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Palaeontological evidence for an Oligocene divergence between Old World monkeys and apes

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Apes and Old World monkeys are prominent components of modern African and Asian ecosystems, yet the earliest phases of their evolutionary history have remained largely undocumented¹. The absence of crown catarrhine fossils older than 20 million years (Myr) has stood in stark contrast to molecular divergence estimates of 25–30 Myr for the split between Cercopithecoidea (Old World monkeys) and Hominoidea (apes), implying long ghost lineages for both clades^{2–4}. Here we describe the oldest known fossil ‘ape’, represented by a partial mandible preserving dental features that place it with ‘nyanzapithecine’ stem hominoids. Additionally, we report the oldest stem member of the Old World monkey clade, represented by a lower third molar. Both specimens were recovered from a precisely dated 25.2-Myr-old stratum in the Rukwa Rift, a segment of the western Branch of the East African Rift in Tanzania. These finds extend the fossil record of apes and Old World monkeys well into the Oligocene epoch of Africa, suggesting a possible link between diversification of crown catarrhines and changes in the African landscape brought about by previously unrecognized tectonic activity⁵ in the East African rift system.

The late Oligocene represents the least-sampled temporal interval in primate evolutionary history³, with only a handful of primates described from all of Afro-Arabia^{6–10}. Possible reasons for an end-Palaeogene gap in the fossil record include limited deposits of appropriate age, particularly from Africa below the equator, complicated by densely vegetated topography in more tropical environments. As a result of this sampling bias, detailed understanding of the early diversification of Old World monkeys and apes has remained elusive. In particular, fossils from this interval are critical for testing the hypothesis of a late Palaeogene (~25–30Myr) hominoid–cercopithecoïd divergence, a result repeatedly retrieved by molecular studies^{2–4}. Recent discoveries from the Rukwa Rift Basin in southwestern Tanzania provide critical data for testing these ideas by revealing a novel glimpse into late Oligocene terrestrial ecosystems from Africa below the equator^{10–12}.

The Rukwa Rift Basin (Fig. 1) records one of the thickest accumulations of sedimentary rock in the entire East African rift system (EARS)¹¹. Work over the past decade has documented a complex and long-lived history of the western branch of the EARS^{5,11} containing continental faunas of both Cretaceous¹² and Oligocene¹⁰ age, the latter spanning, 24–26 Myr (see Supplementary Information, section 1). Palaeontological field research in 2011–12 resulted in the recovery of two well-preserved primate fossils from the Nsungwe 2B locality. These discoveries provide critical data for resolving disparities between molecularly derived divergence estimates and the primate fossil record.

Primates Linnaeus, 1758

Anthropoidea Mivart, 1864

Catarrhini Geoffroy, 1812

Cercopithecoidea Gray, 1821

Nsungwepithecus gen. nov.

Etymology. Prefix ‘Nsungwe’ in reference to the name of the geological formation from which the specimen was recovered; ‘pithecus’ a common primate suffix derived from the Greek pithekos (ape).

Diagnosis. Differs from all other fossil cercopithecoids in exhibiting the following combination of features on the lower third molar (M3): larger than all known ‘victoriapithecids’ other than *Zaltanpithecus*^{13,14}; unbifurcated mesial root; low rounded cusps with pronounced buccal flare; hypoconulid pronounced and centrally positioned; deeply incised distal buccal cleft that extends to the crown base; incomplete bilophodonty, with a small notch in the lophid connecting the protoconid and metaconid and absence of a hypolophid connecting the entoconid and hypoconid; lower degree of mesiodistal elongation and basal inflation than in *Noropithecus*¹⁴; marked buccal enamel wrinkling extending onto the median buccal ridge; shallow and crenulated lingual notch; and a proliferation of accessory cuspidals along the postmetacristid and around the entoconid, including three cuspidals situated in the talonid basin.

Nsungwepithecus gunnelli sp. nov.

Etymology. Specific name is in honour of Gregg F. Gunnell for his many contributions to primate palaeontology.

Holotype. RRBP (Rukwa Rift Basin Project) 11178, left partial mandible preserving M₃ (Fig. 2b; see also Supplementary Information, section 2).

Locality and horizon. Oligocene Nsungwe Formation, locality Nsungwe 2B, near the town of Mbeya, southwestern Tanzania (Fig. 1a). The site is situated 30m above the contact between the Utengule and Songwe members of the Nsungwe Formation. The age of the

fossil-bearing unit is tightly constrained between two volcanic tuffs dated by U-Pb CATIMS (U-Pb chemical abrasion thermal ionization mass spectrometry) geochronology at 25.237 and 25.214 Myr ago (Fig. 1c and Supplementary Information).

Diagnosis. As for genus. For additional description and metrics, see Supplementary Information.

Hominoidea Gray, 1825

Rukwapithecus gen. nov.

Etymology. Prefix ‘Rukwa’ in reference to the Rukwa Rift Basin from which the specimen was recovered; ‘pithecus’ a common primate suffix derived from the Greek pithekos (ape).

Diagnosis. Differs from all other extinct catarrhines in the following combination of characters: long, high-crowned and obliquely implanted lower fourth premolar, with mesial basin elevated high above the longer and more distolingually oriented talonid basin; mesiodistally elongate and crenulated lower molars that increase in length and width distally, and that are subrectangular and waisted in outline; mesial position of lower molar protoconid and hypoconid relative to lingual cusps; deep lower molar hypoflexid formed in part by a pronounced buccal cingulid that surrounds the protoconid mesially, but blends onto the buccal surface of the hypoconid; small lower molar metastylid (=mesoconid¹⁵) distolingual to the metaconid that is more pronounced on M₂–M₃; accessory cuspules in lingual notches of M₂ and M₃; deep lingual notch and distolingual fovea on M₁–M₃; large, well-individuated and buccally positioned hypoconulid on M₁–M₃; cresting between entoconid and hypoconulid weak or absent on M₁–M₃; and M₃ massive and highly crenulated, slightly tapering to a broad and rounded distal margin.

Rukwapithecus fleaglei sp. nov.

Etymology. Specific name is in honour of John G. Fleagle, for his many contributions to the study of primate morphology, behaviour and evolution.

Holotype. RRBP 12444A, a rightmandible bearing lower fourth premolar (P₄) through to M₃ and the ascending ramus (Fig. 2i and Supplementary, section 3).

Locality and horizon. Oligocene Nsungwe Formation, locality Nsungwe 2B (as described above).

Diagnosis. As for genus. For additional description and metrics, see Supplementary Information. Morphological features defining the earliest crown catarrhines have largely been a matter of speculation, with victoriapithecids and proconsuloids often defined primarily by the shared retention of primitive characters relative to later forms, rather than by demonstrable synapomorphies^{14–17}. Poor resolution of the phylogenetic branching pattern among fossil forms near the base of the cercopithecoid–hominoid split is further complicated by an unbalanced fossil record for the two groups, with early cercopithecoids represented by relatively few early–mid Miocene taxa¹⁴ and Miocene apes exhibiting greater taxonomic diversity¹⁵. The presence of taxa as distinctive as *Prohylobates*, *Proconsul* and *Rangwapithecus* in the African early Miocene indicates that the cercopithecoid–hominoid diversification initiated during the Oligocene^{15,18}, yet the only previously described late Oligocene catarrhines, *Kamoyapithecus* and *Saadanius*, are generally regarded as stem forms rather than members of the catarrhine crown clade^{6,8,17}. As such, *Rukwapithecus* and *Nsungwepithecus* are the first described primates that document the presence of crown catarrhines as early as 25 Myr ago. *Nsungwepithecus* represents the first cercopithecoid old enough to confirm the late Palaeogene crown catarrhine divergence estimates derived from molecular studies^{2–4}. *Nsungwepithecus* shares with victoriapithecids numerous features of lower molar morphology including deeply incised buccal clefts, a high degree of buccal flare,

and the lack of a buccal cingulid. Before the late Miocene, the published cercopithecoid record has largely been limited to rare and incomplete materials of *Prohylobates* and *Zaltanpithecus* collected from the early–middle Miocene of northern Africa^{13,14,18–20}, together with a spectacular array of over 2,500 specimens from a single taxon (*Victoriapithecus*) from mid-Miocene deposits in eastern Africa^{14,16,19,21}. Additional cercopithecoid diversity has recently been recognized in early–middle Miocene faunas from Kenya and Uganda, represented by as many as three species within the bilophodont genus *Noropithecus*¹⁴. Collectively, these fossils have been grouped in the Victoriapithecidae (a basal cercopithecoid group), with the acknowledgement that additional, more complete, fossils may reveal this to be a paraphyletic assemblage¹⁴. The recovery of a stem cercopithecoid older than 25Myr ago significantly extends the record of this clade, documenting the presence of a relatively large and incompletely bilophodont monkey in the Oligocene of eastern Africa.

Rukwapithecus shares two features with the Miocene apes and extant hominoids that are not present in cercopithecoids or Fayum stem catarrhines^{15,16}: buccal position of the M₂ hypoconulid, and mesial migration of cusps on the buccal side of lower molars such that the hypoconid is positioned opposite the lingual notch between the metaconid and the entoconid. In particular, *Rukwapithecus* shares numerous features with the early Miocene *Rangwapithecus*^{15,17,22,23}, including cusp position and wear pattern, degree of crenulation and cingulid development, oblique orientation of the cristid obliqua on M₁ and M₂, deep hypoflexid, deep distolingual fovea, and an enlarged M₃. Such features suggest that the lower molar pattern in the *Rukwapithecus*–*Rangwapithecus* clade was fairly conserved across the Oligocene–Miocene transition. *Rukwapithecus* nevertheless differs from *Rangwapithecus* in a number of features, exhibiting for example a narrower mesial fovea, a less tapered distal margin of M₃, and relatively weak cresting between the lower molar entoconid and

hypoconulid. Indeed, bootstrap support for the *Rangwapithecus*–*Rukwapithecus* clade in our parsimony analyses is very low (<50%), arguing against a particularly close (genus level) relationship (Fig. 3 and Supplementary Information, sections 5–7). Parsimony and Bayesian phylogenetic analyses^{24–27} place *Rukwapithecus* as a stem hominoid nested within the ‘nyanzapithecine’ clade (sensu Harrison¹⁵, see Fig. 3), but this result is not particularly robust (see Fig. 3 support values and Supplementary Information). In light of this, we cautiously place *Rukwapithecus* in both ‘Nyanzapithecinae’ and Hominoidea, but recognize that additional data from other parts of the dentition, cranium and postcranium are necessary for further testing and refining these hypotheses.

The Cenozoic era of Africa records a remarkable and deep record of environmental change. During this time, tectonic activity in the prominent East African rift system⁵, uplift of the African plateau^{5,28}, and climate aridification²⁸ had profound implications for Africa’s resident biota. Near the Oligocene–Miocene boundary, collision between the Afro-Arabian and Eurasian landmasses initiated periodic faunal interchange that contributed to the eventual replacement of many resident forms by immigrant species²⁹. Given the paucity of palaeontological data from the 22–30-Myr interval in Afro-Arabia, fossils from the Rukwa Rift provide a rare window into Palaeogene catarrhine diversity during this period of dramatic change in African terrestrial ecosystems, with *Nsungwepithecus* and *Rukwapithecus* together comprising 40% of described late Oligocene anthropoid taxa. The precisely dated stratigraphy of the site suggests that early hominoid and cercopithecoid evolution in eastern Africa took place against the backdrop of previously unrecognized tectonic uplift in the western branch of the EARS⁵, coinciding with the global late Oligocene warming event³⁰, and pre-dating larger-scale faunal shifts that intensified later in the Miocene.

METHODS SUMMARY

Rukwa specimens (RRBP 12444A and RRBP 11178) were scanned at the Ohio University MicroCT (OUmCT) facility in Athens, Ohio, using a GE eXplore Locus in vivo small animal MicroCT scanner. The Rukwapithecus type specimen (RRBP 12444A) was scanned at a slice thickness of 90 μ m, 80 kV, 495mA yielding a voxel size of 0.0930.093 0.09 mm. For a more detailed reconstruction of occlusal surfaces RRBP 12444A was also scanned at a slice thickness of 20 μ m, 80 kV, 495 mA. The latter protocol was also used for the Nsungwepithecus type specimen (RRBP 11178), yielding a voxel size of 0.0230.0230.02mm for high-resolution scans. The resulting volume data (in VFF-format) were exported from MicroView 2.2 (open-source software developed by GE; <http://www.sourceforge.net>) and imported into Avizo 6.3 (Visualization Sciences Group) for image segmentation, visualization and manipulation. Protocols for phylogenetic analysis and high precision CA-TIMS U-Pb zircon ages for the fossiliferous locality are provided in Supplementary Information.

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Supplementary Information is available in the online version of the paper.

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2007; R. Felice co-discovered RRBP 11178. Research was supported by US National Science Foundation (EAR-0617561, EAR/IF-0933619, BCS-1127164), National Geographic Society (CRE), Louis B. Leakey Foundation, Ohio University Heritage College of Osteopathic Medicine, and Ohio University Office of Research and Sponsored Programs.

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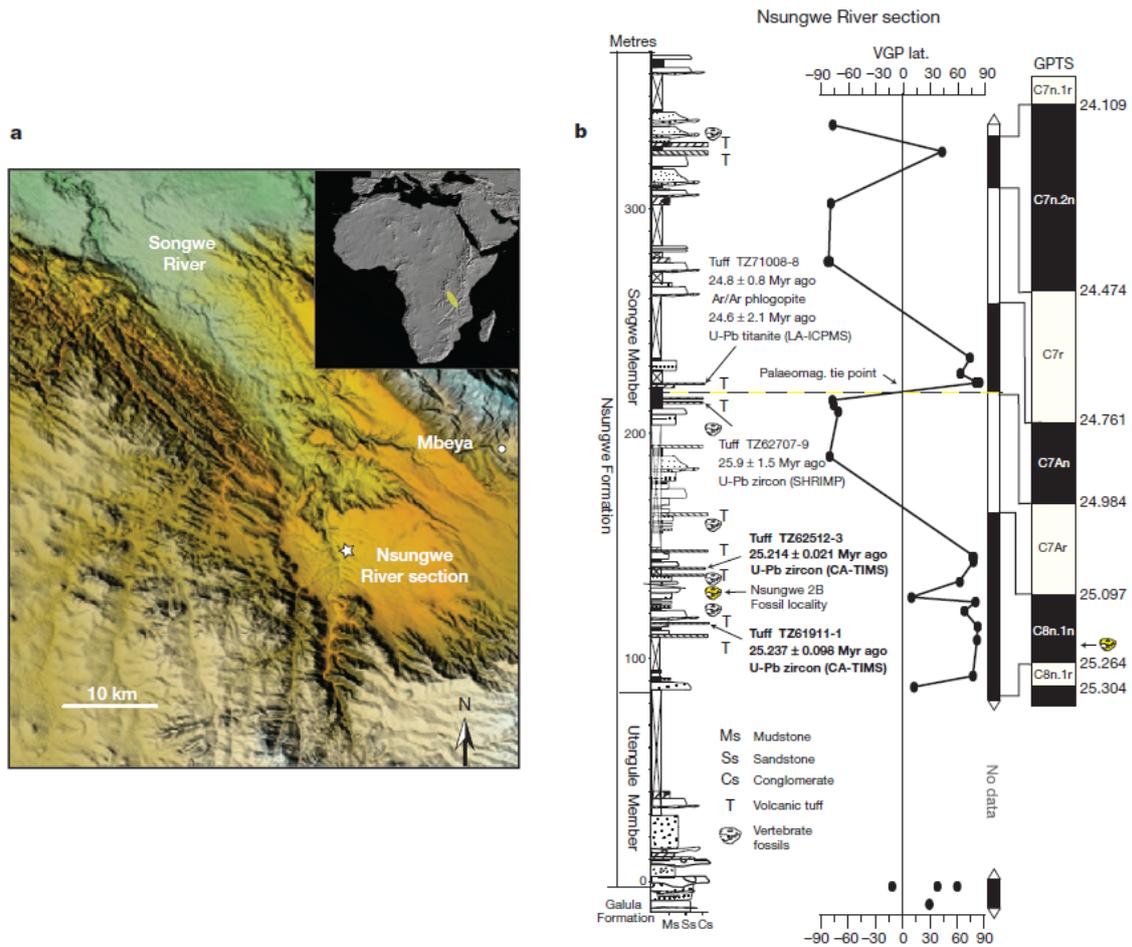


Figure 1 | Location and stratigraphy of the primate-bearing locality (Nsungwe 2B), in southwestern Tanzania. a, Digital elevation model of the study area based on Shuttle Radar Topography Mission data (SRTM). Inset map highlights the position of the Rukwa Rift Basin in eastern Africa (yellow oval). b, Measured stratigraphic section through the Nsungwe Formation, showing the position of Nsungwe 2B in yellow with the positions of two recently dated (via U-Pb CA-TIMS; bold type) carbonatite tuffs and several other dated tuffs (left), interpreted palaeomagnetic reversal stratigraphy of ref. 5 (virtual geomagnetic pole latitude (VGP lat.)) (centre), and ages (Myr ago; right) derived from the global polarity timescale (GPTS). Black bars, normal polarity; white bars, reversed polarity (see Supplementary Information for additional geological details).

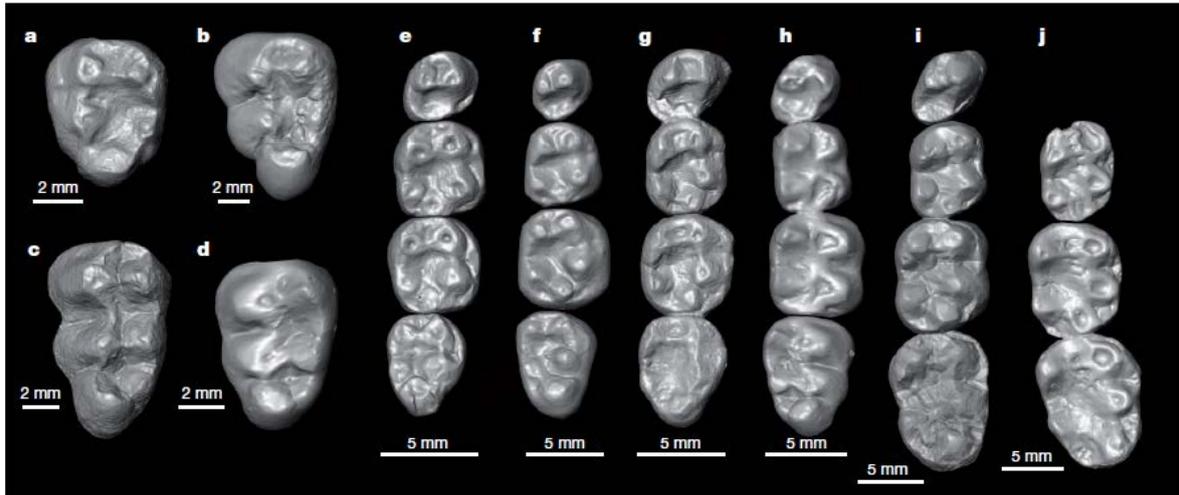


Figure 2 | Comparison of Nsungwe Formation primates with representative stem and crown catarrhines. a, *Propliopithecus sp.* (TQ 4, early Oligocene of Oman), rightM3, reversed for comparison; b, *Nsungwepithecus gunnelli* gen. et sp. nov. (RRBP 11178, late Oligocene of Tanzania), left M3; c, *Noropithecus bulukensis* (KNM-WS 12642, early Miocene of Kenya), right M3, reversed for comparison; d, *Victoriapithecus macinnesi* (KNM-MB 18993, middle Miocene of Kenya), rightM3, reversed for comparison; e, *Propliopithecus haeckeli* (SMN 12638, early Oligocene (?) of Egypt), right P4–M3; f, *Aegyptopithecus Zeuxis* (DPC 3056, early Oligocene of Egypt), right P4–M3; g, *Kalepithecus songhorensis* holotype (KNM-SO 378, early Miocene of Kenya), right P4–M3; h, *Victoriapithecus macinnesi* (KNM-MB 18993, middle Miocene of Kenya), right M1–M3 and reversed left P4; i, *Rukwapithecus fleaglei* gen. et sp. nov. (RRBP 12444A, late Oligocene of Tanzania), right P4–M3; j, *Rangwapithecus gordonii* (KNM-SO 463, early Miocene of Kenya), right M1–M3. See Supplementary Information section 4 for imaging protocols, and Supplementary Videos 1 and 2 for additional views of Nsungwe specimens.

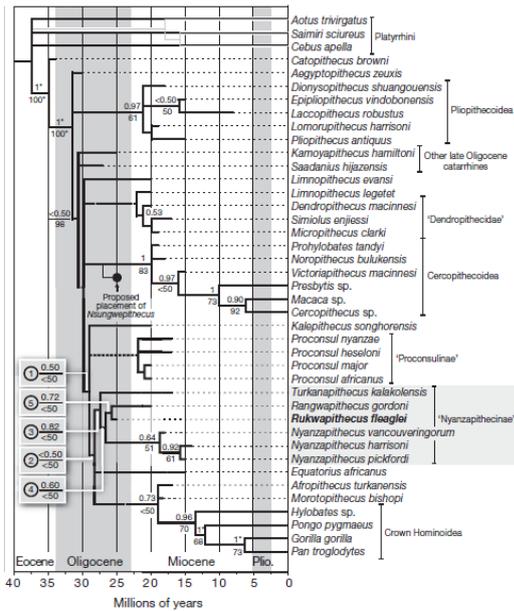


Figure 3 | Phylogenetic placement of *Rukwapithecus*, new genus. Temporally calibrated Adams consensus of four equally parsimonious trees recovered in PAUP 4.0b10 and the ‘allcompat’ tree calculated in MrBayes 3.2, based on analysis of the modified and taxonomically expanded 191-character morphological character matrix of ref. 26 (see Supplementary Information for details; thick dashed lines indicate branches that are not present in the strict consensus of all five trees; asterisks next to support values indicate that that node was constrained in either the parsimony or Bayesian analysis). Eocene *Catopithecus* was constrained as the most basal stem catarrhine due to its retention of several plesiomorphies that demonstrably evolved convergently in later catarrhines and the extant platyrrhine outgroups²⁷. Both analyses congruently placed *Rukwapithecus* as a nyanzapithecline stem hominoid, and, within ‘Nyanzapithecinae’, as the sister taxon of early Miocene *Rangwapithecus*. We obtained the same placement of *Rukwapithecus* when *Lomorupithecus* was removed and scorings for *Afropithecus* and *Morotopithecus* were combined into a single operational taxonomic unit, following an alternative taxonomic hypothesis of ref. 15. Numbers above and below branches are Bayesian posterior probability values and bootstrap values, respectively. We place quotation marks around

‘Nyanzapithecinae’ because reports of more complete materials of *Mabokopithecus* may eventually necessitate reassignment of some or all *Nyanzapithecus* species to the former genus^{15,17} due to taxonomic priority¹⁹, and may result in a name change for ‘Nyanzapithecinae’. The new genus *Nsungwepithecus* was not included in the phylogenetic analyses, and is grafted onto the tree in its proposed placement as the most basal known stem cercopithecoid. Unambiguous synapomorphies for nodes numbered 1–5 are provided in the Supplementary Information. Divergence dates within crown Cercopithecoidea and crown Hominoidea are based on the molecular dating analysis of ref. 4 with independent rates and soft bounds.