Morphological diversity in tenrecs (Afrosoricida, Tenrecidae): Comparing tenrec skull diversity to their closest relatives

Sive Finlay[1,2] and Natalie Cooper[1,2,*]

[1] School of Natural Sciences, Trinity College Dublin, Dublin 2, Ireland.
[2] Trinity Centre for Biodiversity Research, Trinity College Dublin, Dublin 2, Ireland.
*Corresponding author: ncooper@tcd.ie; Zoology Building, Trinity College Dublin, Dublin 2, Ireland.
Tel: +353 1 896 1926.

Keywords: geometric morphometrics, golden moles, morphological diversity, tenrecs

Introduction

Analysing patterns of morphological diversity has important implications for our understanding of ecological and evolutionary traits. For example, from a functional ecology perspective, morphological characteristics of limbs inform us about locomotory style (e.g. Bou et al., 1987) and the trophic niches associated with particular dental morphologies affect speciation and diversification rates through time (Price et al., 2012). Morphological diversity is also an important aspect of evolutionary patterns such as adaptive radiations and convergent evolution. High morphological diversity is a unifying (Losos and Mahler, 2010; Olson and Arroyo-Santos, 2009), although not defining (Glor, 2010; Olson and Arroyo-Santos, 2009), characteristic of adaptive radiations. Furthermore, analysing morphological convergences in groups such as freshwater cichlid fish (Muschick et al., 2012) and anole lizards (Mahler et al., 2013) gives interesting insights into the relative repeatability of evolution (Losos, 2011).

Although studies of morphological diversity have clear implications for our understanding of ecological and evolutionary patterns, apart from a few examples (e.g. Ruta et al., 2013; Goswami et al., 2011; Brusatte et al., 2008), it is still common to study morphological diversity from a qualitative rather than quantitative perspective. However, we need to quantify the morphological similarities and differences among species to gain a better understanding of their ecological interactions and evolutionary history. Unfortunately, morphological diversity is difficult to quantify. Studies are inevitably constrained to measure the diversity of specific traits rather than overall morphologies (Roy and Foote, 1997). In

addition, our perception of morphological diversity is influenced by the trait being used. One study of pterosaurs demonstrated that comparing the diversity of different morphological traits using varying methods produced similar results (Foth et al., 2012). However, it remains unclear whether this finding can be applied to all vertebrate groups: in some species, comparing the relative diversity of cranial and limb morphologies may yield different results (Foth et al., 2012). Furthermore, linear measurements of morphological traits can restrict our understanding of overall morphological variation. A distance matrix of measurements between specific points is unlikely to give a completely accurate representation of a three dimensional structure (Rohlf and Marcus, 1993).

These are important limitations to consider but geometric morphometric approaches help to overcome some of the issues associated with traditional morphological studies (Adams et al., 2004). Morphometric studies based on caliper measurements of particular features can only describe a limited set of distances, ratios and angles which often fail to capture the overall shape of a specific structure (Slice, 2007). Geometric morphometrics circumvents these issues by using a system of Cartesian landmark coordinates to define anatomical points. This method captures more of the true, overall anatomical shape of particular structures (Mitteroecker and Gunz, 2009). These more detailed approaches are useful tools for studying patterns of morphological diversity.

Here we apply geometric morphometric techniques to quantify morphological diversity in a Family of small mammals, the tenrecs. Tenrecs (Afrosoricida, Tenrecidae) are a morphologically diverse group that is commonly cited as an example of both convergent evolution and an

adaptive radiation (Soarimalala and Goodman, 2011; Eisenberg and Gould, 1969). The Family is comprised of 34 species, 31 of which are endemic to Madagascar (Olson, 2013). Body masses of tenrecs span three orders of magnitude (2.5 to ¿ 2,000g); a greater range than all other Families, and most Orders, of living mammals (Olson and 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 and Gould, 1969). Their similarities include examples of morphological, behavioural and ecological convergence (Soarimalala and Goodman, 2011). Tenrecs are one of only four endemic mammalian clades in Madagascar and the small mammal species they resemble are absent from the island (Garbutt, 1999). Therefore, it appears that tenrecs represent an adaptive radiation of species which filled otherwise vacant ecological niches (Soarimalala and Goodman, 2011). The similarities among tenrecs and other small mammals are even more remarkable when you consider their phylogenetic history. Tenrecs were originally classified within the general "Insectivora" clade and only molecular studies revealed their true phylogenetic affinities within the Afrotherian mammals (Stanhope et al., 1998). Therefore, despite initial appearances, tenrecs are more closely related to elephants, manatees and aardvarks than they are to shrews, moles or hedgehogs.

Although tenrecs are often cited as an example of both an adaptive radiation and exceptional convergent evolution, these claims have not been investigated quantitatively. There are qualitative similarities among the hind limb morphologies of tenrecs and several other unrelated species with similar locomotory styles (Salton and Sargis, 2009) but the degree of

morphological similarity has not been established. Morphological diversity is an important feature of adaptive radiations (Losos and Mahler, 2010) and it also informs our understanding of convergent phenotypes (Muschick et al., 2012). Therefore, it is important to quantify patterns of morphological diversity in tenrecs to gain an insight into their evolution. My thesis is the first study to address this issue.

We present the first quantitative study of patterns of morphological diversity in tenrecs. We use geometric morphometric techniques (Rohlf and Marcus, 1993) to compare cranial morphological diversity in tenrecs to that of their closest relatives, the golden moles (Afrosoricida, Chrysochloridae). We expect tenrecs to be more morphologically diverse than golden moles because tenrecs occupy a wider variety of ecological niches. The tenrec Family includes terrestrial, semi-fossorial, semi-aquatic and semi-arboreal species (Soarimalala and Goodman, 2011). In contrast, all golden moles occupy very similar, fossorial ecological niches (Bronner, 1995). Greater ecological variety is often (though not always) correlated with higher morphological diversity (Losos and Mahler, 2010).

Materials and Methods

The methods we used involved several steps of data collection, geometric morphometrics analyses and comparisons of morphological diversity. These included i) data collection, ii)geometric morphometric analyses and iii)estimating morphological diversity. For clarity, Figure 1 summarises all of these steps and we describe them in detail below.

Data collection

One of us (SF) used the collections of five museums: the Natural History Museum, London (BMNH), the Smithsonian Institute Natural History Museum, Washington D.C. (SI), the American Museum of Natural History, New York (AMNH), the Museum of Comparative Zoology, Cambridge M.A. (MCZ) and the Field Museum of Natural History, Chicago (FMNH). We recorded species names as they were written on museum specimen labels and then corrected them to match the taxonomy in Wilson and Reeder's Mammal Species of the World (2005). For recently identified species, which are not included in Wilson and Reeder (2005), we used the taxonomy recorded on the specimen labels. Wilson and Reeder (2005) record 30 species of tenrec but more recent studies indicate that there are now 34 species (Olson, 2013). The additional species belong to the shrew tenrec (*Microgale*) Genus and represent either recognition of cryptic species boundaries (Olson et al., 2004) or discovery of new species (Goodman et al., 2006; Olson and Arroyo-Santos, 2009). Only one of these four recent additions, *M. jobihely*, was present in the museum collections and therefore we could not include the three other newly recognised species in the analyses. We photographed all of the tenrec and golden mole skulls available in the collections. This included 31 of the 34 species in the tenrec Family and 12 of the 21 species of golden moles (Wilson and Reeder, 2005).

We took pictures of the skulls using photographic copy stands consisting of a camera attachment with an adjustable height bar, a flat stage on which to place the specimen and an adjustable light source. To take possible light variability into account, on each day we took a

photograph of a white sheet of paper and used the custom white balance function on the camera to set the image as the baseline "white" measurement for those particular light conditions.

We photographed the specimens with a Canon EOS 650D camera fitted with a EF 100 mm f/2.8 Macro USM lens. We used a remote control (Hähnel Combi TF) to take the photos to avoid shaking the camera and distorting the images. We photographed the specimens on a black material background with a light source in the top left-hand corner of the photograph. We used small bean bags as necessary to hold the specimens in position while being photographed to ensure that they lay in a flat plane relative to the camera and did not tilt in any direction. We used the grid-line function on the live-view display screen of the camera to position the specimens in the centre of each image.

We photographed the skulls in three views: dorsal (top of the cranium), ventral (underside of the skull with the palate roof facing upwards) and lateral (right side of the skull) (Figure 1). When the right sides of the skulls were damaged or incomplete we photographed the left sides and later reflected the images so that they could be compared to pictures of the right sides (e.g. Barrow and Macleod, 2008).

We converted the raw files to binary (grey scale) images and re-saved them as TIFF files (uncompressed files preserve greater detail, RHOI, 2013). Photographs of the specimens from the American Museum of Natural History and the Smithsonian Institute are available on figshare in separate file sets for the dorsal (Finlay and Cooper, 2013b), ventral (Finlay and Cooper, 2013d) and lateral (Finlay and Cooper, 2013c) skull pictures along with the mandibles (Finlay and Cooper, 2013a). Copyright

restrictions from the other museums prevent public sharing of their images however they are available on request.

Geometric morphometric analyses

We used a combination of landmark and semilandmark analysis approaches to assess the shape variability in skull. We used the TPS software suite (Rohlf, 2013) to digitise landmarks and curves on the photos. We set the scale on each image individually to standardise for the different camera heights that I used when photographing my specimens. We created separate data files for each of the three morphometric analyses (skulls in dorsal, ventral and lateral views). One of us (SF) digitised landmarks and semilandmark points on every image individually. Some specimens were too damaged to use in particular views so there were a different total number of images for each analysis. We photographed 182 skulls in dorsal view (148 tenrecs and 34 golden moles), 173 skulls in ventral view (141 tenrecs and 32 golden moles) and 171 skulls in lateral view (140 tenrecs and 31 golden moles).

When using semilandmark approaches there is a potential problem of over - sampling: simpler structures will require fewer semilandmarks to accurately represent their shape (MacLeod, 2012). To ensure that we applied a uniform standard of shape representation to each outline segment (i.e. that simple structures would not be over-represented and more complex features would not be under-represented), we followed the method outlined by MacLeod (2012). For each data set we chose a random selection of photos of specimens which represented the breadth of the morphological data (i.e. specimens from each sub-group of species). We

drew the appropriate curves on each specimen and over-sampled the number of points on the curves. We measured the length of the line and regarded that as the 100%, true length of that outline. We then re-sampled the curves with decreasing numbers of points and measured the length of the outlines. We calculated the length of each re-sampled curve as a percentage of the total length of the curve and then found the average percentage length for that reduced number of semilandmark points across all of the specimens in my test file. We continued this process until I found the minimum number of points that gave a curve length which was at least 95% accurate. We repeated these curve-sampling tests for each analysis to determine the minimum number of semilandmark points which would give accurate representations of morphological shape.

Figure 2 depicts that landmarks and curves which we used for each of the sets of photographs. For landmarks which are defined by dental structures, we used published dental sources (Repenning, 1967; Eisenberg and Gould, 1969; Nowak, 1983; MacPhee, 1987; Knox Jones and Manning, 1992; Davis and Schmidly, 1997; Quérouil et al., 2001; Nagorsen, 2002; Wilson and Reeder, 2005; Goodman et al., 2006; Karataş et al., 2007; Hoffmann and Lunde, 2008; Asher and Lehmann, 2008; Muldoon et al., 2009; Lin and Motokawa, 2010) where available to identify the number and type of teeth in each species. Detailed descriptions of the landmarks can be found in the supplementary material.

After creating the files with the landmarks and semilandmarks placed on each photograph, we used TPSUtil (Rohlf, 2012) to create "sliders" files that defined which points in the TPS files should be treated as semilandmarks (Zelditch et al., 2012). We combined the landmarks and taxonomic identification files into a single morphometrics data object and

carried out all further analyses in R version 3.1.1 (R Core Team, 2014). Data and code for all of our analyses is available on GitHub (REF to paper repository).

At this stage, we either used the full data set (31 species of tenrec and 12 species of golden mole) or a reduced data set with just 17 species of tenrec (Figure 1). We created this reduced data set because the majority of tenrec species (19 out of 31 in my data) belong to the *Microgale* (shrew-like) Genus that has relatively low morphological diversity (Soarimalala and Goodman, 2011; Jenkins, 2003). This may mask signals of higher morphological diversity among other tenrecs. To test this, we created a subset of the tenrec data that included just five of the *Microgale* species, each representing one of the five sub-divisions of *Microgale* outlined by Soarimalala and Goodman (2011), i.e. small, small-medium, medium, large and long-tailed species. We compared the morphological diversity of this subset of tenrecs (n=17: five *Microgale* and 12 non-*Microgale* species) to that of the 12 species of golden moles (dashed arrows in Figure 1). After this selection stage, all further steps in the analyses were the same.

For each analysis, we used the gpagen function in the geomorph package (Adams et al., 2013) to run a general Procrustes alignment (Rohlf and Marcus, 1993) of the landmark coordinates while sliding the semilandmarks by minimising Procrustes distance (Bookstein, 1997). We used these Procrustes-aligned coordinates of all specimens to calculate average shape values for each species which we then used for a principal components (PC) analysis with the plotTangentSpace function (Adams et al., 2013). We selected the number of principal component (PC) axes that accounted for 95% of the variation in the data (Figure 1) and used

these axes to estimate morphological diversity in each Family.

Estimating morphological diversity

We grouped the PC scores for tenrecs and golden moles separately so that we could estimate the diversity of each Family and then compare the two groups (Figure 1). We compared morphological diversity in two ways. First, we used non parametric multivariate analysis of variance (npMANOVA; Anderson, 2001) to test whether tenrecs and golden moles occupied significantly different positions within the morphospaces defined by the PC axes that accounted for 95% of the overall variation in the data (e.g. Serb et al., 2011; Ruta et al., 2013). A significant difference between the two Families would indicate that they have unique morphologies which do not overlap. Second, we compared morphological diversity within tenrecs to the diversity within golden moles. We define morphological diversity as the mean Euclidean distance (sum of squared differences) between each species and its Family centroid (Figure 3). This is summarised in the equation below where n is the number of species in the Family, i is the number of PC axes and c are the average PC scores for each axis (the centroid).

$$Disparity = \frac{\sqrt{\Sigma(PCn_i - PCc_i)^2}}{n} \quad (1)$$

If tenrecs are more morphologically diverse than golden moles, then they should be more dispersed within the morphospaces and have, on average, higher values of mean Euclidean distance.

One possible issue with these analyses is that the two Families have

unequal sample sizes: 31 (or a subset of 17) tenrec species compared to just 12 golden mole species. Morphological diversity is usually decoupled from taxonomic diversity (e.g. Ruta et al., 2013; Hopkins, 2013) so larger groups are not necessarily more morphologically diverse. However, comparing morphological diversity in tenrecs to the diversity of a smaller Family could still bias the results. We used pairwise permutation tests to account for this potential issue.

We tested the null hypothesis that tenrecs and golden moles have the same morphological diversity (the same mean Euclidean distance to the Family centroid). If this is true, when we randomly assign the group identity of each species (i.e. shuffle the "tenrec" and "golden mole" labels) and then re-compare the morphological diversity of the two groups, there will be no significant difference between these results and those obtained when the species are assigned to the correct groupings. We performed this shuffling procedure (random assignation of group identity) 1000 times and calculated the difference in morphological diversity between the two groups for each permutation. This generated a distribution of 1000 values which are calculations of the differences in morphological diversity under the assumption that the null hypothesis (equal morphological diversity in the two Families) is true. This method automatically accounts for differences in sample size because shuffling of the group labels preserves the sample size of each group: there will always be 12 species labelled as "golden mole" and then, depending on the analysis, either 31 or 17 species labelled as "tenrec". Therefore, the 1000 permuted values of differences in morphological diversity create a distribution of the expected difference in diversity between a group of sample size 31 (or 17 in the case of the subsetted tenrec data) compared to a group of sample size 12 under

the null hypothesis that the two groups have the same morphological diversity. We compared the observed measures of the differences in morphological diversity between the two Families to these null distributions to determine whether there were significant differences after taking sample size into account (two-tailed t test).

Results and Discussion

Results

Figure 4 depicts the morphospaces defined by the first two principal component (PC) axes from our principal components analyses (PCAs) of skull and mandible morphologies. The PCAs are based on the average Procrustes -superimposed shape coordinates for skulls in three views (dorsal, ventral and lateral). To compare morphological diversity in the two families, we used the PC axes which accounted for 95% of the cumulative variation in each of the skull analyses: dorsal (n=6 axes), ventral (n=7 axes) and lateral (n=7 axes). First, we compared the position of each Family within the morphospace plots. Tenrecs and golden moles occupy significantly different positions in the dorsal (npMANOVA: $F_{1,42}$=68.13, R^2=0.62, p=0.001), ventral (npMANOVA: $F_{1,42}$=103.33, R^2=0.72 , p=0.001) and lateral (npMANOVA: $F_{1,42}$=76.7, R^2 =0.65, p=0.001) skull morphospaces, indicating that the Families have very different, non-overlapping cranial and mandible morphologies (Figure 4.

Second, we compared the morphological diversity within each Family. Based on our measures of mean Euclidean distance to the Family centroids, tenrec skulls are more morphologically diverse than golden

mole skulls when they are measured in lateral view but not in dorsal or ventral view (Table 1). In contrast, when we analysed morphological diversity of skulls within the sub-sample of 17 tenrecs (including just five *Microgale* species) compared to the 12 golden mole species, we found that tenrec skulls were significantly more morphologically diverse than golden moles in all analyses (Table 1).

The pairwise permutation tests for each analysis confirmed that differences in morphological diversity were not artefacts of differences in sample size (Table 2)

Discussion

Tenrecs are often cited as an example of a mammalian group with high morphological diversity (Olson, 2013; Soarimalala and Goodman, 2011; Eisenberg and Gould, 1969). They are also more ecologically diverse than their closest relatives (Soarimalala and Goodman, 2011; Bronner, 1995) so we predicted that they would be more morphologically diverse than golden moles. However, our results do not support our original prediction, highlighting the importance of quantitative tests of perceived morphological patterns.

In our full analysis, tenrecs only had higher morphological diversity than golden moles when the skulls were measured in lateral view (Table 1). There was no difference in morphological diversity when we analysed the skulls in dorsal or ventral views. This is most likely due to our choice of landmarks. The two outline curves in lateral view (Figure REF) emphasise morphological variation in the back and top of the skulls. These curves summarise overall shape variation but they do not identify

clear anatomical differences because they are defined by relative features rather than homologous structures (Zelditch et al., 2012). Therefore, high morphological diversity in tenrecs when analysed in this view may not indicate biologically or ecologically relevant variation. These lateral aspects of the skull morphology were not visible in the dorsal and ventral photographs so they could not be included in those analyses. In contrast, our landmarks in the dorsal, and particularly ventral, views focus on morphological variation in the overall outline shape of the sides of the skull and palate (Figure REF). The result that tenrecs are no more diverse than golden moles in these areas makes intuitive sense: most tenrecs have broad, non-specialised diets (Olson, 2013) so there is no obvious functional reason why they should have particularly diverse palate morphologies. The different results for our analysis of lateral skull morphologies compared to dorsal and ventral views highlight the importance of using multiple approaches when studying 3D morphological shape using 2D geometric morphometrics techniques (Arnqvist and Mårtensson, 1998).

In addition to the differences among the three skull views, our results indicate that, in skulls at least, the overall morphological diversity within tenrecs is not as large as is often assumed (e.g. Eisenberg and Gould, 1969; Olson, 2013). Studies of morphological variation are sensitive to the sampling used. If a particular morphotype is over-represented then the similarities among those species will reduce the overall morphological variation within the group (Foote, 1991). This appears to be the case for our data; it was only when we included a sub-sample of *Microgale* tenrecs that we found higher morphological diversity in tenrecs compared to golden moles across all three skull analyses (Table 1). While there are clear physical differences among Family members (Olson, 2013; Eisenberg

and Gould, 1969), the majority of tenrecs are very morphologically similar (Jenkins, 2003) so morphological diversity in the Family as a whole is not as large as it first appears. Of course our results are based on skull shape only and analyses of other morphological traits may produce different results, but they do provide an insight into the differences between subjective and quantitative assessments of morphological diversity.

Caveats

As highlighted above, landmark choice and placement will inevitably influence the results of a geometric morphometrics study. Our interest in broad-scale, cross-taxonomic comparisons of cranial morphology constrained our choice of landmarks to those that could be accurately identified in many different species (e.g. Ruta et al., 2013; Goswami et al., 2011; Wroe and Milne, 2007). In contrast, studies that use skulls to characterise morphological variation within species (e.g. Blagojević and Milošević-Zlatanović, 2011; Bornholdt et al., 2008) or to delineate species boundaries within a clade (e.g. Panchetti et al., 2008) tend to focus on more detailed, biologically homologous landmarks (Zelditch et al., 2012). Repeating our analyses with a narrower taxonomic focus may give greater insight into the specific morphological differences among subgroups of tenrecs and golden moles.

The goal of our study was to quantify morphological variation in tenrecs instead of relying on subjective assessments of their high morphological diversity (Olson, 2013; Soarimalala and Goodman, 2011; Eisenberg and Gould, 1969). However, it is difficult to quantify overall morphological diversity because any study is inevitably constrained by its

choice of specific traits (Roy and Foote, 1997). Variation in skull shape is only one aspect of overall morphology. Quantifying variation in other morphological traits could yield different patterns. Therefore future work should extend our approach beyond skulls to gain a more complete understanding of the overall morphological diversity of tenrecs and golden moles.

Conclusions

We have presented the first quantitative investigation of morphological diversity in tenrecs. Our results indicate that, overall, tenrec skulls are not more morphologically diverse than golden moles and that similarities among the species rich *Microgale* tenrecs mask signals of higher morphological diversity among the rest of the Family. Of course the results presented here are restricted to just one axis of morphological variation and further analysis of other traits is required. However, our findings provide a foundation for future investigations and represent a significant step towards a more quantitative understanding of patterns of morphological and evolutionary diversity in tenrecs.

Acknowledgements

We thank Thomas Guillerme, François Gould and the members of NERD club for their insightful discussions and comments. Thank you to museum staff and curators for facilitating our access to their collections: Leona Leonard and Nigel Monaghan (Natural History Museum, Ireland),

Roberto Portela Miguez and Paula Jenkins (Natural History Museum, London), Esther Langan (Smithsonian Institute), Eileen Westwig (American Museum of Natural History), Judy Chupasko (Museum of Comparative Zoology) and Bill Stanley and Steve Goodman (Field Museum).

References

Adams, D. C., E. Otárola-Castillo, and E. Paradis. 2013. geomorph: an R package for the collection and analysis of geometric morphometric shape data. Methods in Ecology and Evolution 4:393–399.

Adams, D. C., F. J. Rohlf, and D. Slice. 2004. Geometric morphometrics: Ten years of progress following the "revolution". Italian Journal of Zoology 71:5–16.

Anderson, M. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32–46.

Arnqvist, G. and T. Mårtensson. 1998. Measurement error in geometric morphometrics; empirical strategies to assess and reduce its impact on measures of shape. Acta Zoologica Academiae Scientiarum Hungaricae 44:73–96.

Asher, R. J. and T. Lehmann. 2008. Dental eruption in Afrotherian mammals. BMC Biology 6:14.

Barrow, E. and N. Macleod. 2008. Shape variation in the mole dentary (Talpidae: Mammalia). Zoological Journal of the Linnean Society 153:187–211.

Blagojević, M. and S. Milošević-Zlatanović. 2011. Sexual shape dimorphism in Serbian roe deer (*Capreolus capreolus* L.). Mammalian Biology - Zeitschrift für Säugetierkunde 76:735–740.

Bookstein, F. 1997. Landmark methods for forms without landmarks: morphometrics of group differences in outline shape. Medical Image Analysis 1:225–243.

Bornholdt, R., L. R. Oliveira, and M. E. Fabián. 2008. Size and shape variability in the skull of *Myotis nigricans* (schinz, 1821) (chiroptera: Vespertilionidae) from two geographic areas in brazil. Brazilian Journal of Biology 68:623–631.

Bou, J., A. Casinos, and J. Ocaña. 1987. Allometry of the limb long bones of insectivores and rodents. Journal of Morphology 192:113–123.

Bronner, G. 1995. Systematic revision of the golden mole genera *Amblysomus*, *Chlorotalpa* and *Calcochloris* (Insectivora: Chrysochloromorpha; Chrysochloridae). Ph.D. thesis.

Brusatte, S., M. Benton, M. Ruta, and G. Lloyd. 2008. Superiority, competition and opportunism in the evolutionary radiation of dinosaurs. Science 321:1485–1488.

Davis, W. and D. Schmidly. 1997. The Mammals of Texas - Online Edition. `http://www.nsrl.ttu.edu/tmot1/Default.htm`.

Eisenberg, J. F. and E. Gould. 1969. The Tenrecs: A Study in Mammalian Behaviour and Evolution. Smithsonian Contributions to Zoology 27:1–152.

Finlay, S. and N. Cooper. 2013a. "Insectivore" mammal mandibles. http://dx.doi.org/10.6084/m9.figshare.717187.

Finlay, S. and N. Cooper. 2013b. "Insectivore" mammal skulls, dorsal view. http://dx.doi.org/10.6084/m9.figshare.705863.

Finlay, S. and N. Cooper. 2013c. "Insectivore" mammal skulls, lateral view. http://dx.doi.org/10.6084/m9.figshare.715890.

Finlay, S. and N. Cooper. 2013d. "Insectivore" mammal skulls, ventral view. http://dx.doi.org/10.6084/m9.figshare.715841.

Foote, M. 1991. Morphological and taxonomic diversity in a clade's history: the blastoid record and stochastic simulations. University of Michigan, Museum of Paleontology Contributions 28:101–140.

Foth, C., S. Brusatte, and R. Butler. 2012. Do different disparity proxies converge on a common signal? Insights from the cranial morphometrics and evolutionary history of *Pterosauria* (Diapsida: Archosauria). Journal of Evolutionary Biology 25:904–915.

Garbutt, N. 1999. Mammals of Madagascar. Pica Press, Sussex.

Glor, R. 2010. Phylogenetic insights on adaptive radiation. Annual Review of Ecology, Evolution, and Systematics 41:251–270.

Goodman, S. M., C. J. Raxworthy, C. P. Maminirina, and L. E. Olson. 2006. A new species of shrew tenrec (*Microgale jobihely*) from northern Madagascar. Journal of Zoology 270:384–398.

Goswami, A., N. Milne, and S. Wroe. 2011. Biting through constraints: cranial morphology, disparity and convergence across living and fossil

carnivorous mammals. Proceedings of the Royal Society B: Biological Sciences 278:1831–1839.

Hoffmann, R. and D. Lunde. 2008. Order Erinaceomorpha Pages 192–297. Princeton University Press, Oxfordshire, UK.

Hopkins, M. 2013. Decoupling of taxonomic diversity and morphological disparity during decline of the Cambrian trilobite family Pterocephaliidae. Journal of Evolutionary Biology 26:1665–1676.

Jenkins, P. 2003. *Microgale*, shrew tenrecs Pages 1273–1278. The University of Chicago Press, Chicago.

Karataş, A., M. Mouradi Gharkheloo, and T. Kankiliç. 2007. Cranial features and karyotypes of two hedgehogs (Insectivora: Erinaceidae) from Iran. Anatomia, Histologia, Embryologia 36:419–423.

Knox Jones, J. and R. Manning. 1992. Insectivores Page 75. Texas Tech University Press, United States of America.

Lin, L.-K. and M. Motokawa. 2010. Mammals of Taiwan, Volume 1. Soricomorpha. `http://mammal.biota.biodiv.tw/`.

Losos, J. 2011. Convergence, adaptation and constraint. Evolution 65:1827–1840.

Losos, J. B. and D. Mahler. 2010. Adaptive radiation: the interaction of ecological opportunity, adaptation and speciation Pages 381–420. Sinauer Association, Sunderland, MA.

MacLeod, N. 2012. Going Round the Bend ii: Extended Eigenshape Analysis. `http://www.palass.org`.

MacPhee, R. 1987. The shrew tenrecs of Madagascar: Systematic revision and holocene distribution of *Microgale* (Tenrecidae, Insectivora). American Museum Novitates Number 2889:1–45.

Mahler, D., T. Ingram, L. Revell, and J. Losos. 2013. Exceptional convergence on the macroevolutionary landscape in island lizard radiations. Science 341:292–295.

Mitteroecker, P. and P. Gunz. 2009. Advances in geometric morphometrics. Evolutionary Biology 36:235–247.

Muldoon, K., D. de Blieux, E. Simons, and P. Chatracth. 2009. The subfossil occurrence and paleoecological significance of small mammals at Ankilitelo Cave, Southwestern Madagascar. Journal of Mammalogy 90:111–1131.

Muschick, M., A. Indermaur, and W. Salzburger. 2012. Convergent evolution within an adaptive radiation of cichlid fishes. Current Biology 22:1–7.

Nagorsen, D. 2002. An identification manual to the small mammals of British Columbia. Ministry of Sustainable Resource Management, Ministry of Water, Land and Air Protection, Biodiversity Branch and Royal BC Museum.

Nowak, R. 1983. Walker's Mammals of the World, 4th edition vol. 1. Johns Hopkins University Press, Baltimore.

Olson, L. E. 2013. Tenrecs. Current Biology 23:R5–R8.

Olson, L. E. and S. M. Goodman. 2003. Phylogeny and biogeography of tenrecs Pages 1235–1242. The University of Chicago Press, Chicago.

Olson, L. E., S. M. Goodman, and A. D. Yoder. 2004. Illumination of cryptic species boundaries in long-tailed shrew tenrecs (Mammalia: Tenrecidae; *Microgale*), with new insights into geographic variation and distributional constraints. Biological Journal of the Linnean Society 83:1–22.

Olson, M. E. and A. Arroyo-Santos. 2009. Thinking in continua: beyond the "adaptive radiation" metaphor. BioEssays 31:1337–1346.

Panchetti, F., M. Scalici, G. Carpaneto, and G. Gibertini. 2008. Shape and size variations in the cranium of elephant-shrews: a morphometric contribution to a phylogenetic debate. Zoomorphology 127:69–82.

Price, S., S. S. B. Hopkins, K. K. Smith, and L. Roth. 2012. Tempo of trophic evolution and its impact on mammalian diversification. Proceedings of the National Academy of Sciences, USA 109:7008–7012.

Quérouil, S., P. Hutterer, M. Colyn, J. Kerbis Peterhans, and E. Verheyen. 2001. Phylogeny and evolution of African shrews (Mammalia: Soricidae) inferred from 16s rRNA sequences. Molecular Phylogenetics and Evolution 20:185–195.

R Core Team. 2014. R: A language and environment for statistical computing. `http://www.R-project.org/`.

Repenning, C. 1967. Subfamilies and Genera of the Soricidae. Geological Survey Professional Paper 565 United States Government Printing Office, Washington.

RHOI. 2013. Revealing Hominid Origins Iinitiative Fossil Photography Protocol, U.C Berkeley. `http://rhoi.berkeley.edu/RHOI_photo/RHOI_Photography_Protocol.html`.

562 Rohlf, F. 2012. Tpsutil ver 1.53. http://life.bio.sunysb.edu/morph/.

563 Rohlf, F. 2013. Tpsdig2 ver 2.17. http://life.bio.sunysb.edu/morph/.

564 Rohlf, J. and L. Marcus. 1993. A revolution in morphometrics. Trends in
565 Ecology and Evolution 8:129–132.

566 Roy, K. and M. Foote. 1997. Morphological approaches to measuring
567 biodiversity. Trends in Ecology and Evolution 12:277–281.

568 Ruta, M., K. Angielczyk, J. Fröbisch, and M. Benton. 2013. Decoupling of
569 morphological disparity and taxic diversity during the adaptive
570 radiation of anomodont therapsids. Proceedings of the Royal Society B:
571 Biological Sciences 280:20131071.

572 Salton, J. A. and E. Sargis. 2009. Evolutionary morphology of the
573 Tenrecoidea (Mammalia) hindlimb skeleton. Journal of Morphology
574 270:367–387.

575 Serb, J., A. Alejandrino, E. Otárola-Castillo, and D. Adams. 2011.
576 Morphological convergence of shell shape in distantly related scallop
577 species (Mollusca: Pectinidae). Zoological Journal of the Linnean
578 Society 163:571–584.

579 Slice, D. 2007. Geometric morphometrics. Annual Review of
580 Anthropology 36:261–281.

581 Soarimalala, V. and S. Goodman. 2011. Les petits mammiferes de
582 Madagascar. Guides sur la diversité biologique de Madagascar
583 Association Vahatra, Antananarivo, Madagascar.

584 Stanhope, M., V. Waddell, O. Madsen, W. de Jong, S. Hedges, G. Cleven,
585 D. Kao, and M. Springer. 1998. Molecular evidence for multiple origins

of insectivora and for a new order of endemic african insectivore mammals. Proceedings of the National Academy of Sciences, USA 95:9967–9972.

Wilson, D. and D. Reeder. 2005. Mammal species of the world. A taxonomic and geographic reference (3rd edition). Johns Hopkins University Press.

Wroe, S. and N. Milne. 2007. Convergence and remarkably consistent constraint in the evolution of carnivore skull shape. Evolution 61:1251–1260.

Zelditch, M., D. Swiderski, and D. Sheets. 2012. Geometric Morphometrics for Biologists, 2nd edition. Academic Press, Elsevier.

List of Figures

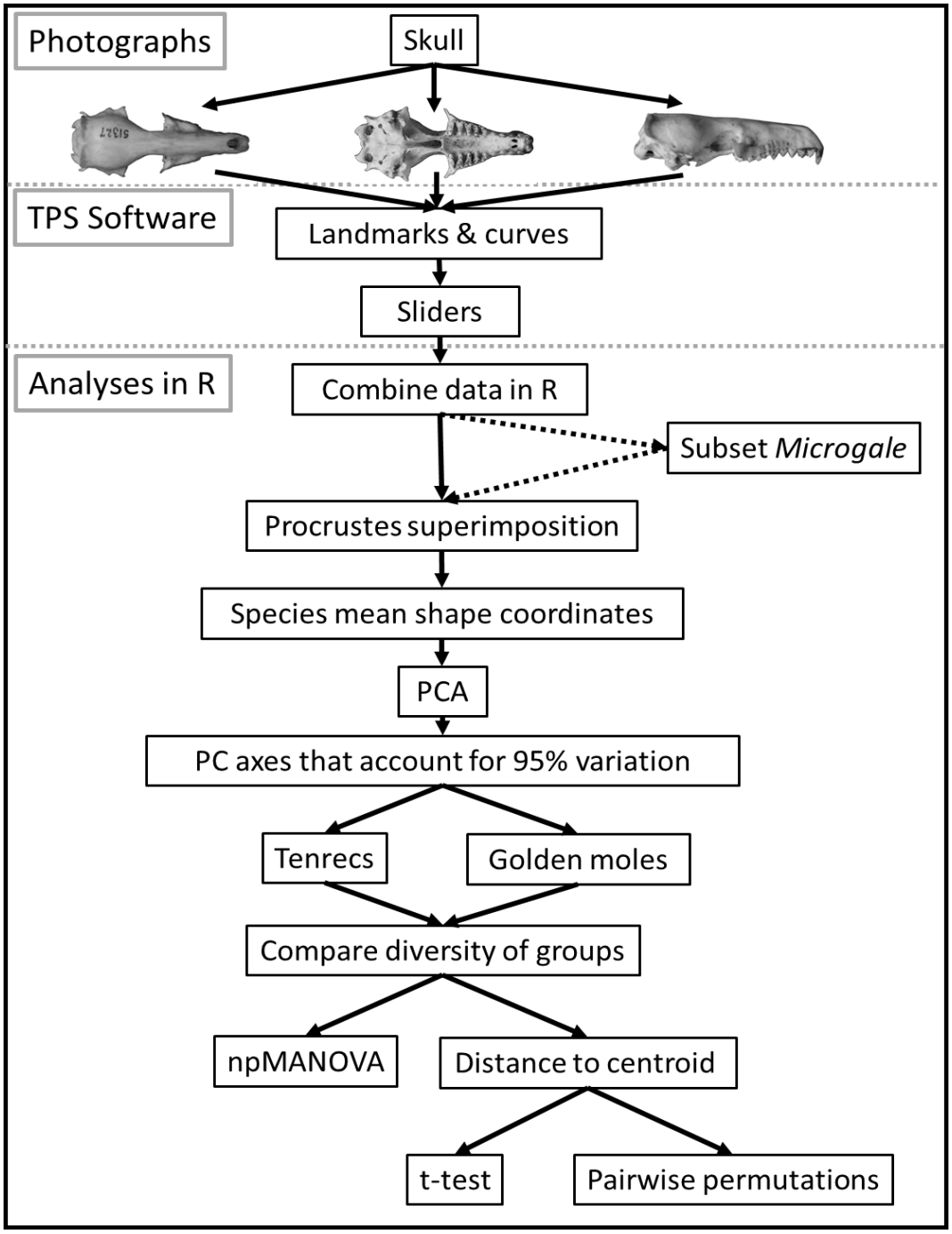

Figure 1: Summary of the main steps in our data collection, processing and analysis protocol. Note that the analyses were repeated separately for each set of photographs: skulls in dorsal, ventral and lateral views. The dashed arrows refer to the stage at which we selected a subsample of the tenrecs (including just five species of the *Microgale* Genus) so that we could compare the morphological diversity of this reduced subsample of tenrec species to the diversity of golden moles.

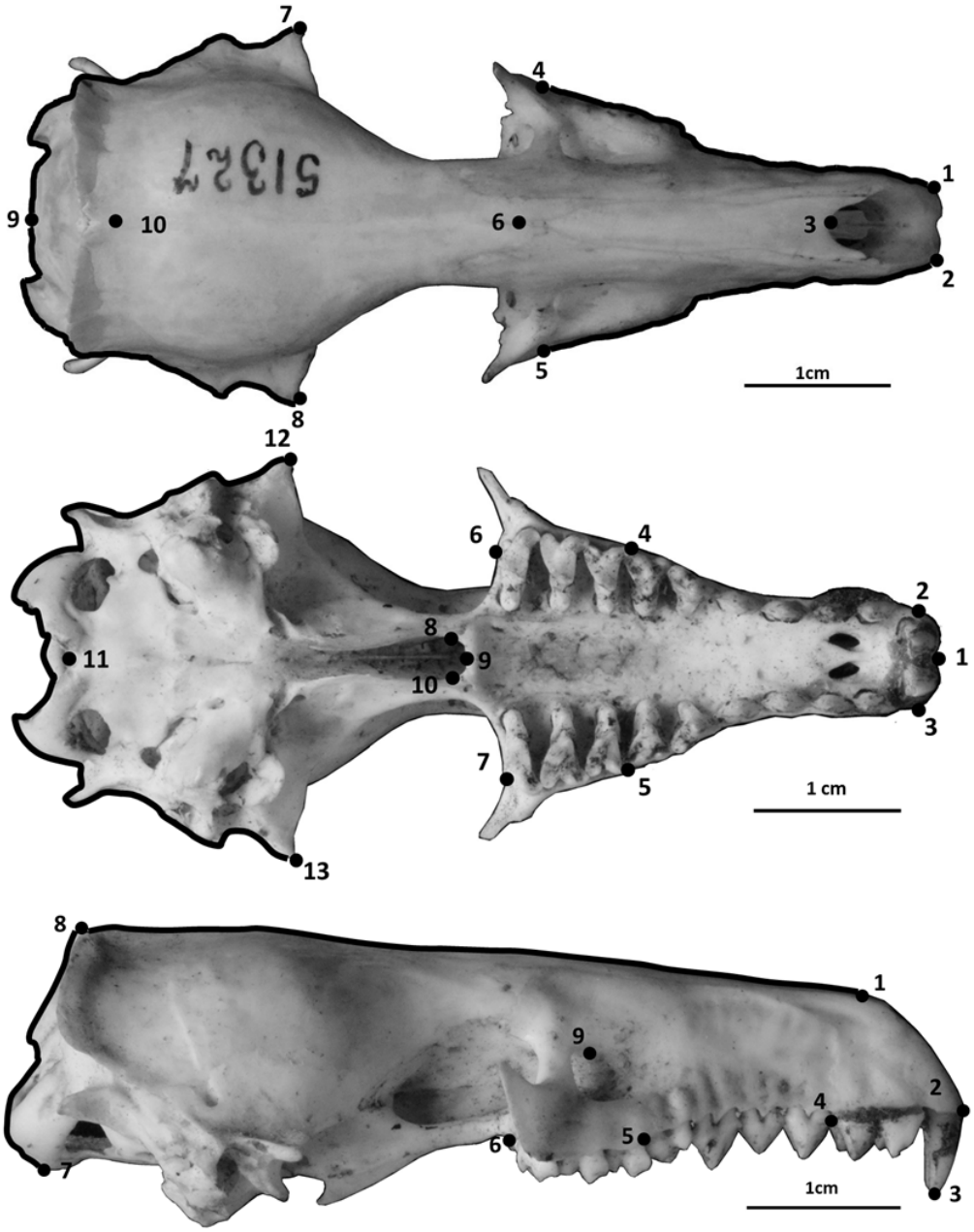

Figure 2: Landmarks (numbered points) and curves (outlines) for the skulls in dorsal,ventral and lateral view. See the supplementary material for detailed landmark descriptions. The skulls are two different specimens of *Potamogale velox* (otter shrew tenrec), museum accession numbers AMNH 51327 (dorsal picture) and BMNH 1934.6.16.2 (ventral and lateral pictures).

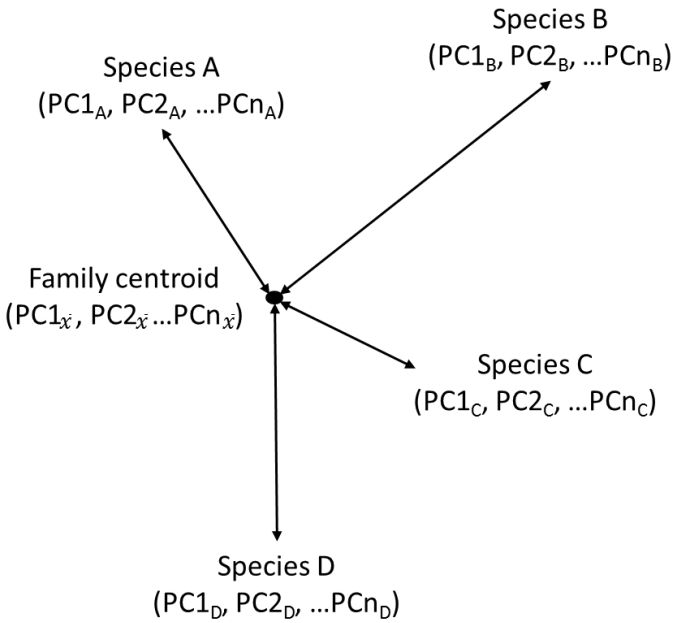

Figure 3: Estimating morphological diversity as the mean Euclidean distance between each species and the Family centroid. Every species had scores on the principal components (PC) axes that accounted for 95% of the variation in the principal components analysis. The number of axes (PCn) varied for each analysis but they were the same within a single analysis. PC scores were used to calculate the Euclidean distance from each species to the Family centroid (average ($\bar{x}$) PC scores for the entire Family). Morphological diversity of the Family is the average value of these Euclidean distances.

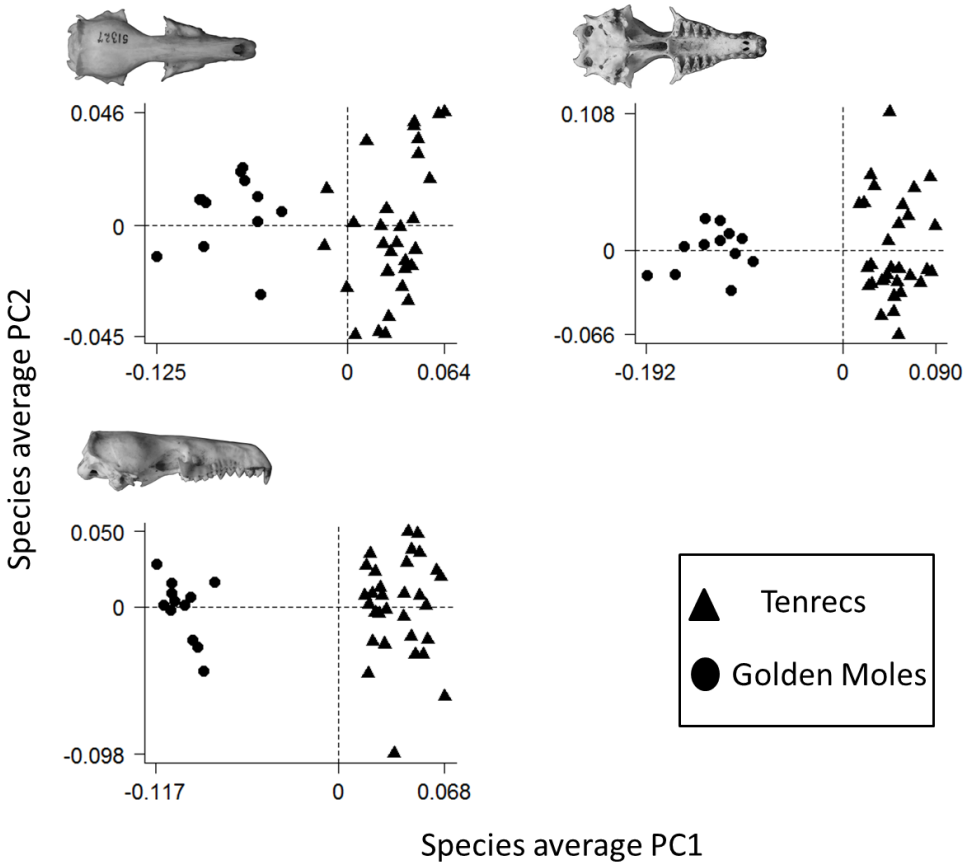

Figure 4: Principal components plots of the morphospaces occupied by tenrecs (triangles, n=31 species) and golden moles (circles, n=12 species) for the skulls in dorsal (top left), ventral (top right) and lateral (bottom left) views. Each point represents the average skull shape of an individual species. Axes are principal component 1 (PC1) and principal component 2 (PC2) of the average scores from principal components analyses of mean Procrustes shape coordinates for each species.

List of Tables

Table 1: Morphological diversity in tenrecs compared to golden moles (12 species). N is the number of tenrec species: 31 species or 17 species including just five representatives of the *Microgale* Genus. Morphological diversity of the Family is the mean Euclidean distance from each species to the Family centroid. Significant differences between the two Families ($p<0.05$) from two-tailed t-tests are highlighted in bold.

N	Analysis	Morphological diversity		t_{df}	p value
		Tenrecs	Golden moles		
		(mean ± s.e)	(mean ± s.e)		
31	Skulls dorsal	0.036 ± 0.0029	0.029 ± 0.0032	$-1.63_{29.88}$	0.11
	Skulls ventral	0.048 ± 0.0034	0.044 ± 0.0041	$-0.68_{26.99}$	0.51
	Skulls lateral	0.044 ± 0.0041	0.032 ± 0.0037	$-2.16_{35.03}$	**0.04**
17	Skulls dorsal	0.044 ± 0.0025	0.029 ± 0.0032	$-3.62_{22.75}$	**<0.01**
	Skulls ventral	0.054 ± 0.0039	0.042 ± 0.0041	$-2.23_{25.46}$	**0.04**
	Skulls lateral	0.054 ± 0.0053	0.031 ± 0.0037	$-3.47_{26.31}$	**<0.01**

Table 2: Results of the permutation analyses comparing the observed differences in morphological diversity to a null distribution of expected results. Morphological diversity of the Family is the mean Euclidean distance from each species to the Family centroid. Results are shown for both the full (N=31 species of tenrec compared to 12 species of golden mole) and reduced (N=17 species of tenrec compared to 12 golden moles) data sets. Significant values ($p<0.05$) indicate that the observed morphological diversity is different to the expected differences under a null hypothesis of equivalent diversities in the two Families.

N	Analysis	Morphological diversity					p value
		Measured values			Permuted values		
		Tenrecs	Golden moles	Difference	Min.	Max.	
31	Dorsal	0.036	0.029	0.007	-0.011	0.009	0.013
	Ventral	0.048	0.044	0.004	-0.014	0.013	0.023
	Lateral	0.044	0.032	0.012	-0.012	0.011	¡0.001
17	Dorsal	0.044	0.029	0.015	-0.011	0.014	¡0.001
	Ventral	0.054	0.042	0.013	-0.017	0.019	0.023
	Lateral	0.054	0.031	0.022	-0.018	0.019	¡0.001