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The Earliest Fossil of the African Clawed Frog (Genus *Xenopus*) from Sub-Saharan Africa

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ABSTRACT.—Although the fossil record of pipoid frogs is more extensive than for other anuran clades, crown-group genera are poorly documented throughout the Cenozoic. We report an isolated neurocranium from the Nsungwe Formation (~25 million years ago; Oligocene) in southwestern Tanzania, providing the earliest evidence for the genus *Xenopus* in sub-Saharan Africa. The specimen is well preserved, allowing us to use three-dimensional geometric morphometrics to compare the shape of this neurocranium to those of all extant species of *Xenopus* based on microcomputed tomography scans. Analyses revealed that this small fossil resembles diminutive extant species of *Xenopus* such as *X. longipes*. The fossil neurocranium preserves well-ossified tectum nasi and septum nasi, the latter separating large ovoid olfactory foramina, contributing to a more-ossified region surrounding the prootic foramen than observed in extant species of similar size. The Nsungwe Formation pipoid fossil contributes new information to the early biogeography and body-size diversification within the genus *Xenopus*.

African clawed frogs in the genus *Xenopus* are found today throughout sub-Saharan Africa and, because of their widespread use as model organisms in biological research, as introduced populations around the world (Measey et al., 2012; Evans et al., 2015). Because all members of the family Pipidae, including *Xenopus*, are predominantly aquatic frogs with a preference for slow-moving bodies of water, they likely have a high potential for fossilization. Indeed, the fossil record for the Pipidae, and more generally the Pipoidea, is extensive and extends into the Mesozoic of both Africa and South America (e.g., Báez and Rage, 1998; Báez et al., 2000; Rage and Dutheil, 2008; Rage et al., 2013; Gómez, 2016). As most of these fossils are not referable to extant genera, many have been described as representing extinct pipoid taxa. When complete body fossils are preserved, the morphology of these extinct taxa is similar enough to living species to suggest a long evolutionary history for the aquatic ecology observed in extant species (Cannatella, 2015). Two extinct taxa (*Singidella* from the Eocene of Tanzania, and *Pachycentrata* from the Upper Cretaceous of Niger) are attributed to the crown-group subfamily Pipinae (Báez and Harrison, 2005; Cannatella, 2015). The fossil record for the other and more species-rich subfamily Xenopodinae remains poorly documented, though several extinct taxa (*Saltenia* from the Late Cretaceous and *Llankibratrachus* and *Shelania* from the Eocene; all from Argentina) have been referred to the larger clade Xenopodimorpha (Trueb and Báez, 2006; Cannatella, 2015). To date, no fossils that can be confidently referred to the extant genus *Xenopus* have been described from the Palaeogene of sub-Saharan Africa, when this genus is thought to have originated (Cannatella, 2015).

Here we report the earliest fossil material from sub-Saharan Africa referable to the extant pipid genus *Xenopus* based on a specimen from the upper Oligocene Nsungwe Formation in the Rukwa Rift Basin of southwestern Tanzania (Fig. 1). Localities from this formation preserve a diverse vertebrate and invertebrate fauna (Stevens et al., 2008, 2009, 2013; Roberts et al., 2010, 2012) from ~25 million years ago (mya) (Roberts et al., 2010, 2012),

including amphibians and reptiles (McCartney et al., 2014; Blackburn et al., 2015; Müller et al., 2018). Isolated vertebrae from the Nsungwe Formation represent the earliest fossil evidence of the family Ptychadenidae (Blackburn et al., 2015), though additional post-cranial and cranial elements of anurans await description. Among the most distinctive of anuran fossils found so far is a small, isolated neurocranium (Fig. 2), described herein as referable to xenopodinomorph pipids based on the presence of an exposed canal for the Eustachian tube on the ventral surface of the otic capsule and frontoparietals that narrow rostrally and lack anterolateral flanges (Cannatella, 1985).

Comparisons to extant species of the genus *Xenopus* reveal xenopodinomorph affinities of the neurocranium. We compare this specimen to neurocrania isolated from microcomputed tomographic (microCT) scans of fluid-preserved specimens representing all extant species in the genus. We use three-dimensional geometric morphometrics to compare the fossil from the Nsungwe Formation with variation seen across the two extant subgenera (*Silurana* and *Xenopus*) in the clade. Our findings are relevant both to understanding the antiquity of crown-group *Xenopus* as well as the historical biogeography of this biologically important taxon.

MATERIALS AND METHODS

Sampling.—For morphological comparisons and statistical analyses, we sampled all 29 currently recognized extant species of *Xenopus*, including primary types of 15 of these species and representatives of species that today occur in the region such as *X. borealis*, *X. laevis*, *X. muelleri*, and *X. victorianus*. We follow the taxonomy for *Xenopus* by Evans et al. (2015) in recognizing two subgenera, *Silurana* and *Xenopus*, as well as three species groups within subgenus *Xenopus* (*amioti*, *laevis*, and *muelleri* species groups). We obtained morphological data for 50 specimens in addition to the isolated neurocranium from the Nsungwe Formation. Institutional abbreviations for the specimens studied are as follows: AMNH, American Museum of Natural History, New York, USA; BMNH, Natural History Museum, London, UK;

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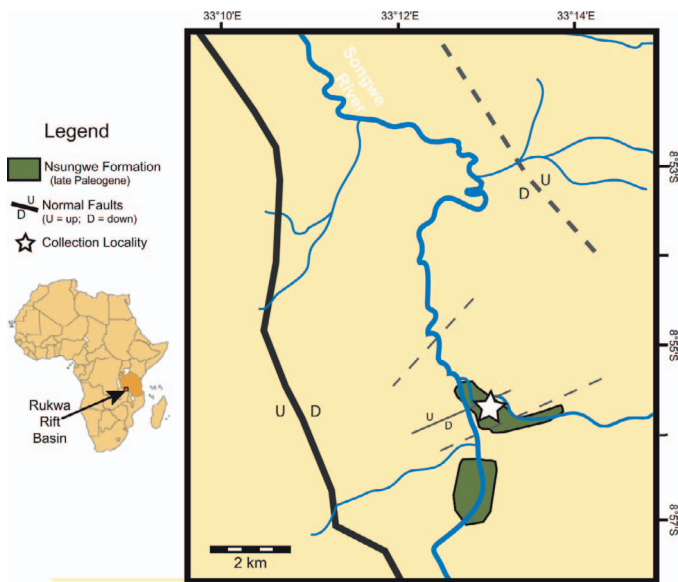


FIG. 1. Location of the Rukwa Rift Basin containing the Nsungwe Formation fossil-bearing localities. Star notes collection locality of RRBP 13274B.

CAS, California Academy of Sciences, San Francisco, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA; MHNG, Museum d'histoire naturelle de Genève, Switzerland; NCSM, North Carolina State Museum, Raleigh, USA; RRBP, Rukwa Rift Basin Project, Tanzanian Antiquities Unit, Dar es Salaam, Tanzania; UF, Florida Museum of Natural History, University of Florida, Gainesville, USA.

Computed Tomography (CT) Scanning.—We performed high-resolution computed tomography (microCT) scanning at the GE Sensing and Inspection Technologies facility (San Carlos, California, USA), and at the University of Florida's Nanoscale Research Facility, using a Phoenix v|tome|x S and Phoenix v|tome|x M (GE Measurement & Control Solutions, Boston, Massachusetts, USA), respectively. All scans were run using a 180-kV X-ray tube containing a diamond-tungsten target, with the voltage, current, and detector capture time adjusted for each scan to maximize absorption range for each specimen. Raw X-ray data were processed using GE's proprietary datos|x software v.2.3 to produce a series of tomogram images and volumes, with final voxel resolutions ranging from 4.5 to 72 μm . The resulting microCT volume files were imported into VG StudioMax v.3.0 (Volume Graphics, Heidelberg, Germany), the neurocrania isolated using VG StudioMax's suite of segmentation tools, and then exported as high-fidelity shapefiles (.ply format). We deposited image stacks (TIFF) and 3D mesh files (STL) in MorphoSource (Supplementary Table S1).

Shape Analyses.—We quantified interspecific shape variation of the neurocranium using three-dimensional geometric morphometric analyses in the R package 'geomorph' v.3.0.3 (Adams and Otárola-Castillo, 2013). Sixteen fixed landmarks were digitized on each shape file corresponding to homologous and repeatable points on the frontoparietal, otic region, and basicranium (Supplementary Fig. S1). We performed a generalized Procrustes analysis to align, rotate, and scale specimen landmark data to a common coordinate system and unit-centroid size to remove variation in position, orientation, and size (Rohlf and Slice, 1990), resulting in a set of shape variables, or Procrustes tangent coordinates, for all specimens. We examined the trends of allometry by assessing the multivariate regression between

neurocranium shape and centroid size (CS, the square root of summed squared distances of landmarks from the configuration centroid, Bookstein, 1991; method RegScore, Drake and Klingenberg, 2008) using Procrustes distances, and we generated a regression plot to visualize this relationship.

We performed a Procrustes multivariate analysis of variance (MANOVA) to test if mean shape differed between the subgenera *Xenopus* and *Silurana* to identify the presence or absence of morphological divergence. A principal component analysis of neurocranium shape variation was performed and the Procrustes-aligned specimens were plotted in two dimensions of tangent space (PC1 and PC2) and grouped by subgenus and species group membership. To aid in the visualization of shape variation in a phylogenetic context, we mapped PC2 scores of each species on the mitochondrial DNA (mtDNA) phylogeny of Evans et al. (2015). Scores for PC2 were extracted for the largest individual of each species and then mapped onto the phylogeny using the continuous ancestral state reconstruction function (contMap) in the R package 'phytools' (Revell, 2012).

RESULTS

Shape Analyses.—A multivariate regression of neurocranium shape on log centroid size exhibited significant positive allometry ($SS = 0.0443$, $MS = 0.0443$, $R^2 = 0.14$, $F_{1,49} = 6.963$, $P < 0.0001$; 10,000 iterations), indicating a neurocranium size-to-shape relationship within *Xenopus* that is similar within the subgenera and species groups (Fig. S2). A MANOVA revealed that mean neurocranium shape differed between the subgenera *Xenopus* and *Silurana* ($SS = 0.0520$, $MS = 0.026$, $R^2 = 0.16$, $F_{2,48} = 4.635$, $P < 0.0001$; 10,000 iterations). A PCA plot of shape variation demonstrated distinct clustering of *Silurana* and *Xenopus* in tangent space (PC1 = 29%, PC2 = 13% variance explained; Fig. 3B, Fig. S3). In contrast, patterns of shape variation among the species groups in subgenus *Xenopus* are largely overlapping in tangent space (Fig. 3B). The PC1 axis describes the shape differences driven by the size of the otic region relative to the length of the frontoparietal. Specimens that have a negative PC1 value possess a large otic capsule and a truncated frontoparietal while specimens that have a positive PC1 value possess a small otic capsule and an elongate frontoparietal. The PC2 axis describes the shape differences driven by the relative length, width, and height of the frontoparietal (independent of the otic region) as well as the relative size of the foramen magnum. *Xenopus* and *Silurana* occupy distinct regions of neurocranium morphospace because of nonoverlapping PC2 values.

Species of *Xenopus* possess a frontoparietal that is elongate, narrow, and dorsoventrally deep as well as a relatively small foramen magnum (negative PC2 values). Species of *Silurana* possess a frontoparietal that is truncated, broad, and dorsoventrally compressed, and have a relatively large foramen magnum (positive PC2 values; see Fig. S4 for warped surfaces of PC1 and PC2 minima and maxima generated using *warpRefMesh* geomorph function). The continuous ancestral state reconstruction of PC2 on the mtDNA phylogeny of *Xenopus* (Evans et al., 2015) illustrates the morphological divergence in neurocranium shape between the two subgenera (Fig. 3A). It also illustrates a tendency for different species groups within *Xenopus* to independently achieve similar negative PC2 values; note that *X. largeni* as well as both the *amieti* and *laevis* species groups all attain similar negative PC2 values. The neurocranium from the Nsungwe Formation occupies the same region of morphospace as the species in the subgenus

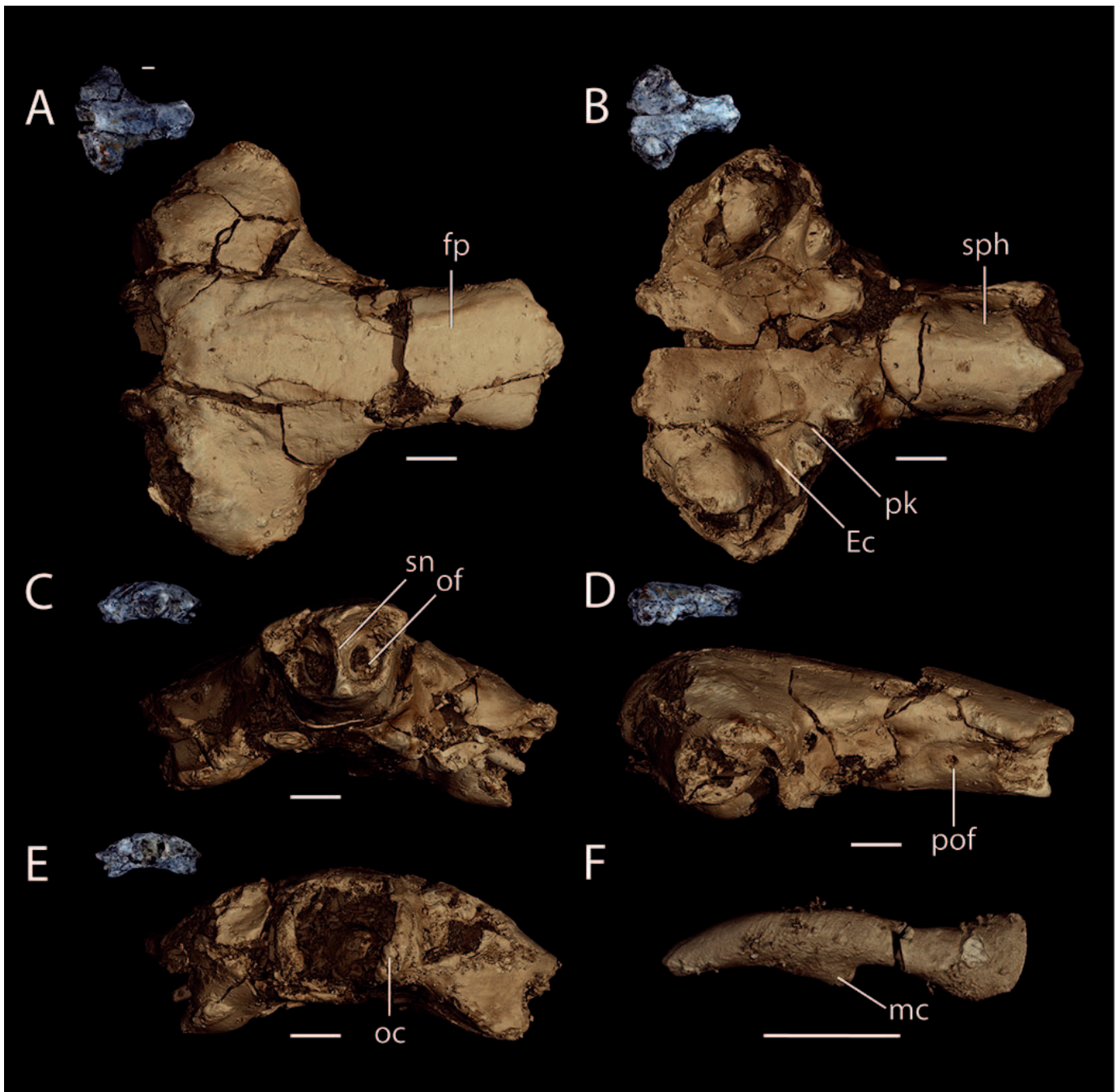


FIG. 2. High-resolution computed tomography (CT) scan of RRBP 13274B showing the neurocranium in dorsal (A), ventral (B), rostral (C), right lateral (D), and caudal (E) views; inset shows color photograph of specimen in same view. Also shown is the left stapes in left lateral view (F), which was isolated from the left otic region in the CT scan. Abbreviations: Ec, Eustachian canal; fp, frontoparietal; mc, attachment site for m. cucullaris; oc, occipital condyle; of, olfactory foramen; pk, palatine knob; pof, prootic foramen; sn, septum nasi; sph, sphenethmoid. Scale bars equal 1 mm.

Xenopus (Fig. 3B) because of the relative proportions of its frontoparietal and small foramen magnum.

SYSTEMATIC PALEONTOLOGY
 AMPHIBIA Linnaeus, 1758
 ANURA Fischer von Waldheim, 1813
 PIPIDAE Gray, 1825
Xenopus Wagler, 1827
 subgenus *Xenopus* sp. indet.

Referred Specimen.—One isolated neurocranium: RRBP 13274B. All of the skeletal elements that are typically synostotically fused

to form the pipid neurocranium are present, though the surfaces are weathered and either crushed or, in some places, missing.

Locality and Age.—RRBP 13274B was collected from locality Nsungwe 2B in the late Oligocene Nsungwe Formation of the Rukwa Rift Basin of southwestern Tanzania (Fig. 1). The Nsungwe 2B locality (~1,200 m above sea level) represents an ash-rich depositional interval, precisely dated to 25.2 mya, within a fluviolacustrine succession interpreted as a semiarid wetlands system that developed in the rift system between 26–24 mya. Age constraint for the fluvial to shallow lacustrine deposits within the sequence are provided by U-Pb and Ar-Ar dating of intercalated volcanic tuffs bracketing fossil localities along with supporting

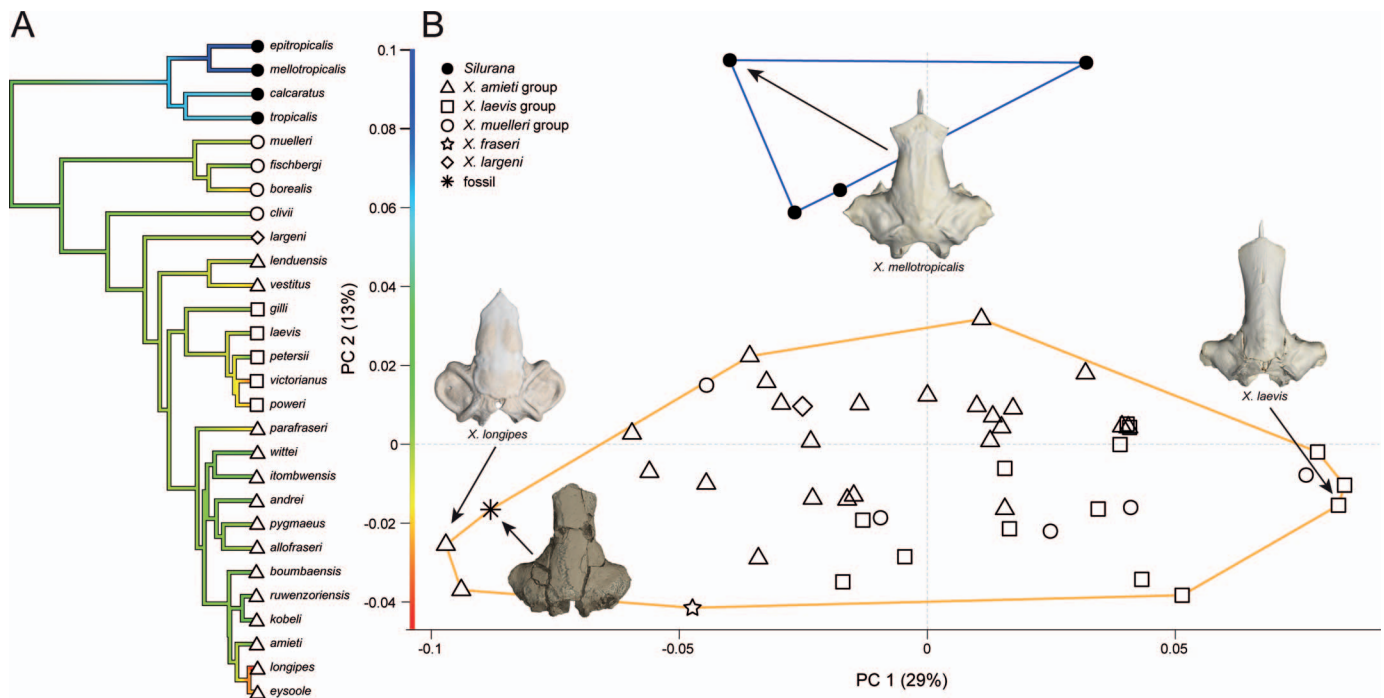


FIG. 3. Relationship of RRBP 13274B to patterns of neurocranium shape observed among extant species in the genus *Xenopus*. (A) Values of PC2 scores for each species are mapped onto the mtDNA phylogeny of Evans et al. (2015), revealing both differences between subgenus *Silurana* and multiple trends towards negative PC2 scores within subgenus *Xenopus*. (B) Morphospace of neurocrania of the genus *Xenopus* defined by PC1 and PC2 scores showing high overlap among species groups within subgenus *Xenopus* and similarities of RRBP 13274B to small species such as *X. longipes*.

magnetostratigraphy, biostratigraphy, and detrital zircon age constraints (Roberts et al., 2012; Stevens et al., 2013).

Description.—RRBP 13274B is an isolated neurocranium (Fig. 2), 9.0 mm long (from the occipital condyle to the anterior extent of the sphenethmoid) and 8.2 mm wide (from otic capsule to otic capsule) that is triangular in dorsal view with prominent otic regions and a narrow and anteriorly tapering braincase. As in other pipids, the sphenethmoid comprises the anterolateral walls of the braincase and preserves the posterior margins of the orbitonasal foramen and the anterior margins of the optic foramen. The sphenethmoid incorporates well-ossified tectum nasi and septum nasi, the latter separating large ovoid olfactory foramina, and is weakly constricted anterior to the optic foramen. There may be a weak embayment at the anterior margin of the dorsal sphenethmoid indicating the presence of the nasals. The neurocranium is crushed anterior to the otic capsules in the region of the prepalatine connection. The right prootic foramen appears to be present and indicates that this foramen is located posterodorsal to the optic foramen on the anterior surface of the otic capsule. The surfaces of the otic region are worn and the posterior regions crushed and, in some places, incomplete. The foramen magnum is bordered by a pair of thin and weakly curved occipital condyles. The otic capsule bears a well-defined and exposed canal on the ventral surface that is oriented obliquely to the long-axis of the neurocranium. In life, the Eustachian tube passed through this canal, the anterior margins of which are formed by the palatine knob and the posterior margin by the ventral region of the otic capsule. The damage to the posterior otic capsules leads to it being difficult to assess the features of the condyloid fossa, jugular and perilymphatic foramina, and the process posteroventral to the condyloid fossa.

The CT-scan revealed a stapes lodged within the left otic capsule, which we digitally isolated (Fig. 2F). This left stapes is complete, preserving the rod-like bony pars media plectri that in

life would have been embedded within the tympanic disc distally (Mason et al., 2009). The proximal stapes is slightly expanded at the articulation with the pars interna plectri. Ventrally, the stapes bears a small bony projection corresponding to one insertion point of the m. cucullaris (Mason et al., 2009). Few pipoid stapes have been figured and described in any detail, precluding further comparisons.

Remarks.—Because the elements of the neurocranium appear to be synostotically fused and the optic foramen is enclosed within bone, we interpret RRBP 13274B as representing an individual that is well past metamorphosis (Trueb and Hanken, 1992).

Comparisons.—The combination of a canal for the Eustachian tubes, a sphenethmoid that encloses the optic foramen, and a palatine knob all support RRBP 13274B being referred to the Pipoida (Cannatella, 1985; Báez and Pugener, 2003; Rage and Dutheil, 2008). The rounded lateral profile and the exposed condition of the Eustachian canal supports an affinity with the genus *Xenopus* (Cannatella and Trueb, 1988). Quantitative assessments of overall shape reveal strong similarities to subgenus *Xenopus* (Fig. 2). Specimen RRBP 13274B is small in comparison to most extant species but similar in both size and shape to the smallest species within subgenus *Xenopus*. In comparison to small species such as *X. longipes*, the lateral walls of the neurocranium, especially in the region of the prootic foramen, appear to be more fully ossified in RRBP 13274B. In subgenus *Silurana*, the otic region is typically displaced anteriorly relative to the occiput, and there is a pronounced constriction of the braincase at the posterior sphenethmoid such that the anterior neurocranium appears widely expanded (Estes, 1975). Further, there is no evidence for a prominent epiotic eminence as found in *Silurana*. Other authors have reported that the septum nasi is poorly ossified in extant species (Báez and Pugener, 1998; Gómez, 2016) and some extinct species (Henrici and Báez, 2001), but our survey of extant diversity shows that this feature is highly

variable and sometimes present and well defined as in RRBP 13274B. Similarly, the lateral reduction of the sphenethmoid in *Xenopus* has been reported as leading to an orbitonasal foramen that is incompletely surrounded by bone (Cannatella and Trueb 1988), though we observed a completely enclosed foramen in some species (*X. boumbaensis*, *X. itombwensis*). We refrain from erecting a new taxon to accommodate this fossil because of the lack of clearly diagnostic features to differentiate it from other species of *Xenopus*.

DISCUSSION

Our analyses based on a synoptic collection of extant species demonstrate the value of sampling all species within the extant clades. If we relied on a small set of exemplars, such as *X. laevis*, *X. muelleri*, and *X. tropicalis* to identify this isolated neurocranium, the combination of characters identified in this fossil could lead to an interpretation that the morphology of the fossil rests outside of the variation observed among living species (Fig. 3B). Instead, by sampling all extant species, we found that the Nsungwe Formation fossil bears clear similarities to smaller extant species within the subgenus *Xenopus*, which occupies a large region of morphospace. As the two subgenera of extant *Xenopus* occupy distinct regions of morphospace, this general approach may facilitate further refinements in the identification of isolated pipid neurocrania from the Cenozoic.

Our morphometric analysis demonstrates a relationship between size and shape in extant species of *Xenopus*. Small species (e.g., *X. longipes*) are generally characterized by a large otic capsule relative to the frontoparietal (negative PC1 values) whereas large species (e.g., *X. laevis*) possess relatively small otic capsules (positive PC1 values). The trend of large braincases and sensory organs (including the otic capsule and inner ear) in small-bodied taxa has been broadly documented in both frogs and salamanders (Hanken, 1984; Yeh, 2002), but this is the first report of cranial allometry in the genus *Xenopus*. The two subgenera of *Xenopus* possess divergent neurocranium shapes, but the neurocranium shape of taxa in the *X. amieti*, *X. laevis*, and *X. muelleri* species groups appear influenced by size more than by clade membership.

Most recent analyses of divergence times within the Pipidae suggest that the divergence of the two subgenera *Silurana* and *Xenopus* occurred in the early Cenozoic (reviewed in Cannatella, 2015; Feng et al., 2017). Recent phylogenetic analyses using mtDNA suggest that crown-group *Silurana* originated 7–10 mya and crown-group *Xenopus* originated 20–23 mya (Evans et al., 2015), though these dates are half those of other previous estimates (Evans et al., 2004). Historical biogeographic analyses suggest that the origin and early diversification of the subgenus *Xenopus* occurred in eastern Africa (Evans et al., 2004) and likely before the end of the Paleogene.

Historically, fossil pipids recovered from the Mesozoic and Cenozoic of both Africa and South America were often attributed to the genus *Xenopus*. Today, however, none of those Cretaceous or Paleogene records are thought to represent crown-group members of *Xenopus*. Báez (1996) pointed out that the skull of the “*Xenopus*-like pipid” reported from the Upper Cretaceous of Niger by de Broin et al. (1974) lacks features to clearly ally this fossil with *Xenopus*. Similarly, recent phylogenetic analyses suggest that *Xenopus romeri* described from the Paleocene of Brazil by Estes (1975, 1977) is more closely related to other extinct xenopodine taxa (Báez and Pugener, 1998). Báez (1996) further noted that fossils from the lower Oligocene of Libya described by Špinar (1980) as *X.* (subgenus *Libycus*)

hasaunus are not referable to *Xenopus*; Špinar (1980) also suggested affinities of this extinct taxon to another extant pipid genus, *Hymenochirus*.

Cenozoic records of *Xenopus* from the Neogene of Africa include two from the Miocene. Ahl (1926) described *Xenopus stromeri* based on an isolated neurocranium from the lower Miocene of Namibia which resembled the long, thin neurocrania of large-bodied *Xenopus* (see also Rage, 2008). Later, Vergnaud-Grazzini (1966) described many associated fossils that she referred to *Xenopus* from the Miocene of Beni-Mellal in Morocco and for which both she and Estes (1975) noted similarities to species in the subgenus *Silurana*. Fossils referred to the genus *Xenopus* are also documented from more recent deposits including the early Pleistocene deposits from Olduvai Gorge (Leakey, 1965, 1971) and the Pliocene and Pleistocene of South Africa (Stromer, 1931; Hendey, 1970). The only previous record of *Xenopus* from the Paleogene (or earlier) of the Afro-Arabian plate is *X. arabiensis* from the late Oligocene of Yemen, described by Henrici and Baéz (2001) as resembling species in the *muelleri* group. Previous to this discovery from the Nsungwe Formation, the earliest occurrence of *Xenopus* in sub-Saharan Africa was from the Miocene of Namibia (Ahl, 1926), although Rage (2008) argued that this material is not referable to *Xenopus*. Taken together with information from molecular phylogenies, the Nsungwe neurocranium and *X. arabiensis* from Yemen suggest that the crown-group of subgenus *Xenopus* attained both a wide geographic distribution and perhaps a wide range of body sizes relatively early in its diversification.

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SUPPLEMENTARY DATA

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