

A Cretaceous mammal from Tanzania

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Krause, D.W., Gottfried, M.D., O'Connor, P.M., and Roberts, E.M. 2003. A Cretaceous mammal from Tanzania. *Acta Palaeontologica Polonica* 48 (3): 321–330.

We report here the discovery of a Cretaceous mammal from the “Red Sandstone Group” of southwestern Tanzania. This specimen is one of only a very few Cretaceous mammals known from Gondwana in general and Africa in particular. The specimen consists of a short, deep left dentary that bore a large, procumbent central incisor, and five single-rooted, hypsodont cheek-teeth. The specimen is very tentatively identified as a sudamericid, and thus may represent the first African record of an enigmatic clade of mammals, the Gondwanatheria, which is otherwise known from the Late Cretaceous and Paleogene of several other Gondwanan landmasses. Unfortunately, the precise age of the specimen could not be determined. If it is pre-Campanian and if its identity as a sudamericid is corroborated through subsequent discoveries, it represents the earliest known gondwanatherian. If the specimen is from the Campanian or Maastrichtian, and again assuming its identification is correct, it has the potential to refute a recently formulated biogeographic hypothesis predicting the absence of certain terrestrial and freshwater vertebrate taxa, including gondwanatherians, in Africa (i.e., those that evolved elsewhere on Gondwana after Africa became an isolated landmass).

Key words: Mammalia, Gondwanatheria, Cretaceous, Gondwana, Africa, Tanzania.

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Introduction

Controversy persists and, indeed, continues to grow as to whether placental mammals arose before or after the Cretaceous/Tertiary boundary, and whether their ancestry and earliest history is Laurasian or Gondwanan (e.g., Hedges et al. 1996; Springer 1997; Springer et al. 1997; Kumar and Hedges 1998; Stanhope et al. 1998; Archibald 1999; Benton 1999a, b; Eastal 1999a, b; Foote et al. 1999a, b; Hedges and Kumar 1999; Rich, Vickers-Rich, and Flannery 1999; Eizirik et al. 2001; Madsen et al. 2001; Murphy et al. 2001; Ji et al. 2002; Waddell et al. 2001; Yang et al. 2003). One camp (e.g., Springer et al. 1997; Stanhope et al., 1998; Eizirik et al. 2001; Murphy et al. 2001; Waddell et al. 2001) has predicted that the most recent common ancestor of crown-group eutherians will turn out to be Gondwanan, and that members of the primitive placental clade Afrotheria (elephants, sirenians, hyraxes, golden moles, aardvarks, and elephant shrews) were present in Africa before the end of the Cretaceous. A mammalian record from the Cretaceous, and especially the Late Cretaceous, of Africa is clearly essential to directly test the competing hypotheses underpinning this controversy.

Unfortunately, while Laurasian Cretaceous mammals are relatively well-known (e.g., Clemens et al. 1979; Kielan-Jaworowska 1992; Cifelli 2001; Luo et al. 2002), the Gondwanan record, particularly that of Africa, suffers from an almost complete lack of fossils. Early Cretaceous Gondwanan mammals are known from Argentina (Bonaparte and Rougier 1987; Rougier et al. 1992; Hopson and Rougier 1993), Australia (Archer et al. 1985; Rich et al. 1989, 1997, 1998, 1999, 2001; Flannery et al. 1995), Cameroon (Brunet et al. 1988, 1990; Jacobs et al. 1988), Morocco (Sigogneau-Russell et al. 1998, and references therein), and perhaps South Africa (C. Forster, personal communication in Rich et al. 1997). Late Cretaceous Gondwanan mammals are known from South America (Marshall and Sempere 1993, and references therein; Pascual et al. 2000; Rougier et al. 2000, 2001), India (Prasad and Sahni 1988; Prasad et al. 1994; Prasad and Godinot 1994; Das Sarma et al. 1995; Anantharaman and Das Sarma 1997; Krause et al. 1997), Madagascar (Krause et al. 1994, 1997; Krause and Grine 1996; Krause 2001, 2002, in press), and perhaps Libya (Nessov et al. 1998). A tooth from the Late Cretaceous of Egypt initially identified as mammalian (Stromer and Weiler 1930) was later shown to be from the pycnodontid fish *Anomoeodus* (Stromer 1936).



Fig. 1. Location of Locality TZ-07 in the Mbeya District of southwestern Tanzania, which yielded the mammal jaw (NMT 02067) described here. Also indicated is the location of productive vertebrate fossil localities in the "Malawi Dinosaur Beds," Mwakasyunguti area, Karonga District, Malawi (Colin and Jacobs 1990; Jacobs et al. 1990, 1992; Gomani 1997).

Other than the Libyan occurrence, based on an isolated caudal vertebra from a Cenomanian horizon (see Rage and Cappetta 2002), there are no previously known Late Cretaceous mammals from the African mainland, an interval of some 35 million years.

Here we report the discovery of a mammalian fossil from the Cretaceous of sub-Saharan Africa. The specimen is a partial lower jaw, recovered from the "Red Sandstone Group" in the Mbeya District of southwestern Tanzania (Fig. 1) by a reconnaissance expedition led by MDG and PMO in July 2002. The only other Mesozoic mammalian fossils recovered from Tanzania include isolated jaws and teeth of haramiyids, triconodonts, and eupantotheres from the Upper Jurassic (Kimmeridgian–Tithonian) Tendaguru Series of southeastern Tanzania (Branca 1916; Dietrich 1927; Heinrich 1991, 1998, 1999, 2001), taxa that are not closely related to the derived taxon that the specimen described here represents.

Abbreviations.—Michigan State University, East Lansing (MSU), National Museums of Tanzania, Dar Es Salam (NMT).

Provenance

The lower jaw (NMT 02067) was collected from locality TZ-07, situated at approximately 8° 56' S, 33° 12' E in the

Mbeya District of southwestern Tanzania (Fig. 1) (precise locality coordinates are on file at the Michigan State University Museum). Locality TZ-07 exposes approximately 140 m of section of the "Red Sandstone Group" (Fig. 2). The section is dominated by thick sequences of red-pink sandstone, with trough and tabular cross-stratification as well as planar stratification, along with minor dark red mudstone lenses. The sediments at TZ-07 are here interpreted as representing deposition by axial, north-west-trending braided fluvial systems, consistent with sediment accumulation in a half-graben rift valley setting. The "Red Sandstone Group" at TZ-07 preserves a relatively abundant and diverse vertebrate fauna (O'Connor et al. in press), contrary to Westcott et al. (1991), who maintained that the deposit was not richly fossiliferous. The fauna includes teleost fishes, turtles, crocodyliforms, titanosaurid? sauropods (including an associated partial skeleton), non-avian theropods, birds (a single limb element), and mammals (the specimen reported here) (O'Connor et al. in press). NMT 02067 was found *in situ* in a sandstone lens approximately one-fifth of the way up from the base of the section at TZ-07 (Fig. 2); dinosaur (and other vertebrate) remains were recovered below, lateral to, and above the specimen, confirming that the mammal jaw is the same age as the "Red Sandstone Group" dinosaurs.

The age of the "Red Sandstone Group", originally named by Spence (1954), is poorly constrained. A stratotype section has not been described and the unit has not been properly defined. Spence regarded it as Cretaceous, based on lithostratigraphic relationships with the Malawi Dinosaur Beds (Mwakasyunguti area, Karonga District), which are Early Cretaceous, perhaps no younger than Aptian (Colin and Jacobs 1990; Jacobs et al. 1990, 1992; Gomani 1997), and which lie about 200 km to the southeast (Fig. 1). Subsequent to Spence's (1954) naming of the unit, Harkin and Harpum (1957) reported the presence of "reptile" bones in the "Red Sandstone Group". Other workers (Biyashev and Pentel'kov 1974; Pentel'kov and Voronovskii 1977) argued for a late Middle Jurassic age based on molluscan and reptilian fossils, while still others (Westcott et al. 1991; Morley et al. 1992; Damblon et al. 1998) assigned a Miocene age to the unit based on palynomorphs and fossil wood.

These seemingly contradictory age assignments are reconcilable, at least in part, based on our preliminary field investigations in 2002, which revealed the presence of two presumably unconformable time-stratigraphic units in the outcrop area explored—one containing dinosaurs and other vertebrate remains that are indisputably Mesozoic, as at TZ-07 where the mammal jaw was collected, and another superficially similar unit, which crops out at a single locality approximately 2 km south of TZ-07 and contains a Tertiary (minimally post-Paleocene) fauna. Although direct correlation of the two units was physically impossible, their relative stratigraphic positions can be safely inferred based

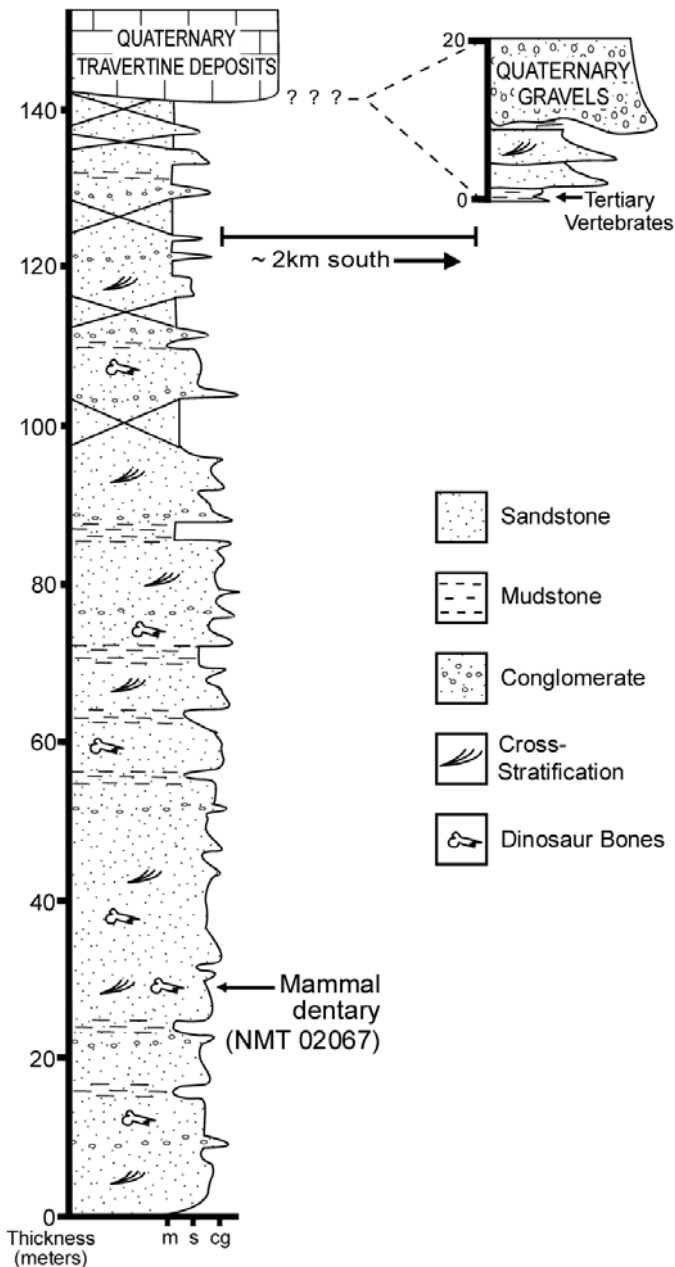


Fig. 2. Measured stratigraphic section of the "Red Sandstone Group" in the Mbeya District of southwestern Tanzania. Section demonstrates level of Locality TZ-07, which yielded the mammal dentary (NMT 02067) described in this report as well as dinosaurs, which were also found above and below this level. Also indicated is the stratigraphic horizon of an area some 2 km to the south that yielded Tertiary vertebrate fossils.

on faunal assemblages and relationship of overlying beds (Fig. 2).

We assign a Cretaceous age to the mammal jaw based on its being found in the lower of these two units, and on the overall fauna at TZ-07, which includes (probable titanosaurid) sauropod and non-avian theropod dinosaurs, as well as megaloolithid dinosaur eggshell (Gottfried et al. in press). In addition, we recovered an osteoglossomorph teleost fish scale at TZ-07 from exactly the same level as the

mammal jaw; osteoglossomorphs have a predominantly (possibly entirely) Cretaceous and later fossil record (see Arratia 1997). In its entirety, this fauna points to a Cretaceous age, which is also consistent with the fact that gondwanatherians have only been found in Cretaceous and younger sediments elsewhere.

Description

NMT 02067 is a heavily abraded partial left dentary (Figs. 3, 4). It lacks sufficient morphological information to allow diagnosis of a new taxon. The nearly complete body of the dentary is short and deep; the posterior aspect of the ramus is broken away along a jagged, roughly vertical fracture through the masseteric fossa, distal to the tooth row (Fig. 3A). Another fracture passes through the body of the dentary obliquely, and is most evident in labial view (stippled in Fig. 3A). This fracture, as revealed by X-ray radiography (Fig. 4), passes inferiorly from the mesial border of the rim of the alveolus for the first cheek-tooth, and posteriorly between the apices of the large roots of the central incisor and the third cheek-tooth. Although all of the tooth crowns are missing or incomplete, devoid of both enamel and cementum, the alveoli and dentine stumps indicate that there was a large, procumbent, laterally compressed central incisor mesially, and five cheek-teeth distally (assuming that all of the cheek-teeth were single-rooted; see below). The incisor is separated from the first cheek-tooth by a short diastema (approximately 2.5 mm) (Fig. 3). A single, large mental foramen is situated on the labial aspect of the dentary inferior to the diastema (Fig. 3A). The masseteric fossa (Fig. 3A) was large and extended anteriorly to a position below the mesial border of the fourth cheek-tooth. Although the symphyseal surface is damaged and abraded, there is no indication that the mandibular symphysis was fused. In lateral view (Fig. 3A, B), the inferior margin of the dentary undulates, being strongly convex mesially and concave distally, with the deepest part of the body of the dentary (8.3 mm) beneath the diastema, and the shallowest part (7.0 mm) beneath the root of the third cheek-tooth.

The incisor is missing its extra-alveolar portion. Its root is implanted at an angle of approximately 55 degrees relative to the horizontal axis of the dentary and, as revealed radiographically (Fig. 4), extends distally to a position below the mesial edge of the root of the third cheek-tooth. The cross-section of the incisor at the rim of the alveolus measures approximately 3.0 mm high and 2.1 mm wide.

The crowns of the two most mesial cheek-teeth are broken away although their roots are still embedded in the jaw. The roots indicate that the first cheek-tooth was perhaps just slightly smaller than the second; both, however, measure approximately 1.5 mm in diameter. The third cheek-tooth is large and curved (convex mesially, concave distally) and was clearly the largest of the cheek-teeth. The crown of this

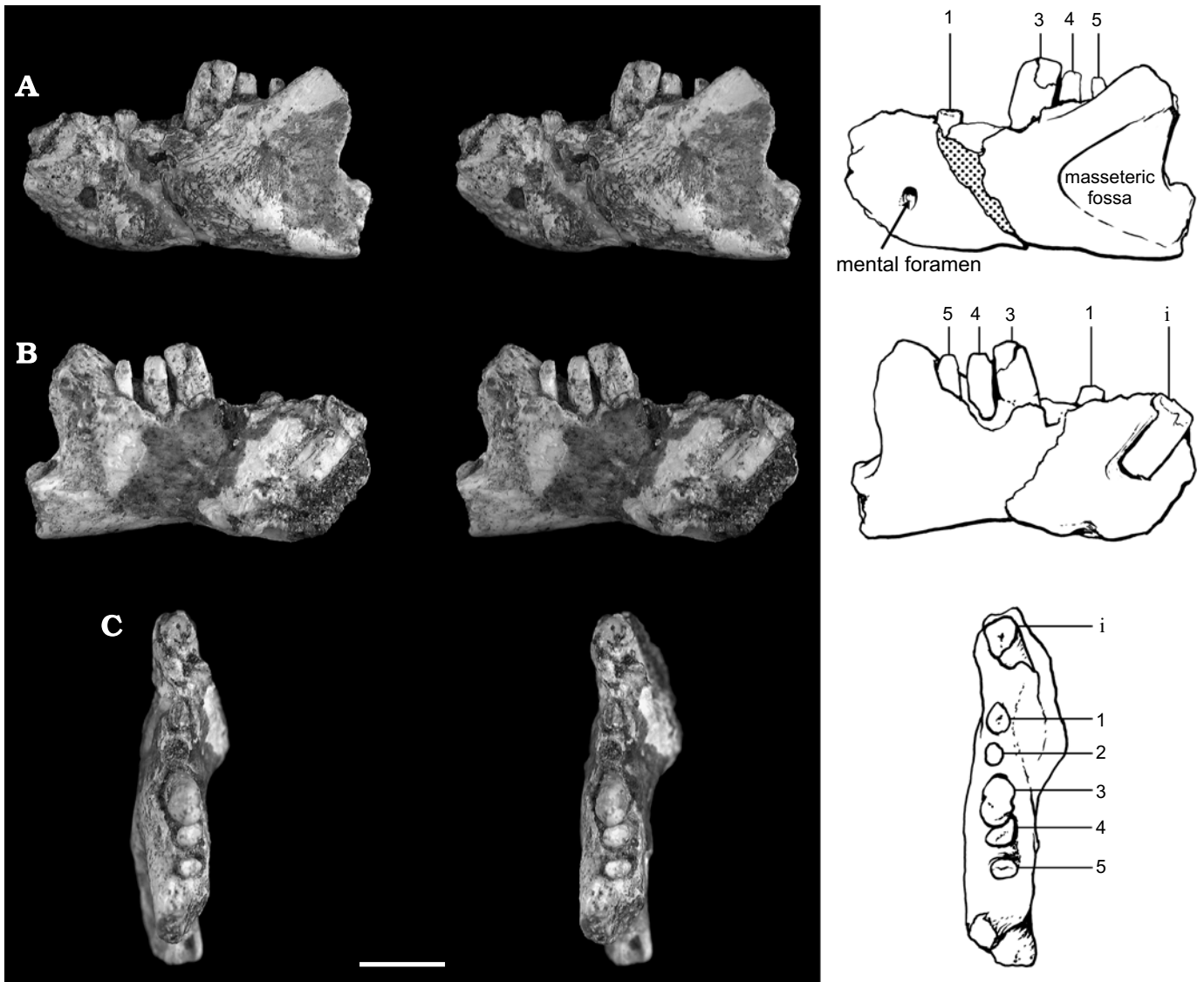


Fig. 3. Stereophotographs and drawings of left dentary of ?sudamericid gondwanatherian mammal (NMT 02067) from the Cretaceous of southwestern Tanzania in labial (A), lingual (B), and occlusal (C) views. Abbreviations: i, incisor; 1-5, cheek-teeth 1-5. Scale bar 5 mm.

tooth is very tall and is represented by a dentine stump, measuring 2.3 mm mesiodistally and 1.9 mm labiolingually, that projects superodistally far out of its alveolus, indicating that it was hypsodont. The tooth was firmly anchored in its alveolus by a large, parallel-sided, posteriorly curving root (Fig. 4). The apex of the root terminates inferiorly approximately three-fourths of the way through the depth of the dentary. The crowns of the fourth and fifth cheek-teeth are represented by much smaller stumps, which also project far superodistally from their alveoli, although they appear slightly less strongly canted distally than the third cheek-tooth. Judging from what is preserved, the fourth cheek-tooth was about the same size as the first and second, while the fifth is notably smaller (approximately 1.0 mm in diameter) and thus the smallest of all of the cheek-teeth. The radiograph (Fig. 4) illustrates that the root

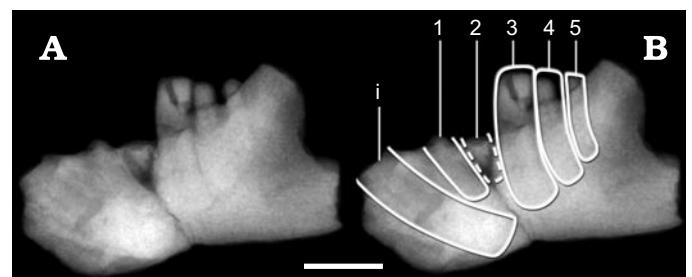


Fig. 4. X-ray radiograph of left dentary of ?sudamericid gondwanatherian mammal (NMT 02067) from the Cretaceous of southwestern Tanzania. A. Unaltered radiograph. B. Radiograph with outlines of tooth roots indicated, and reconstructed coronal outlines of the three distal-most cheek-teeth. Outlines of the roots were developed from several different radiographs, none of which clearly revealed the outline of the root of the second cheek-tooth, which is therefore indicated by a dashed line. Abbreviations: i, incisor; 1-5, cheek-teeth 1-5.

of the fourth cheek-tooth, though smaller in caliber than that of the third cheek-tooth, is also curved and very long, extending through well over one-half of the depth of the dentary. The fifth cheek-tooth, in keeping with its smaller crown, has a still shorter root, which projects less than halfway through the dentary.

Significantly, the radiograph (Fig. 4) of the dentary clearly demonstrates that the roots of the three distal cheek-teeth are firmly anchored in their alveoli, thus indicating that they are truly hypsodont (i.e., not just appearing to be so because they are pulled out of their alveoli). The fact that the teeth are firmly implanted in their alveoli also provides evidence that the three distal cheek-teeth are single-rooted because the crowns sitting atop the roots project far out of their alveoli and are not connected to each other. Furthermore, there is no indication that the crown of the third cheek-tooth was connected to that of the second. Although the outlines of the root for the second cheek-tooth cannot be discerned on the radiograph, the mesial and distal borders of the root of the first cheek-tooth can be interpreted and reveal that the root was obliquely oriented and therefore most likely divergent from that for the second cheek-tooth. This suggests that the first and second cheek-teeth were also single-rooted.

Comparisons and preliminary identification

NMT 02067 superficially resembles the dentaries of several clades of Cenozoic mammals with enlarged, procumbent, laterally compressed central incisors (e.g., rodents, lagomorphs, wombats, the aye-aye, hyraxes, apatemyids, tillo-donts, taeniodonts—see Koenigswald 1988). With the limited morphology available for analysis, it is impossible to rule out the possibility that NMT 02067 is an early member of some taxon with enlarged incisors previously known only from Cenozoic horizons. It is not even possible to rule out Rodentia because the possession of more than four lower cheek-teeth is known in the bathyergid *Heliophobius*, which can have as many as six (though they may not all be in place at the same time and there is some speculation that the increased number is the result of retained deciduous teeth, Woods 1984; Wood 1985). Furthermore, aspects of the anatomy of NMT 02067 are so ambiguous (e.g., occlusal morphology) and so little is known of Gondwanan Cretaceous mammals that we cannot rule out the possibility that NMT 02067 represents a new, previously unknown taxon, possibly even one with little or no enamel on its teeth.

Among Mesozoic mammals, however, only gondwanatherians, and taeniolabidoid and djadochtatheroidean multituberculates, possess a large, procumbent, laterally compressed lower central incisor and dentaries with the follow-

ing suite of features, also exhibited by NMT 02067: body short and deep, unfused mandibular symphysis, distinct diastema, and coronoid process originating far anteriorly (see Pascual et al. 1999). Taeniolabidoid and djadochtatheroidean multituberculates are restricted to the Late Cretaceous and Paleogene of Laurasia (Kielan-Jaworowska and Hurum 2001), whereas gondwanatherians are roughly contemporaneous but known only from a few sites in Gondwana: the Late Cretaceous of Argentina (*Gondwanatherium*, *Ferugliotherium*; Bonaparte 1986a, b, 1988, 1990; Krause et al. 1992; Kielan-Jaworowska and Bonaparte 1996), Madagascar (*Lavanify*; Krause et al. 1997), and India (unnamed form; Das Sarma et al. 1995; Anantharaman and Das Sarma 1997; Krause et al. 1997); the early Paleocene of Argentina (*Sudamerica*; Scillato-Yané 1984, 1985; Bonaparte et al. 1993; Pascual et al. 1999); and the Eocene of Antarctica (unnamed form; Reguero et al. 2002). *Ferugliotherium* is a member of the monotypic Ferugliotheriidae, whereas *Gondwanatherium*, *Sudamerica*, *Lavanify*, and the unnamed forms from India and Antarctica are all assigned to Sudamericidae (Krause and Bonaparte 1993; Krause et al. 1997; Reguero et al. 2002). Gondwanatherians were initially regarded as the earliest known edentates (Scillato-Yané and Pascual 1984, 1985; Mones 1987; Bonaparte 1986a, b, 1990), then as multituberculates (Krause and Bonaparte 1990, 1993; Krause et al. 1992; Bonaparte et al. 1993; Kielan-Jaworowska and Bonaparte 1996), and, most recently, as Mammalia *incertae sedis* (Pascual et al. 1999; Koenigswald et al. 1999).

We tentatively conclude that NMT 02067 is not a multituberculate and is most parsimoniously referred to the Gondwanatheria, and more specifically to the Sudamericidae (i.e., all gondwanatherians save *Ferugliotherium*). This is based, in large part, on the presence of hypsodont cheek-teeth in the specimen, and the assumption that at least the three most distal cheek-teeth were molariform; unfortunately, the occlusal morphology is not preserved. Indeed, the poor preservation of the cheek-teeth precludes observation of synclines and islets (see terminology of Koenigswald et al. 1999) on the crowns of the teeth, if they existed (as they do in sudamericids to varying degrees); it cannot be determined if such synclines and islets are absent because NMT 02067 is in fact not a gondwanatherian, or because NMT 02067 is a primitive gondwanatherian (see below), or because they were once present and are simply not preserved owing to pre- and/or postmortem wear. However, at the very least, it can be concluded, from the shape of the dentine stump representing the third cheek-tooth, that it was not an enlarged, laterally compressed, blade-like tooth of the type found in almost all multituberculates. We assume that it formed the core of a molariform tooth, and that at least the three distal-most teeth of NMT 02067 were molariform. No known multituberculate has more than two molariform teeth in each lower jaw quadrant. Furthermore, no known multituberculate (nor *Ferugliotherium*) pos-

sesses hypsodont cheek-teeth. The presence of hypsodont cheek-teeth is the strongest evidence linking NMT 02067 with sudamericid gondwanatherians.

If NMT 02067 represents a gondwanatherian, the presence of five cheek-teeth indicates that it represents a less derived taxon than *Sudamerica*. Pascual et al. (1999) recently demonstrated the presence of four cheek-teeth, all of them molariform, in the dentary of the sudamericid *Sudamerica*, which is the only definitively identified gondwanatherian represented by a substantial jaw fragment. NMT 02067 also appears less derived than *Sudamerica* (and possibly other sudamericids) in that the incisor is less compressed labiolingually (height:width ratio of 1.43, compared to 2.50 in *Sudamerica ameghinoi*, 2.03 in *Gondwanatherium patagonicum*—Krause et al. 1992; Pascual et al. 1999), the incisor root is much shorter relative to the cheek-tooth row (extending below only the anterior cheek-teeth in the Tanzanian form but below the entire tooth row in *S. ameghinoi*—Pascual et al. 1999), and the diastema is relatively short (presumably a function, at least in part, of the presence of more teeth). NMT 02067 resembles the dentary of *Sudamerica* in that the posterior cheek-tooth crowns (at least the third and fourth) are curved along their height and project superodistally. Koenigswald et al. (1999) suggested that this distally-canted orientation of the posterior cheek-teeth was consistent with a palinally-directed power stroke of the masticatory cycle, which appears to have been present in both multituberculates and gondwanatherians (e.g., Krause 1982; Krause and Bonaparte 1993). Finally, NMT 02067 differs from *Sudamerica* in at least two other character states, the polarity of which cannot be determined at present: a more inferiorly positioned mental foramen and an apparently greater range of variation in the relative sizes of its cheek-teeth.

Biogeographic implications

The following discussion is predicated on the assumption that NMT 02067 is indeed a representative of the Gondwanatheria, an identification that we must stress remains to be verified by more diagnostic material. If confirmed, the presence of a gondwanatherian in the Cretaceous of Africa has important implications for the evolutionary and biogeographic history of Gondwanan mammals. Gondwanatherians are currently regarded as *Mammalia incertae sedis* (Pascual et al. 1999) and, as such, they unfortunately cannot be used to resolve the controversy of whether or not crown-group eutherians (i.e., placentals) arose before or after the Cretaceous/Tertiary boundary, or whether they originated in Laurasia or Gondwana. However, whether from the Early or Late Cretaceous, if our tentative identification is correct, NMT 02067 would provide the first evidence of gondwanatherians on the African mainland, and would be further evidence of cosmopolitanism among Gondwanan mammals of

the Cretaceous (see Krause et al. 1997). If pre-Campanian, NMT 02067 would represent the earliest known gondwanatherian, and a substantial extension of the temporal, as well as geographic, range of the clade (*Gondwanatherium*, from the Campanian of Argentina, was previously regarded as the earliest known gondwanatherian, see Bonaparte 1986b). If from the Campanian or Maastrichtian, NMT 02067 has potentially added utility in addressing recent hypotheses regarding the geographic distribution of Gondwanan mammals and other terrestrial (and freshwater) vertebrates at the end of the Cretaceous.

The discovery of gondwanatherians, which were initially known only from the Late Cretaceous (Campanian) and Paleocene of Argentina, in the Late Cretaceous (Maastrichtian) of both Madagascar and India provided the first evidence for cosmopolitanism among Late Cretaceous Gondwanan mammals (Krause et al. 1997). This discovery also led to the hypothesis that Antarctica may have served as a biotic link between South America and Indo-Madagascar in the Late Cretaceous (gondwanatherians have since been found on the Antarctic Peninsula, though from a much later interval, the Eocene; Reguero et al. 2002). This hypothesized biotic link is also supported by the presence of sister taxa of abelisauroid theropods (Sampson et al. 1998, 2001; Carrano et al. 2002; but see Sereno et al. 2002) and (possibly) peirosaurid and notosuchid crocodyliforms (Buckley and Brochu 1999; Buckley et al. 2000) in the Late Cretaceous of both South America and Indo-Madagascar, and is consistent with Hay et al.'s (1999) recent paleogeographic reconstruction of Gondwana. Hay et al. postulated physical connections between South America and Indo-Madagascar through Antarctica that persisted well into the Late Cretaceous (Krause et al. 1999). A corollary of this hypothesis, discussed by Krause et al. (1997) and Sampson et al. (1998), is that Africa, following its separation from South America in the Early Cretaceous, would have an increasingly endemic fauna, and that representatives of nonmarine taxa that evolved on other Gondwanan landmasses after Africa was already isolated would likely not be found on Africa in the last stages of the Cretaceous.

As Krause et al. (1999: 6) noted, "One of the key stumbling blocks for testing [these] paleobiogeographic hypotheses [...] is the virtual lack of terrestrial and freshwater vertebrates from the post-Cenomanian Late Cretaceous of Africa." Indeed, the record of terrestrial and freshwater vertebrates from the Campanian and Maastrichtian of mainland Africa is restricted to a few sites in North Africa that have yielded scrappy material of only a few taxa (e.g., Gemmelaro 1921; Rauhut and Werner 1997; Churcher 1999). The presence of a purported African Cretaceous gondwanatherian reported here may weaken the "African endemism" corollary outlined above; this is particularly true if the specimen turns out to be from the Campanian or Maastrichtian and if it can be demonstrated that sudamericids, which appear to be highly derived, evolved after the South America-Africa split in the Early Cretaceous. The ultimate biogeo-

graphic significance of NMT 02067 cannot be realized until it is identified with more precision, and until the phylogenetic interrelationships of gondwanatherians are better resolved. Finally, the overall inadequacy of the record of Cretaceous terrestrial and freshwater vertebrates from Africa, coupled with the current controversy concerning the time and place of origin of crown-group eutherians, strongly underscore the strategic importance of continued field research in the “Red Sandstone Group” to collect additional material and to refine the age of the deposit from which NMT 02067, and other vertebrate fossils, were recovered.

Acknowledgments

We thank the Tanzanian Commission on Science and Technology, the Tanzanian Antiquities Unit, the National Museums of Tanzania, and the Tanzanian Ministry of Mines and Mineral Resources, whose cooperation made this research possible. Special thanks go to Director Donatus Kamamba, Chediël Msuya, and Remegius Chami of the Antiquities Unit for facilitating the fieldwork. We are also very grateful for the help we received from government officials and residents of the Mbeya District, Ray Cox and Joe Johns and their staff at the Utengule Country Hotel, Stephan Copes of the Utengule Coffee Estate, Erling Johannsen, and Tim Davenport. The fieldwork was accomplished through the dedicated efforts of participants in the 2002 reconnaissance expedition, including Yasemin Tulu (MSU), who discovered NMT 02067, Erin Rasmusson, and Nancy Stevens. We also thank Virginia Heisey, who skillfully prepared NMT 02067; Marylou Stewart for macrophotography; Allan Kucine for X-ray radiography; Luci Betti-Nash for the drawings in Figs. 1–3; Richard Cifelli, Zofia Kielan-Jaworowska, Matt Lamanna, and Josh Smith for information on purported occurrences of Cretaceous African mammals; and Lou Jacobs and Guillermo Rougier for helpful reviews of the manuscript. The fieldwork aspects of this research were supported by a faculty grant (to MDG) from the Michigan State University Office of the Vice-President for Research and Graduate Studies, and by grants from the Jurassic Foundation (to PMO and MDG) and The Paleobiological Fund (to PMO). The specimen was prepared at the Stony Brook University Vertebrate Fossil Preparation Laboratory, funded by NSF grant EAR-0116517 (to Maureen O’Leary and DWK). Additional support was provided by NSF grant EAR-106477 (to DWK).

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