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Cranial morphological disparity within the adaptive radiation of tenrecs (Afrosoricida, Tenrecidae) is no greater than expected by chance

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Abstract

Introduction

Adaptive radiations, "evolutionary divergence of members of a single phylogenetic lineage into a variety of different adaptive forms" (Futuyma 1998, cited by Losos, 2010) have long-attracted the interests and attentions of naturalists. Some of the most famous examples include cichlid fish and Caribbean *Anolis* lizards (Gavrilets & Losos, 2009). These groups exhibit great variety in both their phenotypic forms and the ecological niches which they occupy.

Each of these groups are uncontroversially accepted as examples of adaptive radiations. However, there has been considerable debate about how adaptive radiations should be defined (REFS) and how to distinguish an adaptively radiated group from just a clade of apparently diverse species. This is an important distinction because we need a consistent means of identifying an adaptive radiation before we can investigate and understand the selective pressures which cause adaptive radiations to develop in some groups and not others (REFS).

One suggestion which has been proposed is that an adaptively radiated clade should show exceptional (i.e. greater than expected by chance) morphological and ecological diversity (Losos & Mahler, 2010). In this case, a group of species would be considered exceptionally diverse if they have more phenotypic and ecological diverstiy than their closest relatives and also if they exhibit greater diversity than expected by chance. However, few putative examples of adaptive radiations have been characterised in this way. Under this definition it is equally important to demonstrate exceptional diversity in both phenotypic variety and the range of ecological niches which the species occupy. However, for the

purposes of this paper we will focus on the first criteria; investigating the evidence for morphological variety.

Phenotypic diversity is commonly measured as morphological disparity; the diversity of organic form (Foote, 1997; Erwin, 2007)). There is no single definition of disparity and it can be calculated in many ways including measures of morphospace occupation (e.g. Goswami et al., 2011; Brusatte et al., 2008) and rate-based approaches that assess the amount of directed change away from an ancestor (O'Meara et al., 2006; Price et al., 2013). Analyses of disparity apply these alternative approaches depending on whether the study is interested in current patterns of morphological diversity or the rate at which they accumulate through time.

Here we investigate current patterns of morphological disparity in tenrecs (Afrosoricida, Tenrecidae) to determine whether they represent an adaptive radiation sensu (Losos & Mahler, 2010). The tenrec family is comprised of 34 species, 31 of which are endemic to Madagascar (Olson, 2013). From a single common ancestor (Asher & Hofreiter, 2006), Malagasy tenrecs diversified into a wide variety of descendant species which convergently resemble distantly related insectivore mammals such as shrews (*Microgale* tenrecs), moles (*Oryzorictes* tenrecs) and hedgehogs (*Echinops* and *Setifer* tenrecs) (Eisenberg & Gould, 1969).

Tenrecs are often cited as an example of an adaptively radiated family which exhibits exceptional morphological diversity (Soarimalala & Goodman, 2011; Olson & Goodman, 2003; Eisenberg & Gould, 1969). However, this apparent exceptional diversity is based on subjective comparisons to other groups and it has not been tested quantitatively. If tenrecs are exceptionally morphologically diverse then, following (Losos

& Mahler, 2010), tenrecs should be more morphologically disparate than expected by chance and they should exhibit significantly more phenotypic diversity than their nearest relatives, the golen moles (Afrosoricida, Chrysochloridae). Here we test these predictions using cranial morphology as a proxy for phenotypic diversity.

Using the most complete morphological data set of tenrecs and golden moles to date we apply geometric morphometric analyses (Rohlf & Marcus, 1993; Zelditch et al., 2012) to quantify morphological disparity among our species. Our results indicate that, on average, tenrecs are more phenotypically diverse than their closest relatives but their morphological diversity is no greater than that which is expected to evolve by chance. Therefore, under strict definitions, the designation of tenrecs as an exceptional adaptive radiation may need to be reconsidered.

These findings highlight the vital importance of testing our common, but often erroneous, expectations about patterns of morphological disparity in groups that exhibit apparent high levels of diversity.

Materials and Methods

Data collection

Morphological data collection

One of us (SF) photographed cranial specimens of tenrecs and golden moles at the Natural History Museum London (NHML), 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 access to 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) and 181 mandibles in lateral view (147 tenrecs and 34 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. Our landmarks (points) and semilandmarks (outline curves) used to represent shape variation in the dorsal skulls and mandibles are depicted in Figures 1 and 2 respectively. Corresponding landmark definitions for each view are in tables 1 and 2. We also placed landmarks and semilandmarks on photographs of ventral and lateral skull views, details 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 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 Development Core Team, 2013) within the geomorph package (Adams et al., 2013). We used the gpagen function to run a general Procrustes alignment (REFS) of the landmark coordinates while sliding the semilandmarks by minimising procrustes distance rather than bending energy (REFS). We used these Procrustes-aligned coordinates of all species (n=43) to calculate average shape values for each species which we then used for a principal components (PC) analysis (REFS) with the plotTangentSpace function (Adams et al., 2013).

Phylogeny

Instead of basing our analyses on individual trees and assuming that their topologies were known without error (e.g. Ruta et al., 2013; Foth et al., 2012; Brusatte et al., 2008; Harmon et al., 2003) we used a distribution of 101 pruned phylogenies derived from the randomly resolved mammalian supertrees in (Kuhn et al., 2011).

Eight species (six *Microgale* tenrecs and two golden moles) in our morphological data were not in the phylogenies. Phylogenetic relationships among the *Microgale* have not been resolved more recently than the (Kuhn et al., 2011) analysis, therefore we added the additional *Microgale* species at random to the *Microgale* genus within each phylogeny (Revell, 2012). We could not use the same approach to add the two missing golden mole species because they were the only representatives of their respective genera within our data. Therefore we randomly added

these species to the common ancestral node (using the findMRCA function in phytools (Revell, 2012)) of all golden moles within each phylogeny. Adding these extra species to the phylogenies created polytomies which we resolved arbitrarily using zero-length branches (Paradis et al., 2004). We calculated pairwise phylogenetic distances among species using the cophenetic function (R Development Core Team, 2013).

Analyses

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; the sum and product of the range and variance of morphospace occupied by each family (Brusatte et al., 2008; Foth et al., 2012; Ruta et al., 2013). We also calculated morphological disparity directly from the Procrustes-superimposed shape data (ZelditchMD, Zelditch et al., 2012). Disparity is expected to be higher in larger groups (REFS). Therefore we repeated our disparity comparisons between the two families using rarefaction (see supplementary material) to confirm that observed differences in disparity between the two groups were not artefacts of differences in sample size.

To test whether tenrecs are more morphologically disparate than expected by chance, we simulated shape evolution (Harmon et al., 2008) of the species-average, Procrustes-superimposed shape coordinates of each tenrec species across our distribution of phylogenies. We took

"chance" to mean the expected shape evolution under a Brownian Motion (BM) model and we repeated 1000 simulations on of shape evolution in BM on each of 101 phylogenies pruned to include tenrec species only. We ran a principal components analysis on each of the simulations and used the PC axes which accounted for 95% of the cumulative variation to calculate disparity metrics.

We compared the observed disparity measure to the corresponding distribution of values and used a two-tailed test to determine whether the observed (true) disparity measures were more or less than that which is expected to evolve under BM.

The majority of tenrecs (19 out of 31 in our data) are members of the *Microgale* (shrew-like) genus which is notable for its relatively low phenotypic diversity (Soarimalala & Goodman, 2011; Jenkins, 2003) and may mask signals of high disparity among other tenrecs. To test this we repeated our simulations of shape evolution excluding *Microgale* species. This reduced our data set for tenrecs from 31 to 12 species.

To test whether tenrecs have significantly different morphologies than golden moles, we used a non parametric MANOVA (Anderson, 2001) to compare morphospace occupation between the two groups (REFS?).

Results

Morphological disparity in tenrecs

We compared observed disparity to the distributions of expected disparity calculated from BM simulations of shape data (1,000 simulations on each

of 101 phylogenies). We present the results from comparing our observed and simulated measures of sum of variance (figures 3 and 4) because all disparity metrics yielded the same patterns: tenrecs have significantly lower disparity than expected under BM. Full results from all disparity metrics and including the ventral and lateral skull views can be found in the supplementary.

Removing the phenotypically similar *Microgale* tenrecs did not qualitatively affect our results; the non-*Microgale* tenrecs still show significantly lower phenotypic disparity than expected by chance (simulation results in the supplementary material).

Morphological disparity in tenrec and golden moles

Figures 5 and 6 depict 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 (n = 6 axes for the dorsal skulls analysis and n = 11 axes for the mandibles) to calculate the disparity of each family.

In the dorsal skulls analysis, tenrecs and golden moles occupy significantly different areas of morphospace (npMANOVA, F = 59.34, R^2 = 0.59, p = 0.001) indicating that the two families have signficantly different skull morphologies. For each of the calculated metrics, tenrecs have higher disparity than golden moles but these differences were not significant for the variance-based calculations. Non-*Microgale* tenrecs also higher disparity than golden moles but none of the comparisons were statistically significant .

Tenrecs and golden moles have significantly different mandible shapes (npMANOVA F = 59.34, R^2 = 0.59, p = 0.001). However, unexpectedly, golden moles appear to have higher disparity than tenrecs in the shape of their mandibles (although these differences are only significant when disparity is calculated as product of variance or ZelditchMD).

We tested whether these results may be artefacts of relatively low phenotypic diversity within *Microgale* tenrecs. However, although golden moles and non-Microgale tenrecs occupy significantly different areas of morphospace (npMANOVA F = 31.6, R^2 = 0.59, p = 0.001), there is no significant difference between the two groups for any metrics of disparity.

Discussion

Our findings provide new insights into phenotypic diversity within the tenrec family. Contrary to previous suggestions (e.g. Eisenberg & Gould, 1969; Olson, 2013), tenrecs do not appear to be exceptional in their morphological diversity. Tenrecs are not more morphologically varied than expected to evolve by chance: they show significantly lower disparity in their morphologies than expected to evolve under Brownian Motion models of evolution.

When we compared tenrecs' cranial morphologies to their closest relatives the resulting patterns were less straightforward. For the analyses of skull shapes we found a trend towards higher disparity in tenrecs than in golden moles although these apparent differences were only significant for some disparity metrics. In contrast, the analyses of the mandibles indicated that golden moles have more diverse mandible shapes although,

again, these results are only significant for some disparity metrics.

These results put a new perspective on the long-standing assumption that tenrecs are an adaptive radiation.

It is evidence that tenrecs are a diverse group, both phenotypically and ecologically. 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 is striking morphological diversity, from the spiny *Echinops, Setifer* and striking *Hemicentetes* to the shrew-like *Microgale*. Furthermore, tenrecs inhabit a variety of ecological niches and habitats including terrestrial, arboreal, semi-aquatic and semi-fossorial forms (REFS). However, our results cast doubt over whether the evident diversity within the tenrec family should be considered to be a true adaptive radiation.

Phenotypic and ecological divergences within a clade are not surprising; most clades have at least small levels of disparity so, when it comes to identifying adaptive radiations, it's important to identify clades which are exceptional in their diversity (Losos & Mahler, 2010). Here we have presented the first quantitative investigation of morphological disparity in tenrecs and our results suggest that perhaps phenotypic variation in tenrecs is not the product of an adaptive radiation in the strict sense of its definition.

All of our simulation analyses agree that tenrecs show significantly lower morphological diversity than that which is expected to evolve under random, BM evolution.

The discrepancies between our analyses of cranial and mandible

disparity could reflect derive from factors associated with the modularity of morphological evolution.

There is strong evidence that morphological variation in skulls and mandibles is derived from differential evolution of integrated developmental modules (reviewed by Klingenberg, 2013). For example, there seems to be two primary modules in the mouse mandible; an alveolar part which holds the teeth and the ascending ramus for muscle attachment and which articulates with the skull (Klingenberg, 2008). Geometric shape covariation is stronger within rather than between these modules.

Our landmarks and curves for the mandibles (figure 2, table 2) include aspects of variation in the dentition but they focus particular attention on the ascending ramus (condyloid, condylar and angular processes). Therefore the higher morphological disparity in golden mole mandibles most likely reflects greater variation in the shape of the muscle attachment areas of the mandible. In contrast it proved impossible to position reliable landmarks on the corresponding articulation areas of the skull in lateral view (see supplementary).

If variation in muscle attachment/articulation sites is driving morphological disparity in mandibles, it is not clear why golden moles should have more disparate articular rami than tenrecs.

While our findings cast doubt on the designation of tenrecs as an adaptive radiation sensu (Losos & Mahler, 2010), there are certain caveats to consider which could modify the interpretation of our results.

Phenoypic variation can evolve for reasons other than adaptive radiation. Therefore, to describe phenotypic divergence as the product of

an adaptive radiations requires exceptional morphological diversity in traits which have specific and proven adaptive significance (Losos & Mahler, 2010). The evolution of cranial shape (both upper skull and mandible), particularly dental morphology, has obvious correlations with dietary specialisations (REFS) and occupation of specific ecological niches (REFS).

Considering the wide ecological diversity of our study species; the fossorial golden moles and semi-fossorial, arboreal, terrestrial and semi-aquatic tenrecs (REFS) it is reasonable to expect that variation in cranial shape should be an adaptive characterstic which allows the animals to survive in their divergent niches. Therefore quantifying the diversity of cranial morphology is a reasonable method of assessing the significance of morphological variety within the context of identifying an adaptive radiation.

Cranial shape similarities are commonly used to delineate species boundaries (REFS) or for cross-taxonomic comparative studies of phenotypic (dis)similarities (REFS). However, disparity studies are inevitably constrained to be measures of diversity within specific traits rather than overall morphology (Roy & Foote, 1997). Therefore it is possible that other morphological proxies of phenotype; analyses of linear measurements and/or discrete characters of either cranial or post-cranial morphologies could yield different results.

However, the results of (Foth et al., 2012) are encouraging. In an analysis of morphological disparity in pterosaurs, they found that disparity calculations based on geometric morphometric characterisation of skull shape yielded broadly similar results compared to analyses of

whole-skeleton discrete characters and limb proportion data sets. Therefore the disparity patterns we find here based on geometric morphometric analyses of cranial shape most likely represent approximations of disparity which are accurate for morphological diversity in the clades.

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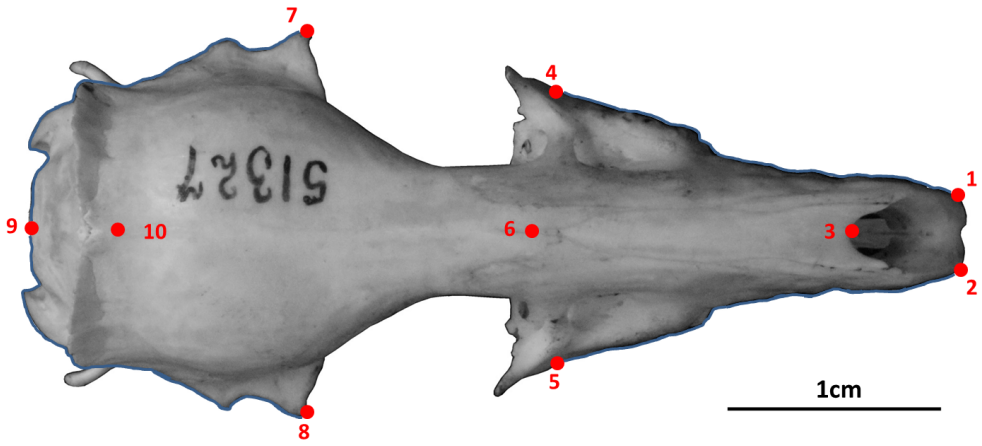

Figure 1: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of skulls in dorsal view. Curves were re-sampled to the same number of evenly-spaced points. See table X for description of curves and landmarks.*Potamogale velox* (Tenrecidae) skull, accession number: AMNH_51327

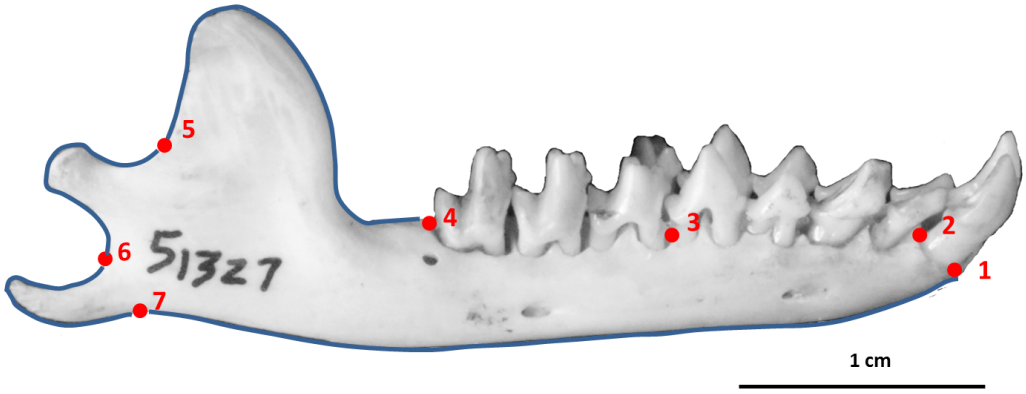

Figure 2: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of mandibles. Curves were re-sampled to the same number of evenly-spaced points. See table X for description of curves and landmarks.*Potamogale velox* (Tenrecidae) mandible, accession number: AMNH_51327

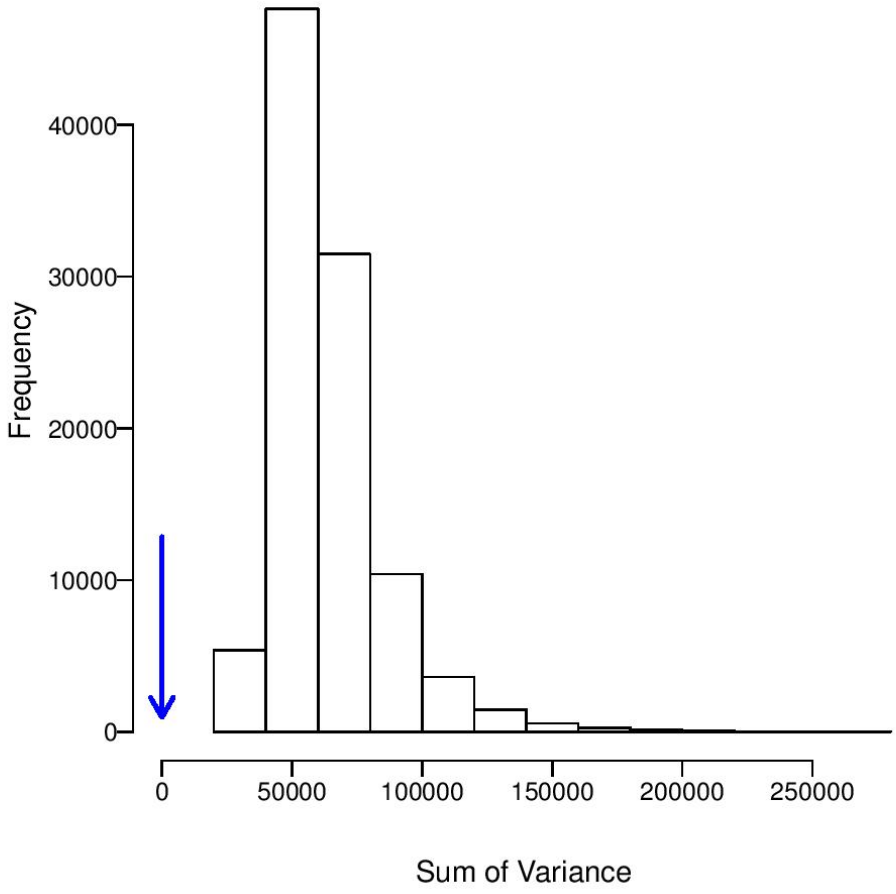

Figure 3: Comparison of the observed and expected disparity in the dorsal skulls. Disparity is measured as sum of variance, blue arrow points to the observed value of disparity (0.0017)

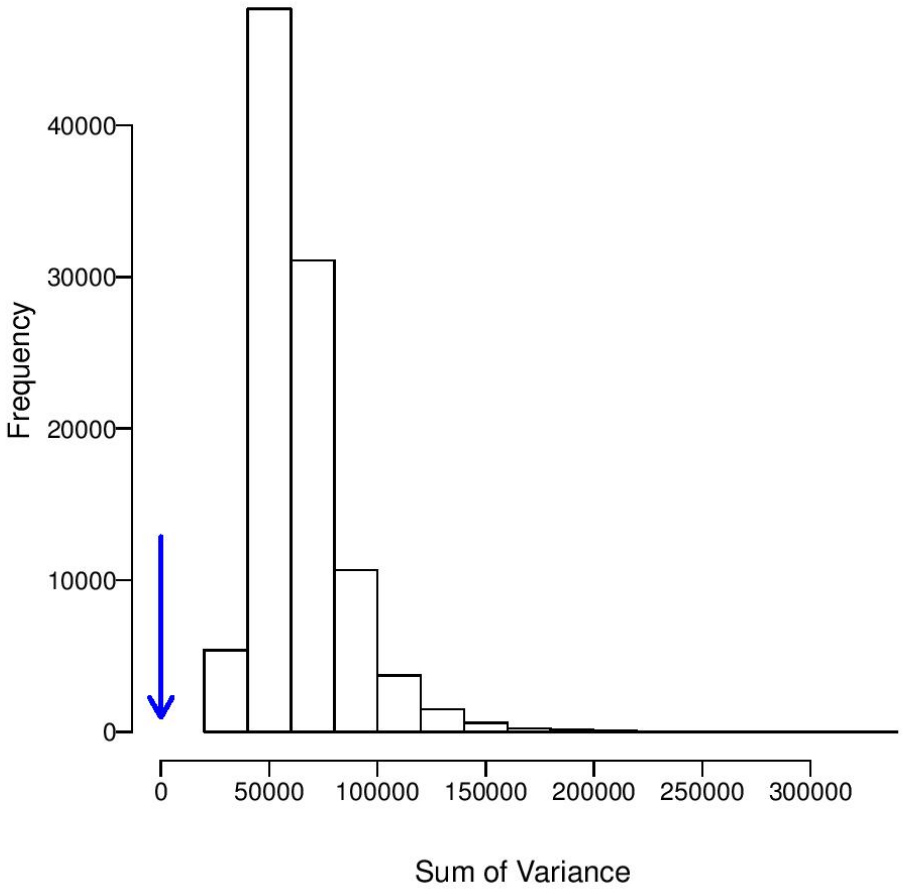

Figure 4: Comparison of the observed and expected disparity in the mandibles. Disparity is measured as sum of variance, blue arrow points to the observed value of disparity (0.0031)

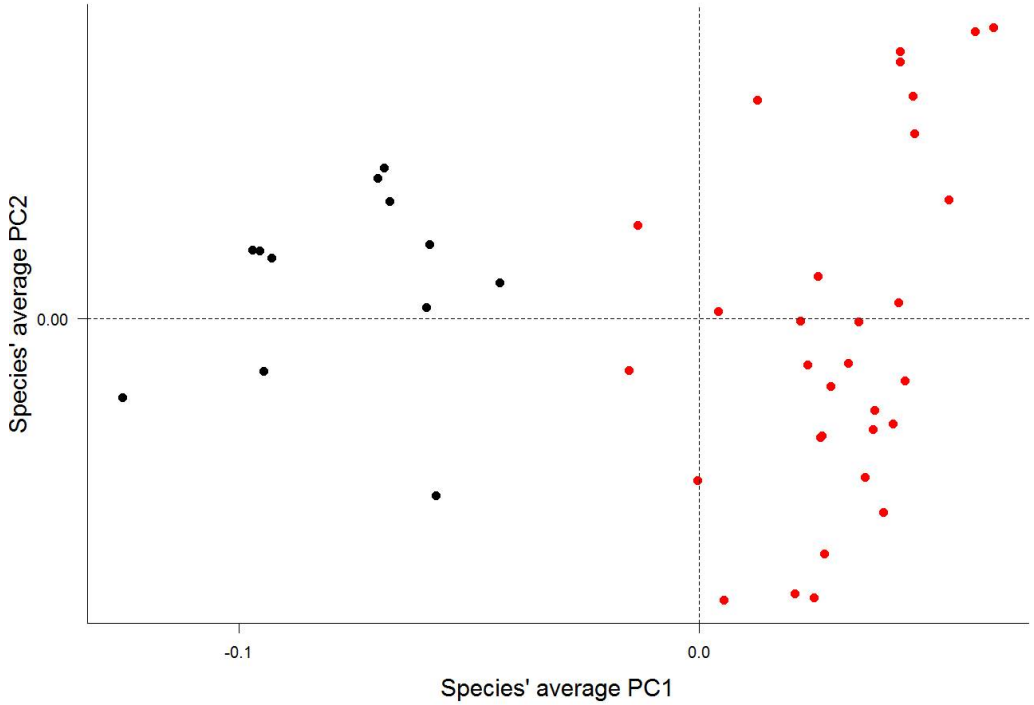

Figure 5: Principal components plot of the dorsal skulls' morphospace occupied by tenrecs (red, n=31) and golden moles (black, n=12). Axes are PC1 and PC2 of the average scores from a PCA analysis of mean Procrustes shape coordinates for each species.

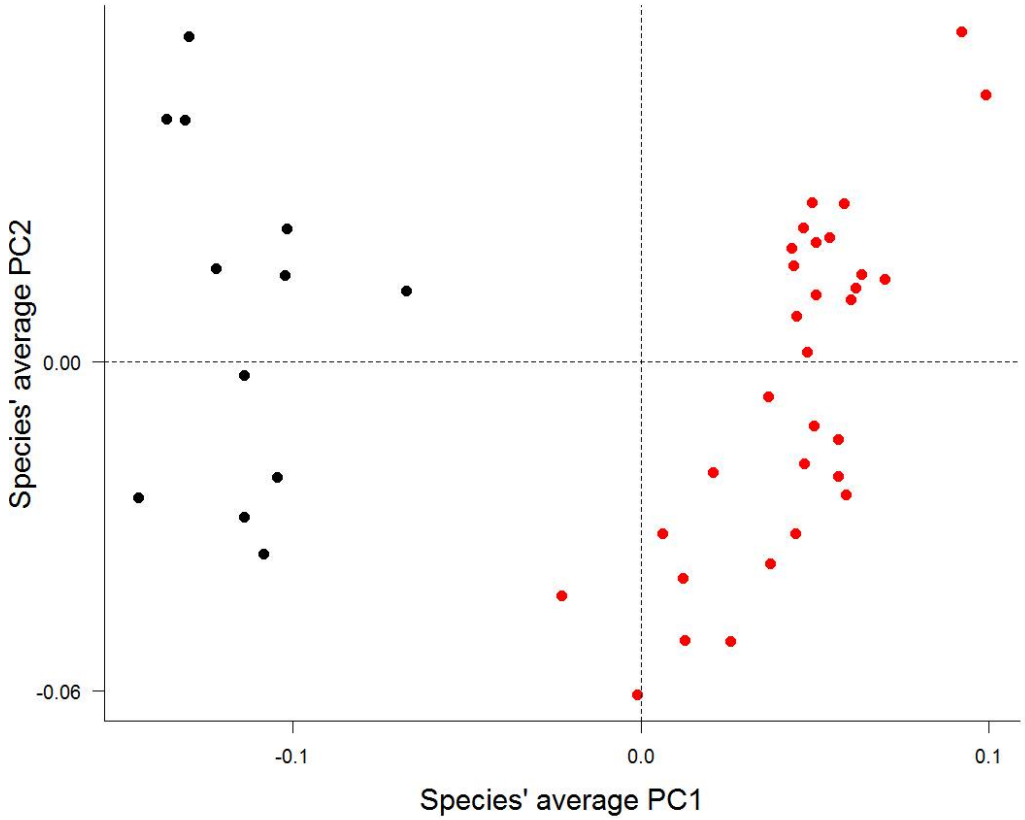

Figure 6: Principal components plot of the mandibles' morphospace occupied by tenrecs (red, n=31) and golden moles(black, n=12). Axes are PC1 and PC2 of the average scores from a PCA analysis of mean Procrustes shape coordinates for each species.

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Table 1: Descriptions of the landmarks (points) and curves (semilandmarks) for the skulls in dorsal view (see Figure 1).

Landmark	**Description**
1 + 2	Left (1) and right (2) anterior points of the premaxilla
3	Anterior of the nasal bones in the midline
4 + 5	Maximum width of the palate (maxillary) on the left (4) and right (5)
6	Midline intersection between nasal and frontal bones
7 + 8	Widest point of the skull on the left (7) and right (8)
9	Posterior of the skull in the midline
10	Posterior intersection between saggital and parietal sutures
Curve A	Outline of the braincase on the left side, between landmarks 9 and 7
(12 points)	(does not include visible features from the lower (ventral) side of the skull)
Curve B	Outline of the palate on the left side, between landamarks 4 and 1
(10 points)	(outline of the rostrum only, not the shape of the teeth)
Curve C	Outline of the braincase on the right side, between landmarks 9 and 8
(12 points)	(does not include visible features from the lower (ventral) side of the skull)
Curve D	Outline of the palate on the right side, between landamarks 5 and 2
(10 points)	(outline of the rostrum only, not the shape of the teeth)

Table 2: Descriptions of the landmarks (points) and curves (semilandmarks) for the mandibles in lateral (buccal) view (see figure 2)

Landmark	**Description**
1	Anterior of the alveolus of the first incisor
2	Posterior of the alveolus of the first incisor
3	Anterior of the alveolus of the first molar
4	Posterior of the alveolus of the last molar
5	Maximum curvature between the coronoid and condylar processes
6	Maximum curvature between the condylar and angular processes
7	Maximum curvature between the angular process and the horizontal ramus
Curve A	Condyloid process (between landmarks 4 and 5, 15 points)
Curve B	Condylar process (between landmarks 5 and 6, 15 points)
Curve C	Angular process (between landmarks 6 and 7, 15 points)
Curve D	Base of the jaw (between landmarks 7 and 1, 12 points)