Running head: CRANIAL MORPHOLOGICAL DISPARITY IN TENRECS

Quantifying cranial morphological disparity in tenrecs (Afrosoricida, Tenrecidae) with implications for their designation as an adaptive radiation

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Keywords: disparity, morphology, geometric morphometrics, tenrecs, golden moles, adaptive radiation

Abstract

Understanding why some clades are more phenotypically diverse than others remains a central challenge in evolutionary biology. This issue is particularly relevant when we consider whether a group represents an adaptive radiation. However, we must be able to identify exceptionally diverse clades before we can determine the selective pressures which led to the evolution of their variety. Tenrecs (Afrosoricida, Tenrecidae) are a family of small mammals and are often cited as an example of a phenotypically diverse, adaptively radiated group. However, this assumption has not been tested. Here we use geometric morphometric analyses of cranial and mandible shape to test whether tenrecs show exceptional morphological disparity. We find that tenrecs are no more morphologically diverse than their sister taxa, the golden moles (Afrosoricida, Chrysochloridae), casting doubt over whether tenrecs should be considered to be an exceptionally diverse group.

Introduction

Phenotypically diverse groups have long attracted the attention of evolutionary biologists, particularly when it comes to the study of adaptive radiations - 'evolutionary divergence of members of a single phylogenetic lineage into a variety of different adaptive forms' (Futuyma 1998, cited by Losos, 2010).

There are many famous examples of adaptive radiations including Darwin's finches, Caribbean *Anolis* lizards and cichlid fish (Gavrilets & Losos, 2009). However, there has been considerable debate about how adaptive radiations should be defined (Glor, 2010; Losos & Mahler, 2010) based on the relative importance of speciation rates, species richness and morphological diversity. One particular issue is whether it is even meaningful to distinguish a specific group of species as an adaptive radiation or not based on arbitrary statistical thresholds of variety (Olson & Arroyo-Santos, 2009).

Despite the controversies and disagreements, there does seem to be a consensus that high morphological diversity is an important criterion for identifying adaptive radiations (Losos & Mahler, 2010; Olson & Arroyo-Santos, 2009). One way to test whether a group shows high morphological diversity is through sister taxa comparisons. For example, Losos and Miles (2002) used this approach to demonstrate exceptional diversity in some but not all clades of iguanid lizards. This is a good way of assessing the relative diversity of a clade but of course there is also a danger that a focal clade's diversity will be judged to be exceptional just because it is more variable than an exceptionally non-diverse sister taxon (Losos & Miles, 2002).

Here we use sister-taxa comparisons to test whether tenrecs (Afrosoricida, Tenrecidae) exhibit the high levels of phenotypic diversity that are expected of an adaptively radiated clade.

The tenrec family contains 34 species, 31 of which are endemic to Madagascar (Olson, 2013). Tenrecs are often cited as an example of an adaptively radiated family which exhibits exceptional morphological diversity (Soarimalala & Goodman, 2011; Olson & Goodman, 2003). Body sizes of extant tenrecs span three orders of magnitude (2.5 to $>$ 2,000g) which is a greater range than all other Families, and most Orders, of living mammals (Olson & Goodman, 2003). Within this vast size range there are tenrecs which convergently resemble shrews (*Microgale* tenrecs), moles (*Oryzorictes* tenrecs) and hedgehogs (*Echinops* and *Setifer* tenrecs) (Eisenberg & Gould, 1969) even though they are not closely related to these species (Stanhope et al., 1998).

However, evidence for claim that tenrecs are exceptionally diverse has not been tested. Here we present the first quantitative investigation of morphological diversity in tenrecs, and how this compares to their closest relatives, the golden moles (Afrosoricida, Chryscholoridae). We apply two dimensional geometric morphometric techniques (Rohlf & Marcus, 1993; Adams et al., 2013) to create morphospace plots that depict cranial and mandible morphological variation in the two Families. We use these morphospaces to compare the relative morphological disparity (Foote, 1997; Wills et al., 1994; Erwin, 2007) within each Family.

Our results show an overall trend for higher morphological diversity in tenrec crania compared to those of golden moles. However, these differences are not statistically significant. These findings indicate that, with regards to cranial shape, tenrecs are no more morphologically diverse than their closest relatives.

In contrast, we found significantly greater morphological disparity in golden mole mandibles compared to tenrecs. These findings cast doubt over whether the apparent phenotypic diversity within tenrecs should be considered to be truly exceptional.

Materials and Methods

Morphological data collection

One of us (SF) photographed cranial specimens of tenrecs and golden moles at the Natural History Museum London (BMNH), the Smithsonian Institute Natural History Museum (SI), the American Museum of Natural History (AMNH), Harvard's Museum of Comparative Zoology (MCZ) and the Field Museum of Natural History, Chicago (FMNH). We photographed the specimens with a Canon EOS 650D camera fitted with an EF 100mm f/2.8 Macro USM lens using a standardised procedure to minimise potential error (see supplementary material for details).

We collected pictures of the skulls in dorsal, ventral and lateral views (right side of the skull) and of the outer (buccal) side of the right mandibles. A full list of museum accession numbers and details on how to access the images can be found in the supplementary material.

In total we collected pictures from 182 skulls in dorsal view (148 tenrecs and 34 golden moles), 173 skulls in ventral view (141 tenrecs and 32 golden moles), 171 skulls in lateral view (140 tenrecs and 31 golden moles) and 182 mandibles in lateral view (147 tenrecs and 35 golden moles), representing 31 species of tenrec (out of the total 34 in the family) and 12 species of golden moles (out of a total of 21 in the family (Asher et al., 2010)). We used the taxonomy of Wilson and Reeder (2005) supplemented with more recent sources (IUCN, 2012; Olson, 2013) to identify our specimens.

We used a combination of both landmarks (type 2 and type 3, (Zelditch et al., 2012)) and semilandmarks to characterise the shapes of our specimens. Figure 1 shows our landmarks (points) and semilandmarks (outline curves) for the skulls in dorsal and ventral views and figure 2 shows the points and curves we used for lateral views of skulls and mandibles. Corresponding definitions of each of the landmarks can be found in the supplementary material.

We digitised all landmarks and semilandmarks in tpsDIG, version 2.17 (Rohlf, 2013). We re-sampled the outlines to the minimum number of evenly spaced semilandmark points required to represent each outline accurately (MacLeod, 2013, details in supplementary material). We used TPSUtil (Rohlf, 2012) to create sliders files (Zelditch et al., 2012) to define which points were semilandmarks. We conducted all subsequent analyses in R version 3.0.2 (R Core Team, 2014) within the geomorph package (Adams et al., 2013). We used the gpagen function to run a general Procrustes alignment (Rohlf & Marcus, 1993) of the landmark coordinates while sliding the semilandmarks by minimising Procrustes distance (Bookstein, 1997). We used these Procrustes-aligned coordinates of all species to calculate average shape values for each species (n = 43) which we then used for a principal components (PC) analysis with the plotTangentSpace function (Adams et al., 2013).

Disparity calculations

We calculated morphological disparity separately for golden moles and tenrecs in each of the morphological datasets. We used the PC axes which accounted for 95% of the cumulative variation to calculate four disparity metrics; 1) the sum of the range, 2) the product of the range, 3) the sum of the variance and 4) the product of the variance of morphospace occupied by each Family (Brusatte et al., 2008; Foth et al., 2012; Ruta et al., 2013).

We used two approaches to test whether tenrecs have significantly different morphologies compared to golden moles. First we compared morphospace occupation between the two groups with non parametric MANOVAs (Anderson, 2001) to test whether tenrecs and golden moles occupy significantly different areas of morphospace (e.g Serb et al., 2011; Ruta et al., 2013).

Secondly, we tested whether tenrecs have significantly higher or lower disparity than golden moles. If the two Families have equal disparity then the designation of each species as being either a tenrec or golden mole should not make any difference to our calculations. Therefore we used pairwise permutation tests to assess whether our data differed from this null hypothesis. We assigned Family identities at random to each specimen and calculated the differences in disparity for these new Family groupings. We repeated these permutations 1000 times to generate a null distribution of the expected differences in Family disparity. We compared our observed (true) measures of the differences in disparity between tenrecs and golden moles to these permuted distributions to test whether the families had significantly different levels of disparity compared to the null hypothesis.

The majority of tenrec species (19 out of 31 in our dataset) are members of the *Microgale* (shrew-like) Genus which is notable for its relatively low phenotypic diversity (Soarimalala & Goodman, 2011; Jenkins, 2003). The strong similarities among these species may mask signals of higher disparity among other tenrecs. Therefore we repeated our Family-level comparisons of disparity excluding the *Microgale* species so that we could compare disparity within the remaining 12 tenrec species to disparity within the 12 species of golden moles.

Results

Morphological disparity in tenrecs and golden moles

Figure 3 depicts the morphospace plots derived from our principal components analyses of average Procrustes-superimposed shape coordinates for each species in our skull and mandible data respectively. We used the principal components axes which accounted for 95% of the cumulative variation (number of axes: n = 7 (dorsal), n = 8 (ventral), n = 8 (lateral) and n = 12 (mandibles)) to calculate the disparity of each Family.

Tenrecs and golden moles clearly have very different cranial and mandible morphologies: in each analysis, the families occupy significantly different areas of morphospace (npMANOVA, table 3). Our comparisons of disparity within each Family yielded different trends for skulls compared to mandibles. In our analyses of the three different views of the skulls, there is an overall trend for tenrecs to have higher disparity than golden moles. However, none of these differences are statistically significant (table 1).

There is a less clear pattern from our analysis of disparity in mandibles. Three of our four metrics indicate that golden moles have significantly higher disparity in the shape of their mandibles than tenrecs (table 1) although one metric (sum of ranges) indicated the opposite result.

The three curves at the back of the mandibles (figure 2) place a particular emphasis on shape variation in the posterior of the bone; the ramus, coronoid, condylar and angular processes. Therefore, higher disparity in golden mole mandibles compared to tenrecs could be driven by greater morphological variation in these structures. To test this idea, we repeated our morphometric analyses of the mandibles with a reduced dataset of points; just the seven landmark points and one single curve at the base of the jaw between landmarks 1 and 7 (figure 2). When we compared disparity with this reduced data set we found that golden moles no longer had significantly higher disparity than tenrecs (table 1).

Morphological disparity in non-*Microgale* tenrecs and golden moles

We repeated our disparity comparisons with a subset of the tenrec specimens to remove the large and phenotypically similar *Microgale* tenrec Genus. In this case we found that tenrecs have significantly higher disparity than golden moles when the skulls are analysed in lateral view (table 2). However, none of the other comparisons in any of the analyses were significant.

Discussion

Our analyses are the first quantitative investigation of morphological disparity in tenrecs. We show that tenrecs' cranial morphologies are no more diverse than their closest relatives and therefore phenotypic variety in tenrecs is perhaps not as exceptional as it first appears.

One apparent anomaly in our results is that we found opposite patterns of disparity among tenrecs and golden moles in the analyses of skulls and mandibles.

When we compared the diversity of skull shapes in the two Families, we found a trend towards higher disparity in tenrecs compared to golden moles but none of these differences were significant (table 1). Even when we removed the phenotypically similar *Microgale* Genus, tenrecs were still no more diverse than golden moles in most of the analyses of their skull shapes (table 2).

In contrast to these patterns from the skull analyses, two of our disparity metrics indicate that golden moles have more disparate mandible shapes than tenrecs (table 1). We recognised that our landmarks and curves for the mandibles focus particular attention on the ascending ramus (condyloid, condylar and angular processes, figure 2). Therefore we deleted the three semilandmark curves around these structures and repeated our disparity calculations. In this case we found no significant difference in disparity between the two Families (table 1). Therefore, our results seem to indicate that golden moles have greater morphological variation in the posterior structures of their mandibles compared to tenrecs.

Given that these posterior structures act as muscle attachment and articulation sites for connections with the upper jaw one might expect that golden moles with highly disparate posterior mandible morphologies should also show high variability in the corresponding mandible articulation areas of the skull. However, we could not locate reliable, homologous points accurately on those areas of the skull pictures in lateral view. Instead, our landmarks and semilandmark curves for the skulls in lateral view focus attention on morphological variation in the dentition and the overall shape of the top and back of the skulls (figure 2). This may explain why golden mole skulls in lateral view do not show the same pattern of higher disparity compared to tenrecs that we see in our analyses of the mandibles. However, further investigation is required to identify possible reasons why golden moles appear to show such variation in the posterior structure of their mandibles.

We used variation in skull and mandible shapes as proxy measures for overall morphological diversity within the two Families. Many other studies also use skulls to study phenotypic variation within species (Blagojević & Milošević-Zlatanović, 2011; Bornholdt et al., 2008), to delineate species boundaries within a clade (e.g. Panchetti et al., 2008) or for cross-taxonomic comparative studies of phenotypic (dis)similarities (e.g. Ruta et al., 2013; Goswami et al., 2011; Wroe & Milne, 2007).

However, studies of morphological disparity are inevitably constrained to measure diversity within specific traits rather than overall phenotypes (Roy & Foote, 1997). Disparity calculations based on skull shape can yield similar results compared to analyses of whole-skeleton discrete characters and limb proportion data sets (Foth et al., 2012). Yet it is still possible that comparing disparity in tenrecs and golden moles using non-cranial morphological measures could produce different results. For example, tenrecs inhabit a wide variety of ecological niches and habitats including terrestrial, arboreal, semi-aquatic and semi-fossorial environments (Soarimalala & Goodman, 2011). In contrast, although golden moles occupy a wide altitudinal, climatic and vegetational spectrum of habitats (Bronner, 1995), they are are all fossorial species which, superficially at least, appear to be less functionally diverse than tenrecs. Therefore, comparing the disparity of limb morphologies within the two Families could indicate that tenrecs have more morphologically diverse limbs than golden moles.

Evidence of exceptional morphological diversity is one criterion for designating a clade as an adaptive radiation (Losos & Mahler, 2010). Our analyses are the first measures of morphological diversity within tenrecs, a group which is commonly cited as an example of an adaptive radiation (Olson, 2013). We found that tenrecs are no more morphologically diverse than their their closest relatives and therefore, within our tests, do not appear to be exceptionally diverse.

The evolution of cranial shape (both upper skull and mandible), particularly dental morphology, has obvious correlations with dietary specialisations and occupation of specific ecological niches (e.g. Wroe & Milne, 2007). Considering the wide ecological diversity of the tenrec Family; semi-fossorial, arboreal, terrestrial and semi-aquatic (Soarimalala & Goodman, 2011), we think that it is reasonable to expect that this variety should be reflected in skull morphology. However, we have not included any measures of the 'adaptiveness' of cranial shape in our analyses and therefore our analyses should not be considered to be an explicit test of whether or not tenrecs are an adaptive radiation (Losos &

Mahler, 2010). Instead we have made the first step towards understanding the apparent phenotypic diversity within tenrecs within a quantitative framework. Future work should focus on explicit measures of the 'adaptiveness' and functional importance of tenrec cranial and post-cranial morphologies to understand the significance of morphological diversity within the Family (e.g. Mahler et al., 2010). However, we also recognise that strict, statistically based categorisations of clades as being adaptive radiations or not is not necessarily biologically meaningful or helpful when it comes to trying to understand patterns of phenotypic diversity (Olson & Arroyo-Santos, 2009).

We have presented the first quantitative study which tests the common claim that tenrecs are an exceptionally diverse group (Olson, 2013; Soarimalala & Goodman, 2011; Eisenberg & Gould, 1969). Focusing on cranial diversity is only one aspect of morphological variation and further analyses are required to test whether other morphological traits yield similar patterns. However, our results provide a clear indication that phenotypic variety within tenrecs is perhaps not as exceptional as it first seems.

Acknowledgements

We thank François Gould, Dean Adams, David Polly, Gary Bronner, Steve Brusatte, Steve Wang, Luke Harmon, Thomas Guillerme and the members of NERD club for insightful discussions and the museum staff and curators for their support and access to collections. Funding was provided by an Irish Research Council EMBARK Initiative Postgraduate Scholarship

(SF) and the European Commission CORDIS Seventh Framework Programme (FP7) Marie Curie CIG grant. Proposal number: 321696 (NC)

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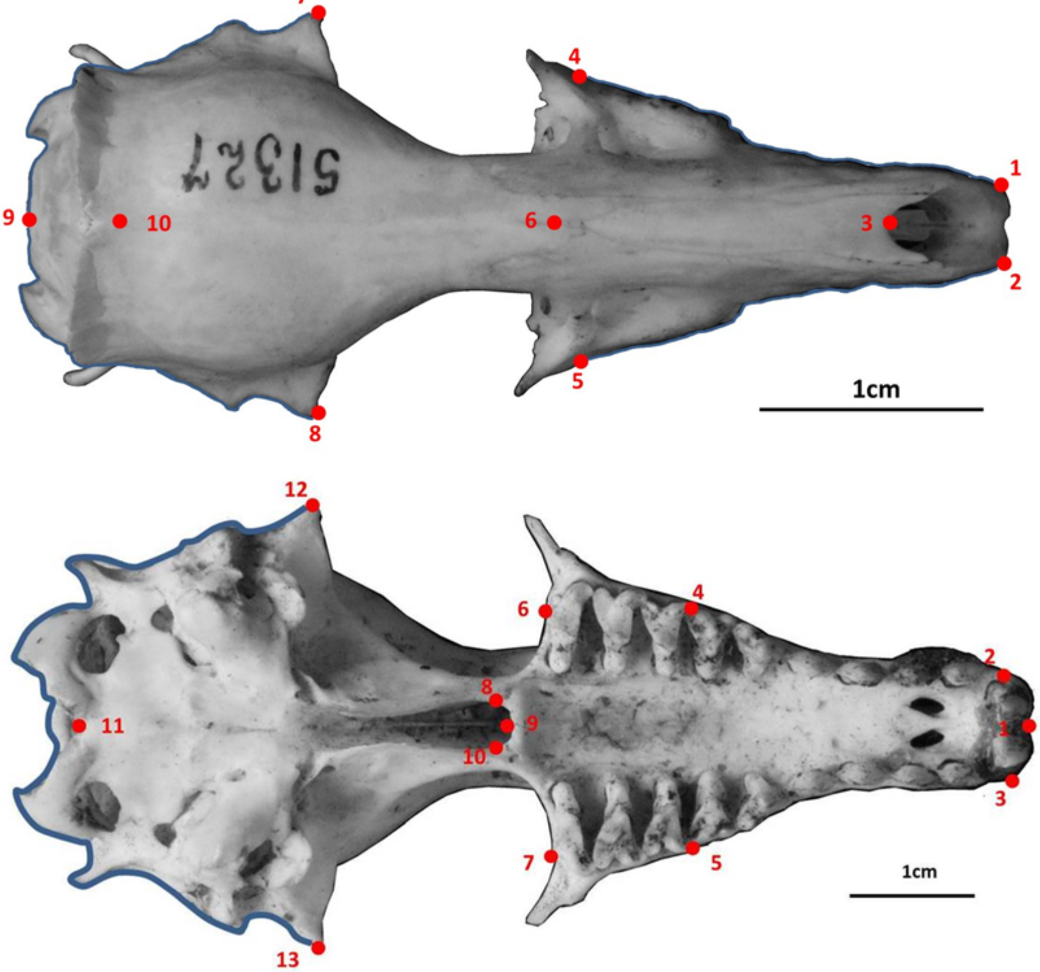

Figure 1: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of skulls in dorsal and ventral views respectively. Curves were re-sampled to the same number of evenly-spaced points. See Supplementary Material for descriptions of the curves and landmarks. The specimens belong to two different *Potamogale velox* (Tenrecidae) skulls: accession number AMNH 51327 (dorsal) and NHML 1934.6.16.2 (ventral)

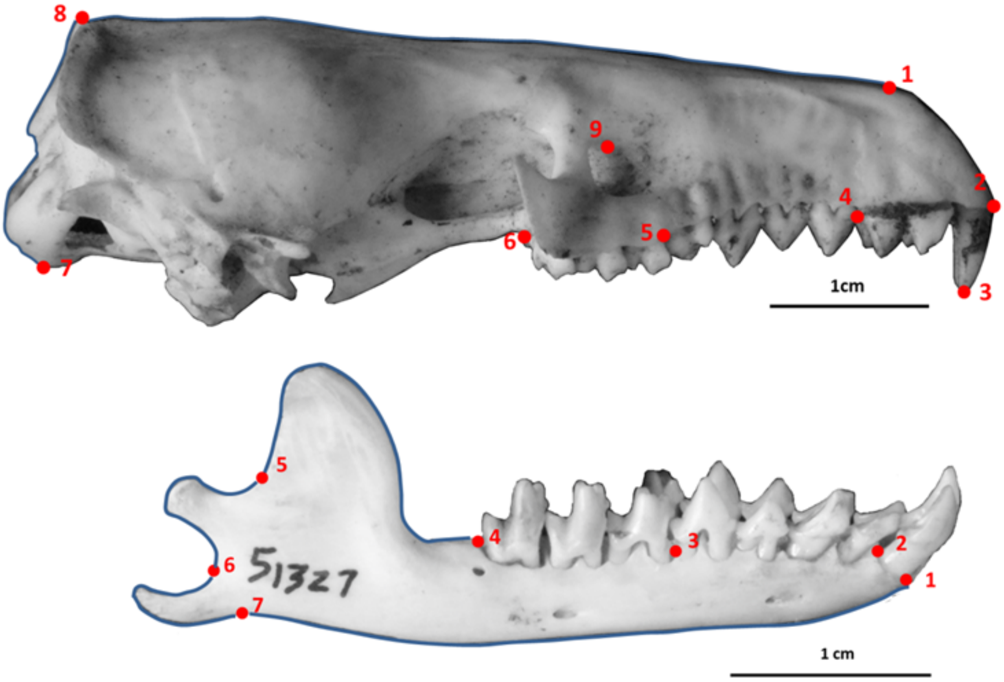

Figure 2: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of lateral views of skulls and mandibles respectively. Curves were re-sampled to the same number of evenly-spaced points. See Supplementary Material for descriptions of the curves and landmarks. The specimens belong to two different *Potamogale velox* (Tenrecidae) skulls: accession number AMNH 51327 (dorsal) and NHML 1934.6.16.2 (ventral)

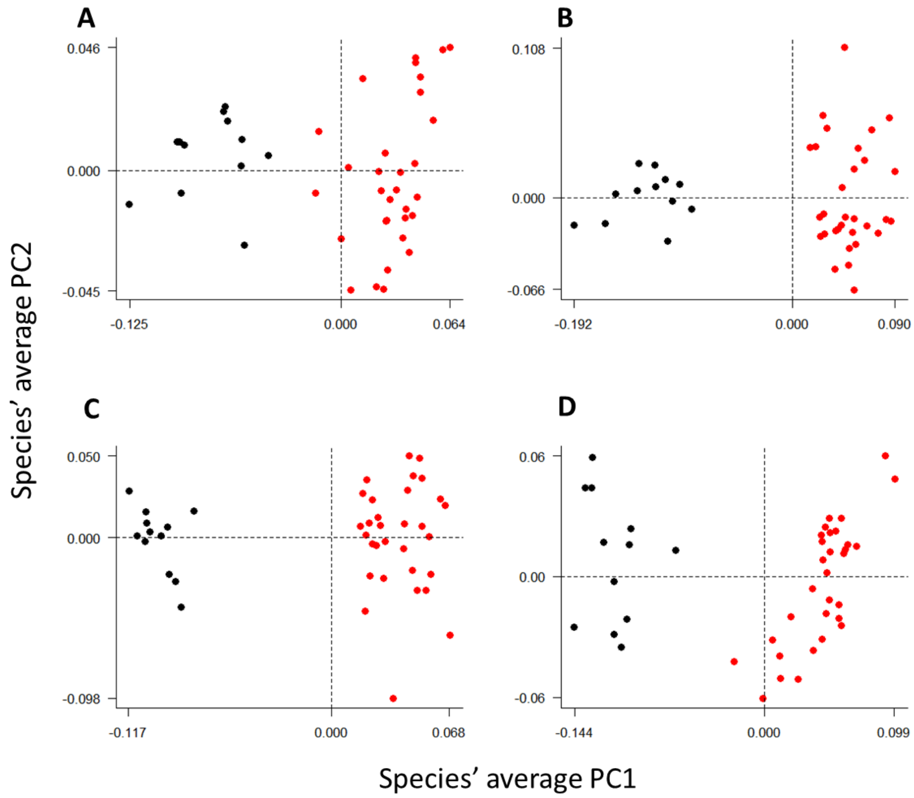

Figure 3: Principal components plots of the morphospaces occupied by tenrecs (red, n = 31 species) and golden moles (black, n = 12) for the skulls: dorsal (A), ventral (B), lateral (C) and mandibles (D) analyses. Axes are PC1 and PC2 of the average scores from a PCA analysis of mean Procrustes shape coordinates for each species.

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Table 1: Disparity comparisons between tenrecs (T) and golden moles (G) for each of our data sets(rows) and four disparity metrics (columns). 'Mandibles:one curve' refers to our shape analysis of mandibles excluding the three curves around the posterior structures of the jaw (figure 2). Significant differences are highlighted in bold with the corresponding p value in brackets. Disparity metrics are: sum of variance, product of variance, sum of ranges and product of ranges

Disparity metric	**SumVar**	**ProdVar**	**SumRange**	**ProdRange**
Skulls dorsal	T>G	T>G	T>G	T>G
Skulls lateral	T>G	T>G	T>G	T>G
Skulls ventral	T>G	G>T	T>G	T>G
Mandibles	G>T	**G>T* (0.008)**	**T>G* (0.025)**	**G>T* (0.009)**
Mandibles:one curve	G>T	G>T	T>G	T>G

Table 2: Disparity comparisons between non-*Microgale* tenrecs (T) and golden moles (G) for each of our data sets(rows) and four disparity metrics (columns). Significant differences are highlighted in bold with the corresponding p value in brackets. Disparity metrics are; sum of variance, product of variance, sum of ranges and product of ranges.

Disparity metric	**SumVar**	**ProdVar**	**SumRange**	**ProdRange**
Skulls dorsal	T>G	T>G	T>G	T>G
Skulls lateral	**T>G* (0.014)**	T>G	**T>G* (0.001)**	**T>G*(0.003)**
Skulls ventral	T>G	T>G	T>G	T>G
Mandibles	T>G	G>T	T>G	G>T

Table 3: npMANOVA comparisons of morphospace occupation for tenrecs and golden moles in each of the four analyses (three views of skulls and mandibles). In each case the two families occupy significantly different areas of morphospace.

Analysis	**F**	$\mathbf{R^2}$	**p value**
Skulls dorsal	66.02	0.62	0.001
Skulls ventral	100.74	0.71	0.001
Skulls lateral	75.07	0.65	0.001
Mandibles	59.34	0.59	0.001