation (Irdinmanhan), Henan Province, China (Fig. 3). As is discussed below, the affinities of *P. pishigouensis*, do not appear to lie with either *Propterodon* or with Hyaenodonta generally. An additional Chinese species, *P. tongi* was named by Liu and Huang (2002) for a dentary with P₁-M₃ from the Huoshipo locality, Yuli Member of the Hedi Formation (Irdinmanhan), Shanxi Province. This species differs from *P. morrisi* in being slightly smaller and in having a more strongly hypercarnivorous morphology, with metaconids lacking at least on M₂-₃, trigonids more open, and talonids more reduced, especially on M₃. Most recently, Bonis et al. (2018) named *Propterodon panganensis* for a dentary preserving P₄-M₁ from the Sharamurunian equivalent Pondaung Formation of Myanmar (Fig. 3). This species has some unusual features (symmetric P₄ protoconid, P₄ and M₁ similar in size, very reduced M₁ talonid) that suggest its relationship to other *Propterodon* requires confirmation, but it is clearly a hypercarnivorous hyaenodont.
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$_2$-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. 1B).

Stratigraphy and Age—Myton Member of the Uinta Formation (Uinta C, Fig. 1A), late Uintan (U$_3$) North American Land Mammal Age (NALMA), late middle Eocene (Prothero, 1996) (Fig. 3).

Diagnosis—Largest known species of Proterodon, with M$_2$ and M$_3$ lengths approximately 11 and 13 mm, respectively, and dentary depth approximately 25 mm beneath M$_3$.

Talonid on M$_3$ relatively large, comparable to M$_2$ talonid. Metaconids on M$_2$-3 present but extremely reduced.

Differential Diagnosis—Differs from P. panganensis in substantially larger size, with dentary more than 100% deeper. Differs from P. morrisi in larger size, approximately 40% longer M$_2$-3, more reduced metaconids on M$_2$-3, and a relatively larger talonid on M$_3$. Differs from P. tongi in larger size, approximately 50% longer M$_2$-3, retention of rudimentary metaconids on M$_2$-3, larger talonids on M$_2$-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 tooth row, the coronoid
process forms an approximately 60-degree angle with the alveolar margin. The process is
elongate and extends well above the tooth row, 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 dorsolaterally. 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,
neat 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 distally, even with 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 M₁.

The metaconid of M₂ 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 M₃. 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 hypocon 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), *Mimocyon longipes* and *Sinopa 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 *Mimocyon* or *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*₂⁻³ in species of *Pyrocyon* (*P. dioctetus, P. strenuus*) and in *Tritemnodon agilis* resembles *Propterodon witteri* in having open trigonids (that is, with the paraconid apex well mesial to the apices of the protoconid and, if present, metaconid) 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 the record during Wa₆, well before the end of the densely sampled portion of the Willwood record (Chew, 2009), and the genus is unknown from Wa₇ through Uintan faunas. *Tritemnodon* is well-documented from the earlier portion of the Bridgerian, particularly Br₂, but has a limited record from Br₃ and no record from the earlier portions of the Uintan (Ui₁₋₂) (Eaton, 1982; Gunnell et al., 2009). A close relationship of *P. witteri* to 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*, M₃ is distinctly larger than M₂ 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 M₂-₃ 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., 2018) (Fig. 5C-D). *Oxyaenoides* has completely lost metaconids on all molars, while *P. witteri* retains small metaconids on M₂₋₃. 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 derived morphologies (open trigonids, trenchant talonids) and less derived morphologies (retained metaconids, elongate talonids) 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. 5E-F). 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 hyaenodons (Rana et al., 2015; Borths et al., 2016; Borths and Seiffert, 2017; Borths and Stevens, 2019a, b). 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. 5G-H) and *P. tongi* (Fig. 5I-J), is quite similar to that of *P. witteri* (Matthew and Granger, 1924, 1925; Liu and Huang, 2002). Trigonid proportions of M$_{2,3}$ 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$_{2,3}$ 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 M₃’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 M₃ 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*. 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. This is also
true in other recent analyses using parsimony (Borths et al., 2016; Borths and Seiffert, 2017).
Most nodes in Bayesian trees recovered by Borths and colleagues (Borths et al., 2016; Borths
and Seiffert, 2017; Borths and Stevens, 2017, 2019a, b) 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, 2019a, 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, 2019a, b), 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. Instead, many individual trees
recover these genera in positions proximate to species of Prototomus (specifically *P. martis* and *P. minimus*) and *Pyrocyon*. This includes trees in which the European genera are successive sister taxa to *Pyrocyon* and trees in which *Preregigens* is the sister taxon of *Prototomus minimus* (with *P. martis* as sister taxon to this clade). 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 Paleocene-Eocene Thermal Maximum, consistent with evidence from the Abbey Wood fauna (Hooker, 2010).

OXYAENODONTA Van Valen, 1971

OXYAENIDAE Cope, 1877

MACHAEROIDINAE Matthew, 1909

*APATAELURUS* Scott, 1937

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

(Fig. 7)

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

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

**Holotype**—IVPP V7997, left dentary preserving P₄-M₁.

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

**Stratigraphy and Age**—Hetaoyuan Formation, Irdinmanhan stage (Wang et al., 2019).
**Revised Diagnosis**—Smallest known species of *Apataelurus*, with P₄ and M₁ lengths approximately 10 and 9 mm, respectively.

**Comparisons and Discussion**—Tong and Lei (1986) described IVPP V7997 as a new species of *Propterodon*, *P. pishigouensis*. Compared to other species referred to *Propterodon*, the most distinctive feature of “*P.*” *pishigouensis* is the shape of the dentary, which is ventrally deflected anteriorly, beginning below the anterior root of P₄ (Tong and Lei, 1986), indicating the presence of an anterior flange (Fig. 7A). 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* (Fig. 7). On P₄, both *A. kayi* and *pishigouensis* have a well-developed paraconid that is nearly as tall as the talonid (Scott, 1938; Tong and Lei, 1986). The paraconid is absent on P₄ 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 P₄ talonids dominated by a tall hypoconid, in *pishigouensis* and *A. kayi*, the talonid is distinctly broader than the remainder of the crown (Scott, 1938; Tong and Lei, 1986). In contrast, P₄ 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 P₄, *P. morrisi*, P₄ is enlarged relative to M₁ (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., 2018).

505 On M₁, a defined metaconid is lacking in *pishigouensis* and *A. kayi* (Scott, 1938; Tong and Lei, 1986), again along with *P. panganensis* (Bonis et al., 2018), but retained in *P. morrisi* (e.g., AMNH FM 21553), with M₁ of *P. tongi* too worn to assess. The primary difference in M₁ 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 *pishigouensis* and *A. kayi*, the talonid is relatively elongate and nearly as tall as the paraconid (Scott, 1938; Tong and Lei, 1986). Talonid morphology is simplified in both *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.

515 Taken together, the mandibular and dental morphology of “*Proterodon* pishigouensis” differs substantially from other species of *Proterodon*, particularly *P. morrisi* and *P. tongi*, but closely matches the morphology of the North American machaeroidine *Apataelurus kayi*. Accordingly, *Proterodon pishigouensis* is recombined as *Apataelurus pishigouensis*. As a species of *Apataelurus*, *A. pishigouensis* differs from *A. kayi* primarily in its somewhat smaller size. The talonid of *A. pishigouensis* may be smaller than that of *A. kayi*, but this is complicated by heavier wear in the type and only described specimen of the North American form. Referral 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 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\(^2\).

**Discussion**

**Hyaenodontine Origins**— Recent assessments of hyaenodont biogeography (Borths et al., 2016; Borths and Stevens, 2017) have supported a European divergence of Hyaenodontinae from *Oxyaenoides*, which was recovered as the sister taxon of Hyaenodontinae in both analyses. This grouping is nested within a broader assemblage of European hyaenodonts comprising taxa referred to Proviverrinae by Solé (2013) and Solé et al. (2015b). More recent studies (Borths and Stevens, 2019a, b; Solé and Mennecart, 2019) complicate this scenario slightly by recovering Prionogalidae and *Thereutherium* within the clade defined by *Oxyaenoides* and Hyaenodontinae,
but the basic biogeographic scenario is unchanged, with Hyaenodontinae deeply nested within a clade of European hyaenodonts. As was noted by Borths and Stevens (2019a) with regard to the position of Prionogalidae, the character support uniting *Oxyaenoides*, *Thereutherium*, Prionogalidae, and Hyaenodontinae consists primarily of features associated with hypercarnivory, specifically reduction of the metaconids and talonids on lower molariform teeth. Hypercarnivory has evolved iteratively in diverse carnivorous mammalian clades and homoplasy in features associated with hypercarnivory is well-documented (Muizon and Lange-Badré, 1997; Holliday and Steppan, 2004; Solé and Ladevèze, 2017). Accordingly, support for a close relationship between *Oxyaenoides* and Hyaenodontinae should be regarded cautiously, despite its recovery in several analyses.

In contrast to the analyses just discussed, results of the current phylogenetic analysis do not place Hyaenodontinae phylogenetically proximate to *Oxyaenoides*, nor do the results of Rana et al.’s (2015) analysis. While the position of Hyaenodontinae is not consistently resolved in the present study, a sister taxon relationship to *Oxyaenoides* is not present in any most parsimonious tree. Some most parsimonious trees (MPTs) do recover Hyaenodontinae as the sister taxon of Proviverrinae, as used by Solé (2013) and Solé et al. (2015b). However, other MPTs recover Hyaenodontinae as the sister taxon of North American and European *Galecyon* or to a clade comprising *Galecyon* plus Holarctic *Arfia*. Still other MPTs place Hyaenodontinae at the base of a diverse grouping that includes all sampled taxa excepting *Arfia* and Proviverrinae, with Asian and North American Limnocyoninae the next diverging clade. There is no particular support in this analysis for a European origin for Hyaenodontinae.

In fact, a European origin appears unlikely. Unlike *Oxyaenoides*, which shares some distinctive dental features with other proviverrines, including a double-rooted P₁ and molar...
talonids with three, more or less equally developed and equidistantly spaced cusps, hyaenodontine dental morphology has little in common with proviverrines. The relatively large P<sub>1</sub> remains single-rooted in *P. morrisi* and *P. tongi* (Matthew and Granger, 1925; Liu and Huang, 2002), while the entoconid and hypoconulid are weakly developed in all species of *Propterodon*. With the exception of a reduced metacingulum on M<sup>1-2</sup>, other distinctive proviverrine dental features enumerated by Solé (2013) (entoconids on P<sub>3-4</sub>, prominent paraconids on P<sub>2-3</sub> and parastyle on P<sub>4</sub>, M<sup>1-2</sup> with metacones taller than paracones) are absent in *Propterodon* (Matthew and Granger, 1925; Lavrov, 1996; Liu and Huang, 2002).

Biogeographic evidence also suggests that derivation of hyaenodontines from within the European Eocene hyaenodont radiation is unlikely. From the late early Eocene through the Eocene/Oligocene transition, Europe was an island isolated from the rest of Holarctica (e.g., Meulenkamp and Sissingh, 2003), resulting in the evolution of a diverse endemic mammalian fauna (Hooker, 1989; Badiola et al., 2009; Danilo et al., 2013). This period encompasses the radiation of proviverrine hyaenodonts (sensu Solé, 2013), which formed the dominant carnivorous element of this endemic European fauna. There is little evidence of mammalian dispersal from Europe to Asia during this interval. In fact, there is some evidence from the fossil record consistent with an earlier Asian record of Hyaenodontinae. 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
both 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 above). 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.

**Late Uintan Carnivore Dispersals**—In addition to *Propterodon*, several other carnivorous taxa that first appear in the late Uintan (Ui$_{2-3}$) have a potential origin outside western North America. Among hyaenodonts, the limnocyonine *Oxyaenodon dysodus* is quite distinct from *Limnocyon potens*, 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). While Morlo and Gunnell (2005) recovered *O. dysodus* and *L. potens* as sister taxa in a phylogenetic analysis of limnocyonines, an earlier analysis of a nearly identical matrix (Morlo and Gunnell, 2003) recovered *O. dysodus* as the sister taxon of Bridgerian *Thinocyon medius*, outside of a monophyletic *Limnocyon* (note that the consensus tree shown in Morlo and Gunnell [2005, fig. 1] is in error; all four shortest trees found by analyzing the published matrix without modification recover *Thinocyon medius* rather than Bridgerian *Limnocyon* as the sister taxon of *L. potens* plus *O. dysodus*). Both Morlo and Gunnell (2003) and Tong and Lei (1986) have noted similarities to the Irdinmanhan Chinese taxon *Prolaena parva*. Taken together, it is plausible
that the appearance of *Oxyaenodon* in the late Uintan reflects immigration from Asia, similar to
the pattern hypothesized for *P. witteri*. A full assessment of the affinities of *Oxyaenodon* is
beyond the scope of this study. Published descriptions and illustrations of material of *O. dysodus*
are inadequate to confidently score the species, and substantial additional material remains
unpublished (Friscia and Dunn, 2016).

The affinities of another late Uintan hyaenodont, the small undescribed taxon or taxa
referred to 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.),
very divergent from both *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. Carnivore dispersals from Asia to North America during the later Uintan would be concordant with evidence for dispersal of other mammals from Asia to North America during this interval, including the chalicotheroid perissodactyl *Grangeria* and the omomyid primate *Macrotarsius* in Ui₂ (Woodburne, 2004). Ui₃ sees additional dispersals including several brontotheriid perissodactyls, and *Mytonolagus*, the oldest known North American lagomorph (Woodburne, 2004; Mihlbachler, 2008).

A complicating factor is the poor quality of the Asian middle Eocene carnivore record. As discussed above, the Lingchan and Arshantan record of hyaenodons 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 hyaenodons 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 Lei, 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 Lei, 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 Lei, 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. As noted above, *Prolaena* can be potentially added to this list although Morlo and Gunnell (2003) were skeptical of a relationship between Asian *Prolaena* and North American *Oxyaenodon*. 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 Lei, 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 hyaenodons 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 in North American carnivorous guilds, from “creodont” to carnivoramorphan dominated, 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   | M₂    | 11.5 | 7.8 | 5.4 | 9.7 | 3.8 | 4.0 | 4.8 |
|                 | M₃    | 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 chron 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.
Figure 5

Comparison of M$_{2-3}$ of *Propterodon witteri* sp. nov. with other middle Eocene hypercarnivorous hyaenodons.

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

(A) *Apataelurus pishigouensis*, IVPP V7997, left dentary with P₄-M₁; (B) *Apataelurus kayi*, CM 11920, right dentary with P₃-M₂ (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 P₄ and M₁ and paraconid on M₁ 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.
