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A FOSSIL GEKKOTAN (SQUAMATA) FROM THE LATE OLIGOCENE NSUNGWE
FORMATION, RUKWA RIFT BASIN, TANZANIA

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-LRH: J. Müller et al.

-RRH: Fossil gekkotan from Tanzania

ABSTRACT.—We describe the first record of a fossil gekkotan from the Late Oligocene Nsungwe Formation in the Rukwa Rift Basin, Tanzania. The specimen consists of an almost complete maxilla containing 23 tooth positions, with 10 teeth still in place. Typical gekkotan features include the tall facial process along with a posteriorly sloping angle, and the presence of unicuspid, pleurodont teeth with large resorption pits. Limited preservation does not allow for a more specific systematic assignment, which is why we refer the specimen to *Gekkota incertae sedis*. The material represents the second record of a Paleogene gekkotan from Africa, and the first one from the central part of the continent.

Key words: Squamata; Gekkota; Oligocene; Tanzania; Nsungwe Formation, Biogeography

Gekkota is a diverse clade of lizards with a cosmopolitan distribution, found in all tropical and subtropical regions of the world and in even in some temperate areas (Han et al., 2004; Bauer, 2013). The widespread success of this highly speciose clade is often attributed to the repeated acquisition and loss of a unique set of integrated morphological adaptations and behaviors permitting adhesion between the digits and a variety of locomotor substrates (e.g., Russell, 2002; Russell and Higham, 2009; Gamble et al. 2012; Higham et al., 2015). Molecular studies consistently place gekkotans as sister to all other crown squamates except dibamids (e.g., Townsend et al., 2004; Wiens et al., 2012; Pyron et al., 2013), which implies that their evolutionary origin was deeper in the Mesozoic, a hypothesis also supported by molecular divergence estimates (Early Jurassic; Jones et al., 2013). The fossil record of gekkotans is surprisingly poor. The oldest known undisputed gekkotan fossil, *Cretaceogekko burmae*, is preserved in amber and dates from the late Early

Cretaceous of Myanmar (Arnold and Poinar, 2008; Daza et al., 2014). Otherwise, only a handful of Cretaceous and Paleogene gekkotans are documented until a richer record emerges throughout the Neogene and Quaternary (Daza et al., 2014). This sparse fossil record likely results from the fragile nature of the gekkotan skeleton, with bones easily destroyed or disarticulated prior to preservation (Evans, 2003).

The fossil record of gekkotans is similarly geographically patchy, with the majority of fossil occurrences documented from North America and Eurasia (Estes, 1983; Daza et al., 2014). On the southern continents, the gekkotan fossil record is limited to a handful of pre-Quaternary occurrences from Africa, South America, Australia, and New Zealand (Rage, 2008; Augé and Rage, 2006; Daza et al., 2014). This is unfortunate, as the majority of extant gekkotan diversity is Gondwanan in distribution (Han et al., 2004), hence a broader geographic sample of gekkotan fossils is needed to test any hypotheses regarding models of vicariance, dispersal, and even the general diversification of the clade.

With respect to continental Africa, pre-Quaternary records are known from the upper Paleocene of Adrar Mgorn, Morocco (Augé and Rage, 2006), the lower Miocene of the Sperrgebiet, Namibia (Rage, 2008), and the upper Miocene of Beni Mellal, Morocco (Rage, 1976). With the exception of the latter record, consisting of several cranial and postcranial remains tentatively assigned to the extant phyllodactylid genus *Tarentola*, all African gekkotan fossil material is extremely fragmentary. Here we report on a Paleogene gekkotan fossil from Africa, recovered from the late Oligocene Nsungwe Formation, in the Rukwa Rift Basin of Tanzania (Fig. 1). The Nsungwe Formation has produced a diverse fauna of invertebrates and vertebrates, both terrestrial and aquatic (e.g., Feldmann et al., 2007; Stevens et al., 2006, 2008, 2013, 2016), including notable records of Paleogene African

herpetofauna, such as snakes and anurans (McCartney et al., 2014; Blackburn et al., 2015).

As the phylogenetic understanding of gekkotan morphology across many genera and larger clades remains unclear (see, e.g., Daza et al., 2011), we refrain from erecting a new taxon, but conservatively refer the newly described material to *Gekkota incertae sedis*.

MATERIALS AND METHODS

The fossil material was subjected to micro-tomographic analysis at the Museum für Naturkunde Berlin using a Phoenix nanotom X-ray tube at 90 kV and 100 μ A, generating 1440 projections with 750 ms per projection, which results in an effective voxel size of 4.7 μ m. Cone-beam reconstruction was performed using the datavox 2 reconstruction software (GE Sensing & Inspection Technologies GMBH phoenix|x-ray datavox 2.0) and the data were visualized using VG Studio Max 3.0 (Volume Graphics GmbH). An interactive 3D image of the specimen can be accessed under

<https://sketchfab.com/models/98f3be8195b4415dae1c657526a125d1>.

RESULTS

SYSTEMATIC PALEONTOLOGY

Reptilia Linnaeus, 1758

Squamata Oppel, 1811

Gekkota Camp, 1923

Gekkota incertae sedis

Diagnosis.—Squamate lizard that can be referred to Gekkota on the basis of a tall facial process of the maxilla in conjunction with a steep posterior sloping angle (Augé, 2005), and the presence of slender, straight and closely spaced unicuspid, pleurodont teeth with well-developed lingual resorption pits.

Referred Specimen.—Rukwa Rift Basin Project (RRBP – collection identifier used by the Tanzanian Antiquities Unit) 13002, right maxilla with fragmentary portions of prefrontal and ?nasal/frontal (Figs. 1A, B, 2).

Locality and Horizon.—Late Oligocene Nsungwe Formation, locality TZ-01, Rukwa Rift Basin, southwestern Tanzania (Fig. 1C). The Nsungwe Formation is subdivided into two members, the lower Utengule Member and the upper Songwe Member with the latter assigned an age of ~24.95 Ma based on biostratigraphy, dated ash beds, and detrital zircon geochronology (Roberts et al., 2010, 2012; Stevens et al., 2013). The specimen comes from the Songwe Member.

Description.— The right maxilla (RRBP 13002; Figs. 1A, B, 2) is abraded but nearly complete, whereas the facial process and the palatal shelf are slightly damaged, and the anterior and posterior tips broken off. The element has an anteroposterior length of 9.1 mm. Large parts of the bone's medial surface are obscured by sediment, but this covering was digitally removed through computed tomography.

The specimen exhibits a tall, roughly triangular facial process that distinctly tapers dorsally (Fig. 2A); however, the process is slightly incomplete along the anterior edge. The dorsal edge of the process is straight and sloping in an anteroventral direction, whereas the dorsal-most tip is capped by a fragmentary piece of bone that is either the remainder of the nasal or the anterolateral process of the frontal; preservation does not allow the determination of differences in bone thickness, which otherwise may be helpful to discriminate between frontal and nasal.

The anteroventral portion of the maxilla reveals the well-preserved posterior half of the external naris. The external naris is relatively small in comparison to the overall size of the bone, and at least its maxillary portion is also distinctly rounded due to the development of a small triangular anterior tip of the facial process that bounds the external naris posterodorsally. The posterior edge of the facial process has an almost straight, ventrally sloping posterior margin between its dorsal tip and dorsoventral mid-height. This point marks the distal-most extent of the ventral process of the prefrontal, the tip and only preserved part of which is still attached (Figs. 2A, B). Such a configuration suggests that the prefrontal had a comparatively narrow, but relatively elongate ventral process. Ventral to this edge, the facial process quickly transitions to the posterodorsal edge of the maxillary body, forming the anteroventral margin of the orbit. The lateral surface of the maxilla (Fig. 2A) further reveals a distinct triangular depression opening towards the orbital region at the posterior base of the facial process, a feature characteristic of many gekkotans (see, e.g., figs. 14-18 in Heinicke et al., 2014). Moreover, there is a row of at least 7 maxillary foramina along the ventrolateral margin of the bone, in addition to one large, anteriorly positioned foramen dorsal to this row and a number of irregularly-distributed, smaller foramina across the lateral surface. The partially damaged surface makes any additional determination difficult.

The medial view (Fig. 2B) reveals a well-developed and comparatively wide palatal shelf with an almost uniform medial expansion along most of the anteroposterior extent of the bone. The shelf slightly increases in width from anterior to posterior until just posterior to the level of the facial process (Fig. 2C). Posterior to this point the shelf tapers significantly, eventually disappearing altogether. In the central area of the maxilla the shelf is slightly elevated, and at its posterior turning point (i.e., where the shelf slopes posteroventrally) there is a well-developed alveolar

foramen. There are at least 23 closely spaced tooth positions on the bone, with 10 pleurodont teeth and an 11th very damaged tooth still in place. Although the maxilla is slightly incomplete, from what is preserved it can be estimated that the tooth count in RRBP 13002 is at the lower end known for gekkotans, and that the tooth row extended posteriorly well beyond the anterior edge of the orbit. The preserved teeth are rather uniform in shape, being straight, slender, and with a single rounded cusp. The more posteriorly positioned teeth are slightly shorter than the central and anterior ones. The resorption pits are well-developed.

DISCUSSION

Molecular phylogenetic analyses subdivide Gekkota into two major clades, Gekkomorpha and Pygopodomorpha (Gamble et al., 2008a,b; Vidal and Hedges, 2009), sometimes also referred to as Gekkonoidea and Pygopodoidea (see, e.g., Daza et al., 2014), the latter being exclusively Australasian in modern distribution. Although only gekkomorphans are found on continental Africa today, it is possible that pygopodomorphs had a formerly wider distribution on the southern landmasses, and maybe even elsewhere. We therefore refrain from assigning the Rukwa gekkotan a priori to Gekkomorpha, as such a conclusion would be solely based on current biogeographic distributions. It should be added that RRBP 13002 differs from the pygopodomorph subclade Diplodactylidae in having a relatively lower tooth count and a tall and steeply sloping facial process (Bauer, 1990; Daza et al., 2014). Nonetheless, these differences are not sufficient to exclude relationships with pygopodomorphs more generally. Gekkomorpha includes four major extant lineages – Eublepharidae, Sphaerodactylidae, Phyllodactylidae, and Gekkonidae – all of which are found in Africa today. No known osteological apomorphies have been documented that reliably characterize most of these clades, as there is considerable

morphological variation across different gekkotan taxa (Daza et al., 2011). Some putative osteological synapomorphies have only been suggested for sphaerodactylids and phyllodactylids (Daza and Bauer, 2012), but none of these characters apply to the maxilla. RRBP 13002 differs from most extant sub-Saharan African gekkotans whose cranial morphology has been described, or at least figured in sufficient detail, (e.g., *Phelsuma*, digimorph.org; *Hemitheconyx*, *Chondrodactylus*, Rieppel, 1984; *Narudasia*, Daza et al., 2011; *Afrogecko*, *Cryptacites*, *Matoatoa*, *Kolekanos*, *Ramigekko*, Heinicke et al., 2014) in its combination of a relatively low tooth count, a tall facial process, and a wide palatal shelf. Taxa coming close to such a morphology are *Narudasia*, which has a similarly low tooth count and also a relatively broad palatal shelf; *Hemitheconyx*, which has a broad palatal shelf and a tall facial process; and *Chondrodactylus*, which has a tall facial process and a low tooth count. Given that the latter two genera are at least partial ground-dwellers, the tall facial process of RRBP 13002 may indicate a similar ecology; also the ground-dwelling genus *Bunopus* from Arabia has a similarly shaped maxilla (Daza et al., 2012). Additional fossil material is needed to confirm such a hypothesis.

Among fossil gekkotans, RRBP 13002 bears resemblance to the Early Cretaceous genus *Hoburogekko* from Mongolia (Daza et al., 2012), which essentially shares all the maxillary characters discussed above. However, given the large temporal and geographic distance it is questionable if these features indicate a close phylogenetic relationship between the two fossils.

Despite its systematic uncertainties, RRBP 13002 is of particular interest as it represents only the second record of a Paleogene gekkotan from Africa. Previously, the only documented Paleogene gekkotan was a late Paleocene record from the northern edge of the continent (Augé and Rage, 2006). The newly described material from the late Oligocene of the Rukwa Rift Basin of Tanzania expands geographic and

temporal ranges for the clade, indicating that at least by the mid-Cenozoic, gekkotans had reached sub-equatorial Africa and were occupying a dynamic landscape characterized by seasonally dry periods with perennial availability of water (Roberts et al., 2012; Stevens et al., 2013). This ecosystem witnessed periodic volcanic activity related to the development of the East African Rift system, and featured the earliest evidence of Old World monkeys and apes, along with a diversity of mammals, crocodylians, snakes, birds, frogs, fishes, and invertebrates (Roberts et al., 2012; Stevens et al., 2013). Notably, this record provides an important datum, breaking a ~20 million year hiatus in the African fossil record of the gekkotan clade.

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FIGURES

FIG 1.—Specimen photograph and locality map. A, RRBP 13002, gekkotan right maxilla in lateral view and B, in medial view (scale bar equals 1 mm); C, map showing the Nsungwe Formation within the Rukwa Rift Basin (Tanzania) and the collection locality, incl. its relative position within Tanzania.

FIG. 2.—RRBP 13002, digital image of gekkotan specimen as derived from computed tomography. A, lateral view; B, medial view; C, occlusal view. Scale bar equals 1 mm. Abbreviations: af, alveolar foramen; fp, facial process of maxilla; mpn, maxillary portion of external naris; n/f fragmentary remainder of either nasal or frontal; prf, ventral portion of prefrontal; ps, palatal shelf.

Figure 1

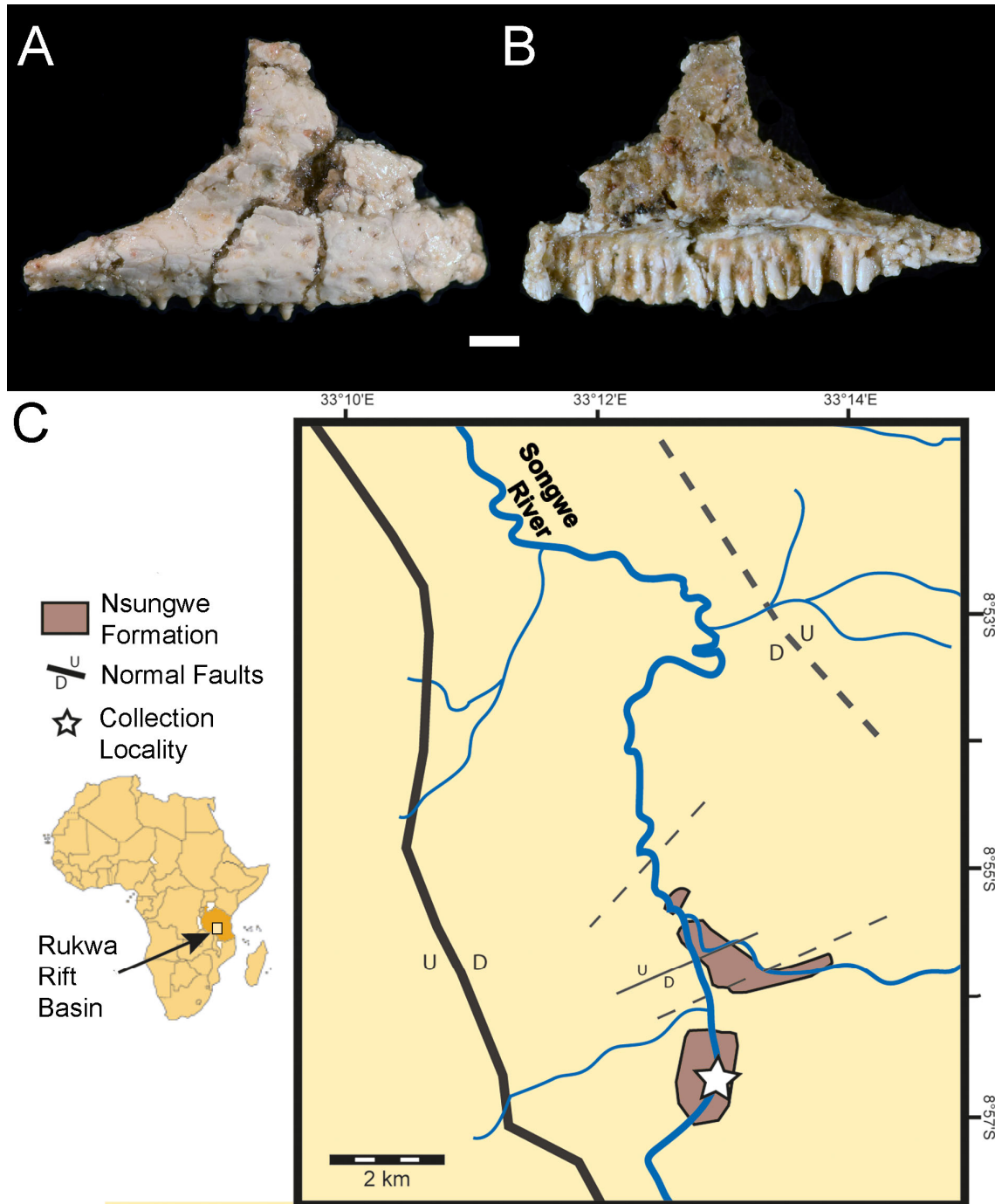


Figure 2

