A HYRACOID FROM THE LATE OLIGOCENE RED SANDSTONE GROUP OF TANZANIA, RUKWALORAX JINOKITANA (GEN. AND SP. NOV.)

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A striking array of fossil hyracoids has been described from northern Africa and the Arabian Peninsula, with several taxa recognized from Paleogene strata not only in the Fayum Depression of Egypt, but also in Morocco, Algeria, Tunisia, Libya and Oman (e.g., Sudre, 1979; Rasmussen, 1989 and references therein; Thomas et al., 1989; Gheerbrant et al., 2005). Hyracoids were abundant in these faunas, comprising up to 90% of the mammalian fauna recovered from the L-41 locality in the Jebel Qatrani Formation of Egypt (Rasmussen and Simons, 1991).

Hyracoids appear to have achieved their apex in diversity during the Paleogene, at which time the group dominated the small-medium sized herbivorous niches in known faunas (Schwartz et al., 1995). During this time, they spanned a rabbit to rhinoceros range in body size, exhibiting a diversity of locomotor and dietary morphologies (Rasmussen et al., 1996). From the bunodont Geniohyus, to the common lophoselenodont Thyrohyrax, hyracoids flourished, assuming a vast array of niches that would later be occupied by immigrant artiodactyls and perissodactyls (Schwartz et al., 1995). Indeed, specializations for limb stabilization attributed to cursoriality in Antilohyrax pectidens suggest that in some ways it converged upon modern springboks in aspects of its locomotor habits (Rasmussen and Simons, 2000), whereas at the other extreme, postcranial specializations of the hind limb later emerged in some procaviids to permit extreme rotation for rock and tree climbing (Fischer, 1986).

Faunal exchange beginning in the Miocene introduced a number of immigrant ungulates to the African continent, with a dramatic decline in hyracoid diversity occurring shortly thereafter (Schwartz et al., 1995). Subsequent to the collision between the Arabian and Eurasian plates, hyracoid diversity in the well-documented faunas of Kenya precipitously decreased as ungulates including boids, giraffids, rhinocerotids, suids, and trigLRILS from the northern continents made their way across the Arabian Peninsula and onto the African continent (Janis, 1993). Hyracoids in turn migrated into Eurasia but over time faired somewhat worse from the standpoint of abundance and taxonomic diversity than did their northern hemisphere counterparts. Today, only three hyrax genera remain, Procavia, Dendrohyrax and Heterohyrax, all 5 kg or smaller and living in Africa and/or extreme southwest Asia (Gheerbrant et al., 2005).

Our understanding of Paleogene hyracoid evolutionary patterns derives largely from northern African faunas (Osborn, 1908; Rasmussen and Simons, 1988; Rasmussen et al., 1990; Thewissen and Simons, 2001; De Blieux and Simons, 2002; De Blieux et al., 2006). In contrast, except for fragmentary specimens from Angola attributed to previously recognized Fayum taxa (Pickford, 1986), the sub-Saharan hyracoid record has been relatively undocumented prior to the rich Neogene faunas of Kenya, Namibia, and South Africa (Whitworth, 1954; Meyer, 1978; Pickford and Fischer, 1987; Pickford, 2003, 2004; Tsujikawa and Pickford, 2006), making regional comparisons of pre- and post-interchange diversity and abundance all but impossible. Although new Oligocene hyracoids have recently been described from Chilga, Ethiopia (Kappelman et al., 2003), and Losodok, Kenya (Rasmussen and Gutierrez, 2009), prior to the discovery reported herein, not a single novel hyracoid taxon has yet been recognized from deposits of this age sub-equatorial Africa (Gheerbrant et al., 2005). Based in southwestern Tanzania, the Rukwa Rift Basin Project (RRBP) is beginning to fill in some of the critical gaps in the vertebrate record of Africa. In particular, recent work in the Songwe Member of the Nsungwe Formation of the Red Sandstone Group has revealed a diverse microfauna of late Oligocene age, preserving invertebrates (Feldmann et al., 2007), fish (Gottfried et al., 2007), anurans (Simons et al., 2006), crocodylians and a diversity of mammals represented by dental and postcranial specimens (Stevens et al., 2005, 2006a, 2006b, 2008, 2009).

Here we describe the earliest hyracoid evidence from the region, represented by an unique pectinate right lower first incisor.

Location

The study area is situated in the Rukwa Rift Basin of southwestern Tanzania (Fig. 1). Fossils were excavated from a small outcrop belt of Red Sandstone Group strata located near the Songwe River, west of Mbeya. Red Sandstone Group deposits are significant because they represent a poorly understood continental rift-fill sequence containing a remarkable number of recently discovered fossil bearing intervals and localities (O’Connor et al., 2006; Stevens et al., 2008). Previous workers have assigned the Red Sandstone Group ages ranging from Jurassic to Miocene-Pliocene (e.g., Spence, 1954; Pentelkov, 1979; Wescott et al., 1991; Kilembwe and Rosendahl, 1992; Dambion et al., 1998). Recent work on the geology and paleontology of the Rukwa Rift Basin suggests that the Red Sandstone Group can be subdivided into at least two distinct stratigraphic units, the >500 m-thick Galula Formation and >300 m-thick Nsungwe Formation (formerly termed units I and II, respectively; see Roberts et al., 2004, 2007). The Galula Formation is assigned a Cretaceous age based on diverse fauna that includes dinosaurs, mammals, crocodyliforms, turtles, and fish (O’Connor et al., 2006). The Nsungwe Formation, which is subdivided into the lower Utengule Member and upper Songwe Member is assigned a Paleogene (~24.95 MY) age based on biostratigraphy, a dated ash bed and detrital zircon geochronology (Roberts et al., 2004, 2007; Stevens et al., 2005, 2006a, 2006b, 2008).

The fossil described herein was discovered in the Songwe Member of the Nsungwe Formation (Red Sandstone Group) at locality TZ-01, from a 3-4 meter thick sequence of poorly sorted, muddy, medium to coarse grained, massive sandstone beds. This interval is incredibly rich in microvertebrates, freshwater crustaceans and molds of freshwater gastropods and bivalves, and is

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sited within the upper 10 m of the Songwe Member and interbedded with a series of thin (0.1-2 m thick) claystones, siltstones, tuffs and cross-bedded, lenticular sandstones. Fossil bearing horizons are interpreted as sheet flood deposits within a small, flashy discharge fluvial system that appears to have drained into a local lake or swamp. Lenticular sandstones represent channelized fluvial deposits, whereas claystones and siltstones represent low-energy overbank deposits, some of which show evidence of palaeosol development. Tuff layers represent ash-flow and fall pyroclastics derived from nearby eruptive centers. Facies associations and faunal data, including the presence of aquatic and semi-aquatic taxa (fish, crustaceans, frogs, and aquatic mollusks), suggests perennial availability of water, but periodic or seasonal climatic fluctuation.

Ongoing geologic efforts in the basin include dating of ash beds and detrital zircon geochronology. An ash-flow tuff bed located ~7 m below the top of the Nsungwe Formation (Songwe Member) and 1.5 meters above the fossil bearing interval at TZ-01 has been dated at ~24.95 Ma (Roberts et al., 2007). This Oligocene age for the top of the Nsungwe Formation is consistent with previous assessments based on mammalian biostratigraphy (Stevens et al., 2005, 2006a, 2006b, 2008).

**MATERIALS AND METHODS**

Linear measurements of the Rukwa specimen were recorded using a National DC2-456H stereomicroscope bundled with Motic Images Plus (version 3.5) software. The accuracy of measurements is on average +/- 0.01 mm. Comparative material consisted primarily of reference specimens, casts and photographs of representative fossil and Recent hyraxes, including *Procavia* (YPM 3617), *Dendrohyrax* (YPM 1430), *Heterohyrax* (BER I 31’91), *Antilohyrax* (DPC 16657, DPC 15689), *Megahyrax* (DPC 8661, KNM RU 16, KNM RU 62, KNM RU 136, KNM RU 215), *Paraphynlodon* (KNM BN 1741), *Prohyrax* (PO AD 2902), *Saghatherium* (CGM 90-1527), *Thyrohyrax* (DPC 17760, DPC 17765), and *Titanohyrax* (CBI 41). Abbreviations: Berg Aukas, Namibia (BER); Chambi, Tunisia (CBI); Cairo Geological Museum (CGM); Duke University Division of Fossil Palates (DPC); Kenya National Museums (KNM); Namibia Geological Survey Museum (NGSM); Arrisdrift, Namibia (PO AD); and Yale Peabody Museum (YPM).

**SYSTEMATIC PALEONTOLOGY**

Order HYRACOIDEA Huxley, 1869

*RUKWALORAX JINOKITANA*, gen. et sp. nov.

**Type Specimen**—RRBP 06183, right central incisor (Fig. 2); specimen of the National Museum of Tanzania.

**Type Locality**—TZ-01, late Oligocene Songwe Member of the Nsungwe Formation of the Red Sandstone Group, Rukwa Rift Basin, southwestern Tanzania.

**Etymology**—Generic epithet incorporates both the East African Rift segment from which the specimen was recovered.
Miocene Arrisdrift deposits in the Orange River Valley of Namibia contain lower central incisors that preserve apical trpectinate morphology only in unworn specimens—these separations rapidly disappear with wear (Pickford, 2003). Pickford and Fischer (1987) described a series of Parapliohyrax specimens from the upper middle Miocene Baringo deposits of Kenya, six of which preserve lower central incisors, all too worn to conclusively determine the number of pectinations, but approximately twice the size of RRPB 06183; ranging in mesiodistal length between 7.9 and 9.4 mm. A deciduous second lower incisor referred to the same taxon and too fragmentary for mesiodistal measurements clearly preserves just 3 pectinations Pickford and Fischer (1987). Rasmussen et al. (1996) described a collection of late Miocene Heterohyrax specimens from Berg Aukas in Namibia, including three lower incisors, each exhibiting three deeply separated pectinations. The only fossil taxon prior to Rukwalorax that has been documented to exceed 3 deeply separated tines on the lower central incisor is the early Oligocene hyperpectinate Antilohyrax, a form known from the lower levels of the Jebel Qatrani Formation of Egypt. Whereas it might be tempting to consider Rukwalorax intermediate in morphology between Antilohyrax and the three-tined forms, the late Oligocene age of the Tanzanian form in combination with a paucity of hyperpectinate hyracines in the fossil record cautions against such speculation at this time.

CONCLUDING REMARKS

Here we describe the oldest small-bodied hyracoid recovered from east Africa, represented by a single pectinate right lower first incisor. The tooth is labiobuccinally narrow and mesiodistally elongate, measuring approximately 3.83 mm at its widest point, exhibiting a mild concavity along its lingual aspect, and an elongate, tapering root centered directly beneath tines two through four. The specimen is distinctive among Paleogene hyracoids in preserving four separate tines on the central lower incisor. Taxa such as Thyrohyrax exhibit only three tines whereas the hyperpectinate Antilohyrax exhibits 10 individual tines. Although Rukwalorax most closely resembles Antilohyrax among Paleogene hyracines in exceeding 3 pectinations on the lower central incisor, the younger age of the Tanzanian deposits precludes its consideration as a directly “intermediate” form between trpectinate and hyperpectinate lower central incisor morphologies. Presence of such a diversity of hyracoid incisor morphologies dating to the earliest Oligocene implies a far greater Eocene and perhaps Paleocene diversity for the clade. Rukwa Rift Basin localities are beginning to provide a rare window into hyracoid evolutionary history prior to the Neogene faunal transition, helping to expand our knowledge of Paleogene vertebrate diversity on the African continent.

ACKNOWLEDGMENTS

We recognize years of collaboration with our late colleague and friend Dr. S. Kapilima of the University of Dar es Salaam. J.-P. Cavigelli skilfully prepared the specimen. We thank Tanzanian colleagues J. Temba and D. Kamamba (Antiquities Division), Field assistance provided by S. Ngasala, E. Rasmussen, and V. Simons. For access to museum collections, we thank: Y. Attia, Z. Magdy, and E. Alamed (CGM); E. Simons and P. Chatrath (DUPC); M. Mungu, E. Mbua and F. K. Manthi (KNM); and G. Schneider (NNSM). Reference casts generously provided by P. Holroyd and R. Tabuce. We appreciate helpful comments on the project from J. Davis, G. Gunnell, J.A. Holman, S. Howard, M. Dawson, and E. Simons. Financial support provided by: National Geographic Society–CRE (2003-2007), LSB Leakey Foundation (2004-2005), Ohio University African Studies Program, Ohio University Research Council, Ohio University College of Osteopathic Medicine Research and Scholarly Affairs Committee, and the National Science Foundation (EAR 0617561).