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# A REVISION OF THE UPPER CRETACEOUS LEPIDOSIRENID LUNGFISHES FROM THE QUSEIR FORMATION, WESTERN DESERT, CENTRAL EGYPT

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ABSTRACT—We evaluate new lungfish remains from the Upper Cretaceous Quseir Formation in the Western Dessert of southern Egypt. Taxa include *Lavocatodus protopteroides*, *L. humei*, *L. giganteus*, and *Protopterus nigeriensis*. We treat *Lavocatodus* as members of Lepidosirenidae based on the presence of a well-defined medial articular surface, in the absence of a symphyseal surface of corresponding prearticular bones. Material of *L. protopteroides* represents the first example of an adult specimen, supporting the retention of the species as valid, and not a junior synonym of *L. humei*. Specimens of *L. humei* are the most abundant in the assemblage, and all exhibit the medial articular surface, a feature that is absent from specimens of *Ceratodus*; therefore, we reassign additional specimens of '*C.*' *humei* to *Lavocatodus*. New specimens of *L. giganteus* extend the temporal and spatial ranges of the species (the type material of *L. giganteus* is from Paleocene deposits of In Farghas, Mali). Finally, a new specimen of *Protopterus* represents the oldest record of the genus in Egypt. The prearticular is confidently assigned to *Protopterus* based on the presence of only three ridges on the tooth plate, a medial symphyseal suture, a coronoid process, and a shallow tooth crown plus prearticular depth. We further assign it to *P. nigeriensis* based the length and merger of tooth ridges. Furthermore, the oldest Cenomanian specimens reported from the Sudan Wadi Milk Formation are assigned to *P. nigeriensis*, which would extend the temporal range of *P. nigeriensis* by roughly 14 Ma.

## INTRODUCTION

Lungfishes (Dipnoi) are osteichthyan fishes with an extensive record throughout the Paleozoic and to a lesser extent during the Mesozoic and Cenozoic (Clack et al., 2011). Based on extant representatives within the Lepidosirenidae and Neoceratodontidae, lungfishes possess a high degree of cartilage in their skeletons that ossifies relatively late during development (Ahlberg and Trewin, 1994; Johanson et al., 2005; Johanson et al., 2009). This likely accounts for the fact that fossilized remains of lungfishes, especially during the Mesozoic and Cenozoic, are often restricted to the hardest elements, such as the skull roof, jaws, and isolated tooth plates. Mesozoic forms are most diverse in Gondwana, especially in the fossil record of the Australian landmass, with fewer taxa currently known from South America and Africa. Several studies conducted over the past decade have closely examined the lungfish record in South America and Africa, concentrating primarily on members of Ceratodontiformes (e.g., Churcher and de Iuliis, 2001; Churcher et al., 2006; Apesteguía et al., 2007; Soto and Perea, 2010; Cione et al., 2011; Cione and Gouiric-Cavalli, 2012). These reviews suggest a strong similarity of both South American and African taxa with Australian forms. Prompted by the recovery of new lungfish remains from the Upper Cretaceous Quseir Formation (Fig. 1) in the Western Dessert of southern Egypt, we evaluate the new fossils in the context of previous research on northern Africa lungfish faunas and provide additional perspectives on the Egyptian assemblage of lungfishes. These efforts are being conducted as part of the Mansoura University Vertebrate Paleontology Initiative, a collaborative network among Mansoura University, Ohio University, and the Denver Museum of Nature and Science that was established to promote field, laboratory, and museum research along with training opportunities for a range of students and researchers from Egypt and abroad.

**Institutional Abbreviations—AMNH**, American Museum of Natural History, New York, U.S.A.; **MNHN**, Muséum National d'Histoire Naturelle, Paris, France; **MUVP**, Mansoura University vertebrate paleontology collections, Mansoura, Egypt; **TMM**, Texas Memorial Museum at The University of Texas at Austin, Austin, Texas, U.S.A.; **Vb**, Technische Universität Berlin, Berlin, Germany.

Ensemble divisions for MNHN species utilized by Werner (1994), Martin (1995), and Gloy (1997) are also utilized here. **HGO**, from the West of Hoggar; **HGS**, from the South of Hoggar; **IBC**, from In Beceten of southern Niger; **TGE**, or from Morocco, Algeria, and/or Mali.

## GEOLOGIC SETTING

Sequences of the Quseir Formation, together with the overlying Duwi and Dakhla formations, represent a Campanian through Paleocene succession exposed throughout central and southern Egypt (Klitzsch et al., 1979; Tantawy et al., 2001). Exposures of the Quseir Formation are accessible in multiple areas near both Kharga Oasis and Dakhla Oasis, Western Desert, southern Egypt (Fig. 1). The sequences include a variety of depositional environments, ranging from fluviatile and estuarine to various marine facies, most of which preserve vertebrate and
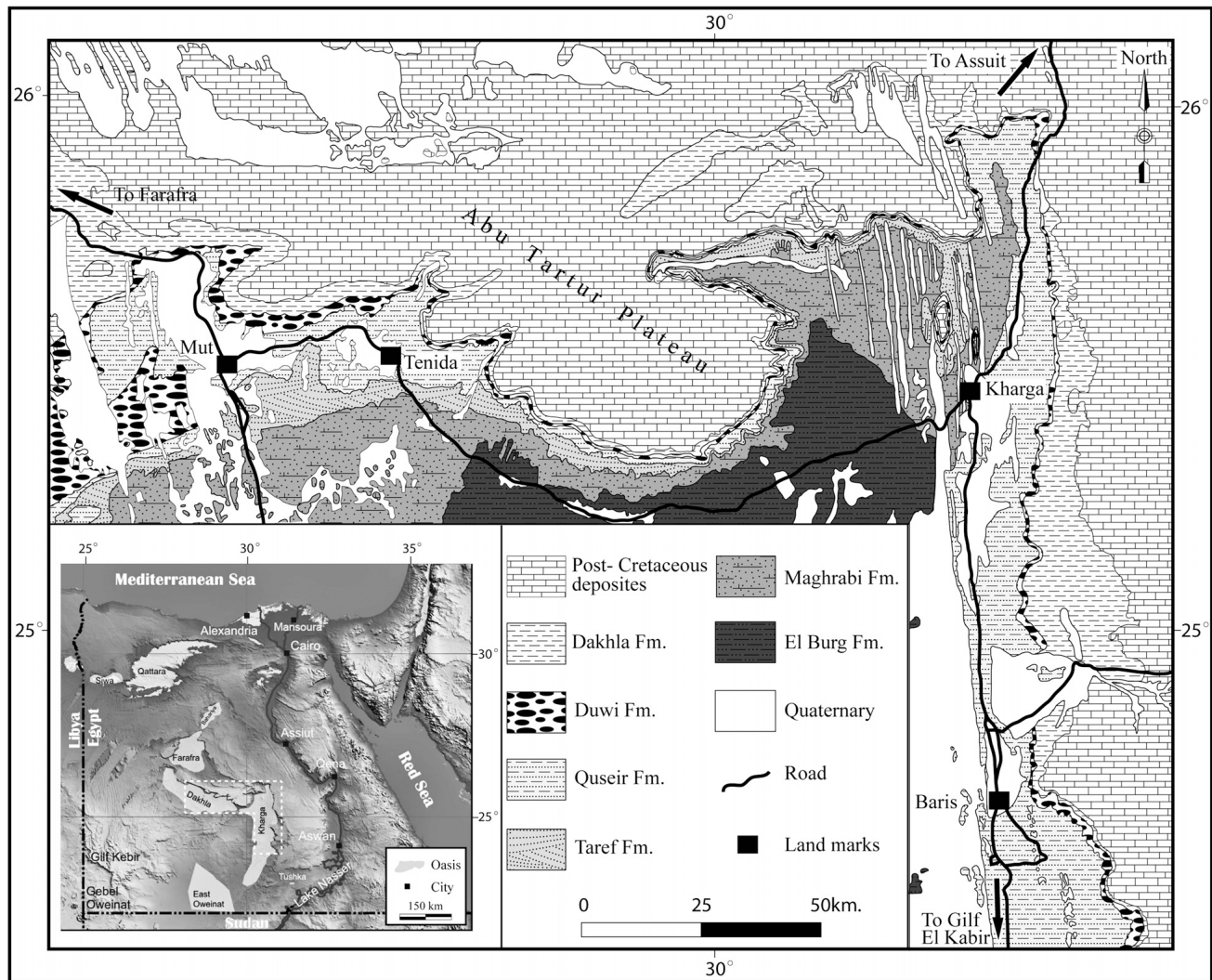
*Corresponding author.

FIGURE 1. Location and geologic map of the Dakhla and Kharga oases of the Western Desert, southern Egypt, depicting outcrops of Upper Cretaceous rock units. The Mansoura University Vertebrate Paleontology (MUVP) initiative has conducted field reconnaissance through these sequences near the towns of Mut, Kharga, Tineida, and Baris. The lungfish materials described in this report were recovered from the Quseir Formation. The white dashed lines on the inset map indicate the position of the field area. Modified after (El Khawaga et al., 2005).

invertebrate fossils characteristic of their respective depositional settings (Klitzsch et al., 1979; Hendriks, 1984; Hermina, 1990; Klitzsch and Schandelmeier, 1990; Tantawy et al., 2001; Mahmoud, 2003; O'Connor et al., 2010).

The type section of the lower-middle Campanian Quseir Formation is located at Gebel Atshan in the Quseir area, Red Sea coast (Youssef, 1957). An additional stratigraphic section was measured near the town of Teneida in the Dakhla Oasis field area. Thirty meters of the upper part of the Quseir Formation are exposed in the region and consist of slope-forming variegated shale (purple, gray, and green) alternating with hard bands of sandstone and siltstone. Occasional thin phosphatic beds exhibiting bioturbation (e.g., burrows) are intercalated in the upper part of the sequence. Vertebrate fossils, including fishes, turtles, crocodyliforms, and dinosaurs, were collected primarily from these units, representing nearshore-marine to fluvial depositional environments (O'Connor et al., 2010). These units also preserve abundant petrified wood and the lungfish materials described herein.

## MATERIALS AND METHODS

The dipnoan fossils described in this report consist mainly of partial tooth plates, although some are complete, along with additional, partial jaw elements. Material was recovered by surface collection from the localities listed in Table 1. All remains were accessioned into the Mansoura University Vertebrate Paleontology (MUVP) collections at Mansoura University, Mansoura (Nile Delta), Egypt. Comparative fossil materials from Africa examined were †*Protopterus nigeriensis* MNHN-F-IBC 1804 (holotype) and MNHN-F-IBC 1751. Comparative extant materials examined were *Protopterus aethiopicus* UF 137272 and UF 147058 and *Protopterus annectens* AMNH 55226 and TMM M-1129. A guide to tooth plate orientation is provided in Figure 2.

## SYSTEMATIC PALEONTOLOGY

SARCOPTERYGII Romer, 1955
DIPNOI Müller, 1844
CERATODONTIFORMES (Berg, 1940)

TABLE 1. Locality and specimen information

| Field no. | MUVP no. | Figure | Location | Taxon |
|---|---|---|---|---|
| LKE 10027 | MUVP 38 | Figure 3 | Baris | *Lavocatodus protopteroides* |
| DVP 08 47 | MUVP 39 | | Tineida | *Lavocatodus humei* |
| DVP 08 58 | MUVP 40 | Figure 4 | Tineida | *Lavocatodus humei* |
| DVP 08 73B | MUVP 41 | | Tineida | *Lavocatodus humei* |
| DVP 08 73C | MUVP 42 | | Tineida | *Lavocatodus humei* |
| DVP 08 73D | MUVP 43 | | Tineida | *Lavocatodus humei* |
| LKE 10115 | MUVP 44 | | Tineida | *Lavocatodus humei* |
| LKE 10129B | MUVP 45 | | Tineida | *Lavocatodus humei* |
| DVP 08 25A | MUVP 46 | Figure 4 | Baris | *Lavocatodus humei* |
| DVP 08 25B | MUVP 47 | | Baris | *Lavocatodus humei* |
| LKE 10008 | MUVP 48 | | Baris | *Lavocatodus humei* |
| LKE 10081 | MUVP 49 | | | *Lavocatodus humei* |
| LKE 10093 | MUVP 50 | | Tineida | *Lavocatodus humei* |
| DVP 08 74 | MUVP 51 | Figure 5 | Tineida | *Lavocatodus giganteus* |
| LKE 10125A | MUVP 52 | | Tineida | *Lavocatodus giganteus* |
| LKE 10125B | MUVP 53 | | Tineida | *Lavocatodus giganteus* |
| LKE 10129A | MUVP 54 | | Tineida | *Lavocatodus giganteus* |
| DVP 08 73A | MUVP 55 | | Tineida | *Lavocatodus giganteus* |
| LKE 10014A | MUVP 56 | | Baris | *Lavocatodus giganteus* |
| LKE 10014B | MUVP 57 | Figure 6 | Baris | *Protopterus nigeriensis* |



FIGURE 3. Lower right tooth plate and prearticular (MUVP 38) of *Lavocatodus protopteroides* in ventral view (left) and occlusal view (right).

LEPIDOSIRENIDAE (Bonaparte, 1841)
*LAVOCATODUS* Martin, 1995

**Remarks**—Species of *Lavocatodus* were "left in Lepidosireniformes incertae sedis" by Otero (2011:238) because the suture of the lateral and medial bony mandibular elements were not known at that time. We have recovered a single dentition with a partially preserved prearticular preserving a well-defined symphyseal surface on the tooth plate. Herein, we consider *Lavocatodus* to be lepidosirenids, as per the redefined diagnosis of the Lepidosirenidae by Kemp (1998).

LAVOCATODUS PROTOPTEROIDES (Tabaste, 1963)
(Fig. 3)

**Referred Material**—MUVP 38, lower right tooth plate on a partially preserved right prearticular bone.

**Description**—Tooth plate with four preserved ridges. The mesial-most ridge is gracile and reflected anterobuccally. Ridges
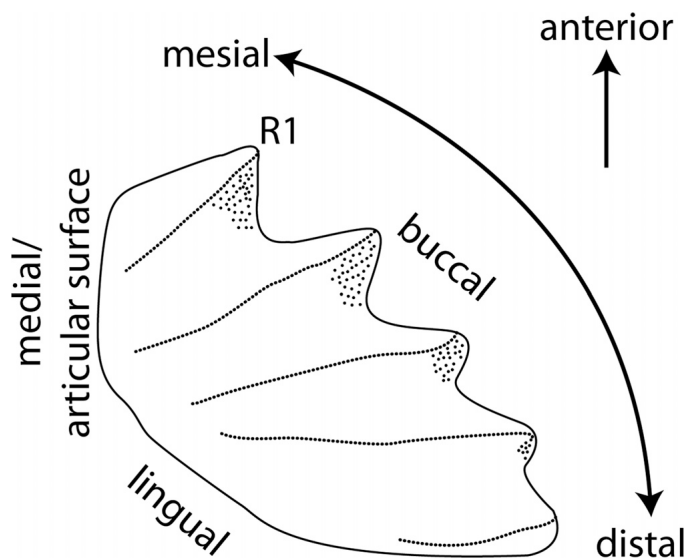
extend lingually from each crest and converge strongly towards the lingual apex of the tooth plate. Ridges 2 and 3 are long (~3.25 cm), curved buccoposteriorly, and taper to a sharp point. The fourth ridge is broken. There is a well-defined, 3.75-cm flat medial surface for articulation with its antimere.

**Discussion**—*Lavocatodus protopteroides* was previously called "*Ceratodus*" *protopteroides*, then later '*Protopterus*' *protopteroides*. According to Gloy (1997:58), *L. protopteroides* is somewhat similar to, but cannot be the same as, *Lavocatodus* '*Protopterus*' *humei* (Priem 1914), because in *L. humei* the second and more posterior ridges do not converge towards the articular surface. "*Dieser Meinung kann nicht entsprochen werden, da bei der Familie der Ceratodontidae Anlage und Verlauf der Kämme andersartig ist (GILL 1972). Bei der vermeintlich nahverwandten Art* Ceratodus humei *laufen der zweite Kamm und die folgenden Kämme nicht auf die Symphyse zu. Desweiteren liegen die Kammansätze (zweiter Kamm und folgende) vor der Symphyse (TABASTE 1963; SCHAAL 1984).*" This is contrary to the hypothesis that *L. protopteroides* was an extreme variation of *L. humei* (Martin, 1984) or that sensu Gloy (1997) specimens of *L. protopteroides* were actually early ontogenetic stages of *L. humei* (Werner and Gayet, 1997).

We were unable to personally observe all of the specimens to which Gloy referred. However, according to the unpublished dissertation, there is shared morphology between *Lavocatodus protopteroides* and *L. humei*, although specimens of *L. protopteroides* are much smaller (see Gloy, 1997:78, appendix 5). There were no adult-stage forms of *L. proptopteroides* available in the dissertation by Gloy, nor was any consideration given regarding the maximum size of the taxon. Given the sheer size of the new specimen (MUVP 38) relative to others assigned to *L. protopteroides*, we consider MUVP 38 to represent an adult. For the purposes of this contribution, we retain the designation of *L. protopteroides* as valid, and not merely as a junior synonym of *L. humei*.

*LAVOCATODUS HUMEI* (Priem, 1914)
(Fig. 4)

**Referred Material**—Upper tooth plates: MUVP 39, MUVP 40, MUVP 41, MUVP 42, MUVP 43, MUVP 44, MUVP 45; lower tooth plates: MUVP 46, MUVP 47, MUVP 48, MUVP 49, MUVP 50.

**Description**—All dentitions of *Lavocatodus humei* documented here are isolated and detached from supporting jaw



FIGURE 2. Line drawing of generalized tooth plate and orientation guide. **Abbreviation**: **R1**, ridge 1.
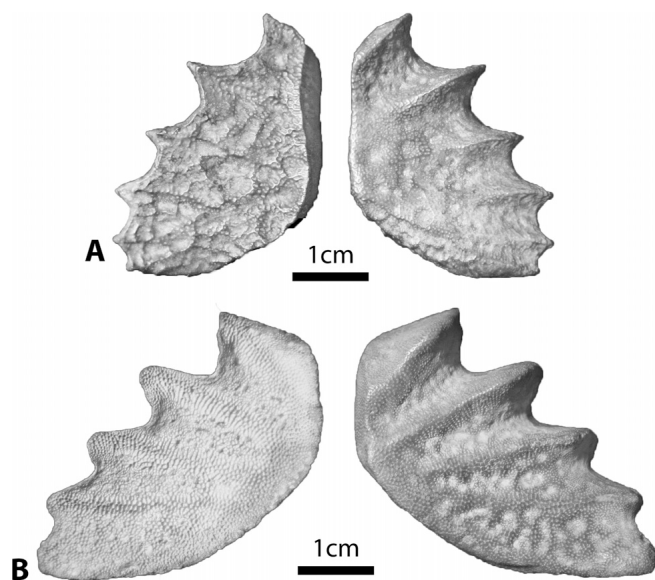
FIGURE 4. Tooth plates of *Lavocatodus humei*. **A**, upper left tooth plate (MUVP 40) in dorsal (left) and occlusal (right) views. **B**, lower right tooth plate (MUVP 47) in ventral (left) and occlusal (right) views.
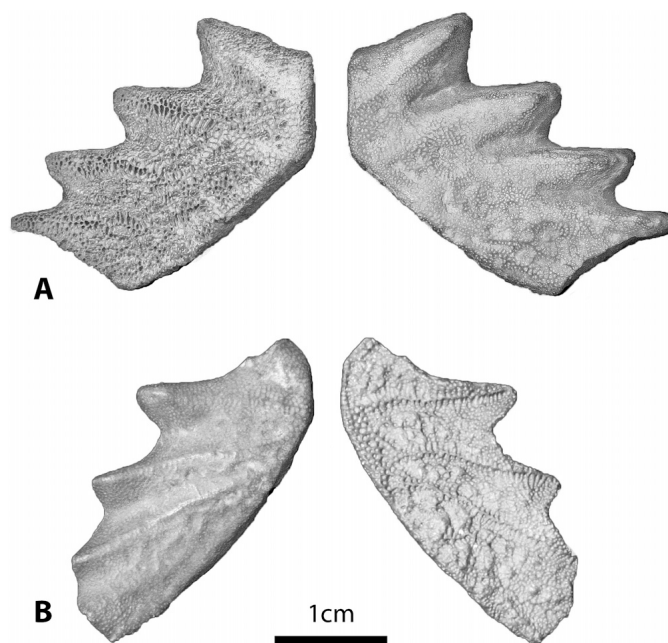


FIGURE 5. Tooth plates of *Lavocatodus giganteus*. **A**, upper left tooth plate (MUVP 55) in dorsal (left) and occlusal (right) views. **B**, lower left tooth plate (MUVP 51) in occlusal (left) and ventral (right) views.

elements. The basal surface of each tooth plate is marked by numerous nutrient grooves that align with the occlusal ridges. MUVP 40 is a complete upper left tooth plate (Fig. 4A). The mesial-most ridge of MUVP 40 is 1 cm long and directed buccally, not anteriorly. There are four additional ridges that appear to fan out buccoposteriorly. Ridges are furthest apart mesially and gradually get closer to one another towards the distal margin of the tooth plate. The fifth ridge is shorter than the fourth and does not extend to the apex formed by the medial and lingual margins of the tooth plate. There is wear and some pitting on the flattened lingual side of the occlusal surface, but the ridges are still well defined. The articular surface is ~2 cm in length and slightly worn. Additional upper tooth plates also exhibit the subtriangular shape of MUVP 40, but have lost either the first (mesial-most) ridge or the distal fourth and fifth ridges, or some combination of both. MUVP 46 is a complete lower right tooth plate, with five well-defined ridges (Fig. 4B). The mesial-most ridge is particularly tall compared with more distal ridges. The articular surface, relative to the mesiodistal length of the tooth plate, is shorter in this and other lower tooth plates, when compared with the relative length of the symphyseal surface in upper tooth plates. The lingual margin curves buccally such that the posterior margin is co-linear with the fifth, distal-most ridge. The first ridge is 1.5 cm long and the articular surface is 1.7 cm long (Fig. 4B). As with upper dentitions, the tendency is to break through the articular surface at the first ridge, between the third and fourth ridges, or both (supplemental imagery is available at Morphobank.org; username = 850; password = egypt).

**Discussion**—*Lavocatodus humei* is the most abundant taxon in the collection thus far and is also represented by the greatest size variability among all recovered lungfishes. It is taxonomically equivalent to specimens assigned to '*Ceratodus*' *humei* by Churcher and de Iuliis (2001) in their review of the generic and specific diagnoses of specimens formally described by Priem (1914), Arambourg and Joleaud (1943), Tabaste (1963), and Martin (1984). For reasons described above, we reassign those specimens to the genus *Lavocatodus*, *sensu* Martin (1995).

## *LAVOCATODUS GIGANTEUS* Martin, 1995
(Fig. 5)

**Referred Material**—Upper tooth plates: MUVP 51, MUVP 52, MUVP 53, MUVP 54; lower tooth plates: MUVP 55, MUVP 56.

**Description**—All of the upper tooth plates are missing their mesial-most ridge, the most complete of which (MUVP 55) is from the left side (Fig. 5A). On three upper right tooth plates (MUVP 51, MUVP 52, MUVP 54), the second and third ridges are preserved and indicate a low, buccolingual profile for the tooth, although it is slightly greater than in lower tooth plates of this taxon. The medial articular surface is partly preserved on two upper tooth plates (MUVP 52 and MUVP 53), creating a rounded angle with the lingual surface. Unlike the convex condition in *Lavocatodus humei*, the lingual margin of the tooth plate in *L. giganteus* is linear as it moves towards the posterior edge plate. Lower tooth plates are more rectangular, rather than triangular. MUVP 56 is a lower, left tooth plate missing only its fifth (and possibly sixth) distal-most ridge(s) (Fig. 5B). All ridges are directed sharply buccoposteriorly. There is a sharp angle between the first ridge and articular surface, as well as between the articular surface and the lingual margin (Fig. 5B).

**Discussion**—*Lavocatodus giganteus* was erected as the type species of *Lavocatodus* by Martin (1995). In doing so, he singled out an upper tooth plate specimen (HGS 25) previously described as *Protopterus humei* by Martin (1984). That specimen and the type specimen (TGE 4292) of *L. giganteus* described by Martin (1995) are from the Paleocene deposits of In Farghas, Mali. Thus, new specimens described here extend the range of the taxon and reach of freshwater systems both geographically across what is the present day Sahara and temporally by about 13 million years back to the middle of the Campanian. Additionally, it is probable that some specimens previously identified as *Neoceratodus africanus* should be reassigned to *L. giganteus* (e.g., specimen HGO 7; Martin, 1984:fig. 26). Whereas the name 'giganteus' reflects the large size of the type specimen, specimen

HGS 25 is considered a small (~3 cm length) subadult, with high, unworn ridges. Specimens described here are considerably more worn on the occlusal surface and larger than HGS 25, but less worn and smaller than TGE 4292. This indicates that at least for upper tooth plates of *L. giganteus*, the low profile of the plate is maintained throughout ontogeny.

SARCOPTERYGII Romer, 1955
DIPNOI Müller, 1844
CERATODONTIFORMES (Berg, 1940)
LEPIDOSIRENIDAE (Bonaparte, 1841)
*PROTOPTERUS NIGERIENSIS* Martin, 1997
(Fig. 6)

**Referred Material**—Nearly complete lower left tooth plate with three well-developed ridges in situ on a partial prearticular bone, MUVP 57.

**Synonyms**—*Protopterus* sp. Werner, 1994:228 and Tafel 3, figs. 2, 5, and 6.

**Description**—The prearticular bone of MUVP 57 is 1.7 cm at its longest and 0.7 cm at its deepest. Medially, there is a rough symphyseal surface for articulation with its antimere. In lateral view, a coronoid process is present posterordorsally on the prearticular, although it is broken (Fig. 6C). Elsewhere, the surface of the prearticular is dimpled and looks somewhat porous. The tooth plate is 1.35 cm from the anterior-most end of the articular surface to the distal-most end of the third ridge. The articular surface of the tooth plate is relatively flat and parallel with the symphyseal surface of the prearticular bone, as it is in modern representatives of Lepidosirenidae (Criswell, 2011). Ridges are tall (~0.35 cm), narrow, and relatively unworn, retaining vestigial tubercles on the first and second ridges. The tallest part of the third ridge is broken. The relative length of each ridge increases from mesial to distal (4.5, 5.5, and 7 mm, respectively). Ridges 2 and 3 are joined lingually and there is a single ridge extending from their merger to the origin of ridge 1.

**Discussion**—The presence of only three ridges, midline-fused right and left prearticulars, and a coronoid process on the prearticular (Criswell, 2011:characters 17 and 18) are among diagnostic characters of crown Lepidosirenidae, i.e., *Protopterus* or *Lepidosiren*. Although there are no formal jaw character to distinguish between *Protopterus* from *Lepidosiren*, Criswell (2011:37) also states that the prearticular " ... is wider in Lepidosiren, running in a nearly straight line across the anterior mar-

gin before curving laterally." In addition, the crown height of the prearticular tooth plus the depth of the prearticular in of *Lepidosiren* is roughly 2/3 the anteroposterior length of the tooth in lateral view vs. 1/2 or less in *Protopterus* (Criswell, 2011:fig. 1.53). Based on the combined characters of tooth number, sutures, and size and shape of the prearticular, we assign MUVP 57 to *Protopterus*. This is supported loosely by geography in that no species of *Lepidosiren* have been recovered from Africa (Otero, 2011).

The presence of tubercles on the first and second ridges is indicative of the subadult growth phase of modern *Neoceratodus*, but not for members of Lepidosirenidae, a group that typically exhibit cusps on the third distal-most ridge (Kemp, 2003). However, it is not unreasonable to presume that earlier forms of Lepidosirenidae, which collectively with extant forms are considered the sister taxon to *Neoceratodus*, would maintain cusps for some phase of growth on the first and second ridges. The length of the third ridge is approximately 1.5 times longer than the first ridge in MUVP 57, unlike in the Eocene lepidosirenid specimens from Mali (Martin, 1995). The Malian form represents *Protopterus elongus* and exhibits a third ridge that is twice the length of the first ridge. Relative ridge length in MUVP 57 is more similar to Eocene Egyptian specimens assigned to *P. elongus* (Murray et al., 2010). The relative length of the third and first ridges of the prearticular tooth plate in the Coniacian-Santonian lepidosirenid *Protopterus nigeriensis* (IBC 1751; paratype) from Niger is approximately 1.5 (Martin, 1997). The ridges in MUVP 57 also bifurcate, similar to the condition in IBC 1751. For these reasons, we assign this MUVP 57 to *P. nigeriensis*, making it the youngest (by about 14 million years) and easternmost representative of the species.

*Protopterus nigeriensis* bears a strong resemblance to Cenomanian specimens from the Sudan Wadi Milk Formation that have been assigned to *Protopterus* sp. by Werner (1994; Vb-703, Vb-706, and Vb-707), analyzed in great detail by Gloy (1997), and mentioned briefly in Werner and Gayet (1997). We tentatively reassign the Sudan Wadi Milk specimens (Vb-703, Vb-706, and Vb-707) to *P. nigeriensis*, based on the description by Gloy (1997).

BIOGEOGRAPHIC OBSERVATIONS

Extant members of the Lepidosirenidae are located on the continents of Africa and South America. The clade has been the subject of several studies promoting a vicariance model to account
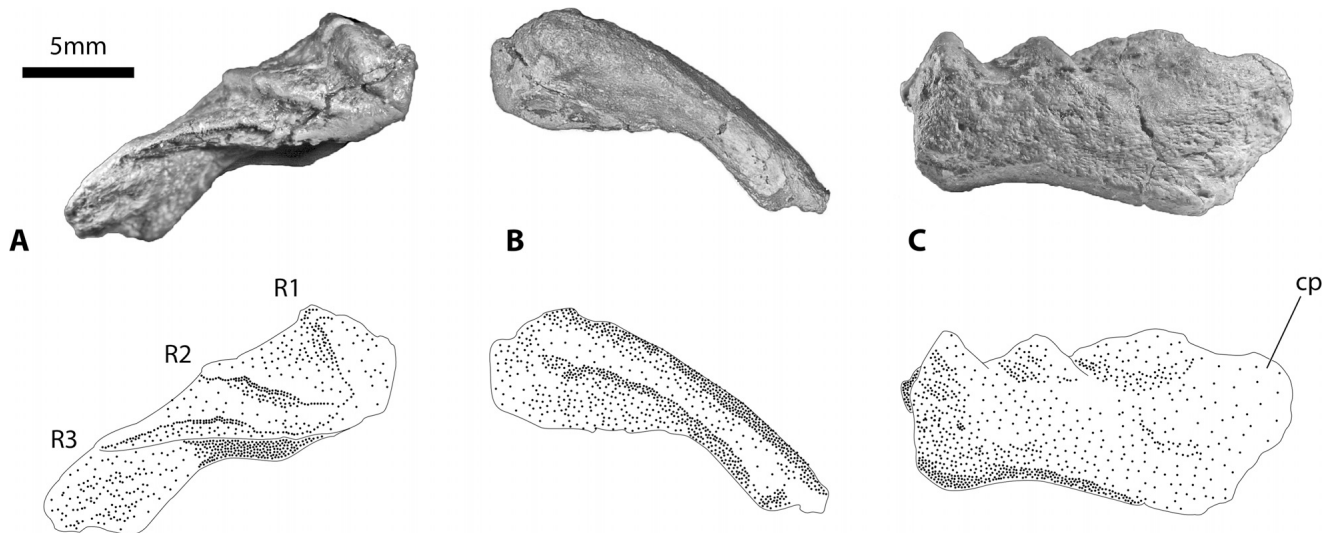


FIGURE 6. Left prearticular and prearticular tooth plate with line drawings (MUVP 57) of *Protopterus nigeriensis*. **A**, ventral view; **B**, dorsal view; **C**, lateral view. **Abbreviations**: **cp**, coronoid process; **R1–R3**, ridges 1–3.

for their distribution, given their classification as primarily freshwater fishes (Myers, 1938). Extant members of Lepidosirenidae are strictly confined to freshwater due to a physiological intolerance of saline water. From what can be gleaned from the fossil record, the Mesozoic paleoenvironments with lungfish remains were predominantly freshwater, with the limited possibility of marine influence (Cavin et al., 2007). Therefore, it is logical to hypothesize that the extant members of Lepidosirenidae were established on both Africa and South America prior to the breakup of those continents, which was well underway by late Early Cretaceous (Smith et al., 1994; Hay et al., 1999). A recent molecular phylochronology analysis for extant lungfishes is consistent with this hypothesis, with an estimated divergence time of 120 Ma (165–95 Ma) for African and South American lungfishes (Heinecke et al., 2009).

Among Cretaceous lungfishes, Lepidosirenidae is confidently known from Africa and only questionably known from South America. As reported here, we can add to this record new material of *Lavocatodus* from the Quseir Formation. We consider *Lavocatodus* part of the Lepidosirenidae because the genus has a well-defined symphyseal surface on the tooth plate, as per the revised diagnosis of the clade by Kemp (1998). *Lavodatodus* is distributed extensively across northern Africa, as documented in previous accounts of taxa now attributed to the genus (Martin, 1995). As far as the published record, there are no accounts of *Lavocatodus* from South America; however, there are similarities to the Argentinian taxon *Atlantoceratodus iheringi* (Ameghino 1899), a taxon currently considered more closely related to Ceratodontidae and Neoceratodontidae than to Lepidosirenidae (Apesteguía et al., 2007; Cione et al., 2007). Specimens described for *A. iheringi* are problematic because the first, mesial-most ridge is broken off in all upper dentitions. Therefore, it is not clear if that ridge would be characteristically mesial as it is in all neoceratodontids. The four distal-most ridges are preserved, however, and they are directed buccoposteriorly. In addition, they have a low profile and are short from a true mediolingual apex (rather than a rounded mediolingual apex as in Ceratodontidae) to the buccal extent of all ridges, much like *Lavocatodus giganteus* specimen MUVP 56) from this study and the type specimen described by Martin (1984, 1995). We suggest a further analysis of the specimens of *A. iheringi* to determine if they are synonymous with *L. giganteus*.

*Lepidosiren* also was reported in Cretaceous deposits of Laguno Umayo, Peru, by Sigé (1968, 1972) and Schultze (1991), findings that would have represented the earliest confirmed occurrence of crown clade Lepidosirenidae on South America. However, a revision of the stratigraphy at that locality reassigned the age to the Late Paleocene–Early Eocene (Sigé, 2004). Additional specimens of *Lepidosiren* from the Paleocene through Miocene are found mostly in western equatorial South America (Stirton, 1953; Arratia and Cione, 1996). Thus far, no fossils from eastern regions of South America are known; however, extant *Lepidosiren* are distributed extensively across the continent (Criswell, 2011).

By contrast, the fossil record of *Protopterus* in Africa is extensive, spanning a great extent of northern and central Africa (Otero, 2011). The oldest Cenomanian specimens reported from the Sudan Wadi Milk Formation, as a result of this study, are assigned to *Protopterus nigeriensis*. If those specimens do represent *P. nigeriensis*, that would extend the temporal range by ∼14 million years, suggesting an origin of *Protopterus* in the present day southeastern Saharan region, with radiations extending both west and north through the Cretaceous.

## ACKNOWLEDGMENTS

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