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## THE EARLIEST RECORD OF THE ENDEMIC AFRICAN FROG FAMILY PTYCHADENIDAE FROM THE OLIGOCENE NSUNGWE FORMATION OF TANZANIA

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The Ranoidea is a cosmopolitan radiation of frogs comprising 19 families and more than 2400 extant species (nearly 40% of all anurans; Ford and Cannatella, 1993; Scott, 2005; Bossuyt et al., 2006; Blackburn and Wake, 2011; Barej et al., 2014). Studies using time-calibrated molecular phylogenies suggest a Cretaceous origin for the Ranoidea (Bossuyt and Roelants, 2009), but the Mesozoic and early Cenozoic fossil record of this diverse clade remains poor (Rage, 1984; Roček, 2000; Roček and Rage, 2000; Rage and Roček, 2003). Although many fossils have been attributed to the Ranoidea, typically few diagnostic characteristics are provided to assign fossils to specific taxa within the clade (e.g., de Broin et al., 1974; Rage, 1984). The Ranoidea is thought to have initially diversified in Africa (Bossuyt et al., 2006; Rage et al., 2013), but the African fossil record of anurans in the Mesozoic and Paleogene is generally poor, with the Afro-Arabian record limited primarily to pipoid frogs (e.g., Henrici and Báez, 2001; Trueb et al., 2005; Rage and Dutheil, 2008; Rage et al., 2013) or taxonomically enigmatic fossils (Flynn and Brunet, 1989; Jacobs et al., 1990; Roček, 2000; Evans et al., 2008; Rage and Dutheil, 2008; Rage et al., 2013).

Here we report the earliest record of the endemic African ranoid frog family Ptychadenidae from the late Oligocene Nsungwe Formation in the Rukwa Rift Basin of southwestern Tanzania (Fig. 1). Paleogene anuran fossils are typically rare, but they constitute approximately 13% of materials collected from localities in the Nsungwe Formation. Radiometrically dated at ~25 Ma (Roberts et al., 2010, 2012; Stevens et al., 2013), Nsungwe Formation localities preserve a diverse vertebrate fauna and a number of novel invertebrate taxa (Stevens et al., 2008, 2009, 2013; Roberts et al., 2010, 2012). Nsungwe Formation anuran fossils include vertebrae preserving a unique sacral morphology that provides the earliest record of the Ptychadenidae, the earliest definitive record of any family within the diverse ranoid clade Natatanura (sensu Frost et al., 2006), and the first late Oligocene record of anurans from Africa below the equator.

**Institutional Abbreviations**—CAS, Herpetology Collection, California Academy of Sciences, San Francisco, California, U.S.A.; KU, Department of Herpetology, University of Kansas Natural History Museum and Biodiversity Institute, Lawrence, Kansas, U.S.A.; MCZ, Department of Herpetology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; RRB, Rukwa Rift Basin Project, Tanzanian Antiquities Unit, Dar es Salaam, Tanzania.

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### SYSTEMATIC PALEONTOLOGY

ANURA Fischer von Waldheim, 1813

PTYCHADENIDAE Dubois, 1987

Gen. et sp. indet.

(Fig. 2)

**Referred Specimens**—Two isolated compound sacra: RRB 07615 and RRB 05113.

**Locality and Age**—RRB 07165 was collected from locality Nsungwe 2; RRB 05113 was collected from locality TZP-2; both localities are in the late Oligocene Nsungwe Formation in the Rukwa Rift Basin of southwestern Tanzania (Fig. 1). Both localities are from fluviolacustrine successions that were deposited as part of a semiarid wetlands system that developed between 25.5 and 24.5 Ma. These are fluvial to shallow lacustrine deposits bracketed by precisely dated volcanic tuffs with supporting magnetostratigraphy and biostratigraphy (Roberts et al., 2012; Stevens et al., 2013).

**Description**—RRB 07615 is a block-like partial anuran composite sacral element. The presence of both transverse processes and sacral diapophyses, a large spinal foramen on each side of the vertebrae, and two prominent posterior condyles all indicate that this element represents the fusion of the last presacral and sacral vertebrae. Both transverse processes of the presacral vertebra are broken, although the preserved base of the left process indicates that it projected anterolaterally rather than directly laterally. The sacral diapophysis is missing on the right and broken distally on the left. The composite element is broader than tall, being ~3.5 mm in height and ~4.5 mm at its minimum width. The centrum is concave anteriorly and bears two condyles posteriorly. In anterior view, the centrum is dorsoventrally compressed, as is the neural canal, but this does not appear to reflect postmortem distortion. The articular surfaces of the prezygapophyses are oriented approximately 45° from horizontal. In posterior view, the neural canal is dorsoventrally compressed, slightly more so than in anterior view. The articular facets of the prominent posterior condyles are separated by a sulcus and are rounder than the anterior cotyle. In dorsal view, the sacral condyles are visible whereas the anterior portion of the centrum is not. The element is rectangular in dorsal view, being wider than long. A low-lying neural spine is present at the midline of the fused neural arches, with a poorly defined lamina extending posteriorly along each sacral diapophysis. In lateral view, a prominent foramen for passage of the spinal nerve marks the position of fusion between the presacral vertebra and the sacrum (Fig. 2C).

RRB 05113 is similar in size and morphology to RRB 07615. Although somewhat more fragmentary in missing the

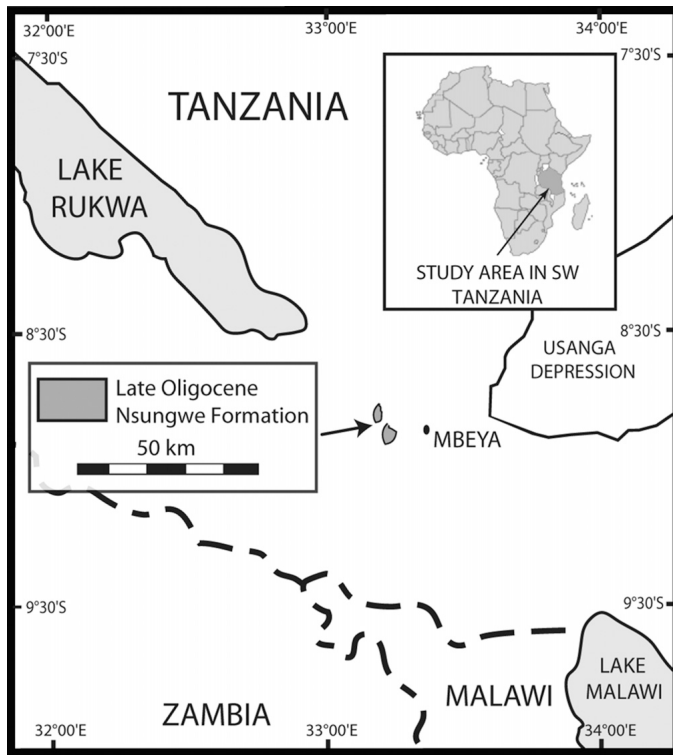


FIGURE 1. Location of Rukwa Rift Basin containing the Nsungwe Formation fossil-bearing localities.

transverse processes, the specimen preserves a complete dorsal surface, centrum, and prezygapophyses.

**Comparisons**—These two isolated specimens bear features that among modern frogs are found consistently only in the Ptychadenidae. Both specimens exhibit complete fusion of the last presacral vertebra and sacrum into a composite element with anteriorly projecting transverse processes that give an ‘X’-shaped appearance in dorsal view. They also exhibit on each side a characteristic foramen above the centrum that serves as the outlet for the spinal nerve. The fusion of these two vertebrae has been suggested as a synapomorphy of the Ptychadenidae (Clarke, 1981; Scott, 2005). Fusion of these elements is found variably among other anurans, including several North American species of Ranidae. However, the composite element in ranids can be distinguished from the ptychadenid

morphology in that the transverse processes of the eighth presacral vertebra in ranids are directed laterally (rather than anterolaterally) and sacral transverse processes are more expanded distally (see Discussion). The fossils described here could not be referred to a specific genus or species within the Ptychadenidae and do not exhibit features allowing for diagnosing a new taxon.

We base our comparison with extant ptychadenids on both specimens (Appendix 1) and depictions provided of Recent and Miocene ptychadenids by Vergnaud-Grazzini (1966). The morphology of the ptychadenid composite element comprising the eighth presacral vertebra and sacrum is readily distinguishable from that of other taxa with fusion of those elements. In ptychadenids, the fused element is ‘X’-shaped in dorsal view because the transverse processes of the eighth presacral vertebra project anterolaterally and the sacral diapophyses project posterolaterally. In the Ranidae sensu stricto, the presacral transverse processes project directly laterally (compare Vergnaud-Grazzini, 1966:fig. 30, Lynch, 1965:fig. 1, Ramaswami, 1933:fig. 2, and Holman, 1963:fig. 2; *Rana palmipes*, KU 301761; *R. warszewitschii*, KU 41126) and the sacral transverse processes are weakly dilated. Unlike the morphology in many ranids, the neural arches of the composite element in *Ptychadena* lack deep grooves and fossae on the dorsal surface and exhibit a single minute low-lying neural spine. The composite element found in some species of the Dendrobatidae may be distinguished from ptychadenids by its more boxy shape, with greater dorsoventral compression relative to ranids and ptychadenids, together with shorter transverse processes and generally smaller size (e.g., *Oophaga granulifer*, KU 110223–27; *O. pumilio*, KU 68256–58, 95006–07). In dendrobatids and ranids, fusion is frequently incomplete or even absent in some or most individuals of a species (see Holman, 1963; Lynch, 1965). For example, a large series of *Rana palmipes* (n = 46; KU 152842–87) collected from Santa Cecilia, Ecuador, contains examples with incomplete fusion and/or left-right asymmetries in 12 individuals and complete absence of fusion in four juveniles (Holman, 1963; Lynch, 1965). Fusion of the eighth presacral vertebra and sacrum was reported in *Rhinoderma* (family Rhinodermatidae) by Grant et al. (2006), but our examination of 12 individuals (KU 68685, 125367–68, 161572–74, MCZ A-8554, 9646–48, 9650, 93619) revealed fusion in only one specimen that exhibited left-right asymmetry suggestive of a developmental abnormality (KU 161574). In addition, the sacral vertebra of *Rhinoderma* is easily distinguishable from ptychadenids in bearing broadly expanded transverse processes. Our survey of representatives of other families in the diverse ranoid clade Natatanura (sensu Frost et al., 2006) did not reveal fusion of the eighth presacral vertebra and sacrum (Appendix 1).

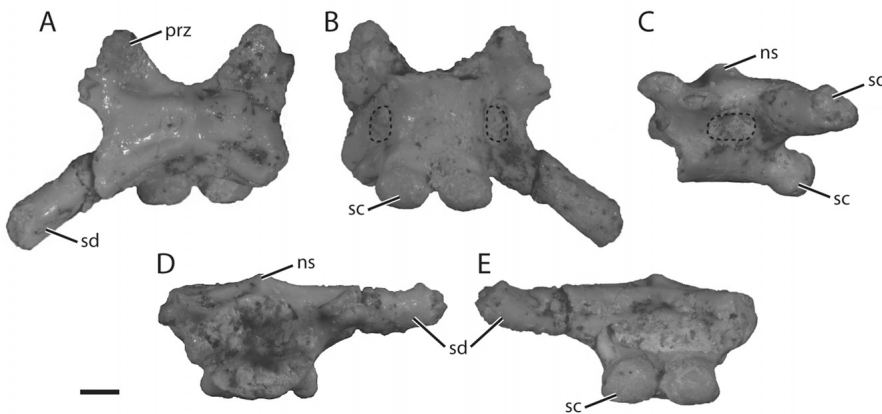


FIGURE 2. RRBP 07615 (Ptychadenidae indet.) in dorsal (A), ventral (B), left lateral (C), anterior (D), and posterior (E) views. Anterior is to the top for both A and B, and to the left in C. Approximate boundaries of spinal foramina indicated with dashed lines. **Abbreviations:** prz, prezygapophysis; ns, neural spine; sc, sacral articular condyles; sd, sacral diapophysis. Scale bar equals 1 mm.

## DISCUSSION

The Neobatrachia likely originated in the middle Mesozoic, with estimates based on time-calibrated molecular phylogenies ranging from the Jurassic to Early Cretaceous (Bossuyt and Roelants, 2009). The Cretaceous record of neobatrachians is restricted to Gondwana (Báez et al., 2012), although most African records from the Mesozoic or Paleogene are poorly documented (e.g., Báez and Werner, 1996; Roček, 2000; Roček and Rage, 2000; Rage and Roček, 2003; but see Evans et al., 2008). Putative ranoid frogs are documented from Afro-Arabia in the Cretaceous of Sudan (Báez and Werner, 1996), the middle Eocene of Namibia (Rage et al., 2013), and the Miocene of Saudi Arabia (Thomas et al., 1982) in addition to a diverse record from Pliocene and Pleistocene units (e.g., van Dijk, 2003, 2006). Laloy et al. (2013) suggest that the enigmatic anuran *Thaumastosaurus* from the Eocene of western Europe is referable to the Ranoidea and possibly even the Natatanura, although this requires further analysis with greater taxon sampling.

Fossils have frequently been referred to Ranoidea based on fragmentary remains of ilia or, in some cases, elements of the pectoral girdle consistent with a fermisternal condition (e.g., Rage, 1984; Rage et al., 2013). However, the earliest Eocene record attributed to Ranidae is based on a displasiocoelous presacral vertebra (Roček and Rage, 2000); based on the distribution of this trait, this record is best characterized as Ranoidea incertae sedis. Unraveling the phylogenetic affinities of fossil anurans is complicated by the fact that the taxonomic inclusiveness of both Ranidae and Ranoidea are often not explicit (for one exception, see Rage, 1984) and that the large radiation of ranoid frogs is now divided into several families (Blackburn and Wake, 2011). Hence, it remains difficult to interpret the taxonomic affinities of many fossils identified as 'ranid' or 'ranoid' in the literature, and most fossils previously attributed to the Ranidae are best considered as members of the broader clade Ranoidea unless specific morphologies are described to align them specifically with the Ranidae (Folie et al., 2012). Unfortunately, few lineages within the Ranoidea, particularly among the diverse Natatanura, exhibit documented skeletal apomorphies, and many of those that are known are also found in other anuran lineages (Scott, 2005). In contrast, the composite presacral and sacral vertebrae described herein preserve morphology that is diagnostic among ranoids and distinctive to Ptychadenidae.

Ptychadenidae is thought to be among the earliest diverging lineages of Natatanura, a large and diverse clade within Ranoidea (Bossuyt et al., 2006; Pyron and Wiens, 2011). Living ptychadenids comprise approximately 50 species in three genera (*Hildebrandtia*, *Lanzarana*, *Ptychadena*) and are restricted to sub-Saharan Africa (Blackburn and Wake, 2011), with the exception of two extant species of *Ptychadena* that occur in the Nile Delta (Baha El Din, 2006; Dehling and Sinsch, 2013). Each ptychadenid genus exhibits the complete and symmetrical fusion of the last presacral vertebra with the sacrum (Vergnaud-Grazzini, 1966; Clarke, 1982; Scott, 2005), and the distinctive anterolateral orientation of the transverse process of the last presacral vertebra distinguishes these fused vertebral elements from those of other anurans. Based on molecular studies, ptychadenids are predicted to have diverged from other ranoids by the Oligocene (Bossuyt et al., 2006), but prior to the highly constrained ages of the Rukwa fossils. The earliest previous record of Ptychadenidae hailed from middle Miocene Beni Mellal in Morocco (Vergnaud-Grazzini, 1966). Fossil ptychadenids are also known from Pleistocene sites on Madagascar (Burney et al., 2008). More recent faunas from Morocco suggest that ptychadenids and other Afrotropical anurans may have experienced local extinctions in northwestern Africa by the Late Miocene (Blain et al., 2013).

Several anuran lineages exhibit fusion of specific vertebral elements, but few of these fusion patterns are unique to a given clade (Lynch, 1973; Trueb, 1973). For example, fusion of the first

two presacral vertebrae is found in many modern frogs (Lynch, 1973; Cannatella and Trueb, 1988; Ford, 1990; Scott, 2005; van Dijk, 2006; Blackburn, 2008) and fusion of the second and third presacral vertebrae is found in some species of the hyloid family Dendrobatidae (Silverstone, 1975; Grant et al., 2006). Fusion of the sacral vertebra to the urostyle is also well documented, with variable incorporation of one or more presacral vertebrae into the composite element (Holman, 1963; Lynch, 1973; Trueb, 1973; Cannatella and Trueb, 1988; Pugener and Maglia, 2009). Although not previously discussed in works related to ptychadenid anatomy, fusion of the eighth presacral vertebra and sacrum is present in other anurans, including as intraspecific and ontogenetic variation in some species of Ranidae sensu stricto (Noble, 1931; Ramaswami, 1933; Taylor, 1942; Holman, 1963; Lynch, 1965). In many cases, these fusions occur at low frequency or exhibit asymmetries that suggest abnormal development (see Comparisons). Symmetrically fused vertebrae occur in certain species of North American and Asian Ranidae (Ramaswami, 1933; Holman, 1963; Lynch, 1965) and a handful of other lineages, including some species of the endemic Central and South American family Dendrobatidae (Noble, 1922; Silverstone, 1975; Grant et al., 2006). However, the Ptychadenidae remains the only major clade of frogs diagnosed based on this specific vertebral fusion pattern and associated distinctive transverse process morphology.

Work in the Nsungwe Formation of southwestern Tanzania has revealed the earliest evidence of the Ptychadenidae, a family of ranoid frogs endemic to Africa. These discoveries provide the first definitive evidence that crown-group Natatanura diversified by the late Oligocene. Continued exploration of different facies of the Nsungwe Formation reveals a number of distinct habitats with differing taphonomic modes of preservation (e.g., Roberts et al., 2010). Such work provides opportunities for recognizing an unprecedented level of paleobiological diversity at the Paleogene-Neogene transition on the African continent, offering a window into the evolution of modern African faunas and demonstrating how organisms diversify and respond to environmental change through time.

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- APPENDIX 1. Specimens examined of the families in the diverse ranoid clade Natatanura.
- Ceratobatrachidae—*Ceratobatrachus guentheri*, KU 128664; *Discodeles guppyi*, KU 98472; *Platymantis guppyi*, KU 93741, 98166
- Conrauidae—*Conraua goliath*, MCZ A-15738
- Dicroglossidae—*Limnonectes blythii*, KU 155636; *L. ibanorum*, KU 155676; *Quasipaa boulengeri*, KU 311902; *Sphaerotheca breviceps*, KU 203853
- Mantellidae—*Aglyptodactylus madagascariensis*, KU 153468; *Boehmantis microtympanum*, KU 173083; *Boophis tephraomystax*, KU 206445; *Gephyromantis plicifer*, KU 153469–70; *Guibemantis bicalcaratus*, KU 153454–55; *G. liber*, KU 153456; *Mantidactylus albofrenatus*, KU 153457; *M. femoralis*, KU 153460, 173082; *M. guttulatus* KU 153461–64; *M. lugubris*, KU 153465–66; *M. ulcerosus*, KU 153471–72
- Micrixalidae—Via X-ray: *Micrixalus fuscus*, MCZ A-1274, A-107662
- Nyctibatrachidae—Via X-ray: *Nyctibatrachus anamallaeinsis*, MCZ A-25599; *N. major*, MCZ A-15405
- Petropedetidae—*Petropedetes cameronensis*, KU 129704–05; *P. martiensseni*, MCZ A-25381
- Phrynobatrachidae—*Phrynobatrachus acridoides*, MCZ A-138216; *P. acutirostris*, KU 155158; *P. dendrobates*, MCZ A-14660
- Ptychadenidae—*Hildebrandtia ornata*, CAS 154656, KU 170523; *Ptychadena mascareniensis*, CAS 131481, *P. mossambica*, MCZ A-28622; *P. cf. oxyrhynchus*, CAS 141762; *P. superciliaris*, KU 154360–61
- Pyxicephalidae—*Amietia angolensis*, KU 154366–67; *A. fuscigula*, KU 195817–18, MCZ A-5970, A-12677; *Pyxicephalus adpersus*, KU 220957, MCZ A-21359; *Tomopterna cryptotis*, MCZ A-24014
- Ranidae—*Hylarana galamensis*, MCZ A-85227; *H. glandulosa*, KU 155661; *H. grisea*, KU 93769; *H. papua*, KU 93778; *Meristogenys jerboa*, KU 155608; *Pelophylax perezii*, KU 148630; *Odorrana hosii*, KU 155666, 155671; *O. margaretae*, KU 311904; *Staurois natator*, KU 152225
- Ranixalidae—Via X-ray: *Indirana phrynoderma*, MCZ A-20885–86
- Rhacophoridae—*Chiromantis xerampelina*, KU 195924; *Polypedates leucomystax*, KU 154002; *Rhacophorus schlegelii*, KU 153178).

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