Journal of Vertebrate Paleontology

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/ujvp20

Introduction to *Adalatherium hui* (Gondwanatheria, Mammalia) from the Late Cretaceous of Madagascar

David W. Krause , Joseph R. Groenke , Simone Hoffmann , Raymond R. Rogers & Lydia J. Rahantarisoa

To cite this article: David W. Krause , Joseph R. Groenke , Simone Hoffmann , Raymond R. Rogers & Lydia J. Rahantarisoa (2020) Introduction to *Adalatherium hui* (Gondwanatheria, Mammalia) from the Late Cretaceous of Madagascar, Journal of Vertebrate Paleontology, 40:sup1, 4-18, DOI: 10.1080/02724634.2020.1805455

To link to this article: https://doi.org/10.1080/02724634.2020.1805455

Society of Vertebrate Paleontology Memoir 21
Journal of Vertebrate Paleontology
Volume 40, Supplement to Number 2:4–18

MEMOIR ARTICLE

INTRODUCTION TO *ADALATHERIUM HUI* (GONDWANATHERIA, MAMMALIA) FROM THE LATE CRETACEOUS OF MADAGASCAR

DAVID W. KRAUSE, *,[1,2] JOSEPH R. GROENKE, [3] SIMONE HOFFMANN, [4] RAYMOND R. ROGERS, [5] and LYDIA J. RAHANTARISOA [6]
[1]Department of Earth Sciences, Denver Museum of Nature & Science, Denver, Colorado 80205, U.S.A., David.Krause@dmns.org;
[2]Department of Anatomical Sciences, Stony Brook University, Stony Brook, New York 11794-8081, U.S.A.;
[3]Department of Biomedical Sciences, Ohio University Heritage College of Osteopathic Medicine, Ohio University, Athens, Ohio 45701, U.S.A., groenke@ohio.edu;
[4]Department of Anatomy, New York Institute of Technology, College of Osteopathic Medicine, Old Westbury, New York 11568, U.S.A., shoffm04@nyit.edu;
[5]Geology Department, Macalester College, 1600 Grand Avenue, St. Paul, Minnesota 55105, U.S.A., rogers@macalester.edu;
[6]Département de Sciences de la Terre et de l'Environnement, Université d'Antananarivo, Antananarivo (101), Madagascar, ralyhanta@yahoo.fr

ABSTRACT—*Adalatherium hui* is a latest Cretaceous (Maastrichtian) gondwanatherian mammal based on only a single specimen, a virtually complete, articulated, and well-preserved skull and postcranial skeleton. The specimen is the most complete and best preserved of any mammaliaform from the Mesozoic of the southern supercontinent Gondwana. It was discovered in the Anembalemba Member of the Maevarano Formation in the Mahajanga Basin of northwestern Madagascar. The holotype specimen includes the only complete lower jaw and the only postcranial remains known for Gondwanatheria, which, other than the cranium of *Vintana sertichi* (also from the latest Cretaceous of Madagascar), are represented only by isolated teeth and fragmentary dentaries. Despite being represented by an immature individual, *A. hui* is third only to *V. sertichi* and *Coloniatherium cilinskii* as the largest Mesozoic mammaliaform (based on body fossils) from Gondwana. Here, we (1) review the paucity of mammaliamorph skull and postcranial skeletal material from the Mesozoic of Gondwana relative to the record from Laurasia; (2) review the systematic paleontology of *A. hui*; (3) provide an overview of the history of discovery of the holotype specimen; (4) detail the preservation of the holotype, its preparation history, and the imaging techniques used to study it; (5) provide an overview of the geological context of *A. hui*, which indicates that the species lived close to the end-Cretaceous extinction event in a highly seasonal, semiarid climate; and (6) estimate the body mass of *A. hui* in the context of other Mesozoic mammaliaforms.

Citation for this article: Krause, D. W., J. R. Groenke, S. Hoffmann, R. R. Rogers, and L. J. Rahantarisoa. 2020. Introduction to *Adalatherium hui* (Gondwanatheria, Mammalia) from the Late Cretaceous of Madagascar; pp. 4–18 in D. W. Krause and S. Hoffmann (eds.), *Adalatherium hui* (Mammalia, Gondwanatheria) from the Late Cretaceous of Madagascar. Society of Vertebrate Paleontology Memoir 21. Journal of Vertebrate Paleontology 40(2, Supplement). DOI: 10.1080/02724634.2020.1805455.

INTRODUCTION

The record of Mesozoic mammaliaforms from the southern supercontinent Gondwana pales in comparison with that from its northern counterpart, Laurasia. A survey of Mesozoic mammaliaform species, and the localities from which they are known, extracted from the last major compendium on Mesozoic mammaliaforms (Kielan-Jaworowska et al., 2004), underscores this strong disparity (Table 1). For the Cretaceous, when Pangaea was undergoing its greatest degree of fragmentation, there are greater than eight times more mammaliaform species and mammaliaform-producing localities known from Laurasia (299 species from 156 localities) than from Gondwana (36 species from 18 localities). This imbalance between northern and southern supercontinents is even greater for the Late Jurassic (68 species from 19 Laurasian localities; four species from one Gondwanan locality), roughly the same for the Middle Jurassic (15 species from 14 Laurasian localities; two species from two Gondwanan localities), but not nearly as great for the Late Triassic–Early Jurassic (25 species from 22 Laurasian localities; 10 species from seven Gondwanan localities).

Although many additional Mesozoic mammaliaform taxa have been described since Kielan-Jaworowska et al.'s (2004) compendium, the majority have come from China; strikingly, the number of new Mesozoic mammaliaform species (37) from China named during the 2005–2014 decade is more than in all prior decades combined (21; see Meng, 2014:fig. 1). During the same decade (2005–2014), only 16 new Mesozoic mammaliaform species from all Gondwanan landmasses combined were named, and only two more have been added since 2014 (data from Krause et al., 2019:supplemental table 4). As such, the prodigious disparity in knowledge of the evolutionary history of Mesozoic mammaliaforms between Laurasia and Gondwana has only increased since the compendium by Kielan-Jaworowska et al. (2004).

The imbalance in knowledge is exacerbated not only by the relatively few species and localities but also by the relative incompleteness of the specimens from Gondwana. Despite the fact that the vast majority of the mammaliaform fossil record is composed of isolated jaws and teeth, there is a considerable number of important, relatively complete specimens (composed of skull

---

*Corresponding author.

TABLE 1. Number of mammaliaform-bearing localities or local faunas (numerator) and named species[1] of mammaliaforms (denominator) based on body fossils (i.e., not traces) from Mesozoic horizons on each of the major landmasses of the world. Compiled from Kielan-Jaworowska et al. (2004); see discussion in text.

	Laurasia			Gondwana					
Epoch	N. AM.[2]	EUR.[3]	ASIA[4]	S. AM.	AFR.	ANT.	MAD.	IND.	AUST.
Late Cretaceous	81/156	12/6	21/55	8/14	1/0	0/0	1/1	2/2	0/0
Early Cretaceous	15/14	7/46	20/22	1/1	2/13	0/0	0/0	0/0	3/5
Late Jurassic	12/35	4/29	3/4	0/0	1/4	0/0	0/0	0/0	0/0
Middle Jurassic	0/0	8/12	7[5]/2	1/1	0/0	0/0	1/1	0/0	0/0
Late Triassic – Early Jurassic	4/3	13/18	5/4	0/0	3/2	0/0	0/0	4/8	0/0

[1] "Named species" here is conservatively taken to mean any species (i.e., the second name in the Linnaean binomial) that is fully named but not qualified with (usually preceded by) a question mark, aff., cf., or quotation marks. We do include species in which the generic name is qualified with a question mark, aff., cf., or quotations marks. In other words, "cf. Genus species", "aff. Genus species", "?Genus species" , or ""Genus" species" are counted but "Genus cf. species", "Genus aff. species", "Genus ?species", or "Genus "species"" are not. Unnamed or indeterminate forms (e.g., "Gen. et sp. nov.", "Gen. et sp. indet.", or "Genus sp.") are not counted.

[2] For these purposes, Greenland is included in North America.

[3] It must be noted that there is increasing evidence that Cretaceous vertebrates of southern Europe had strong Gondwanan affinities (e.g., Krause et al. [2019] and references therein).

[4] Asia, as used here, does not include the Indian subcontinent.

[5] One or more of these localities may be Late Jurassic.

and/or articulated postcranial skeletal material) of a broad taxonomic range of taxa now known from the Mesozoic of Laurasian landmasses. Most of these have been recovered during the past three decades (see Kielan-Jaworowska et al., 2004, and references therein, as well as Luo et al., 2003, 2007a, 2007b, 2011, 2015a, 2015b, 2017; Hu et al., 2005, 2010; Kielan-Jaworowska et al., 2005; Luo and Ji, 2005; Luo and Wible, 2005; Martin, 2005, 2013; Hu, 2006; Ji et al., 2006, 2009; Li and Luo, 2006; J. Meng et al., 2006, 2011; Sereno, 2006; Wible et al., 2007, 2019; Bolortsetseg, 2008; Hurum and Kielan-Jaworowska, 2008; Kusuhashi et al., 2009; Yuan et al., 2009, 2013; Gao et al., 2010; Ladevèze et al., 2010; Zheng et al., 2013; Zhou et al., 2013, 2019; Bi et al., 2014, 2016, 2018; Hou and Meng, 2014; Martin et al., 2015; Q.-J. Meng et al., 2015, 2017; Smith and Codrea, 2015; Xu et al., 2015; Han and Meng, 2016; Rougier et al., 2016; Chen et al., 2017; Han et al., 2017; Csiki-Sava et al., 2018; Huttenlocker et al., 2018; Jäger et al., 2019; Mao and Meng, 2019; Wang et al., 2019; Mao et al., 2020) and have come from the following areas and horizons: (1) Late Triassic of Texas—partial skull of the stem mammaliaform *Adelobasileus*; (2) Late Triassic of Greenland—partial skull and postcranial skeleton of the haramiyid *Haramiyavia*; (3) Early Jurassic of Wales—associated elements composed of almost every element of the skull and postcranium of the morganucodontan *Morganucodon*; (4) Early Jurassic of China—several skulls of the stem mammaliaform *Sinoconodon* and the mammaliaforms *Morganucodon* and *Hadrocodium*; (5) Early Jurassic of Arizona—partial skull and associated postcranial elements of the 'triconodont' *Dinnetherium*; (6) Late Jurassic of Colorado—partial skull and postcranial skeleton of the basal mammaliaform *Fruitafossor* and partial skulls of the multituberculate *Glirodon* and the triconodontid *Priacodon*; (7) Late Jurassic of Portugal—partial skulls of a diversity of paulchoffatiid multituberculates, skull and partial postcranial skeleton of the docodontan *Haldanodon*, and fragmentary skulls and postcranial skeletons of the cladotherians *Dryolestes* and *Henkelotherium*; (8) Middle–Late Jurassic of China—partial skull and postcranium of the enigmatic mammaliaform *Megaconus*; partial to nearly complete skulls and postcrania of the euharamiyidans *Arboroharamiya*, *Maiopatagium*, *Qishou*, *Shenshou*, *Vilevolodon*, and *Xianshou*; nearly complete skull and postcranium of the multituberculate *Rugosodon*; partial skulls and postcrania of the docodontans *Castorocauda*, *Agilodocodon*, *Docofossor*, and *Microdocodon*; skull and postcranium of the enigmatic gliding form *Volaticotherium*; partial skull and postcranium of the shuotheridian *Pseudotribos*; and partial skull and anterior part of postcranial skeleton of the eutherian *Juramaia*; (9) Early Cretaceous of China—skulls and/or postcranial skeletons of the multituberculates *Jeholbaatar*, *Liaobaatar*, and *Sinobaatar*; the eutriconodontans *Chaoyangodens*, *Gobiconodon*, *Jeholodens*, *Juchilestes*, *Liaoconodon*, *Repenomamus*, and *Yanoconodon*; the 'symmetrodontans' *Akidolestes*, *Anebodon*, *Lactodens*, *Maotherium*, and *Zhangheotherium*; the stem therian *Origolestes*; and the eutherians *Acristatherium*, *Ambolestes*, *Eomaia*, and *Sinodelphys*; (10) Early Cretaceous of Montana—jaws and postcranial elements of the eutriconodontan *Gobiconodon*; (11) Early Cretaceous of Utah—cranium of the enigmatic mammaliaform *Cifelliodon*; (12) Early Cretaceous of Spain—nearly complete skull and postcranium of the eutriconodontan *Spinolestes*; (13) Late Cretaceous of Romania—partial skulls of the multituberculates *Barbatodon*, *Kogaionon*, and *Litovoi*; (14) Late Cretaceous of Uzbekistan—nearly complete skull of the eutherian *Daulestes*; (15) Late Cretaceous of Mongolia—skulls (and partial skulls) and/or postcrania of the multituberculates *Bulganbaatar*, *Catopsbaatar*, *Chulsanbaatar*, *Kamptobaatar*, *Kryptobaatar*, *Mangasbaatar*, *Nemegtbaatar*, *Sloanbaatar*, and *Tombaatar*; the metatherians *Asiatherium* and *Deltatheridium*; and the eutherians *Asioryctes*, *Barunlestes*, *Kennalestes*, *Ukhaatherium*, and *Zalambdalestes*; and (16) Late Cretaceous of China—skulls (and partial skulls) of the multituberculates *Guibaatar*, *Kryptobaatar*, and cf. *Tombaatar*; skull and partial postcranium of the multituberculate *Yubaatar*; and skull of the eutherian *Kennalestes*.

Thus, there are approximately 75 mammaliaform genera (uncertainty centers around the taxonomic status of several forms, particularly paulchoffatiid multituberculates) represented by skull and/or postcranial material from the Mesozoic of Laurasia. By extreme contrast, there are only five mammaliaform genera from the entire Mesozoic of Gondwana that are represented by anything more than isolated elements (primarily jaws and teeth). These include the nearly complete skulls and

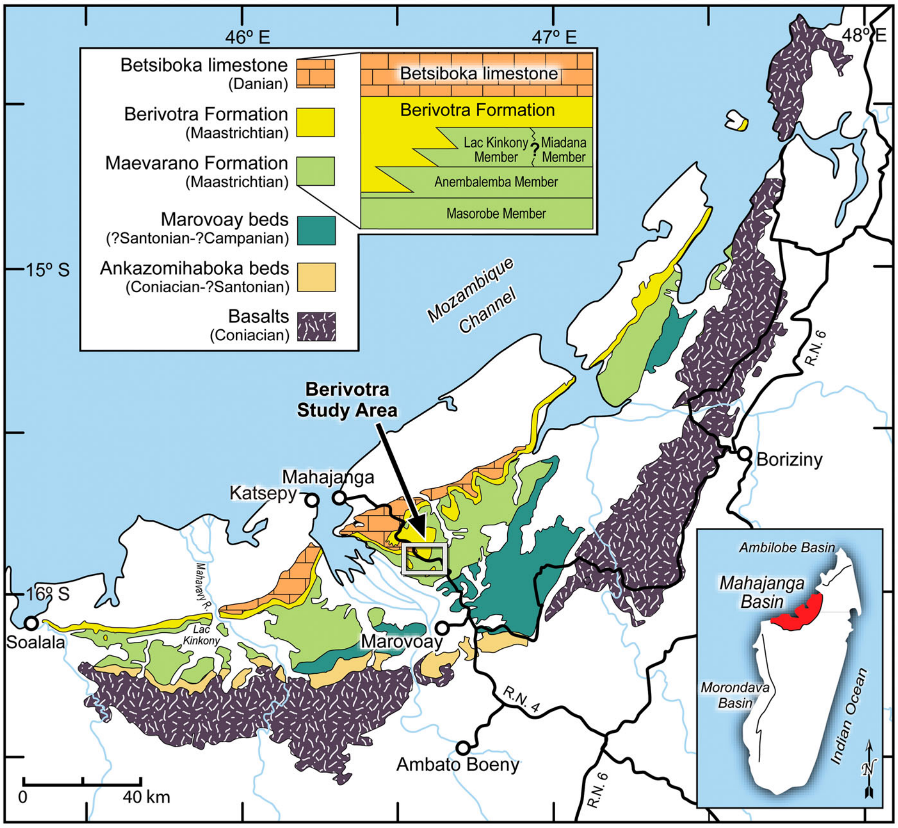

FIGURE 1. Outcrop map of Upper Cretaceous and Paleocene strata in the Mahajanga Basin of northwestern Madagascar (see inset); the Berivotra Study Area is highlighted (rectangle). The holotype specimen of *Adalatherium hui* (UA 9030) was recovered from locality MAD99-15 in the Anembalemba Member of the Maevarano Formation, which is of latest Cretaceous (Maastrichtian) age.

postcrania of the morganucodontans *Megazostrodon* and *Erythrotherium* from the Early Jurassic (likely Hettangian–Sinemurian) of southern Africa (Crompton and Jenkins, 1968; Crompton, 1974; Jenkins and Parrington, 1976; Gow, 1986), skulls and partially articulated postcranial skeletons of the stem therian *Vincelestes* from the Early Cretaceous (Hauterivian–Barremian) of Argentina (e.g., Bonaparte and Rougier, 1987; Rougier et al., 1992; Rougier, 1993), partial crania and lower jaws of the dryolestoid *Cronopio* from the earliest Late Cretaceous (early Cenomanian) of Argentina (Rougier et al., 2011), and the cranium of the gondwanatherian *Vintana* from the latest Late Cretaceous (Maastrichtian) of Madagascar (Krause, 2014; Krause et al., 2014). Among these, *Vincelestes*, *Cronopio*, and *Vintana* are the only mammalian taxa occurring after the beginning of Pangaean fragmentation (*Vincelestes* and *Cronopio* from West Gondwana and *Vintana* from East Gondwana). Furthermore, it is noteworthy that there are no mammaliaform skulls or postcranial skeletons known from the ~30 million years of the post-early Cenomanian Late Cretaceous from all of Gondwana other than the recently described cranium of *Vintana* from the Maastrichtian of Madagascar (Krause, 2014; Krause et al., 2014).

In this volume, we describe a mammalian specimen from the Anembalemba Member (uppermost Cretaceous, Maastrichtian) of the Maevarano Formation, Mahajanga Basin, northwestern Madagascar (Fig. 1). This specimen, Université d'Antananarivo (UA) 9030, is more complete than that of any previously known mammaliaform from the Cretaceous and, indeed, the entire Mesozoic of Gondwana. In addition to UA 9030, the entire sample of mammalian specimens known from the Maevarano Formation consists of nine isolated, mostly fragmentary teeth representing five species (*Lavanify miolaka* [Gondwanatheria, Sudamericidae; Krause et al., 1997]; Sudamericidae, gen. et sp. indet. [Gondwanatheria; Krause, 2013]; ?Multituberculata, gen. et sp. indet. [Krause, 2013]; Marsupialia, gen. et sp. indet. [Krause, 2001], but see Averianov et al. [2003] and Archibald and Averianov [2012]; and Mammalia, gen. et sp. indet. [Krause et al., 1994]), a femur assigned to Multituberculata, gen. et sp. indet. (Krause et al., 2017), and the cranium of *Vintana sertichi* (Gondwanatheria, Sudamericidae; Krause, 2014; Krause et al., 2014). Specimen UA 9030 was preliminarily described by Krause, Hoffmann, et al. (2020) and assigned to a new genus and species of gondwanatherian mammal, *Adalatherium hui*, which was allocated to a new family, Adalatheriidae.

The holotype and only known specimen of *Adalatherium hui*, UA 9030, is composed of a virtually complete, articulated, and well-preserved skull and postcranial skeleton (Fig. 2A) that allows for a full skeletal reconstruction (Fig. 2B, C). The primary objectives of this volume are to describe and illustrate, in detail, the anatomical structure of UA 9030 and to compare it with the known skull and postcranial skeletal material of other Mesozoic mammaliaforms. The rest of this introductory chapter is focused on reviewing the systematic paleontology of *A. hui*, detailing the circumstances of discovery of the holotype specimen, providing methodological information related to the mechanical and digital preparation of the specimen, placing the new taxon in geological context, and estimating the body mass of UA 9030 and comparing it with the body masses of other Mesozoic mammaliaforms.

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
ALLOTHERIA Marsh, 1880
GONDWANATHERIA Mones, 1987

ADALATHERIIDAE Krause, Hoffmann, Wible, and Rougier, 2020 (in Krause, Hoffmann, et al., 2020)

ADALATHERIUM Krause, Hoffmann, Wible, and Rougier, 2020 (in Krause, Hoffmann, et al., 2020)

Type Species—*Adalatherium hui* Krause, Hoffmann, Wible, and Rougier, 2020 (in Krause, Hoffmann, et al., 2020).

Included Species—Type species only.

Etymology—*Adala* (Malagasy), meaning 'crazy'; therium (Latinized form of the Greek *θηριον*), meaning 'beast.' Together, 'crazy beast,' in reference to the many unique morphological attributes of the new taxon.

Diagnosis—As for type and only known species.

ADALATHERIUM HUI Krause, Hoffmann, Wible, and Rougier, 2020 (in Krause, Hoffmann, et al., 2020)

(Fig. 2A)

Holotype Specimen—UA (Université d'Antananarivo) 9030, virtually complete, articulated, and well-preserved skull and postcranial skeleton.

Referred Specimens—None.

Etymology—In esteemed reference to Yaoming Hu, who passed away on April 12, 2008, during the beginning phases of research on this specimen while a postdoctoral associate at Stony Brook University, and in recognition of his many contributions to the knowledge of Mesozoic and Paleogene mammals.

Type Locality—Locality MAD99-15, Berivotra Study Area of northwestern Madagascar, southeast of the port city of Mahajanga (Fig. 1). Locality coordinates on file at the Denver Museum of Nature & Science and the Université d'Antananarivo.

Age and Distribution—Known only from the Upper Cretaceous (Maastrichtian) Anembalemba Member, Maevarano Formation, Mahajanga Basin, northwestern Madagascar (Fig. 1; Rogers et al., 2000, 2007; Krause et al., 2010).

Diagnosis—(Modified from Krause, Hoffmann, et al., 2020: supplementary information.) Differs from all other Mesozoic mammaliaforms (except, in some cases, *Vintana*, as noted) in possessing: (1) quadrangular upper postcanine tooth crowns with four major cusps and three connecting perimetric ridges mesially, lingually, and distally that border, on three sides, a central valley that opens buccally; (2) lower postcanine tooth crowns with four major cusps arranged in diamond pattern and connected by four perimetric crests; (3) prominent mesiobuccal basin on two distalmost lower postcanines; (4) two large, curved, open-rooted upper incisors, each with buccally restricted enamel (there are indications from the alveoli that this feature is shared with *Vintana*); (5) large internasal vacuity; (6) five large infraorbital foramina (compared with three or fewer in other Mesozoic mammaliaforms, except *Vincelestes*, which also has five but they are not uniformly large); (7) facial process of lacrimal extremely large, contacting septomaxilla and excluding frontal and nasal from contact with maxilla (shared with *Vintana*); (8) large foramen in lacrimal (not related to nasolacrimal duct but possibly for large ethmoidal neurovascular bundle); (9) extreme plethora of nasal foramina, both large and small (some Mesozoic multituberculates [e.g., *Nemegtbaatar*] approach this condition); (10) relatively large intranarial process of septomaxilla (shared with *Vintana*); (11) presence of septomaxillary canal; (12) large paranasal sinus arising from anterior vestibule of nasal cavity, anterior to crista semicircularis; (13) very large, midline (seemingly unpaired) incisive foramen; (14) extraordinarily deep zygomatic arch; (15) secondary bony canal in inner ear that parallels cochlear ganglion canal and likely enclosed network of vasculature (shared with *Vintana*); (16) straight and distinctly separate canal, presumably for lagenar nerve, between cochlear canal apex and internal acoustic meatus; (17) thin, single-layered primary osseous lamina in inner ear that lacked habenulae perforatae, with cochlear nerve branches presumably passing along surface of osseous lamina (possibly shared with *Vintana*); (18) masseteric fossa positioned relatively high dorsally on ascending ramus of dentary; (19) at least 28 trunk vertebrae (with potentially as many as 31), 12 of which are from lumbar region; (20) tail short with almost all 24 caudal vertebrae (all except three distalmost wider than long); (21) tibia strongly bowed anteroposteriorly and compressed mediolaterally; and (22) trochleated facet on distal end of astragalus for articulation with navicular.

Further differs from all gondwanatherians except *Vintana* in being larger and in having molariform teeth that are approximately as wide as they are long. Further differs from the ferugliotheriids *Ferugliotherium* and *Trapalcotherium* in having relatively high-crowned postcanine teeth. Differs from sudamericids in lacking cementum-filled infundibula on postcanine teeth. Further differs from *Lavanify*, *Bharratherium*, and *Vintana* in not possessing modified radial enamel (prisms separated by prominent interrow sheets of interprismatic matrix). Further differs from *Galulatherium* in having stepped differential in height between diastema and postcanine alveolar portion, in more dorsal position of mental foramen on dentary, and in possessing enamel on teeth. Further differs from *Vintana* in (1) exhibiting lesser angle between floor of nasal cavity and nasopharynx; (2) having relatively small orbits (relative to cranial size); (3) having less prominent internarial process on premaxilla; (4) possessing premaxilla that is relatively short and does not contact lacrimal, jugal, palatines, and vomer; (5) possessing single (rather than paired) incisive foramen that is relatively large and bounded by both premaxillae and maxillae (rather than lying completely within premaxillae); (6) possessing an upper canine; (7) possessing many more nasal foramina (*Vintana* has only a single, very large foramen in each nasal); (8) lacking massive, ventrally directed flange on zygomatic process of jugal; (9) maxillae meet in midline (palatines not intervening); (10) lacrimal foramen in relatively lateral position on lacrimal (not inside orbit); (11) lacking contact between vomer and palatines; and (12) cochlear canal more strongly curved.

CIRCUMSTANCES OF DISCOVERY

UA 9030 was collected as part of the long-term and still ongoing Mahajanga Basin Project. Although initiated by Stony Brook University in 1993, the Mahajanga Basin Project has developed into a large-scale collaborative project involving several U.S. institutions (Denver Museum of Nature & Science, Macalester College, Ohio University, and Stony Brook University) and the Université d'Antananarivo. The project has undertaken 13 expeditions in over 25 years and, recently, has expanded beyond the Mahajanga Basin into the Ambilobe Basin to the north (Farke and Sertich, 2013) and the Morondava Basin to the south (Burch and Sertich, 2011; Marshall et al., 2015). These expeditions have approximately septupled the previously known species diversity of Late Cretaceous vertebrates from Madagascar and have resulted in the discovery of specimens of lungfish, ray-finned fishes, frogs, turtles, snakes, non-ophidian squamates, crocodyliforms, non-avian dinosaurs, birds, and mammals (see faunal list in Krause, Hoffmann, et al., 2020:table S2).

The circumstances of discovery of UA 9030, the holotype and only known specimen of *Adalatherium hui*, were unusual and, in fact, serendipitous. The specimen was collected on July 15, 1999, from locality MAD99-15 in the Berivotra Study Area, in a large plaster jacket originally thought to contain only the partial, poorly preserved skeleton of a medium-sized crocodyliform, as field-identified on the basis of several osteoderms (Fig. 3). The crocodyliform was discovered by Joseph A. Rabarison, then a graduate student at the Université d'Antananarivo, and collected by him and Dr. Michael D. Gottfried of Michigan State University. Preparation of the contents of the jacket,

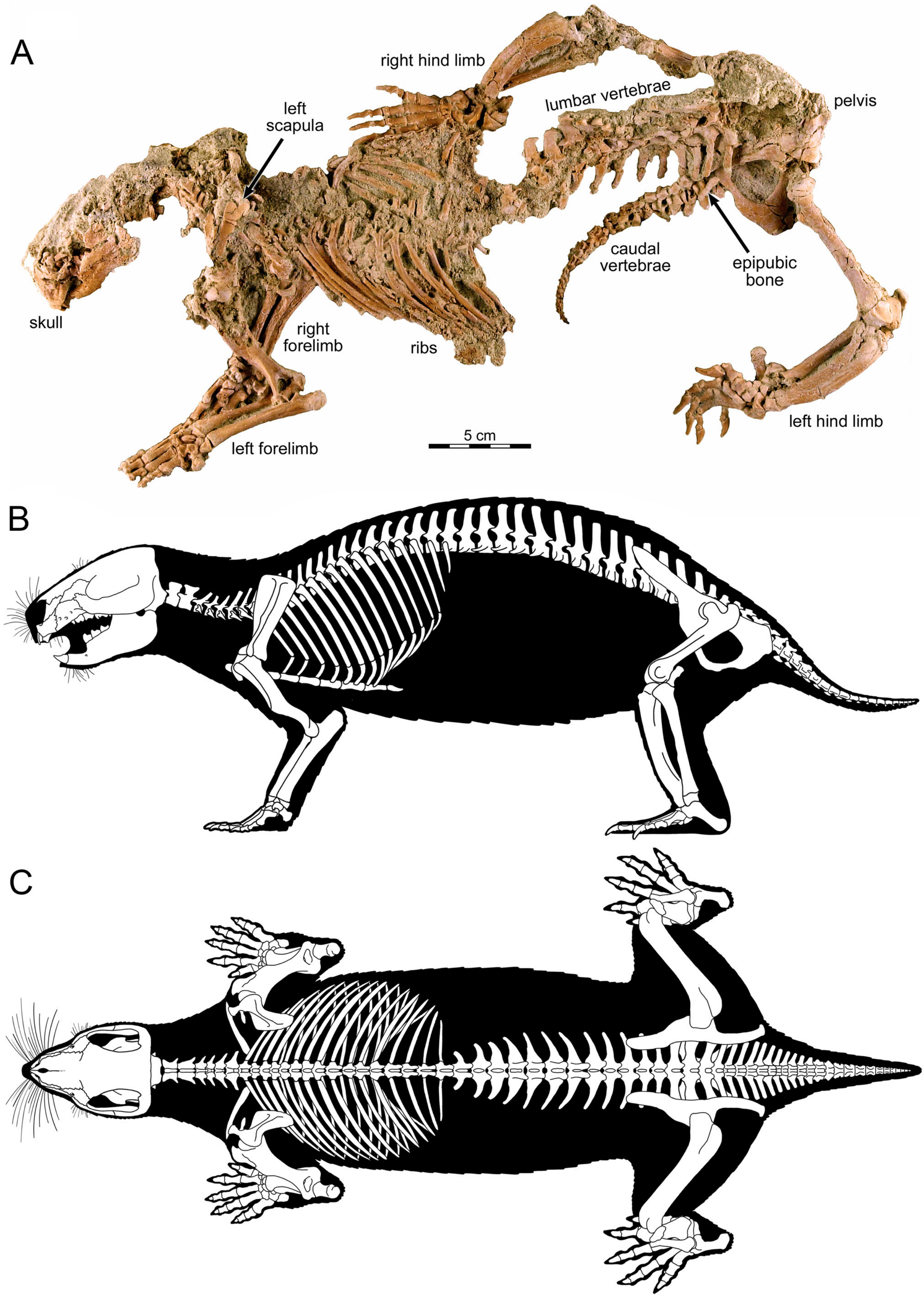

FIGURE 2. *Adalatherium hui*. **A**, photograph of skull and postcranial skeleton of holotype specimen (UA 9030). **B**, **C**, skeletal reconstructions in left lateral and dorsal views, respectively.

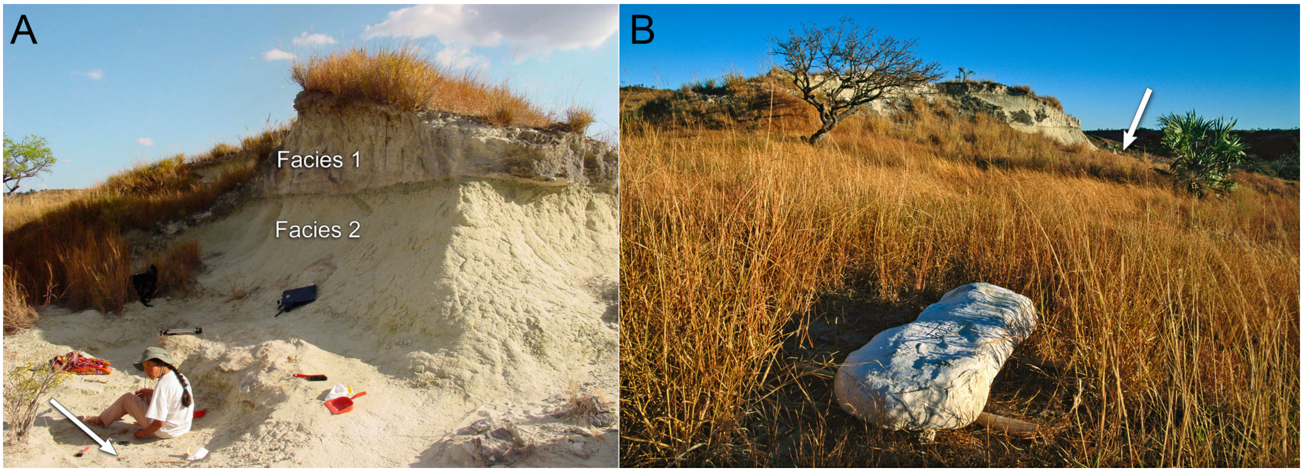

FIGURE 3. Locality MAD99-15, type locality of *Adalatherium hui*, in the Anembalemba Member of the Maevarano Formation, Berivotra Study Area, Mahajanga Basin, northwestern Madagascar. **A**, close-up view looking south-southwest, with site where holotype specimen, UA 9030, was discovered indicated by white arrow. Also indicated are the two different facies, Facies 1 and Facies 2, constituting the Anembalemba Member. **B**, more distant view of locality (indicated by white arrow), looking north, with plaster jacket (in foreground) containing crocodyliform specimens (see text) and UA 9030.

---

beginning in December 2002, by Virginia Heisey in the Stony Brook University Vertebrate Fossil Preparation Laboratory, unexpectedly revealed the presence of not only a crocodyliform but the virtually complete skull and postcranial skeleton of the mammalian specimen described herein. Further preparation also revealed the presence of a skull and postcranial skeleton of a hatchling crocodyliform (Whatley and Buckley, 2004), subsequently identified by Joseph J. W. Sertich (pers. comm., September 2018) as referable to the notosuchian *Miadanasuchus oblita*, lying some 5 cm beneath the mammalian specimen.

SPECIMEN PREPARATION AND SCANNING METHODS

Mechanical Preparation

UA 9030 was manually prepared by V. Heisey in the Vertebrate Fossil Preparation Laboratory at Stony Brook University (SBU), beginning in December 2002. When it was first recognized that the plaster jacket also contained the specimen of a mammal (through exposure of the left humero-ulnar joint), a portable X-ray unit from SBU Division of Laboratory Animal Resources was employed to discover how much of the skeleton was present and to guide further preparation.

The bone surfaces of the top side (as preserved in the sediment) were prepared under magnification using steel insect pins and carbide needles over the course of six months. Bulk matrix was also removed from the periphery. The specimen was then radiographically imaged in the SBU Medical Center Radiology Unit. Digital photographs, including stereopairs, were also taken of the exposed side of the skeleton. A supporting bed, composed of commercially available urethane insulating spray foam, with an aluminum foil separator, was then constructed to cradle the exposed surface. The specimen was turned over onto the bed and most of the remaining matrix prepared away, after which a second bed of the same materials was created so that both sides of the skeleton potentially could be viewed for study. Following upon another session of photography, the skull was removed and, prior to detailed preparation and removal of the dentaries from the cranium, micro-computed tomography (μCT)-scanned (see below).

In the first half of 2006, the left forelimb (except the humerus), the left hind limb, a small block posterior to the shoulder containing four anterior thoracic vertebrae, another block containing 12 thoracic vertebrae, the pelvis, and the series of caudal vertebrae were removed from the postcranial skeleton. Postcranial materials were molded and cast by J.R.G.; this was done to preserve and record spatial associations (especially of the carpals and tarsals) at the time of burial. After molding, the left antebrachium, carpus, and manus and the entire left hind limb were disarticulated to the extent deemed possible by V. Heisey, with all isolated elements again molded and cast. Prior to molding, a number of more delicate and highly trabeculated elements of the specimen were treated with cyclododecane, which was liquefied and injected into exposed trabecular areas to provide structural support; this material subsequently sublimated. Specimens were mounted in plasticine clay and block-molded with Silicones XT-475 RTV silicone with GI-202A catalyst; this product was chosen because it was marketed to be a low-durometer, low-oil, long-lasting product. Vinac B-15 solubilized in acetone was applied as a mold separator. To prevent potential loss of associations among the disarticulated elements, particularly the carpals, tarsals, and sesamoids, form-fit silicone mold storage mounting bases were created by replicating half of each mold that had been made of the separated elements. Because of the significance of the specimen and the condition of preservation after preparation, it was determined that the benefits of molding additional portions of the skull and postcranium were outweighed by the high potential for irreparable damage.

In the spring of 2013, reassessment of materials used to house UA 9030 occurred. The original foil-and-urethane beds used to support the articulated portion of the postcranium had warped and lost conformity to the specimen over time, putting the specimen at risk. After documenting positional information via medical CT scan (see below), the specimen was transferred by J.R.G. to a bed of generally established archival materials (matte fiberglass impregnated with Epo-Tek 301 epoxy support, with partially embedded polyester batting wrapped in an archival polytetrafluoroethylene separator). During the same time frame, the mechanically disarticulated postcranial remains were removed from the form-fit silicone housings and placed in acrylic boxes with polyethylene supports.

In March 2016, the decision was made to deliberately separate the articulated postcranium into anterior and posterior portions in order to effectively μCT scan this portion of the skeleton (see below). This also led to a more stable curation outcome for the extremely fragile specimen. Two sets of 'clamshell' beds were created for this purpose, using Specialist bandages for support with polyester batting and polytetrafluoroethylene as cushion and separator, respectively.

Computed Tomography

For both research and archival purposes, UA 9030 underwent X-ray computed tomography a number of times at several facilities between 2003 and 2019. Discovery of UA 9030 roughly coincided with the beginning of widespread use of CT imaging in paleontology (see Ketcham and Carlson, 2001; Carlson et al., 2003; Sutton, 2008), and CT scan data have been integral to the comprehensive study of various fossils, both large and small, from the Mahajanga Basin (e.g., Sampson and Witmer, 2007; Kley et al., 2010; Evans et al., 2014; Krause, 2014; Krause et al., 2014). Some data sets are used in multiple chapters of this volume, and, so as to avoid redundancy of description, these are summarized below in this chapter. Scan description varies because different facilities have preferences for how scan data are reported. The data sets are presented chronologically; not all were used for descriptive work.

In August 2003, a block of matrix containing the disarticulated cranium and jaws was scanned at the High-Resolution X-ray Computed Tomography Facility in the Department of Geological Sciences at the University of Texas at Austin, Austin, Texas, U.S.A. The Bio-Imaging Research scanning system used an image intensifier detector and a 225 kV FeinFocus microfocal X-ray source. The specimen was scanned at 120 kV, 0.2 μA. The resulting data set preserves the association of the dentaries and a hyoid element relative to the cranium. It was used in initial descriptive work performed by D.W.K. and Y. Hu. The resultant 1024 × 1024 × 1404 voxel data set is composed of 0.063 mm × 0.063 mm × 0.072 mm voxels.

In part owing to lag time following the untimely passing of Y. Hu and in part because of work associated with the publication of monographic works on *Majungasaurus* (Sampson and Krause, 2007), *Simosuchus* (Krause and Kley, 2010), and *Vintana* (Krause, 2014), and other projects, research on UA 9030 was delayed but resumed in 2013 and the specimen was scanned several more times to target specific anatomical regions. In March 2013, the isolated left forelimb (except the humerus) and hind limb, the partial series of 12 thoracic vertebrae, as well as the pelvis and caudal vertebrae, were μCT-scanned on the GE eXplore Locus in vivo μCT scanner at the Ohio University μCT Facility, Athens, Ohio, U.S.A. The ulna, radius, femur, tibia, fibula, parafibula, calcaneus, and cuboid were scanned at 80 kV, 498 μA, and a size of 0.089564 mm × 0.089564 mm × 0.089564 mm; the thoracic and caudal vertebrae, pelvis, metacarpals, metatarsals, remaining tarsals, all carpals, and pedal and manual proximal and intermediate phalanges were also scanned at 80 kV and 498 μA, but with a resultant voxel size of 0.044782 mm × 0.044782 mm × 0.044782 mm. One additional scan was performed for the distal pedal and manual phalanges at 70 kV, 114 μA, and a voxel size of 0.019927 mm × 0.019927 mm × 0.019927 mm. MicroView and VFFtoRAW were used to create 16-bit TIFF slices of the μCT data sets.

In March 2013, the remaining blocks of matrix from the original preparation were scanned with a GE Lightspeed VCT 64-source medical CT scanner in Stony Brook University Department of Radiology, Stony Brook, New York, U.S.A. Two data sets (data set 1: kV = 140, μA = 250, 512 × 512 × 669 voxels, voxel size = 0.3789 mm × 0.3789 mm × 0.625 mm; data set 2: kV = 140, μA = 250, 512 × 512 × 568 voxels, voxel size = 0.3789 mm × 0.3789 mm × 0.625 mm) were generated to confirm that no additional materials possibly related to UA 9030 remained to be prepared. None were found.

Three different attempts were made to generate data for study of the skull when later review of the 2003 data set found it unsuitable for description in light of subsequent advances in scan technology and output resolution. The first of these occurred in November 2013 with the GE Phoenix v|tome|x s scanner at the Microscopy and Imaging Facility at the American Museum of Natural History, New York, New York, U.S.A. Two resultant data sets of the dentaries (kV = 150; μA = 260; 990 × 990 × 1955 voxels; voxel size = 0.0447 mm × 0.0447 mm × 0.0447 mm) and the cranium (kV = 150; μA = 260; 990 × 990 × 2403 voxels; voxel size = 0.04629 mm × 0.04629 mm × 0.04629 mm) were produced but not utilized for the study due to difficulties in determining clear suture and fragment boundaries in some areas.

Another series of scans was performed at Avonix Imaging in Plymouth, Minnesota, U.S.A., in July 2014. Scanning was performed on a Nikon Metrology MCT225 industrial μCT scanner (225 kV microfocus reflection target X-ray tube; Perkin Elmer XRD 1621 AN3 ES detector panel). Raw scan data were converted to 16-bit TIFF stacks using VG Studio Max (Volume Graphics) for study. The cranium was scanned in two parts. The first reconstructed scan volume encompassed the anterior part of the cranium (kV = 160; μA = 58; 1491 × 1378 × 1890 voxels; voxel size = 0.0362 mm × 0.0362 mm × 0.0362 mm); the second included the posterior part of the cranium (kV = 160; μA = 58; 1652 × 1505 × 1605 voxels; voxel size = 0.0362 mm × 0.0362 mm × 0.0362 mm). The scans were later stitched and cropped in Fiji (U.S. National Institutes of Health, Bethesda, Maryland, U.S.A.) into a single working volume (1286 × 1090 × 2840 voxels; voxel size = 0.0362 mm × 0.0362 mm × 0.0362 mm). Both dentaries and one upper postcanine tooth (left PC5) constituted a third scan (kV = 160; μA = 58; 915 × 818 × 1808 voxels; voxel size = 0.0453 mm × 0.0453 mm × 0.0453 mm). These data sets were originally intended to form the basis for all cranial segmentations and descriptions. It was later determined that certain aspects of the cranial morphology (sutures, petrosal) were insufficiently resolved to use the Avonix data as a basis for description of the osseous portions of the cranium but were sufficiently resolved for use in the lower jaw and dental reconstructions.

The data sets ultimately used to study craniofacial morphology of UA 9030 were generated in April 2015 at the High-Resolution X-ray Computed Tomography Facility in the Department of Geological Sciences at the University of Texas at Austin. The scanning was performed on a North Star Imaging scanner with a 225 kV FeinFocus microfocal X-ray source and Perkin Elmer detector. The first scan (kV = 190; μA = 250; 1655 × 1821 × 4429 voxels; voxel size = 0.0224 mm × 0.0224 mm × 0.0224 mm) was of the entire cranium, whereas a second close-up scan (kV = 160; μA = 150; 1621 × 1340 × 1308 voxels; voxel size = 0.00613 mm × 0.00613 mm × 0.00613 mm) targeted the preserved ear region.

In March 2016, prior to the transfer of the postcranium onto the present archival housings, the articulated specimen (excluding the left antebrachium, carpus, and manus, left hind limb, thoracic vertebrae 5–16, pelvis, and caudal vertebrae) was again scanned with the GE Lightspeed VCT 64-source medical CT scanner in Stony Brook University Department of Radiology (kV = 140; μA = 360; 512 × 512 × 1970 voxels; voxel size = 0.3457 mm × 0.3457 mm × 0.2 mm). The purpose of this scan was to digitally preserve, to the extent possible given the coarseness of the scan, the spatial relationship between the areas that were to be separated (see above). The specimen was subsequently split to facilitate μCT scanning in October 2016, using the GE Phoenix v|tome|x s scanner at the Microscopy and Imaging Facility at the American Museum of Natural History, with the anterior part (kV = 200; μA = 230; voxel size = 0.10828451 mm × 0.10828451 mm × 0.10828451 mm) and posterior part (kV = 200; μA = 230; voxel size = 0.0890563 mm × 0.0890563 mm × 0.0890563 mm) scanned separately. In addition, a focused scan of the pectoral region (kV = 200; μA = 230; voxel size = 0.06523045 mm × 0.06523045 mm × 0.06523045 mm) was conducted.

In May 2018, a small block containing disarticulated anterior thoracic vertebrae was scanned on the Nikon XTek XT H 225 μCT scanner at Yale University, New Haven, Connecticut, U.S.A. (voxel size = 0.02630699 mm × 0.02630699 mm × 0.02630699 mm). In 2019, the pelvis was rescanned on a Bruker SkyScan 1173 at the New York Institute of Technology Visualization Center, Old Westbury, New York (kV = 130; μA = 61; voxel size = 0.071 mm × 0.071 mm × 0.071 mm).

Digital Preparation

Data processing, digital segmentation of voxels, polygon generation, and imaging followed general Mahajanga Basin Project protocols (e.g., Evans et al., 2014; Krause, 2014; Krause et al., 2014). Avizo 7 (Visualization Sciences Group [VSG]), 8 (FEI), and 9 (FEI/Thermo Fisher Scientific), Amira 6 (FEI/Thermo Fisher Scientific), and Dragonfly 3.0 were used to generate surfaces. Additional details relevant to each study can be found in the subsequent chapters.

GEOLOGICAL CONTEXT

Stratigraphy and Sedimentology

The skeleton of *Adalatherium hui* was recovered from locality MAD99-15 in the Anembalemba Member of the Maevarano Formation (Rogers et al., 2000). Within the Berivotra Study Area, the Anembalemba Member ranges in thickness from 10 to 15 m and consists of two distinct sandstone facies, referred to as Facies 1 and Facies 2 (Rogers et al., 2000; Rogers, 2005). Both facies are clearly present at locality MAD99-15 (Fig. 3A). Facies 1 consists of fine- to coarse-grained, moderately sorted, light greenish gray sandstones that exhibit high-angle trough and tabular cross-bedding; this facies is interpreted to represent stream flow in an aggrading channel setting. Facies 2, by contrast, is characterized by very poorly sorted, fine- to coarse-grained sandstones that are light olive gray in color, typically massive in structure, and with a much higher clay fraction than Facies 1. Diverse and independent lines of evidence indicate that Facies 2 was deposited as a fine-grained debris flow initiated by surges of rainfall (Rogers, 2005). The vast majority of the well-preserved, articulated or associated vertebrate remains from the Anembalemba Member, and of the Maevarano Formation in general, has been recovered from the debris-flow deposits of Facies 2.

Geochronology

Available data indicate that the Maevarano Formation is of Maastrichtian age. This evidence is derived from various sources. Most significantly, the Anembalemba and Miadana members of the Maevarano Formation interfinger with lower portions of the marine Berivotra Formation, which is known to be Maastrichtian in age on the basis of invertebrate and elasmobranch fish fossils (Besairie, 1972; Gottfried et al., 2001; Abramovich et al., 2002; Rahantarisoa, 2007). Moreover, magnetostratigraphic data identify a reversal near the top of the Berivotra Formation (only 30 m above the top of the Anembalemba Member in the Berivotra Study Area), which is interpreted as the shift that occurred from Chron 30N to Chron 29R at approximately 66.3 Ma (Casey et al., 2003; Dennis-Duke, 2005). Finally, Cretaceous flood basalts overlying the Ankazomihaboka sandstones but stratigraphically well below the Maevarano Formation have been dated at between 92 (Turonian) and 84 (Santonian) Ma. The basalts appear to have been emplaced during a period of extensive mafic magmatism on Madagascar associated with rifting between the Indian subcontinent and the island that opened the Mascarene Basin (e.g., Storey et al., 1995, 1997; Melluso et al., 1997, 2001, 2009; Torsvik et al., 1998, 2000; Yatheesh et al., 2006, 2013; Torsvik and Cocks, 2017). Concerted and intensive efforts to further constrain the age of the Maevarano Formation by dating materials within the unit using radioisotopic approaches have so far been unsuccessful but are ongoing.

Taphonomy

The UA 9030 specimen was found at or very near the erosional surface at locality MAD99-15. The anterior portion of the skeleton was buried resting on its right side while the posterior portion was buried from above; as such, the skeleton, as preserved, is twisted some 90° along its longitudinal axis (Fig. 2A; Krause, Hoffmann, et al., 2020:ED fig. 1). Although obviously compressed during burial, the specimen is very well preserved, with the exception of a few areas of both the skull and postcranial skeleton that were damaged, presumably by the action of swelling clays (smectites) that were hydrated by meteoric waters linked to modern-day plant root infiltration (Odom, 1984; Francischini et al., 2020). The damage caused by this process (the expansion and contraction of entombing clay) is so severe in several small areas that little remains but finely broken fragments. The contrast in preservational quality is particularly evident in the skull, the anterior part of which is very well preserved but the posterior part of the cranium (orbitotemporal, posterior palate, basicranial, and occipital regions), the distal cheek teeth, and the medial aspects of the lower jaws are of relatively poor preservation quality, represented in some areas only by finely comminuted bone.

Similarly, in the postcranial skeleton, preservation in most areas is so exquisite that tiny elements such as the distal-most caudal vertebrae, the smallest carpals and tarsals, phalangeal sesamoids, and even non-osseous tissues (e.g., costal cartilages) are preserved, largely in articular relationship. However, taphonomic processes took their toll on preservation of the cervical and anterior thoracic axial skeleton and parts of the pectoral region, although some structure is preserved in these areas. The sacrum and left os coxa are fragmented to the point of being almost unrecognizable. The forelimbs (except for the right humerus) are pristine, more or less side by side, in articulation. Three distal phalanges of the left manus were not discovered in articulation due to modern erosion but were recovered from the surface during excavation. The intermediate phalanx of digit IV and one distal phalanx (probably also of digit IV) have not been recovered. Overall, however, the vast majority of the postcranial axial skeleton is preserved in articulation; this includes the vertebrae (except the four anterior-most thoracics), ribs, sternum, and even costal cartilages. The tail, which was quite short, was curled under the pelvis and between the legs; as a result, the distal terminus is directed anteriorly. Although the left hind limb is in articulation with the os coxa, twisting of the postcranial skeleton along its longitudinal axis resulted in the positioning of the right hind leg above the pelvis and thoracic and lumbar vertebrae whereas the left hind leg lies below the pelvis and the lumbar and caudal vertebrae. All of the elements of both of these hind legs are preserved, most of them in excellent condition. The left part of the pelvis suffered some damage (it was at the edge of the plaster jacket) but was largely recovered and repaired during preparation. The right part of the pelvis is missing. One of the epipubic bones has not been identified, but the other lies anterior to the left pubis and across the transverse processes of the proximal caudal vertebrae (Fig. 2A).

It is clear from the completeness and generally exquisite preservation of UA 9030 that it had not been exposed to weathering for a significant period of time, or perhaps even at all, prior to burial. The individual represented by UA 9030 was likely buried soon after death or perhaps even while still alive (the same holds true for the associated hatchling specimen of the crocodyliform *Miadanasuchus* buried only a few centimeters beneath UA 9030). This inference is based not only on the completeness and excellent preservation of the skeleton, including the presence of costal cartilages and tiny manual and pedal sesamoids, but also on the observation that the interiors of the bones were not infilled with sediment. This may be the result of the presence of soft tissues covering the bones when the individual was buried in an exceptionally thick deposit (>2 m) of Facies 2. The tightly articulated nature of the specimen is consistent with this interpretation.

Paleoecology and Paleoclimatology

Interpretations of the paleoecology and paleoclimatology of the Maevarano Formation are based on previous work and only briefly summarized here. In essence, *Adalatherium* lived on a terrestrial alluvial floodplain in a highly seasonal (pronounced dry and wet seasons), semiarid climate. The presence and abundance of multitaxic vertebrate fossil bone beds in the Anembalemba Member, the same rock unit from which UA 9030 was extracted, are reflective of localized mortality in desiccating channel belts, with burial of articulated and/or associated skeletons under massive, recurrent debris flows (Rogers et al., 2000, 2007, 2013; Rogers, 2005; Rogers and Krause, 2007; Krause et al., 2010). Cyanobacterial poisoning via toxic algal blooms in shrinking pools of water during dry seasons may also at least partially explain the mass mortality revealed by the repetitive bone beds (Rogers and Krause, 2007; Rogers et al., 2017, 2018). Drought-adapted species such as conchostracans (Stigall and Hartman, 2008) and lungfish (Marshall and Rogers, 2012) have been recovered from the Anembalemba Member, as have necrophagous and osteophagous insect feeding traces (e.g., mandibular-carved borings and puparial chambers) on vertebrate bone, all of which are additional indications of prolonged dry seasons (Roberts et al., 2007; Rogers and Krause, 2007). The varicolored (but mostly red), oxidized paleosols of the immediately underlying rock unit, the Masorobe Member, also reveal abundant evidence of a parched, dryland environment (e.g., carbonate nodules; pervasive root mottling with long, vertically oriented traces). Employing 'climofunctions' developed by Sheldon et al. (2002), Kast et al. (2008) estimated that the Mahajanga Basin received anywhere from 430 to 1100 mm of precipitation annually at the time that *Adalatherium* lived, but it is likely that that precipitation fell in a relatively short period of time, presumably triggering the aforementioned debris flows. Finally, also consistent with an interpretation of a highly seasonal, semiarid climate is the fact that, paleogeographically, the Mahajanga Basin lay at approximately 30°S in the Maastrichtian, some 15° farther south than today, in what has been interpreted to be the subtropical desert belt (e.g., de Wit, 2003; Wells, 2003; Schettino and Scotese, 2005; Ali and Krause, 2011:fig. 5b; Reeves, 2014; Torsvik and Cocks, 2017).

BODY MASS OF *ADALATHERIUM HUI* AND OTHER MESOZOIC MAMMALIAFORMS

The estimated length (84 mm) and width (57 mm) of the cranium of *Adalatherium hui* (UA 9030; cranial size (square root of [cranial length × cranial width]) = 69.2 mm) are substantially smaller than the 124.1 mm length and 83.4 mm width measured for the holotype cranium of *Vintana sertichi* (UA 9972; cranial size = 101.7 mm; Kirk et al., 2014). These cranial size metrics for UA 9030 of *A. hui* yield an estimated body mass of 2.36 kg, with a 95% confidence interval of 1.53–3.64 kg (Krause, Hoffmann, et al., 2020). Krause, Hoffmann, et al. (2020) employed other measures (cranial length, cranial width, humeral and femoral lengths, and diaphyseal circumferences) and averaged them to yield an overall body mass estimate of 3.08 kg for UA 9030, spanning a range from 1.78 to 5.22 kg. With an overall body mass estimate of 8.74 kg (spanning a range from 6.65 to 10.83 kg based on cranial length, width, and size estimates), *V. sertichi* is almost three times larger than *A. hui* and is currently the largest Mesozoic mammaliaform known from Gondwana (Krause, Hoffmann, et al., 2020; recalculated from Kirk et al., 2014). Among all Mesozoic mammaliaforms worldwide, *V. sertichi* is second in estimated body mass only to the carnivorous *Repenomamus giganticus* from the Early Cretaceous of China (skull length = 160 mm; estimated body mass = 12–14 kg; Hu et al., 2005). *Coloniatherium cilinskii*, a mesungulatid dryolestoid from the Late Cretaceous of Argentina, could potentially be larger than *V. sertichi*, but it is not known from sufficiently well-preserved fossil material to derive a confident estimate of body mass. At present, *C. cilinskii* is represented only by fragmentary lower jaws, isolated teeth, and petrosals. Cranial length estimates for *C. cilinskii* range from 87 to 161.5 mm depending upon the comparative sample analyzed (Rougier et al., 2009). This range of values brackets the known cranial length of *V. sertichi* (101.7 mm) but exceeds the cranial length estimated here for *A. hui* (84 mm). Further evidence that *A. hui* was smaller than *C. cilinskii* is provided by estimates of dentary length (80 mm in *C. cilinskii* according to Rougier et al., 2000; ~65 mm in *A. hui*). Despite being considerably smaller than *R. giganticus*, *V. sertichi*, and probably *C. cilinskii*, *A. hui* is still very large compared with other gondwanatherians (Gurovich, 2008), and Mesozoic mammaliaforms generally (Alroy, 1999; Kielan-Jaworowska et al., 2004). It is also worth noting that the estimated body mass of UA 9030 is almost certainly lower than would be typical of adult specimens of *A. hui*. Specimen UA 9030 clearly represents a subadult individual, as indicated by its still not fully erupted distal postcanine teeth (Krause, Hu, et al., 2020) and the presence of unfused epiphyses on several long bones and metapodials (Hoffmann, Hu, et al., 2020). Based on the stages of these parameters, however, Krause, Hoffmann, et al. (2020) concluded that UA 9030 was probably nearly fully grown. Based on current knowledge, *A. hui* therefore appears to be the third largest mammaliaform known on the basis of body fossils from the Mesozoic of Gondwana.

The large size of Mesozoic mammaliaforms such as *R. giganticus*, *V. sertichi*, *C. cilinskii*, and *A. hui* is of interest in the context of what Clemens et al. (2003:236) succinctly described as "common knowledge," which "holds that Mesozoic mammals, suffering under the tyranny of the dinosaurs, were very small creatures." Alroy (1999) estimated the average body mass of mammals at the end of the Cretaceous to have been only ~80 g (range = 11–590 g). In their compendium of Mesozoic mammaliaforms, Kielan-Jaworowska et al. (2004:5) stated that "The vast majority of early mammals … were shrew to mouse sized, a pattern that persisted through the entire 155-Ma history of mammals in the Mesozoic." This "common knowledge" has recently been disputed for placental mammals on the basis of genomic evidence (Romiguier et al., 2013). Nonetheless, small body size has been an important component of some adaptive scenarios for mammaliaform evolution, such as the nocturnal bottleneck hypothesis (e.g., Gerkema et al., 2013). According to this scenario, small body size in Mesozoic mammaliaforms was accompanied by increased risk of predation, which in turn favored increased nocturnal activity as an antipredator strategy. Over macroevolutionary timescales, adaptation for a nocturnal habitus led to a loss of some visual abilities (e.g., tetrachromatic vision) and a compensatory expansion in auditory, olfactory, and somatosensory capabilities (Hall et al., 2012). Although the ecological, behavioral, and physiological consequences of small body size are too numerous to review here, it is important to note how profoundly the received wisdom regarding very small body mass in Mesozoic mammaliaforms has shaped our current understanding of mammalian evolution and adaptations (e.g., Walls, 1942; Crompton, 1980; Luo, 2007; Smith et al., 2010; Hut et al., 2012; Maor et al., 2017; Grossnickle, 2020).

In this context, it is worth noting that there is increasing evidence that many other Mesozoic mammaliaforms were much larger than shrews and mice, or even rats (Weil, 2005). Not all of the larger Mesozoic taxa are represented by crania or even complete dentaries, thus precluding precise comparisons, but even fairly complete jaws are sufficient to reveal the presence of many species larger than brown rats (*Rattus norvegicus*, average ~400 g; Nowak, 1991) and, in some cases, even guinea pigs (*Cavia porcellus*, average ~1 kg; Nowak, 1991). These taxa include, for instance, *Steropodon galmani* and *Kollikodon ritchei* from the Early Cretaceous of Australia (Archer et al., 1985; Flannery et al., 1995; Pian et al., 2016); *Vincelestes neuquenianus* from the Early Cretaceous of Argentina (Rougier, 1993); *Repenomamus robustus* and *Laioconodon hui* from the Early Cretaceous of China (Li et al., 2001; Hu et al., 2005; Meng et al., 2011); *Catopsbaatar catopsaloides* and *Mangasbaatar udanii* from the Late Cretaceous of Mongolia (Kielan-Jaworowska et al., 2005; Rougier et al., 2016); *Yubaatar zhongyuanensis* from the Late Cretaceous of China (Xu et al., 2015); *Gobiconodon ostromi* and *Cifelliodon wahkarmoosuch* from the Early Cretaceous of the U.S.A. (Jenkins and Schaff, 1988; Huttenlocker et al., 2018); *Didelphodon vorax* from the Late Cretaceous of Canada and the U.S.A. (Gordon, 2003; Wilson et al., 2016); and *Schowalteria clemensi* from the Late Cretaceous of Canada (Fox and Naylor, 2003).

Taxa represented exclusively or largely by dental remains provide even less precise estimates of body size, varying greatly depending upon energy demands and methods of food processing (Copes and Schwartz, 2010; Hopkins, 2018). Nonetheless, Clemens et al. (2003), employing an arbitrary boundary of >5 mm in length or width of individual cheek teeth, listed a number of taxa categorized as 'large' for Mesozoic mammaliaforms. These included a possible new, unnamed dryolestid from the Early Cretaceous of Australia (Clemens et al., 2003); the multituberculates *Meniscoessus robustus*, *Bubodens magnus*, *Cimolodon nitidus*, and *Cimolomys gracilis* (although subsequent body mass estimates by Wilson et al. [2012] for *C. nitidus* and *C. gracilis* of 179 and 287 g, respectively, put them below average brown rat size) and the marsupial '*Pediomys*' *florencae* (now *Protolambda florencae*; see Davis, 2007), all from the Late Cretaceous of North America; the mesungulatid dryolestoids *Coloniatherium cilinskii* (discussed above) and *Mesungulatum houssayi*, and *Gondwanatherium patagonicum*, a gondwanatherian, from the Late Cretaceous of Argentina (Bonaparte, 1990); and an indeterminate mammal from the Late Cretaceous of Madagascar (Krause et al., 1994). To this list can be added the Late Cretaceous North American multituberculates *Essonodon browni* and multiple species of *Meniscoessus* (*M. collomensis*, *M. conquistus*, *M. intermedius*, *M. major*, and *M. seminoensis*; see Lillegraven, 1987; Wilson et al., 2010, 2012); the marsupials *Eodelphis browni*, *Eodelphis cutleri*, and *Didelphodon coyi* (see Fox and Naylor, 2006); and the eutherian *Altacreodus magnus* (see Lillegraven, 1969; Fox, 2015).

Finally, it is also important to note that the large Mesozoic mammaliaforms enumerated above are based on body fossils. Recently discovered trackways suggest the presence of other large Mesozoic mammaliamorphs, including on Gondwanan landmasses. Tracks of Mesozoic mammaliaforms are, in general, rare (see recent summaries in Lockley et al. [2017], Mateus et al. [2017:fig. 8], and Stanford et al. [2018]), and many of them "are of questionable value" because they are isolated, of mediocre preservation, and/or lack comparative material in the form of skeletal remains (Lockley et al., 2017:221). Nonetheless, if correctly attributed, some comparative statements can be made about their size. The manus of *A. hui* measures roughly 5.0 cm in length and 3.3 cm in width, whereas the pes is approximately 7.3 cm long and 4.5 cm wide. Although tracks made by *A. hui* would presumably have been slightly larger than these dimensions due to the presence of soft tissues, the autopodia of *A. hui* are substantially larger than those of most Mesozoic trackmakers thought to represent mammaliaforms. This conclusion clearly relates to the various species of *Ameghinichnus* from the Late Triassic/Early Jurassic of South Africa (Olsen and Galton, 1984) and the Jurassic of South America (Casamiquela, 1964; de Valais, 2009), North America (Szajna and Silvestri, 1996), and Europe (Gierliński et al., 2004); *Ameghinichnus*? ichnospecies from the Jurassic of South America (de Valais, 2009); *Catocapes angolanus* from the Early Cretaceous of Angola (Marzola et al., 2014; Mateus et al., 2017); *Brasilichnium elusivum* and *Brasilichnium saltatorium* from the Early Cretaceous of Brazil (Leonardi, 1981; Buck et al., 2017b); *Koreasaltipes jinjuensis* from the Early Cretaceous of Korea (Kim et al., 2017); Morphotype B from the Early Cretaceous of Maryland (Stanford et al., 2018); *Schadipes crypticus* and *Schadipes*, ichnosp. indet., from the Late Cretaceous of Colorado (Lockley and Foster, 2003); ichnogenus indet. from the Late Cretaceous (Cenomanian) of Tunisia (Contessi, 2013); and ichnogenus indet. from the Early Cretaceous of Morocco (Klein et al., 2018). A few recently described tracks are generally larger; although their proportions vary, they were made by animals that were likely also smaller than *A. hui*. These include ichnogenus indet. from the Middle Jurassic of Argentina (de Valais, 2009); *Sederipes goddardensis* (Morphotype A) from the Early Cretaceous (Aptian) of Maryland (Stanford et al., 2018); *Aracoaraichnium leonardii* from the Early Cretaceous of Brazil (Buck et al., 2017a); and ichnogenus indet. from the Late Cretaceous of Colorado (Lockley et al., 2017). One isolated track that represents an animal almost certainly larger than *A. hui* has been ascribed to Morphotype C from the Early Cretaceous of Maryland; the track is ~11.4 cm long and ~5.9 cm wide (Stanford et al., 2018:figs. 6j [not 6i as stated], 7c).

The preservation of both the skull and feet of *A. hui* motivates us to make additional observations about Mesozoic mammaliaform trackmakers and their relative body sizes. Marzola et al. (2014:181) estimated that the Early Cretaceous Angolan trackmaker, later named *Catocapes angolanus*, by Mateus et al. (2017) (the validity of which has been questioned by Stanford et al., 2018), represented an animal "as big as a modern raccoon … comparable in size to *Repenomamus*." Mateus et al. (2017:230) reiterated the comparison with the extant raccoon (*Procyon lotor*) but went further and identified *C. angolanus* as the "largest known mammaliamorph from the Early Cretaceous … unmatched in size by the coeval skeletal fossil record," thus implying that *C. angolanus* was larger than even *R. giganticus*. The two isolated tracks of *C. angolanus*, not identifiable as either manus or pes, average 2.7 cm in length and 3.2 cm in width. Raccoon footprints, by contrast, are typically much larger: manus 6.4–7.6 cm long, 6.4 cm wide; pes 6.4–10.2 cm long, 5.7 cm wide (e.g., Shomon, 1953; Halfpenny and Biesiot, 1986). Furthermore, raccoons are notorious for being highly variable in body mass (depending on gender, geography, and season); they typically range from 8 to 26 kg, with the maximum recorded weight being 29.4 kg (Zeveloff, 2002). Both *R. giganticus* (12–14 kg) and *V. sertichi* (~9 kg) fall within this range, but *A. hui* is much smaller (~3.1 kg). Nevertheless, both the manus and pes of the subadult individual of *A. hui* appear to be considerably larger than the tracks assigned to *Catocapes angolanus*. Within the context of manual and pedal dimensions and body mass estimated from skeletal dimensions for *A. hui*, *C. angolanus* was smaller than *A. hui*, which, in turn, was much smaller than a raccoon. Indeed, the footprints of *C. angolanus* appear to be very similar in size to those of *Mustela nigripes*, the black-footed ferret (both manus and pes tracks are 2.9 cm long and 3.2 cm wide; Halfpenny and Biesiot, 1986), which has a body mass of only 645–1,125 g (Anderson et al., 1986). Furthermore, as pointed out by Stanford et al. (2018), several other Early Cretaceous trackmakers were as large or larger than *C. angolanus*.

We therefore support the conclusion of Stanford et al. (2018:10) that "*Catocapes* is clearly not the largest Early Cretaceous mammalian track morphotype presently known." Much work obviously needs to be done and more discoveries of associated or articulated skulls and postcranial skeletons need to be made in order to reliably compare track size with body mass in Mesozoic mammaliaforms.

CONCLUSIONS

The holotype and only known specimen (UA 9030) of the gondwanatherian *Adalatherium hui* is the most complete and best preserved of any Mesozoic mammaliaform from Gondwana. Details concerning the systematic paleontology of *A. hui*, the discovery and preparation of UA 9030 and the digital imaging methods used to study it, its geological context, and its body size relative to other Mesozoic mammaliaforms from Gondwana (third largest) are summarized in this chapter. The following chapters in this volume provide detailed descriptions and copious illustrations of the skeletal anatomy of *A. hui*, followed by a concluding chapter on its phylogenetic relationships.

ACKNOWLEDGMENTS

We thank the 1999 field crew for their efforts and, in particular, J. A. Rabarison, who discovered UA 9030, and both he and M. D. Gottfried for collecting it. We also thank the Ministries of Mines and Higher Education of the Republic of Madagascar and the Department of Paleontology, the Université d'Antananarivo, for permission to conduct research in Madagascar, and B. Andriamihaja and his staff (Madagascar Institut pour la Conservation des Ecosystèmes Tropicaux) and the villagers of Berivotra for logistical support of field work. For assistance in imaging and digital postprocessing of UA 9030, we gratefully acknowledge the following individuals and institutions: T. Zimmerman, Division of Laboratory Animal Resources, Stony Brook University (SBU); L. Caronia, W. Mattera, C. K. Mazzarese, and H. Nicoleau, Department of Radiology, SBU; J. Thostenson and M. Hill, American Museum of Natural History; J. Diehm and B. Reuther, Avonix Imaging; M. Colbert, D. Edey, J. Maisano, and R. Racicot, University of Texas at Austin; P. O'Connor, Department of Biomedical Sciences, Ohio University; B.-A. S. Bhullar, Department of Geology and Geophysics, Yale University; T. Salerno, Department of Anatomical Sciences, SBU; L. Dougan, Department of Earth Sciences, Denver Museum of Nature & Science; and K. Hurdle, New York Institute of Technology Visualization Center. V. Heisey, Department of Anatomical Sciences, SBU, was responsible for the mechanical preparation of UA 9030. L. Betti-Nash, Department of Anatomical Sciences, SBU, rendered Figure 1 and assisted with the final layout of the other figures. S. Hartman drew the skeletal reconstructions of *Adalatherium* in Figure 2B and C. The late M. Stewart, Media Services, SBU, took the photograph in Figure 2A. Randrianarisata, Madagascar Institut pour la Conservation des Ecosystèmes Tropicaux, took the photograph in Figure 3A; and M. Stenzel, National Geographic Society, took the photograph in Figure 3B.

Financial support for discovery and collection of UA 9030 in 1999 was provided by the National Geographic Society (grant 6400-99) and the National Science Foundation (grant EAR-9706302), and support for subsequent analysis was provided by a series of grants from the National Science Foundation (EAR-9706302, EAR-0106477, EAR-0446488, EAR-1122642, EAR-1528273, and EAR-1664432 to D.W.K. and DEB-1501497 and MRI-1828305 to S.H.), and a grant from the Office of the Vice President for Research, SBU (2005–2007), to support the late Y. Hu as a postdoctoral associate.

ORCID

David W. Krause http://orcid.org/0000-0001-7860-6828
Joseph R. Groenke http://orcid.org/0000-0002-9527-1887
Simone Hoffmann http://orcid.org/0000-0001-8984-0601
Raymond R. Rogers http://orcid.org/0000-0002-1557-2058
Lydia J. Rahantarisoa http://orcid.org/0000-0003-3216-6630

LITERATURE CITED

Abramovich, S., G. Keller, T. Adatte, W. Stinnesbeck, L. Hottinger, D. Stueben, Z. Berner, B. Ramanivosoa, and A. Randriamanantenasoa. 2002. Age and paleoenvironment of the Maastrichtian–Paleocene of the Mahajanga Basin, Madagascar: a multidisciplinary approach. Marine Micropaleontology 47:17–70.

Ali, J. R., and D. W. Krause. 2011. Late Cretaceous bioconnections between Indo-Madagascar and Antarctica: refutation of the Gunnerus Ridge causeway hypothesis. Journal of Biogeography 38:1855–1872.

Alroy, J. 1999. The fossil record of North American mammals: evidence for a Paleocene evolutionary radiation. Systematic Biology 48:107–118.

Anderson, E., S. C. Forrest, T. W. Clark, and L. Richardson. 1986. Paleobiology, biogeography, and systematics of the black-footed ferret, *Mustela nigripes* (Audubon and Bachman), 1851. Great Basin Naturalist Memoirs 8:11–62.

Archer, M., T. F. Flannery, A. Ritchie, and R. E. Molnar. 1985. First Mesozoic mammal from Australia—an Early Cretaceous monotreme. Nature 318:363–366.

Archibald, J. D., and A. O. Averianov. 2012. Phylogenetic analysis, taxonomic revision, and dental ontogeny of the Cretaceous Zhelestidae (Mammalia: Eutheria). Zoological Journal of the Linnean Society 164:361–426.

Averianov, A. O., J. D. Archibald, and T. Martin. 2003. Placental nature of the alleged marsupial from the Cretaceous of Madagascar. Acta Palaeontologica Polonica 48:149–151.

Besairie, H. 1972. Géologie de Madagascar. I. Les terrains sédimentaires. Annales Géologiques de Madagascar 35:1–463.

Bi, S., Y. Wang, G. Jian, S. Xia, and J. Meng. 2014. Three new Jurassic euharamiyidan species reinforce early divergence of mammals. Nature 514:579–584.

Bi, S., X. Zheng, J. Meng, X. Wang, N. Robinson, and B. Davis. 2016. A new symmetrodont mammal (Trechnotheria: Zhangheotheriidae) from the Early Cretaceous of China and trechnotherian character evolution. Scientific Reports 6:26668.

Bi, S., X. Zheng, X. Wang, N. E. Cignetti, S. Yang, and J. R. Wible. 2018. An Early Cretaceous eutherian and the placental-marsupial dichotomy. Nature 558:390–395.

Bolortsetseg, M. 2008. Description of three new specimens of cimolodontans and a phylogenetic study of the postcranial anatomy of Multituberculata (Mammalia, Synapsida). Ph.D. dissertation, The City University of New York, New York, New York, 304 pp.

Bonaparte, J. F. 1990. New Late Cretaceous mammals from the Los Alamitos Formation, northern Patagonia. National Geographic Research 6:63–93.

Bonaparte, J. F., and G. W. Rougier. 1987. Mamíferos del Cretácico Inferior de Patagonia; pp. 343–359 in Actas IV Congreso Latinoamericano de Paleontología, Santa Cruz de la Sierra, Bolivia, 27–30 July 1987, Vol. 1.

Buck, P. V., A. M. Ghilardi, L. B. R. Fernandes, and M. A. Fernandes. 2017a. A new ichnotaxon classification of large mammaliform trackways from the Lower Cretaceous Botucatu Formation, Paraná Basin, Brazil. Palaeogeography, Palaeoclimatology, Palaeoecology 485:377–388.

Buck, P. V., A. M. Ghilardi, B. C. P. M Peixoto, L. B. R. Fernandes, and M. A. Fernandes. 2017b. A new tetrapod ichnotaxon from Botucatu Formation, Lower Cretaceous (Neocomian), Brazil, with comments on fossil track preservation on inclined planes and local paleoecology. Palaeogeography, Palaeoclimatology, Palaeoecology 466:21–37.

Burch, S. H., and J. J. W. Sertich. 2011. Giant pterosaur remains from the Campanian of the Morondava Basin, western Madagascar. Journal of Vertebrate Paleontology 31(Program and Abstracts):80A.

Carlson, W. D., T. Rowe, R. A. Ketcham, and M. W. Colbert. 2003. Applications of high-resolution X-ray computed tomography in petrology, meteoritics and palaeontology; pp. 7–22 in F. Mees, R. Swennen, M. Van Geet, and P. Jacobs (eds.), Applications of X-ray Computed Tomography in the Geosciences. Geological Society, Special Publications 215, London.

Casamiquela, R. M. 1964. Estudios icnológicos. Problemas y métodos de la icnología con aplicación al estudio de pisadas mesozoicas (Reptilia, Mammalia) de la Patagonia. Colegio Industrial Pío IX, Buenos Aires, Argentina, 229 pp.

Casey, M., R. Rogers, M. Jackson, and G. Buckley. 2003. Magnetic stratigraphy of the Upper Cretaceous Maevarano Formation (Campanian (?)–Maastrichtian), northwestern Madagascar. Journal of Vertebrate Paleontology 23(3, Supplement):39A.

Chen M., Z.-X. Luo, and G. P. Wilson. 2017. The postcranial skeleton of *Yanoconodon allini* from the Early Cretaceous of Hebei, China, and its implications for locomotor adaptation in eutriconodontan mammals. Journal of Vertebrate Paleontology. 37:e1315425.

Clemens, W. A., G. P. Wilson, and R. E. Molnar. 2003. An enigmatic (synapsid?) tooth from the Early Cretaceous of New South Wales, Australia. Journal of Vertebrate Paleontology 23:232–237.

Contessi, M. 2013. First report of mammal-like tracks from the Cretaceous of North Africa (Tunisia). Cretaceous Research 42:48–54.

Copes, L. E., and G. T. Schwartz. 2010. The scale of it all: postcanine tooth size, the taxon-level effect, and the universality of Gould's scaling law. Paleobiology 36:188–203.

Crompton, A. W. 1974. The dentitions and relationships of the Southern African Triassic mammals *Erythrotherium parringtoni* and *Megazostrodon rudnerae*. Bulletin, British Museum (Natural History), Geology 24:399–443.

Crompton, A. W. 1980. Biology of the earliest mammals; pp. 1–12 in K. Schmidt-Nielsen, L. Bolis, and C. R. Taylor (eds.), Comparative Physiology: Primitive Mammals. Cambridge University Press, New York, New York.

Crompton, A. W., and F. A. Jenkins Jr. 1968. Molar occlusion in Late Triassic mammals. Biological Reviews 43:427–458.

Csiki-Sava, Z., M. Vremir, J. Meng, S. L. Brusatte, and M. A. Norell. 2018. Dome-headed, small-brained island mammal from the Late Cretaceous of Romania. Proceedings of the National Academy of Sciences of the United States of America 115:4857–4862.

Davis, B. M. 2007. A revision of "pediomyid" marsupials from the Late Cretaceous of North America. Acta Palaeontologica Polonica 52:217–256.

Dennis-Duke, B. 2005. Revisiting the magnetostratigraphy of the Upper Cretaceous Berivotra and Maevarano formations, northwestern Madagascar. Senior Honors thesis, Macalester College, Saint Paul, Minnesota, 139 pp.

de Valais, S. 2009. Ichnotaxonomic revision of *Ameghinichnus*, a mammalian ichnogenus from the Middle Jurassic La Matilde Formation, Santa Cruz province, Argentina. Zootaxa 2203:1–21.

de Wit, M. J. 2003. Madagascar: heads it's a continent, tails it's an island. Annual Review of Earth and Planetary Sciences 31:213–248.

Evans, S. E., J. R. Groenke, M. E. H. Jones, A. H. Turner, and D. W. Krause. 2014. New material of *Beelzebufo*, a hyperossified frog (Amphibia: Anura) from the Late Cretaceous of Madagascar. PLoS ONE 9:e87236.

Farke, A. A., and J. J. W. Sertich. 2013. An abelisauroid theropod dinosaur from the Turonian of Madagascar. PLoS ONE 8:e62047.

Flannery, T. F., M. Archer, T. H. Rich, and R. Jones. 1995. A new family of monotremes from the Cretaceous of Australia. Nature 377:418–420.

Fox, R. C. 2015. A revision of the Late Cretaceous–Paleocene eutherian mammal *Cimolestes* Marsh 1889. Canadian Journal of Earth Sciences 52:1137–1149.

Fox, R. C., and B. G. Naylor. 2003. A Late Cretaceous taeniodont (Eutheria, Mammalia) from Alberta, Canada. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 229:393–420.

Fox, R. C., and B. G. Naylor. 2006. Stagodontid marsupials from the Late Cretaceous of Canada and their systematic and functional implications. Acta Palaeontologica Polonica 51:13–36.

Francischini, H., S. G. Lucas, P. Dentzien-Dias, and C. L. Schultz. 2020. Recent root damages of fossilized vertebrate remains from New Mexico, USA; pp. 139–150 in S. Martínez, A. Rojas, and F. Cabrera (eds.), Actualistic Taphonomy in South America. Springer Nature, Cham, Switzerland.

Gao, C.-L., G. P. Wilson, Z.-X. Luo, A. M. Maga, Q.-J. Meng, and X. Wang. 2010. A new mammal skull from the Lower Cretaceous of China with implications for the evolution of obtuse-angled molars and "amphilestid" eutriconodonts. Proceedings of the Royal Society B: Biological Sciences 277:237–246.

Gerkema, M. P., W. I. L. Davies, R. G. Foster, M. Menaker, and R. A. Hut. 2013. The nocturnal bottleneck and the evolution of activity patterns in mammals. Proceedings of the Royal Society B: Biological Sciences 280:20130508.

Gierliński, G., G. Pieńkowski, and G. Niedźwiedzki. 2004. Tetrapod track assemblage in the Hettangian of Sołtyków, Poland, and its paleoenvironmental background. Ichnos 11:195–213.

Gordon, C. L. 2003. A first look at estimating body size in dentally conservative marsupials. Journal of Mammalian Evolution 10:1–21.

Gottfried, M. D., J. A. Rabarison, and L. L. Randriamiaramanana. 2001. Late Cretaceous elasmobranchs from the Mahajanga Basin of Madagascar. Cretaceous Research 22:491–496.

Gow, C. E. 1986. A new skull of *Megazostrodon* (Mammalia, Triconodonta) from the Elliot Formation (Lower Jurassic) of Southern Africa. Palaeontologia Africana 26:13–23.

Grossnickle, D. M. 2020. Feeding ecology has a stronger evolutionary influence on functional morphology than on body mass in mammals. Evolution 74:610–628.

Gurovich, Y. 2008. Additional specimens of sudamericid (Gondwanatheria) mammals from the early Paleocene of Argentina. Palaeontology 51:1069–1089.

Halfpenny, J. C., and E. A. Biesiot. 1986. A Field Guide to Mammal Tracking in Western America. Johnson Books, Boulder, Colorado, 161 pp.

Hall, M. I., J. M. Kamilar, and E. C. Kirk. 2012. Eye shape and the nocturnal bottleneck of mammals. Proceedings of the Royal Society B: Biological Sciences 279:4962–4968.

Han, G., and J. Meng. 2016. A new spalacolestine mammal from the Early Cretaceous Jehol Biota and implications for the morphology, phylogeny, and palaeobiology of Laurasian 'symmetrodontans.' Zoological Journal of the Linnean Society 178:343–380.

Han, G., F. Mao, S. Bi, Y. Wang, and J. Meng. 2017. A Jurassic gliding euharamiyidan mammal with an ear of five auditory bones. Nature 551:451–456.

Hoffmann, S., Y. Hu, and D. W. Krause. 2020. Postcranial morphology of *Adalatherium hui* (Mammalia, Gondwanatheria) from the Late Cretaceous of Madagascar; pp. 133–213 in D. W. Krause and S. Hoffmann (eds.), *Adalatherium hui* (Mammalia, Gondwanatheria) from the Late Cretaceous of Madagascar. Society of Vertebrate Paleontology Memoir 21. Journal of Vertebrate Paleontology 40 (2, Supplement).

Hopkins, S. S. B. 2018. Estimation of body size in fossil mammals; pp. 7–22 in D. A. Croft, D. F. Su, and S. W. Simpson (eds.), Methods in Paleoecology, Reconstructing Cenozoic Terrestrial Environments and Ecological Communities. Springer Nature, Cham, Switzerland.

Hou, S., and J. Meng. 2014. A new eutriconodont mammal from the early Cretaceous Jehol Biota of Liaoning, China. Chinese Science Bulletin 59:546–553.

Hu, Y. 2006. Postcranial morphology of *Repenomamus* (Eutriconodonta, Mammalia): implications for the higher-level phylogeny of mammals. Ph.D. dissertation, The City University of New York, New York, New York, 405 pp.

Hu, Y., J. Meng, C. Li, and Y. Wang. 2010. New basal eutherian mammal from the Early Cretaceous Jehol biota, Liaoning, China. Proceedings of the Royal Society B: Biological Sciences 277:229–236.

Hu, Y., J. Meng, Y. Wang, and C. Li. 2005. Large Mesozoic mammals fed on young dinosaurs. Nature 433:149–152.

Hurum, J. H., and Z. Kielan-Jaworowska. 2008. Postcranial skeleton of a Cretaceous multituberculate mammal *Catopsbaatar*. Acta Palaeontologica Polonica 53:545–566.

Hut, R. A., N. Kronfeld-Schor, V. van der Vinne, and H. De la Iglesia. 2012. In search of a temporal niche; environmental factors; pp. 281–304 in A. Kalsbeek, M. Merrow, T. Roenneberg, and R. G. Foster (eds.), Progress in Brain Research, The Neurobiology of Circadian Timing 199.

Huttenlocker, A. K., D. M. Grossnickle, J. I. Kirkland, J. A. Schultz, and Z.-X. Luo. 2018. Late-surviving stem mammal links the lowermost Cretaceous of North America and Gondwana. Nature 558:108–112.

Jäger, K. R. K., Z.-X. Luo, and T. Martin. 2019. Postcranial skeleton of *Henkelotherium guimarotae* (Cladotheria, Mammalia) and locomotor adaptation. Journal of Mammalian Evolution 27:349–372.

Jenkins, F. A., Jr., and F. R. S. Parrington. 1976. The postcranial skeletons of the Triassic mammals *Eozostrodon*, *Megazostrodon*, and *Erythrotherium*. Philosophical Transactions of the Royal Society B 273:387–431.

Jenkins, F. A., Jr., and C. R. Schaff. 1988. The Early Cretaceous mammal *Gobiconodon* (Mammalia, Triconodonta) from the Cloverly Formation in Montana. Journal of Vertebrate Paleontology 8:1–24.

Ji, Q., Z.-X. Luo, C.-X. Yuan, and A. R. Tabrum. 2006. A swimming mammaliaform from the Middle Jurassic and ecomorphological diversification of early mammals. Science 311:1123–1127.

Ji, Q., Z.-X. Luo, S. Zhang, C.-X. Yuan, and L. Xu. 2009. Evolutionary development of the middle ear in Mesozoic therian mammals. Science 326:278–281.

Kast, S., R. Rogers, and K. Curry Rogers. 2008. Reconstructing Late Cretaceous climate in the Mahajanga Basin of northwestern Madagascar. Journal of Vertebrate Paleontology 28(3, Supplement):99A.

Ketcham, R. A., and W. D. Carlson. 2001. Acquisition, optimization and interpretation of X-ray computed tomographic imagery: applications to the geosciences. Computers & Geosciences 27:381–400.

Kielan-Jaworowska, Z., R. L. Cifelli, and Z.-X. Luo. 2004. Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure. Columbia University Press, New York, New York, 630 pp.

Kielan-Jaworowska, Z., J. H. Hurum, and A. V. Lopatin. 2005. Skull structure in *Catopsbaatar* and the zygomatic ridges in multituberculate mammals. Acta Palaeontologica Polonica 50:487–512.

Kim, K. S., J. D. Lim, M. G. Lockley, L. Xing, and Y. Choi. 2017. Korean trackway of a hopping, mammaliaform trackmaker is first from the Cretaceous of Asia. Cretaceous Research 74:188–191.

Kirk, E. C., S. Hoffmann, A. D. Kemp, D. W. Krause, and P. M. O'Connor. 2014. Sensory anatomy and sensory ecology of *Vintana sertichi* (Mammalia, Gondwanatheria) from the Late Cretaceous of Madagascar; pp. 203–222 in D. W. Krause (ed.), *Vintana sertichi* (Mammalia, Gondwanatheria) from the Late Cretaceous of Madagascar. Society of Vertebrate Paleontology Memoir 14. Journal of Vertebrate Paleontology 34(6, Supplement).

Klein, H., A. Lagnaoui, G. D. Gierliński, H. Saber, J. N. Lallensack, M. Oukassou, and A. Charrière. 2018. Crocodylomorph, turtle and mammal tracks in dinosaur-dominated Middle–?Jurassic and mid-Cretaceous ichnoassemblages of Morocco. Palaeogeography, Palaeoclimatology, Palaeoecology 498:39–52.

Kley, N. J., J. J. W. Sertich, A. H. Turner, D. W. Krause, P. M. O'Connor, and J. A. Georgi. 2010. Craniofacial morphology of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar; pp. 13–98 in D. W. Krause and N. J. Kley (eds.), *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. Society of Vertebrate Paleontology Memoir 10. Journal of Vertebrate Paleontology 30(6, Supplement).

Krause, D. W. 2001. Fossil molar from a Madagascan marsupial. Nature 412:497–498.

Krause, D. W. 2013. Gondwanatheria and ?Multituberculata (Mammalia) from the Late Cretaceous of Madagascar. Canadian Journal of Earth Sciences 50:324–340.

Krause, D. W. (ed.). 2014. *Vintana sertichi* (Mammalia, Gondwanatheria) from the Late Cretaceous of Madagascar. Society of Vertebrate Paleontology Memoir 14. Journal of Vertebrate Paleontology 34(6, Supplement), 222 pp.

Krause, D. W., and N. J. Kley (eds.). 2010. *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. Society of Vertebrate Paleontology Memoir 10. Journal of Vertebrate Paleontology 30(6, Supplement), 236 pp.

Krause, D. W., S. Hoffmann, and S. Werning. 2017. First postcranial remains of Multituberculata (Allotheria, Mammalia) from Gondwana. Cretaceous Research 80:91–100.

Krause, D. W., G. V. R. Prasad, W. von Koenigswald, A. Sahni, and F. E. Grine. 1997. Cosmopolitanism among Gondwanan Late Cretaceous mammals. Nature 390:504–507.

Krause, D. W., J. J. W. Sertich, P. M. O'Connor, K. Curry Rogers, and R. R. Rogers. 2019. The Mesozoic biogeographic history of Gondwanan terrestrial vertebrates: insights from Madagascar's fossil record. Annual Review of Earth and Planetary Sciences 47:519–553.

Krause, D. W., J. J. W. Sertich, R. R. Rogers, S. C. Kast, A. H. Rasoamiaramanana, and G. A. Buckley. 2010. Overview of the discovery, distribution, and geological context of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar; pp. 4–12 in D. W. Krause and N. J. Kley (eds.), *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. Society of Vertebrate Paleontology Memoir 10. Journal of Vertebrate Paleontology 30(6, Supplement).

Krause, D. W., Y. Hu, S. Hoffmann, J. R. Groenke, J. A. Schultz, A. R. Evans, W. von Koenigswald, and G. W. Rougier. 2020. Dental morphology of *Adalatherium hui* (Mammalia, Gondwanatheria) from the Late Cretaceous of Madagascar; pp. 97–132 in D. W. Krause and S. Hoffmann (eds.), *Adalatherium hui* (Mammalia, Gondwanatheria) from the Late Cretaceous of Madagascar. Society of Vertebrate Paleontology Memoir 21. Journal of Vertebrate Paleontology 40(2, Supplement).

Krause, D. W., J. H. Hartman, N. A. Wells, G. A. Buckley, C. A. Lockwood, C. E. Wall, R. E. Wunderlich, J. A. Rabarison, and L. L. Randriamiaramanana. 1994. Late Cretaceous mammals. Nature 368:298.

Krause, D. W., S. Hoffmann, Y. Hu, J. R. Wible, G. W. Rougier, E. C. Kirk, J. R. Groenke, R. R. Rogers, J. B. Rossie, J. A. Schultz, A. R. Evans, W. von Koenigswald, and L. J. Rahantarisoa. 2020. Skeleton of Cretaceous gondwanatherian mammal from Madagascar reflects long-term insularity. Nature 581:421–427.

Krause, D. W., S. Hoffmann, J. R. Wible, E. C. Kirk, J. A. Schultz, W. von Koenigswald, J. R. Groenke, J. B. Rossie, P. M. O'Connor, E. R. Seiffert, E. R. Dumont, W. L. Holloway, R. R. Rogers, L. J. Rahantarisoa, A. D. Kemp, and H. Andriamialison. 2014. First cranial remains of a gondwanatherian mammal reveal remarkable mosaicism. Nature 515:512–517.

Kusuhashi, N., Y. Hu, Y. Wang, T. Setoguchi, and H. Matsuoka. 2009. Two eobaatarid (Multituberculata; Mammalia) genera from the Lower Cretaceous Shahai and Fuxin formations, northeastern China. Journal of Vertebrate Paleontology 29:1264–1288.

Ladevèze, S., M. W. Colbert, and T. Smith. 2010. 3D computational imaging of the petrosal of a new multituberculate mammal from the Late Cretaceous of China and its paleobiologic inferences. Comptes Rendus Palevol 9:319–330.

Leonardi, G. 1981. Novo icnogênero de tetrápode Mesozóico da Formação Botucatu, Araraquara, SP. Anais da Academia Brasileira de Ciencias 53:795–805.

Li, G., and Z.-X. Luo. 2006. A Cretaceous symmetrodont therian with some monotreme-like postcranial features. Nature 439:195–200.

Li, J., Y. Wang, Y. Wang, and C. Li. 2001. A new family of primitive mammal from the Mesozoic of western Liaoning, China. Chinese Science Bulletin 46:782–785.

Lillegraven, J. A. 1969. Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. The University of Kansas Paleontological Contributions 50:1–122.

Lillegraven, J. A. 1987. Stratigraphic and evolutionary implications of a new species of *Meniscoessus* (Multituberculata, Mammalia) from the Upper Cretaceous Williams Fork Formation, Moffat County, Colorado; pp. 46–56 in J. E. Martin and G. E. Ostrander (eds.), Papers in Vertebrate Paleontology in Honor of Morton Green. Dakoterra, Special Paper 3.

Linnaeus, C. 1758. Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Laurentii Salvii, Stockholm, 824 pp.

Lockley, M. G., and J. Foster. 2003. Late Cretaceous mammal tracks from North America. Ichnos 10:269–276.

Lockley, M. G., N. A. Matthews, and B. Breithaupt. 2017. A new mammal track from the Laramie Formation (Maastrichtian) at the Fossil Trace locality, Golden, Colorado. Cretaceous Research 78:221–227.

Luo, Z.-X. 2007. Transformation and diversification in early mammal evolution. Nature 450:1011–1019.

Luo, Z.-X., and Q. Ji. 2005. New study on dental and skeletal features of the Cretaceous "symmetrodontan" mammal *Zhangheotherium*. Journal of Mammalian Evolution 12:337–357.

Luo, Z.-X., and J. R. Wible. 2005. A Late Jurassic digging mammal and early mammalian diversification. Science 308:103–107.

Luo, Z.-X., Q. Ji, and C.-X. Yuan. 2007a. Convergent dental adaptations in pseudo-tribosphenic and tribosphenic mammals. Nature 450:93–97.

Luo, Z.-X., P. Chen, G. Li, and M. Chen. 2007b. A new eutriconodont mammal and evolutionary development in early mammals. Nature 446:288–293.

Luo, Z.-X., Q. Ji, J. R. Wible, and C.-X. Yuan. 2003. An Early Cretaceous tribosphenic mammal and metatherian evolution. Science 302:1934–1940.

Luo, Z.-X., C.-X. Yuan, Q-J. Meng, and Q. Ji. 2011. A Jurassic eutherian mammal and divergence of marsupials and placentals. Nature 476:442–445.

Luo, Z.-X., S. M. Gatesy, F. A. Jenkins Jr., W. W. Amaral, and N. H. Shubin. 2015a. Mandibular and dental characteristics of Late

Triassic *Haramiyavia* and their ramifications for basal mammal evolution. Proceedings of the National Academy of Sciences of the United States of America 112:E7101–E7109.

Luo, Z.-X., Q.-J. Meng, Q. Ji, D. Liu, Y. G. Zhang, and A. I. Neander. 2015b. Evolutionary development in basal mammaliaforms as revealed by a docodontan. Science 347:760–764.

Luo, Z.-X., Q. J. Meng, D. M. Grossnickle, D. Liu, A. I. Neander, Y. G. Zhang, and Q. Ji. 2017. New evidence for mammaliaform ear evolution and feeding adaptation in a Jurassic ecosystem. Nature 548:326–329.

Mao, F., and J. Meng. 2019. A new haramiyidan mammal from the Jurassic Yanliao Biota and comparisons with other haramiyidans. Zoological Journal of the Linnean Society 186:529–552.

Mao, F., Y. Hu, C. Li, Y. Wang, M. H. Chase, A. K. Smith, and J. Meng. 2020. Integrated hearing and chewing modules decoupled in a Cretaceous stem therian mammal. Science 367:305–308.

Maor, R., T. Dayan, H. Ferguson-Gow, and K. E. Jones. 2017. Temporal niche expansion in mammals from a nocturnal ancestor after dinosaur extinction. Nature Ecology & Evolution 1:1889–1895.

Marsh, O. C. 1880. Notice on Jurassic mammals representing two new orders. American Journal of Science 20:235–239.

Marshall, M. S., and R. R. Rogers. 2012. Lungfish burrows from the Upper Cretaceous Maevarano Formation, Mahajanga Basin, northwestern Madagascar. Palaios 27:857–866.

Marshall, M. S., J. J. W. Sertich, I. M. Miller, and M. Andrianarivo. 2015. Stratigraphy and paleontology of a new nearshore dinosaur-bearing succession from the Late Cretaceous of the Morondava Basin, western Madagascar. Geological Society of America Abstracts with Programs 47:566.

Martin, T. 2005. Postcranial anatomy of *Haldanodon exspectatus* (Mammalia, Docodonta) from the Late Jurassic (Kimmeridgian) of Portugal and its bearing for mammalian evolution. Zoological Journal of the Linnean Society 145:219–248.

Martin, T. 2013. Mammalian postcranial bones from the Late Jurassic of Portugal and their implications for forelimb evolution. Journal of Vertebrate Paleontology 33:1432–1441.

Martin, T., J. Marugan-Lobon, R. Vullo, H. Martin-Abad, Z.-X. Luo, and A. D. Buscalioni. 2015. A Cretaceous eutriconodont and integument evolution in early mammals. Nature 526:380–384.

Marzola, M., O. Mateus, A. S. Schulp, L. L. Jacobs, M. J. Polcyn, and V. Pervov. 2014. Early Cretaceous tracks of a large mammaliamorph, a crocodylomorph, and dinosaurs from an Angolan diamond mine. Journal of Vertebrate Paleontology 34 (Program and Abstracts):181.

Mateus, O., M. Marzola, A. S. Schulp, L. L. Jacobs, M. J. Polcyn, V. Pervov, A. O. Gonçalves, and M. L. Morais. 2017. Angolan ichnosite in a diamond mine shows the presence of a large terrestrial mammaliamorph, a crocodylomorph, and sauropod dinosaurs in the Early Cretaceous of Angola. Palaeogeography, Palaeoclimatology, Palaeoecology 471:220–232.

Melluso, L., V. Morra, P. Brotzu, and J. J. Mahoney. 2001. The Cretaceous igneous province of central–western Madagascar: evidence for heterogeneous mantle sources, crystal fractionation and crustal contamination. Journal of Petrology 42:1249–1278.

Melluso, L., V. Morra, P. Brotzu, A. Razafiniparany, V. Ratrimio, and D. Razafimathatratra. 1997. Geochemistry and Sr-isotopic composition of the Late Cretaceous flood basalt sequence of northern Madagascar: petrogenetic and geodynamic implications. Journal of African Earth Sciences 24:371–390.

Melluso, L., H. C. Sheth, J. J. Mahoney, V. Morra, C. M. Petrone, and M. Storey. 2009. Correlations between silicic volcanic rocks of the St Mary's Islands (southwestern India) and eastern Madagascar: implications for Late Cretaceous India–Madagascar reconstructions. Journal of the Geological Society, London 166:283–294.

Meng, J. 2014. Mesozoic mammals of China: implications for phylogeny and early evolution of mammals. National Science Review 1:521–542.

Meng, J., Y. Wang, and C.-K. Li. 2011. Transitional mammalian middle ear from a new Cretaceous Jehol eutriconodont. Nature 472:181–185.

Meng, J., Y. Hu, Y. Wang, X. Wang, and C.-K. Li. 2006. A Mesozoic gliding mammal from northeastern China. Nature 444:889–893.

Meng, Q.-J., Q. Ji, Y. G. Zhang, D. Liu, and D. M. Grossnickle. 2015. An arboreal docodont from the Jurassic and mammaliaform ecological diversification. Science 347:764–768.

Meng, Q.-J., D. M. Grossnickle, D. Liu, Y. G. Zhang, A. I. Neander, Q. Ji, and Z.-X. Luo. 2017. New gliding mammaliaforms from the Jurassic. Nature 548:291–296.

Mones, A. 1987. Gondwanatheria, un nuevo orden de mamíferos sudamericanos (Mammalia: Edentata: ?Xenarthra). Comunicaciones Paleontológicas del Museo de Historia Natural de Montevideo 18:237–240.

Nowak, R. M. (ed.). 1991. Walker's Mammals of the World. Johns Hopkins University Press, Baltimore, Maryland, 1629 pp.

Odom, I. E. 1984. Smectite clay minerals: properties and uses. Philosophical Transactions of the Royal Society of London A 311:391–409.

Olsen, P. E., and P. M. Galton. 1984. A review of the reptile and amphibian assemblages from the Stormberg of southern Africa, with special emphasis on the footprints and the age of the Stormberg. Palaeontologica Africana 25:87–100.

Pian, R., M. Archer, S. J. Hand, R. M. D. Beck, and A. Cody. 2016. The upper dentition and relationships of the enigmatic Australian Cretaceous mammal *Kollikodon ritchiei*. Memoirs of Museum Victoria 74:97–105.

Rahantarisoa, L. J. 2007. Biostratigraphie et paléoecologie du Maastrichtien de Berivotra (Mahajanga). Ph.D. dissertation, Université d'Antananarivo, Antananarivo, Madagascar, 126 pp.

Reeves, C. 2014. The position of Madagascar within Gondwana and its movements during Gondwana dispersal. Journal of African Earth Sciences 94:45–57.

Roberts, E. M., R. R. Rogers, and B. Z. Foreman. 2007. Continental insect borings in dinosaur bone: examples from the Late Cretaceous of Madagascar and Utah. Journal of Paleontology 81:201–208.

Rogers, R. R. 2005. Fine-grained debris flows and extraordinary vertebrate burials in the Late Cretaceous of Madagascar. Geology 33:297–300.

Rogers, R. R., and D. W. Krause. 2007. Tracking an ancient killer. Scientific American 296(2):42–51.

Rogers, R. R., J. H. Hartman, and D. W. Krause. 2000. Stratigraphic analysis of Upper Cretaceous rocks in the Mahajanga Basin, northwestern Madagascar: implications for ancient and modern faunas. Journal of Geology 108:275–301.

Rogers, R. R., D. W. Krause, K. Curry Rogers, A. Rasoamiaramanana, and L. Rahantarisoa. 2007. Perspectives on the paleoenvironment and paleoecology of the Late Cretaceous Malagasy theropod *Majungasaurus crenatissimus*; pp. 21–31 in S. D. Sampson and D. W. Krause (eds.), *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. Society of Vertebrate Paleontology Memoir 8. Journal of Vertebrate Paleontology 27(2, Supplement).

Rogers, R. R., D. W. Krause, K. Curry Rogers, J. R. Groenke, P. M. O'Connor, and J. J. W. Sertich. 2017. Twenty years of taphonomic observations and insights in the Upper Cretaceous Maevarano Formation, Madagascar. Journal of Vertebrate Paleontology 37 (Program and Abstracts):186.

Rogers, R. R., D. W. Krause, K. Curry Rogers, P. M. O'Connor, J. J. W. Sertich, J. R. Groenke, and S. H. Burch. 2018. Taphonomy of the Maevarano Formation vertebrate assemblage: life and death in the Late Cretaceous of Madagascar; p. 714 in 5th International Paleontological Congress, Paris, France, Abstract Book. July 9–13, 2018.

Rogers, R. R., D. W. Krause, S. C. Kast, M. S. Marshall, L. Rahantarisoa, C. R. Robins, and J. J. W. Sertich. 2013. A new, richly fossiliferous member comprised of tidal deposits in the Upper Cretaceous Maevarano Formation, northwestern Madagascar. Cretaceous Research 44:12–29.

Romiguier, J., V. Ranwez, E. J. P. Douzery, and N. Galtier. 2013. Genomic evidence for large, long-lived ancestors of placental mammals. Molecular Biology and Evolution 30:5–13.

Rougier, G. W. 1993. *Vincelestes neuquenianus* Bonaparte (Mammalia, Theria) un primitivo mamífero del Cretácico Inferior de la Cuenca Neuquina. Ph.D. dissertation, Universidad de Buenos Aires, Buenos Aires, Argentina, 720 pp.

Rougier, G. W., S. Apesteguía, and L. C. Gaetano. 2011. Highly specialized mammalian skulls from the Late Cretaceous of South America. Nature 479:98–102.

Rougier, G. W., J. R. Wible, and J. A. Hopson. 1992. Reconstruction of the cranial vessels in the Early Cretaceous mammal *Vincelestes neuquenianus*: implications for the evolution of the mammalian cranial vascular system. Journal of Vertebrate Paleontology 12:188–216.

Rougier, G. W., A. M. Forasiepi, R. V. Hill, and M. J. Novacek. 2009. New mammalian remains from the Late Cretaceous La Colonia Formation, Patagonia, Argentina. Acta Palaeontologica Polonica 54:195–212.

Rougier, G. W., M. J. Novacek, R. Pascual, J. N. Gelfo, and D. Cladera. 2000. New Late Cretaceous mammals from Argentina and the survival of Mesozoic lineages in the Patagonian Early Tertiary. Journal of Vertebrate Paleontology 20(3, Supplement):65A.

Rougier, G. W., A. S. Sheth, B. K. Spurlin, M. Bolortsetseg, and M. J. Novacek. 2016. Craniodental anatomy of a new Late Cretaceous multituberculate mammal from Udan Sayr, Mongolia. Palaeontologia Polonica 67:197–248.

Sampson, S. D., and D. W. Krause (eds.). 2007. *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. Society of Vertebrate Paleontology Memoir 8. Journal of Vertebrate Paleontology 27(2, Supplement), 184 pp.

Sampson, S. D., and L. D. Witmer. 2007. Craniofacial anatomy of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar; pp. 32–102 in S. D. Sampson and D. W. Krause (eds.), *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. Society of Vertebrate Paleontology Memoir 8. Journal of Vertebrate Paleontology 27(2, Supplement).

Schettino, A., and C. R. Scotese. 2005. Apparent polar wander paths for the major continents (200 Ma to the present day): a palaeomagnetic reference frame for global plate tectonic reconstructions. Geophysical Journal International 163:727–759.

Sereno, P. C. 2006. Shoulder girdle and forelimb in multituberculates: evolution of parasagittal forelimb posture in mammals; pp. 315–366 in M. T. Carrano, T. J. Gaudin, R. W. Blob, and J. R. Wible (eds.), Amniote Paleobiology: Perspectives on the Evolution of Mammals, Birds, and Reptiles. A Volume Honoring James Allen Hopson. The University of Chicago Press, Chicago, Illinois.

Sheldon, N. D., G. J. Retallack, and S. Tanaka. 2002. Geochemical climofunctions from North American soils and application to paleosols across the Eocene-Oligocene boundary in Oregon. Journal of Geology 110:687–696.

Shomon, J. J. 1953. Animal tracks—and how to know them. Virginia Wildlife Magazine, Reprint D-11.

Smith, F. A., A. G. Boyer, J. H. Brown, D. P. Costa, T. Dayan, S. K. Morgan Ernest, A. R. Evans, M. Fortelius, J. L. Gittleman, M. J. Hamilton, L. E. Harding, K. Lintulaakso, S. K. Lyons, C. McCain, J. G. Okie, J. J. Saarinen, R. M. Sibly, P. R. Stephens, J. Theodor, and M. D. Uhen. 2010. The evolution of maximum body size of terrestrial mammals. Science 330:1216–1219.

Smith, T., and Codrea, V. 2015. Red iron-pigmented tooth enamel in a multituberculate mammal from the Late Cretaceous Transylvanian 'Haţeg Island.' PLoS ONE 10:e0132550.

Stanford, R., M. G. Lockley, C. Tucker, S. Godfrey, and S. M. Stanford. 2018. A diverse mammal-dominated, footprint assemblage from wetland deposits in the Lower Cretaceous of Maryland. Scientific Reports 8:741.

Stigall, A. L., and J. H. Hartman. 2008. A new spinicaudatan genus (Crustacea: 'Conchostraca') from the Late Cretaceous of Madagascar. Palaeontology 51:1053–1067.

Storey, M., J. J. Mahoney, and A. D. Saunders. 1997. Cretaceous basalts in Madagascar and the transition between plume and continental lithosphere mantle sources; pp. 95–122 in J. J. Mahoney and M. F. Coffin (eds.), Large Igneous Provinces. Continental, Oceanic, and Planetary Flood Volcanism. Geophysical Monograph 100. American Geophysical Union, Washington, D.C.

Storey, M., J. J. Mahoney, A. D. Saunders, R. A. Duncan, S. P. Kelly, and M. F. Coffin. 1995. Timing of hot spot-related volcanism and the breakup of Madagascar and India. Science 267:852–855.

Sutton, M. D. 2008. Tomographic techniques for the study of exceptionally preserved fossils. Proceedings of the Royal Society B: Biological Sciences 275:1587–1593.

Szajna, M. J., and S. M. Silvestri. 1996. A new occurrence of the ichnogenus *Brachychirotherium*: implications for the Triassic-Jurassic mass extinction event; pp. 275–283 in M. Morales (ed.), The Continental Jurassic. Museum of Northern Arizona Bulletin 40.

Torsvik, T. H., and L. R. M. Cocks. 2017. Earth History and Palaeogeography. Cambridge University Press, Cambridge, U.K., 317 pp.

Torsvik, T. H., R. D. Tucker, L. D. Ashwal, E. A. Eide, N. A. Rakotosolofo, and M. J. de Wit. 1998. Late Cretaceous magmatism in Madagascar: palaeomagnetic evidence for a stationary Marion hotspot. Earth and Planetary Science Letters 164:221–232.

Torsvik, T. H., R. D. Tucker, L. D. Ashwal, L. M. Carter, B. Jamtveit, K. T. Vidyadharan, and P. Venkataramana. 2000. Late Cretaceous India-Madagascar fit and timing of break-up related magmatism. Terra Nova 12:220–224.

Walls, G. L. 1942. The Vertebrate Eye and Its Adaptive Radiation. Cranbrook Institute of Science, Bloomfield Hills, Michigan, 785 pp.

Wang, H., J. Meng, and Y. Wang. 2019. Cretaceous fossil reveals a new pattern of mammalian middle ear evolution. Nature 576:102–105.

Weil, A. 2005. Living large in the Cretaceous. Nature 433:116–117.

Wells, N. A. 2003. Some hypotheses on the Mesozoic and Cenozoic paleoenvironmental history of Madagascar; pp. 16–34 in S. M. Goodman and J. P. Benstead (eds.), The Natural History of Madagascar. The University of Chicago Press, Chicago, Illinois.

Whatley, R., and G. A. Buckley. 2004. A hatchling crocodyliform from the Upper Cretaceous Maevarano Formation, Madagascar. Journal of Vertebrate Paleontology 24(3, Supplement):128A.

Wible, J. R., S. L. Shelley, and S. Bi. 2019. New genus and species of djadochtatheriid multituberculate (Allotheria, Mammalia) from the Upper Cretaceous Bayan Mandahu Formation of Inner Mongolia. Annals of Carnegie Museum 85:285–327.

Wible, J. R., G. W. Rougier, M. J. Novacek, and R. J. Asher. 2007. Cretaceous eutherians and Laurasian origin for placental mammals near the K/T boundary. Nature 447:1003–1006.

Wilson, G. P., M. Dechesne, and I. R. Anderson. 2010. New latest Cretaceous mammals from northeastern Colorado with biochronologic and biogeographic implications. Journal of Vertebrate Paleontology 30:499–520.

Wilson, G. P., E. G. Ekdale, J. W. Hoganson, J. J. Calede, and A. Vander Linden. 2016. A large carnivorous mammal from the Late Cretaceous and the North American origin of marsupials. Nature Communications 7:13734.

Wilson, G. P., A. R. Evans, I. J. Corfe, P. D. Smits, M. Fortelius, and J. Jernvall. 2012. Adaptive radiation of multituberculate mammals before the extinction of dinosaurs. Nature 483:457–460.

Xu, L., X. Zhang, H. Pu, S. Jia, J. Zhang, J. Lü, and J. Meng. 2015. Largest known Mesozoic multituberculate from Eurasia and implications for multituberculate evolution and biology. Scientific Reports 5:14950.

Yatheesh, V., G. C., Bhattacharya, and K. Mahender. 2006. The terrace like feature in the mid-continental slope region off Trivandrum and a plausible model for India-Madagascar juxtaposition in immediate pre-drift scenario. Gondwana Research 10:179–185.

Yatheesh, V., P. J. Kurian, G. C. Bhattacharya, and S. Rajan. 2013. Morphotectonic architecture of an India-Madagascar breakup related anomalous submarine terrace complex on the southwest continental margin of India. Marine and Petroleum Geology 46:304–318.

Yuan, C., L. Xu, X. Zhang, Y. Xi, Y. Wu, and Q. Ji. 2009. A new species of *Gobiconodon* (Mammalia) from western Liaoning, China and its implication for the dental formula of *Gobiconodon*. Acta Geologica Sinica 83:207–211.

Yuan, C.-X., Q. Ji, Q.-J. Meng, A. R. Tabrum, and Z.-X. Luo. 2013. Earliest evolution of multituberculate mammals revealed by a new Jurassic fossil. Science 341:779–783.

Zeveloff, S. I. 2002. Raccoons: A Natural History. Smithsonian Books, Washington, D.C., 200 pp.

Zheng, X., S. Bi, X. Wang, and J. Meng. 2013. A new arboreal haramiyid shows the diversity of crown mammals in the Jurassic period. Nature 500:199–202.

Zhou, C.-F., S. Wu, T. Martin, and Z.-X. Luo. 2013. A Jurassic mammaliaform and the earliest mammalian evolutionary adaptations. Nature 500:163–167.

Zhou, C.-F., B.-A. S. Bhullar, A. I. Neander, T. Martin, and Z.-X. Luo. 2019. New Jurassic mammaliaform sheds light on early evolution of mammal-like hyoid bones. Science 365:276–279.

Submitted November 6, 2018; revisions received May 29, 2020; accepted May 31, 2020.

Memoir Editors: Lars Werdelin and Patrick O'Connor.