First postcranial remains of Multituberculata (Allotheria, Mammalia) from Gondwana

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A B S T R A C T

Multituberculata (Allotheria) are generally regarded as the evolutionarily most successful and longest-lived (Middle Jurassic to late Eocene) clade of Mesozoic and early Paleogene mammals. Despite this “reputation” and the fact that the group is particularly well represented in both taxonomic diversity and relative abundance on Laurasian landmasses during the Cretaceous and Paleocene, multituberculata are exceedingly poorly represented on the southern supercontinent Gondwana. Previous records on Gondwanan landmasses have been based on fragmentary dental remains and all except the three most recently published (each represented by a single isolated tooth or fragment of tooth) have been disputed and allocated to either Haramiyida or Gondwanatheria. Furthermore, several previous records, disputed or not, are based on fragmentary dental remains of a type (plagiaulacoid) that has evolved independently several times in mammalian evolution.

Here we place on record a multituberculate femur from the Upper Cretaceous (Maastrichtian) Mahavaro Formation of the Mahajanga Basin, Madagascar. This specimen, although fragmentary as well, exhibits a number of features common to all multituberculata femora: neck cylindrical in cross section and set apart from shaft; greater trochanter prominent, extending proximally beyond head, inclined dorsally, and separated from neck by deep incisure; lesser trochanter prominent and protruding ventrally; posttrochanteric fossa present on ventral aspect, lateral to lesser trochanter; subtrochanteric tubercle present on dorsal aspect, distal to incisure between greater trochanter and neck; diaphysis straight, elliptical in cross section (slightly compressed dorsoventrally); and third trochanter absent. Three of these features (prominent, ventrally placed lesser trochanter; presence of posttrochanteric fossa; presence of subtrochanteric tubercle) are regarded as autapomorphies of Multituberculata. This specimen therefore not only independently and conclusively confirms the presence of the clade on Madagascar—previously based on a small molar fragment—but on the entire supercontinent as well.

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1. Introduction

Whereas multituberculata are among the most common and speciose mid-late Mesozoic and early Paleogene mammals on the Laurasian supercontinent, represented by literally thousands of isolated teeth and jaws from hundreds of localities but also by skulls and postcranial skeletons, their record on Gondwanan landmasses is extremely sparse (e.g., Kielan-Jaworowska et al., 2004; Weil and Krause, 2008; Rich and Vickers-Rich, 2012; Krause, 2013; Wilson, 2014). This disparity in abundance and diversity may be owing, in part, to the relatively poor fossil record of early mammals on Gondwana (Kielan-Jaworowska et al., 2004; Rich and Vickers-Rich, 2012) but enough is known to at least suggest that it is real. Not only are individual specimens of multituberculata exceedingly rare, but those that have been recovered are fragmentary, almost exclusively isolated teeth, leading to controversy surrounding their identity. Included among these specimens is a small fragment of a molar, composed of only two cusps, from the Late Cretaceous of Madagascar that Krause (2013) provisionally referred to the Multituberculata. Here we describe the first postcranial remains of a multituberculate from Gondwana, a fragmentary but morphologically distinctive proximal femur that bears a number of characteristic features of Multituberculata. This specimen was discovered at the same locality, MAD93–35, as the molar...
fragment, in the Upper Cretaceous (Maastrichtian) Anembalemba Member of the Maevarano Formation, in the Berivotra Study Area of the Mahajanga Basin, northwestern Madagascar (Fig. 1). Our objectives here are to document this record, thereby confirming that multituberculates were indeed present on Madagascar in the Late Cretaceous, and Gondwana as a whole, and to discuss the paleobiogeographic implications of this occurrence.


2. The record of Gondwanan multituberculates

The following records have been purported to represent Multituberculata on Gondwanan landmasses (listed from earliest publication to latest, with original taxonomic assignment and age in parentheses):

1) *Hahnodon taqueti* Sigogneau-Russell, 1991 (Hahnodontidae, Plagiaulacoidea?; Early Cretaceous, Morocco) — based on an isolated m2. Butler and Hooker (2005) argued that this taxon (and the entire family) should be referred to the Haramiyida but Hahn and Hahn (2006, p. 185) concluded that “the morphology of the Hahnodontidae supports their referral to the multituberculates, whereas their mode of wear contradicts it.” Meng et al. (2014) supported the conclusion of Butler and Hooker (2005) on the basis of root structure.

2) *Denisodon moroccensis* Hahn and Hahn, 2003 (Hahnodontidae, Paulchoffatioidea, Plagiaulacida; Early Cretaceous, Morocco) — based on an isolated m2. The statements (see #1 above) by Butler and Hooker (2005) and Hahn and Hahn (2006) also pertain to *D. moroccensis*, the single specimen of which Butler and Hooker suggested might be an m1 of *H. taqueti*.

3) Hahnodontidae, gen. et sp. indet. (Hahnodontidae, Paulchoffatioidea, Plagiaulacida; Early Cretaceous, Morocco) — based on two isolated teeth, a distal upper premolar (P3 or P4) and a fragmentary lower incisor, described by Hahn and Hahn (2003). Neither Butler and Hooker (2005) nor Hahn...
and Hahn (2006) explicitly discussed these specimens but the former removed the entire family from Multituberculata.

4) Ferugliotherium windhauseni Bonaparte, 1986 (Ferugliotheriidae, ?Multituberculata; Late Cretaceous, Argentina) — originally based on a single, isolated, worn molariform tooth identified as m2. To this taxon have been referred, in some cases questionably, specimens from various other tooth positions, including incisors, premolars, and molars (Bonaparte, 1990; Krause et al., 1992; Krause, 1993; Kielan-Jaworowska and Bonaparte, 1996). This is the most controversial taxon listed here; the complex history of the specimen assignments, which includes differing opinions by Kielan-Jaworowska et al. (2004), Gurovich (2006), Pascual and Ortiz-Jaureguizar (2007), and Gurovich and Beck (2009), were most recently reviewed by Krause (2014) and need not be repeated here. Suffice it to say that this species, based on its holotypic specimen, and the entire family Ferugliotheriidae are currently regarded as low-crowned gondwanatherians (e.g., Gurovich and Beck, 2009; Krause, 2013, 2014), which, like multituberculates, are members of Allotheria (Krause et al., 2014a). Undermining a conclusive determination of whether ferugliotheriids are multituberculates or gondwanatherians is the absence of any specimen that includes both multituberculate-like premolars and gondwanatherian-like molars.

5) Vucettichia gracilis Bonaparte, 1990 (Gondwanatheriidae, Gonwanatheria, ?Paratheria; Late Cretaceous, Argentina) — this taxon was established on the basis of two heavily worn teeth, identified as upper molars. Krause (1993) demonstrated that they represented teeth of Ferugliotherium windhauseni, which was considered a multituberculate by Bonaparte (1990); but see comments in #4 above.

6) Argentodites coloniensis Kielan-Jaworowska, Ortiz-Jaureguizar, Viyetes, Pascual, and Goin, 2007 (Multituberculata, ?Cimolodonta, superfamily and family incertae sedis; Late Cretaceous, Argentina) — based on a nearly complete left p4, without roots. Gurovich and Beck (2009), p. 32) concluded that the single specimen representing this taxon should be referred to "Ferugliotherium or a closely related taxon." Rougier et al. (2009) agreed with this assessment but Ortiz-Jaureguizar and Pascual (2011) did not, maintaining that Argentodites was likely a cimolodontan.

7) Trapalotherium mutatensus Rougier, Chornogubsky, Casadio, Arango, and Giallombardo, 2009 (?Multituberculata, Ferugliotheriidae; Late Cretaceous, Argentina) — based on an isolated specimen identified as left m1. Ferugliotheriids are currently regarded as low-crowned gondwanatherians (e.g., Gurovich and Beck, 2009; Krause, 2013, 2014), but see section on Ferugliotherium (#4) above.

8) Corriebaatar marywaitersae Rich, Vickers-Rich, Flannery, and nine others, 2009 (Cimolodonta, Corriebaataridae; Early Cretaceous, Australia) — based on a fragmentary left dentary bearing p4 and mesial root of m1. Record not disputed.

9) ?Multituberculata (Late Cretaceous, Madagascar) — based on a molar fragment with two cusps described by Krause (2013). Record tentative but not disputed.

10) Indobaatar zofiae Parmar, Prasad, and Kumar, 2013 (Eobaataridae; Early/Middle Jurassic, India) — based on what was described as an isolated left P4. Record not disputed.

Of the occurrences listed above, the multituberculate affinities of only the three most recently published specimens have not (yet) been disputed. As such, based on the current literature, the only unquestioned records of Multituberculata on Gondwanan landmasses, one of which was tentative when originally published, are based on three taxa represented by three isolated teeth or fragments of teeth. Furthermore, it must be noted that some of the previous records of multituberculates on Gondwanan landmasses, both disputed and so far undisputed, have been based only on dental characters associated with plagiaulacoidy. Plagiaulacoidy is the condition in which one or more distal premolars (and, in some cases, the first molar) have become laterally compressed and blade-like, with an apical edge that is serrated (Simpson, 1933). Associated with these blade-like teeth are enlarged, procumbent incisors; brachydont, crushing or grinding molars; and significant diastema in the lower jaw and sometimes in the upper jaw. Unfortunately for the purposes of identifying isolated teeth, plagiaulacoidy has evolved independently in a number of mammalian taxa; indeed, it is often hailed as a prime example of evolutionary convergence in mammalian dentitions (e.g., Simpson, 1933; Gingerich, 1977; Ungar, 2010; Acorn, 2014). In addition to being ubiquitous among multituberculates (except arguably in Taeniola-bidioidea [sensu Williamson et al., 2016], in which the blade-like premolars have undergone secondary reduction), plagiaulacoid dentitions are known in a number of marsupial (Diprotodontia — Balbaridae, Burramyidae, Hypsiprymnodontidae, Macroqodidae, Phalangeridae, Potoriidae; Polydolopomorphida — Bonapartheriidae, Polydolopidae; Paucituberculata — Abderitiidae, Caenolestidae) and placental (Plesiadiformes — Carpolesitidae, Saxoilidae) taxa (e.g., Simpson, 1933; Rose, 1975; Parker, 1977; Marshall, 1981; Rich et al., 2009, fig. 3; Ungar, 2010; Abello, 2013; Beck, 2016; Prufrock et al., 2016; Goin et al., 2016). In addition, if ferugliotheriids are gondwanatherians and plagiaulacoid lower premolars are correctly assigned to the group (Kielan-Jaworowska and Bonaparte, 1996; Kielan-Jaworowska et al., 2007; Gurovich and Beck, 2009), then gondwanatherians can be added to the list. It is generally agreed that plagiaulacoid premolars evolved for the purpose of slicing (e.g., Simpson, 1933; Parker, 1977; Krause, 1982; Biknevicius, 1986; Wall and Krause, 1992; Dumont et al., 2000; Dennis, 2002; McNamara, 2014).

3. Systematic paleontology

Mammalia Linneaus, 1758
Allotheria Marsh, 1880
Multituberculata Cope, 1884
Family indet.
Gen. et sp. indet.

Despite the abundance and diversity of multituberculates, to our knowledge not a single multituberculate species has been named on the basis of isolated postcranial remains. We choose to not deviate from that practice, in part because of precedent but primarily because we do not consider the specimen described below, DMNH EPV.100010, to be diagnostic at the familial, generic, or species level.

3.1. Specimen

DMNH EPV.100010 is a slightly eroded proximal portion of a right femur (Fig. 2A–F).

3.2. Locality, stratigraphy, and age

DMNH EPV.100010 was discovered at locality MAD93-35 in the Anembalemba Member of the Maevvarano Formation, in the Berivotra Study Area of the Mahajanga Basin, northwestern Madagascar (Fig. 1; see also Rogers et al., 2000, for geological map of the Berivotra Study Area [fig. 2], graphic stratigraphic logs [fig. 7] and outcrop views [fig. 8] of the Anembalemba Member, and regional
cross-section illustrating stratigraphic relations among Upper Cretaceous and Tertiary rock units in the Berivotra Study Area (fig. 11). Coordinates for locality MAD93-35 are on file at the Denver Museum of Nature and Science and at the University of Antananarivo. The Maevarano Formation has been confidently dated as late Late Cretaceous (Maastrichtian) in age (see Krause et al., 2014b, and references therein).

3.3. Description

DMNH EPV.100010 is described here as if in a horizontal, flexed position with dorsal, ventral, medial, and lateral surfaces, and proximal and distal ends. The length of the preserved fragment is 25.7 mm; if proportioned as other multituberculate femora, it was probably about 32–34 mm long in life. The cross-section of the femoral shaft is elliptical, with a maximum diameter (mediolaterally) of 4.8 mm and a minimum diameter (dorsoventrally) of 4.1 mm. In addition to missing its distal end, DMNH EPV.100010 does not preserve the apices of the greater and lesser trochanters and nor the femoral head.

DMNH EPV.100010 possesses a very large and long greater trochanter that leans dorsally as it ascends toward its apex. Even though incomplete, the greater trochanter would have extended much farther proximally than where the proximal-most end of the

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Fig. 2. Right femora of Multituberculata. A–F, Multituberculata gen et sp. indet. (DMNH EPV.100010) from the Late Cretaceous of Madagascar in A) dorsal, B) medial, C) ventromedial, D) ventral, E) lateral, and F) proximal (medial to left, dorsal to top) views. Specimen is missing the apices of the greater and lesser trochanters, the femoral head, and the distal end. G–I, ?, Eucozammon sp. (AMNH 16325) from the Paleocene of U.S.A. in G) dorsal, H) medial, and I) ventral views (modified from Granger and Simpson, 1929, fig. 21). J–L, Nemegtbaatar gohiensis (composite including ZPAL MgM-l81) from the Late Cretaceous of Mongolia in J) dorsal, K) medial, and L) ventral views (modified from Kielan-Jaworowska et al., 2004, fig. 8.13B). Abbreviations: fn, femoral neck; gt, greater trochanter; i, incisure between femoral neck and greater trochanter; lt, lesser trochanter; ptf, posttrochanteric fossa; stf, subtrochanteric fossa; stt, subtrochanteric tubercle; tf, trochanteric fossa.
femoral head would have been if preserved. The femoral head is, in fact, missing but the neck on which it sat projects proximomedially at an angle of approximately 44° relatively to the lateral margin of the diaphysis, thus resulting in a deep incisure between the greater trochanter and femoral neck. At the base of the greater trochanter lies a prominent trochanteric fossa, best seen in ventromedial (Fig. 2C) and proximal (Fig. 2F) views; although still containing some hard, adherent matrix, it is clear that it was elliptical in shape and very deep. Just as the apex of the greater trochanter and femoral head are broken off, so too is the apex of the lesser trochanter, thus precluding observation of its shape. Despite the breakage, the large base of the lesser trochanter is preserved, unmistakably indicating the existence of this feature on the ventral surface of the femur. Extending from the base of the lesser trochanter are three ridges: a short one passing distally onto the diaphysis, another short one extending onto the neck of the femur, and a longer, more robust one, the intertrochanteric ridge, extending proximally onto the greater trochanter and forming the ventral wall of the trochanteric fossa. A posttrochanteric fossa (of Kielan-Jaworowska and Gambaryan, 1994; divided trochanteric [digital] fossa of Simpson and Elftman, 1928) is present as a shallow depression lateral to the base of the lesser trochanter; it is elliptical in shape and horizontally oriented (i.e., parallel to the long axis of the diaphysis). There is no trace of a third trochanter.

A small but distinct subtrochanteric tubercle is present on the dorsal surface of DMNH EPV.100010, at the base of the greater trochanter. Associated with the subtrochanteric tubercle is a shallow fossa immediately lateral to it. DeBey and Wilson (2014, p. 363) introduced the term subtrochanteric tubercle for such a structure but described it as lying “between portions of a proximodistally bisected subtrochanteric tubercle,” thus dividing the tubercle into medial and lateral portions. We use the terms subtrochanteric tubercle and subtrochanteric fossa slightly differently, restricting the tubercle to only that portion lying at the base of the greater trochanter on the dorsal side (medial portion of tubercle in DeBey and Wilson’s terminology) and the fossa to the proximodistally aligned depression lateral to the tubercle. Lateral to the subtrochanteric fossa is another raised area that DeBey and Wilson (2014, fig. 9A) labeled the “distal ridge.” Our rationale for modifying this terminology is based on the muscle attachments inferred by Kielan-Jaworowska and Gambaryan (1994, fig. 42D). These authors show nothing attaching to the subtrochanteric tubercle (medial portion of DeBey and Wilson), but illustrate M. vastus lateralis originating from the region in which the subtrochanteric fossa and the distal ridge (lateral portion? Of DeBey and Wilson) are located. As such, the tubercle is not functionally divided into medial and distal portions.

4. Comparisons

4.1. Size

DMNH EPV.100010, with an estimated length of 32–34 mm, represents an animal just slightly smaller than *Ptilodus kummnae* (femoral length ~36 mm: see Krause and Jenkins, 1983, table 1), a medium-sized multituberculate. The body mass of *P. kummnae* was estimated by Wilson et al. (2012) to be 110 g, the size of small rat species such as the *Asian Rattus* *lesue* and the *Australian R. fuscipes* (see Breed and Taylor, 2000). Interestingly, although precise size comparisons are impossible, the isolated, fragmentary molar specimen (FMNH PM 61152) from the same strata (and, indeed, the same locality — MAD93-35) as DMNH EPV.100010 that was tentatively assigned to the Multituberculata by Krause (2013) represents a similarly sized animal, suggesting that the two specimens could represent the same species.

4.2. Comparisons of DMNH EPV.100010 with femora of other multituberculates

Femora are known for a number of multituberculate species representing a broad range of higher taxa, and two representative examples are provided in Fig. 2 (G–I, ?Eucosmodon sp.; J–L, *Nemegtbaatar gobiensis*) for comparison. Lists of these species, and the femoral specimens attributed to them, are provided by Krause and Jenkins (1983, pp. 200–201) and DeBey and Wilson (2014, table S4). To these lists can be added *Chulsanbaatar vulgaris* (ZPAL MM-M/70a, IB5, 99a — Kielan-Jaworowska and Gambaryan, 1994), *Slavenbaatar mirabilis* (ZPAL MM-M/20 — Kielan-Jaworowska and Gambaryan, 1994), *Meniscosemus robustus* (MOR 882 — Hunter et al., 1997); *Mangasbaatar udanii* (PSS-MAE 141 — provisionally described by Bolortsetseg (2008) as the “Udan Multi” but more recently named by Rougier et al., 2016), *Rugosodon eurasiacus* (BMNH 1142 — Yuan et al., 2013), *Yubataar zhongyuansensis* (HGM 41HIII0111 — Xu et al., 2015), and *Sphenopsalis nobilis* (IVPP V19030 — Mao et al., 2016). Yuan et al. (2013) also scored the femur of *Sinobaatar*, but none has ever been described or illustrated, either for the holotypic specimen of *S. lingyuansensis* (IVPP V12517, see Hu and Wang, 2002) or for other skeletal specimens that have since been discovered (Luo et al., 2016).

Across this taxonomic diversity, there are several ubiquitous or nearly ubiquitous morphological features of the proximal portion of the femur. Kielan-Jaworowska and Gambaryan (1994, pp. 63, 84) listed seven such attributes: (1) head spherical, with extensive articular surface; (2) neck long and constricted, set apart from shaft at angle of 50–60°; (3) greater trochanter prominent, extending proximally beyond head and separated from it by deep incurse; (4) absence of third trochanter; (5) lesser trochanter, at confluence of greater trochanter and neck, plate-like, convex lateroproximally, concave mediadistally, and strongly protruding ventrally; (6) presence of posttrochanteric fossa; and (7) presence of subtrochanteric tubercle. Of these, Kielan-Jaworowska and Gambaryan (1994) regarded the last three as autapomorphies of Multituberculata.

DeBey and Wilson (2014, p. 366) refined and added to these attributes of multituberculate femora as follows: (1) articular head surface “greater than hemispherical”; (2) neck “cylindrical in cross section”; (3) “a greater trochanter that is aligned with the shaft [. . .] is dorsally recumbent as well as curved medially, and exhibits a large rugose area for muscle attachment on the lateral surface”; (4) “a lesser trochanter [. . .] that terminates abruptly rather than passing into a ridge as in most mammals”; and (5) “a straight shaft that is elliptical in cross section, larger mediolaterally.”

Each of these features is discussed in the context of DMNH EPV.100010 below.

4.2.1. Head and neck

The femoral head is not preserved on DMNH EPV.100010 but the neck is long and cylindrical, as in other multituberculates. Although Kielan-Jaworowska and Gambaryan (1994, p. 63) characterized the femoral neck of multituberculates as “forming an angle of 50–60° to the shaft,” the angle in DMNH EPV.100010 is only approximately 44°. To investigate this potential discrepancy, we measured femoral neck-shaft angles (also known as the caput-collum-diaphyseal angle) in a range of multituberculata taxa based on both published and unpublished photographs and drawings (Table 1). Precision is difficult but measurement error is likely within 2–3° (perhaps higher for those femora with relatively incomplete diaphyses). In addition to the specimens listed in Table 1, Bolortsetseg (2008) measured the angle as 42° in *Ectypodus* sp. (BT03049), 45° in *Kryptobaatar dashzevegi* (MAE 00–22), and 60° in *Mangasbaatar udanii* (PSS-MAE 141). This broader sample generally confirms the
The greater trochanter of DMNH EPV.100010, even though its apex is not preserved, is directed dorsally. Furthermore, the greater trochanter is massive, as in other multituberculates, and clearly would have extended far proximal to where the head (character 247) would have been located. Although the apex of the lesser trochanter of DMNH EPV.100010 is not preserved, its base indicates that it was very well developed, in the position typical for multituberculates (ventrally rather than medially on the femur), and projected out from the diaphysis. Such a condition is not present in stem mammals and is otherwise found only in tituberculates (e.g., *Zhangheotherium*, *Maotherium*, eutherians, and metatherians (e.g., Kielan-Jaworowska et al., 2004; Yuan et al., 2013). Like *Rugosodon*, it has a low greater trochanter relative to the femoral head but, like cimolodontans and the Madagascan taxon, the greater trochanter is directed dorsally.

### 4.2.3. Lesser trochanter

Although the apex of the lesser trochanter of DMNH EPV.100010 is not preserved, its base indicates that it was very well developed, in the position typical for multituberculates (ventrally rather than medially on the femur), and projected out from the diaphysis. Such a condition is not present in stem mammals and is otherwise found only in tituberculates (e.g., *Zhangheotherium*, *Maotherium*, eutherians, and metatherians (e.g., Kielan-Jaworowska et al., 2004; Yuan et al., 2013). DeBey and Wilson (2014, p. 366) described the lesser trochanter of multituberculates as terminating "abruptly rather than passing into a ridge as in most mammals." This is generally true but must be qualified. DMNH EPV.100010 exhibits a very short ridge extending distally from the base of the lesser trochanter to connect to the diaphysis. However, such ridges have been described or illustrated for the femora of a few other multituberculate taxa as well (e.g., *Catopsalis joyneri* — Deischl, 1964, fig. 29; *Catopsalis alexanderi* — Middleton, 1982, pl. 1, fig. 6; *Mesodma sp.* — Deischl, 1964, fig. 21D; *Meniscoessus robustus* — Hunter et al., 1997, fig. 18L, M; *Ptilodus kummae* — Krause and Baird, 1979, text-fig. 1G; *Mesodma sp.* — Deischl, 1964, fig. 23; *Hell Creek and Tullock morphotype Mu9* — Deischl and Jenkins, 1983, fig. 20E; *Catopsbaatar catopsaloides* — Mount Laurel, 1982, pl. 1, fig. 6; *Meniscoesous robustus* — Hunter et al., 1997; *Sphenopsalis nobilis* — Mao et al., 2016, p. 442 and fig. 12A2). The ridge is faintly visible in several Hell Creek and Tullock formation morphotypes but the condition in Mu9 is similarly similar to that of DMNH EPV.100010 in this regard (DeBey and Wilson, 2014, fig. 11).

### 4.2.4. Posttrochanteric fossa

The posttrochanteric fossa is a depression immediately lateral to the lesser trochanter. It is ubiquitously present on multituberculate femora, and appears to be moderately deep to deep in most taxa (e.g., *Ptilodus* — Gidley, 1909, fig. 5 [also Krause and Baird, 1979, text-fig. 1G]; *Eucosmodon* — Granger and Simpson, 1929, fig. 21C [also Krause and Jenkins, 1983, fig. 20]; Mount Laurel Formation multituberculate — Krause and Baird, 1979, text-fig. 1F; *Catopsalis* — Middleton, 1982, fig. 6; Bissekty Formation multituberculate — Kielan-Jaworowska and Nesson, 1992, fig. 5G; *Kryptobaatar dashzevegi* — Kielan-Jaworowska and Gambaryan, 1994, fig. 2A; *Ectypodus* sp. — Bolortsetseg, 2008, fig. 13.2; *Catopsbaatar catopsaloides* — Hurum and Kielan-Jaworowska, 2008, fig. 8A5, 7B; Hell Creek and Tullock formation morphotypes Mu1, 3, 5, 6, 7, 8, 10 — DeBey and Wilson, 2014, figs. 3C, 5B, 7B, 8C, 9E, 10C, and 12C, respectively); and *Ptilodus kummae* (pers. obs., DWK). Such a strong inclination appears to not be present in *Nemegtbaatar gobiensis* — Kielan-Jaworowska and Gambaryan (1994, figs. 16C, 42A) and *Sphenopsalis nobilis* (Mao et al., 2016, fig. 12A2). We disagree with the statement by Hurum and Kielan-Jaworowska (2008, p. 556) that the greater trochanter is not inclined in *Eucosmodon* and *Kryptobaatar dashzevegi*.

### 4.2.5. Subtrochanteric tubercle and fossa

A subtrochanteric tubercle on the dorsal surface, at the junction of the greater trochanter and femoral neck, is clearly present in.
DMNH EPV.100010. This feature is variably developed in Multituberculata, in some cases distinct (e.g., ?Eucosmodon — Granger and Simpson, 1929, fig. 21; Stogimys kuszmauli — Deischl, 1964, fig. 31a [also Krause and Jenkins, 1983, fig. 20A]; Bissekty Formation multituberculata — Kielan-Jaworska and Nesov, 1992, fig. 5E; Kryptobaatar — Kielan-Jaworska and Gambaryan, 1994, fig. 3; Nemegtbaatar — Kielan-Jaworska and Gambaryan, 1994, fig. 16B; Chulsanbaatar — Kielan-Jaworska and Gambaryan, 1994, fig. 24B, C), in some cases poorly developed and indistinct (e.g., ?Madagascar, has been discovered (Hoffmann, 2016; Hoffmann et al., 2012), Krause et al., (2014a), and references therein). Postcranial elements of the earliest multituberculata (mid-level of femoral head) and in lacking the third trochanter.}

In sum, therefore, if the femora of ?late Cretaceous) is controversial. The clade is regarded by some as basal mammals or basal mammaliaforms outside Allotheria (e.g., Rowe, 1993; Jenkins et al., 1997; Luo et al., 2015) and by others as crown mammals within Allotheria (e.g., Butler, 2000; Zheng et al., 2013; Bi et al., 2014; Krause et al., 2014a). Knowledge of the postcranial skeleton is extremely limited. Postcranial elements of the earliest haramiyidans, Haramiyavi, although known, remain undescribed (Jenkins et al., 1997; Luo et al., 2015) but do not include femora (Luo, pers. comm., 2017).

Other possible haramiyidans include Arboroharamiya, Shenhou, and Xianshou (assigned to Eleutherodontidae within Haramiyida by Luo et al., 2015) but to Euharamiyida within Allotheria by Bi et al., 2014). The femur of Arboroharamiya was only briefly described, and as having a head that is “not spherical but cylindrical” (Zheng et al., 2013, p. 201). Other characteristics of the proximal femur are derived from scorings in the phylogenetic analyses of Zheng et al. (2013: “neck present, head spherical [contra main article] and inflected medially”; greater trochanter “directed dorsolaterally”; and third trochanter “absent”) and Bi et al. (2014, Sl: greater trochanter at “mid-level of femoral head”). Shenhou was scored by Bi et al. (2014) as differing from Arboroharamiya and Xianshou in having no femoral neck but all three taxa were characterized as having a greater trochanter that is dorsolaterally directed and short (mid-level of femoral head) and in lacking the third trochanter. Additionally, in Shenhou and Xianshou, the lesser trochanter was scored as “small to absent.” Luo et al. (2015), however, rescored several of these characters based on observation of figures in Bi et al. (2015; see, for instance, Extended Data fig. 4a) and Luo’s “own assessment of fossil specimens” of Arboroharamiya, Shenhou, and Xianshou as follows: Character 281 — Arboroharamiya and Xianshou were rescored as in Shenhou, with the “neck absent and head ori- ented dorsally” (as opposed to “neck present, head spherical and inflected medially”); Character 285 — the position of the lesser trochanter in Arboroharamiya, Shenhou, and Xianshou was rescored as on the “medial side of the shaft” (as opposed to on “the ventromedial or ventral side”); and Character 286 — the size of the lesser trochanter in Shenhou and Xianshou was rescored as “large” (as opposed to “small to absent”). The presence or absence of a posttrochanteric fossa, a subtrochanteric tubercle, or a subtrochanteric fossa in Arboroharamiya, Shenhou, and Xianshou is unknown.

In sum, therefore, if the femora of Arboroharamiya, Shenhou, and Xianshou are representative of Haramiyida and correctly scored by Luo et al. (2015), it would appear that the femora of haramiyidans and multituberculata (including that of DMNH EPV.100010) are highly distinctive, particularly in the presence/absence of a femoral neck (absent in haramiyidans, present in multituberculata), orientation of the femoral head (dorsally in haramiyidans, inflected medially in multituberculata), orientation of the greater trochanter (directed dorsolaterally in haramiyidans, directed dorsally in multituberculata), relative size of the greater

The phylogenetic position of Haramiyida (Late Triassic to ?Late Cretaceous) is controversial. The clade is regarded by some as basal mammals or basal mammaliaforms outside Allotheria (e.g., Rowe, 1993; Jenkins et al., 1997; Luo et al., 2015) and by others as crown mammals within Allotheria (e.g., Butler, 2000; Zheng et al., 2013; Bi et al., 2014; Krause et al., 2014a). Knowledge of the postcranial skeleton is extremely limited. Postcranial elements of the earliest haramiyidans, Haramiyavi, although known, remain undescribed (Jenkins et al., 1997; Luo et al., 2015) but do not include femora (Luo, pers. comm., 2017).

Other possible haramiyidans include Arboroharamiya, Shenhou, and Xianshou (assigned to Eleutherodontidae within Haramiyida by Luo et al., 2015) but to Euharamiyida within Allotheria by Bi et al., 2014). The femur of Arboroharamiya was only briefly described, and as having a head that is “not spherical but cylindrical” (Zheng et al., 2013, p. 201). Other characteristics of the proximal femur are derived from scorings in the phylogenetic analyses of Zheng et al. (2013: “neck present, head spherical [contra main article] and inflected medially”; greater trochanter “directed dorsolaterally”; and third trochanter “absent”) and Bi et al. (2014, Sl: greater trochanter at “mid-level of femoral head”). Shenhou was scored by Bi et al. (2014) as differing from Arboroharamiya and Xianshou in having no femoral neck but all three taxa were characterized as having a greater trochanter that is dorsolaterally directed and short (mid-level of femoral head) and in lacking the third trochanter. Additionally, in Shenhou and Xianshou, the lesser trochanter was scored as “small to absent.” Luo et al. (2015), however, rescored several of these characters based on observation of figures in Bi et al. (2015; see, for instance, Extended Data fig. 4a) and Luo’s “own assessment of fossil specimens” of Arboroharamiya, Shenhou, and Xianshou as follows: Character 281 — Arboroharamiya and Xianshou were rescored as in Shenhou, with the “neck absent and head ori- ented dorsally” (as opposed to “neck present, head spherical and inflected medially”); Character 285 — the position of the lesser trochanter in Arboroharamiya, Shenhou, and Xianshou was rescored as on the “medial side of the shaft” (as opposed to on “the ventromedial or ventral side”); and Character 286 — the size of the lesser trochanter in Shenhou and Xianshou was rescored as “large” (as opposed to “small to absent”). The presence or absence of a posttrochanteric fossa, a subtrochanteric tubercle, or a subtrochanteric fossa in Arboroharamiya, Shenhou, and Xianshou is unknown.

In sum, therefore, if the femora of Arboroharamiya, Shenhou, and Xianshou are representative of Haramiyida and correctly scored by Luo et al. (2015), it would appear that the femora of haramiyidans and multituberculata (including that of DMNH EPV.100010) are highly distinctive, particularly in the presence/absence of a femoral neck (absent in haramiyidans, present in multituberculata), orientation of the femoral head (dorsally in haramiyidans, inflected medially in multituberculata), orientation of the greater trochanter (directed dorsolaterally in haramiyidans, directed dorsally in multituberculata), relative size of the greater
trocchanter (at mid-level of femoral head in haramiyidans, above level of femoral head in multituberculates), and position of the lesser trochanter (on medial side of diaphysis in haramiyidans, on ventromedial or ventral side of diaphysis in multituberculates). The proximal femora of haramiyidans and multituberculates are similar in possessing a large lesser trochanter and in lacking a third trochanter.

4.5. Comparison conclusions

Despite its fragmentary nature, DMNH EPV.100010 is indubitably a multituberculate femur. Multituberculate femora are highly distinctive and can easily be distinguished from those of other allotherians, as well as from those of other mammaliaforms in general (Simpson and Elftman, 1928; Granger and Simpson, 1929; Krause and Jenkins, 1983; Kielen-Jaworowska and Gambaryan, 1994; DeBey and Wilson, 2014). In particular, DMNH EPV.100010 exhibits at least three multituberculate apomorphies: a prominent lesser trochanter that is directed ventrally, a posttrochanteric fossa, and a subtrochanteric tubercle.

5. Paleobiogeographic implications and concluding remarks

The identification of multituberculates from Gondwana landmasses on the basis of dental remains has proven controversial (see Section 2 above). However, the recovery of a distinctive and diagnostic element, a femur, from the Late Cretaceous of Madagascar independently and firmly establishes their presence, both on Madagascar specifically and on the southern supercontinent as a whole. Despite this new record, it is becoming clearer that there was a substantial disparity in diversity and abundance in various vertebrate taxa relative to northern, Laurasian landmasses. Parallels exist. For instance, among mammaliaforms, docodonts were widely distributed in the Jurassic of Europe, Asia, and North America, but were rare to absent in Gondwana (Rougier et al., 2015, and references therein). Similarly, among squamates, lizards are diverse and abundant in Laurasia but exceedingly rare, especially relative to snakes, on Gondwana (Krause et al., 2003, and references therein). Among squamates, lizards are diverse and abundant in Laurasia but exceedingly rare, especially relative to snakes, on Gondwana (Krause et al., 2003, and references therein). Similarly, among lissamphibians, salamanders appear to have been diverse and abundant in the Mesozoic of Laurasia but relatively uncommon on Gondwana (Gardner and Rage, 2016, and references therein). This points to a fundamental division of at least some terrestrial tetrapod clades during the initial fragmentation of Pangea into the Laurasian and Gondwanan supercontinents that profoundly influenced their distributions.

With the presence of multituberculates on Madagascar in the Late Cretaceous (Maastrichtian) confirmed, obvious paleobiogeographic questions arise: how, when, and from where did they get to the island, or were they already on Madagascar before it separated from other Gondwanan landmasses? The fossil record, both earlier in time on Madagascar and the rest of Gondwana, is still woefully inadequate to provide clear answers. That said, there is growing evidence, primarily from the examination of ghost lineages of vertebrate taxa that were among the least capable of overwater dispersal (e.g., large dinosaurs, terrestrial crocodyliforms), that several taxa were on Madagascar before it was fully isolated (Ali and Krause, 2011). Because the origin of multituberculates dates back to the Middle Jurassic (Butler and Hooker, 2005), they also could have been represented on what became the island of Madagascar well before it separated from the Indian subcontinent (~85~90 Ma), Antarctica (~120 Ma), and even Africa (~165 Ma) (see Ali and Krause, 2011, and references therein for review of Gondwanan fragmentation).

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