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Overview of the discovery, distribution, and geological context of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar

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OVERVIEW OF THE DISCOVERY, DISTRIBUTION, AND GEOLOGICAL CONTEXT OF *SIMOSUCHUS CLARKI* (CROCODYLIFORMES: NOTOSUCHIA) FROM THE LATE CRETACEOUS OF MADAGASCAR

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ABSTRACT—*Simosuchus clarki* is a bizarre, pug-nosed notosuchian crocodyliform known only from the Upper Cretaceous (Maastrichtian) Maevarano Formation in the Mahajanga Basin of northwestern Madagascar. When originally named and described in 2000, *S. clarki* was based entirely on a single specimen that included a nearly complete skull and lower jaw preserved in articulation with the anterior and mid-trunk portions of the postcranial skeleton, as well as several associated elements from the posterior region. The species is now represented by three additional partial and nearly complete articulated skeletons, as well as numerous isolated elements (mostly teeth), that permit detailed description of its entire bony anatomy, the primary subject of other chapters in this volume. These specimens were discovered as part of the ‘Mahajanga Basin Project,’ initiated in 1993 and conducted jointly by Stony Brook University and the Université d’Antananarivo, in the Berivotra and Masiakakoho study areas. The best-preserved specimens of *S. clarki* were entombed in massive, poorly sorted, clay-rich debris flow deposits (facies 2 of the Anembalemba Member) that accumulated in channel belts in response to exceptional rainfall events. *Simosuchus*, along with its contemporaries in the Maevarano assemblage, lived in a strongly seasonal, semi-arid climate some 20 million years after Madagascar separated from the India/Seychelles block and became an island isolated in the Indian Ocean.

INTRODUCTION

In 2000, Buckley et al. announced the discovery of a remarkably complete and exquisitely preserved specimen of a new mesoeucrocodylian crocodyliform, *Simosuchus clarki*, from the Upper Cretaceous Maevarano Formation, Mahajanga Basin, northwestern Madagascar (Fig. 1). This specimen, Université d’Antananarivo (UA) specimen number 8679, designated as the holotype, consists of a virtually complete and undistorted skull and lower jaw as well as the majority of the postcranial skeleton, though much of the posterior trunk and caudal regions are missing (Fig. 2). *Simosuchus clarki* was characterized by Buckley et al. (2000:941) as having among its most salient features “an extremely blunt snout, a tall, rounded skull, an anteriorly shifted jaw joint and clove-shaped, multicused teeth,” and therefore deviating significantly from the ‘typical’ crocodyliform Bauplan of “an elongate snout with an array of conical teeth, a dorsoventrally flattened skull and a posteriorly positioned jaw articulation.” A preliminary phylogenetic analysis suggested a close relationship to the South American notosuchian *Uruguaysuchus* (see Rusconi, 1933). Subsequent analyses (e.g., Tykoski et al., 2002; Pol, 2003; Sereno et al., 2003; Turner and Calvo, 2005; Turner and Buckley, 2008; Sereno and Larsson, 2009) have largely corroborated placement of *Simosuchus* within Notosuchia. One notable exception is Carvalho et al. (2004), who placed *Simosuchus*, along with *Chimaerasuchus*, outside of Notosuchia within a new taxon, Chimaerasuchidae. For a more detailed overview and reassessment of the phylogenetic relationships of *Simosuchus*, see Turner and Sertich (this volume).

Pending a more thorough analysis of function, various aspects of the cranial and postcranial morphology (e.g., anterolaterally

positioned external nares; laterally positioned orbits; short, flat, shovel-like snout; deep skull; posteroventrally positioned occipital condyle; short, underslung mandible; enlarged processes on cervical vertebrae) suggested to Buckley et al. (2000) a terrestrial, perhaps burrowing, lifestyle for *Simosuchus*. The morphology of the foliform, multicused teeth indicated an herbivorous diet to the authors; this hypothesis was supported by cranial features (relatively anterior position of jaw joint, short mandible) that are inconsistent with the condition seen in most other crocodyliforms, where advantages of both force and velocity related to carnivory are gained through relatively posterior placement of the jaw joint.

The report by Buckley et al. (2000) was based exclusively on the holotype and only known specimen, UA 8679, discovered during the 1998 field season, which was the fourth of nine such field seasons of the Mahajanga Basin Project, conducted jointly by Stony Brook University and the Université d’Antananarivo. Since its inception in 1993, the Mahajanga Basin Project has resulted in the discovery of a considerable diversity of vertebrates, including ray-finned fishes, anurans, turtles, snakes, non-ophidian squamates (‘lizards’), crocodyliforms, birds, non-avian dinosaurs, and mammals (see most recent review in Krause et al., 2006). The crocodyliform assemblage is particularly diverse and, in addition to *S. clarki*, includes *Mahajangasuchus insignis* (see Buckley and Brochu, 1999; Turner and Buckley, 2008), *Arariipesuchus tsangatsangana* (see Turner, 2006), *Miadanasuchus oblita* (see Buffetaut and Taquet, 1979; Simons and Buckley, 2009), and at least two other taxa that, though announced in preliminary fashion (Buckley and Brochu, 1996; Buckley et al., 1997, 2003), are still in various stages of description and analysis. Some of these taxa contributed substantially to a preliminary analysis of the biogeographic relationships of Cretaceous crocodyliforms by Turner (2004).

*Corresponding author.

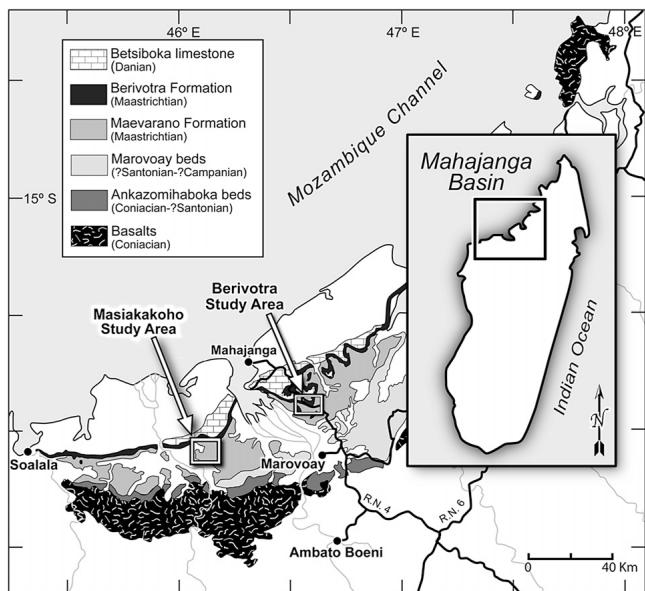


FIGURE 1. Map depicting the outcrop area of Cretaceous and Paleocene strata in the Mahajanga Basin of northwestern Madagascar and the Berivotra and Masiakakoho study areas of the Mahajanga Basin Project. Question marks in legend indicate current uncertainty concerning age estimates.

Since the discovery of the holotype specimen of *S. clarki* in the 1998 field season, subsequent expeditions have resulted in the discovery of three additional, partially articulated specimens: FMNH PR 2596, represented by a nearly complete, though poorly preserved skull, lower jaw, and postcranial skeleton (Fig. 3); FMNH PR 2597, which includes a nearly complete though distorted skull and lower jaw and articulated anterior postcranial skeleton (Fig. 4); and FMNH PR 2598, represented by a well-preserved and articulated caudal skeleton in association with portions of the skull, lower jaw, and appendicular skeleton (Fig. 5). These three specimens in particular fill critical gaps in knowledge and permit documentation of virtually the entire skeletal anatomy, including the osteodermal covering, of this bizarre crocodyliform (Figs. 6, 7). They also have permitted the identification of various isolated elements (primarily teeth) in the Mahajanga Basin Project collections. Despite the recovery of these additional specimens, *S. clarki* remains one of the rarer elements of the vertebrate assemblage from the Maevarano Formation.

This volume expands significantly upon the preliminary report by Buckley et al. (2000) and details current knowledge of *S. clarki* by incorporating the new material. Owing to the relatively complete representation of bony elements, and their often exquisite preservation, this volume is devoted primarily to detailed documentation of the osteology of *S. clarki* by region: head skeleton by Kley et al., postcranial axial skeleton by Georgi and Krause, appendicular skeleton by Sertich and Groenke, and bony integument (osteoderms) by Hill. These descriptions, in concert, allow for a reassessment of phylogenetic and biogeographic relationships of *S. clarki* by Turner and Sertich. The objectives of this introductory chapter are to review the history of discovery of specimens of *S. clarki* and to place this taxon in taxonomic, geographic, and geological context, thereby ‘setting the stage’ for the chapters that follow.

Institutional Abbreviations—FMNH, The Field Museum, Chicago; UA, Université d'Antananarivo, Antananarivo, Madagascar.

SYSTEMATIC PALEONTOLOGY

ARCHOSAURIA Cope, 1869
CROCODYLOMORPHA Walker, 1970
CROCODYLIFORMES Hay, 1930 (sensu Clark, in Benton and Clark, 1988)

MESOEUCROCODYLIA Whetstone and Whybrow, 1983
NOTOSUCHIA Gasparini, 1971

SIMOSUCHUS Buckley, Brochu, Krause, and Pol, 2000

Type Species—*Simosuchus clarki* Buckley, Brochu, Krause, and Pol (2000).

Included Species—Type species only.

Etymology—From *simos* (Greek, σιμός), pug-nosed, and *Souchos* (Greek, Σοῦχος), the Egyptian crocodile-headed god Sobek (Sebek).

Diagnosis—As for type and only known species.

SIMOSUCHUS CLARKI Buckley, Brochu, Krause, and Pol, 2000

Simosuchus clarki Buckley, Brochu, Krause, and Pol, 2000:941, fig. 1.

Type Specimen—UA 8679 (Fig. 2): articulated skull (including left and right pairs of palpebrals), lower jaw, nearly complete element of hyobranchial apparatus (ceratobranchial I?), and anterior and mid-trunk portions of postcranial skeleton, including all eight cervical and first 13 dorsal vertebrae and almost all of their associated ribs, nearly complete pectoral girdle and forelimbs (missing only left phalanges IV-3 and V-2), and anterior dorsal, anterior ventral, and forelimb osteoderms. Numerous teeth (approximately 25); two posterior dorsals, one possible sacral, and three proximal caudal vertebrae; several partial ribs; fragmentary right pubis; various complete (both astragali) and fragmentary elements (both femora, left tibia) of the hind limbs; and numerous osteoderms and osteoderm fragments were recovered in association with the articulated portion of the skeleton. Discovered by L. L. Randriamiaramanana of the Université d'Antananarivo on July 4, 1998.

Etymology—For James M. Clark, “in recognition of his contributions to crocodyliform systematics” (Buckley et al., 2000:941).

Type Locality and Horizon—Locality MAD98-17 (see cover illustration), Berivotra Study Area, Anembalemba Member, Maevarano Formation, Mahajanga Basin, northwestern Madagascar (locality coordinates on file at the Université d'Antananarivo, Stony Brook University, and The Field Museum).

Age and Distribution—Known only from the Late Cretaceous (Maastrichtian) of northwestern Madagascar, in the Berivotra and Masiakakoho study areas of the Mahajanga Basin (Fig. 1).

Localities and Referred Specimens—Specimens of *Simosuchus clarki* (in addition to the holotype) have been recovered from 18 localities (other than the type locality) within the Anembalemba and Masorobe members of the Maevarano Formation, but the majority of these is comprised of isolated teeth.

The Berivotra Study Area yielded (organized by locality, with ‘MAD’ and the locality’s year of discovery as prefix): MAD93-06: UA 9755—isolated tooth; MAD93-14: UA 9756—isolated tooth; MAD93-18: FMNH PR 2824—nearly complete fifth? cervical vertebra, UA 9753—nearly complete right femur; MAD93-33: FMNH PR 2591—isolated tooth, FMNH PR 2592—isolated tooth; MAD93-34: UA 9757—isolated tooth; MAD93-35: FMNH PR 2600—isolated tooth; MAD93-73: UA 9758—isolated tooth; MAD95-11: FMNH PR 2593—isolated tooth; MAD96-01: UA 9759—isolated tooth, UA 9760—isolated tooth; MAD98-25: FMNH PR 2594—isolated tooth; MAD03-03: UA 9762—partial frontal and 36 partial osteoderms; MAD03-09: UA 9761—isolated tooth; MAD05-36: FMNH PR 2597—partial skeleton including articulated but somewhat distorted skull and lower jaw; parts of all of the cervical vertebrae and at least the six anterior-most dorsal vertebrae; approximately 13 dorsal

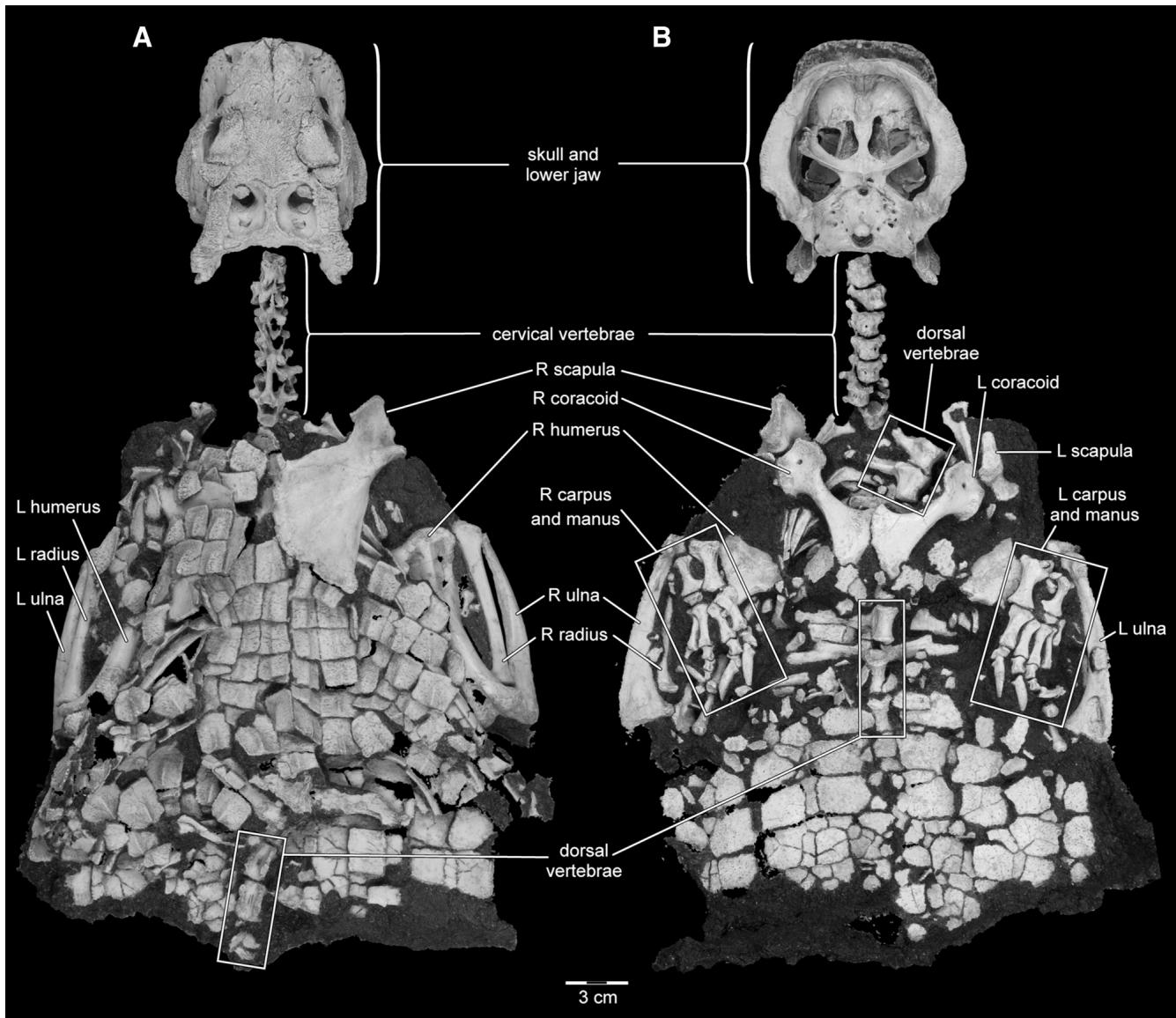


FIGURE 2. Painted cast of UA 8679, the holotype of *Simosuchus clarki*, in **A**, dorsal, and **B**, ventral views. This specimen consists primarily of a virtually complete, well-preserved, and articulated skull and lower jaw and most (primarily the anterior and mid-trunk portions) of the postcranial skeleton. Isolated elements (including those from the posterior part of the skeleton) found associated with the specimen are not shown. Painted cast is illustrated because original specimen was prepared and parts of it disarticulated for study purposes. **Abbreviations:** **L**, left; **R**, right.

ribs (both left and right) in addition to numerous associated rib fragments; partial right and left scapulae; right coracoid; partial left coracoid; right humerus; proximal right radius and ulna; partial left radius; left radiale; fragmentary appendicular elements; numerous associated osteoderms and osteoderm fragments; MAD05-37: FMNH PR 2598—skeleton including portions of the skull and lower jaw (fragmentary right quadratojugal, angular, and surangular); centrum of second? dorsal vertebra and nearly complete caudal vertebral series (with several chevron bones and articulated, unfused ribs on the most proximal vertebrae); fragmentary right coracoid; proximal right humerus; proximal left ulnare; partial right manus including MC-I-MC-IV with five associated phalanges; right and proximal left femora; right tibia; right calcaneum and astragalus; fragments of three metatarsals and six pedal phalanges; rib fragments; numerous articulated and associated appendicular (femoral), dorsal and ventral trunk, and caudal osteoderms (Note: Association

of some elements not in direct articulation is equivocal because FMNH PR 2599 was found nearby), FMNH PR 2599—right articulated calcaneum and astragalus and left calcaneum (Note: Association of these elements is equivocal but is based on size and state of preservation; they were found very near to FMNH PR 2598, but that specimen has a right calcaneum and astragalus in close association with the rest of the skeleton and appears to represent a slightly larger individual); MAD05-42: UA 9854—isolated tooth.

The Masiakakoho Study Area yielded (by locality, with ‘MAD’ and the locality’s year of discovery as prefix): MAD03-17: UA 9776—left distal tibia, five phalanges, partial centrum of first caudal vertebra, and numerous osteoderms and osteoderm fragments; FMNH PR 2596—nearly complete, articulated, but poorly preserved skeleton including entire crushed skull and lower jaw; all eight cervical vertebrae; an undetermined number of dorsal vertebrae (because of poor preservation and osteodermal cover)

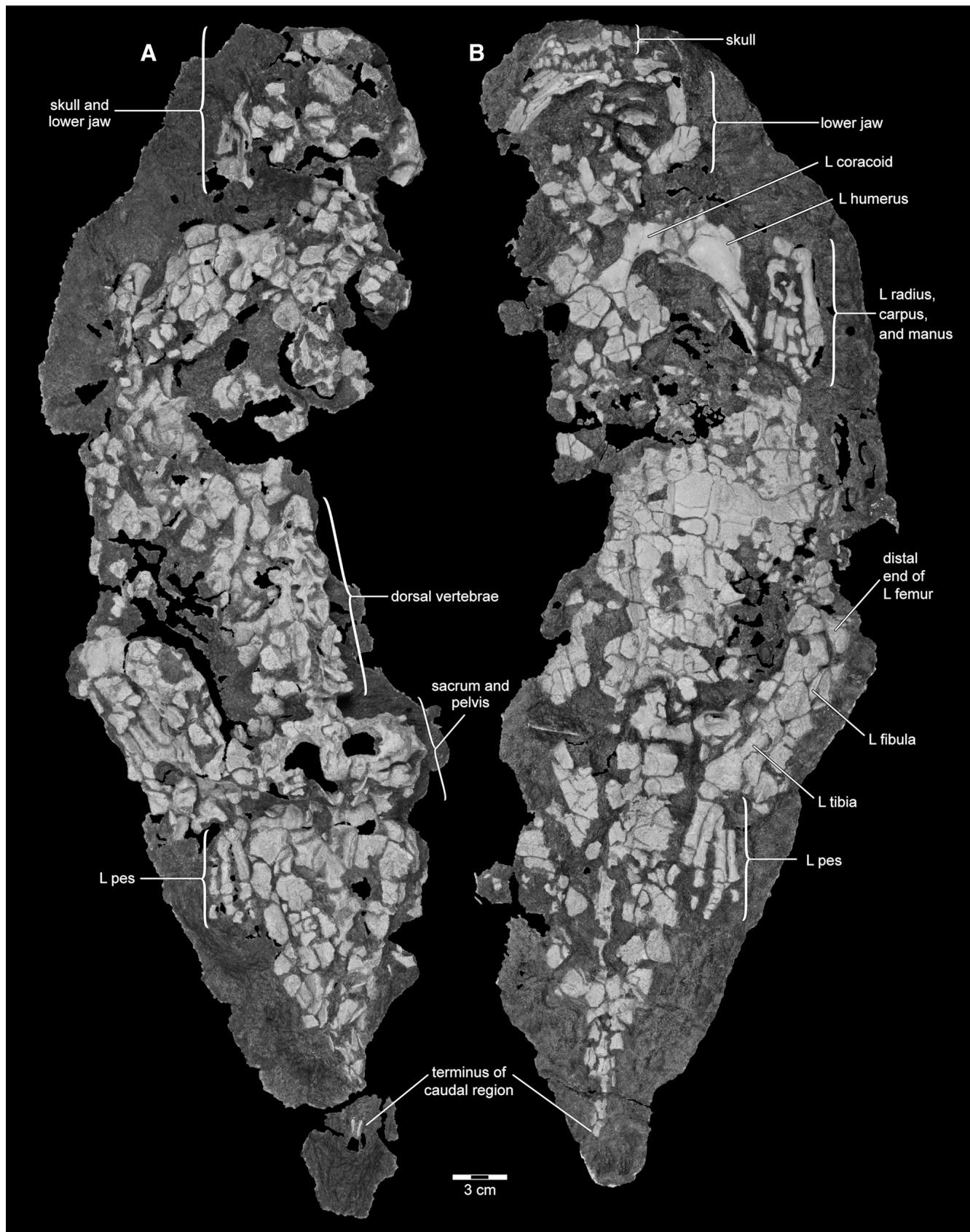


FIGURE 3. Painted cast of FMNH PR 2596, crushed skull and lower jaw and nearly complete, articulated but poorly preserved postcranial skeleton of *Simosuchus clarki*, in **A**, dorsal, and **B**, ventral views. Osteoderms surround the endoskeleton of this specimen and obscure many elements. Painted cast is illustrated because, owing to mottling, it is very difficult to distinguish between bone and matrix on the original specimen. **Abbreviation:** **L**, left.

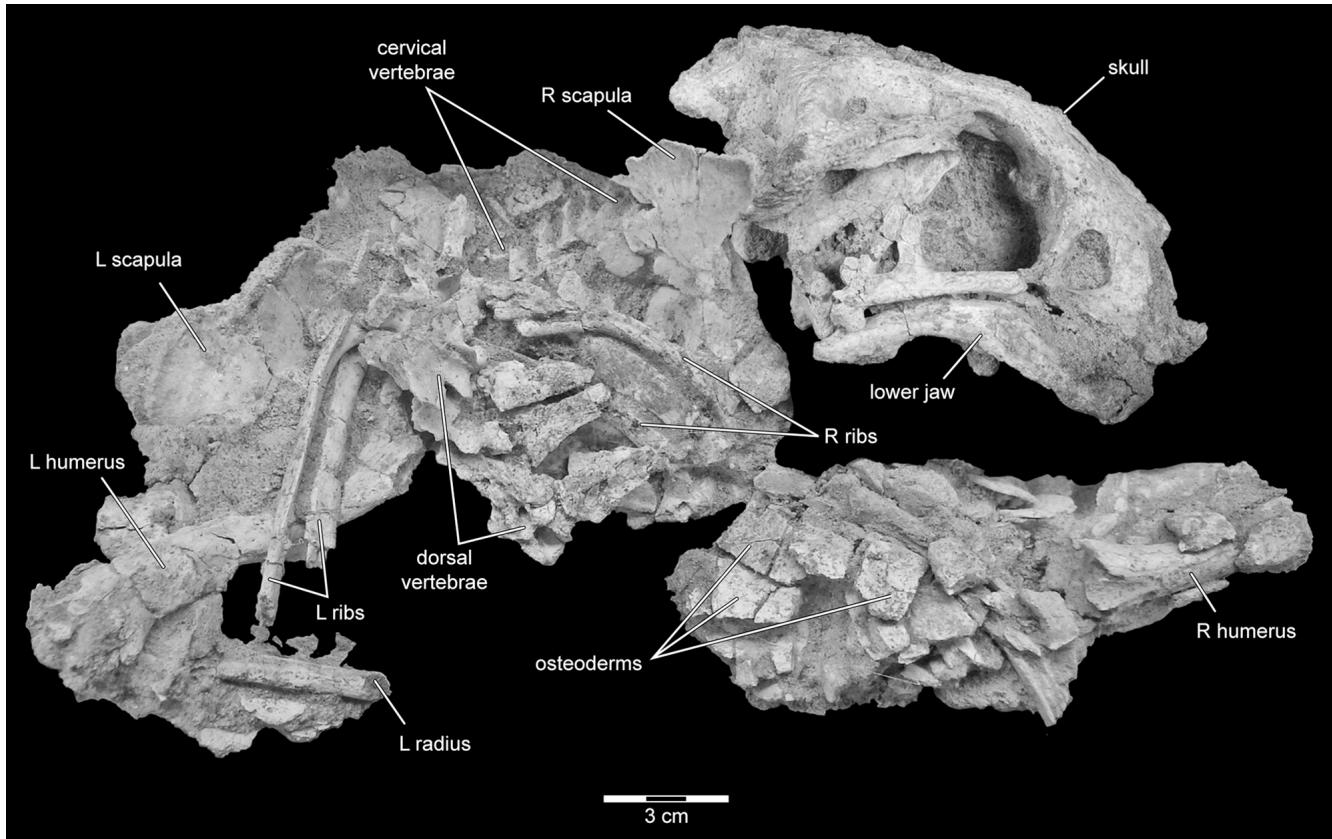


FIGURE 4. FMNH PR 2597, skull and lower jaw in right lateral view and partial skeleton in posteroventral view of *Simosuchus clarki*. Specimen includes nearly complete, articulated, but somewhat distorted skull and lower jaw (photographed prior to isolation from rest of specimen and more detailed preparation); all cervical and the first six anterior dorsal vertebrae; several ribs and rib fragments; parts of both forelimbs; and numerous osteoderms and osteoderm fragments. Isolated elements found associated with the specimen are not shown. Abbreviations: L, left; R, right.

but at least the posterior-most seven; both sacral vertebrae; 12 caudal vertebrae; several fragmentary ribs; nearly complete but poorly preserved left forelimb preserving all elements except for distal carpal 4, pisiform, digit V, and phalanges I-1 and I-2, II-2 and II-3, III-4, and IV-2 and IV-3; articulated distal right humerus and proximal radius and ulna; broken and distorted portions of both ilia, both ischia, and both pubes; proximal right femur; nearly complete but poorly preserved left hind limb preserving all elements except the distal tarsals, MT V, and phalanges III-4 and IV-2–IV-4; associated appendicular, dorsal and ventral trunk, and caudal osteoderms; MAD03-23: UA 9754—right ectopterygoid, two complete osteoderms, and numerous osteoderm fragments; MAD05-59: FMNH PR 2595—isolated tooth.

Diagnosis—See Turner and Sertich (this volume).

GEOLOGICAL CONTEXT

Simosuchus clarki is known only from the Anembalemba and Masorobe members of the Maevarano Formation in the Berivotra and Masiakakoho study areas of the Mahajanga Basin, northwestern Madagascar. The Maevarano Formation, named and described by Rogers et al. (2000), consists of sediments eroded from crystalline highlands to the east that form the north-south ‘backbone’ of the island. Basalts emplaced during the breakup of the Madagascar-India block (comprising Madagascar, the Seychelles, and the Indian subcontinent) (Storey et al., 1995, 1997; Torsvik et al., 1998, 2001), upon weathering, provided an

additional source of clays (e.g., saponite) to the aggrading Maevarano alluvial plain (Rogers, 2005; Kast et al., 2008). Rogers et al. (2000) identified, named, and described three members of the Maevarano Formation in the Berivotra Study Area: Masorobe, Anembalemba, and Miadana. The Masorobe and Anembalemba members also crop out in the Masiakakoho Study Area. A fourth, still-unnamed, vertebrate-bearing member has been identified in the Lac Kinkony area further to the west (Gaffney et al., 2009; Rogers and Krause, 2010).

The Masorobe Member, the basal member of the Maevarano Formation, yields several definitive clues to the paleoenvironment and paleoclimate in which *S. clarki* lived. This rock unit, over 80 m thick in the type section, is broadly exposed in both the Berivotra and Masiakakoho study areas. It is oxidized, predominantly reddish in color, and consists of generally coarse-grained, poorly sorted sandstones with relatively minor intercalations of claystone and siltstone. Primary stratification in the form of tabular and trough cross-bedding is developed in the sandstones but paleosol lithologies dominate the unit. Evidence of pedogenesis is provided by “color banding, superbly developed root casts (with drab root halos and occasional calcareous encrustations), root mottling (often with a strong vertical fabric), caliche, and rare slickensides” (Rogers et al., 2000:282). These features are consistent with an interpretation of parched dryland soils. Geochemical and X-ray diffraction analyses of the paleosols of the Masorobe Member by Kast et al. (2008), coupled with ‘climofunctions’ developed by Sheldon et al. (2002), indicate that paleoprecipitation in the Mahajanga Basin was between 430

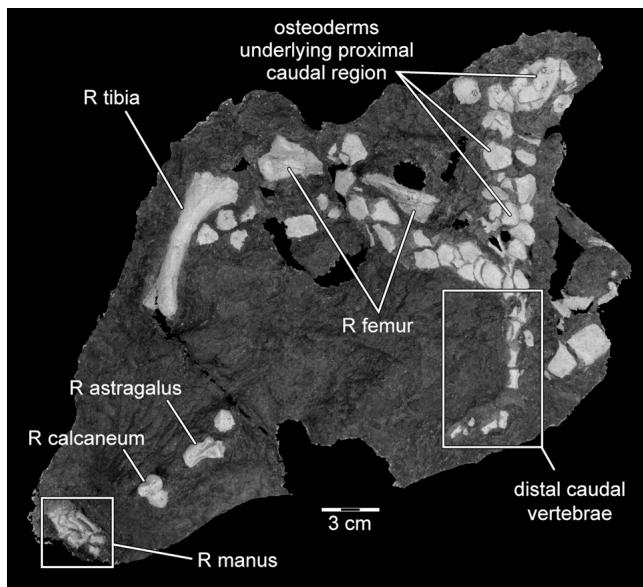


FIGURE 5. Cast of FMNH PR 2598, partial skeleton of *Simosuchus clarki*, in ventral view. Specimen includes associated elements of the skull and lower jaw, the second? dorsal centrum and nearly complete caudal vertebral series (including several chevron bones), rib fragments, elements of both forelimbs and both hind limbs, and numerous trunk and caudal osteoderms. Tail was curled dorsally and anteriorly to lie on the dorsal aspect of the trunk prior to burial. Painted cast is illustrated because original specimen was prepared and disarticulated in sections for study purposes. Isolated elements found associated with the specimen are not shown. **Abbreviation:** **R**, right.

and 1100 mm annually. These data, in concert with evidence for recurrent flooding in the form of fine-grained debris flow deposits in both the Masorobe Member and the overlying Anembalemba Member (see below), suggest a highly seasonal, semi-arid climate in the Mahajanga Basin during the latest Cretaceous. At this time, Madagascar was drifting northward toward the equator

and the Mahajanga Basin was already situated at approximately 25–30°S (e.g., Royer et al., 1992; Scotese, 1998), thereby entering the subtropical desert belt (de Wit, 2003; Wells, 2003). Vertebrate fossils are much less common and generally less well preserved than in the overlying Anembalemba Member, but the Masorobe has yielded several specimens of *S. clarki*, including a nearly complete, articulated skeleton (FMNH PR 2596; Fig. 3). This specimen is of additional interest in that it is associated with meniscate burrows, currently being described in detail by R. Rogers and colleagues.

The Anembalemba Member is also broadly exposed in both the Berivotra and Masiakakoho study areas. In contrast to the Masorobe Member, however, it is a relatively thin unit (only 10–15 m thick) and paleosol development is relatively poor. Rogers et al. (2000) recognized two predominant facies, designated facies 1 and facies 2, within the Anembalemba Member. Facies 1 consists primarily of light-colored, poorly sorted sandstones and is characterized by pervasive evidence of primary stratification (small- to medium-scale tabular and trough cross-bedding) reflective of stream flow. Facies 2 is also comprised of poorly sorted sandstones but they are of a darker, greenish color, have a much larger clay fraction, and are generally massive in structure. Rogers (2005) interpreted facies 2 as representative of recurrent, large-scale, cohesive, debris flow events as torrential precipitation eroded sediments from weathered basalts to the southeast. The fine-grained debris flows triggered by exceptionally heavy rains rapidly made their way northwestward toward the Mozambique Channel along dry stream courses, and entombed the remains of vertebrate animals that had perished during the dry season in the channel belts. As a result, vertebrate remains are indeed abundantly and exquisitely preserved in the Anembalemba Member, including most of the known specimens of *S. clarki*. Abundant feeding traces on vertebrate bone by both invertebrates (e.g., necrophagous and osteophagous carion insect borings and puparial chambers) and vertebrates (e.g., tooth marks) provide evidence of carcass utilization, presumably primarily during periods of environmental stress caused by drought (as also evidenced by the occurrence and surface preservation of conchostracans; Stigall and Hartman, 2008), and significant intervals of time between death and final burial (Rogers et al., 2003, 2007; Roberts et al., 2007; Rogers and

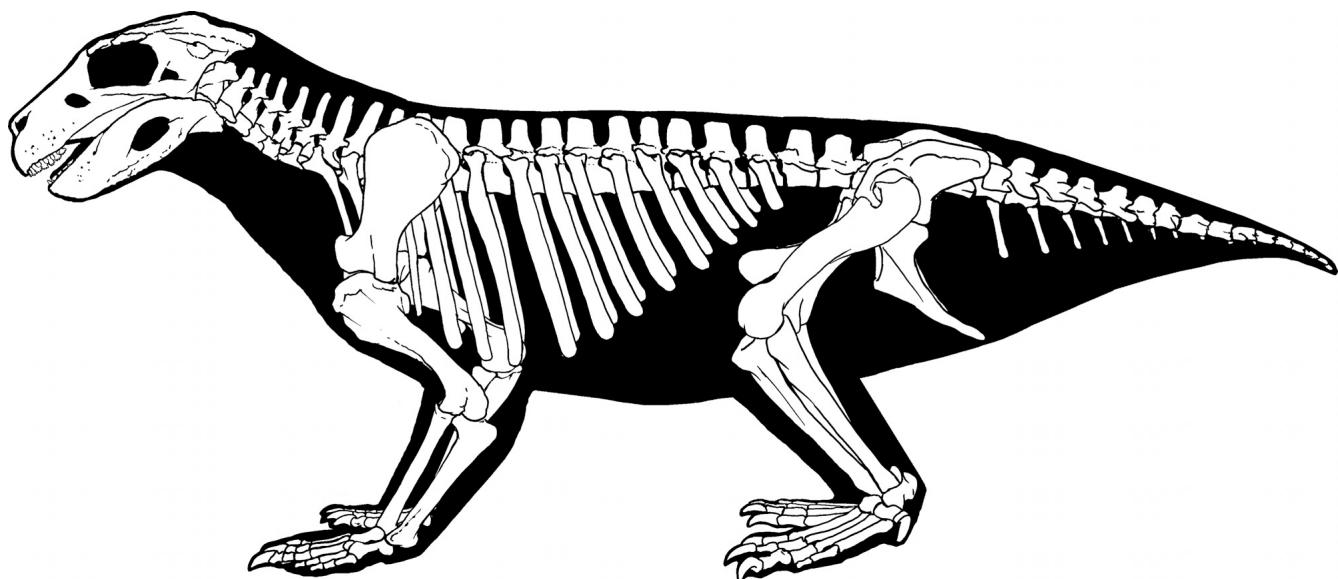


FIGURE 6. Skeletal anatomy of *Simosuchus clarki* in left lateral view. Reconstruction based on a composite of specimens, primarily UA 8679 (type specimen), FMNH PR 2596, FMNH PR 2597, and FMNH PR 2598.

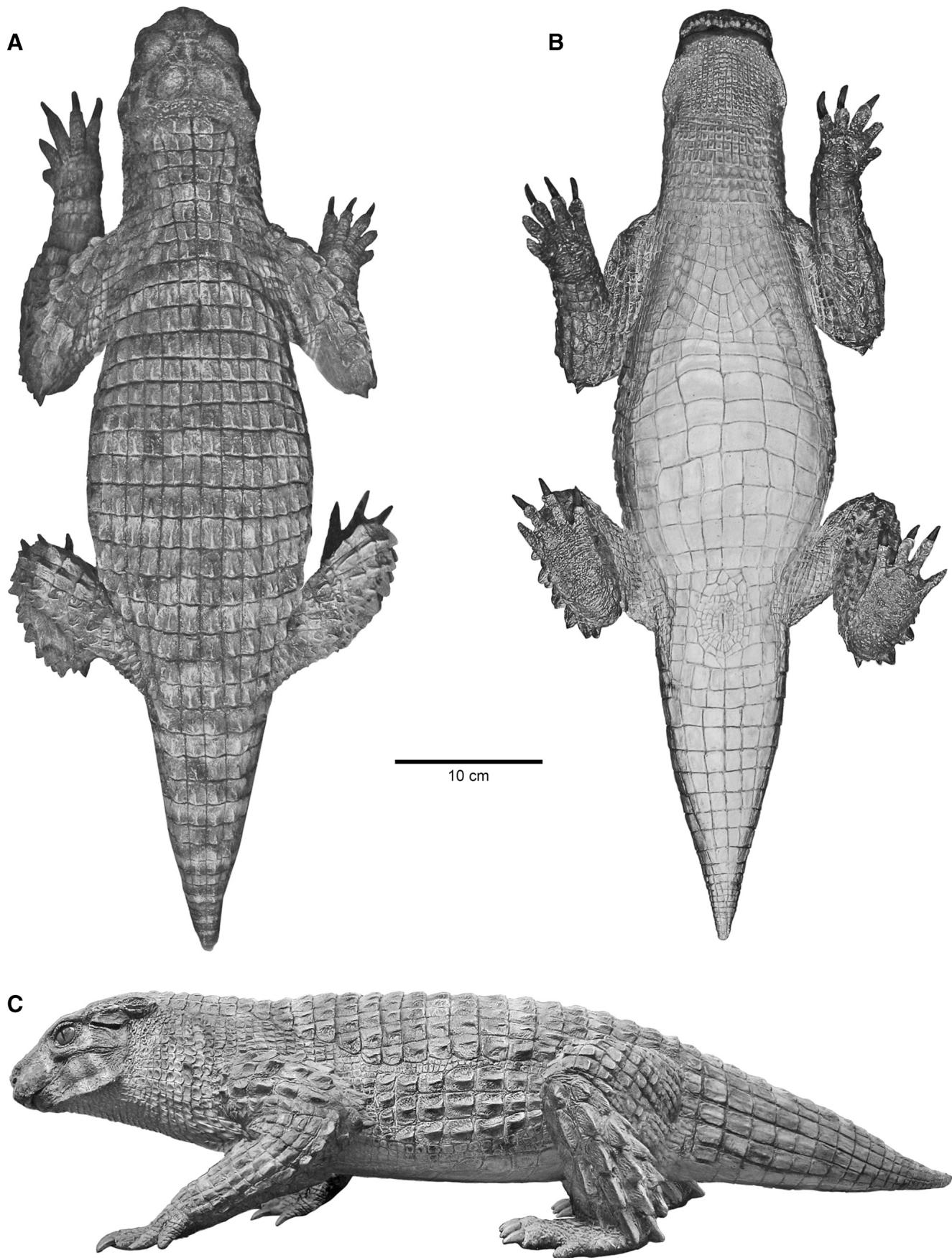


FIGURE 7. Fleshed out reconstruction of *Simosuchus clarki* in **A**, dorsal; **B**, ventral; and **C**, left lateral views. Based on photographs of sculpture by B. Filipović. Photographs adjusted digitally by L. Betti-Nash.

Krause, 2007). This is consistent with the fact that, buried alongside spectacularly preserved specimens, many bones, presumably from animals that died weeks or months before burial, show evidence of advanced weathering and surface degradation. On a broader temporal scale, however, the occurrence of specimens of *S. clarki* (and those of many other vertebrate species) in both the Masorobe and Anembalemba members suggests that not much time passed between deposition of the two members (alternatively, of course, *S. clarki* may have been a long-lived species).

The 25 m thick Miadana Member, currently identified only in the Berivotra Study Area (Rogers et al., 2000), lies at the top of the formation and is separated from the overlying marine Berivotra Formation by a disconformity. It consists of a mix of fine- to coarse-grained, generally massive sediments including claystone, siltstone, and sandstone. Unlike the underlying Anembalemba and Masorobe members, it is not extensively exposed and, to date, has not yielded remains of *S. clarki*. Nor has the unnamed new member that crops out in the Lac Kinkony area.

At least the upper portions of the Maevarano Formation (Miadana and Anembalemba members, and the unnamed new member) are of latest Cretaceous (Maastrichtian) age. The Anembalemba Member, from which most of the terrestrial and freshwater vertebrate fossils were recovered, is intercalated with, as well as overlain by, the marine Berivotra Formation, which is dated as Maastrichtian on the basis of its contained invertebrate and vertebrate fossils (Besairie, 1972; Gottfried et al., 2001; Abramovich et al., 2002; Rahantarisoa, 2007). Preliminary magnetostratigraphic data are consistent with this assessment in indicating the presence of a reversal near the top of the Berivotra Formation (Casey et al., 2003; Dennis-Duke, 2005). This is interpreted as the shift that occurred from Chron 30N to Chron 29R, dated at approximately 65.8 Ma (Ogg et al., 2004). It therefore appears that *Simosuchus* and its contemporaries in the Maevarano assemblage lived at a time long after Madagascar became an island isolated in the Indian Ocean. Basalts that incompletely rim Cretaceous sediments of the Mahajanga Basin and underlie the Ankazomihaboka sandstones (Fig. 1) have been dated at approximately 88 Ma (Coniacian) and correlated with the event that separated the Seychelles and Indian subcontinent from Madagascar (Storey et al., 1995, 1997; Torsvik et al., 1998, 2001).

Curiously, Masters et al. (2006:403) recently stated that the Maastrichtian age for the fossiliferous strata of the Maevarano Formation is only a minimum age because “the fossils are allochthonous” and that the Maevarano Formation “could be as old as 88 million years.” There is currently no evidence whatsoever to indicate that the formation is anything other than Maastrichtian (Rogers et al., 2007). Moreover, Masters et al.’s (2006) unsubstantiated assertion that “the fossils are allochthonous” is contrary to a wealth of sedimentologic and taphonomic data indicating that the fossils in question are in fact buried at, or in very close proximity to, the site of mortality (Rogers et al., 2000, 2007; Rogers, 2005; Rogers and Krause, 2007). The fossils of the Maevarano Formation are preserved in their life habitats, and there is no indication of postmortem exhumation or reworking. Unfortunately, the statements by Masters et al. (2006) have been employed by Ali and Aitchison (2008:159) to argue that an 88 Ma age for the Maevarano fossil assemblage “would certainly be more amenable with the paleogeographic model” that they devised. Amenable perhaps, but contrary to all available evidence.

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