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Macroscelideans (Myohyracinae and Rhynchocyoninae) from the late Oligocene Nsungwe formation of the Rukwa Rift Basin, southwestern Tanzania

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ABSTRACT

The fossil record of macroscelidean mammals is notoriously patchy, with a significant spatial and temporal gap separating faunas from the early Oligocene localities of northern Africa and the early Miocene localities of eastern and southern Africa. Here we describe fossil macroscelideans representing Myohyracinae and Rhynchocyoninae recovered from a rift-fill sequence of richly fossiliferous sandstones in the late Oligocene Nsungwe Formation in the Rukwa Rift Basin of southwestern Tanzania. Radiometrically dated to 25.2 Ma, a new Palaeogene myohyracine taxon (*Rukwasengi butleri*) is represented by a partial maxilla (RRBP 05409) preserving a lightly worn M2-M3. The M2 exhibits a less hypsodont and mesiodistally elongate morphology than the early Miocene *Myohyrax oswaldi*, and the three-rooted M3 exhibits a tiny mesially positioned fossette. A new rhynchocyonine (*Oligorhynchocyon songwensis*) is represented by specimens more brachyodont than the early Miocene *Miorhynchocyon*. Taken together these finds document a rare window into macroscelidean evolutionary history with diversification of the group near the Palaeogene-Neogene Transition (PNT). Continued exploration offers a refined perspective on mid-Cenozoic faunal and ecosystem dynamics on continental Africa, expanding opportunities for recognising trends in palaeobiological diversity across habitat types and through time.

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Palaeogene; palaeoecology; mammal evolution; Afrotheria; Cenozoic; elephant shrew; sengi

Introduction

Unravelling the origin and affinities of macroscelideans (also termed sengis, or elephant shrews) has long presented a palaeontological puzzle. Modern sengis are small insectivorous mammals characterised by rapid hind limb-dominant locomotion and an elongate flexible snout. Extant sengis consist of 20 species within six described genera, all restricted to continental Africa (Heritage et al. 2020). Often described as 'living fossils', their evolutionary history has been linked with mixodectid insectivores (Schlosser 1910), Glires (Novacek 1984), Menotyphla (Haeckel 1866; Gregory 1910), condylarthrans (Hartenberger 1986; Simons et al. 1991; Zack et al. 2005; Tabuce et al. 2007; Penkrot et al. 2008), and prior to a more expanded African Cenozoic fossil record, some of their members were originally described as hyracoids or even marsupials. More recently, macroscelideans have been grouped among afrotherians, an array of endemic African mammals that includes modern tubulidentates, tenrecoids, hyracoids, sirenians, and proboscideans united first on the basis of molecular sequence data (e.g., Stanhope et al. 1998; Murphy et al. 2001; Asher et al. 2003; Asher 2007; Hedges et al. 2015) and later supported by morphological features (e.g., Sánchez-Villagra et al. 2007; Seiffert 2007; Tabuce et al. 2007, 2008; Wible et al. 2007; Asher and Lehman 2008; O'Leary et al. 2013).

Importantly, temporal and spatial sampling gaps in early Cenozoic fossil-bearing sites on continental Africa have obscured macroscelidean evolutionary history across the Palaeogene-Neogene Transition (PNT). Palaeogene sengi discoveries were long limited to two now-extinct subfamilies from localities in northern Africa. Taxonomy follows Holroyd (2010). Metoldobotinae includes a single described genus (*Metoldobotes*) from the early Oligocene Fayum Depression of Egypt (Schlosser 1910; Simons et al. 1991). Herodotiinae includes *Chambius* from the late Early or early Middle Eocene Chambi Massif in Tunisia (e.g., Hartenberger 1986; Tabuce 2018), *Nemenchatherium* from the mid-late Eocene Bir el Ater, Algeria, and the late Middle or Late Eocene locality of Dur At-Talah, Libya (Tabuce et al. 2001), *Eotmantsoius* represented by a single tooth also from Dur At-Talah, Libya (Tabuce et al. 2012), and *Herodotius* from Oligocene localities in the Fayum Depression of Egypt (Simons et al. 1991). Localities in Namibia have revealed interesting materials including an enigmatic tooth from the Silica North locality (Pickford et al. 2008) and other materials interpreted as Eocene in age (but see Seiffert 2010; Coster et al. 2012; Marivaux et al. 2012; Sallam and Seiffert 2016 for a range of alternative age interpretations extending into the Oligocene or even the Miocene).

Metoldobotes has remained an uncontested sengi by most. Seiffert (2007) and Asher and Seiffert (2010) reviewed arguments for and against including herodotiines (*Nementchatherium, Chambius* and *Herodotius*) in the Macroscelidea. In recent years, additional significant and well-preserved herodotiine specimens have been described from sites in northern Africa (Tabuce et al. 2012; Tabuce et al. 2008). But until recently, the subsequent record for the group has been interrupted by a ~ 9 Ma hiatus in the fossil record until the recovery of Miocene and more recent faunas of eastern (Kenya) and southern (South Africa, Namibia) Africa, with localities that preserve an array of forms more similar to modern rhynchocyonine sengis (see review in Holroyd 2010). Also common in Miocene faunas are members of the Myohyracinae (Patterson 1965), the now-extinct subfamily of macroscelideans originally interpreted as hyracoids with tooth specialisations reflecting herbivorous diets (e.g., Butler 1984). The sengi fossil record expands

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considerably throughout the Neogene, with macrosceledines documented by at least 18 Ma (e.g., Butler 1984) and mylomygalines documented in the early Pleistocene of South Africa (reviewed in Holroyd 2010). Today only rhynchocyonines and macroscelidines remain.

Fossils from the Rukwa Rift Basin of southwestern Tanzania offer a rare window into the mid-Cenozoic of the African continental vertebrate record in general and that of sengis specifically. Specimens recovered from the ~25 Ma Nsungwe Formation reveal a rich fauna of late Oligocene invertebrates (Feldmann et al. 2007; Roberts et al. 2016; Epa et al. 2018), fishes (Stevens et al. 2016; Claeson et al. 2021), anurans (Blackburn et al. 2015 & 2019), lepidosaurs (McCartney et al. 2014; McCartney et al. 2021; Müller et al. 2018), and a diversity of mammals (Stevens et al. 2005, 2006, 2008, 2009a, 2009b, 2013) including sengis.

Here we describe Palaeogene evidence of both Myohyracinae and Rhynchocyoninae from Africa south of the equator. These discoveries offer insight into the geographic and temporal expansion and evolutionary significance of Palaeogene macroscelideans from the interior of the African continent.

Location

Specimens described herein derive from continental strata in the Rukwa Rift Basin of southwestern Tanzania, from a rock unit that represents the earliest known Cenozoic sedimentary record of rifting (Roberts et al. 2012) in the Western Branch of the East African Rift System (Figure 1). Fossil-bearing localities are situated in the Songwe River valley at approximately 8° 56′ S, 33° 12′ E and are part of a laterally continuous series of interbedded fluvial sandstones, floodplain and channel fill palaeosols, lacustrine siltstones, and devitrified airfall tuffs (bentonites) comprising the Songwe Member of the Nsungwe Formation (Roberts et al. 2004 & 2010; Lawrence et al. 2021). Specimens were recovered from variable discharge, flashy fluvial deposits (some of which have been overprinted by paedogenesis) at localities TZ-01, TZ-01S, and TZP-2. The fauna is dominated by small (<4 cm) specimens, including numerous teeth, jaws, and postcranial elements from microsites that preferentially preserve isolated elements (Stevens et al. 2005, 2006, 2008, 2009a, 2009b, 2013; Stevens et al. 2016; McCartney et al. 2014, 2021; Blackburn et al. 2015, 2019; Müller et al. 2018; Claeson et al. 2021). Fossil localities are bracketed by a series of well-dated volcanic ash beds that demonstrate a roughly similar age of ~25 Ma for all three localities (Roberts et al. 2012; Stevens et al. 2013) from which the sengi specimens were recovered.

Materials and methods

Specimens were collected by standard palaeontological hand-quarrying methods. Fieldwork was conducted under permits issued by the Tanzanian Commission for Science and Technology (COSTECH) and the Tanzania Antiquities Unit. Specimens are designated with RRBP, Rukwa Rift Basin Project (identifier used by the Tanzania Antiquities Unit), Dar es Salaam, Tanzania.

After mechanical preparation at the Ohio University Palaeobiology Preparation and Imaging Facility, specimens were µCT scanned at the Shared Materials Instrumentation Facility (SMiF) at Duke University, Durham, NC on a Nikon XTH 225 ST scanner. Specimens were scanned using an isotropic voxel size of 0.010 mm, at a voltage of 113 kV and amperage of 124 µA. Digital models were constructed through segmentation and visualised using the volume rendering and isosurface modules in Avizo Lite 9.2.0. Digital data including DICOM stacks and mesh models are available on MorphoSource. The following standard sengi tooth measurements were obtained on dental specimens (following Butler 1984) using a Nikon SMZ-1500 stereomicroscope bundled with a Motic 10.0 MP digital camera (Motic ImagePlus Version 3.0): on molars, maximum length (mesiodistal), maximum breadth (buccolingual); on premolars: maximum length (mesiodistal), maximum buccolingual breadth at distal cusps and at mesial cusps. Comparative material consisted primarily of reference specimens and casts of representative fossil and Recent macroscelideans examined in person by NJS at the following institutions: National Museums of Kenya (NMK/KNM), Duke University Division of Fossil Primates (DPC), United States National Museum of Natural History-

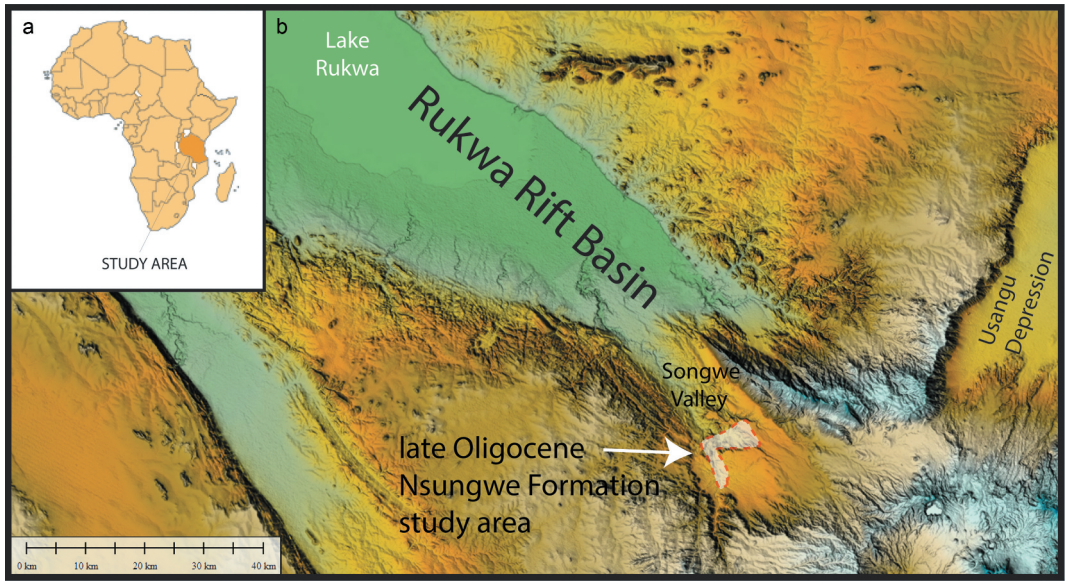

Figure 1. Geological context. Specimens were recovered from the Songwe Member of the late Oligocene Nsungwe Formation in the Rukwa Rift Basin of southwestern Tanzania. **A**, Geographic position of the Rukwa Rift Basin in eastern Africa (Tanzania shaded) and **B**, Digital elevation model showing the outcrop distribution of the Nsungwe Formation study area at the southern end of the Rukwa Rift Basin in the Songwe Valley.

Smithsonian Institution (USNM). Specimen casts were kindly provided by R. Asher, P. Holroyd, and R. Tabuce. For less accessible specimens, observations were supplemented with photographic comparisons.

Results

Systematic palaeontology

Order Macroscelidea Butler 1956
Family Macroscelididae Bonaparte 1838
Subfamily Myohyracinae Andrews 1914
Rukwasengi butleri new genus and species
Figure 2

Type Specimen

RRBP 05409, partial right maxilla preserving M2-M3 (Figure 2A-E).

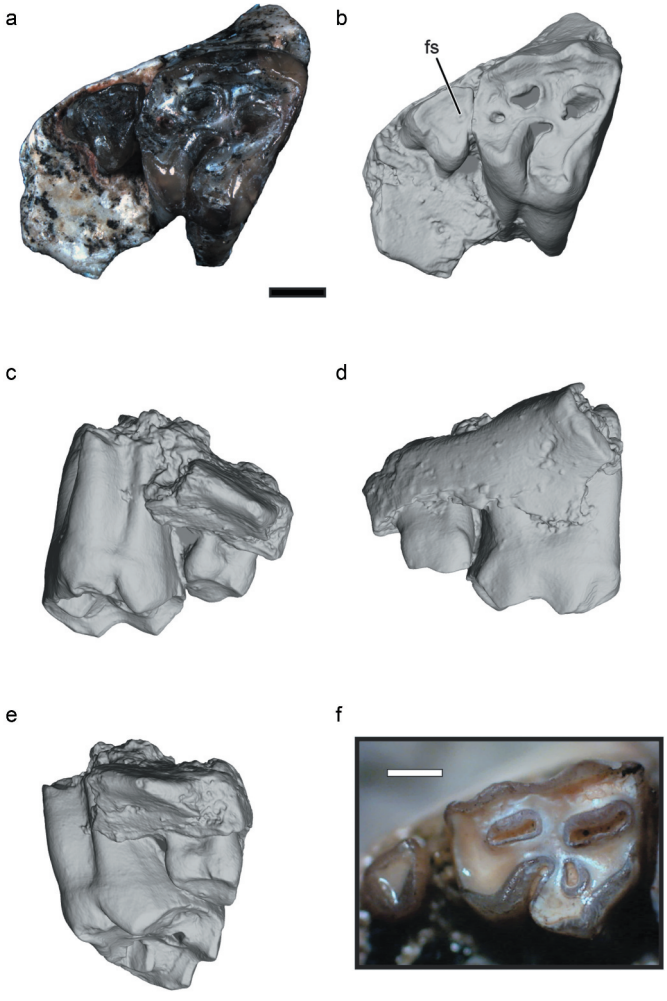

Figure 2. **Nsungwe formation Myohyracine**. Photograph (A) and digital renderings (B–E) of the late Oligocene *Rukwasengi butleri* (RRBP 05409, holotype) upper right molars (M2-3) in occlusal (A, B), lingual (C), buccal (D), and posterior (E) views. Photograph of *Myohyrax oswaldi* (KNM-RU 3763) in occlusal view (F) for reference. The lead line to "fs" calls out the small fossette on M3. Scale bars equal 1 mm.

Type Locality

TZP-2, late Oligocene Songwe Member of the Nsungwe Formation, Mbeya Region, southwestern Tanzania.

Etymology

Generic epithet incorporates the name of the rift segment from which the specimen derives (Rukwa), and the common term for macroscelidean (sengi). Specific epithet in honour of sengi expert Percy Butler.

Diagnosis

Differs from rhynchocyonine macroscelideans in possessing pronounced fossettes on upper molar teeth. Cheek teeth are less hypsodont and shorter mesiodistally than early Miocene *Myohyrax* and *Protypotheroides*. Further differs from *Myohyrax* in M2 buccolingual breadth exceeding mesiodistal length, M2 with a single more buccally positioned anterior fossette and two posterior fossettes (one buccal and one more centrodistally positioned), and a relatively larger and three-rooted M3 exhibiting a small mesially positioned fossette. Differs from *Namasengi* in exhibiting less individuated upper molar cusps, and from both *Namasengi* and *Promyohyrax* in lacking a buccal sinus on upper molars. Further differs from *Promyohyrax* in being larger, relatively more buccolingually broad, and having less buccally inflated M2. Further differs from herodotiines in lacking a buccal cingulum on upper molars, and in exhibiting a relatively smaller M3.

Description

RRBP 05409 is a partial right maxilla preserving moderately worn and closely approximated M2-M3 (Figure 2A-E). The M2 measures 2.45 mm in mesiodistal length, and 3.3 mm in buccolingual breadth at the broadest point near the base of the mesial cusps. Although worn, it is apparent that the paracone is slightly taller and more buccally positioned than is the metacone. A strong, mesially curved lingual sulcus is present. The lingual margins of the protocone and hypocone are sharp in outline and directed anteriorly. Three rounded fossettes are present in the M2 occlusal surface, two positioned in the buccal half of the tooth, and a third smaller and more central fossette distally. The third molar is three-rooted and triangular in outline, measuring 1.2 mm by 1.5 mm in maximum mesiodistal and buccolingual dimensions, respectively. The lightly worn M3 closely approximates M2 within the maxilla and exhibits a round, very small, mesially positioned fossette.

Remarks

Rukwasengi resembles Palaeogene herodotiines and metoldobotines (and not early Miocene myohyracines; Figure 2F) in exhibiting an M2 that is broader buccolingually than mesiodistally. Notably, the *Rukwasengi* M3 is also three rooted and exhibits a distinctive, small mesially positioned fossette. It is relatively smaller than the M3 in herodotiines, yet relatively larger than the M3 in *Myohyrax*. *Rukwasengi* expands the eastern African record for myohyracines earlier by at least 4 Ma, offering a glimpse into the mid-Cenozoic gap in the sengi fossil record.

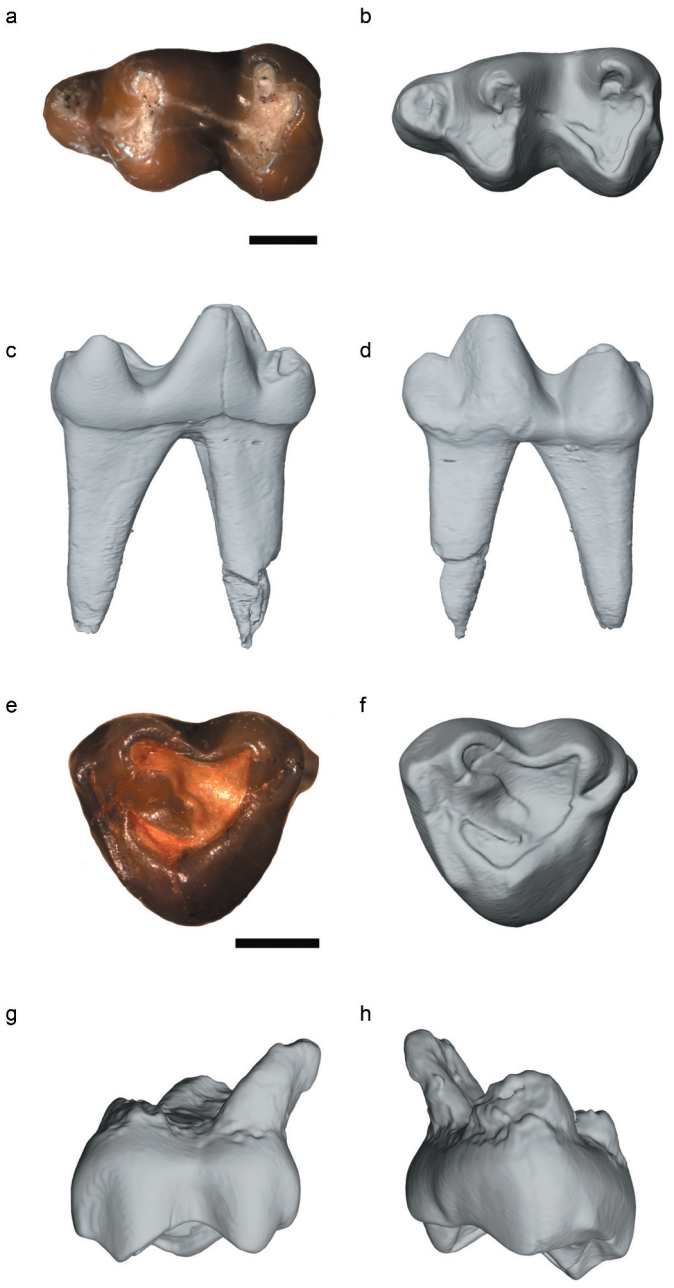

Figure 3. Nsungwe formation Rhynchocyonine. Photograph (A) and digital rendering (B–D) of the late Oligocene *Oligorhynchocyon songwensis* (RRBP 08086, holotype) left lower fourth premolar in occlusal (A, B), buccal (C), and lingual (D) views. Photograph (E) and digital rendering (F-H) of *Oligorhynchocyon songwensis* (RRBP 07433, referred specimen) upper left molar (M2 or M3) in occlusal (E, F), buccal (G), and lingual (H) views. Scale bars equal 1 mm.

Order Macroscelidea Butler 1956
Family Macroscelididae Bonaparte 1838
Subfamily Rhynchocyoninae Gill, 1872
Oligorhynchocyon songwensis new genus and species.
Figure 3

Type Specimen

RRBP 08086, left p4 (Figure 3A-D).

Type Locality

TZ-01S, late Oligocene Songwe Member of Nsungwe Formation, Mbeya Region, southwestern Tanzania.

Etymology

Generic epithet incorporates the age of the rock unit from which the specimen derives (Oligo), and a modern sengi taxon (rhynchocyon). Specific epithet references the Songwe River along which the fossil locality is located.

Diagnosis

Cheek teeth larger and more mesiodistally elongate than Palaeogene metoldobotines and herodotiines; lacking characteristic fossettes/fossettids observed in myohyracines; more brachyodont than mylomygalines, *Pronasilio*, and modern *Rhynchocyon*. Distinct from Miocene *Miorhynchocyon* species in lacking p4 anterobuccal cingulid, and in possessing weaker p4 cristid obliqua that meets the posterior wall of the trigonid lower and closer to the metaconid (rather than in a position midway between protoconid and metaconid). Further differs from *M. meswae* in relatively lower paraconid height in relation to metaconid, and from both *M. meswae* and *M. rusingae* in smaller size. Differs from *M. clarki* in being more brachyodont, with p4 relatively longer mesiodistally in relation to buccolingual breadth, sharper margins of the buccal cusps, and a pronounced p4 posterior cingulid. More brachyodont than *M. gariepensis*, with a much lower paraconid and less pronounced and basally inflated trigonid cusps. More brachyodont than materials referred to *Eorhynchocyon* and *Namasengi*. Further differs from *Namasengi* in exhibiting a wider p4 talonid.

Description

RRBP 08086 is a lightly worn two-rooted and molariform left p4 (Figure 3A-D) measuring 4.1 mm in mesiodistal length, 1.95 mm buccolingual breadth at the broadest point near the distal cusps, and 1.8 buccolingual breadth across the protoconid and metaconid. RRBP 08086 lacks a strong anterobuccal cingulid, exhibiting a very faint rugosity in that position. The low, wide paraconid is lingually positioned and reaches only half the height of the other trigonid cusps. It is well-individuated and linked to the protoconid by a small paracristid that ascends along the posterobuccal aspect of the cusp to a notch between the paraconid and protoconid. A prominent preprotocristid descends along the anterolingual aspect of the protoconid to terminate in the same notch, meeting the paracristid just posterobuccal to the paraconid. The transversely aligned protoconid and metaconid are tall and subequal in size, and connected by a narrow protocristid, forming a steep and unbroken posterior trigonid wall, at the base of which a weak cristid obliqua terminates just buccal to the rise of the metaconid. The hypoconid and entoconid are transversely aligned and subequal in size, although the entoconid is sharper in outline and there is no evidence of an entostylid near its anterior slope. Trigonid and talonid basins are steeply sloped lingually and cusp heights are uneven across the tooth, with the protoconid and metaconid approximately 50% taller than the paraconid, entoconid and hypoconid. Distal to the entoconid, a posterior cingulid rises to terminate at a hypoconulid expansion along the posthypocristid.

Referred specimen

Collected nearby in locality TZ-01, RRBP 07433 is a lightly worn three-rooted left upper molar (M2 or M3) (Figure 3E-H). The molar measures 2.8 mm in mesiodistal length, and 2.6 mm in buccolingual breadth. The tooth is brachyodont yet crestiform, with cusps largely subsumed in crests. The large paracone connects through a preparacrista to the well-developed and anteriorly projecting parastyle. A pronounced anterior cingulum is visible. The preprotocrista is wide and extends approximately halfway to a point between the paracone and the parastyle. A strong postprotocrista extends from the protocone, branching to form a basin distolingual to the metacone. RRBP 07433 preserves the bases of three roots that appear subequal in size. More brachyodont than early Miocene rhynchocyonines (including *M. clarki*), RRBP 07433 is consistent in size with RRBP 08086 and so provisionally referred to the same taxon here.

Remarks

Two specimens, RRBP 08086 (locality TZ-01S) and RRBP 07433 (locality TZ-01) document the presence of rhynchocyonines in the Oligocene Nsungwe Formation. RRBP 08086 is a well-preserved lower p4 and RRBP 07433 is a lightly worn isolated upper molar. Smaller than *Miorhynchocyon meswae* and *M. rusingae*, these specimens are clearly rhynchocyonine although more brachyodont and distinctive from early Miocene forms. Rukwa specimens expand the record for Rhynchocyoninae into the Palaeogene of eastern Africa, further addressing the mid-Cenozoic gap in the sengi fossil record.

Discussion and Conclusions

The Rukwa macroscelideans are significant in representing the earliest evidence of both myohyracines and rhynchocyonines from eastern Africa. Sengi fossils have been reported from localities as early as Eocene in age (e.g., Hartenberger 1986) yet for decades only a handful of pre-Miocene genera were known (Simons et al. 1991; Hartenberger 1986; Tabuce et al. 2001, 2012, 2017; Seiffert 2007; Pickford et al. 2008). Palaeogene taxa have generally been assigned to either Metoldobotinae or Herodotiinae (e.g., Simons et al. 1991; Seiffert 2007 but see Senut and Pickford 2021), with morphological evidence documenting well-differentiated rhynchocyonines and myohyracines by the early Miocene (Butler 1995). Molecular studies retrieve divergence estimates for crown macroscelidids (rhynchocyonines, macroscelidines) by the early Oligocene (Heritage et al. 2020).

Until recently, the oldest definitive fossil evidence of rhynchocyonines (*Miorhyncocyon meswae*, Butler 1984) in eastern Africa derived from the early Miocene Meswa Bridge locality in Kenya. Two different species (*Miorhynchocyon clarki*, Butler 1969; *M. rusingae*, Butler and Hopwood 1957) are recognised from the nearby Songhor locality with an age estimate of ~20 Ma. *Miorhynchocyon* is found in a host of localities with the last occurrence recorded at the ~14 Ma Fort Ternan locality (*M. rusingae*, Butler 1969). Two high-crowned rhynchocyonines (*Brachyrhynchocyon* and *Hypsorhynchocyon*; Senut 2008) have been recognised from the early Miocene locality of Northern Sperrgebiet in Namibia, documenting a wide geographic distribution for the group. Interesting materials have recently been described from Eocliff in the Sperrgebiet, Namibia, interpreted as Eocene in age (Senut and Pickford 2021). Additional species have also been postulated but not formally described from the early Miocene of Uganda (Butler 1984).

Myohyracines (represented by *Myohyrax oswaldi*) are common in the ~20 Ma Chamtwara and Songhor localities in Kenya and in sites from the Miocene of Namibia (e.g., Senut 2003), persisting until at least ~13 Ma based on fossils from Fort Ternan, Kenya and Bosluts Pan, South Africa (Holroyd 2010). A second species of *Myohyrax* (*M. pickfordi*, Senut 2008) and a larger myohyracine genus (*Protypotheroides*) have been described from the ~20 Ma Langental deposits in Namibia (Stromer 1922; Patterson 1965; Pickford et al. 2008), along with materials from the Eocliff in the Sperrgebiet, Namibia (Senut and Pickford 2021), suggesting a more diverse radiation awaits discovery for that group.

Presence of rhynchocyonine and myohyracine fossils from the Nsungwe Formation in the Rukwa Rift Basin documents that both groups were present in eastern Africa by 25 Ma, prior to the PNT. Continental rift-fill deposits of the Nsungwe Formation offer an important window into the evolutionary history of late Oligocene terrestrial and freshwater biotas in eastern Africa, providing data on mammalian diversification against the backdrop of rift development in the Western Branch of the East African Rift System.

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Conflicts of interest

No potential conflict of interest was reported by the authors.

Data statement and data availability

This published work, including the novel genus *Rukwasengi* (urn:lsid:zoobank.org:act:E60CFB69-1F55-41F2-BC9A-79079C6EBE62), novel species *butleri* (urn:lsid:zoobank.org:act:E360C064-23CA-45DC-B9A8-C2012241584A), novel genus *Oligorhynchocyon* (urn:lsid:zoobank.org:act:6ACC3E77-2D4A-4806-ACE1-440ADDAC3B2E), and novel species *songwensis* (urn:lsid:zoobank.org:act:9B8C3D70-EFCB-424F-BC65-A4FDCD879130), along with the associated nomenclatural acts, have been registered in ZooBank under urn:lsid:zoobank.org:pub:7525A261-F757-4917-96EA-ADC6128D1535. μCT data and associated mesh (PLY) files are hosted at Morphosource (www.morphosource.org).

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