Features

Recent additions to the fossil record of tenrecs and golden moles

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Tenrecs (Tenrecidae) are a diverse clade of small afrotherians, with slightly over 30 species in eight genera on the island of Madagascar, and three species in two genera distributed in the African tropics, from Liberia in the west to Kenya in the east. Golden moles (Chrysochloridae) are the extant sister clade of tenrecs, and are less ecologically and taxonomically diverse, consisting of just over 20 small, subterranean species throughout subsaharan Africa, most of which are in Southern Africa and few (3 spp.) in central and eastern Africa. Phylogenetic estimates exist for both groups, although more data have been published for tenrecids (e.g., Olson & Goodman 2003; Asher & Hofreiter 2006; Poux et al. 2008; Everson et al. 2016) than chrysochlorids (Bronner 1995; Asher et al. 2010). Unfortunately, the nomenclature for the two clades and the subgroups within each varies among authors. Here, for reasons outlined in Asher & Helgen (2010) and in contrast to some of my esteemed colleagues in the IUCN Afrotheria specialist group, I use Tenrecoidea (McDowell 1958) for the clade consisting of all descendants of the last common ancestor of extant tenrecs and golden moles, Chrysochloridae for the clade of golden moles, and Tenrecidae for the clade of tenrecs, including extant African (*Potamogale* and *Micropotamogale*) and Malagasy species (i.e., Tenrecinae following Asher & Helgen 2010: figs. 1, 2 and pp. 6-7).

Descriptions of chrysochlorid and tenrecid fossils have appeared in the literature sporadically over the past century (Broom 1941, 1948; Butler 1984; Mein & Pickford 2003; Asher & Seiffert 2010) and consist of fragmentary jaws, teeth, skulls, and the occasional skeletal element. Thus far, reports of tenrec fossils are known from the African continent, but no chrysochlorid has been recovered from Madagascar. In contrast to primates (Fleagle 2013), tenrecs do not have an abundant Malagasy subfossil record, although the long-enigmatic Malagasy "aardvark" *Plesiorycteropus* (Macphee 1994) may represent an extinct, large-bodied tenrec (Buckley 2013). Uncontroversial remains of fossil tenrecs and golden moles generally come from Neogene (roughly 23-2.5 million years ago) exposures in South Africa, Namibia, and near Lake Victoria in east Africa. To date, the oldest potential records include those of Gheerbrant (1994) and Seiffert et al. (2007), who described North African dental remains of possibly insectivoran-grade afrotheres from (respectively), the late Paleocene (just over 56 million years ago) and late Eocene (around 33.5 million years ago). Asher & Avery (2010) reported more complete, but much younger, cranioskeletal remains of *Chrysochloris arenosa* and *C. bronneri* from the early Pliocene (around 5 million years ago) of Langebaanweg, South Africa. Another recent Namibian discovery is that of Pickford (2018a), who described and figured a left mandible of a new tenrec, *Promicrogale namibiensis*, with a canine (c), three premolars (p) and three molars (m) from deposits interpreted to represent the early Miocene, just over 20 million years in age, in what is today Elisabethfeld, Namibia.

Until 2015, the fossil record of animals potentially related to golden moles and tenrecs were primarily limited to fragments of Miocene or younger skulls and teeth. This record has improved recently with publications in the *Communications of the Geological Survey of Namibia* by Martin Pickford (2015a, b, c; 2018b). Pickford described fossils from Namibia, including the localities "Black Crow" and "Eocliff", as shown on his map in Pickford 2015c: fig. 2 (available via the link for "volume 16" here:

http://www.mme.gov.na/publications/?designation=gsn), and interpreted to sample (respectively) the Lutetian and Bartonian. Following Cohen et al. (2013), these marine stages are over 41.2 and 37.8 million years old, respectively, making the fossils potentially the oldest yet known for either group. Dental terminology is key to evaluate this material, and relevant cusps are shown for *Setifer setosus*, *Potamogale velox*, and *Didelphis virginiana* in Fig. 1 based on homologies established by Butler (1937) and Patterson (1956; for further details and justification see Asher & Sanchez-Villagra, 2005).

Black Crow

Pickford (2015a) named an isolated lower molar from this Namibian locality *Diamantochloris*, which exhibits distinctive features such as a mesiodistally compressed trigonid and large talonid basin. The talonid resembles that of the North African Oligocene fossil *Eochrysochloris* (Seiffert et al. 2007: fig. 5), and---despite their names---neither *Eochrysochloris* nor *Diamantochloris* have chrysochlorid-like molars. The fossil in Pickford (2015a) was complemented by a later description (Pickford 2018b) of a diminutive right mandible with p3-m2, plus upper cheek teeth tentatively associated based on size. Some extant chrysochlorids, such as *Chrysochloris asiatica*, lack a talonid basin altogether; others (e.g., *Amblysomus hottentotus* and the fossil *Prochrysochloris*) show a small heel with a single cusp and no basin, a morphology also evident in Pickford's photographs of *Namachloris* (Pickford 2015b: fig. 26). It is possible to have a protocone on the upper molars with an un- or minimally-basined talonid heel (e.g., *Amblysomus*, *Potamogale*, and *Solenodon*; see Asher & Sánchez-Villagra 2005 and *Namachloris* Pickford 2015b: figs. 23-25). However, the talonid basin on the Black Crow molars figured by Pickford (2015a: fig. 7; 2018b: figs. 1-2) is, to my knowledge, larger than that seen in any living or fossil chrysochlorid, and also appears larger than the talonid basin illustrated for at least some of the Namibian fossil tenrecs (e.g., *Namagale*, Pickford 2015c: fig. 20).

The basined talonid of the lower molar, and correspondingly small ectoflexid just buccal (or lateral, on the cheek side) to it, are informative regarding the shape of the occluding upper molars of *Diamantochloris*. The uppers would have exhibited not only a prominent protocone (as do some extant chrysochlorids) to occlude with the talonid, but also a metacone and unenlarged paracone, in contrast to the anatomically "zalambdodont" (in reference to the triangular shape of the Greek letter lambda) upper molars of tenrecs and golden moles, in which the metacone is small or absent and the paracone large (see Fig. 1 and Asher & Sánchez-Villagra 2005). Two isolated upper molars assigned by Pickford (2018b: fig. 5) to *Diamantochloris* do in fact show prominent metacones; these are lingual to a large stylar region with a projecting parastyle and without any hint of a hypocone. A maxilla fragment containing a P4 and broken M1 assigned to *Diamantochloris* show conule-like emarginations (Pickford 2018b: fig. 4) on the pre- and post-protocrista buccal to its M1 protocone, a morphology reminiscent of the North African *Widanelfarasia* (Seiffert et al. 2007: fig. 2B) and *Dilambdogale* (Seiffert 2010: fig. 6). The stylar region of *Diamantochloris* is larger than that of, say, the much older North African fossil *Todralestes* (Gheerbrant et al. 2016: fig. 7) or indeed another todralestid also found at Black Crow (*Namalestes* Morales & Pickford 2018: fig. 4). Todralestids also have prominent metacones and large, basined talonids, and Morales & Pickford (2018:78) used possession of a "well-developed metacone" to exclude *Namalestes* from "the basal Tenrecoidea". While some ancestral, insectivoran-grade afrothere likely had prominent metacones, I agree with Morales & Pickford (2018) regarding *Namalestes*. The teeth of *Diamantochloris* resemble those of African insectivoran-grade mammals of uncertain affinity, such as *Widanelfarasia* (Seiffert et al. 2007), more than those of chrysochlorids. The phylogenetic analysis of Seiffert (2010: fig. 12) weakly supports *Todralestes*, *Dilambdogale*, and *Widanelfarasia* as successively distant sister-taxa to a tenrec-golden mole clade. *Diamantochloris* shows dental morphology consistent with a similar phylogenetic placement, outside of the crown clade of living tenrecs and golden moles.

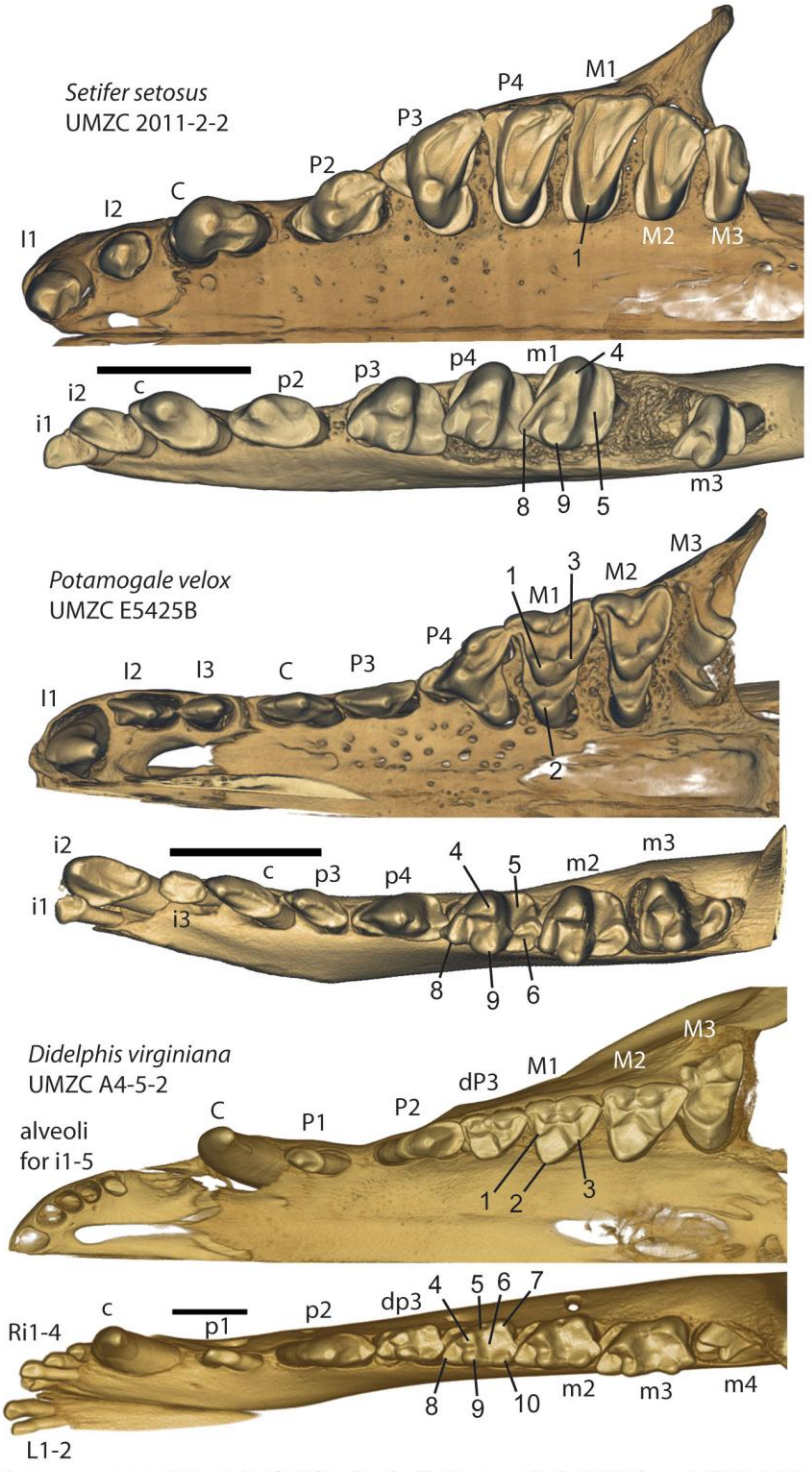

Fig. 1. Dental cusp nomenclature in *Setifer* (top), *Potamogale* (middle) and *Didelphis* (bottom) following Butler (1937), Patterson (1956) and Asher & Sanchez-Villagra (2005). Upper & lower case I, C, P, and M indicate (respectively) upper and lower incisors, canines, premolars, and molars. “d” indicates a deciduous tooth. Individual cusps are 1 = paracone, 2 = protocone, 3 = metacone, 4 = protoconid, 5 = ectoflexid, 6 = talonid basin, 7 = hypoconid, 8 = paraconid, 9 = metaconid, 10 = entoconid. Scale bars = 5mm. UMZC = University Museum of Zoology, Cambridge. Images derived from CT scans taken at the Cambridge Biotomography Centre (www.cbc.zoo.cam.ac.uk/) and reconstructed in 3D using Drishti 2.6.4 (Limaye 2012).

A feature of the *Diamantochloris* mandible that would greatly strengthen its identification as a chrysochlorid is Pickford's interpretation that it shows an articulation of the lower jaw (or dentary) angular process with the hyoid bone. Such a feature is unique to golden moles (Bronner 1991). Based on the p3-m2 dentary fragment, which ends posteriorly at the exposed m2 root and lacks any remnant of the condyle or jaw angle, Pickford (2018b 61): writes "the bend in the mandible of *Diamantochloris* at the junction between the premolar and molar rows, indicates that this genus may have been endowed with a hyoid-mandible articulation. However, more completely preserved fossils are required to confirm or falsify this inference." There appears to be some torsion of the alveolar row in the mandibular fragment of *Diamantochloris*, such that the posterior teeth appear to occlude in a slightly more lingual direction than the anterior teeth (Pickford 2018b: fig. 7). However, as Pickford notes, this is by itself not sufficient to signify a dentary-hyoid articulation and further material is needed to confirm this intriguing possibility.

Eocliff chrysochlorids

Compared to the Black Crow fossils, fossils from Eocliff (Pickford 2015b, c) are more complete and diagnostic. Pickford (2015b) named *Namachloris arenatans* based on multiple individuals with associated skulls, jaws, teeth, and postcranial elements. Many of these elements show unique, shared characters with extant golden moles, such as reduction of the metacone, talonid, and the coronoid process of the dentary, distinct anterolateral processes of the premaxilla, prominent nuchal crests and domed occiput, elongate medial epicondyle of the humerus and metacromion of the scapula, compressed and comma-shaped first rib, keeled manubrium sterni, among other features. In my view, Pickford (2015b) has made a convincing case that *Namachloris* is the anatomically best preserved fossil species of golden mole yet known.

The species epithet for this taxon, "arenatans", is based on the interpretation that *Namachloris* was "fully adapted to sand swimming" as documented in the extant *Eremitalpa granti* (Fielden et al. 1990). *Eremitalpa* differs from most other chrysochlorid genera in its peculiar locomotor regime in which its foraging tunnels collapse behind it as it moves in its sandy burrowing medium (Gasc et al. 1986; Narins et al. 1997). Some populations of the Western Cape mole (*Chrysochloris asiatica*) occur in arid and sandy substrates of the west coast and Namaqualand of South Africa, but most populations are present in more mesic areas of the Western Cape. In general, chrysochlorids are known from regions with much more rainfall than the Namib desert of northwestern South Africa and southern Namibia, such as *Amblysomus hottentotus,* widespread throughout the Eastern Cape and Kwazulu-Natal provinces of South Africa. Several, much more rare chrysochlorid species, also exist in areas throughout South Africa and other countries with substantially more rainfall than the Namib desert (Bronner & Jenkins 2005; chapters by Bronner et al. in Child et al. 2016).

Most golden moles are not "sand-swimmers" but have activity patterns highly dependent on the frequency of rains. They tend to dig both transient, superficial burrows and more permanent, deep burrows with seasonally durable nesting chambers (Bronner 1995; Hickmann 1990). Asher & Avery (2010) noted that the humeral dimensions of *Eremitalpa* are unusual for chrysochlorids of its body size and are approximated only by the much larger *Chrysospalax*, a taxon which, so far as is known, generally forages on the surface (Maddock & Hickman 1985; Skinner & Smithers 1990). The humeral distal margin (including the medial epicondyle) in *Eremitalpa* and *Chrysospalax* is large compared to non-chrysochlorids, but for a golden mole it is narrow. Relative to the overall length of the humerus, *Eremitalpa* has a mean length:distal width ratio near 1.4, similar to the ratio in the extinct *Chrysochloris arenosa* but in contrast to extant species such as *C. asiatica* and similarly-sized *Amblysomus*, *Neamblysomus*, and *Chlorotalpa*. As a proportion of humeral length, the medial epicondyle in most golden moles is significantly longer than in *Eremitalpa,* leading to a mean length:distal width ratio close to 1.0, with no overlap with either *Eremitalpa* or *C. arenosa* (Asher & Avery 2010: fig. 2). Asher &

Avery (2010) interpreted the smaller epicondyle of *Eremitalpa* and the extinct *C. arenosa* as evidence for a smaller muscle mass of the extrinsic digital flexors, muscles relevant to the dorsoventral (or parasagittal) digging motion of this and other subterranean mammals (Rose & Emry 1983). Relative to the arm-movements that typify parasagittal digging in the "sandy loam" and "alluvium" of most chrysochlorid habitats, the "pure, loose dune sand" (Skinner & Smithers 1990:24) of *Eremitalpa* habitats would presumably entail less recruitment of extrinsic digital flexors while digging; this may also be the case for the larger, surface-foraging *Chrysospalax*. Extrinsic digital flexors are obviously still important for locomotion, but unlike most other chrysochlorid species, *Eremitalpa* is not known to typically construct permanent burrows and may not use these flexor muscles as much as other chrysochlorids. Complicating this assessment is the fact that one of the rarest chrysochlorid taxa, *Cryptochloris wintoni* (and possibly *C. zyli*), occurs sympatrically with *Eremitalpa* but retains the low humeral length:width ratio of extant golden moles such as *Chrysochloris* and *Amblysomus* (Asher & Avery 2010: fig. 6). As of this writing there is no explanation for this difference, for example if *Cryptochloris* and *Eremitalpa* occupy distinct micro-habitats in the areas where they co-occur. Clearly more data on the habitat of *C. wintoni* would be needed to determine if and how the two species differ in locomotor strategy.

Pickford (2015b:182) writes that the "humerus of *Namachloris arenatans* is almost as broad distally as it is long due to the extreme elongation of the medial epicondyle". This would suggest a ratio close to one, as seen in non-sand-swimming chrysochlorids and unlike the atypical, sand-swimming habitat of *Eremitalpa*. However, photographs of the *Namachloris* humerus (Pickford 2015b: fig. 33) suggest a length of about 14mm and a distal margin (from supinator crest laterally to medial tip of the epicondyle) of about 8mm. This humeral length is slightly larger than the average in *Amblysomus hottentotus* (Asher & Avery 2010: table 1) but the length:distal width ratio of ca. 14:8 (= 1.75) is even larger than that seen in *Eremitalpa* (ca. 1.4; Asher & Avery 2010:fig. 2) and would be consistent with a "sand-swimming" locomotor capacity. Such measurements taken from 2D photographs undoubtedly have error, and whether these photos, or the description of Pickford (2015b:182) of the *Namachloris* humerus as "almost as broad distally as it is long", are accurate must await further analysis.

Another recent paper based on these Namibian chrysochlorid remains is Mason et al. (2017), who compare the auditory anatomy of *Namachloris* with that of extant chrysochlorids. Using microCT scans of two of the Eocliff skulls (GSN Na 1 and 2), they reveal a number of important and diagnostic features. Mason et al. suggest that *Namachloris* had a highly coiled cochlea, likely between 3 to 3.5 turns, resembling the coiling of around 1100° seen in extant chrysochlorids (Crumpton et al. 2015). They also note that the mallear morphology of *Namachloris* lacks the hypertrophy seen in several extant species, such as *Eremitalpa* and *Chrysochloris* and, proportionally, is more similar to the non-hypertrophied malleus of *Amblysomus hottentotus*. These new data further illuminate the mosaic nature of the chrysochlorid middle ear, showing for example that increased coiling (three turns or more in all species known so far) likely evolved prior to mallear hypertrophy (not present in *Namachloris* and some living species), consistent with previous studies (e.g., Crumpton et al. 2015) and amenable to further testing via phylogenetic analysis.

Mason et al. (2017) also comment on one of the more controversial aspects of these fossils: their age. Pickford et al. (2013: table 2) list K-Ar radiometric dates of 40-45 million years based on samples of "phonolite cobbles from the overlying Gemsboktal Conglomerate", supporting their interpretation of a Lutetian age (41.2-47.8 following Cohen et al. 2013) for the "Black Crow" locality which yielded the right lower molar discussed above. The more complete and diagnostic fossils for both tenrecids and chrysochlorids are from the younger locality, Eocliff. Biochronologically, the fauna of Eocliff does not appear to be unambiguously Eocene. Mason et al. (2017) note the radiometric data from Pickford et al. (2008, 2013) in support of a Lutetian age, but also acknowledge some contradictory evidence from biostratigraphy. For example, they note Sallam & Seiffert's (2016) suggestion that a locality with anthracotheres (a group which has no African record at all prior to ca. 35Ma) could be, at the oldest, near the Eocene-Oligocene boundary in age. Coster et al. (2012) similarly argued for a post-Eocene age for these Namibian limestone deposits based on the rodent fauna. Marivaux et al. (2014) went further, suggesting a Miocene age. An Eocliff fauna including hyracoids such as "*Rupestrohyrax lacustris*" (a possible synonym of *Titanohyrax angustidens*) and rodents such as *Metaphiomys* and *Neophiomys* ("*Phiomys aff. phiomyoides*" in Pickford et al., 2014) have first appearance dates after the Eocene-Oligocene boundary and suggest that the Eocliff tenrecs and golden moles are post-Eocene. Even if it is a late Paleogene or Neogene fossil, *Namachloris* still comprises the anatomically most complete record of a pre-Pliocene golden mole.

Eocliff tenrecids

Pickford (2015c) described three genera of tenrecs from Eocliff: *Namagale*, *Sperrgale*, and *Arenagale*. His taxonomy implies a close relationship of *Namagale* to potamogalines and of *Sperrgale* and *Arenagale* to tenrecines (i.e., Malagasy tenrecs following the taxonomy of Asher & Helgen 2010). He assigns numerous, isolated jaw and cranial elements to each taxon. Postcranially, he assigns two isolated distal humeri to *Namagale* (Pickford 2015c: table 1), tarsal elements, fore- and hindlimb elements, and pelvic elements to *Sperrgale* (2015c: table 3), and tarsal elements to *Arenagale* (2015c: table 6). As with the remains of *Namachloris*, these fossil tenrecids were found in dense concentrations of many individuals, perhaps as a result of predator regurgitates and/or scats, some of which "contain one or two skeletons of small mammals" (Pickford 2015c: 124). It is not clear which tenrecid elements are associated from any single pellet, or which elements were associated based on size and/or relative abundance. In any event, given the associations presented by Pickford (2015c) and with the qualifications noted above regarding the age of Eocliff, these fossils represent the anatomically most complete, pre-Pliocene fossil tenrecs yet known.

The holotype of *Namagale grandis* (Pickford 2015c: fig. 6) shows molars with a large stylar shelf and an M3 with an elongate parastyle but no metastyle. The M2 on this specimen shows both paracone and a small metacone, situated close to each other, and a protocone at the tooth's lingual margin. Lower molars assigned to *Namagale* (Pickford 2015c: figs. 15-16) show a small, teardrop-shaped talonid basin. Such features are reminiscent of the unworn dental morphology of extant *Potamogale*. Malagasy tenrecids have a reduced/absent metacone and talonid basin, and are thus relatively more zalambdodont.

Fossils assigned to the diminutive *Sperrgale* similarly possess upper molars with prominent metacones and paracones, a lingual protocone, and the distinctive M2-M3 stylar morphology noted above for *Namagale*. Indeed, the metacone in *Sperrgale* appears to be larger than that of *Namagale* and unlike anything seen among Malagasy tenrecs; it also has a small, teardrop-shaped talonid basin, as in the extant *Potamogale* (Fig. 1). The third Eocliff tenrecid, *Arenagale*, also shows a metacone (Pickford 2015c: fig. 33) which, among the three Eocliff tenrecids, appears to contribute the least to the stylar shelf and thus exhibit some similarity to tenrecines rather than potamogalines. Lower molars have not yet been figured or described for *Arenagale* so it is unclear if this taxon had basined talonids. All of the Eocliff fossils assigned to tenrecs by Pickford (2015c) exhibit a cleft between the para- and metastyles on at least some of their cheek teeth (character #79 in Asher et al. 2010), resembling a number of insectivoran-grade afrotheres and other zalambdodont mammals (see Asher 1999).

Based on the combined morphology-DNA dataset and strict consensus of eight MP trees shown in Asher et al. (2010), a number of hard-tissue characters optimize as shared-derived characters for tenrecids as a whole (relative to chrysochlorids as their sister taxon, and *Elephantulus* and *Procavia* as successively distant outgroups to the tenrecoid clade), and for potamogalines to the exclusion of other tenrecids. This does not mean that these characters lack homoplasy or do not occur in other groups, only that they optimize as shared derived of varying consistency on optimal cladograms in Asher et al. (2010). For example, fully grown tenrecids lack a major contribution of the entotympanic to the auditory bulla (character #6, state 0, numbered according to Asher et al. 2010), have a ring-like ectotympanic (#10, 0), a squamosal contribution to the mastoid tubercle (#24, 1), a maxilla that extends posterior to the toothrow on the ventrum of the pterygoid (#46, 1), and a reduced zygomatic arch (#51, 1). Potamogalines show a closed tubal canal (character #8, state 1), a semiphaneric ectotympanic (#9, 1), medially positioned foramen for the ascending pharyngeal artery (#18, 1), a fenestrate basioccipital (#22, 1), a frontal bone anteroposteriorly shorter than the parietal (#43, 2), reduction of the lacrimal foramen (#55, 0), a reduced scapular metacromion and acromion (#108 and #110, 1), lack a humeral epicondylar foramen (#118, 1), and show an iliopectineal tubercle (#133, 1).

Most of these features are currently either unknown or undocumented in the Eocliff tenrecs, as basicrania, complete skulls, and most of the postcranial skeleton are not yet published. However, there are a few characters that could help to test the assertion that *Sperrgale* and *Arenagale* are more closely related to tenrecines than potamogalines, and that *Namagale* is related to potamogalines. As noted above, extant potamogalines have reduced lacrimal foramina, lack an entepicondylar foramen on their distal humerus, and show an iliopectineal tubercle on each os coxae. Pickford (2015c: 127) notes that *Namagale* has a lacrimal foramen (unlike potamogalines); humeri and pelvic elements are listed for *Sperrgale*, and humeri for *Namagale*, but the requisite anatomical details have not yet been figured or described.

Phylogeny is not typology, and a patent lacrimal foramen (for example) would not disqualify *Namagale* as a close relative to the two extant potamogaline genera, *Micropotamogale* and *Potamogale*, as implied by the taxonomy of Pickford (2015c). Similarly, presence of upper molar metacones would not necessarily disqualify todralestids (or *Diamantochloris*) from a close evolutionary relationship to tenrecids or chrysochlorids, as noted above. Ultimately, the assignment of a given taxon to this or that clade will require a phylogenetic analysis. I agree with Pickford (2015b, c) that the fossils from Eocliff represent tenrecids and chrysochlorids, two clades of insectivoran-grade afrotheres that have long suffered from a limited fossil record. Hopefully, the Eocliff fossils are amenable to further study, including a quantitative phylogenetic analysis. MicroCT scans of the kind already published by Mason et al. (2017) represent the kind of detailed anatomical investigation that can enable future phylogenetic analyses. Particularly with more efforts to establish their phylogenetic affinities, these fossils will prove to be among the most important and anatomically well-known to shed light on the still enigmatic evolutionary history of endemic African mammals.

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