HISTORICAL BIOLOGY
https://doi.org/10.1080/08912963.2024.2370015

RESEARCH ARTICLE

Oldest record of a crown anomaluroid rodent from sub-Saharan Africa: a new genus and species from the early Oligocene Topernawi Formation of northern Kenya

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ABSTRACT

Anomaluroid rodents (i.e. Anomaluridae + Zenkerellidae) have a long evolutionary history in Africa dating back to at least the middle Eocene, but Palaeogene fossil members of the anomaluroid crown group have never been found south of the Sahara. Here, we describe the oldest crown anomaluroid from sub-Saharan Africa, *Eliwourus topernawiensis* (new genus and species) from the early Oligocene Topernawi Formation of northern Kenya. Bayesian phylogenetic tip-dating analysis of a combined molecular-morphological dataset places ~29.5 Ma *Eliwourus* as an advanced stem anomalurid, and suggests that crown Anomaluridae originated ~28.2 Ma. The gliding behaviour seen in all crown anomalurids had, therefore, likely evolved before the close of the early Oligocene. Bayesian geocoordinates analysis places the origin of crown Anomaluroidea (~47.2 Ma) in northern Africa, and identifies a stem anomalurid dispersal into equatorial eastern Africa in the latest Eocene or earliest Oligocene. We present the first quantitative analysis of the pace of anomaluroid dental evolution and confirm a remarkably slow or bradytelic rate of phenotypic change, despite significant transformations in postcranial morphology related to the evolution of gliding behaviour during the same interval. The Topernawi area was evidently sufficiently forested during the early Oligocene to support both arboreal rodents and primates.

ARTICLE HISTORY
Received 4 March 2024
Accepted 16 June 2024

KEYWORDS
Oligocene; Turkana; Kenya; anomalurid; anomaluroid; rodent

Introduction

The rodent family Anomaluridae, members of which are also known as ‘scaly-tailed flying squirrels’, had an ancient evolutionary origin in Afro-Arabia (Sallam et al. 2010; Heritage et al. 2016; Marivaux et al. 2017; Fabre et al. 2018) and are now represented by at least six extant species that are traditionally placed in two genera (*Anomalurus* and *Idiurus*) (Kingdon 2013). These species are found in diverse environments across peri-equatorial Africa, from Sierra Leone to Tanzania. Extant anomalurids are arboreal and are distinctive in bearing a gliding membrane or patagium that is not present in *Zenkerella* (family Zenkerellidae), the extant anomaluroid sister taxon of Anomaluridae. Gliding behaviour and its associated anatomical specialisations are assumed to have been present in the ancestral crown anomalurid (Heritage et al. 2016; Marivaux et al. 2017; Fabre et al. 2018).

The phylogeny and antiquity of Anomaluroidea has only recently been clarified through DNA sampling of *Zenkerella* (Heritage et al. 2016; Fabre et al. 2018); this genus is evidently a very distant relative of crown anomalurids, potentially having diverged from Anomaluridae as early as the middle Eocene, and has accordingly been placed in its own family (Heritage et al. 2016; Marivaux et al. 2017; Fabre et al. 2018). Previously published phylogenetic analyses that either excluded *Zenkerella* (Marivaux et al. 2005; Sallam et al. 2010, 2010) or placed the genus within crown Anomaluridae (Marivaux et al. 2011, 2015), left open the possibility that middle Eocene African zegdoumyids might be stem anomalurids. More recent analyses that have included living and extinct zenkerellids have instead placed zegdoumyids as stem anomaluroids, i.e. as successive sister taxa of Zenkerellidae + Anomaluridae (Heritage et al. 2016; Marivaux et al. 2017; Fabre et al. 2018). Within this context, the oldest crown anomaluroid fossils that occur within the latitudinal distribution of modern species (i.e. fossil species belonging to the genera *Nonanomalurus*, *Paranomalurus* and *Zenkerella* from sites in Kenya and Uganda) date to the early Miocene (Lavocat 1973; Pickford et al. 2013). All older candidate crown anomaluroids are from the late Eocene and early Oligocene of northern Africa (Jaeger et al. 1985; Sallam et al. 2010, 2010; Coster et al. 2015; Marivaux et al. 2017), with the exception of undescribed specimens from the early Oligocene of Oman (Thomas et al. 1992) and an isolated occurrence in southeast Asia (middle or late Eocene of Myanmar; Dawson et al. 2003; Marivaux et al. 2005).

The current absence of Palaeogene crown anomaluroids from sub-Saharan Africa might be explained by that region’s exceptionally poor terrestrial Eocene and Oligocene fossil record. However, multiple rodent-bearing sites of Oligocene age in southern Tanzania (Rukwa; Stevens et al. 2006) and northern Kenya (Lokone,

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Losodok, Nakwai; Rasmussen and Gutierrez 2009; Ducrocq et al. 2010; Marivaux et al. 2012) have not yet yielded crown anomaluroid fossils. Anomaluroids have also never been reported from a series of rodent-bearing localities in the Sperrgebiet region of Namibia (Eocliff, Eoridge, and Silica North and South) that are probably late Oligocene or earliest Miocene in age (Seiffert 2010; Coster et al. 2012; Sallam and Seiffert 2016b, 2020) but have been claimed to be as old as Bartonian or middle Eocene (Pickford 2018).

Here, we describe a new stem anomalurid genus and species that has recently been discovered in the late early Oligocene Topernawi Formation that is exposed in the Ekitale Basin on the west side of Lake Turkana in northern Kenya (Figure 1) (Princehouse and Aoron 2020). The new taxon is represented by only one specimen, a mandible bearing M_{1-3} and the roots of P_4. In this study, we place the new taxon into phylogenetic context by combining molecular and morphological data in a Bayesian tip-dating analysis, and use the resulting time-scaled tree to assess both anomaluroid biogeography and the pace of phenotypic evolution within the clade.

The locality that yielded the studied specimen ('Hill 2') is geochronologically tightly constrained, having been deposited between a basalt dating to 29.7 ± 0.5 and a felsic ignimbrite dating to 29.24 ± 0.08 Ma (Sousa et al. 2022). The specimen is therefore late Rupelian (late early Oligocene) in age, and as such is not only the oldest sub-Saharan anomalurid but also the oldest sub-Saharan member of crown Anomaluroidea. The Topernawi Formation is 92 m thick in the type section, is highly volcaniclastic, and includes both fluvial deposits and high-density debris flows (Sousa et al. 2022). Most of the vertebrate fossil-bearing localities, including Hill 2, occur in Unit 4 of the Formation, below the capping ignimbrite. These localities have also yielded remains of phiomorph hystricognathous rodents, as well as anthropoid primates, macroscelideans, hyracoids (geniohyids and *Thyrohyrax*), embrithopods, proboscideans, anthracotheriid artiodactyls and hyainailuroids. The Topernawi fauna is close in age to the well-sampled Quarries I and M of the Jebel Qatrani Formation in the Fayum region of northern Egypt (Seiffert 2006), and allows for a comparison of northern versus equatorial faunas during a phase in African prehistory that was characterised both by widespread extinction and significant geological upheaval (de Vries et al. 2021).

Materials and methods

Collection

Most mammalian fossils from the Topernawi localities have been recovered through surface prospecting, including the specimen discovered here (KNM TP-102508).

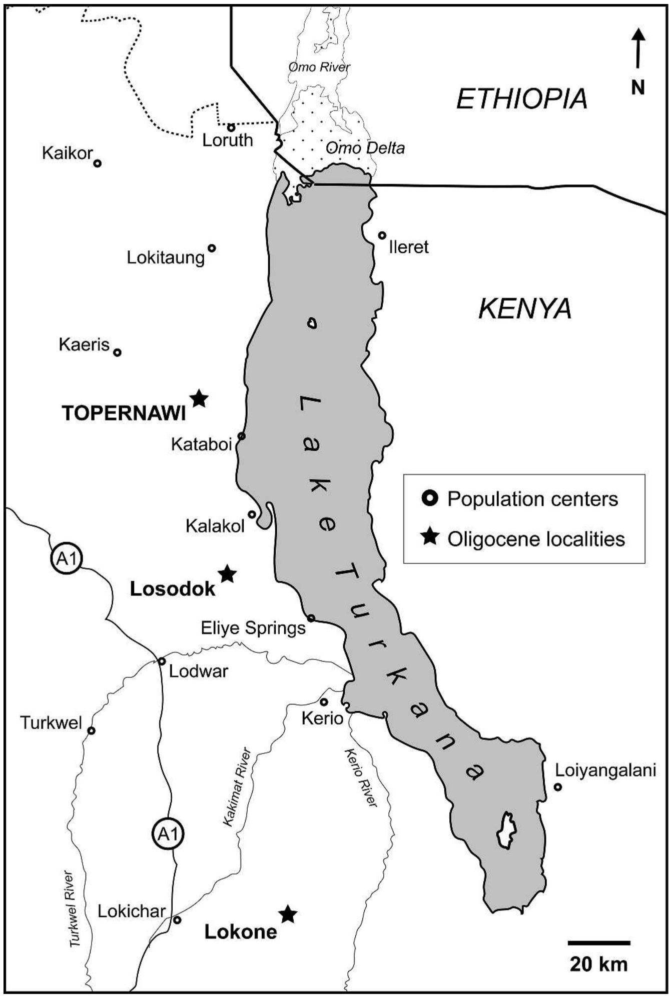

Figure 1. Map of the Turkana area of northern Kenya, showing the geographic position of the Topernawi region and other Oligocene localities in the region.

Imaging

A silicone (Affinis light-body) mould of KNM TP-102508 taken at the Turkana Basin Institute facility in Turkwel, Kenya, was micro-CT scanned at Duke University's Shared Materials Instrumentation Facility. Small air pockets that remained in the moulding compound, and which appeared on the inverse digital surface model as 'bubbles', were digitally removed in Avizo to produce the digital surfaces figured here. Images of the original model, the digitally cleaned model, and progressive smoothing iterations of the cleaned model are permanently archived in the Open Science Framework (OSF) repository associated with this study: DOI 10.17605/OSF.IO/5H9ME

Phylogenetic analyses

To place the new taxon within Anomaluroidea, we ran a total evidence Bayesian tip-dating analysis (hereafter BTD) (Ronquist et al. 2012) with implementation of the fossilised birth–death prior on branch lengths (FBD) (Zhang et al. 2015) in MrBayes 3.2.7 (Ronquist and Huelsenbeck 2003). For these purposes, we added KNM TP-102508 to the morphological character matrix of Marivaux et al. (2017) and combined that 158-character matrix with 7,467 DNA base positions from four mitochondrial loci (COX1, CYTB, ND2 and ND4) and two nuclear loci (IRBP and vWF). We included the extant anomaluromorph sister taxon of Anomaluroidea (the springhare *Pedetes*, family Pedetidae) as a DNA-only taxon to further constrain the temporal framework for anomaluroid evolution, as the dental character homologies of *Pedetes*' highly autapomorphic cheek teeth are currently unclear and open to debate. We used stepping-stone analyses in MrBayes to calculate the likelihoods of two alternative placements – one in which *Pedetes* was placed outside of a clade that includes anomaluroids plus early-middle Eocene zegdoumyids (i.e. thereby situating zegdoumyids as stem anomaluroids), and one in which *Pedetes* was placed closer to crown anomaluroids than to zegdoumyids (i.e. situating zegdoumyids as stem anomaluromorphs). We used the greedy algorithm (Lanfear et al. 2012) in PartitionFinder v. 2.1.1 (Lanfear et al. 2017) to find a combinatorial partitioning scheme, and appropriate evolutionary models for resulting partitions, using the Bayesian Information Criterion (BIC). The optimal scheme identified by this analysis included nine subsets, five of which were assigned the GTR+I+G model [i.e. a General Time Reversible model that includes a parameter for invariant sites (I) and a parameter for rate heterogeneity among variable sites (G)], and four of which were assigned the GTR+G model (see, e.g. Yang 1994). The Markov *k* model was applied to the morphological partition, and 95 of the morphological characters were treated as ordered. The BTD analysis employed flat [i.e. beta (1,1)] priors for the parameters extinctionpr and fossilizationpr, an exp(10) setting for igrvarpr and speciationpr, and sampleprob was set to 0.005. The clockratepr parameter was set to be approximately flat [i.e. normal(0.01,100)]. The prior for the root node age was based on the age of the oldest taxon in the matrix, *Tribosphenomys* [i.e. treeagepr = truncatednormal(60.91,60.92,1.0)]. Several hard constraints were employed for taxa outside of crown Anomaluromorpha (see settings files in the OSF repository). The MCMC analysis was run for 60 million generations, sampling every 1000 generations, with four runs and four chains and a temp setting of 0.10. The 50,000 post-burnin trees retained in the posterior distribution were summarised using an allcompat (majority rule plus compatible groups) consensus.

We also ran (1) a non-clock Bayesian analysis of the molecular partition (using the same partitioning and model scheme as was used in the combined BTD analysis) and (2) a BTD analysis of the morphological partition alone (using the same settings pertaining to the morphological partition as were used in the combined BTD analysis). As a means for testing the hypothesis of slow or bradytelic evolution of anomaluroid dental characters (Sallam et al. 2010; Marivaux et al. 2017), we also ran a non-clock analysis of the morphological partition that was constrained to fit the allcompat topology derived from the BTD analysis, with the aim of comparing the resulting morphological branch lengths to the time-scaled branch lengths derived from the BTD analysis. All input data, settings and output data associated with the phylogenetic analyses are permanently archived in the Open Science Framework (OSF) repository associated with this study.

Finally, we used MBASR (Heritage 2021) to obtain posterior probabilities for all possible ancestral states at all nodes (for all morphological characters) throughout the time-scaled tree derived from the BTD analysis. The input and output files are permanently archived in the Open Science Framework (OSF) repository associated with this study.

Biogeographic analysis

We used the software BayesTraits v4.0.1 (Meade and Pagel 2022) to model ancestral biogeography as a continuous variable and within a Bayesian framework. As input, the analysis uses a time-scaled phylogenetic tree and geocoordinates for each tree tip. The included GeoModel fits the phylogenetic network to Earth's surface by using a maximum likelihood search for the joint geolocations of all internal nodes. Our analysis was run for 30 million iterations, sampling every 1000 iterations, and with the option for variable rates enabled. The initial five million iterations were discarded as burn-in, yielding 25,000 post-burn-in samples. For each internal tree node, we interpret the mean geocoordinates from the posterior distribution to represent the peak estimate for its geolocation. As an input tree, we modified the result from the total evidence BTD analysis by pruning away outgroup taxa and leaving only anomaluromorph and zegdoumyid tips. The geocoordinates of type specimen localities were used as input data for fossil species. For extant species, we started with geographic range polygons (IUCN 2023) and then used furthest-point-sampling to draw sets of evenly spaced locations from within them. The ranges of all extant species were sampled at the same density with between-point spacing at ~130 km.

Anatomical terminology

We use the dental nomenclature of Marivaux et al. (2017) (Figure 2).

Institutional abbreviations

KNM, National Museums of Kenya, Kenya; DPC, Duke Lemur Center Museum of Natural History, U.S.A.

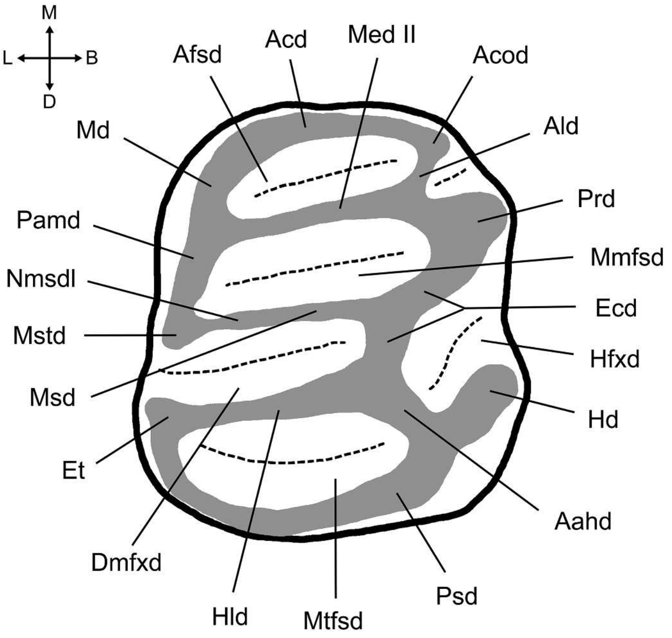

Figure 2. Terminology used to describe cusps, crests, and basins on an anomaluroid right lower molar, following Marivaux et al. (2017). Directional terms: M, mesial; B, buccal; D, distal; L, lingual. Terminology for cusps and crests: Aahd, anterior arm of hypoconid; Acd, anterocingulid (or anterolophid); Acod, anteroconid; Afsd, anterofossettid; Ald, anterolophulid; Dmfxd, distal mesoflexid; Ecd, ectolophid; Et, entoconid; Hd, hypoconid; Hfxd, hypoflexid; Hld, hypolophid; Md, metaconid; Med II, metalophulid II; Mmfsd, mesial mesofossettid; Msd, mesolophid; Mstd, mesostylid; Mtfsd, metafossettid; Nmsdl, lingual neo-mesolophid; Pamd, posterior arm of the metaconid; Prd, protoconid; Psd, posterolophid.

Systematic paleontology

Rodentia Bowdich, 1821
Anomaluromorpha Bugge, 1974
Anomaluroidea Gervais, 1849
Anomaluridae Gervais, 1849

Eliwourus, new genus
LSID urn:lsid:zoobank.org:act:89039C15-4FBD-4AA7-BA1D-52B43F3467B5
Figure 3

Etymology

Combination of *eliwo*, Turkana for strange, and *urus*, Greek for tail, mimicking other generic names within Anomaluridae (i.e. *Anomalurus*, *Idiurus*, *Shazurus*).

Type species

Eliwourus topernawiensis, new species.

LSID urn:lsid:zoobank.org:act:59C124C3-2564-4EFA-A13B-5E8FE4C7E5E8

Geographic distribution and age

Topernawi Formation, west side of Lake Turkana, northern Kenya, late early Oligocene (29.7 ± 0.5 to 29.24 ± 0.08 Ma).

Diagnosis

Eliwourus differs from other Palaeogene and early Miocene anomalurids in combining the following features: relatively thick crests on M_{1-3}; accessory spurs in the M_1 anteroflexid; relatively close approximation of the entoconid and mesostylid cusps, particularly on M_{2-3}; relatively close approximation of the mesolophid and the hypolophid on all lower molars, and accordingly restricted distal mesoflexids, particularly on M_{2-3}; metalophulid II crests that are relatively obliquely oriented with respect to the mesolophid, with the buccal part of the mesial mesofossettid being mesiodistally more expanded than the lingual part; and short anterior arms of the entoconid. *Eliwourus* further differs from early Miocene *Paranomalurus bishopi* in being smaller (based on M_1 size), and in having relatively mesiodistally compressed anteroflexids on M_{2-3}; it differs from some individuals of *P. bishopi* in lacking a notch that separates the protoconid from the buccal part of the anterolophid. *Eliwourus* further differs from early Miocene '*Paranomalurus*' *walkeri* in lacking anterolophulids and pronounced mesiobuccal foveae, lacking buccal spurs on the protoconids, and being larger (based on M_1 size). *Eliwourus* further differs from early Oligocene '*Paranomalurus*' *riodeoroensis* (known from M_{2-3}) in being slightly larger, and in having lower and more robust crests and more restricted anteroflexids.

Eliwourus topernawiensis, new species

Etymology

In reference to the Topernawi area, and the Topernawi Formation, in which the fossil was found.

Holotype and only referred specimen

KNM TP-102508, a partial right mandible with crowns of M_{1-3} and roots of P_4.

Type locality

Hill 2, Topernawi region, Kenya.

Diagnosis

As for genus.

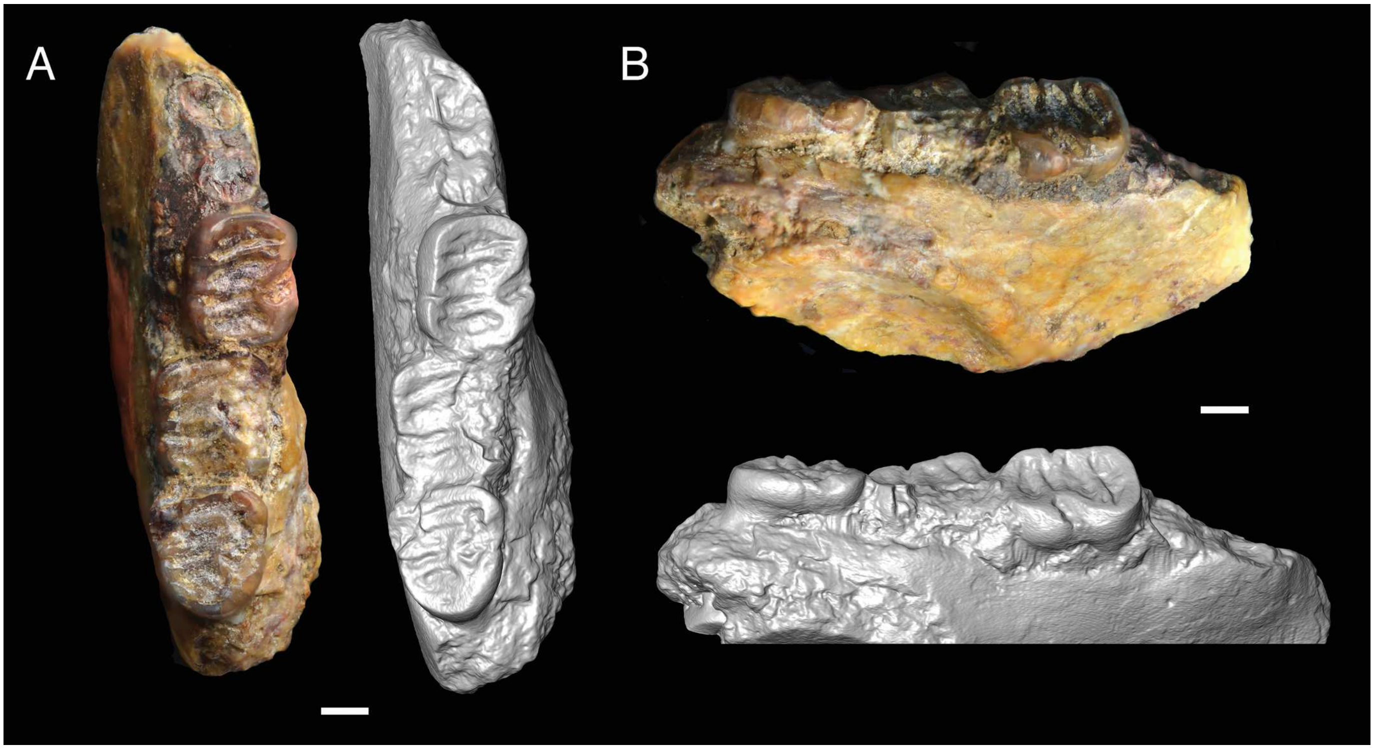

Figure 3. KNM TP-102508, holotype and only specimen of *Eliwourus topernawiensis*, a partial right mandible with crowns of M_{1-3} and roots of P_4 in occlusal (A) and buccal (B) views. Photographs of the specimen are shown alongside a digital model derived from micro-CT scanning of a mould, in the same orientation. Scale bar = 1 mm.

Description

KNM TP-102508 (Figure 3A,B) preserves a small part of the mandibular corpus, with corporal bone extending approximately 1 mm anterior to the mesial root of P_4, the same distance posterior to the distal terminus of the M_3 crown, and about 3.5 mm ventrally. There is a deep concavity on the lateral portion of the corpus delimited by an obliquely (posterodorsally) oriented masseteric ridge; its anterior border extended to at least the posterior portion of M_1. The mesiodistal distance across the two P_4 roots is 2.96 mm.

The M_1 (Figure 3A; mesiodistal length (MDL) = 3.15 mm, trigonid buccolingual width (triBLW) = 2.57 mm, talonid buccolingual width (talBLW) = 2.82 mm) is the best preserved of the three molars, showing no signs of breakage but moderate wear that left the tooth with fairly thick crests, and shallow basins. A robust, long, and mesially convex anterolophid forms the mesial border of the tooth, and connects the metaconid to the protoconid. There is no hint of an anterolophulid nor is there an associated concavity on the buccal wall of the tooth mesiolingual to the protoconid (mesiobuccal fovea), as occurs in some fossil anomalurids, most notably '*Paranomalurus*' *walkeri*. A short accessory crest extends buccally from the metaconid into the anterofossettid. Distally, a complete metalophulid II extends obliquely distolingually from the protoconid to the region of the posterior arm of the metaconid, enclosing the anterofossettid distally. A distinct but short neomesolophid runs lingually from the mesostylid to meet a low and weak mesolophid that connects to the distal portion of the ectolophid, dividing the mesoflexid into a relatively capacious oval mesial mesofossettid and much more restricted gutter-like distal mesoflexid. This crest is roughly paralleled by a slightly more robust hypolophid, which runs distolingually from the mesial portion of the anterior arm of the hypoconid and then curves mesiolingually to meet the entoconid. The mesostylid and entoconid are closely approximated, with only a narrow and shallow sulcus separating the two cusps. A thick and mesially concave posterolophid forms the distal border of the tooth, joining the entoconid and hypoconid and enclosing the distal basin (the metafossettid). The hypoconid bears a short mesiobuccally oriented projection that forms the distal wall of the hypoflexid.

The M_2 (Figure 3A; MDL = 2.90 mm) is badly damaged, with about 30% of the crown morphology missing due to breakage. The crowns of both M_2 and M_3 are displaced and tilted lingually with respect to that of M_1, apparently due to post-mortem distortion. The preserved morphology of M_2 largely resembles that of M_1, with the following differences: the anterolophid is not as robust, and the mesial border of the tooth is not as strongly convex; there is no accessory crest projecting lingually into the anterofossettid; and the anterofossettid is more mesiodistally compressed.

The M_3 (Figure 3A; MDL = 3.09 mm; triBLW = 2.48 mm; talBLW = 2.78) differs from M_{1-2} in having a more triangular shape; i.e. tapering distally with a strongly convex posterolophid. The mesiolingual portion of the crown is missing, as is some enamel in the region of the protoconid and the buccal part of the metalophulid II. M_3 shows even more marked reduction in the size of the anterofossettid, and also has a more mesiodistally compressed mesoflexid. The metalophulid II is oriented relatively transversely, rather than being distolingually oriented as on M_{1-2}. The metafossettid is approximately circular in shape.

Results

Anomaluroid phylogeny and the position of *Eliwourus*

The BTD stepping-stone analysis of the combined dataset, testing two different placements of *Pedetes*, unambiguously favours placing Pedetidae as a sister taxon of Anomaluroidea to the exclusion of Zegdoumyidae (Figure 4; estimated marginal log-likelihood (LnL)

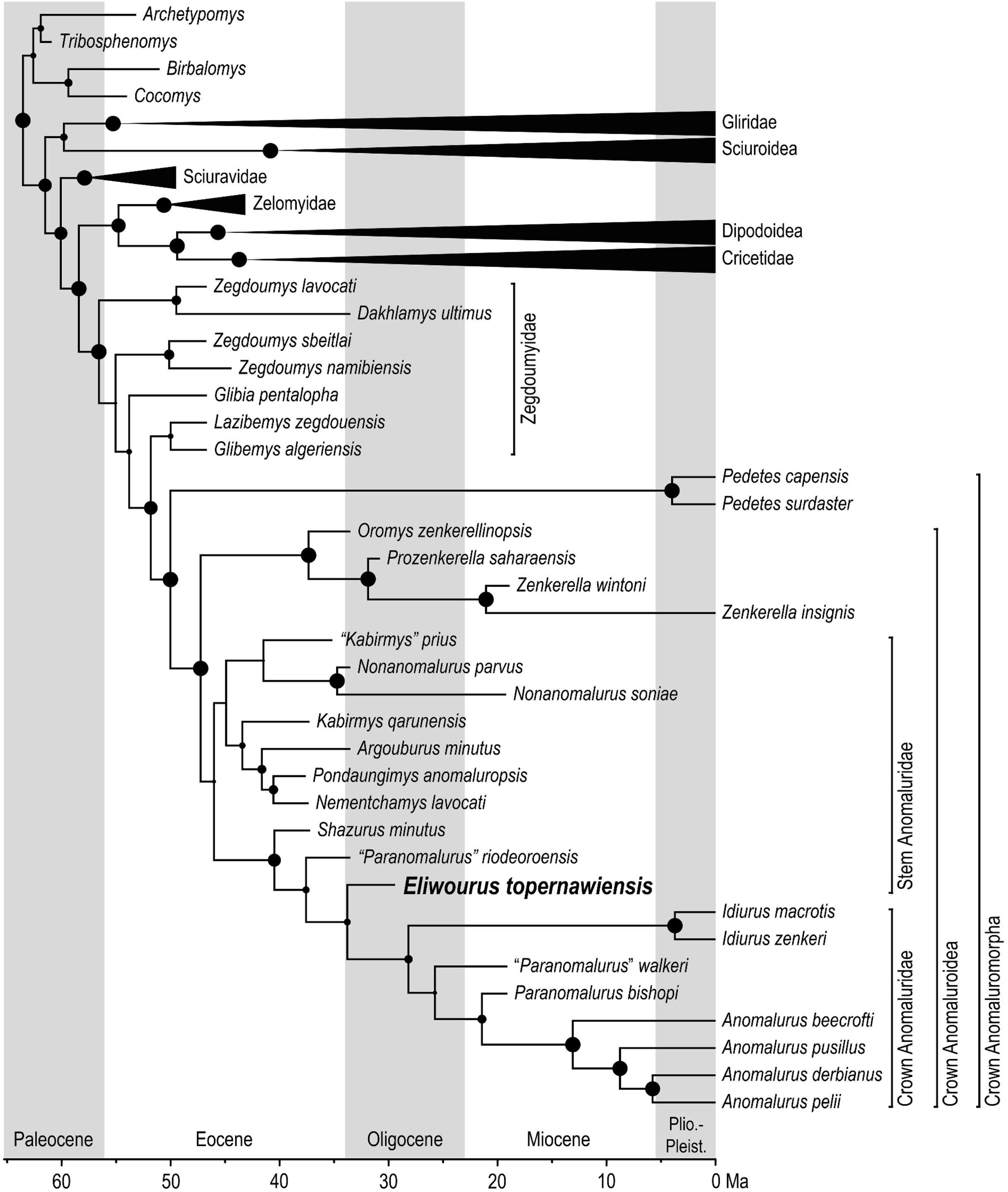

Figure 4. 'Allcompat' consensus derived from Bayesian tip-dating analysis of a combined molecular-morphological matrix of living and extinct anomaluroids and other rodents. Cricetidae, Dipodidae, Gliridae, and Sciuroidea are collapsed (full results are available in the associated OSF data repository). Circles at nodes are scaled relative to posterior probability (note, for instance, that the node for *Pedetes* is supported by a posterior probability of 1.0).

of −44204.51), rather than as the sister taxon of an anomaluroid-zegdoumyid clade (LnL = −44343.04). The primary BTD analysis reported here showed clear signs of topological convergence of the independent runs (average standard deviation of split frequencies = 0.006 and minimum effective sample size of 117.46). Within Anomaluroidea, BTD places *Eliwourus* as a stem anomalurid, diverging from the anomalurid stem at approximately the Eocene-Oligocene boundary (~34 Ma). A more inclusive anomalurid clade that also contains the advanced stem anomalurids *Shazurus* and '*P.*' *riodeoroensis* is well-supported (posterior probability (PP) of 0.87). A clade containing nementchamyids (*Argouburus*, *Kabirmys qarunensis*, *Nementchamys*, *Pondaungimys*), *Nonanomalurus*, and '*Kabirmys*' *prius* is placed along the most basal part of the anomalurid stem (i.e. to the exclusion of Zenkerellidae) with only weak support (PP = 0.37). The origin of crown Anomaluridae is estimated to have occurred at ~28.2 Ma (median age estimate; 95% HPD (highest posterior density) = 22.7–34.2 Ma), i.e. in the latest part of the Rupelian stage (latest early Oligocene), while the estimate for the origin of crown Anomaluroidea is ~47.2 Ma (95% HPD = 44.0–51.0 Ma), i.e. in the earliest part of the Lutetian stage (earliest middle Eocene). The age estimate for crown Anomaluromorpha was 50.0 Ma (95% HPD = 46.5–53.7 Ma). The early Miocene species of *Paranomalurus* are placed as consecutive stem anomalurines (i.e. the stem leading to the extant genus *Anomalurus*, including *Anomalurus beecrofti*, which is sometimes placed in the genus '*Anomalurops*'), with *P. bishopi* closer to crown Anomalurinae than '*P.*' *walkeri*. These results, combined with the much more basal placement of '*P.*' *riodeoroensis*, show *Paranomalurus* to be paraphyletic and in need of revision. Within crown Anomaluridae, crown Anomalurinae is identified as only including extant taxa of the genus *Anomalurus*, is well-supported (PP = 1.0) and is estimated to have originated at ~13.1 Ma, while crown Idiurinae (i.e. members of the genus *Idiurus*) is similarly well-supported (PP = 1.0) and is estimated to have originated at ~3.7 Ma. Results within Anomalurinae are consistent with those found by Fabre et al. (2018), with *Anomalurus* (=*Anomalurops*) *beecrofti* being the sister taxon of an *Anomalurus* (*pusillus*, (*derbianus*, *pelii*)) clade. All of the species divergences within the latter anomalurine clade are placed in the late Miocene.

Ancestral state reconstruction in MBASR identified three morphological characters of interest given the placement of *Eliwourus*. One trait was identified as a synapomorphy of the clade containing *Eliwourus* and all younger anomalurids (character 125: change from protoconid smaller than metaconid, to protoconid equal to metaconid), and two changes were identified as autapomorphies of *Eliwourus* (character 146: change from anterior arm of the entoconid absent, to anterior arm of the entoconid low and short; character 147: change from crests lophodont, to crests present but low).

Pace of phenotypic evolution in anomaluroids

We provide a novel test of the hypothesis that anomaluroids exhibit bradytelic evolution of morphological (primarily dental) characters through the later Palaeogene and Neogene (Sallam et al. 2010; Marivaux et al. 2017) by running a non-clock analysis of the morphological partition constrained to fit the allcompat topology derived from the combined BTD analysis. Plotting the resulting branch lengths – which are representations of phenotypic change – against geological time (Figure 5) allows a graphical display of temporal trends in evolutionary rates. Using this approach, if the branches all show a similar evolutionary rate over time, the resulting slopes of the plotted branches will be roughly similar. Plotted

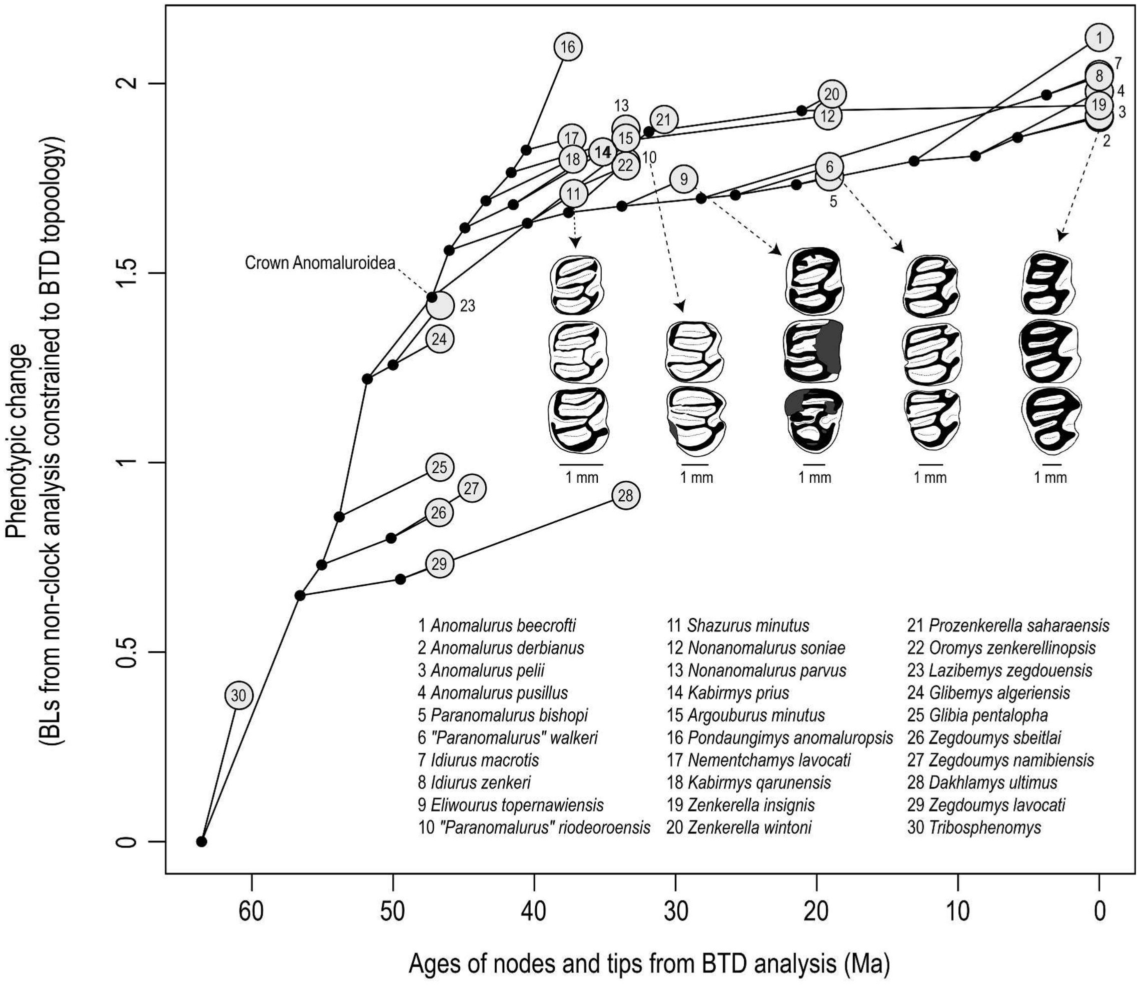

Figure 5. Plot showing pace of phenotypic change in living and extinct anomaluroids. On the y-axis, branch lengths from a non-clock Bayesian phylogenetic analysis that was constrained to fit the 'allcompat' consensus tree derived from Bayesian tip-dating analysis of molecular and morphological data shown in Figure 4. On the x-axis, time in millions of years. Tips are shown as numbers within circles, and nodes are marked with small back circles, to allow legibility. Line drawings of stem and crown anomalurids (scaled to the same M_1 width) are, from left to right, *Shazurus minutus* (early late Eocene, Egypt); '*Paranomalurus*' *riodeoroensis* (earliest Oligocene, Western Sahara); *Eliwourus topernawiensis* (early Oligocene, Kenya); '*Paranomalurus*' *walkeri* (early Miocene, Kenya); *Anomalurus derbianus* (Recent, Uganda).

branches with very steep positive slopes indicate rapid rates of phenotypic change, while branches with more gradual positive slopes indicate less rapid rates. If there has been no evolutionary change over a given time period, plotted branches through that phase will be flat (i.e. a slope of 0).

The clade including crown anomalurids and more advanced stem anomalurids (i.e. *Shazurus* and younger relatives) clearly show a dramatic slowdown in phenotypic evolution starting in the middle Eocene (Figure 5), when there is a shift from strongly positive slopes along older branches to less steep branches for all later African anomalurid lineages. Zenkerellids and nonanomalurids show convergent slowing in rates of phenotypic change with those seen in African anomalurids, but those slowdowns occur later, close to the Eocene-Oligocene boundary. The only terminal branch that maintains the same pace of dental evolution as seen in more basal anomaluroid branches, with no evidence for slowing rates, is that leading to *Pondaungimys*, the only known Asian anomaluroid and a taxon that is estimated to have dispersed out of Afro-Arabia after ~40.6 Ma.

Bayesian geocoordinates analysis

Bayesian geocoordinates (=BCG) analysis of stem and crown anomaluroids (Figure 6), using the tree derived from the combined BTD analysis, places the origin of crown Anomaluroidea (~47.2 Ma) in northeast Africa, near the border of modern Egypt and Libya. The geographic origins of stem Pedetidae and all other early-diverging anomaluroid clades are similarly placed in northern Africa, either in Libya (Pedetidae and Zenkerellidae) or near the border of Algeria and Mali (Nonanomaluridae). Independent dispersals from northern Africa into eastern Africa are inferred to have occurred either in the late Eocene or earliest Oligocene (stem

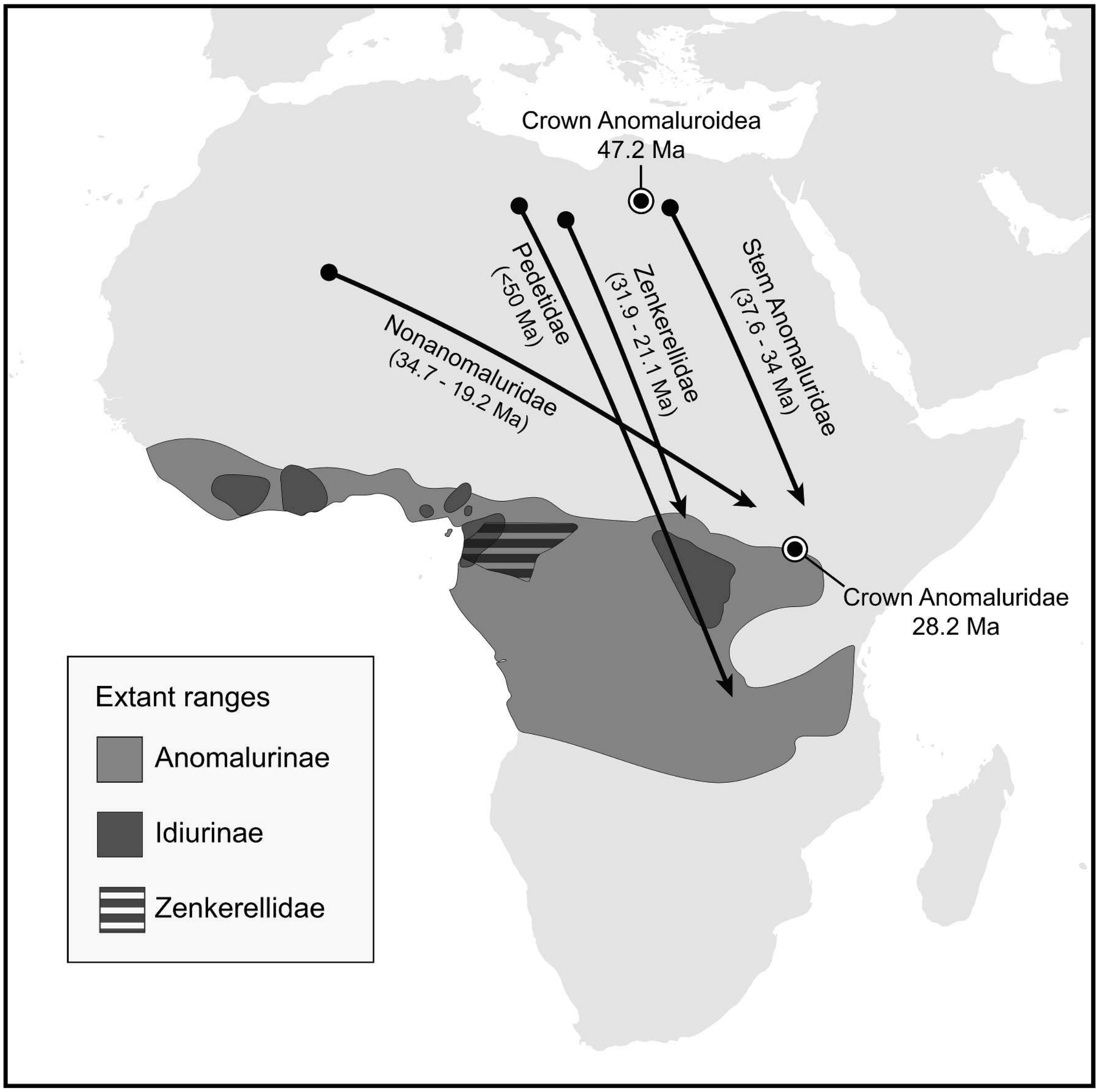

Figure 6. Summary of key nodes and inferred dispersal directions from the Bayesian geocoordinates analysis, showing multiple independent dispersals of anomaluromorph lineages into sub-Saharan Africa.

anomalurid branches leading to crown Anomaluridae) or in the early Oligocene or early Miocene (Nonanomaluridae and Zenkerellidae). The origin of crown Anomaluridae (~28.2 Ma) is placed in eastern Africa, near the border of modern Kenya and Uganda.

Discussion and conclusions

Though the single known specimen of *Eliwourus* only provides information from three lower molar teeth, the comprehensive phylogenetic, phenotypic and biogeographic analyses presented here allow us to place this poorly known taxon into a new scenario for the evolution of African anomaluroids that can be further tested and refined with additional fossil discoveries. *Eliwourus* is identified as the oldest known anomaluroid (and pan-anomalurid) from sub-Saharan Africa and is the closest known fossil relative of crown anomalurids.

In the absence of contradictory evidence from the fossil record, we assume that the ancestral crown anomalurid (i.e. the common ancestor of the extant gliding forms *Anomalurus* and *Idiurus*) had a patagium and was capable of gliding behaviour. We therefore further assume that our age estimates for two nodes – the ancestrally non-gliding crown Anomaluroidea (~46.3 Ma) and the ancestrally gliding crown Anomaluridae (~28.2 Ma) – constrain the temporal window for the evolution of gliding behaviour to a ~19 million-year-long interval that stretches from the middle Eocene through the early Oligocene. The combined results of the BTD and BGC analyses suggest that the earliest splits within Anomaluroidea all occurred in northern Africa, and that *Eliwourus*' origin in eastern Africa can be traced back to at least the earliest Oligocene, following a stem anomalurid dispersal from northeastern Africa that occurred in either the late Eocene or the earliest Oligocene. Our analyses further place the origin of the anomalurid crown group – and therefore gliding behaviour and its requisite morphological adaptations – in eastern Africa only ~1.0–1.5 Ma after the deposition of the *Eliwourus*-bearing Topernawi Formation. Unless anomalurid gliding behaviour evolved very rapidly in this relatively short ~1.0–1.5 Ma window at the terminus of the ~19 Ma-long anomalurid stem lineage, it appears likely that gliding stem anomalurids would have been present in eastern Africa during the time period represented by the Topernawi Formation, and possibly much earlier. Recovery of postcranial remains of *Eliwourus* would likely help to refine our understanding of the pace and timing of the evolution of anomalurid gliding behaviour.

The inclusion of molecular data does not have a strong effect on the estimated time of origin of crown Anomaluroidea; BTD analysis of morphological data alone (results available in OSF repository) place this node at ~46.3 Ma, a difference of only about 1 Ma from the BTD results of the combined molecular-morphological dataset. However, the molecular data have a profound influence on the time of origin of crown Anomaluridae, with an estimate of only ~15.4 Ma based on morphology alone – a difference of ~12.8 Ma from the estimate provided by BTD analysis of the combined molecular-morphological dataset. Available sequence data for anomalurids therefore imply a much greater phylogenetic depth of the anomalurine-idiurine split than could be inferred from dental morphology alone. This result is consistent with the bradytelic pace of evolution of anomalurid dental features through the later Palaeogene and early Miocene that has previously been suggested (Sallam et al. 2010; Marivaux et al. 2017), and which we demonstrate quantitatively here in a novel way (Figure 5). The relatively dramatic transformations of the postcranium that evolved to facilitate anomalurid gliding behaviour evidently occurred with few correlated changes in dental morphology or dietary preferences.

The onset of anomaluroids' dental evolutionary stasis in the middle Eocene roughly coincides with the dispersal of hystricognathous rodents into Afro-Arabia from Asia, based on previously published BTD analyses of the latter clade (Sallam and Seiffert 2016a, 2020; de Vries et al. 2021). Over the subsequent ~20 million years, hystricognaths underwent a significant adaptive radiation in Afro-Arabia and came to dominate the rodent faunas of that landmass (Wood 1968; Jaeger et al. 1985, 2010; Fejfar 1987; Holroyd 1994; Stevens et al. 2006, 2009; Pickford et al. 2008; Rasmussen and Gutierrez 2009; Sallam et al. 2009, 2011; Coster et al. 2010, 2012, 2015; Marivaux et al. 2012, 2014, 2017; Sallam and Seiffert 2016a, 2020; Pickford 2018; Marivaux and Boivin 2019; Al-Ashqar et al. 2021), strongly suggesting that endemic anomaluroids and their zegdoumyid relatives were replaced in the region, at least in terrestrial niches (Seiffert 2012). All extant African hystricognaths are either fully terrestrial (petromurids and thryonomyids) or burrowers (heterocephalids and bathyergids) (e.g. Happold 2013), and at present there is no evidence from the fossil record indicating that any Afro-Arabian hystricognaths ever occupied arboreal niches. Given the null hypothesis that early hystricognaths were terrestrial, one possible explanation for long-term stasis in anomaluroid dental evolution after the middle Eocene is that early competition with terrestrial hystricognaths helped to drive the evolution of anomaluroid arboreality, and that anomalurids and zenkerellids thereby avoided competition with hystricognaths and other Afro-Arabian mammals by entering into relatively narrow arboreal niches in which they could specialise on otherwise unexploited dietary resources. This hypothesis gains support from the discovery of de Vries et al. (2021) that early African hystricognaths rapidly evolved towards the ancestral anomaluroid dental topographic morphospace following their arrival in the middle Eocene, and that anomaluroids were displaced from that morphospace.

Following the inferred dispersal of stem anomalurids into equatorial eastern Africa in the later Eocene, the group disappears from the fossil record of central and northeast Africa. There is no record of Anomaluridae in any of the >100 known mammal-bearing localities of the latest Eocene-early Oligocene Jebel Qatrani Formation of northern Egypt, which together document ~5 million years of geological time and diverse paleoenvironments (Bown and Kraus 1988), nor are they present in coeval sites in Libya (Zallah) (Fejfar 1987; Coster et al. 2012, 2015), where two zenkerellid teeth have been found (Coster et al. 2015). 'Anomaluridae' has been reported in faunal lists from the more southerly early Oligocene Taqah locality in Oman (Thomas et al. 1992), but the specimens on which this occurrence is based have never been described or figured. Given the disappearance of anomalurids in northern Africa by the earliest Oligocene (i.e. post-dating the age of the stem anomalurid-bearing earliest Oligocene Dakhla deposits of Western Sahara), and inferred dispersal into equatorial Africa close to the Eocene–Oligocene boundary, it is reasonable to hypothesise that this apparent local extinction (or latitudinal range contraction) was related to the major climatic changes that were occurring across the planet during that interval (Prothero and Berggren 1992; Zachos et al. 2001; Coxall et al. 2005), and which appear to have impacted Afro-Arabian small mammal faunas (Seiffert 2007, 2012; de Vries et al. 2021).

Extant anomaluroids are not well studied. Naturalistic observations of extant *Zenkerella*, for instance, are still very limited, and almost nothing is known about its behaviour and ecology (Dinets 2017; Adejumo et al. 2020; Da Cunha et al. 2024) despite being the sole living descendant of a lineage that dates back to the early middle Eocene. An important taxonomic implication of anomaluroids' remarkably slow pace of dental evolution since the middle Eocene is a high potential for cryptic species diversity – not only in a fossil record that is dominated by dental remains but also within geographically widespread extant species that are relatively uniform in dental morphological variation but are nevertheless very poorly sampled for confirmatory sequence data. Anomaluroids appear to be an excellent candidate group for exploration of cryptic diversity through both increased field sampling of DNA and museomic approaches (see for instance Fabre et al. 2018).

Acknowledgments

Thanks to M. Borths, J. Kibii, S. Maikweki, F.K. Manthi, P. Mbete, C. Riddle, and J. Yatich for specimen access; to R. Muthoni and T. Gichunge for digitizing specimens from Topernawi; to L. Marivaux and K.C. Beard for casts of anomaluroids from Dakhla and Zallah; to the Turkana Basin Institute for logistical and infrastructure support during fieldwork; and to the many members of the Topernawi Research Project field crews and the Topernawi community. We also thank Michelle Arnal, Laurent Marivaux and an anonymous reviewer for their comments.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

National Science Foundation grants BCS-2124790 to Patricia Princehouse, BCS-2124792 to Natasha Vitek, BCS-1824745 to Dorien de Vries, and BCS-1231288 to Erik Seiffert; Leakey Foundation Research Grant to Dorien de Vries.

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