



Original article

A new assemblage of Cenozoic lungfishes (Dipnoi: Lepidosirenidae) from the late Oligocene Nsungwe Formation, Rukwa Rift Basin, southwestern Tanzania [☆]

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ARTICLE INFO

Article history:

Received 4 February 2020

Revised 14 August 2020

Accepted 15 September 2020

Available online 2 December 2020

Keywords:

Protopterus

Lungfish

Dentary

Pterygoid

Tooth plate

Tanzania

ABSTRACT

Lungfish (Dipnoi) date back to the Devonian, and some fossil taxa as well as extant African lungfishes are known for their ability to aestivate, tolerating low-oxygen environments associated with seasonal drying. Extant lungfishes are separated into two families: Lepidosirenidae (*Protopterus* in Africa and *Lepidosiren* in South America) and Neoceratodontidae (*Neoceratodus* in Australia). African lungfishes were more geographically and phylogenetically diverse on the continent in the past than they are today, with only 5% of extinct taxa recorded from the sub-Saharan fossil record. Given the sparse record of Lepidosirenidae fossils from continental Africa, any new materials are important for understanding diversification of the clade. Here we describe new lungfish fossils cautiously referable to *Protopterus annectens* and *Protopterus aethiopicus*, which are strongly supported sister taxa based on the molecular phylogeny. Specimens were collected from the late Oligocene Nsungwe Formation in the Rukwa Rift Basin (RRB) of southwestern Tanzania. The late Oligocene Nsungwe Formation represents a sequence of continental rift-fill deposits of the Songwe sub-basin of the RRB and is subdivided into the lower Utengule and upper Songwe members. Recovery of such material from the Paleogene of Africa below the equator addresses a sizable gap in the lungfish fossil record. It also expands the Nsungwe Formation fauna that includes invertebrates, alestid fishes, ptychadenid anurans, snakes, and several clades of mammals, deepening paleoecological insights into the late Oligocene record of the continental African interior. At present, *P. aethiopicus* and *P. dolloi* have an extensive modern eastern African distribution associated with the rift lakes and a region where extant members of *P. annectens* are not presently known. Fossil specimens described herein document presence of the clade during Paleogene volcanic activity in the western branch of the Eastern African Rift System.

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1. Introduction

Lungfish (Dipnoi) date back to the Devonian, and some fossil taxa as well as extant African lungfishes are known for their ability to aestivate, tolerating low-oxygen environments associated with seasonal drying. Extant lungfish are separated into two families: Lepidosirenidae, represented by *Protopterus* in Africa and *Lepidosiren* in South America, and Neoceratodontidae, represented by

a single genus (*Neoceratodus*) in Australia. *Protopterus* is further divided into four geographically restricted species, all found in sub-Saharan freshwater ecosystems (Berra, 2007).

African lungfishes were more geographically and phylogenetically diverse on the continent in the past than they are today, with only 5% of extinct taxa recorded from the sub-Saharan fossil record (Otero, 2011). The Cenozoic lungfish record documents *Protopterus* sp. from a number of sites in Kenya, including Rusinga, Loperet, Ombo, Lothagam, Omo River, and East Turkana. Pleistocene deposits in Manonga Valley in central Tanzania have long been the only Cenozoic lungfish records from that country (Stewart, 1997). Given the sparse record of Lepidosirenidae fossils from continental Africa,

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any new materials are important for understanding diversification of the clade.

Here we describe new lungfish fossils collected from the late Oligocene Nsungwe Fm. in the Rukwa Rift Basin (RRB) of southwestern Tanzania (Fig. 1). Recovery of such material from the Paleogene of Africa below the equator addresses a sizable gap in the lungfish fossil record. It also expands the Nsungwe Fm. fauna that includes crabs, gastropods, and termites (e.g., Feldmann et al., 2007; Roberts et al., 2016; Epa et al., 2018), alestid fishes (Stevens et al., 2016), ptychadenid anurans (Blackburn et al., 2015, 2019), snakes (McCartney et al., 2014, this volume), and several clades of mammals (Stevens et al., 2005, 2006, 2009a, 2009b, 2013), deepening paleoecological insights into the late Oligocene record of the continental African interior (Roberts et al., 2010, 2012; Stevens et al., 2013).

2. Geological and geographical setting

The late Oligocene Nsungwe Fm. represents a sequence of continental rift-fill deposits of the Songwe sub-basin of the Rukwa Rift Basin and is subdivided into the lower Utengule and upper Songwe members (Roberts et al., 2010, 2012). All lungfish material described herein was recovered from the Songwe Mb., assigned a late Oligocene age, 25–26 Ma based on biostratigraphy and high-precision U-Pb and Ar/Ar dating of intercalated ashbeds (Stevens et al., 2005, 2006, 2008, 2009a, 2009b, 2013; Roberts et al., 2010, 2012). The new specimens were all recovered from fluvial depositional facies (i.e., facies associations 3 and 4 following Roberts et al., 2010) within the middle portion of the Songwe Mb. along both the Songwe River section at the TZP2 locality and the Nsungwe River section at localities Nsungwe 2b and 3 (Fig. 1). All specimens were collected on expeditions conducted by the Rukwa Rift Basin Project (RRBP) between 2002 and 2016.

3. Material and methods

Lungfish fossils were mechanically prepared by K. Whitman at the Ohio University Vertebrate Fossil Preparation Facility. Specimens were photographed using a Canon Digital Rebel EOS camera with macro-lens at multiple focal points creating image stacks of 4–9 pictures per specimen. Focused photomontages were then assembled from stacks of images using the program Helicon Focus (version 7.6.1 Lite) to generate the figure plates.

Cast of the five fossil lungfish specimens (RRBP 04147, 05429, 09059, 08314, and 16189) described in this paper are held at Ohio University and are available for study upon request; original fossils are permanently reposit with the Tanzania Antiquities Division.

Extant materials used for comparative purposes include *Protopterus aethiopicus* (UF 137272, 147058) and *Protopterus annectens* (AMNH 55226, TMM M-1129), along with specimens described by Criswell (2015). Fossils examined include †*Protopterus elongus* (AMNH 22202, 22204, 22205, 22206, 22123) and †*Protopterus nigriensis* (MNHN-F-IBC 180 [holotype], MNHN-F-IBC 1751, MUVF 57). We cautiously refer specimens to taxa in this text and note the similarities of Rukwa taxa with the modern species of *Protopterus*, in particular *P. aethiopicus*, *P. annectens*, and *P. dolloi*. We consider the adult morphological comparative study by Criswell (2015) and the ontogenetic study by Bemis (1984) when using relative size to distinguish taxa. Morphological descriptions and tentative assignments follow terminology based on Criswell (2015) using an apomorphic approach, rather than the meristic approach previously employed by Poll (1961). As noted in figure captions, some line drawings of extant taxa are based on CT renderings from Criswell (2015).

Abbreviations: AMNH, American Museum of Natural History, New York, NY, USA; MNHN, Muséum National d'Histoire Naturelle, Paris, France; RRBP, Rukwa Rift Basin Project, Tanzanian Antiquities Unit/National Museum of Tanzania, Dar es Salaam, Tanzania; TMM, Texas Memorial Museum, Austin, Texas, USA; UF, Florida Museum of Natural History.

4. Systematic paleontology

Osteichthyes Huxley, 1880

Sarcopterygii Romer, 1955

Dipnoi Müller, 1845

Lepidosirenidae Bonaparte, 1841

Protopterus (Owen, 1839)

Protopterus cf. *annectens*

Figs. 2(A, B), 3(A, B), 4(A, B), 5(A–C)

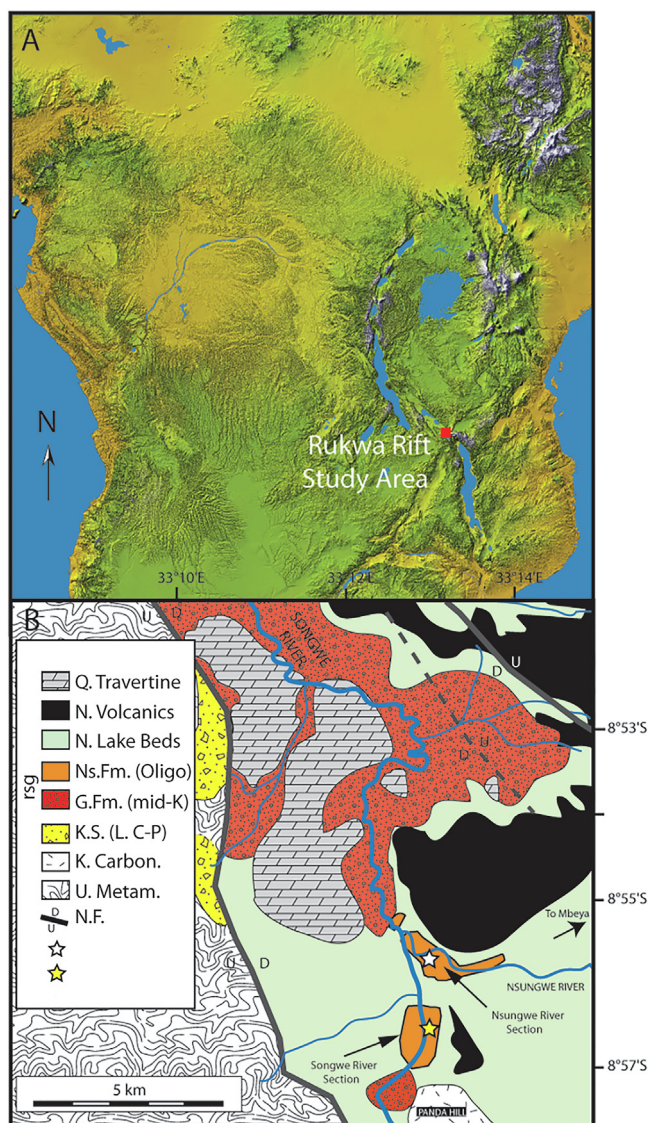


Fig. 1. Location of field area in southwestern Tanzania that produced fossil lungfish specimens. White star: Nsungwe Formation Type Locality; yellow star: TZ1-South Locality. Abbreviations: D, down; G.Fm. (mid-K), Galula Formation (mid-Cretaceous); K. Carbon., Cretaceous Carbonate; K.S. (L. C-P), Karoo Supergroup (Lower Carboniferous-Permian); N., Neogene; N.F., Normal Fault; Ns.Fm., Nsungwe Formation; rsg, Red Sandstone Group; Q., Quaternary; U, Up; U. Metam., Ubendian Metamorphics.

Referred material: RRBP 05429, right pterygoid with tooth plate; RRBP 16189, right prearticular with tooth plate.

Horizon: Late Oligocene, ~25 Ma.

Locality: TZP2 (RRBP 05429) and Nsungwe 3 (RRBP 16189), Mbeya Region, Tanzania.

Depositional environment: Fluvial facies.

Description: RRBP 05429 is a partial right pterygoid and pterygoid tooth plate, missing the anterior process and anterior ridge of the latter (Figs. 2(A), 3(B)). The middle (second) and posterior (third) ridges of the tooth plate are associated with the middle and posterior processes of the pterygoid. The tooth plate is slightly displaced and the posterior tooth plate ridge is not aligned with the posterior process of the pterygoid (Fig. 3(B)). There are signs of compression, preserved as multiple fractures. Tooth plate ridges are sharp and shallow without tubercles and are not worn (Fig. 2(A), 3(B)). The posterior tooth ridge is fractured just distal to the distal-most end of the middle tooth ridge; however, the posterior process of the pterygoid is at least twice the length of the middle tooth ridge and middle pterygoid process. The middle and posterior tooth ridges meet at a distinct sharp angle near where the symphysis would be preserved (Fig. 2(B)) and a central connecting ridge to the anterior ridge of the tooth plate is preserved. The symphyseal margin, while incomplete, follows that central connecting ridge (Fig. 2(A)) similar to the condition in other species such as of *P. annectens* and *P. dolloi*, but not *P. aethiopicus* (Bemis, 1986; Criswell, 2015; Fig. 2(B, C, E)).

The pterygoid bone of RRBP 05429 is posteriorly tapered, elongate, and ventrally directed (Fig. 2(A)) as seen in *Protopterus* (Bemis, 1986; Criswell, 2015) with a straighter ventral margin like in *P. annectens* or *Lepidosiren* (Fig. 3(A, E)) compared to an arched ventral margin in *P. aethiopicus* (Fig. 3(B)). The expansive, wing-like process known in extant species of lepidosirenid lungfishes (Fig. 3(A, C, E)) is missing, probably due to erosion. The pterygoid bone of RRBP 05429 preserves evidence of a moderately defined ascending dorsal process that would have articulated with the supraorbital bone (Fig. 3(B)). That ascending process is incomplete and preserves only the proximal portion, which begins just dorsal to the middle pterygoid process and extends posterior to the posterior pterygoid process (Fig. 3(B)) as is seen in other species of *Protopterus* (Bemis, 1986; Criswell, 2015; Fig. 3(A, C)). The preserved portion of the ascending process also is not as medially directed as in *P. aethiopicus* or *P. dolloi* (Fig. 2(A, C, E)) and in that sense more closely resembles *Lepidosiren* or *P. annectens* (Bemis, 1984; Criswell, 2015; Fig. 2(B)); however, this may be an artifact of preservation. The posterior flange is straight in lateral view and tapers distally (Fig. 3(B)). On the tooth plate, the middle and posterior tooth ridges are present and the anterior tooth plate ridge is fractured along with the anterior process of the pterygoid bone itself. RRBP 05429 is unlike the Cretaceous *P. nigeriensis* (Martin, 1997), which has a short posterior tooth ridge, only one-quarter longer than the middle tooth ridge and a middle and posterior tooth ridge that remain separate from one another near a flat symphyseal margin. RRBP 05429 is unlike the Eocene *P. elongus* (Martin, 1995), which has a short posterior tooth ridge and posterior pterygoid process that are nearly perpendicular to the pterygoid symphysis. *P. elongus* also exhibits a short middle tooth ridge and short middle pterygoid process that join together far from the symphysis before sending a long, bent connecting ridge, towards the anterior tooth ridge.

RRBP 16189 is a partial right deeply crowned prearticular tooth plate and partial right prearticular bone (Figs. 4, 5). The anterior tooth ridge in RRBP 16189 (Fig. 4(B)) is anterolaterally directed at nearly a 45° angle with the prearticular symphysis. The anterior tooth ridge is joined to the middle and posterior tooth ridges by a short central connecting ridge that does not following the margin of the symphysis. The middle tooth ridge is approximately perpendicular to the symphysis. The posterior tooth ridge bifurcates from the middle ridge and remains flush with the prearticular bone; however, it is fractured just proximal to the distal extent of the

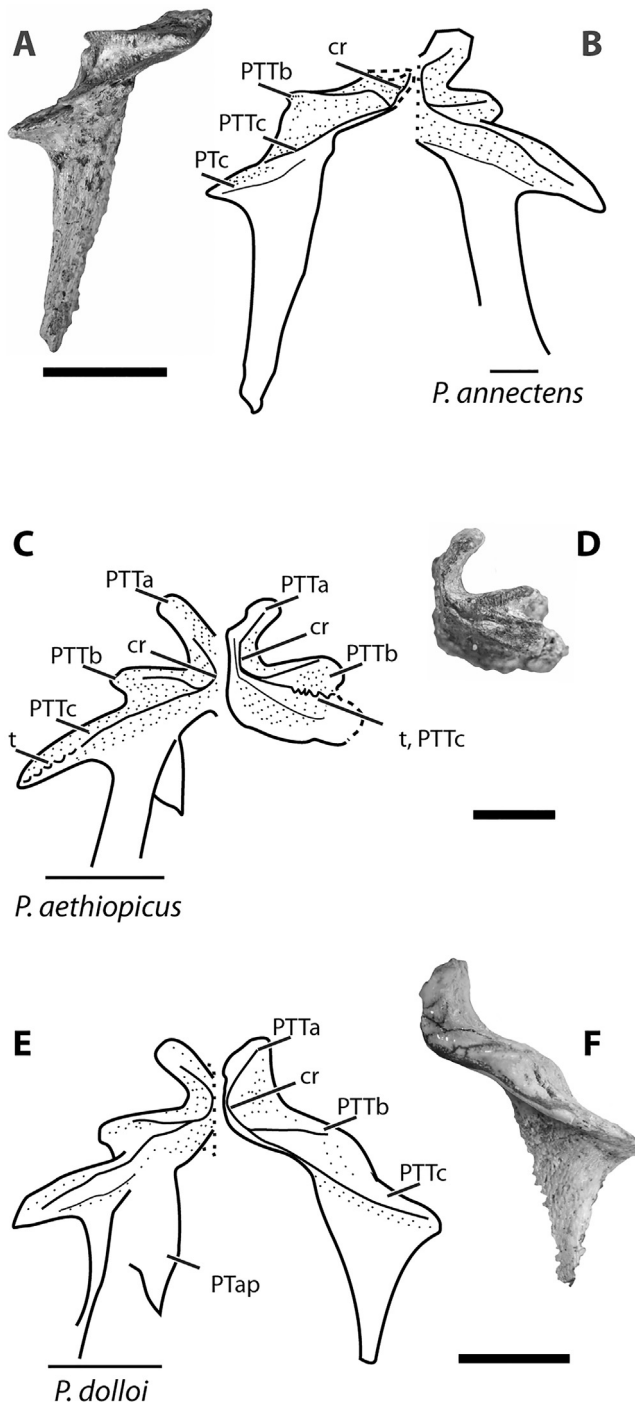


Fig. 2. Pterygoids in occlusal view. **A.** RRBP 05429, *Protopterus* cf. *annectens*, photo and line drawing of right pterygoid. **B.** Line drawing of left pterygoid of *Protopterus annectens* based on CT renderings by Criswell (2015). **C.** Line drawing of right pterygoid of *Protopterus aethiopicus* based on CT renderings in Criswell (2015). **D.** RRBP 04147, *Protopterus* cf. *aethiopicus*, line drawing and photo of left pterygoid tooth plate. **E.** Line drawing of right pterygoid of *Protopterus dolloi* based on CT renderings by Criswell (2015). **F.** RRBP 09059, *Protopterus* sp., line drawing and photo of left pterygoid. Abbreviations: cr, connecting ridge; PTTa-c, pterygoid ridges, anterior, middle, posterior; PTap, anterior process of the pterygoid; PTTa-c, pterygoid tooth ridges, anterior, middle, posterior; t, tubercle. Scale bars: 5 mm (A-D, F) 2.5 mm (E).

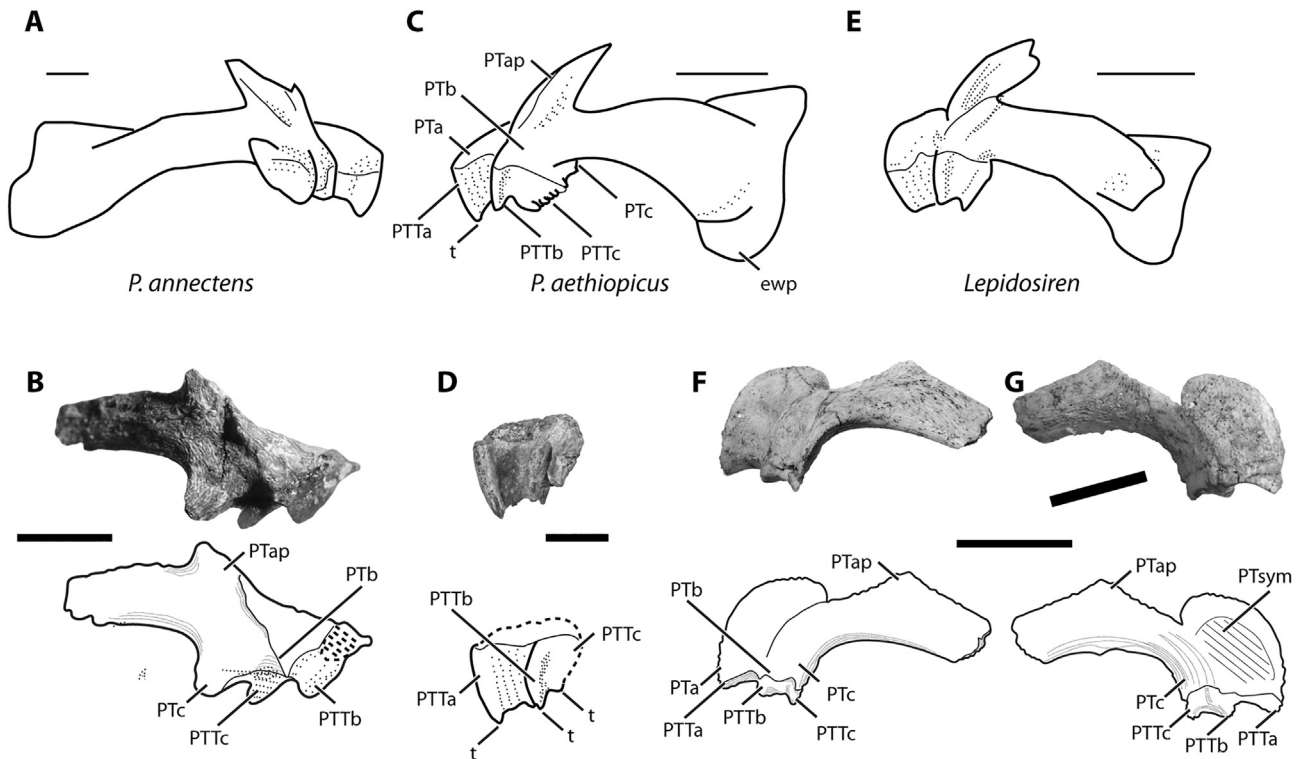


Fig. 3. Pterygoids in lateral and symphyseal views. **A.** Line drawings of right lateral pterygoid of *Protopterus annectens* based on CT renderings by Criswell (2015). **B.** RRBP 05429, *Protopterus* cf. *annectens*, photo and line drawing of right lateral pterygoid. **C.** Line drawings of left lateral pterygoid *Protopterus aethiopicus* based on CT renderings Criswell (2015). **D.** RRBP 04147, *Protopterus* cf. *aethiopicus*, photo and line drawing of left lateral pterygoid tooth plate. **E.** Line drawing of left lateral pterygoid of *Lepidosiren* based on CT renderings by Criswell (2015). **F, G.** RRBP 09059, *Protopterus* sp., photo and line drawing of left lateral pterygoid in lateral (F) and symphyseal (G) view. Abbreviations: cr, connecting ridge; ewp, expansive wing-like process; PTA-c, pterygoid ridges, anterior, middle, posterior; PTap, anterior process of the pterygoid; PTsym, pterygoid symphyseal surface; PTTa-c, pterygoid tooth ridges, anterior, middle, posterior; t, tubercle. Scale bars: 5 mm.

middle tooth ridge, and thus, its complete extent is not known. The ridges are tall and do not preserve tubercles. A worn surface is present on the anterior tooth ridge which was probably due to grinding use during life, rather than erosion, given the well-defined, unworn ridges on the symphyseal surface (Figs. 4(C), 5(B, C)). The anterior ridge is in roughly the same position of the tall cusp in *P. annectens* (Fig. 5(A)). Given the present wear and relative size of RRBP 16189 compared to extant specimens of *P. annectens* and *P. aethiopicus*, it would resemble *P. annectens* (Bemis, 1984) which are noted to have more wear of the anterior ridge at the same size as *P. aethiopicus*. RRBP 16189 is unlike the Cretaceous *P. nigeriensis* (Martin, 1997) and Oligocene *P. libycus* (Stromer, 1910), both of which lack a connecting ridge between the anterior, middle, and posterior tooth ridges.

The symphyseal surface of the prearticular bone (RRBP 16189) is nearly straight and rugose and would have interlocked tightly with its antimeres (Fig. 5(B)). In lateral view (Fig. 5(C)), at the anterior end of the prearticular, there is no bulbous ventral prominence as is present in *P. aethiopicus* (Fig. 5(D)). Rather, there is a shallow shelf supporting the anterior ridge of the prearticular tooth plate (Fig. 5(C)), similar to that in *P. annectens* as rendered in Criswell (2015) (Fig. 5(A)) and *Lepidosiren* (Bemis, 1984). A slightly deeper shelf supporting the second ridge of the prearticular is also present. Nothing else remains of the prearticular bone in RRBP 16189.

Protopterus cf. *aethiopicus* Heckel, 1851

Figs. 2(C, D), 3(C, D), 4(C, D), 5(D, E)

Referred material: RRBP 04147, nearly complete left pterygoid tooth plate with little bone preserved; RRBP 08314, nearly complete right prearticular with tooth plate.

Horizon: Late Oligocene, 24.95 Ma.

Locality: TZP2, Mbeya Region, Tanzania.

Depositional environment: Fluvial facies.

Description: RRBP 04147 is a nearly complete, robust, deeply-crowned left pterygoid tooth plate with a minimal amount of pterygoid bone preserved immediately dorsal to the anterior and middle tooth plate ridges (Figs. 2(D), 3(D)). The anterior and middle pterygoid tooth plate ridges are complete and the posterior ridge is fractured just distal to the end of the middle tooth plate ridge. The anterior tooth ridge is set far apart from the middle and posterior tooth ridges and is joined by a bent central connecting ridge that follows the margin of the symphysis a short distance before turning distally towards the bifurcation of the middle and posterior ridges (Fig. 2(D)) and resembles *P. aethiopicus* (Bemis, 1986; Criswell, 2015; Fig. 2(C)) more than other species of *Protopterus* in that regard (Criswell, 2015). In lateral view (Fig. 3(D)), the deeply crowned anterior tooth ridge most resembles *P. aethiopicus* as rendered in Criswell (2015) and all sharing a prominent tubercle at the distal end of the crown (Bemis, 1984; Fig. 3(C, D)).

RRBP 08314 is a nearly complete, robust, moderately crowned right prearticular tooth plate and partial right prearticular bone. In occlusal view (Fig. 4(D)), the symphyseal surface of the prearticular bone is somewhat straight and worn. The posterior tooth ridge follows the margin of the pterygoid bone. In lateral view, at the anterior end of the prearticular, there is a bulbous ventral prominence, separated from the remainder of the prearticular by a distinct notch (Fig. 5(E)) and similar to that in *P. aethiopicus* that were figured in Ngasala (2015) and Bemis (1986; AMNH 55220) (Fig. 5(D)). The coronoid process and angular process are broken away at roughly the point where those processes would have forked. There is a well-defined keel on the ventral aspect of the prearticular

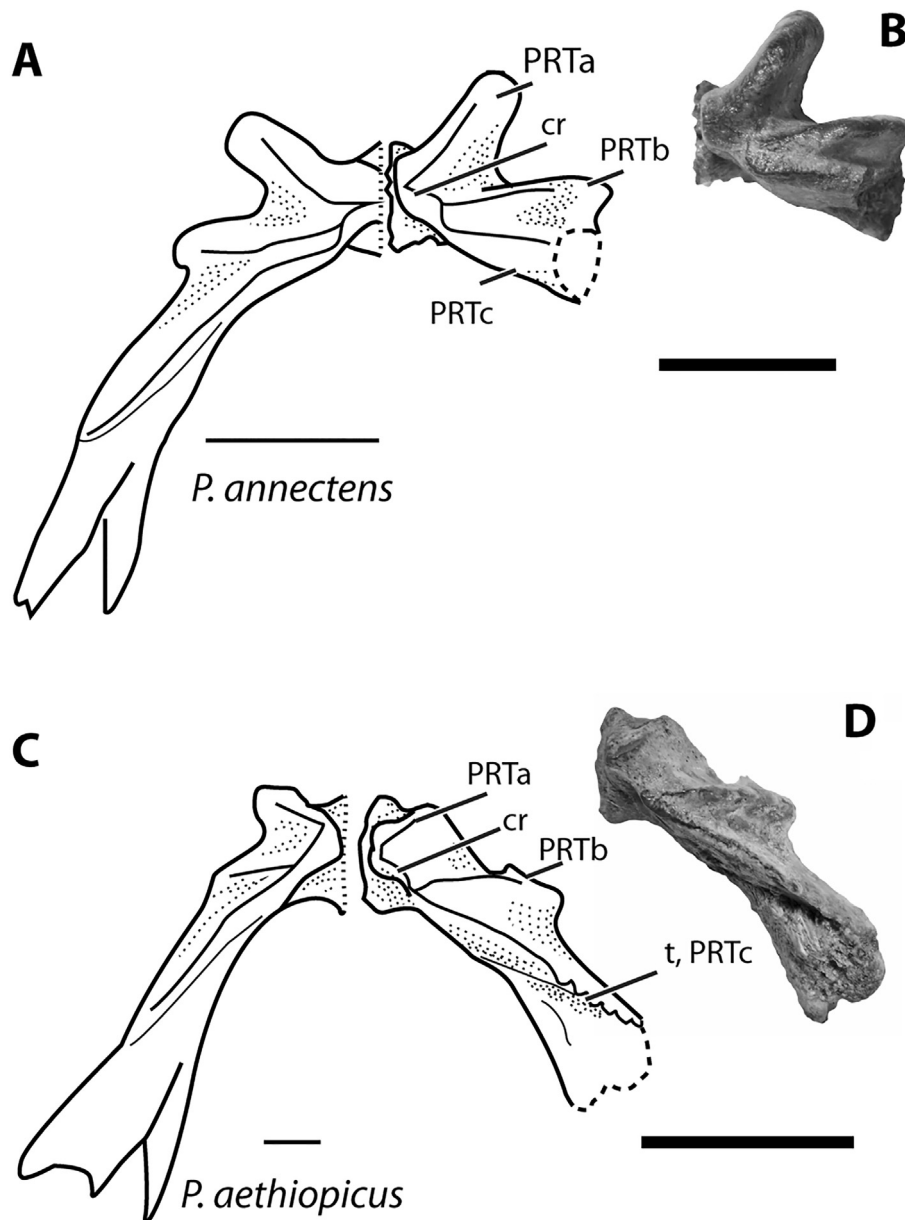


Fig. 4. Preaticulars in occlusal view. **A.** Line drawing of left prearticular of *Protopterus annectens* based on CT renderings by Criswell (2015). **B.** RRBP 16189, *Protopterus* cf. *annectens*, line drawing and photo of right prearticular. Abbreviations: cr, connecting ridge; PRTa-c, prearticular ridges, anterior, middle, posterior; PRTan, angular process of the prearticular; PRTcor, coronoid process of the prearticular; PRTa-c, prearticular tooth ridges, anterior, middle, posterior; t, tubercle. Scale bars: 5 mm.

(Fig. 5(E)) where the angular bone would articulate and form the mandibular canal much like that seen in *P. aethiopicus* (Fig. 5(D)) and Bemis (1986; AMNH 55220). The keel on RRBP 08314 begins ventral to the middle tooth ridge, just posterior to the notch demarcating the ventral prominence. In other species of *Protopterus*, the keel and groove are longer than the angular bone that it accepts (Criswell, 2015).

In occlusal view of RRBP 08314 (Fig. 4(D)), the anterior prearticular tooth ridge is set far apart from the middle and posterior tooth ridges and is joined by a bent central connecting ridge that follows the margin of the symphysis a short distance before turning distally towards the bifurcation of the middle and posterior ridges. The middle tooth ridge is approximately perpendicular to the symphysis. The posterior tooth ridge bifurcates from the middle ridge remaining flush with the prearticular bone. In lateral view, the ridges are tall. There is a different type of mineral on the upper-

most crown on the tubercles relative to the base of the tooth base. On the distal portion of the posterior tooth ridge, there are several tubercles that form the peak of the tooth ridge (Fig. 4(D), 5(E)), as in *P. aethiopicus* (Fig. 5(D)) and as described in Bemis (1984).

In lateral view of RRBP 08314, the middle ridge is not as deep as the anterior ridge; however, both are massive and similar to that in *P. aethiopicus* (Fig. 5(E)) and Bemis (1984, 1986). The peaks of the occlusal surfaces of the anterior and middle tooth ridges (Fig. 5(E)) exhibit well demarcated tubercles that appear to be mineralized differently than the remainder of the tooth plate as in *P. aethiopicus* (Bemis, 1984). The space between the anterior and middle ridge is greater than the distance between the middle and posterior tooth plate ridges (Fig. 4(D)). This is due to the straight and prominent flat central ridge across the symphyseal margin that connects the anterolaterally directed anterior ridge with the middle and posterior ridges, as in *P. aethiopicus* (Fig. 4

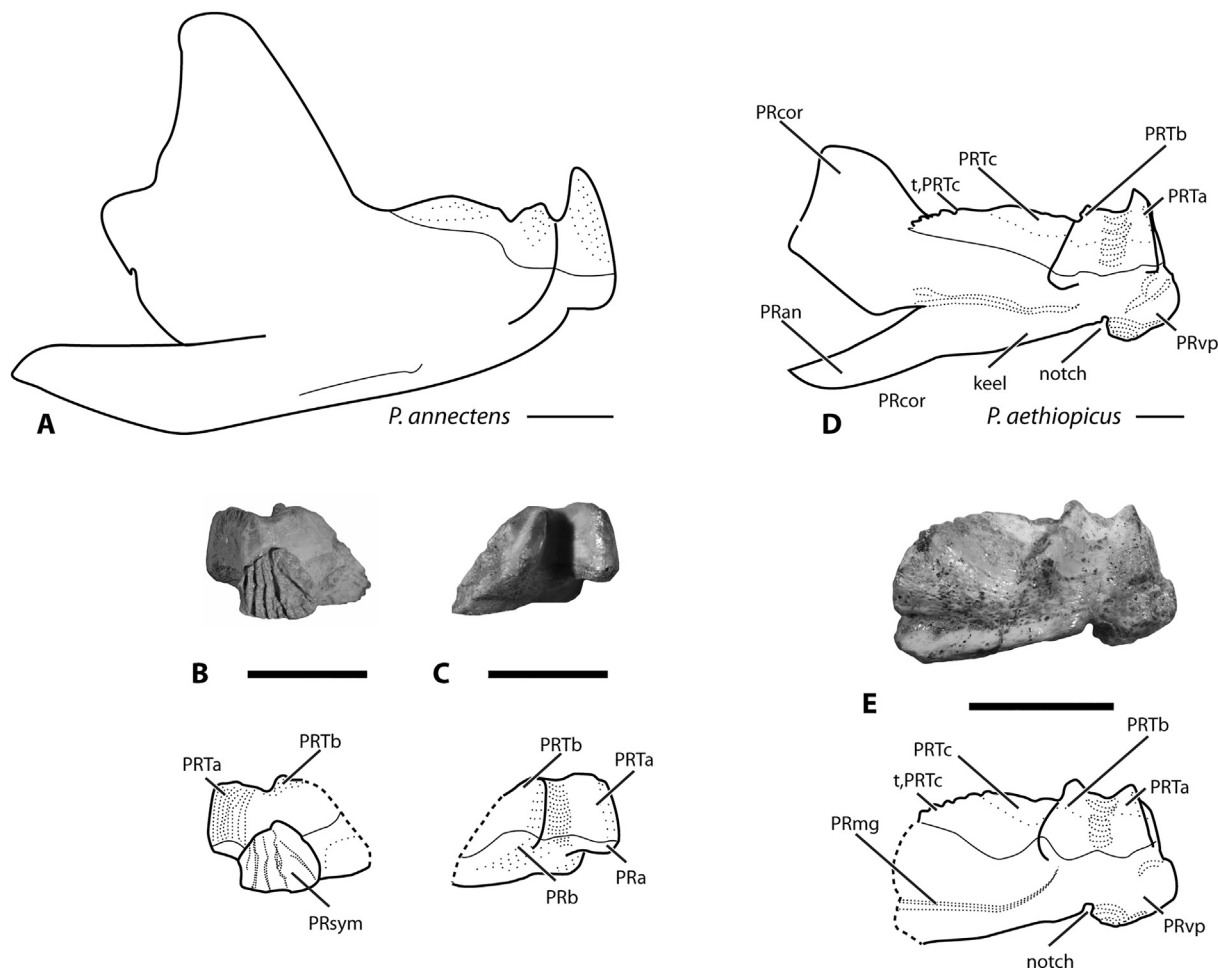


Fig. 5. Prearticulars in lateral and symphyseal view. **A.** Line drawing of right prearticular of *Protopterus annectens* based on CT renderings by Criswell (2015). **B, C.** RRBP 16189, *Protopterus* cf. *annectens*, line drawing and photo of right prearticular in symphyseal (B) and right lateral (C) view. **D.** Line drawings of right prearticular of *Protopterus aethiopicus* based on photo in (Ngasala, 2016). **E.** RRBP 08314, *Protopterus* cf. *aethiopicus*, line drawing and photo of right prearticular. Abbreviations: cr, connecting ridge; PRa-c, prearticular ridges, anterior, middle, posterior; PRan, angular process of the prearticular; PRcor, coronoid process of the prearticular; PRTa-c, prearticular tooth ridges, anterior, middle, posterior; t, tubercle. Scale bars: 5 mm.

(C, D)) as rendered by Criswell (2015). The middle and posterior ridges form a v-shaped bifurcation (Fig. 4(D)) as drawn in Bemis (1986).

The prearticular specimen RRBP 08314 is unlike the Cretaceous *P. nigeriensis* (Martin, 1997) and Oligocene *P. libycus* (Stromer, 1910), both of which lack a connecting ridge between the anterior, middle, and posterior tooth ridges. RRBP 08314 is unlike the Cretaceous *P. nigeriensis* (Martin, 1997), which has a short posterior tooth ridge, only one-quarter longer than the middle tooth ridge and a middle and posterior tooth ridge that remain separate from one another near a flat symphyseal margin. RRBP 08314 also is unlike the Eocene *P. elongus* (Martin 1995), which has a shorter posterior tooth ridge and posterior pterygoid process that are nearly perpendicular to the pterygoid symphysis, a short middle tooth ridge and middle pterygoid process that join together far from the symphysis before sending a long, bent connecting ridge, towards the anterior tooth ridge. It is unlike the Miocene *P. polli* (Dartevelle and Casier, 1949), which was described as having four crests (Martin, 1995; Otero, 2011).

Protopterus sp.

Fig. 2(F), 3(F, G)

Referred material: RRBP 09059, left pterygoid and pterygoid tooth plate.

Horizon: Late Oligocene, 25.2 Ma.

Locality: Nsungwe 2B, Mbeya Region, Tanzania.

Depositional environment: Fluvial facies.

Description: RRBP 09059 is a greatly worn, partial left pterygoid bone and equally worn left pterygoid tooth plate (Fig. 2(F), 3(F, G)). It is almost indiscernible as a lepidosirenid except for the distinct, three-ridge tooth plate. Of the Tanzanian tooth plates prepared for this study, it is the least like any of the extinct or extant species of *Protopterus* known to date, including the other specimens from Rukwa. The tooth plate ridges are without tubercles, greatly worn and shallow, preserving little of the crown (Fig. 2(F), 3(F, G)). The anterior tooth ridge is set far from the middle and posterior tooth ridges, joined by a gently curving central connecting ridge and similar to the condition in *P. dolloi* (Fig. 2 (E)) as rendered in Criswell (2015). The middle and posterior tooth ridges meet at a distinct sharp angle near where the symphysis would be preserved. The posterior process of the pterygoid is at least twice the length of the middle tooth ridge and middle pterygoid process; however, the distal ends of both middle and posterior ridges are highly worn and likely do not represent their potential length. In fact, in lateral view, it is difficult to discern any prominent pterygoid processes (Fig. 3(F)). The symphyseal margin, while incomplete, is flat and large (Fig. 3(G)). There is a bulbous prominence on the pterygoid bone of RRBP 09059 dorsal to the anterior

tooth ridge that follows the contour of the symphysis (Fig. 3(F, G)), and in lateral view, is most similar to the condition in certain examples of *Lepidosiren* (Fig. 3(E)) or *P. dolloi*, albeit in a much more prominent fashion and unlike *P. amphibius* as seen in Criswell (2015). The pterygoid bone tapers greatly into a posterior flange. Remnants of an ascending process are set far from the anterior and posterior ridges, present halfway along the length of the posterior flange (Fig. 3(F, G)). RRBP 09059 is missing the expansive, wing-like process known in extant species of Lepidosirenidae (Fig. 3(A, C, E)) probably due to taphonomy. RRBP 09059 is unlike the Cretaceous *P. nigeriensis* (Martin, 1997), in which the posterior tooth ridge is short, is only one-quarter longer than the middle tooth ridge, and the middle and posterior tooth ridge remain separate from one another near a flat symphyseal margin. It is also unlike the Eocene *P. elongus* (Martin 1995), in which the posterior tooth ridge is shorter and the posterior pterygoid process is nearly perpendicular to the pterygoid symphysis. Moreover, *P. elongus* also exhibits a short middle tooth ridge and middle pterygoid process that join together far from the symphysis before extending a long, bent connecting ridge, towards the anterior tooth ridge. It is unlike the Miocene *Protopterus polli* (Dartevelle and Casier, 1949), a form that is described as having four crests (Martin, 1995; Otero, 2011).

5. Discussion

Lepidosireniform lungfishes from the Cenozoic African fossil record include two described genera, *Lavacatodus* and *Protopterus* (Martin, 1995). Based on molecular data, the radiation of modern *Protopterus* is estimated to have occurred between the Late Cretaceous and early Paleogene (Tokita et al., 2005). All Rukwa specimens are referred to *Protopterus* based on possessing a distinctive tooth plate exhibiting three columnar petrodentine ridges. These specimens represent the first described *Protopterus* records from the Paleogene, more specifically the Oligocene, of southwest Tanzania and expand both the temporal and geographic extent of the genus (see Otero, 2011 for a biogeographic review).

Among many fragments of lungfish fossils, there are four diagnosable species of *Protopterus* resembling the modern form in the African fossil record: *P. libycus* (early Oligocene, Fayum Depression, Egypt; Stromer, 1910), *P. polli* (Miocene, Congo, Dartevelle and Casier, 1949), *P. elongus* (Eocene, Tamaguielt, Mali; Martin, 1995; see also late Eocene of Birket Qarun, Egypt; Murray et al., 2010), and *P. nigeriensis* (Martin, 1997). We distinguish the fossils from Rukwa from named extinct species of *Protopterus* based on tooth-plate ridge number, presence of connecting ridges, position of tooth ridges, and when possible, the shape of the jaw bones themselves. We are cautious to name taxa at this stage and instead note the similarities of Rukwa taxa with the modern species of *Protopterus*, in particular *P. aethiopicus*, *P. annectens* and *P. dolloi*, and consider the adult morphological comparative study by Criswell (2015) and the ontogenetic study by Bemis (1984) when using relative size to distinguish taxa.

Protopterus aethiopicus and *P. annectens* are strongly supported sister taxa based on the molecular phylogeny reported by Tokita et al. (2005), with weaker support for *P. dolloi* as their sister taxon. The estimated divergence time of *P. aethiopicus* and *P. annectens* is between 42 and 25.6 Ma (Tokita et al., 2005). Importantly, volcanism in eastern Africa began during the Oligocene in the Ethiopian zone and more southward in the northern Kenyan rift at 33–30 Ma (Chorowicz, 2005.) At present, *P. aethiopicus* and *P. dolloi* have an extensive modern eastern African distribution associated with the rift lakes. The modern distribution of *P. annectens* is primarily restricted to western Africa with one exception – a report from easternmost Kenya listed specimens of *P. annectens*, including

the specimen referred in this publication, AMNH 55229. Specimens resembling *P. aethiopicus*, *P. annectens* and *P. dolloi* described herein document presence of the clade during Paleogene volcanic activity in the western branch of the Eastern African Rift System, a region where extant members of *P. annectens* are not presently known (Paugy et al., 2008; Froese and Pauly, 2019). Increased research in this paleontologically under-sampled interval in the African Cenozoic record reveals a snapshot into the diversification and biogeographic distribution of these fascinating fishes at a tectonically important interval on the African continent, consistent with the hypothesis made by Otero (2011).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Olga Otero and an anonymous reviewer for their constructive comments on earlier versions of this manuscript, K. Whitman who prepared the fossils, and A. Ramon who helped with figures. Field and laboratory research was supported by the National Science Foundation BCS_1638796, EAR_1349825, BCS_1127164, EAR_0617561/EAR_0854218 and the National Geographic Society. S. Ngasala acknowledges Michigan State University for graduate funding that supported his dissertation work on these materials, M.D. Gottfried recognizes the Department of Earth and Environmental Sciences for support of this research.

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