LETTERS

# The evolution of mammal-like crocodyliforms in the Cretaceous Period of Gondwana

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**Fossil crocodyliforms discovered in recent years[1–5] have revealed a level of morphological and ecological diversity not exhibited by extant members of the group. This diversity is particularly notable among taxa of the Cretaceous Period (144–65 million years ago) recovered from former Gondwanan landmasses. Here we report the discovery of a new species of Cretaceous notosuchian crocodyliform from the Rukwa Rift Basin[6] of southwestern Tanzania. This small-bodied form deviates significantly from more typical crocodyliform craniodental morphologies, having a short, broad skull, robust lower jaw, and a dentition with relatively few teeth that nonetheless show marked heterodonty. The presence of morphologically complex, complementary upper and lower molariform teeth suggests a degree of crown–crown contact during jaw adduction that is unmatched among known crocodyliforms, paralleling the level of occlusal complexity seen in mammals and their extinct relatives[7–12]. The presence of another small-bodied mammal-like crocodyliform in the Cretaceous of Gondwana indicates that notosuchians probably filled niches and inhabited ecomorphospace that were otherwise occupied by mammals on northern continents.**

Specimens of the new notosuchian crocodyliform were recovered from several locations in the middle Cretaceous Galula Formation[6] exposed in the Mbeya Region of southwestern Tanzania. The new crocodyliform adds a small-bodied constituent to the terrestrial vertebrate fauna of continental Africa, and exemplifies the extreme mammal-like heterodonty realized by Gondwanan notosuchians during the Cretaceous. Given the scarcity of Cretaceous-age vertebrate assemblages from subequatorial Africa[6,13], and indeed much of Gondwana, the new form is crucial for exploring the evolutionary dynamics of terrestrial faunas on southern landmasses.

Archosauria Cope, 1869
Crocodyliformes Hay, 1930 (sensu Clark in Benton and Clark, 1988)
Mesoeucrocodylia Whetstone and Whybrow, 1983
Notosuchia Gasparini, 1971
*Pakasuchus kapilimai* gen. et sp. nov.

**Etymology.** From *Paka*, Kiswahili for 'cat' in reference to the short, low skull with molariform teeth reminiscent of carnassials in mammalian carnivores, and *souchos* (Gr.), crocodile; and *kapilimai*, in honour of the late Professor Saidi Kapilima (University of Dar es Salaam), a key contributor to the Rukwa Rift Basin Project.

**Holotype.** RRBP (Rukwa Rift Basin Project (Tanzanian Antiquities Unit)) 08631 is an articulated skull and skeleton (Figs 1, 2).

**Referred material.** RRBP 05103, partial skull preserving left maxilla, lower jaw and eight postcaniniform teeth (Fig. 2).

**Type locality and horizon.** Locality RRBP 2007-04, ~20 km south of Lake Rukwa, Rukwa Rift Basin, Tanzania (see Supplementary Information); Galula Formation, mid-Cretaceous[6].

**Diagnosis.** *Pakasuchus* differs from other crocodyliforms in possessing the following unique combination of characters: extreme heterodonty with reduced tooth count (8 lower quadrant, 5 upper quadrant); trenchant molariform cheek-teeth with paired rostrocaudally-oriented crests; rostroventrolaterally projecting pterygoid flanges; dorsally flared squamosal at contact with parietal; biplanar articular–quadrate articulation bracketed laterally by an expanded surangular; reduced osteoderms in thorax, with a normal complement of osteoderms surrounding the tail.

**Description and comparison.** The holotype (RRBP 08631) of *Pakasuchus* is represented by a virtually complete, exquisitely preserved articulated skull and skeleton (skull length, 7 cm; snout-vent length, 30 cm; Fig. 1). The tapered skull is low and broad and generally similar to those of many notosuchians[5,14,15]. External sculpture on the facial elements is reduced or absent altogether, whereas the dorsal surface of the cranium shows moderate sculpturing. The maxilla is vertical, with limited exposure on the dorsal surface of the rostrum (Fig. 1b). The external nares face rostrally, as is typical of many terrestrial crocodyliforms[1–3,14–16].

The maxilla preserves an alveolar trough rather than individual alveoli. A complete palatine–pterygoid secondary palate is present. The fused pterygoids form the roof and caudal margins of the choanal groove and include a rostrolaterally directed pterygoid flange. There is no antorbital fenestra (Fig. 1b), similar to the condition in the South American notosuchians *Mariliasuchus*[2] and *Adamantinasuchus*[3]. The lower jaw is deep and has a laterally expanded para-alveolar shelf, an enlarged mandibular fenestra and a rostrally extended splenial that forms one-third of the symphysis (Figs 1, 2). The hypertrophied lower caniniform tooth has a distinct alveolus, whereas the postcaniniform teeth are situated in an undulating alveolar trough. The quadrate–articular joint is bi-planar, with both horizontal and near-vertical articular surfaces (Fig. 2k, l). The articular is flat rather than concave, indicating the potential for substantial rostrocaudal translation of the lower jaw. The dorsally expanded surangular forms an enhanced lateral buttress for the jaw joint (Fig. 2l), further constraining movements of the lower jaw.

*Pakasuchus* shows extreme variation in dental size and shape, with distinct caniniform, premolariform and molariform teeth (Fig. 2). Although the specimen was preserved with the jaws closed, X-ray

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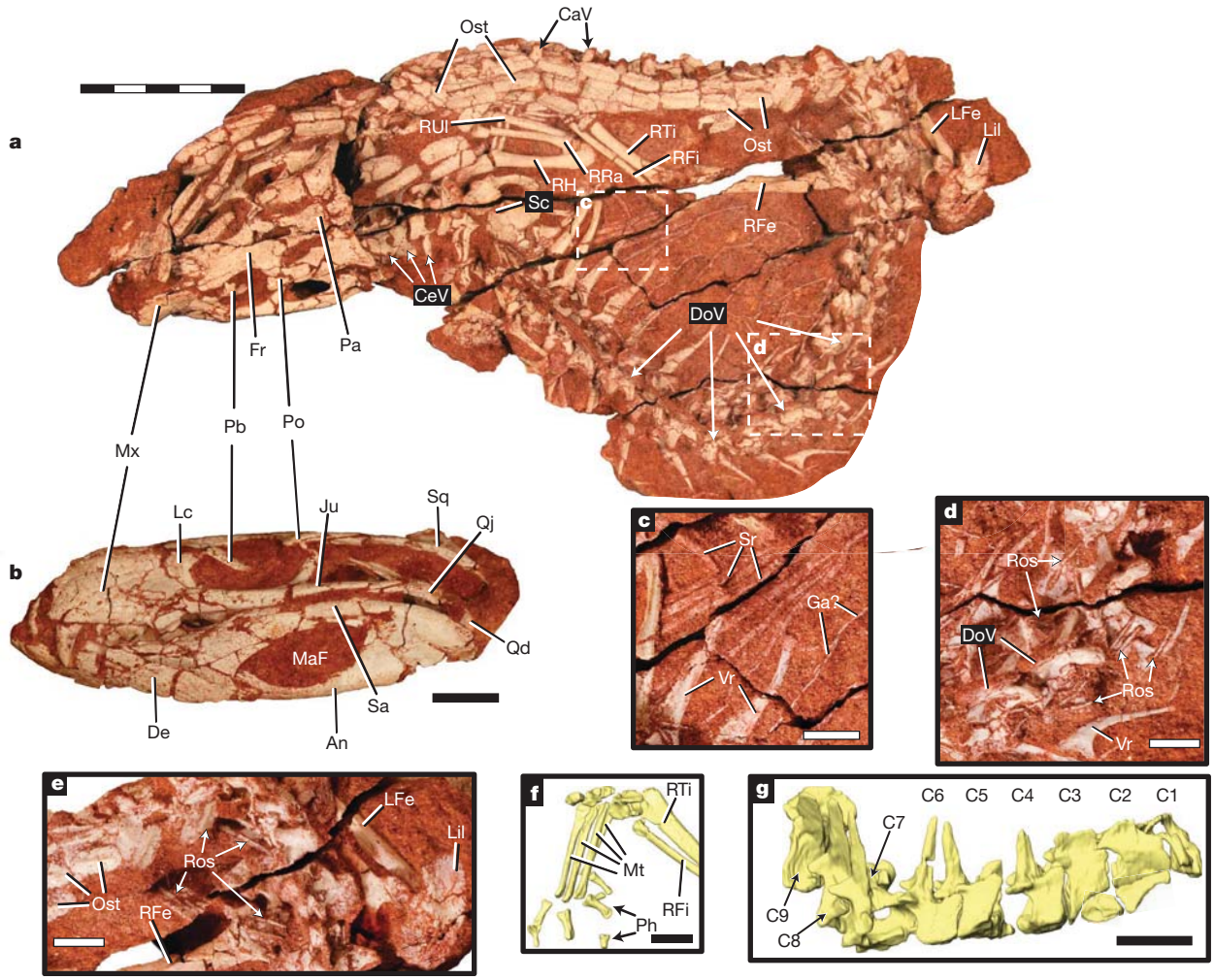


**Figure 1 | *Pakasuchus kapilimai*.** **a–g**, RRBP (Rukwa Rift Basin Project) 08631, holotype specimen. **a**, Skeleton in dorsal view. **b**, Skull in left lateral view. **c**, Vertebral and sternal ribs. **d**, Reduced trunk osteoderms. **e**, Transition from reduced trunk osteoderms to normal tail osteoderms. **f**, Reconstructed micro-CT scan of distal hind limb (extracted from within matrix). **g**, Reconstructed micro-CT scan of cervical vertebrae in right lateral view. Dashed boxes (white) in **a** indicate the positions of **c** and **d**. Scale bars: 5 cm in **a**; 1 cm in **b–g**. Abbreviations: An, angular; CaV, caudal vertebra; CeV, cervical vertebra; De, dentary; C1–C9, cervical vertebrae and position; DoV, dorsal vertebrae; Fr, frontal; Ga?, gastralia; Ju, jugal; Lc, lacrimal; LFe, left femur; Lil, ilium; MaF, mandibular fenestra; Mt, metatarsal; Mx, maxilla; Ost, caudal osteoderm; Pa, parietal; Pb, palpebral; Ph, phalanges; Qd, quadrate; Qj, quadratojugal; RRa, right radius; RFe, right femur; RFi, right fibula; RH, right humerus; Ros, reduced osteoderms; RTi, right tibia; RUl, right ulna; Sa, surangular; Sc, scapula; Sq, squamosal; Sr, sternal rib; Vr, vertebral rib.

computed tomography of the holotype and referred specimen reveals a dental formula of five (5) maxillary and eight (8) mandibular teeth (Figs 1,2). Incisiform teeth as described in other notosuchians[2,3,17–19] either are not preserved or were absent in *Pakasuchus*. All teeth in the post-caniniform series show a distinct constriction between the crown and root (Fig. 2). The maxillary dentition is characterized by an enlarged caniniform tooth in position one that is immediately followed by a small conical tooth (Fig. 2a). Two large molariforms occupy positions three and four, and the ultimate tooth is a small molariform tooth at the extreme caudal end of the alveolar trough. The lower dentition consists of a large caniniform in position one, followed immediately by five small 'premolariform' teeth in positions two through six. Positions seven and eight accommodate two molariform teeth situated opposite the two large maxillary molariforms.

*Pakasuchus* is unique among crocodyliforms, including the dentally diverse notosuchians, in having fully complementary upper and lower molariform cheek-teeth (Fig. 2c–j). The crown on both upper and lower molariforms has two parallel, rostrocaudally oriented crests separated by a longitudinal trough (Fig. 2d, g). This degree of complementary occlusal morphology maximizes crown–crown contact, providing two shearing edges separated by a trough for processing food. Importantly, microcomputed tomography (microCT) of unerupted molariform tooth crowns reveals that the complex trough-crest morphology observed in the working dentition is primary in nature and not the result of wear (Supplementary Fig. 3). The complex morphology and high degree of occlusal precision of the cheek teeth in *Pakasuchus* shows a level of sophistication otherwise seen only in mammals. Moreover, the morphology of the elongate quadrate–articular joint (Fig. 2k, l) provides additional evidence for the derived nature of jaw mobility in this form, with potential movements limited to rotation and rostrocaudal translation of the lower jaw. Although it has been hypothesised that other notosuchians possessed proal kinematics (anterior displacement during the power stroke)[2,4,14,15], no other form has such highly corresponding molariform occlusal morphology. The organization of opposing molariform occlusal surfaces (for example, canted occlusal surfaces) indicates that maximum crown–crown contact would probably have occurred during upward (orthal) and anterior (proal) displacement of the lower jaw during adduction.

The postcranial skeleton of *Pakasuchus* is characterized by long, gracile limbs and an elongated and relatively mobile thorax (Fig. 1). *Pakasuchus* is unique among crocodyliforms in having extremely reduced osteoderms in the trunk region (Fig. 1d), in contrast to the heavily armoured condition characterizing virtually all living and

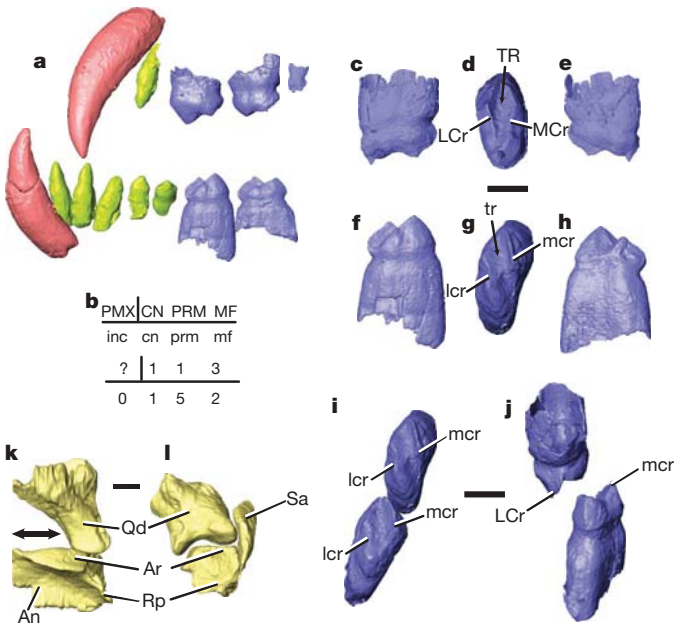


**Figure 2 | Reconstruction of the dentition of *Pakasuchus kapilimai* derived from X-ray computed tomography scans.** **a**, Composite reconstruction of left dentition (RRBP 08631, RRBP 05103) to illustrate size and shape heterodonty in dental series. **b**, Dental classification (above) by tooth position and quadrant-specific (below) dental formula. **c–h**, Lateral (**c**, **f**), occlusal (**d**, **g**), and lingual (**e**, **h**) views of left upper (**c–e**) and left lower (**f–h**) molariform teeth (RRBP 05103). **i**, Occlusal view of left first and second lower molariform teeth (RRBP 05103). **j**, Oblique caudodorsal view of left upper and lower molariform teeth to illustrate complementarity of occlusal surfaces (RRBP 05103). **k, l**, Right jaw (quadrate–articular) joint in medial (**k**) and caudal (**l**) views (RRBP 08631). Colour coding: red, caniniform; green, premolariform; blue, molariform teeth. Arrow (**k**) indicates potential sliding movement at quadrate-articular articulation. Scale bars = 0.5 cm. Abbreviations: An, angular; Ar, articular; CN/cn, caniniform; inc, incisiform; LCr/lcr, lateral crest on molariform; MCr/mcr, medial crest on molariform; MF/mf, molariform; PRM/prm, premolariform; PMX, premaxillary dentition; Qd, quadrate; Rp, retroarticular process; Sa, surangular; Tr/tr, molariform trough. Upper case indicates upper dentition, lower case indicates lower dentition.

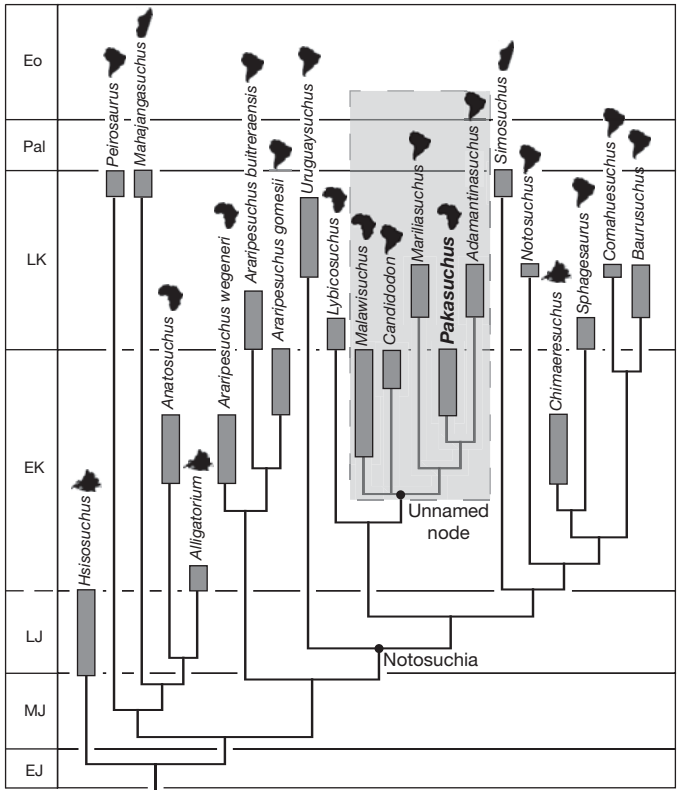


**Figure 3 | Phylogenetic relationships of *Pakasuchus kapilimai* within crocodyliforms.** Stratigraphically calibrated phylogeny of the restricted notosuchian data set with geography indicated by silhouettes: Africa, South America, Madagascar and Asia (China). See Supplementary Information for the analysis protocol, data matrix, character list and discussion. Abbreviations: EJ, Early Jurassic; EK, Early Cretaceous; Eo, Eocene; LJ, Late Jurassic; LK, Late Cretaceous; MJ, Middle Jurassic; Pal, Palaeocene.

extinct members of the clade. A bizarre exception to the otherwise reduced armour in *Pakasuchus* is found in the tail, which is encased in osteoderms. Trunk osteoderms consist of bilaterally symmetrical, longitudinally oriented ossifications positioned dorsal to the vertebral column, vertebral ribs and limb girdles (Fig. 1d). Together, the forward-facing external nares and long, gracile limbs indicate that *Pakasuchus* probably occupied a primarily terrestrial, rather than aquatic, niche. The reduced dorsal body armour further enhances this ecomorphological model in that it would have permitted a more active foraging mode for an organism in a terrestrial environment by allowing reduced weight and increased mobility.

A phylogenetic analysis of representatives of all major mesoeucrocodyliform groups positions *Pakasuchus* within Notosuchia (Fig. 3). Characters in support of this placement include only moderate sculpturing on the dorsal aspect of the skull, smooth alveolar margins and regional differentiation of the dentition. *Pakasuchus* in turn shares a number of features (for example, a jugal that does not extend rostral to the orbit, an ultimate maxillary tooth that is less than or equal to half the size of the penultimate maxillary tooth and molarization of cheek-teeth) with a less inclusive clade that comprises *Mariliasuchus*[2], *Adamantinasuchus*[3], *Malawisuchus*[15] and *Candidodon*[20]. Significantly, these taxa are all small-bodied 'middle' Cretaceous (Aptian–Turonian) forms known exclusively from South America and Africa, each interpreted as an atypical crocodyliform with respect to both anatomical (for example, regionally differentiated dentition) and ecological (for example, terrestrial rather than aquatic) characteristics.

The most distinctive features of the group are craniodental specializations related to divergent feeding strategies, which are distinctly different from the condition found in extant crocodylians or inferred from other extinct crocodyliforms. In conjunction with extremely small body size, many notosuchians express marked heterodonty, including postcaniniform dentitions with multi-cusped teeth[15] and/or complete molarization[2,14,21] of cheek-teeth, convergent with patterns in various non-mammalian cynodont[7,8] and mammalian lineages[9–11]. Further exemplifying such trends within Notosuchia, *Pakasuchus kapilimai* shows an additional reduction in the number of postcaniniform teeth combined with precise complementarity between upper and lower molariform teeth (Fig. 2). *Pakasuchus* parallels the level of occlusal complexity found in adaptations that are considered integral during the radiation of mammals.

The clade of notosuchians that shows the highest degree of heterodonty is restricted to the late Early and early Late Cretaceous of Africa and South America (Fig. 3), still united as a single, large landmass (West Gondwana) until near the Early–Late Cretaceous boundary[22]. The diversity of West Gondwanan mammal-like crocodyliforms during this temporal span is interesting in light of the paucity of mammalian taxa recovered from these areas relative to those known from contemporaneous Laurasian terrestrial faunas[11]. Gondwanan mammals that are known from this timeframe are typically either relictual representatives of cosmopolitan archaic therian groups (for example, eutriconodontans)[11] or members of Gondwanan-restricted clades that show highly derived morphologies (for example, extreme hypsodonty in gondwanatherians)[23–25]. By contrast, Cretaceous Laurasian mammalian assemblages consist of multituberculates, metatherians and basal eutherians, groups that appear to be restricted or absent altogether from contemporaneous Gondwanan assemblages[11]. Crocodyliform

and mammalian diversification patterns suggest that faunal dynamics were different on the northern and southern landmasses, perhaps related to the differential radiation of small-bodied terrestrial forms. Fossil evidence recovered so far indicates that multituberculate, metatherian and eutherian mammals radiated broadly in Laurasia, with notosuchian crocodyliforms and gondwanatherian and 'archaic' mammalian lineages occupying similar niches (for example, small-bodied, terrestrial faunivores) throughout Gondwana.

Notosuchian crocodyliforms have been interpreted to exhibit either mammal-like[4,15] or herbivorous reptile-like[1] dental morphologies, no doubt related to alteration in the fundamental signalling pathways that underlie both individual tooth development[26–28] and global organization of the dental arcade[29,30]. Notosuchian craniodental novelty probably represents an example of evolutionary-developmental experimentation by a clade in the absence of potentially competitive ecomorphs from other major tetrapod groups (that is, mammals). After the Mesozoic, a number of crocodyliform lineages, including notosuchians, either became extinct, or experienced a marked canalization in morphology as reflected by the restricted bauplan of extant crocodylians. The disappearance of so many intriguing Cretaceous forms might therefore reflect a reduction in ecomorphospace owing to environmental change, the arrival or emergence of new forms, or both.

## METHODS SUMMARY

The small size and state of preservation of the specimens (that is, upper and lower jaws recovered in a closed position) prompted the use of high-resolution X-ray microCT to elucidate details of morphology related to the teeth and jaws. X-ray microCT was conducted at the Ohio University μCT Facility (GE eXplore Locus *in-vivo* microCT scanner) using the following protocol: 85 kVp, 400 mA and a slice thickness of 0.045 mm. VFF and DICOM files were compiled into three-dimensional reconstructions with visualizations obtained using the AMIRA 4.1 Advanced Graphics Package.

**Received 22 December 2009; accepted 25 March 2010.**


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**Supplementary Information** is linked to the online version of the paper at www.nature.com/nature.

**Acknowledgements** We thank: D. Kamamba, F. Ndunguru (Tanzania Antiquities Unit), P. Msemwa (Tanzania Museum of House of Culture), I. Marobhe (University of Dar es Salaam), and the Tanzania Commission for Science and Technology for support; J.P. Cavigelli and V. Heisey for specimen preparation; M. Getty, E. Lund, S. Burch, V. Simons, E. Simons, J. Garcia-Massini, G. Masai, and A. Mussa for field assistance; P. Sereno, E. Gomani, and C. Chiumia for specimen access; J. Sidote for digital processing assistance. This research was supported by the US National Science Foundation (NSF EAR-0617561, EAR-0854218), the National Geographic Society (CRE), the University of the Witwatersrand, the Michigan State University Office of Research and Graduate Studies, and the Ohio University College of Osteopathic Medicine and Ohio University Office of Research and Sponsored Programs.

**Author Contributions** P.M.O., N.J.S., E.M.R. and M.D.G. developed the field project. P.M.O., J.J.W.S., N.J.S., T.L.H. and R.R. conducted the research. P.M.O., J.J.W.S., N.J.S., E.M.R., M.D.G. and S.E.N. wrote the manuscript. P.M.O., N.J.S., E.M.R., M.D.G., Z.A.J., and J.T. excavated the specimens.

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