

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 bovids, giraffids, rhinocerotids, suids, and tragulids 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 fared 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; Kilembe and Rosendahl, 1992; Damblon 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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situated 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 paleosol development. Tuff layers represent ash-flow and air-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 molluscs), 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), *Megalohyrax* (DPC 8661, KNM RU 16, KNM RU 62, KNM RU 136, KNM RU 215), *Parapliohyrax* (KNM BN 1741), *Prohyrax* (PQ AD 2962), *Saghatierium* (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 Pri-

mates (DPC); Kenya National Museums (KNM); Namibia Geological Survey Museum (NGSM); Arrisdrift, Namibia (PQ AD); and Yale Peabody Museum (YPM).

SYSTEMATIC PALEONTOLOGY

Order HYRACOIDEA Huxley, 1869

RUKWALORAX JINOKITANA, gen. et sp. nov.

Fig. 2

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

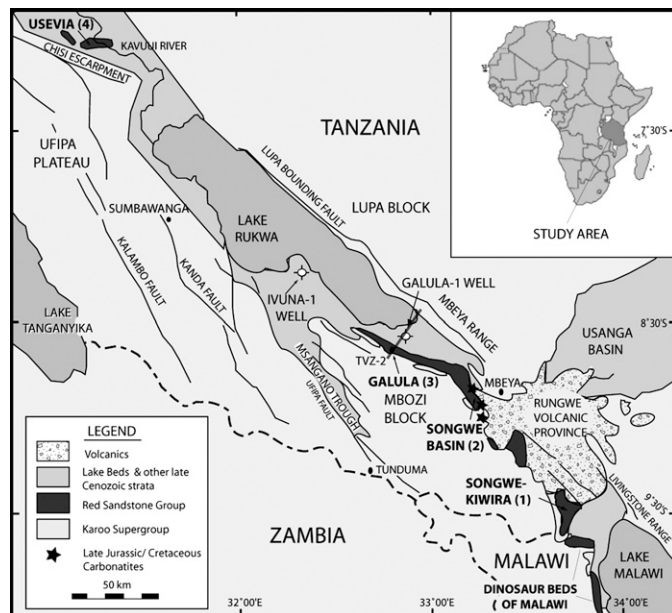
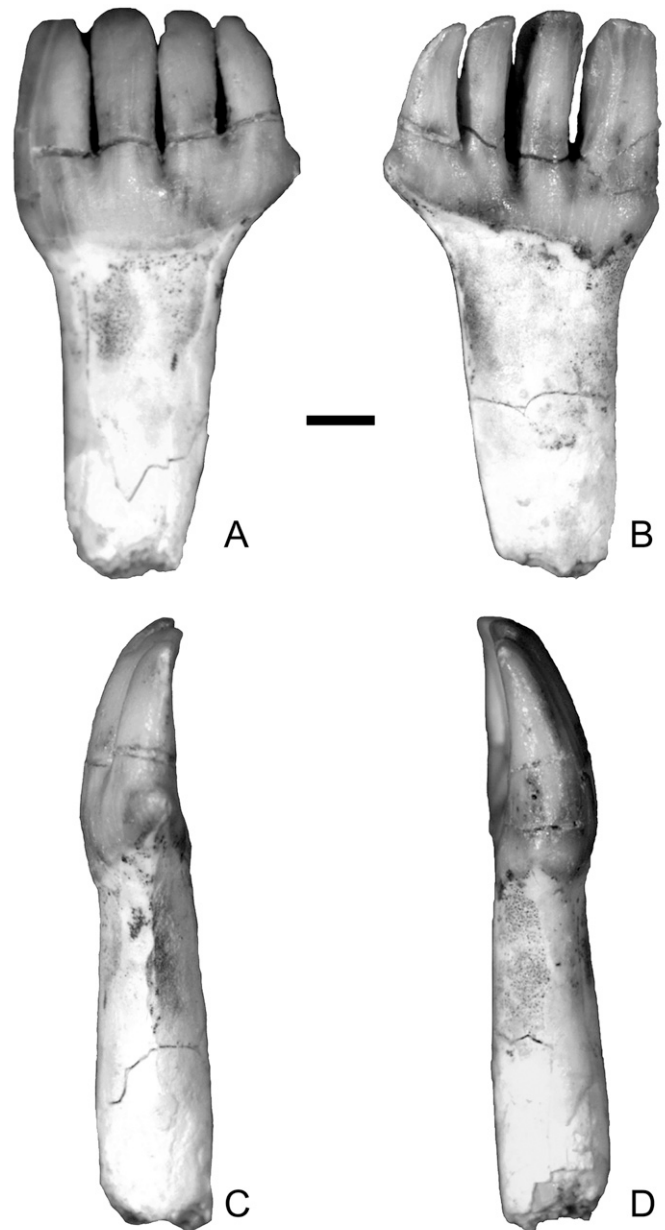


FIGURE 1. Geologic setting and outcrop area of the Red Sandstone Group in the Rukwa Rift Basin, southwestern Tanzania. RRBP 06183 was collected in the Songwe (outcrop area 2), about 15 km southwest of the town of Mbeya.

FIGURE 2. Type specimen of *Rukwalorax jinokitana* (RRBP 06183), lower right central incisor. A, labial view; B, lingual view; C, mesial view; D, lateral view. Scale bar equals 1 mm.

("Rukwa"), and the creature made popular by the writer Theodor Seuss Geisel ("lorax"); specific epithet combines the Swahili words for tooth ("jino") and comb ("kitana").

Diagnosis—Differs from all Paleogene and early Neogene hyracoids by preserving four individual deeply separated pectinations on a lower central incisor of this size.

Description—Pectinate right lower first incisor bearing four individual tines, each less than 1 mm across and approximately 2 mm in length. The tooth is labiolingually narrow and mesiodistally elongate, measuring approximately 3.83 mm at its widest point. It exhibits a mild concavity along its lingual aspect, and an elongate and tapering root centered directly beneath tines two through four. The mesial placement of tine one results in an asymmetric morphology reminiscent of hyracoids such as *Antilohyrax* that exhibit a triangular wedge of alveolar bone between the central incisors (Rasmussen and Simons, 2000). Individual tines are roughly circular in cross section, with subtle crests running longitudinally along the mesial and distal aspects of individual tines, also seen in *Antilohyrax* (Rasmussen and Simons, 2000: fig 1b). Tine morphology varies slightly, with the mesial tine somewhat more conical in outline, and the distal tine somewhat more mesiodistally expanded, than the central tines.

Discussion—Based on the crown shape and root morphology, the specimen is clearly a central lower incisor. Other than hyracoids, few taxa exhibit comb-like incisor morphology. Mammalian tooth combs are most often comprised of multiple individual teeth that are used in grooming (e.g., those observed in prosimian primates), rather than by multiple pectinations on a single tooth. Macroscelideans preserving complex lower incisors (e.g., Senut, 2008) exhibit greater variability in size among the individual pectinations and lack the deeply separated tine morphology exhibited by *Antilohyrax* and *Rukwalorax*. Certain chiropterans exhibit lower central incisors bearing multiple shallow lobes that are thought to function in prey capture/feeding (e.g., Greenhall and Schutt, 1996). These tend to be more bead-like in structure, and none exhibit the deeply separated tine morphology that characterizes the Rukwa specimen. Dermopterans exhibit labiolingually compressed individual teeth bearing multiple tines (Rasmussen and Simons, 2000), that based on behavioral observations and microwear analyses are thought to be used in processing foliage (Rose et al., 1981), and perhaps also in grooming (Aimi and Inagaki, 1988). Yet the Rukwa specimen differs from the pectinate lower incisors of the dermopteran *Cynocephalus* in having tines that are more uniform in size and shape, quite similar to the condition observed in the hyperpectinate hyracoid, *Antilohyrax*. No obvious striations are apparent that would suggest that these comb-like teeth are used in fur grooming in either *Antilohyrax* or *Rukwalorax* (Rasmussen and Simons, 2000; pers. obs.), although such behaviors have been observed in captive *Procavia* individuals (pers. comm. Christine Janis). Likely taxa that possess comb-like tooth morphology use them for a variety of purposes, including both dietary processing and grooming.

Hyracoid lower central incisor morphology varied considerably early in the Paleogene, ranging from forms possessing spatulate to bladelike teeth that preserve no pectinations (e.g., *Titanohyrax*), to those preserving 10 deeply separated tines (e.g., *Antilohyrax*). *Antilohyrax* specimen DPC 15689 preserves a four-tined i3 (De Blieux and Simons, 2002), but the tooth in that position differs drastically in shape and orientation from the distinctive hyracoid lower central incisor morphology of the Rukwa specimen. Based upon previously known specimens, major experimentations in lower central incisor tine number and morphology would appear to have occurred in the early Oligocene. Then and thereafter, the tripectinate condition is by far the most common among hyracoid lower central incisors, with differences in the degree of separation of the three individual tines or tines. Specimens of *Prohyrax hendeyi* from the early middle Miocene Arrisdrift deposits in the Orange River Valley of

Namibia contain lower central incisors that preserve apical tripectinate 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 RRBP 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 hyracoids 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 labiolingually 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 hyracoids 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 tripectinate 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.

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LITERATURE CITED

- Aimi, M., and H. Inagaki. 1988. Grooved lower incisors in flying lemurs. *Journal of Mammalogy* 69:138–140.
- Court, N., and J.-L. Hartenberger. 1992. A new species of hyracoid mammal *Titanohyrax* from the Eocene of Tunisia. *Palaeontology* 35:309–317.
- Damblon, F., P. Gerrienne, H. D'Outrelepond, D. Delvaux, H. Beeckman, and S. Back. 1998. Identification of a fossil wood specimen in the Red Sandstone Group of southwestern Tanzania: stratigraphic and tectonic implications. *Journal of African Earth Sciences* 26:387–396.
- De Blieux, D., and E. L. Simons. 2002. Cranial and dental anatomy of *Antilohyrax pectidens*: a late Eocene hyracoid (Mammalia) from the Fayum, Egypt. *Journal of Vertebrate Paleontology* 22:122–136.
- De Blieux, D. E., M. R. Baumrind, E. L. Simons, P. S. Chatrath, G. E. Meyer, and Attia, Y. S. 2006. Sexual dimorphism of the internal mandibular chamber in Fayum Pliohyracidae (Mammalia). *Journal of Vertebrate Paleontology* 26:160–169.
- Feldmann, R. M., P. M. O'Connor, N. J. Stevens, M. D. Gottfried, E. M. Roberts, S. Ngasala, E. L. Rasmussen, and S. Kapilima. 2007. A new freshwater crab (Decapoda: Brachyura: Potamonautidae) from the Paleogene of Tanzania, Africa. *Neues Jahrbuch für Geologie und Paläontologie* 8:71–78.
- Fischer, M. S. 1986. Die Stellung der Schliefer (Hyracoidea) im phylogenetischen System der Eutheria Zugeich ein Beitrag zur Anpassungsgeschichte der Procaviidae. *Courier Forschungsinstitut Senckenberg* 84:1–132.
- Gheerbrant, E., D. D. Domning, and P. Tassy. 2005. Paenungulata (Sirenia, Proboscidea, Hyracoidea and relatives). In: *The Rise of Placental Mammals* (eds. J. D. Archibald and K. D. Rose) pp 84–105.
- Gottfried, M. D., Stevens, N. J., O'Connor, Roberts, E. M., Ngasala, S. 2007. A new fossil record for the African lungfish *Protopterus* from the Paleogene of Tanzania. *Journal of Vertebrate Paleontology*. 27(Suppl.3):83A.
- Greenhall, A. M., and W. A. Schutt. 1996. *Diaemus youngi*. *Mammalian Species*. 533:1–7.
- Huxley, T. H. 1869. An introduction to the classification of animals. John Churchill and Sons, London.
- Janis, C. M. 1993. Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annual Review of Earth and Planetary Science* 24:467–500.
- Kappelman, J., D. T. Rasmussen, W. J. Sanders, M. Feseha, T. Bown, P. Copeland, J. Crabaugh, J. Fleagle, M. Glantz, A. Gordon, B. Jacobs, M. Maga, K. Muldoon, A. Pan, L. Pyne, B. Richmond, T. Ryan, E. Seiffert, S. Sen, L. Todd, M. Wiemann, and A. Winkler. 2003. Oligocene mammals from Ethiopia and faunal exchange between Afro-Arabia and Eurasia. *Nature* 426:549–552.
- Kilembe, E. A., and B. R. Rosendahl. 1992. Structure and stratigraphy of the Rukwa rift. *Tectonophysics* 209:143–158.
- Meyer, G. 1978. Hyracoidea. In: Maglio and Cooke, eds. *Evolution of African Mammals*, pp 284–314.
- O'Connor, P. M., M. D. Gottfried, N. J. Stevens, E. M. Roberts, and S. Kapilima. 2006. A new vertebrate fauna from the Cretaceous Red Sandstone Group, Rukwa Rift Basin, southwestern Tanzania. *Journal of African Earth Sciences* 44:277–288.
- Osborn, H. F. 1908. New fossil mammals from the Fayum Oligocene, Egypt. *Bulletin of the American Museum of Natural History* 24:265–272.
- Pentelkov, V. G. 1979. New data on age and correlation of Mesozoic rocks of the Rukwa trough, southwestern Tanzania. *Doklady Akademii Nauk USSR* 245:113–116.
- Pickford, M. 1986. Première découverte d'une faune mammaliene terrestre paléogène d'Afrique sub-saharienne. *Comptes Rendus Académie Sciences Paris* 302:1205–1210.
- Pickford, M. 2003. Middle Miocene Hyracoidea from the lower Orange River Valley, Namibia. *Memoir of the Geological Survey of Namibia* 19:199–206.
- Pickford, M. 2004. Revision of the Early Miocene Hyracoidea (Mammalia) of East Africa. *Comptes Rendus Palevol* 3:675–690.
- Pickford, M. and M. S. Fischer. 1987. *Parapliohyrax ngororaensis*, a new hyracoid from the Miocene of Kenya, with an outline of the classification of Neogene Hyracoidea. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 175:207–234.
- Rasmussen, D. 1989. The evolution of the Hyracoidea: A review of the fossil evidence. *The Evolution of Perissodactyls* 57–78.
- Rasmussen, D., and E. Simons. 1991. The oldest Egyptian Hyracoids (Mammalia: Pliohyracidae): New species of *Sagatherium* and *Thy-*
- ohyrax* from the Fayum. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 182:187–209.
- Rasmussen, D. T., and E. L. Simons. 1988. New Oligocene Hyracoids from Egypt. *Journal of Vertebrate Paleontology* 8:67–83.
- Rasmussen, D. T., M. Gagnon, and E. L. Simons. 1990. Taxeopody in the carpus and tarsus of Oligocene Pliohyracidae (Mammalia: Hyracoidea) and the phyletic position of Hyraxes. *Proceedings of the National Academy of Sciences of the United States of America* 87:4688–4691.
- Rasmussen, D. T., M. Pickford, P. Mein, B. Senut, and G. C. Conroy. 1996. The earliest Procaviid hyracoid from the Late Miocene of Namibia. *Journal of Mammalogy* 77:745–754.
- Rasmussen, D. T., and E. L. Simons. 2000. Ecomorphological diversity among Paleogene Hyracoids (Mammalia): a new cursorial browser from the Fayum, Egypt. *Journal of Vertebrate Paleontology* 20:167–176.
- Rasmussen, T., and M. Gutierrez. 2009. A mammalian fauna from the late Oligocene of northwestern Kenya. *Palaeontographica Abt. A* 288:1–52.
- Roberts, E. M., P. M. O'Connor, R. A. Armstrong, N. J. Stevens, and M. D. Gottfried. 2007. U-Pb geochronology of detrital zircons from the Rukwa Rift Basin, Tanzania: New data on the pre-Neogene tectonic and sedimentary evolution of the Western Branch of the East African Rift System. *Geological Society of America, Abstracts with Programs* 39:505.
- Roberts, E. M., P. M. O'Connor, M. D. Gottfried, N. J. Stevens, S. Kapilima, and S. Ngasala. 2004. Revised stratigraphy and age of the Red Sandstone Group in the Rukwa Rift Basin, Tanzania. *Cretaceous Research* 25:749–759.
- Rose, K. D., A. L. Walker and L. L. Jacobs. 1981. Function of the mandibular tooth comb in living and extinct mammals. *Nature* 289:583–585.
- Schwartz, G. T., D. T. Rasmussen, and R. J. Smith. 1995. Body-size diversity and community structure of fossil hyracoids. *Journal of Mammalogy* 76:1088–1099.
- Simons, and V. F. H., J. A. Holman, M. D. Gottfried, N. J. Stevens. 2006. Locomotor morphology and ecological implications of Paleogene African frogs. *Journal of Vertebrate Paleontology* 26:125A.
- Spence, J. 1954. The geology of the Galula coalfield, Mbeya District, Tanganyika. *Geological Survey Department B*, 25:34 pp.
- Stevens, N. J., P. A. Holroyd, E. M. Roberts, P. M. O'Connor, and M. D. Gottfried. 2009. *Kahawamys mbeyaensis* (n. gen., n. sp.) (Rodentia: Thryonomyoidea) from the late Oligocene Rukwa Rift Basin, Tanzania. *Journal of Vertebrate Paleontology* 29:631–634.
- Stevens, N. J., P. M. O'Connor, M. D. Gottfried, E. M. Roberts, and S. Ngasala. 2005. An anthropoid primate humerus from the Rukwa Rift Basin, Paleogene of southwestern Tanzania. *Journal of Vertebrate Paleontology* 25:986–989.
- Stevens, N. J., S. Ngasala, M. D. Gottfried, P. M. O'Connor, and E. M. Roberts. 2006a. Macroscelideans from the Oligocene of southwestern Tanzania. *Journal of Vertebrate Paleontology* 26:128A.
- Stevens, N. J., P. M. O'Connor, M. D. Gottfried, E. M. Roberts, S. Ngasala, and M. Dawson. 2006b. *Metaphiomys* (Rodentia: Phiomidae) from the Paleogene of southwestern Tanzania. *Journal of Paleontology* 80:407–410.
- Stevens, N. J., M. D. Gottfried, E. M. Roberts, S. Ngasala, S. Kapilima, and P. M. O'Connor. 2008. Paleontological exploration in Africa: A view from the Rukwa Rift Basin of Tanzania. In: *Elwyn Simons, A Search for Origins, Developments in Primatology: Progress and Prospects*, pp. 159–180.
- Sudre, J. 1979. Nouveaux mammifères Eocènes du Sahara occidental. *Paleovertebrata* 9:83–115.
- Thewissen, J., and E. L. Simons. 2001. Skull of *Megalohyrax eocaenus* (Hyracoidea, mammalia) from the Oligocene of Egypt. *Journal of Vertebrate Paleontology* 21:98–106.
- Thomas, H., J. Roger, S. Sen, C. Bourdillon-de-Grissac, and Z. Al-Sulaimani. 1989. Découverte de vertébrés fossiles dans l'Oligocène inférieur du Dhofar (Sultanat d'Oman). *Geobios* 22:101–120.
- Tsujikawa, H. and M. Pickford. 2006. Additional specimens of hyracoidea (Mammalia) from the Early and Middle Miocene of Kenya. *Annales de Paléontologie* 92:1–12.
- Whitworth, T. 1954. The Miocene Hyracoids of East Africa. *British Museum of Natural History, Fossil Mammals of Africa* 7:1–58.
- Wescott, W. A., W. N. Krebs, D. W. Engelhardt, and S. W. Cunningham. 1991. Newbiostratigraphic age dates from the Lake Rukwa rift basin in western Tanzania. *American Association of Petroleum Geologists Bulletin* 75:1255–1263.