

1 SIVE FINLAY^{1,2} AND NATALIE COOPER^{1,2,*}

2 ¹ School of Natural Sciences, Trinity College Dublin, Dublin 2, Ireland.

3 ² Trinity Centre for Biodiversity Research, Trinity College Dublin, Dublin
4 2, Ireland.

5 *Corresponding author: Natalie Cooper; ncooper@tcd.ie; Zoology

6 Building, Trinity College Dublin, Dublin 2, Ireland. Tel: +353 1 896 1926.

7 Introduction

8 Analysing patterns of morphological diversity has important implications
9 for our understanding of ecological and evolutionary traits. For example,
10 from a functional ecology perspective, morphological characteristics of
11 limbs inform us about locomotory style (e.g. Bou et al., 1987) and the
12 trophic niches associated with particular dental morphologies affect
13 speciation and diversification rates through time (Price et al., 2012).
14 Morphological diversity is also an important aspect of evolutionary
15 patterns such as adaptive radiations and convergent evolution. High
16 morphological diversity is a unifying (Losos and Mahler, 2010; Olson and
17 Arroyo-Santos, 2009), although not defining (Glor, 2010; Olson and
18 Arroyo-Santos, 2009), characteristic of adaptive radiations. Furthermore,
19 analysing morphological convergences in groups such as freshwater
20 cichlid fish (Muschick et al., 2012) and anole lizards (Mahler et al., 2013)
21 gives interesting insights into the relative repeatability of evolution (Losos,
22 2011).

23 Although studies of morphological diversity have clear implications
24 for our understanding of ecological and evolutionary patterns, apart from
25 a few examples (e.g. Ruta et al., 2013; Goswami et al., 2011; Brusatte et al.,
26 2008), it is still common to study morphological diversity from a
27 qualitative rather than quantitative perspective. However, we need to
28 quantify the morphological similarities and differences among species to
29 gain a better understanding of their ecological interactions and
30 evolutionary history. Unfortunately, morphological diversity is difficult to
31 quantify. Studies are inevitably constrained to measure the diversity of
32 specific traits rather than overall morphologies (Roy and Foote, 1997). In
33 addition, our perception of morphological diversity is influenced by the
34 trait being used. One study of pterosaurs demonstrated that comparing
35 the diversity of different morphological traits using varying methods
36 produced similar results (Foth et al., 2012). However, it remains unclear
37 whether this finding can be applied to all vertebrate groups: in some
38 species, comparing the relative diversity of cranial and limb morphologies
39 may yield different results (Foth et al., 2012). Furthermore, linear
40 measurements of morphological traits can restrict our understanding of
41 overall morphological variation. A distance matrix of measurements

42 between specific points is unlikely to give a completely accurate
43 representation of a three dimensional structure (Rohlf and Marcus, 1993).

44 These are important limitations to consider but geometric
45 morphometric approaches help to overcome some of the issues associated
46 with traditional morphological studies (Adams et al., 2004).
47 Morphometric studies based on caliper measurements of particular
48 features can only describe a limited set of distances, ratios and angles
49 which often fail to capture the overall shape of a specific structure (Slice,
50 2007). Geometric morphometrics circumvents these issues by using a
51 system of Cartesian landmark coordinates to define anatomical points.
52 This method captures more of the true, overall anatomical shape of
53 particular structures (Mitteroecker and Gunz, 2009). These more detailed
54 approaches are useful tools for studying patterns of morphological
55 diversity.

56 Here we apply geometric morphometric techniques to quantify
57 morphological diversity in a Family of small mammals, the tenrecs.
58 Tenrecs (Afrosoricida, Tenrecidae) are a morphologically diverse group
59 that is commonly cited as an example of both convergent evolution and an
60 adaptive radiation (Soarimalala and Goodman, 2011; Eisenberg and
61 Gould, 1969). The Family is comprised of 34 species, 31 of which are
62 endemic to Madagascar (Olson, 2013). Body masses of tenrecs span three
63 orders of magnitude (2.5 to $\geq 2,000$ g); a greater range than all other
64 Families, and most Orders, of living mammals (Olson and Goodman,
65 2003). Within this vast size range there are tenrecs which convergently
66 resemble shrews (*Microgale* tenrecs), moles (*Oryzorictes* tenrecs) and
67 hedgehogs (*Echinops* and *Setifer* tenrecs, Eisenberg and Gould, 1969). Their
68 similarities include examples of morphological, behavioural and
69 ecological convergence (Soarimalala and Goodman, 2011). Tenrecs are one
70 of only four endemic mammalian clades in Madagascar and the small
71 mammal species they resemble are absent from the island (Garbutt, 1999).
72 Therefore, it appears that tenrecs represent an adaptive radiation of
73 species which filled otherwise vacant ecological niches (Soarimalala and
74 Goodman, 2011). The similarities among tenrecs and other small
75 mammals are even more remarkable when you consider their
76 phylogenetic history. Tenrecs were originally classified within the general

77 "Insectivora" clade and only molecular studies revealed their true
78 phylogenetic affinities within the Afrotherian mammals (Stanhope et al.,
79 1998). Therefore, despite initial appearances, tenrecs are more closely
80 related to elephants, manatees and armadillos than they are to shrews,
81 moles or hedgehogs.

82 Although tenrecs are often cited as an example of both an adaptive
83 radiation and exceptional convergent evolution, these claims have not
84 been investigated quantitatively. There are qualitative similarities among
85 the hind limb morphologies of tenrecs and several other unrelated species
86 with similar locomotory styles (Salton and Sargis, 2009) but the degree of
87 morphological similarity has not been established. Morphological
88 diversity is an important feature of adaptive radiations (Losos and Mahler,
89 2010) and it also informs our understanding of convergent phenotypes
90 (Muschick et al., 2012). Therefore, it is important to quantify patterns of
91 morphological diversity in tenrecs to gain an insight into their evolution.

92 We present the first quantitative study of patterns of morphological
93 diversity in tenrecs. We use geometric morphometric techniques (Rohlf
94 and Marcus, 1993) to compare cranial morphological diversity in tenrecs
95 to that of their closest relatives, the golden moles (Afrosoricida,
96 Chrysochloridae). We expect tenrecs to be more morphologically diverse
97 than golden moles because tenrecs occupy a wider variety of ecological
98 niches. The tenrec Family includes terrestrial, semi-fossorial, semi-aquatic
99 and semi-arboreal species (Soarimalala and Goodman, 2011). In contrast,
100 all golden moles occupy very similar, fossorial ecological niches (Bronner,
101 1995). Greater ecological variety is often (though not always) correlated
102 with higher morphological diversity (Losos and Mahler, 2010). However,
103 our results reveal that, in skulls at least, morphological diversity in tenrecs
104 is not as great as it first appears.

105 **Materials and Methods**

106 The methods we used involved several steps of i) data collection, ii)
107 geometric morphometric analyses and iii) estimating morphological
108 diversity. For clarity, Figure 1 summarises all of these steps and we
109 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, 2013a), ventral (Finlay and Cooper, 2013c) and lateral (Finlay and Cooper, 2013b) skull pictures. Copyright restrictions from the other museums prevent public sharing of their images but they are available on request.

Geometric morphometric analyses

We used a combination of landmark and semilandmark analysis approaches to assess the shape variability in the skulls. 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 used when photographing the 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. Our final data sets included photographs of 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

178 over - sampling: simpler structures will require fewer semilandmarks to
179 accurately represent their shape (MacLeod, 2012). To ensure that we
180 applied a uniform standard of shape representation to each outline
181 segment (i.e. that simple structures would not be over-represented and
182 more complex features would not be under-represented), we followed the
183 method outlined by MacLeod (2012). For each data set we chose a random
184 selection of photos of specimens which represented the breadth of the
185 morphological data (i.e. specimens from each sub-group of species). We
186 drew the appropriate curves on each specimen and over-sampled the
187 number of points on the curves. We measured the length of the line and
188 regarded that as the 100%, true length of that outline. We then re-sampled
189 the curves with decreasing numbers of points and measured the length of
190 the outlines. We calculated the length of each re-sampled curve as a
191 percentage of the total length of the curve and then found the average
192 percentage length for that reduced number of semilandmark points across
193 all of the specimens in my test file. We continued this process until we
194 found the minimum number of points that gave a curve length which was
195 at least 95% accurate. We repeated these curve-sampling tests for each
196 analysis to determine the minimum number of semilandmark points
197 which would give accurate representations of morphological shape.

198 Figure 2 depicts that landmarks and curves which we used for each of
199 the sets of photographs. For landmarks which are defined by dental
200 structures, we used published dental sources (Repenning, 1967; Eisenberg
201 and Gould, 1969; Nowak, 1983; MacPhee, 1987; Knox Jones and Manning,
202 1992; Davis and Schmidly, 1997; Quéroutil et al., 2001; Nagorsen, 2002;
203 Wilson and Reeder, 2005; Goodman et al., 2006; Karataş et al., 2007;
204 Hoffmann and Lunde, 2008; Asher and Lehmann, 2008; Muldoon et al.,
205 2009; Lin and Motokawa, 2010) where available to identify the number
206 and type of teeth in each species. Detailed descriptions of the landmarks
207 can be found in the supplementary material.

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

213 carried out all further analyses in R version 3.1.1 (R Core Team, 2014).
214 Data and code for all of our analyses is available on GitHub (Finlay and
215 Cooper, 2015).

216 At this stage, we either used the full data set (31 species of tenrec and
217 12 species of golden mole) or a reduced data set with just 17 species of
218 tenrec (Figure 1). We created this reduced data set because the majority of
219 tenrec species (19 out of 31 in our data) belong to the *Microgale*
220 (shrew-like) Genus that has relatively low morphological diversity
221 (Soarimalala and Goodman, 2011; Jenkins, 2003). This may mask signals
222 of higher morphological diversity among other tenrecs. To test this, we
223 created a subset of the tenrec data that included just five of the *Microgale*
224 species, each representing one of the five sub-divisions of *Microgale*
225 outlined by Soarimalala and Goodman (2011), i.e. small, small-medium,
226 medium, large and long-tailed species. We compared the morphological
227 diversity of this subset of tenrecs (n=17: five *Microgale* and 12
228 non-*Microgale* species) to that of the 12 species of golden moles (dashed
229 arrows in Figure 1). After this selection stage, all further steps in the
230 analyses were the same.

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

241 **Estimating morphological diversity**

242 We grouped the PC scores for tenrecs and golden moles separately so that
243 we could estimate the diversity of each Family and then compare the two
244 groups (Figure 1). We compared morphological diversity in two ways.
245 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).

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

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 would 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 subsetting 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

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.

311 Based on our measures of mean Euclidean distance to the Family
312 centroids, tenrec skulls are more morphologically diverse than golden
313 mole skulls when they are measured in lateral view but not in dorsal or
314 ventral view (Table 1). In contrast, when we analysed morphological
315 diversity of skulls within the sub-sample of 17 tenrecs (including just five
316 *Microgale* species) compared to the 12 golden mole species, we found that
317 tenrec skulls were significantly more morphologically diverse than golden
318 moles in all analyses (Table 1).

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

322 Discussion

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

331 In our full analysis, tenrecs only had higher morphological diversity
332 than golden moles when the skulls were measured in lateral view (Table
333 1). There was no difference in morphological diversity when we analysed
334 the skulls in dorsal or ventral views. This is most likely due to our choice
335 of landmarks. The two outline curves in lateral view (Figure 2) emphasise
336 morphological variation in the back and top of the skulls. These curves
337 summarise overall shape variation but they do not identify clear
338 anatomical differences because they are defined by relative features rather
339 than homologous structures (Zelditch et al., 2012). Therefore, high
340 morphological diversity in tenrecs when analysed in this view may not
341 indicate biologically or ecologically relevant variation. These lateral
342 aspects of the skull morphology were not visible in the dorsal and ventral
343 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 2). 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). 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.

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

380 as large as it first appears. The goal of our study was to quantify
381 morphological variation in tenrecs instead of relying on subjective
382 assessments of their high morphological diversity (Olson, 2013;
383 Soarimalala and Goodman, 2011; Eisenberg and Gould, 1969). However, it
384 is difficult to quantify overall morphological diversity because any study
385 is inevitably constrained by its choice of specific traits (Roy and Foote,
386 1997). Variation in skull shape is only one aspect of overall morphology.
387 Quantifying variation in other morphological traits could yield different
388 patterns. Therefore future work should extend our approach beyond
389 skulls to gain a more complete understanding of the overall morphological
390 diversity of tenrecs and golden moles. While recognising these limitations,
391 our results provide valuable insights into the differences between
392 subjective and quantitative assessments of morphological diversity.

393 **Conclusions**

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

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414 **References**

- 415 Adams, D. C., E. Otárola-Castillo, and E. Paradis. 2013. geomorph: an R
416 package for the collection and analysis of geometric morphometric
417 shape data. *Methods in Ecology and Evolution* 4:393–399.
- 418 Adams, D. C., F. J. Rohlf, and D. Slice. 2004. Geometric morphometrics:
419 Ten years of progress following the "revolution". *Italian Journal of*
420 *Zoology* 71:5–16.
- 421 Anderson, M. 2001. A new method for non-parametric multivariate
422 analysis of variance. *Austral Ecology* 26:32–46.
- 423 Arnqvist, G. and T. Mårtensson. 1998. Measurement error in geometric
424 morphometrics; empirical strategies to assess and reduce its impact on
425 measures of shape. *Acta Zoologica Academiae Scientiarum Hungaricae*
426 44:73–96.
- 427 Asher, R. J. and T. Lehmann. 2008. Dental eruption in Afrotherian
428 mammals. *BMC Biology* 6:14.
- 429 Barrow, E. and N. Macleod. 2008. Shape variation in the mole dentary
430 (Talpidae: Mammalia). *Zoological Journal of the Linnean Society*
431 153:187–211.
- 432 Blagojević, M. and S. Milošević-Zlatanović. 2011. Sexual shape
433 dimorphism in Serbian roe deer (*Capreolus capreolus* L.). *Mammalian*
434 *Biology - Zeitschrift für Säugetierkunde* 76:735–740.
- 435 Bookstein, F. 1997. Landmark methods for forms without landmarks:
436 morphometrics of group differences in outline shape. *Medical Image*
437 *Analysis* 1:225–243.

- 438 Bornholdt, R., L. R. Oliveira, and M. E. Fabián. 2008. Size and shape
439 variability in the skull of *Myotis nigricans* (schinz, 1821) (chiroptera:
440 Vespertilionidae) from two geographic areas in brazil. Brazilian Journal
441 of Biology 68:623–631.
- 442 Bou, J., A. Casinos, and J. Ocaña. 1987. Allometry of the limb long bones
443 of insectivores and rodents. Journal of Morphology 192:113–123.
- 444 Bronner, G. 1995. Systematic revision of the golden mole genera
445 *Amblysomus*, *Chlorotalpa* and *Calcochloris* (Insectivora:
446 Chrysochloromorpha; Chrysochloridae). Ph.D. thesis.
- 447 Brusatte, S., M. Benton, M. Ruta, and G. Lloyd. 2008. Superiority,
448 competition and opportunism in the evolutionary radiation of
449 dinosaurs. Science 321:1485–1488.
- 450 Davis, W. and D. Schmidly. 1997. The Mammals of Texas - Online Edition.
451 <http://www.nsr1.ttu.edu/tmot1/Default.htm>.
- 452 Eisenberg, J. F. and E. Gould. 1969. The Tenrecs: A Study in Mammalian
453 Behaviour and Evolution. Smithsonian Contributions to Zoology
454 27:1–152.
- 455 Finlay, S. and N. Cooper. 2013a. "Insectivore" mammal skulls, dorsal view.
456 <http://dx.doi.org/10.6084/m9.figshare.705863>.
- 457 Finlay, S. and N. Cooper. 2013b. "Insectivore" mammal skulls, lateral
458 view. <http://dx.doi.org/10.6084/m9.figshare.715890>.
- 459 Finlay, S. and N. Cooper. 2013c. "Insectivore" mammal skulls, ventral
460 view. <http://dx.doi.org/10.6084/m9.figshare.715841>.
- 461 Finlay, S. and N. Cooper. 2015. GitHub data and code repository.
462 https://github.com/SiveFinlay/Diversity_Paper.
- 463 Foote, M. 1991. Morphological and taxonomic diversity in a clade's
464 history: the blastoid record and stochastic simulations. University of
465 Michigan, Museum of Paleontology Contributions 28:101–140.
- 466 Foth, C., S. Brusatte, and R. Butler. 2012. Do different disparity proxies
467 converge on a common signal? Insights from the cranial morphometrics

- 468 and evolutionary history of *Pterosauria* (Diapsida: Archosauria). Journal
469 of Evolutionary Biology 25:904–915.
- 470 Garbutt, N. 1999. Mammals of Madagascar. Pica Press, Sussex.
- 471 Glor, R. 2010. Phylogenetic insights on adaptive radiation. Annual Review
472 of Ecology, Evolution, and Systematics 41:251–270.
- 473 Goodman, S. M., C. J. Raxworthy, C. P. Maminirina, and L. E. Olson. 2006.
474 A new species of shrew tenrec (*Microgale jobihely*) from northern
475 Madagascar. Journal of Zoology 270:384–398.
- 476 Goswami, A., N. Milne, and S. Wroe. 2011. Biting through constraints:
477 cranial morphology, disparity and convergence across living and fossil
478 carnivorous mammals. Proceedings of the Royal Society B: Biological
479 Sciences 278:1831–1839.
- 480 Hoffmann, R. and D. Lunde. 2008. Order Erinaceomorpha Pages 192–297.
481 Princeton University Press, Oxfordshire, UK.
- 482 Hopkins, M. 2013. Decoupling of taxonomic diversity and morphological
483 disparity during decline of the Cambrian trilobite family
484 Pterocephaliidae. Journal of Evolutionary Biology 26:1665–1676.
- 485 Jenkins, P. 2003. *Microgale*, shrew tenrecs Pages 1273–1278. The University
486 of Chicago Press, Chicago.
- 487 Karataş, A., M. Mouradi Gharkheloo, and T. Kankiliç. 2007. Cranial
488 features and karyotypes of two hedgehogs (Insectivora: Erinaceidae)
489 from Iran. Anatomia, Histologia, Embryologia 36:419–423.
- 490 Knox Jones, J. and R. Manning. 1992. Insectivores Page 75. Texas Tech
491 University Press, United States of America.
- 492 Lin, L.-K. and M. Motokawa. 2010. Mammals of Taiwan, Volume 1.
493 Soricomorpha. <http://mammal.biota.biodiv.tw/>.
- 494 Losos, J. 2011. Convergence, adaptation and constraint. Evolution
495 65:1827–1840.

- 496 Losos, J. B. and D. Mahler. 2010. Adaptive radiation: the interaction of
497 ecological opportunity, adaptation and speciation Pages 381–420.
498 Sinauer Association, Sunderland, MA.
- 499 MacLeod, N. 2012. Going Round the Bend ii: Extended Eigenshape
500 Analysis. <http://www.palass.org>.
- 501 MacPhee, R. 1987. The shrew tenrecs of Madagascar: Systematic revision
502 and holocene distribution of *Microgale* (Tenrecidae, Insectivora).
503 American Museum Novitates Number 2889:1–45.
- 504 Mahler, D., T. Ingram, L. Revell, and J. Losos. 2013. Exceptional
505 convergence on the macroevolutionary landscape in island lizard
506 radiations. *Science* 341:292–295.
- 507 Mitteroecker, P. and P. Gunz. 2009. Advances in geometric morphometrics.
508 *Evolutionary Biology* 36:235–247.
- 509 Muldoon, K., D. de Blieux, E. Simons, and P. Chatrath. 2009. The
510 subfossil occurrence and paleoecological significance of small mammals
511 at Ankilitelo Cave, Southwestern Madagascar. *Journal of Mammalogy*
512 90:111–1131.
- 513 Muschick, M., A. Indermaur, and W. Salzburger. 2012. Convergent
514 evolution within an adaptive radiation of cichlid fishes. *Current Biology*
515 22:1–7.
- 516 Nagorsen, D. 2002. An identification manual to the small mammals of
517 British Columbia. Ministry of Sustainable Resource Management,
518 Ministry of Water, Land and Air Protection, Biodiversity Branch and
519 Royal BC Museum.
- 520 Nowak, R. 1983. Walker's Mammals of the World, 4th edition vol. 1. Johns
521 Hopkins University Press, Baltimore.
- 522 Olson, L. E. 2013. Tenrecs. *Current Biology* 23:R5–R8.
- 523 Olson, L. E. and S. M. Goodman. 2003. Phylogeny and biogeography of
524 tenrecs Pages 1235–1242. The University of Chicago Press, Chicago.

- 525 Olson, L. E., S. M. Goodman, and A. D. Yoder. 2004. Illumination of
526 cryptic species boundaries in long-tailed shrew tenrecs (Mammalia:
527 Tenrecidae; *Microgale*), with new insights into geographic variation and
528 distributional constraints. *Biological Journal of the Linnean Society*
529 83:1–22.
- 530 Olson, M. E. and A. Arroyo-Santos. 2009. Thinking in continua: beyond
531 the "adaptive radiation" metaphor. *BioEssays* 31:1337–1346.
- 532 Panchetti, F., M. Scalici, G. Carpaneto, and G. Gibertini. 2008. Shape and
533 size variations in the cranium of elephant-shrews: a morphometric
534 contribution to a phylogenetic debate. *Zoomorphology* 127:69–82.
- 535 Price, S., S. S. B. Hopkins, K. K. Smith, and L. Roth. 2012. Tempo of
536 trophic evolution and its impact on mammalian diversification.
537 *Proceedings of the National Academy of Sciences, USA* 109:7008–7012.
- 538 Quérrouil, S., P. Hutterer, M. Colyn, J. Kerbis Peterhans, and E. Verheyen.
539 2001. Phylogeny and evolution of African shrews (Mammalia:
540 Soricidae) inferred from 16S rRNA sequences. *Molecular Phylogenetics*
541 *and Evolution* 20:185–195.
- 542 R Core Team. 2014. R: A language and environment for statistical
543 computing. <http://www.R-project.org/>.
- 544 Repenning, C. 1967. Subfamilies and Genera of the Soricidae. Geological
545 Survey Professional Paper 565 United States Government Printing
546 Office, Washington.
- 547 RHOI. 2013. Revealing Hominid Origins Initiative Fossil Photography
548 Protocol, U.C Berkeley. [http:](http://rhoi.berkeley.edu/RHOI_photo/RHOI_Photography_Protocol.html)
549 [//rhoi.berkeley.edu/RHOI_photo/RHOI_Photography_Protocol.html](http://rhoi.berkeley.edu/RHOI_photo/RHOI_Photography_Protocol.html).
- 550 Rohlf, F. 2012. Tpsutil ver 1.53. <http://life.bio.sunysb.edu/morph/>.
- 551 Rohlf, F. 2013. Tpsdig2 ver 2.17. <http://life.bio.sunysb.edu/morph/>.
- 552 Rohlf, J. and L. Marcus. 1993. A revolution in morphometrics. *Trends in*
553 *Ecology and Evolution* 8:129–132.

- 554 Roy, K. and M. Foote. 1997. Morphological approaches to measuring
555 biodiversity. *Trends in Ecology and Evolution* 12:277–281.
- 556 Ruta, M., K. Angielczyk, J. Fröbisch, and M. Benton. 2013. Decoupling of
557 morphological disparity and taxic diversity during the adaptive
558 radiation of anomodont therapsids. *Proceedings of the Royal Society B:
559 Biological Sciences* 280:20131071.
- 560 Salton, J. A. and E. Sargis. 2009. Evolutionary morphology of the
561 Tenrecoidea (Mammalia) hindlimb skeleton. *Journal of Morphology*
562 270:367–387.
- 563 Serb, J., A. Alejandrino, E. Otárola-Castillo, and D. Adams. 2011.
564 Morphological convergence of shell shape in distantly related scallop
565 species (Mollusca: Pectinidae). *Zoological Journal of the Linnean
566 Society* 163:571–584.
- 567 Slice, D. 2007. Geometric morphometrics. *Annual Review of
568 Anthropology* 36:261–281.
- 569 Soarimalala, V. and S. Goodman. 2011. *Les petits mammifères de
570 Madagascar. Guides sur la diversité biologique de Madagascar*
571 *Association Vahatra, Antananarivo, Madagascar.*
- 572 Stanhope, M., V. Waddell, O. Madsen, W. de Jong, S. Hedges, G. Cleven,
573 D. Kao, and M. Springer. 1998. Molecular evidence for multiple origins
574 of insectivora and for a new order of endemic african insectivore
575 mammals. *Proceedings of the National Academy of Sciences, USA*
576 95:9967–9972.
- 577 Wilson, D. and D. Reeder. 2005. *Mammal species of the world. A
578 taxonomic and geographic reference (3rd edition).* Johns Hopkins
579 University Press.
- 580 Wroe, S. and N. Milne. 2007. Convergence and remarkably consistent
581 constraint in the evolution of carnivore skull shape. *Evolution*
582 61:1251–1260.
- 583 Zelditch, M., D. Swiderski, and D. Sheets. 2012. *Geometric Morphometrics
584 for Biologists*, 2nd edition. Academic Press, Elsevier.

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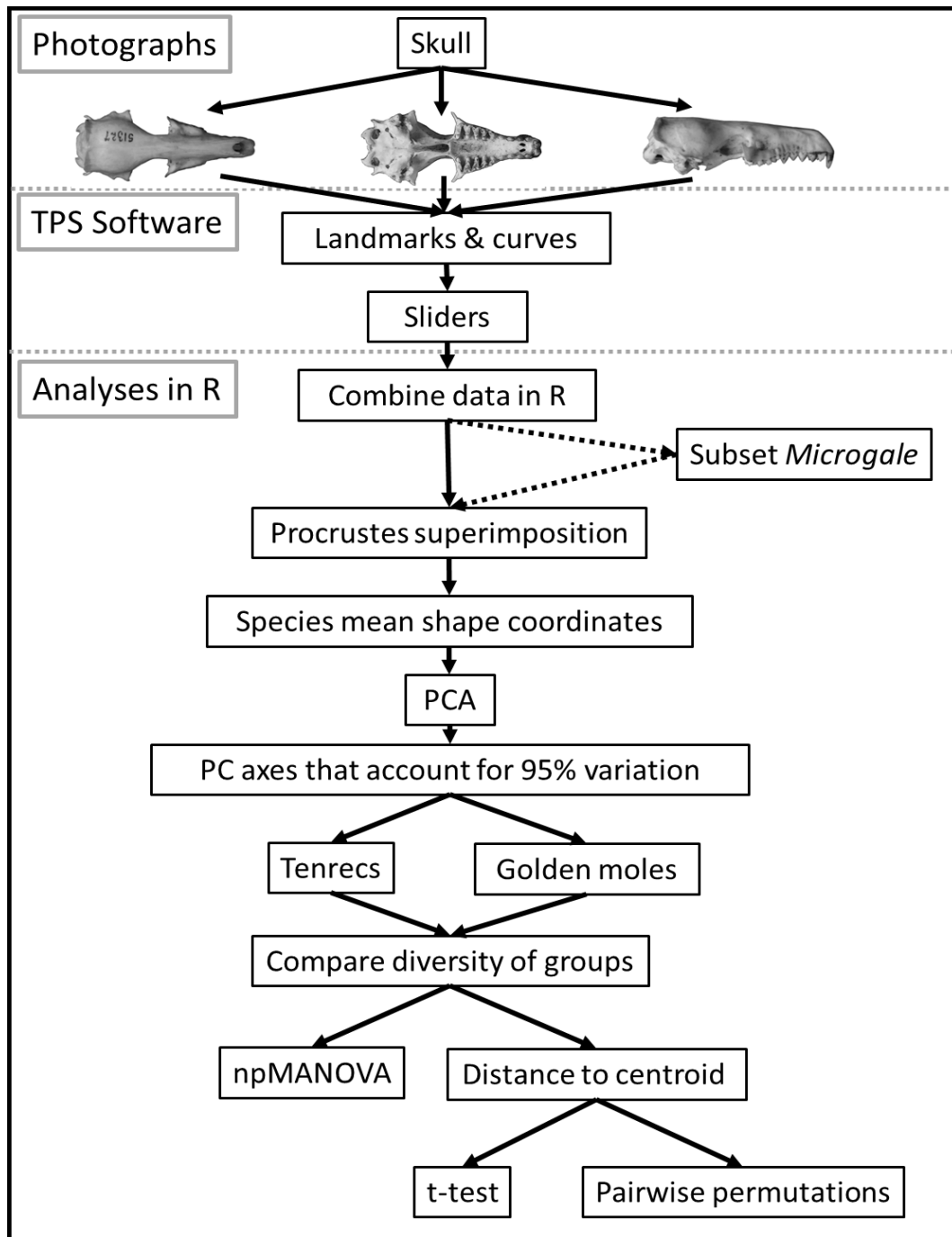


Figure 1: Summary of the main steps in our data collection, processing and analysis protocol. Note that the analyses were repeated separately for each set of photographs: skulls in dorsal, ventral and lateral views. The dashed arrows refer to the stage at which we selected a subsample of the tenrecs (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.

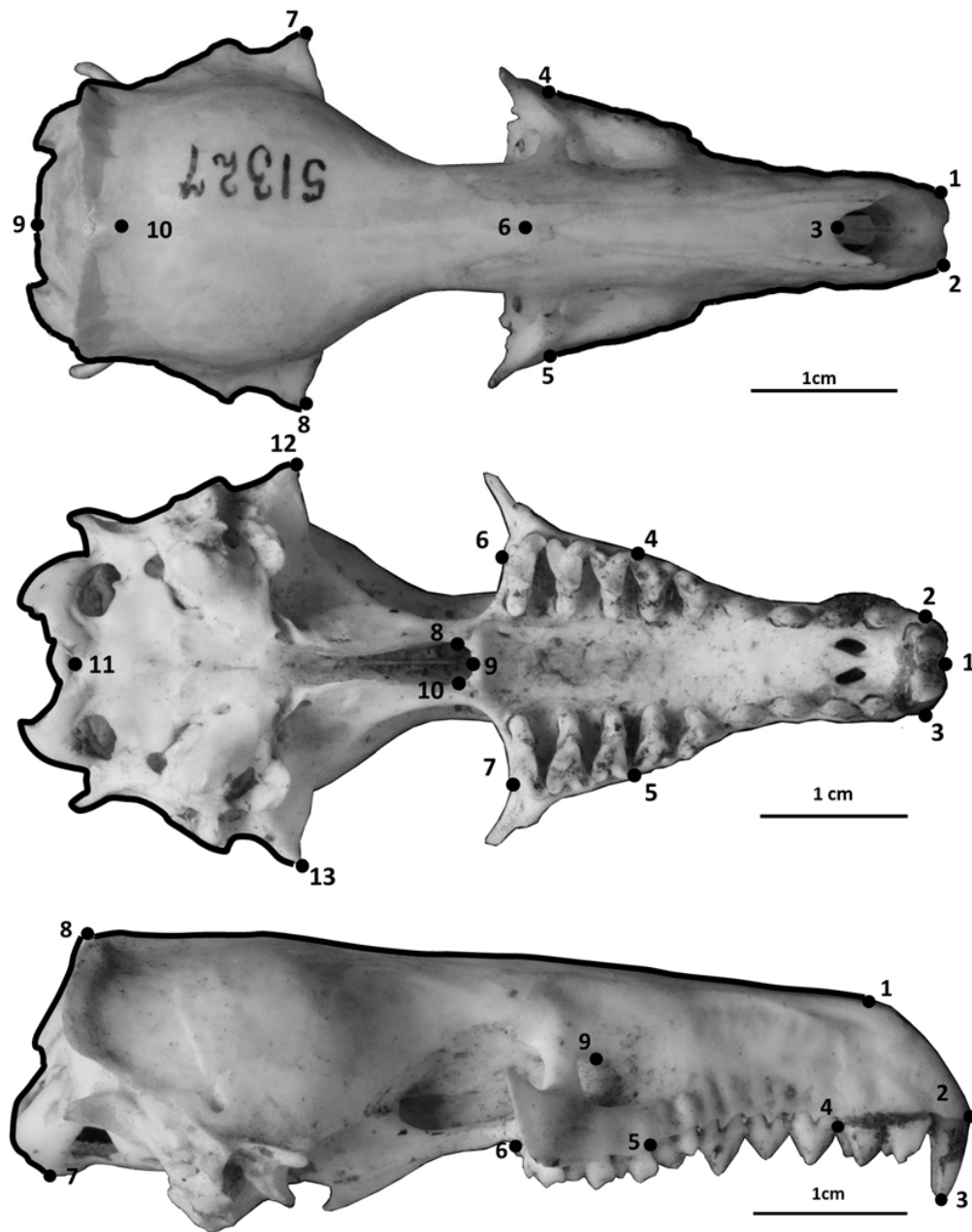


Figure 2: Landmarks (numbered points) and curves (outlines) for the skulls in dorsal, ventral and lateral view. See the supplementary material for detailed landmark descriptions. The skulls are two different specimens of *Potamogale velox* (otter shrew tenrec), museum accession numbers AMNH 51327 (dorsal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

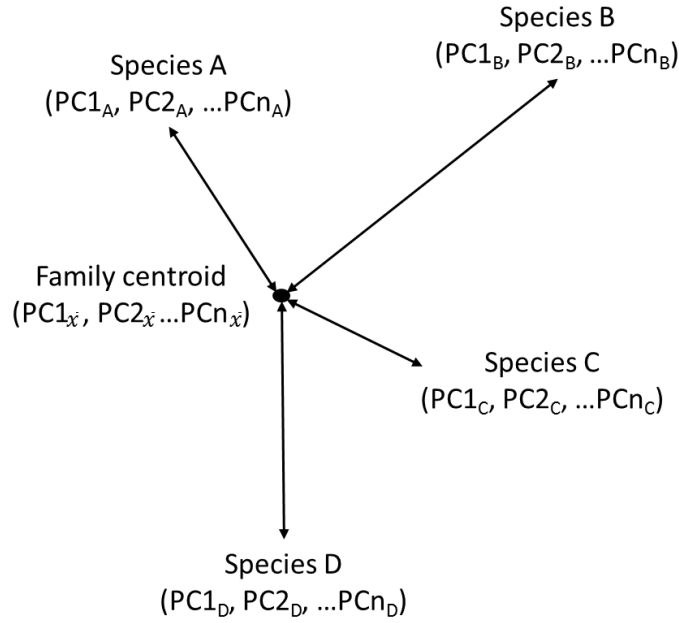


Figure 3: Estimating morphological diversity as the mean Euclidean distance between each species and the Family centroid. Every species had scores on the principal components (PC) axes that accounted for 95% of the variation in the principal components analysis. The number of axes (PCn) varied for each 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.

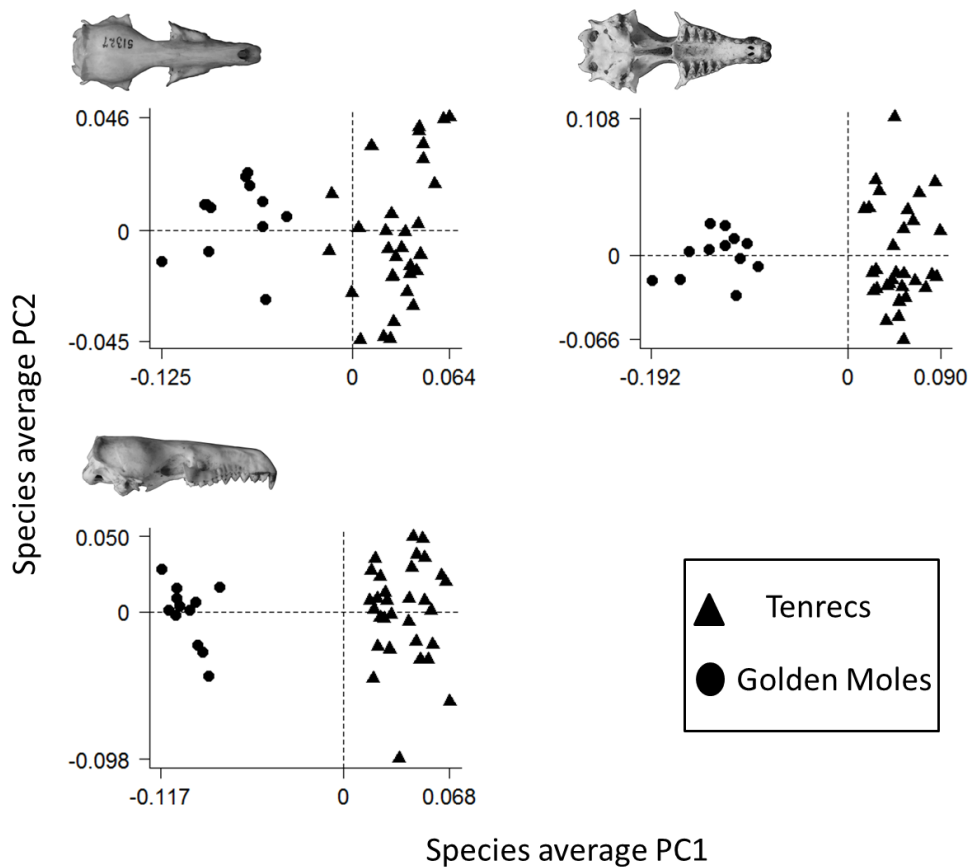


Figure 4: Principal components plots of the morphospaces occupied by tenrecs (triangles, $n=31$ species) and golden moles (circles, $n=12$ species) for the skulls in dorsal (top left), ventral (top right) and lateral (bottom left) views. Each point represents the average skull shape of an individual 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.

592 **List of Tables**

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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 (mean \pm s.e)	Golden moles (mean \pm s.e)		
31	Skulls dorsal	0.036 \pm 0.0029	0.029 \pm 0.0032	-1.63 _{29.88}	0.11
	Skulls ventral	0.048 \pm 0.0034	0.044 \pm 0.0041	-0.68 _{26.99}	0.51
	Skulls lateral	0.044 \pm 0.0041	0.032 \pm 0.0037	-2.16 _{35.03}	0.04
17	Skulls dorsal	0.044 \pm 0.0025	0.029 \pm 0.0032	-3.62 _{22.75}	<0.01
	Skulls ventral	0.054 \pm 0.0039	0.042 \pm 0.0041	-2.23 _{25.46}	0.04
	Skulls lateral	0.054 \pm 0.0053	0.031 \pm 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