



A New Species of *Agriotherium* from North America, and Implications for Understanding Transformations in the Metaconid-Entoconid Complex of Bears

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Abstract

New material of *Agriotherium* from the late Hemphillian (~6 Ma) Quiburis Formation in Arizona, North America is reported. These specimens represent a new species, *Agriotherium hendeyi*, sp. nov., of small size and with a bucco-lingually narrow lower dentition distinguishing it from North American “*Agriotherium*” *schneideri* as well as the genotype and other Old World species of *Agriotherium*. Strikingly, the m1 metaconid-entoconid complex of the new species exhibits a morphologically transitional state between the pattern observed in *Indarctos* (three cusps) and the typical *Agriotherium* pattern (two cusps). Together with a review of the variation in *A. africanum*, a geometric morphometric analysis permits identification and discussion of a proposed transformation pathway from the *Indarctos* pattern to the *Agriotherium* pattern. It is shown that the two cusps in the metaconid-entoconid complex in *Agriotherium* correspond to the two entoconids in *Indarctos*, whereas the ancestral metaconid is reduced or lost in *Agriotherium*. From a developmental perspective, the metaconid fused to the anterior entoconid as a result of the shortening of the talonid, rather than via replacement of the metaconid by a posterior shift of the entoconid, presumably under selective pressure towards a more typically hypercarnivorous tooth morphology and carnivorous diet.

Keywords *Agriotherium* · *Indarctos* · Ursidae · Miocene · Hemphillian NALMA · Quiburis Formation · Metaconid-entoconid complex

Abbreviations

AMNH American Museum of Natural History, New York, USA
AMNH F AM Frick collection (Fossil Mammals), Division of Paleontology, AMNH, USA
AMNH M Mammalogy (Vertebrate Zoology) collections, AMNH, USA

IVPP Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China
L Specimens housed in Iziko South African Museum, Cape Town, South Africa
P/p upper/lower premolar
M/m upper/lower molar
Hh3 Hemphillian3, late Hemphillian North American Land Mammal Age (NALMA)
Hh4 Hemphillian4, latest Hemphillian NALMA
MN Neogene land Mammal Zones of Europe

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Introduction

The large-sized, geographically widespread, Miocene-Pleistocene bear *Agriotherium* and its Miocene relative *Indarctos* have been known for more than a century. *Agriotherium* was first established by Wagner (1837) for *A. sivalense* from the Pinjor layer of the Siwalik Group in South Asia. However, *Hyaenarctos long* was used instead

for the genus name, because it is better known, until Sellards (1916) clarified the priority of *Agriotherium*. The earliest described specimens of *Indarctos* initially were assigned to *Hyaenarctos* (later *Agriotherium*), but Pilgrim (1913) erected *Indarctos* based on *I. salmontanus* from the middle Siwalik Group (described in detail by Pilgrim 1914) and recognized its distinction from *Agriotherium*.

After recognition of these two genera as distinct, differences and similarities have been debated. Now, the generally recognized differences of the two genera include: typically more reduced P1–3/p1–3 of *Agriotherium*; larger P4 parastyle of *Agriotherium*; subdivided P4 hypocone (in most prior literature considered as a protocone) in *Indarctos* (at least in later-diverging species); square-shaped M1 in *Indarctos* (somewhat trapezoidal in *Agriotherium*); longer M2 talon of *Indarctos*; p4 with medial ridge in *Agriotherium*; m1 with only one lower-crowned entoconid in *Agriotherium* (a pair of higher-crowned entoconids in *Indarctos*); and mandible with a premasseteric fossa in *Agriotherium* (Frick 1926; Stach 1957; Hendey 1980; Qiu and Schmidt-Kittler 1983; Petter and Thomas 1986). All but one of the above differences have been widely accepted: the nature of the m1 metaconid-entoconid complex. Traditionally, the three cusps on the posterolingual side of the *Indarctos* m1 are identified as the metaconid and a bicuspid entoconid, whereas the two cusps on the m1 of *Agriotherium* are identified as the metaconid and a single-cusped entoconid. Although a single entoconid is typical of most mammals, the *Indarctos* pattern of a bicuspid entoconid is generally seen in Miocene Ursidae; i.e., it also occurs in the early-diverging hemicyonine ursids, stem ursid *Ballusia* and *Ursavus*, stem Indarctini *Miomaci*, and probably represents the plesiomorphic state for *Indarctos*/*Agriotherium* (Frick 1926; Ginsburg and Morales 1998; Qui et al. 2014; de Bonis et al. 2017). The *Agriotherium* pattern is generally interpreted as enlargement and posterior shift of the metaconid, with loss of the posterior entoconid cusp (here we use the terminology of Rabeder 1999 referring to the posterior entoconid as entoconid1, although we do not assume or imply that this cusp is homologous to the entoconid1 in cave bears). This hypothesis, however, has not yet been documented in the fossil record, as there is no specimen or taxon showing a morphological transition between the two patterns.

Hendey (1980) proposed an alternative hypothesis for the origin of the *Agriotherium* pattern. He argued that it was derived from the *Indarctos* pattern by reduction of the metaconid, and enlargement of the anterior entoconid (entoconid2). Hendey's opinion was driven by the highly variable pattern in *A. africanum* from Langebaanweg in South Africa, in which he observed coeval specimens with a typical *Agriotherium* pattern (L50004), a typical *Indarctos* pattern (L50446), and a morphologically transitional pattern (L50006) with a rather small metaconid and a pair of relatively large entoconids. He interpreted this wide-ranging intraspecific variation as evidence of gradual loss of the metaconid from

the *Indarctos* pattern to the *Agriotherium* pattern. This hypothesis, however, received little subsequent attention. For example, Petter and Thomas (1986) still viewed the *Agriotherium* pattern as the metaconid-entoconid2 pattern without discussing Hendey's (1980) results. Qiu and Schmidt-Kittler (1983) are the only authors who specified a basis for their disagreement with Hendey's inferences. They thought that the rapid loss of the metaconid, with replacement by the entoconid in its topological position on the talonid, did not have any functional significance and would not have been favored by natural selection. Hunt (1998) noted that the m1 of North American "A." *schneideri* still had an *Indarctos* pattern and indicated that Hendey's opinion probably was unreliable. Therefore, few later researchers accepted Hendey's hypothesis, and the metaconid-entoconid2 inference is still the dominant hypothesis for the *Agriotherium* m1 lingual talonid cusp pattern, though there remains no direct fossil evidence documenting that pathway of transformation from the *Indarctos* pattern.

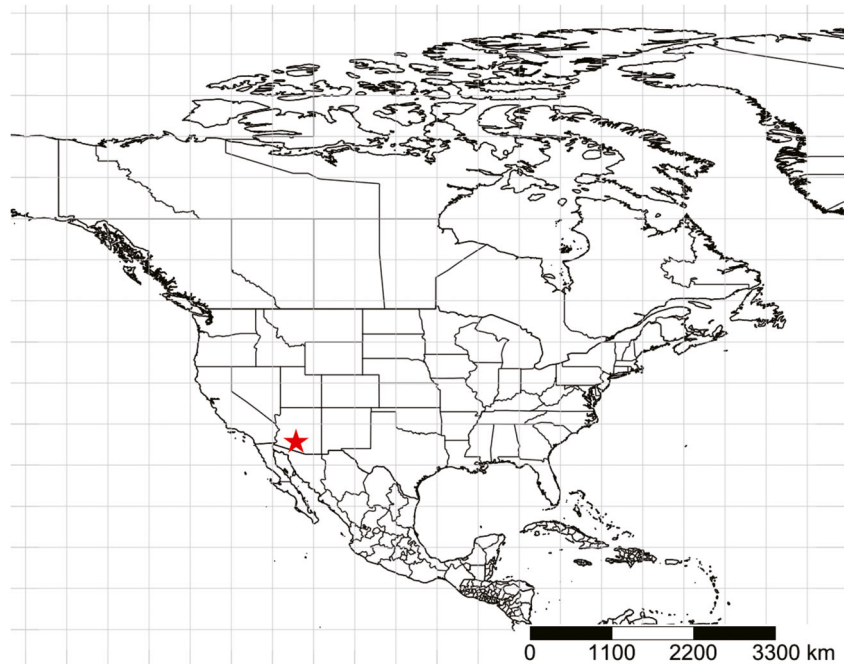
In this work, we report new material of a previously unknown, late Hemphillian (~6 Ma) species of *Agriotherium* from the Quiburis Formation, Arizona, North America (Fig. 1). The new specimens represent a new, small-sized species of *Agriotherium*, with characters that differ markedly from the larger species "A." *schneideri*. It is especially noteworthy that the m1 of the new species shows a morphologically transitional state between the *Indarctos* and *Agriotherium* patterns, thus providing evidence for inferring the pathway of cusp pattern shift between the fixed states typifying other species of those two taxa (other than the highly variable conditions observed in *A. africanum*). The specimens of South African *A. africanum* that support Hendey's transformation hypothesis, further supported in this analysis, are discussed next in the context of this new material from Arizona.

Materials and Methods

Terminology for the skull and dentition follows, with minor modifications, Qui et al. (2014) and Rabeder (1999), respectively. Parts of figure plots were made in the software package ggplot2 (Wickham 2016) in R (R Development Core Team 2016).

For geometric morphometric analyses, the package geomorph (Adams and Otárola-Castillo 2013) in R was used. Thirteen landmarks, including seven contour landmarks and six cusp landmarks (separation grooves were chosen instead of cusp apexes, as they can still be clearly defined even in moderately worn teeth), were identified on m1. Landmark descriptions for m1 (Fig. 2): 1. anteriormost point of the tooth; 2. most buccal point of trigonid; 3. buccal concavity between trigonid and talonid; 4. buccal point of talonid immediately buccal to hypoconid; 5. posterior point of talonid immediately behind hypoconid distal end; 6. lingual point of talonid immediately

Fig. 1 Location map for the Quiburis Formation, Arizona, USA. Background from <https://www.simplemappr.net>



lingual to anterior entoconid; 7. lingual concavity between paraconid and protoconid; 8. separation (here defined as the joint between the cusp ridges and separation groove) between paraconid and protoconid; 9. separation between protoconid and metaconid; 10. separation between metaconid and anterior entoconid; 11. separation between anterior and posterior entoconids; 12. separation between hypoconid and mesoconid; 13. separation between mesoconid and protoconid Fig. 3.

Specimens

The specimens described herein were recovered from the Quiburis Formation of southern Arizona, housed in the Frick collection of fossil mammals at the AMNH. For comparison, *Indarctos* from Baode, Shanxi, China (specimens and casts in IVPP, and specimens in AMNH), *A. inexpectans* (in IVPP),

“*A.* *schneideri* (in AMNH), and casts of *A. africanum*, *A. palaeindicum*, *A. sivalense*, *A. insigne*, and *A. roblesi* (all in AMNH) were examined for comparison. Photos of original specimens of *A. africanum* from the Iziko South African Museum were kindly provided by A. Valenciano. Quotation marks are used for “*Agriotherium*” *schneideri* to reflect doubt about assignment of this species to *Agriotherium*.

All data generated or analyzed during this study are included in this published article, or available in publications cited in the text.

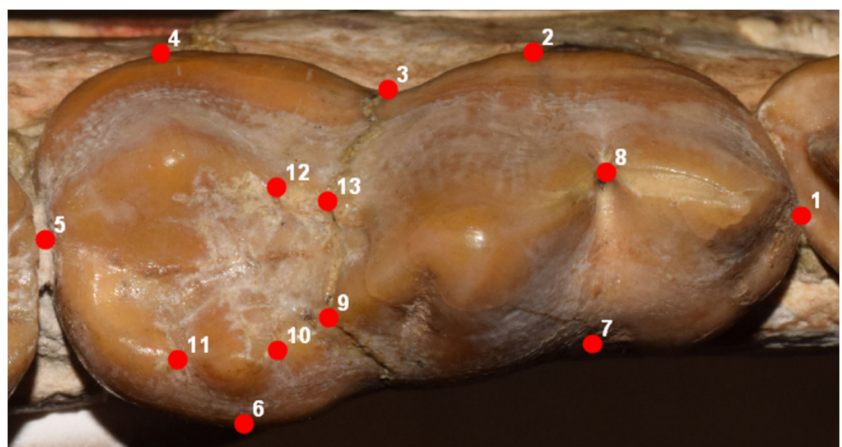
Systematic Paleontology

Order **Carnivora** Bowdich, 1821

Family **Ursidae** Fischer [de Waldheim], 1814

Genus ***Agriotherium*** [A. Wagner], 1837

Fig. 2 Landmarks on lower m1 for geometric morphometric analyses



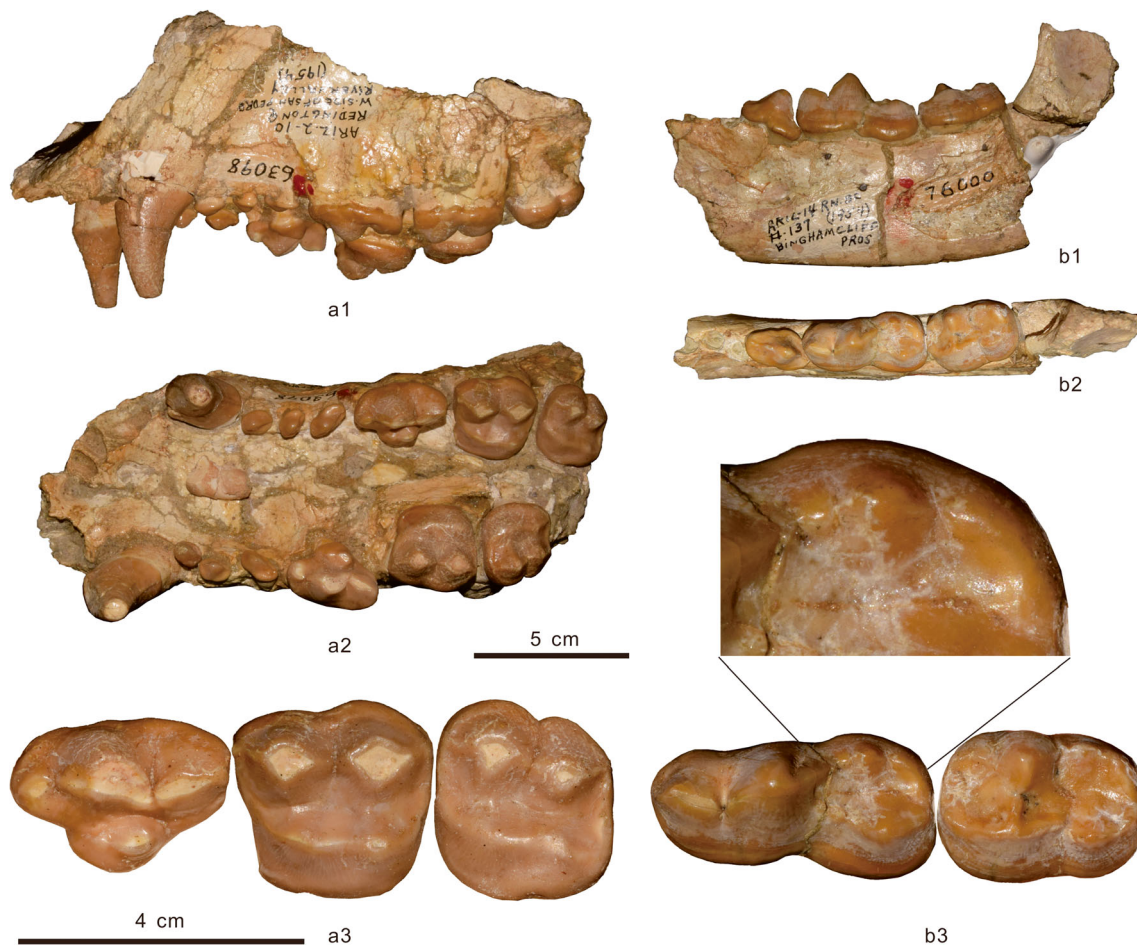


Fig. 3 *Agriotherium hendeyi* **a1–3**, AMNH F:AM 63098 paratype, lateral view, ventral view and dentition (occlusal view); **b1–3**, AMNH F:AM 76000 holotype, lateral view, ventral view, and dentition (occlusal view). Scale bar = 5 cm for a1,2 b1, 2; and 4 cm for a3, b3

Agriotherium hendeyi, sp. nov.

Etymology Named in honor of Dr. Q.B. Hendey, who first recognized the transitional pattern and pathway of m1 talonid cusps from the typical *Indarctos* pattern to the typical *Agriotherium* pattern.

Holotype AMNH F:AM76000, a partial mandible with p4–m2 and alveoli of p1–p3 and m3, from Bingham Cliff Prospect, Quiburis Formation, Arizona.

Paratype AMNH F:AM63098, a crushed rostrum with nearly complete dentition, only lacking the incisors, from Reington Quarry, Quiburis Formation, Arizona.

Age Known only from the Late Hemphillian (Hh3) NALMA, ~6 Ma.

Diagnosis A small species of *Agriotherium*. Lower dentition bucco-lingually narrow. Premolars not reduced in number; P4 with large parastyle and weakly subdivided hypocone; M2

lacking a talon; p4 with distinct medial ridge; m1 with ridge-like mesoconid and (variably) with tiny metaconid.

Differential Diagnosis Differs from *Miomaci* in having distinctly larger size, smaller premolars, larger P4 parastyle, absence of M2 talon, p4 without posterior accessory cusp, m1 with much smaller metaconid; differs from *Indarctos* in having larger P4 parastyle, anteroposteriorly shorter M1, much shorter M2 talon, distinct medial ridge of p4, and much smaller m1 metaconid; differs from “A.” *schneideri* in being much smaller in size, and having shorter M2 talon and much smaller m1 metaconid; differs from *A. sivalense* in being smaller in size, and having weaker buccal concavity in m2 and absence of buccal concavity in p4; differs from *A. palaeindicum* in having less triangular P4 without buccal concavity and presence of m1 metaconid; differs from *A. inexpectans* in having m1 metaconid and absence of m2 buccal concavity; differs from *A. africanum* in being smaller in size, and having distinctly bucco-lingually narrower lower dentition; differs from *A. roblesi* in being distinctly smaller in size and having shorter M2 talon; differs from *A. insigne* in

being slightly smaller in size and having weaker cingula in M1/M2.

Description

Maxilla and Upper Dentition AMNH F:AM 63098 preserves a partial rostrum, broken just behind M2. The specimen is laterally crushed and deformed, therefore non-dental cranial characters cannot be analyzed.

No incisors are preserved. Judging from the alveoli, I1 and I2 were similar in size, whereas I3 was distinctly larger. The upper canine is of moderate size; two prominent ridges are present, one at the anteromedial and another at the posterior side. All three anterior premolars are present. P1 is single-rooted, whereas P3 is clearly double-rooted, while the number of roots in P2 is unclear. All premolars are anterolingually rotated relative to the long axis of the toothrow. The degree of anterolingual rotation in P1 is smaller than that of P2 and P3. P1 and P2 are subequal in size, with the latter being slightly narrower, whereas P3 is distinctly more elongated anteroposteriorly. Lingual cingula are present in all three premolars but indistinct and discontinuous, whereas the buccal cingulum is absent.

P4 is robust. Its buccal contour is convex. The inner lobe is not enlarged relative to other ursids. It is located slightly anterior to the middle of the tooth, and contains a large cusp posteriorly and a smaller cusp anterior to it. The buccal cingulum is absent, whereas the lingual cingulum is only present on the posterolingual side. The P4 parastyle is large and slightly lingually turned relative to the long axis of the upper cheek tooth row. There is an anterolingual ridge on the paracone, linked to

the boundary of the paracone and inner lobe. At the anterolingual end of this ridge, there is no distinct cusp nor even a small bump (which would indicate the presence of a protocone), in contrast to the condition in *Indarctos*. Based on this, and consistent with the results of other work in progress by the senior author (QJ), the cusp dominating the inner lobe in *A. hendeyi* therefore is identified as the hypocone. The hypocone is large and weakly subdivided, with the anterior portion (anterior hypocone) rather low and weakly distinct from the larger posterior portion (posterior hypocone). The apex of the posterior hypocone is located slightly anterior to the carnassial notch.

M1 is nearly square in shape. The buccal part is slightly longer than the lingual part. The buccal contour is distinctly concave between the paracone and the metacone, whereas the anterior contour is only slightly concave and the lingual contour is nearly straight (slightly convex). The cingula are very weak. The presence of a buccal cingulum is only slightly indicated between the paracone and the metacone, and the lingual cingulum is only weakly exhibited at the anterolingual corner. The paracone and metacone are subequal in size. No parastyle or metastyle is present. The M1 protocone and metaconule form an almost continuous ridge, with nearly no interruption. The apex of the metaconule represents the highest point of the protocone-metaconule ridge, and posteriorly this ridge diverges slightly from the paracone-metacone axis. The small transverse ridge between the paracone and protocone seen in other ursids is absent, and the medial ridge of the metaconule is also indistinct, in contrast to their presence in most specimens of *Indarctos*.

M2 is roughly square in shape, although unlike in M1, the width across the metacone is smaller than that across the

Table 1 Measurements of the materials described in this work. Note that for the m1 talonid length, the mesoconid is also taken, as in *A. africanum* it is indistinguishable from the hypoconid, so a

measurement of both is convenient for comparison. For the m2, however, the mesoconid is undistinguished from the protoconid, so the talonid length is only taken from the anterior tip of the hypoconid

Teeth	F: AM63098 maxilla			Right		
	Left			Length	Width	Height
C	Length	Width	Height	Length	Width	Height
P1	24.82	17.06		24.42	18.32	
P2	10.42	8.44	6.38	9.82	7.72	6.24
P3	10.12	7.24	6.72	10.52	7.42	6.82
	13.88	6.92	6.42	13.38	8.02	6.00
P4	Length	Width	Inner lobe length	Length	Width	Inner lobe length
	30.42	21.14	14.92	29.68	20.82	14.38
M1	Length	Anterior width	Posterior width	Length	Anterior width	Posterior width
M2	27.82		24.42	28.18	25.22	27.72
Teeth	25.32			25.92	25.88	25.42
	F: AM76000, mandible					
p4	Length	Width	Height			
	21.96	13.12	14.70			
m1	Length	Anterior width	Posterior width	Talonid length		
m2	39.72	10.38	15.82	15.42		
	29.02	21.00	19.92	11.08		

paracone (Table 1). The talon is absent, and the anterior and posterior borders of M2 are parallel to each other. The buccal contour has a prominent concavity, as in M1, but is even more pronounced. Cingula are indistinct. The paracone is slightly larger than the metacone. The protocone and metaconule are similar in height, and the ridge connecting them is continuous without interruption. Its direction is not in the anteroposterior sagittal plane of the tooth, but forms a stronger angle with the sagittal plane compared with its orientation in M1.

Mandible and Lower Dentition AMNH F:AM 76000 is a mandibular fragment, from the p1 alveolus to the anterobasal part of the ascending ramus. The preserved teeth (p4–m2) are all unworn and the mandible is rather shallow, indicating a young age for the animal. In the preserved part, two mental foramina are present. The anterior foramen is smaller and located at the level of the p2, whereas the posterior one is larger and located below the posterior part of p4. No premasseteric fossa can be seen in the preserved part.

The three anterior premolars are represented by alveoli. They are crowded (presumably influenced partially by its young age and anteroposteriorly short mandibular ramus) and single-rooted. The p4 is ovoid or triangular in shape, with a convex posterolingual corner. The main cusp is tall, and sits at the center of the tooth, above the bucco-lingual basal constriction of the tooth crown. The anterior and posterior accessory cusps are indistinct, only indicated by an inflection in the anterior/posterior ridges of the main cusp. A weak medial ridge is present at the posterolingual corner; it is not connected to the apex of the main cusp.

The m1 is relatively slender. There are prominent constrictions between the trigonid and talonid on both the buccal and lingual sides. The m1 has a tall protoconid and a somewhat lower paraconid. The most peculiar character of m1 is the extremely reduced metaconid; it is a diminutive cusp, much smaller than the two entoconids on the talonid. There is a strong posterolingual ridge of the protoconid connecting the metaconid and protoconid. The mesoconid is rather low and ridge-like, but it is still clearly distinguished from the hypoconid. The single hypoconid occupies the buccal part of the talonid, and there are two entoconids on the lingual side. The two entoconid cusps are similar in length, although the anterior one is distinctly taller and stouter.

The m2 is robust. Its buccal wall is sloped, whereas the lingual wall is nearly vertical. The protoconid is the dominant cusp on the buccal side of the trigonid. The paraconid is present, but indistinct at the anterobuccal side of m2. Unlike on m1, the m2 metaconid is prominent and distinctly taller than the protoconid. The anterior ridge of the metaconid is nearly absent, so the premetaconid is not directly connected to the metaconid. The mesoconid is absent on m2, and the hypoconid is slightly stronger than on m1. Two subequal-sized entoconids are present at the posterolingual corner of the tooth, but the separation of the two cusps is less distinct than on m1.

The m3 is represented by a single alveolus. Judging from the alveolus, it is distinctly smaller than the m2.

The m1 Metaconid-Entoconid Complex in *Agriotherium* and *Indarctos*

Before comparing the material of the new taxon with other known species, homologies of the m1 cusps should be clarified. The m1 metaconid-entoconid complex in *Agriotherium*, and its comparison with *Indarctos*, have been discussed for nearly a century (see Introduction). As noted, Hende (1980) provided good evidence showing that *Indarctos*-like, *Agriotherium*-like, and morphologically transitional patterns are all present among individuals within a single species, *A. africanum*. The morphologically transitional forms also first show a reduction of the metaconid rather than the entoconid1, as most other authors had proposed. Later authors, however, may or may not give explicit reasons to discount Hende's hypothesis, and none explained the variation pattern seen in *A. africanum*.

As has been shown repeatedly (Renaud et al. 2006), the direction of evolution is often strongly correlated with intraspecific variation, as high intraspecific variability represents the pattern with the least developmental constraint, therefore providing the basic materials to be selected, the so-called "line of least resistance" (Schluter 1996, 2000). The intraspecific variation of *A. africanum* thus provides an excellent chance to survey a cusp pattern transition between the fixed conditions typical of other species of *Agriotherium* and of *Indarctos*. Our newly described southernmost U.S. material of *A. hendeyi* indicates that the highly variable (including a transitional morphotype) pattern observed in *A. africanum* does not solely represent the variation in a single local population, but instead exemplifies a transformational pathway based on the transitional states observed in at least two widely geographically-separated species near the phylogenetic transition between other species typical of the two genera. In *A. africanum*, PQ45114 (Fig. 4e1) and L50004 (Fig. 4f1) already have achieved the typical *Agriotherium* pattern, where the metaconid is totally lost; one large metaconid and two entoconids are present in L50446 (Fig. 4a), as is typical of *Indarctos*; whereas a transitional pattern of one rather small metaconid and two entoconids are present in L50006 (Fig. 4c). A similar transitional pattern of a small metaconid and two entoconids occurs in the North American *Agriotherium hendeyi* specimens from the Quiburis Formation (Fig. 4g), suggesting that the pattern shift in this lineage was achieved by reduction of the metaconid, as Hende (1980) proposed.

Besides the above evidence from the intraspecific and interspecific variation of Old World forms that was discussed by Hende (1980), now supported by the presence of a fixed transitional morphotype in the new North American species, three additional pieces of evidence also support an m1 metaconid-reduction hypothesis:



Fig. 4 Comparison of m1 (top) and m2 (bottom) in selected specimens of *Agriotherium* and *Indarctos*. **a–f**: *A. africanum* (S. Africa); **a**, L50446 (mirrored), **b**, L50003, **c**, AMNH FM 105148, cast of L50006, **d**, AMNH FM 105149, cast of L50007 (mirrored), **e**, AMNH FM 105140,

cast of PQ45114 (mirrored), **f**, AMNH FM 105146, cast of L50004. **g**: *A. hendeyi* sp. nov. AMNH F:AM 63098 (North America). **h**: *Indarctos* cf. *I. atticus* AMNH F:AM 22332 (Shanxi, China). M: metaconid; E2: entoconid2; E1: entoconid1

- 1) In *Indarctos*, there is often a concavity in the lingual contour between the metaconid and entoconid2, marking the boundary between the trigonid and talonid (Fig. 4h1). In most specimens of South African *A. africanum* and the new North American species *A. hendeyi*, this concavity is present just anterior to the anterior cusp in the metaconid-entoconid complex, especially in PQ45114 of *A. africanum* (Fig. 4e1). This suggests that the cusp behind this concavity represents the entoconid2, as in *Indarctos*.
- 2) In *Indarctos*, there is always a well-developed mesoconid on the buccal side of m1, between the protoconid and hypoconid, immediately buccal to the metaconid. In most specimens of *Agriotherium*, the mesoconid is reduced or fused with the hypoconid without separation. Both the metaconid and mesoconid are rather small in *A. hendeyi*. In *A. africanum* specimen L50446 (Fig. 4a), both cusps are well developed as in *Indarctos*, in contrast to L50006, PQ45114, and L50004 (Fig. 4c, e1, f1), in which the mesoconid is absent on all teeth and the metaconid is either absent or extremely small (reduced from the ancestral ursid condition). This intraspecific variation pattern suggests that the mesoconid and metaconid, both located at the boundary with talonid, have a synchronous development. The absence of the m1 mesoconid in most species of *Agriotherium* indicates the disappearance of the m1 metaconid in these species.
- 3) Teeth are serially homologous structures, and there is often strong similarity among adjacent teeth (Butler 1937, 1939; Kavanagh et al. 2007; Evans et al. 2016). The structure and variation of m2 therefore also provides support for inferences about the origins of the patterns seen in m1.

Like m1, the m2 of *A. africanum* also exhibits substantial variation, especially in the development of the metaconid. The metaconid is variable, from being large (Fig. 4b, f2) as it is ancestrally for ursids, to distinctly reduced (Fig. 4d), to being totally lost (Fig. 4e2). The *A. africanum* specimen of particular interest is L50006, with associated m1 and m2 that exhibit highly similar morphologies (Fig. 4e1, e2). In the m2, it is clear that the metaconid is totally lost, potentially via fusion with the medial ridge of the protoconid (as can be seen at a morphologically transitional stage in L50007, Fig. 4d), and this ridge turns posteriorly and connects directly with entoconid2. A lingual concavity is also present between the trigonid and entoconid2 on the m2 of L50007. As tooth morphology is determined by epithelial signals and involves differential activation of homeobox genes in the mesenchyme (Jernvall and Thesleff 2000), the patterns of variation of different teeth in one individual, and perhaps to a lesser extent in one population, should arise via the same developmental pathway. Therefore, the variation of m1 in *A. africanum* should be similar to that of m2, and the loss of the metaconid in m2 therefore would indicate that this also is the cusp that is lost in m1. This serial homology inference, on the other hand, is tempered by different developmental blocks for some features between m1 and m2, as we can see in some specimens of *A. africanum* (e.g., L50004) and in most species of *Agriotherium* (including *A. hendeyi*), in which only m1 loses the metaconid, whereas m2 does not.

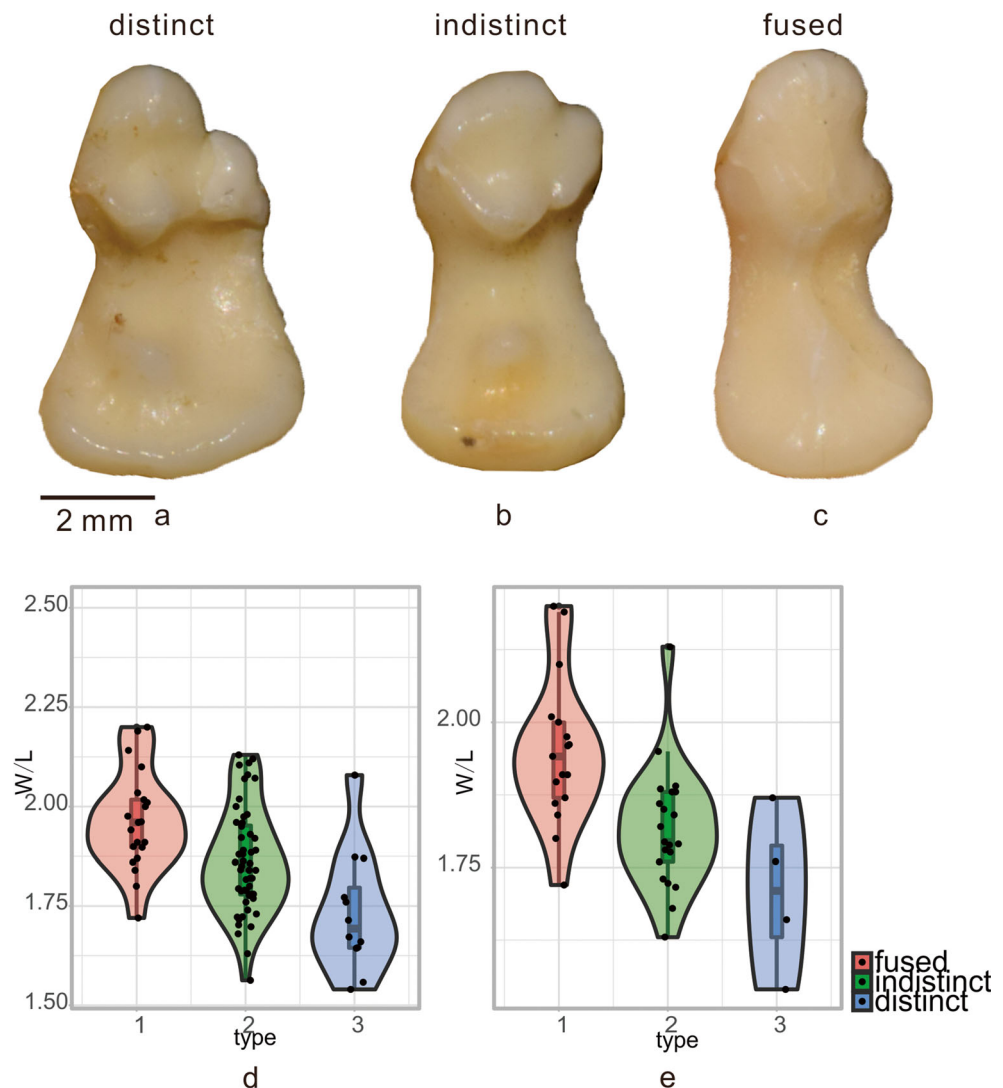
In cusp evolution within *Agriotherium*, the metaconid is lost on m1 and m2. From a developmental perspective, the

primordium for the metaconid could be viewed as having become fused with that of other cusps, either the protoconid or more likely the entoconid2. Distinct cusps are developed from the secondary enamel knots of the tooth germ (Jernvall and Thesleff 2012). When limited space pushes two originally separated secondary enamel knots closer to each other, the two knots may fuse, which causes cusp fusion in subsequent development (Pispa et al. 1999; Jernvall and Thesleff 2000). This pattern of transformation can be seen in the paracone-metacone of weasels (*Mustela*), for example, in which species with an anteroposteriorly elongated M1 always have clear differentiation of the paracone and metacone (Fig. 5a), whereas species with an anteroposteriorly shortened M1 tend to have either two closely proximate cusps or only a single cusp, representing a fused paracone and metacone (Fig. 5b, c). Plots of between- and within- species variation both show that anteroposterior shorter teeth tend to have a fused paracone-metacone, although there is considerable overlap in L/W ratios among specimens with distinct (two widely separated cusps),

indistinct (two closely appressed cusps often with one reduced in size), and fused (Fig. 5d, e).

The talonid (including the mesoconid) of *Agriotherium* is typically shorter than that of *Indarctos*. Decrease of talonid length shortens the distances between the second enamel knots of the metaconid and mesoconid relative to the anterior talonid cusps. To better understand the patterns that might result from this developmental process of talonid shortening influencing cusp fusion, we performed a geometric morphometric analysis of the lower m1 in *A. hendeyi*, *A. africanum*, “*A.*” *schneideri*, and *Indarctos* spp. (*I. atticus* and *I. zdanskyi*) (Fig. 6). A PCA analysis on the tangent space shows that *A. africanum* is clearly different from the morphospace occupied by *Indarctos* and “*A.*” *schneideri*. *Agriotherium africanum* shows wide variation on the PC1 axis, which mainly represents the degree of shortening of the anterior talonid portion of the tooth (see the warp grids (red outlines indicate the tooth

Fig. 5 Variation of the M1 paracone and metacone in extant *Mustela*: **a**, fully separated (*M. vison* AMNH M271485), **b**, partially fused (*M. putorius* AMNH M163437), **c**, fully fused (*M. nigripes* AMNH M40078); and violin-plot and boxplot of the width/length ratio versus degree of paracone-metacone fusion, in **d**, *Mustela* spp.; **e**, ferret group (*Mustela putorius*, *M. eversmanni* and *M. nigripes*)



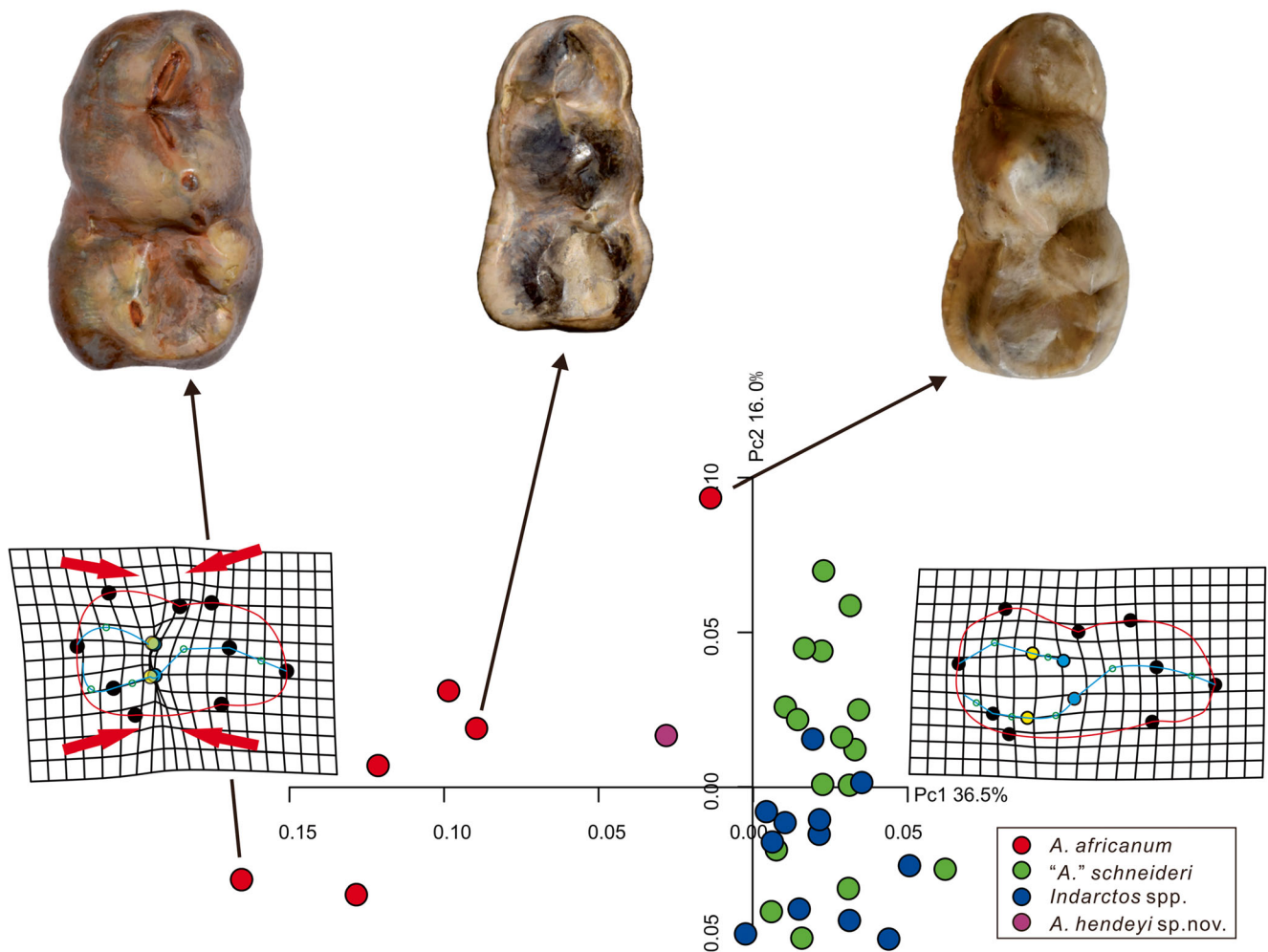


Fig. 6 Geometric morphometric analysis of the lower m1 of *A. hendeyi* (Arizona, USA, N. America), *A. africanum* (S. Africa), “*A.*” *schneideri* (Arizona, Texas, California, Oklahoma, and Florida, USA, N. America) and *Indarctos* spp. (*I. atticus* and *I. zdanskyi* sample from Samos, Greece and Shanxi and Gansu provinces, north China). The plot represents PC1 versus PC2 in a PCA analysis. The warp grid represents the logical value indicating the deformation grids for shapes along X-axis. The large circles in the warp grid indicate the landmarks, with emphasis on the anterior

(filled with blue) and posterior (filled with yellow) borders of the mesoconid and metaconid, respectively (in the left side these two circles are overlapped). The red lines the warp grid indicate the tooth contour and the blue lines indicate the ridges connecting the cusps, while the small green circles indicate the cusp apices. The red arrows indicate the movement of anterior and posterior borders of the mesoconid and metaconid, according to landmark position and grid deformation

contour and blue lines indicate the cusp ridge) in Fig. 6). The extreme variant in *A. africanum* (L50446) is basically *Indarctos*-like, but in the PCA tangent space it is still distinct from *Indarctos* (PC1 score for *A. africanum* is lower than that of any *Indarctos*). The PC1 and PC2 scores of *A. hendeyi* are within the range of variation along each axis for specimens of *A. africanum*, but when assessing both axes simultaneously, *A. hendeyi* is markedly distinct from the morphospace occupied by *A. africanum*. Overall, the geometric morphometric analysis suggests that species of *Agriotherium* generally have a strong shortening of the anterior part of the talonid. This shortening results in the fusion of the mesoconid and metaconid to their most proximate posterior cusps, namely of the mesoconid to the hypoconid and the

metaconid to the entoconid2 (red arrows in Fig. 6). Therefore, the cusp transition seen in some species of *Agriotherium* can be readily explained by a simple developmental process of cusp fusion in proximate secondary enamel knots associated with talonid shortening. This cusp transformation then would have been driven by selection towards a more hypercarnivorous diet, which in the evolution of Carnivora is typically associated with shortening or loss of the talonid (and emphasis on a shearing crest rather than distinct cusps), rather than a direct selection for replacement of the metaconid by entoconid2. This could explain the major question posed by Qiu and Schmidt-Kittler (1983) about the potential functional significance of this transition of loss of the ancestral metaconid and its replacement by entoconid2.

Distinctness of the New Quiburis Formation Species, *Agriotherium hendeyi*, from Other Species of *Agriotherium* and *Indarctos*

The specimens reported herein belong to a species that is quite different from all known North American *Agriotherium* as well as from Old World species of *Agriotherium* and *Indarctos*. This new species represents a relatively small-sized *Agriotherium*, comparable to *A. palaeindicum* in size. The large P4 parastyle and the absence of the M2 talon preclude assignment to *Indarctos*.

Compared with *A. sivalense*: *A. sivalense* is the type species of *Agriotherium*. It was a medium-sized *Agriotherium* from Pinjor layer of the Siwalik Group, the earliest Pleistocene (Cautley and Falconer 1836; Lydekker 1884; Colbert 1935; Nanda 2008). *Agriotherium hendeyi* differs from *A. sivalense* in its slightly smaller size, absence of a buccal concavity on P4, non-subdivided M2 protocone, and weaker anterior and posterior accessory cusps on p4. The large age difference is consistent with the marked morphological differentiation of *Agriotherium hendeyi* from *A. sivalense*.

Compared with *A. palaeindicum*: *A. palaeindicum* was the second *Agriotherium* species identified from the Siwalik Group, presumably from late Miocene-aged levels (Lydekker 1884). *Agriotherium hendeyi* is similar in size to *A. palaeindicum*, but it differs from the latter in having a subdivided P4 hypocone, less triangular shape of P4, wider M1, and less constricted M2 metacone. The original mandibular material assigned to *A. palaeindicum* probably represents *I. punjabensis* (Colbert 1935) instead, so a direct comparison of the lower dentition is impossible.

Compared with *A. inexpetans*: *A. inexpetans* was established based on several isolated lower teeth that belong to a single individual from Jiegou, Gansu Province, northern China (Qiu et al. 1991). *Agriotherium inexpetans* is even smaller than the Quiburis *A. hendeyi*, but the lower m1 talonid morphology is already typical for *Agriotherium*, so differs from the *Indarctos*-*Agriotherium* transitional condition in *A. hendeyi*. *Agriotherium hendeyi* is further distinct from *A. inexpetans* in having a bucco-lingually more slender lower dentition, less distinct m2 buccal concavity, and more anteriorly located m2 metaconid.

Compared with *A. insigne*: *A. insigne* was first described from Montpellier (MN 14), France, based on an upper jaw with P4–M2 (Gervais 1853, 1859). More lower dentitions were recognized later from this area (Stehlin 1907; Viret 1939). In general, *A. hendeyi* is slightly smaller than *A. insigne*. The lower dentition is also narrower than that of *A. insigne*, and the cingulum/cingulid is also weaker in both upper and lower dentitions of *A. hendeyi*. *Agriotherium intermedium* is a rather poorly defined species from Weże (MN15), Poland (Stach 1957), with a broken upper dentition and a lower m1. It is smaller than *A. insigne*, but the preserved

M2 and m1 also exhibit a well-developed cingulum/id. Therefore, this species is probably a synonym of *A. insigne*. Small observed differences between *A. intermedium* and *A. insigne* may be explained as due to geographic or chronological differences (Weże is younger by one MN biochron).

Compared with *A. roblesi*: *A. roblesi* is a huge bear, named based on one M1 and one M2 from Venta del Moro of Spain (Morales and Aguirre 1976) with an age of MN 13 (Van der Made et al. 2006). The Quiburis *A. hendeyi* is much smaller than *A. roblesi*, and the M2 has no talon as opposed to the presence of a talon in *A. roblesi*.

Compared with *A. africanum*: *A. africanum* is the best-known species of *Agriotherium*, as it is represented by a nearly complete cranium, several mandibles and numerous teeth and postcranial bones. The species was found at Langebaanweg, South Africa (Hendey 1972) and was described in detail by Hendey (1980). As discussed above, the dentition of *A. africanum* exhibits great variation, but *A. hendeyi* is generally smaller than *A. africanum*. The dentition of *A. hendeyi* is also narrower. Most M2 s of *A. africanum* have a weakly-developed talon and a strong transverse ridge between the paracone and protocone, which are absent in *A. hendeyi*.

Compared with *A. aecuatorialis*: *A. aecuatorialis* was established from several isolated teeth from Nkondo, Uganda and Mabaget, Kenya (Morales et al. 2005). Morales et al. (2005) considered it distinct from *A. africanum* based on its weaker and simplified P4 hypocone. Considering the great variation among individuals within *A. africanum*, however, *A. aecuatorialis* could be conspecific with *A. africanum*, but more specimens of *A. aecuatorialis* are needed to test this possibility. In any case, *A. aecuatorialis* as currently recognized differs from *A. hendeyi* in its larger size, larger P4 inner lobe, and stronger anterior concavity of M1.

Compared with other species of North American *Agriotherium*: There are several named species of *Agriotherium* from North America, including *A. schneideri*, *A. gregoryi*, *A. coffeyi*, and *A. guymonensis*. *Agriotherium schneideri* was described by Sellards (1916) from Upper Bone Valley (Hh4, Hunt 1998; Tedford et al. 2004); the holotype is a mandible of moderate size. Though somewhat worn, it can be seen that m1 still retains an *Indarctos*-pattern of talonid cusps, with presence of both a large metaconid and two smaller entoconids. *Agriotherium gregoryi* was described by Frick (1921) from the Eden local fauna, California (Hh3, Hunt 1998; Tedford et al. 2004) based on three isolated teeth; the holotype is a heavily worn P4 of large size. Its poor preservation led most later authors to regard *A. gregoryi* as a nomen dubium or a synonym of *A. schneideri* (Dalquest 1986; Miller and Carranza-Castaóeda 1996; Hunt 1998). A third North American species, *A. coffeyi*, was found at Coffee Ranch, Texas and the Guymon-Optima quarries, Oklahoma (Dalquest 1986), both aged Hh3 (Hunt 1998; Tedford et al. 2004). The holotype

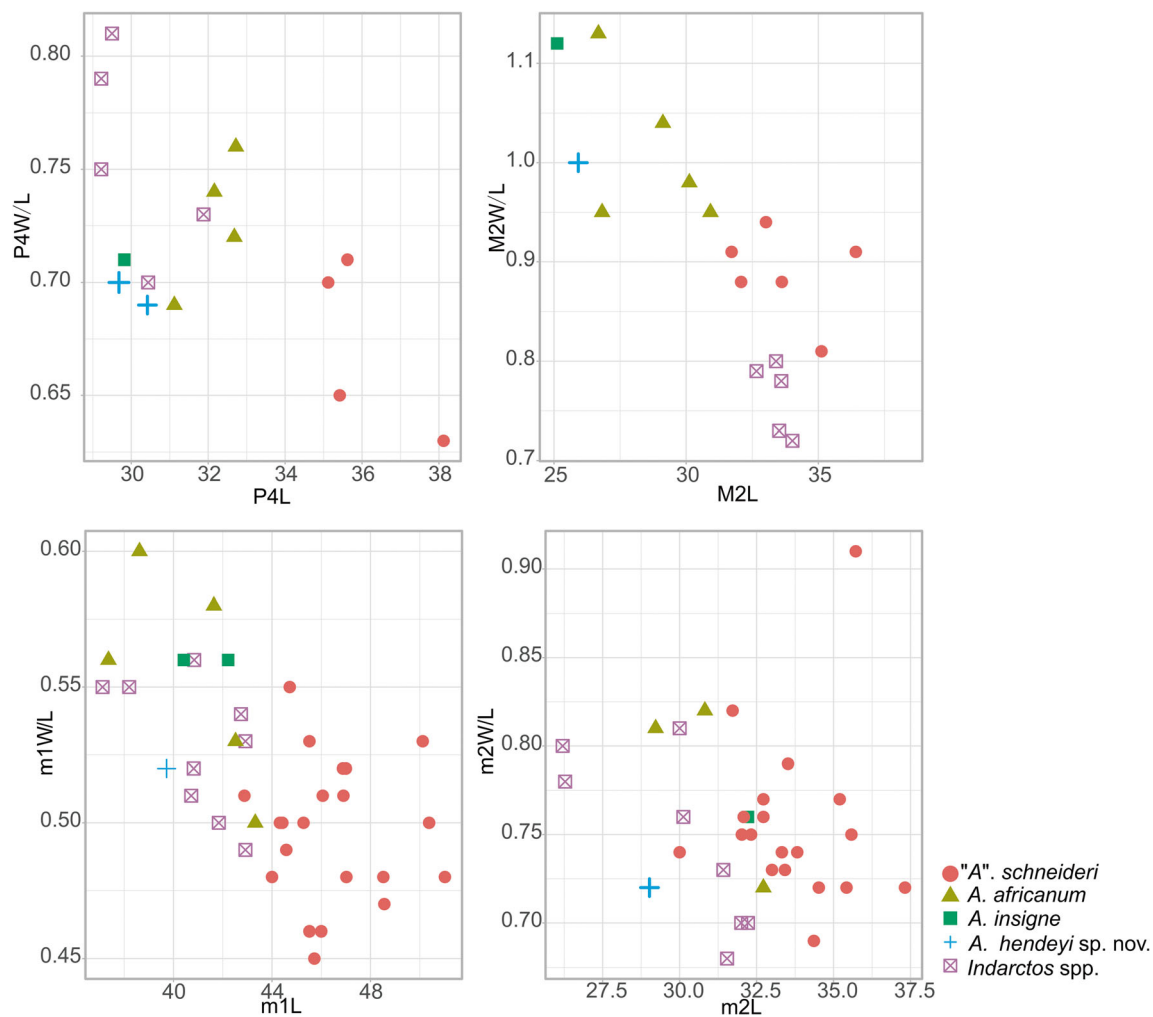


Fig. 7 Bivariate plots of tooth measurements for *Agriotherium hendeyi* and related taxa. Taxon names and symbols indicated in figure legend. L = length (in millimeters); W/L = length/width proportion; P4 = fourth

upper premolar; M2 = second upper molar; m1 = first lower molar; m2 = second lower molar

mandible has unworn teeth, representing a very large individual. However, lower m1 also exhibits an *Indarctos*-pattern, as in *A. schneideri*. The main character that led Dalquest (1986) to erect a new species is the double-rooted p3, which is in fact quite variable in North American *Agriotherium* (personal observation of QJ from AMNH collections). All later authors considered this species also to be a synonym of *A. schneideri* (Miller and Carranza-Castañeda 1996; Hunt Jr 1998). *Agriotherium guymonensis* was mentioned in footnote of Frick (1937), but he did not provide any diagnosis or description, and therefore this species should be viewed as nomen nudum. According to our observations on the material mentioned by Frick (1937), this material is should be assigned to *A. schneideri*.

Therefore, there is only a single valid species previously known from North America, for which *A. schneideri* has priority. Although it also occurs in the Quiburis Formation of Arizona, it is much larger than the new species *A. hendeyi*

and retains the more typical *Indarctos*-like pattern of its talonid cusps, so these two species can be readily distinguished even from within the same formation.

Agriotherium schneideri, however, is not typical for *Agriotherium*. As noted above, the m1 of this species has an *Indarctos*-like primitive ursid pattern, clearly differentiating it from the smaller-sized new species *A. hendeyi* with a more derived condition very close to that of typical *Agriotherium*. Large numbers (~30) of m1 s from the Quiburis Formation from the AMNH Frick collection document that the *Indarctos*-like pattern of the talonid is stable and fixed in *A. schneideri*, not an occasional occurrence via intraspecific variation as in *A. africanum*. The metaconid-entoconid complex is a key character distinguishing *Indarctos* from *Agriotherium*. The assignment of *A. schneideri* to *Agriotherium* is therefore doubtful, because all specimens assigned to it possess a fixed, *Indarctos*-like metaconid-entoconid complex pattern, and it now should be referred to



Fig. 8 Reconstruction of *Agriotherium hendeyi*. Artwork by Qigao Jiangzuo

provisionally as “*A.*” *schneideri*. A more complete description and discussion of the taxonomic position of that species will be the topic of another work, but the morphometric analysis and measurements of the teeth from the Quiburis Formation (Figs. 6 and 7) clearly document the distinctness of *A. hendeyi* from all other specimens and taxa discussed in this work. *Agriotherium hendeyi* differs from “*A.*” *schneideri* (including the synonymized taxa noted above) in its much smaller size (especially compared with the “*A.*” *schneideri* specimens from the same formation, Fig. 7), distinctly shorter M2 talonid, more robust upper dentition, less developed p4 anterior accessory cusp, and a fixed, nearly *Agriotherium*-patterned m1 talonid.

In summary, *A. hendeyi* from the Quiburis Formation of Arizona is clearly distinct from all known species of *Agriotherium*, warranting the new taxon and species name proposed here. A reconstruction of the head of *A. hendeyi* is shown in Fig. 8.

Conclusions

Through detailed description and comparison of new specimens from the Quiburis Formation of Arizona, a new species of *Agriotherium*, *A. hendeyi* is established. The new species is small in size and has a bucco-lingually narrow dentition. The m1 of the new species exhibits a similar cusp pattern to that seen in some specimens of *A. africanum*. This suggests that the condition in *A. hendeyi* from the Quiburis Formation, and some specimens within the wide variation observed in *A. africanum*, represent the morphologically transitional form from the *Indarctos*-pattern (ancestral condition for ursids) to the more derived cusp pattern typical of the type and other species of *Agriotherium*. In morphological and geometric morphometric analyses of the metaconid-entoconid complex, the two cusps in the lingual part of the m1 talonid in

Agriotherium are interpreted as two entoconids, such that the ancestral metaconid is reduced or lost and fused with entoconid2, based on multiple lines of evidence and inference. This anatomical transition is interpreted as resulting from a developmental process of talonid shortening under selection pressure towards a more carnivorous diet, rather than via direct selection for replacement of the metaconid by the entoconid2.

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Compliance with Ethical Standards

Competing Interests The authors declare no competing interests.

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