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

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Morphological diversity is often studied qualitatively. However, to truly understand the evolution of exceptional diversity, it is important to take a quantitative approach instead of relying on subjective, qualitative assessments. Here, we present a quantitative analysis of morphological diversity in a Family of small mammals, the tenrecs (Afrosoricida, Tenrecidae).

Tenrecs are often cited as an example of an exceptionally morphologically diverse group. However, this assumption has not been tested quantitatively. We use geometric morphometric analyses of skull shape to test whether tenrecs are more morphologically diverse than their closest relatives, the golden moles (Afrosoricida, Chrysochloridae). Tenrecs occupy a wider range of ecological niches than golden moles so we predict that they will be more morphologically diverse.

Contrary to our expectations, We find that tenrec skulls are only more morphologically diverse than golden moles when measured in lateral view. Furthermore, similarities among the species-rich *Microgale* tenrec Genus appear to mask higher morphological diversity in the rest of the Family. These results reveal new insights into the morphological diversity of tenrecs and highlight the importance of using quantitative methods to test qualitative assumptions about patterns of morphological diversity.

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7 Introduction

8 Analysing patterns of morphological diversity (the variation in physical
9 form (Foote, 1997) has important implications for our understanding of
10 ecological and evolutionary traits. Increasingly, many studies recognise
11 the importance of quantifying the degree of morphological diversity
12 instead of relying on subjective assessments of diversity in form (e.g.
13 Ruta et al., 2013; Hopkins, 2013; Goswami et al., 2011; Drake and
14 Klingenberg, 2010; Price et al., 2010; Brusatte et al., 2008). We need to
15 quantify the morphological similarities and differences among species to
16 gain a better understanding of their ecological interactions and
17 evolutionary history.

18 Unfortunately, morphological diversity is difficult to quantify. Many
19 studies are constrained to measuring the diversity of specific traits rather
20 than overall morphologies (Roy and Foote, 1997). In addition, our
21 perception of morphological diversity is influenced by the trait being
22 measured, and results may depend on the particular trait being analysed
23 (Foth et al., 2012). Furthermore, linear measurements of morphological
24 traits can restrict our understanding of overall morphological variation;
25 a distance matrix of measurements among specific points is unlikely to
26 give a complete representation of a three dimensional structure (Rohlf
27 and Marcus, 1993). Geometric morphometric approaches can circumvent
28 some of these issues by using a system of Cartesian landmark
29 coordinates to define anatomical points (Adams et al., 2004, and
30 references therein). This method captures more of the true, overall

31 anatomical shape of particular structures (Mitteroecker and Gunz, 2009).
 32 In particular, two-dimensional geometric morphometric approaches are
 33 commonly used to analyse 3D morphological shape and are appropriate
 34 for cross-species comparisons (e.g. Muschick et al., 2012; Panchetti et al.,
 35 2008; Wroe and Milne, 2007). Any bias from 2D representation of a 3D
 36 structure is unlikely to be a significant issue for interspecific studies as
 37 the overall shape variation among species is greater than discrepancies
 38 introduced by using 2D morphometric techniques (Cardini, 2014). These
 39 more detailed approaches are useful tools for studying patterns of
 40 morphological diversity.

41 Here we apply geometric morphometric techniques to quantify
 42 morphological diversity in a family of small mammals, the tenrecs.
 43 Tenrecs (Afrosoricida, Tenrecidae) are a morphologically diverse group
 44 that researchers often identify as an example of both convergent
 45 evolution and an adaptive radiation (Soarimalala and Goodman, 2011;
 46 Eisenberg and Gould, 1969). The family is comprised of 34 species, 31 of
 47 which are endemic to Madagascar (Olson, 2013). Body masses of tenrecs
 48 span three orders of magnitude (2.5 to > 2,000g): a greater range than all
 49 other families, and most orders, of living mammals (Olson and
 50 Goodman, 2003). Within this vast size range there are tenrecs which
 51 resemble shrews (*Microgale* tenrecs), moles (*Oryzorictes* tenrecs) and
 52 hedgehogs (*Echinops* and *Setifer* tenrecs, Eisenberg and Gould, 1969). The
 53 similarities among tenrecs and other small mammal species include
 54 examples of morphological, behavioural and ecological convergence
 55 (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 through gradual morphological specialisations (Poux et al., 2008).

The claims that tenrecs are an example of both an adaptive radiation and convergent evolution 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.

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: McGee and Wainwright, 2013; Losos and Mahler, 2010) correlated with higher morphological diversity. However, our results reveal that, in skulls at least, morphological diversity in tenrecs is not as great as it first appears.

Materials and Methods

Our methods involved 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) collected data from five museums: Natural History Museum, London (BMNH), Smithsonian Institute Natural History Museum, Washington D.C. (SI), American Museum of Natural History, New York (AMNH), Museum of Comparative Zoology, Cambridge M.A. (MCZ) and Field Museum of Natural History, Chicago (FMNH). We used the taxonomy in Wilson & Reeder's Mammal Species of the World (2005), except for the recently discovered tenrec species *Microgale jobihely* (Goodman et al., 2006). We photographed all of the intact tenrec and golden mole skulls available in the collections. This included 31 of the 34 species in the tenrec family (Olson, 2013) and 12 of the 21 species of golden moles (Wilson and Reeder, 2005).

We took pictures of the skulls using photographic copy stands. To take possible light variability into account, we took a photograph of a white sheet of paper each day 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 and using a remote control (Hähnel Combi TF) to avoid camera shake. We photographed the specimens on a black material background with a light source in the top left-hand corner of the photograph and a scale bar placed below the specimen. We used small bean bags to hold the specimens in position to ensure that they lay in a flat plane relative to the camera, and used the grid-line function on the live-view display screen of the camera to position the specimens in the centre of each image.

All skulls were photographed in three views: dorsal, ventral and lateral (right side) (Figure 1). When the right sides of the skulls were damaged or incomplete, we photographed the left sides and later reflected the images (e.g. Barrow and Macleod, 2008). 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). Details of the total sample size for each species can be found in the supplementary material.

After taking the photographs we used the Canon Digital Photo Professional software (Canon, 2013) to convert the raw files to binary (grey scale) images and re-save 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 Natural History Museum are available on figshare (dorsal; Finlay and Cooper (2013a), ventral; Finlay and Cooper (2013c) and lateral; Finlay and Cooper (2013b)). Copyright restrictions from the other museums prevent public sharing of their images but they are available from the authors on request.

Geometric morphometric analyses

We used a combination of landmark and semilandmark 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 (dorsal, ventral and lateral views). One of us (SF) digitised landmarks and semilandmark points on every image individually.

Figure 2 depicts the landmarks and curves which we used for each skull view. For landmarks defined by dental structures, we used published dental sources where available (Repenning, 1967; Eisenberg and Gould, 1969; Nowak, 1983; MacPhee, 1987; Knox Jones and

149 Manning, 1992; Davis and Schmidly, 1997; Quéroutil et al., 2001;
 150 Nagorsen, 2002; Wilson and Reeder, 2005; Goodman et al., 2006; Karataş
 151 et al., 2007; Hoffmann and Lunde, 2008; Asher and Lehmann, 2008;
 152 Muldoon et al., 2009; Lin and Motokawa, 2010) to identify the number
 153 and type of teeth in each species. Detailed descriptions of the
 154 landmarks, as well as an example figure of landmarks on golden mole
 155 skulls, can be found in the supplementary material.

156 When using semilandmark approaches there is a potential problem
 157 of over-sampling: simpler structures will require fewer semilandmarks
 158 to accurately represent their shape (MacLeod, 2012). To ensure that we
 159 applied a uniform standard of shape representation to each outline
 160 segment (i.e. that simple structures would not be over-represented and
 161 more complex features would not be under-represented), we followed
 162 the method outlined by MacLeod (2012) to determine the minimum
 163 number of semilandmark points which would give accurate
 164 representations of morphological shape. We used 54 points for skulls in
 165 dorsal view (10 landmarks, 44 semilandmarks across 4 curves), 73 points
 166 for skulls in ventral view (13 landmarks, 60 semilandmarks) and 44
 167 points for skulls in lateral view (9 landmarks and 35 semilandmarks
 168 across 2 curves). See Figure 2 and the supplementary material for more
 169 details.

170 After creating the files with the landmarks and semilandmarks
 171 placed on each photograph, we used TPSUtil (Rohlf, 2012) to create
 172 "sliders" files that defined which points in the TPS files should be

173 treated as semilandmarks (Zelditch et al., 2012). We combined the
174 landmarks and taxonomic identification files into a single
175 morphometrics data object and carried out all further analyses in R
176 version 3.1.1 (R Core Team, 2014).

177 Next we used the `gpagen` function in version 2.1 of the `geomorph`
178 package (Adams et al., 2014; Adams and Otárola-Castillo, 2013) to run a
179 general Procrustes alignment (Rohlf and Marcus, 1993) of the landmark
180 coordinates while sliding the semilandmarks by minimising Procrustes
181 distance (Bookstein, 1997). We used these Procrustes-aligned coordinates
182 of all specimens to calculate average shape values for each species which
183 we then used for a principal components (PC) analysis with the
184 `plotTangentSpace` function (Adams and Otárola-Castillo, 2013). We
185 selected the number of principal component (PC) axes that accounted
186 for 95% of the variation in the data (Figure 1) and used these axes to
187 estimate morphological diversity in each family.

188 The majority of tenrec species (19 out of 31 in our data) belong to the
189 *Microgale* (shrew-like) genus that has relatively low morphological
190 diversity (Soarimalala and Goodman, 2011; Jenkins, 2003). This may
191 mask signals of higher morphological diversity among other tenrecs. To
192 test this, we created a subset of the tenrec data that included just five of
193 the *Microgale* species, each representing one of the five sub-divisions of
194 *Microgale* outlined by Soarimalala & Goodman (2011), i.e. small,
195 small-medium, medium, large and long-tailed species. We repeated the
196 general Procrustes alignment described above using this reduced data

197 set. We then compared the morphological diversity of the full data set
198 (31 species of tenrec) or a reduced data set with just 17 species of tenrec
199 (five *Microgale* and 12 non-*Microgale* species; Figure 1) to that of the 12
200 species of golden moles.

201 **Estimating morphological diversity**

202 We grouped the PC scores for tenrecs and golden moles separately so
203 that we could estimate the diversity of each family and then compare the
204 two groups (Figure 1). We compared morphological diversity in two
205 ways. First, we used non parametric multivariate analysis of variance
206 (npMANOVA; Anderson, 2001) to test whether tenrecs and golden
207 moles occupied significantly different positions within the
208 morphospaces defined by the PC axes that accounted for 95% of the
209 overall variation in the data (e.g. Serb et al., 2011; Ruta et al., 2013). A
210 significant difference between the two families would indicate that they
211 have unique morphologies which do not overlap. Second, we compared
212 morphological diversity within tenrecs to the diversity within golden
213 moles.

214 Morphological diversity (variation in form) is more commonly
215 referred to as morphological disparity (Foote, 1997). There are many
216 different methods for measuring disparity. Calculations based on
217 summary (principal component) axes of shape variation are popular
218 (e.g. Ruta et al., 2013; Foth et al., 2012; Brusatte et al., 2008; Wainwright,
219 2007) while other methods include calculating disparity directly from

Procrustes shape variables (Zelditch et al., 2012) or rate-based approaches which depend on phylogenetic branching patterns (e.g. Price et al., 2013, 2010; O'Meara et al., 2006). There is no single best method of measuring disparity (Ciampaglio et al., 2001) and each method makes different assumptions which are appropriate for different situations. Therefore, for clarity, we have chosen to measure variation in physical form using a clear, easily-interpretable method which captures variation in morphological diversity.

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 is the average PC score for each axis (the centroid).

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

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

242 of a smaller family could still bias the results. We used pairwise
243 permutation tests to account for this potential issue.

244 We tested the null hypothesis that tenrecs and golden moles have the
245 same morphological diversity (the same mean Euclidean distance to the
246 family centroid). If this is true, when we randomly assign the group
247 identity of each species (i.e. shuffle the "tenrec" and "golden mole"
248 labels) and then re-compare the morphological diversity of the two
249 groups, there should be no significant difference between these results
250 and those obtained when the species are assigned to the correct
251 groupings.

252 We performed this shuffling procedure (random assignation of group
253 identity) 1000 times and calculated the difference in morphological
254 diversity between the two groups for each permutation. This generated
255 a distribution of 1000 values which are calculations of the differences in
256 morphological diversity under the assumption that the null hypothesis
257 (equal morphological diversity in the two families) is true. This method
258 automatically accounts for differences in sample size because shuffling
259 of the group labels preserves the sample size of each group: there will
260 always be 12 species labelled as "golden mole" and then, depending on
261 the analysis, either 31 or 17 species labelled as "tenrec". Therefore, the
262 1000 permuted values of differences in morphological diversity create a
263 distribution of the expected difference in diversity between a group of
264 sample size 31 (or 17 in the case of the tenrec data subset) compared to a
265 group of sample size 12 under the null hypothesis that the two groups

266 have the same morphological diversity. We compared the observed
267 measures of the differences in morphological diversity between the two
268 families to these null distributions to determine whether there were
269 significant differences after taking sample size into account (two-tailed t
270 test). Data and code for all of our analyses are available on GitHub
271 (Finlay and Cooper, 2015).

272 Results

273 Figure 4 depicts the morphospaces defined by the first two principal
274 component (PC) axes from our principal components analyses (PCAs) of
275 skull and mandible morphologies. The PCAs are based on the average
276 Procrustes-superimposed shape coordinates for skulls in three views
277 (dorsal, ventral and lateral).

278 To compare morphological diversity in the two families, we used the
279 PC axes which accounted for 95% of the cumulative variation in each of
280 the skull analyses: dorsal (n=6 axes), ventral (n=7 axes) and lateral (n=7
281 axes). First, we compared the position of each family within the
282 morphospace plots. Tenrecs and golden moles occupy significantly
283 different positions in the dorsal (npMANOVA: $F_{1,42}=68.13$, $R^2=0.62$,
284 $p=0.001$), ventral (npMANOVA: $F_{1,42}=103.33$, $R^2=0.72$, $p=0.001$) and
285 lateral (npMANOVA: $F_{1,42}=76.7$, $R^2=0.65$, $p=0.001$) skull morphospaces,
286 indicating that the families have very different, non-overlapping cranial
287 and mandible morphologies (Figure 4). For each analysis, PC1

summarises a morphological change from the foreshortened, "squat" shape of golden mole skulls at one extreme to the rostrally elongated shape of tenrecs (particularly the *Microgale*) at the other extreme.

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

310 morphological patterns.

311 In our full analysis, tenrecs only had higher morphological diversity
 312 than golden moles when the skulls were measured in lateral view (Table
 313 1). There was no difference in morphological diversity when we
 314 analysed the skulls in dorsal or ventral views. This is most likely due to
 315 our choice of landmarks. The two outline curves in lateral view (Figure
 316 2) emphasise morphological variation in the back and top of the skulls.
 317 These curves summarise overall shape variation but they do not identify
 318 clear anatomical differences because they are defined by relative features
 319 rather than homologous structures (Zelditch et al., 2012). Therefore, high
 320 morphological diversity in tenrecs when analysed in this view may not
 321 indicate biologically or ecologically relevant variation. These lateral
 322 aspects of the skull morphology were not visible in the dorsal and
 323 ventral photographs so they could not be included in those analyses. In
 324 contrast, our landmarks in the dorsal, and particularly ventral, views
 325 focus on morphological variation in the overall outline shape of the sides
 326 of the skull and palate (Figure 2). The result that tenrecs are no more
 327 diverse than golden moles in these areas makes intuitive sense: most
 328 tenrecs have non-specialised insectivorous or faunivorous diets (Olson,
 329 2013) so there is no obvious functional reason why they should have
 330 particularly diverse palate morphologies. Similarly, while there are
 331 anatomical differences among tenrec tooth morphologies (Asher and
 332 Sánchez-Villagra, 2005) more work is required to determine if and how
 333 those differences correspond to variation in diet or feeding ecology. The
 334 different results for our analysis of lateral skull morphologies compared

335 to dorsal and ventral views highlight the importance of using multiple
336 approaches when studying 3D morphological shape using 2D geometric
337 morphometrics techniques (Arnqvist and Mårtensson, 1998). Future
338 analyses could use 3D geometric morphometric approaches to test
339 whether similar patterns emerge.

340 Landmark choice and placement will inevitably influence the results
341 of a geometric morphometrics study. Our interest in broad-scale,
342 cross-taxonomic comparisons of cranial morphology constrained our
343 choice of landmarks to those that could be accurately identified in many
344 different species (e.g. Ruta et al., 2013; Goswami et al., 2011; Wroe and
345 Milne, 2007; Goswami, 2006). In contrast, studies that use skulls to
346 characterise morphological variation within species (e.g. Blagojević and
347 Milošević-Zlatanović, 2011; Giannini et al., 2010; Flores et al., 2010;
348 Bornholdt et al., 2008) or to delineate species boundaries within a clade
349 (e.g. Panchetti et al., 2008) tend to focus on more detailed, biologically
350 homologous landmarks (Zelditch et al., 2012). Repeating our analyses
351 with a narrower taxonomic focus may give greater insight into the
352 specific morphological differences among subgroups of tenrecs and
353 golden moles.

354 In addition to the differences among the three skull views, our
355 results indicate that, in skulls at least, the overall morphological
356 diversity within tenrecs is not as large as is often assumed (e.g.
357 Eisenberg and Gould, 1969; Olson, 2013). Studies of morphological
358 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 (the *Microgale*) are very morphologically similar (Jenkins, 2003) so morphological diversity in the family as a whole is not as large as it first appears.

The goal of our study was to quantify morphological variation in tenrecs instead of relying on subjective assessments of their high morphological diversity. 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). While the skull is widely regarded as a good model for studying morphological variation (e.g. Blagojević and Milošević-Zlatanović, 2011; Flores et al., 2010; Giannini et al., 2010), 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. While recognising these limitations, our results provide valuable insights into the differences between subjective and quantitative assessments of morphological diversity.

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 aspect 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.

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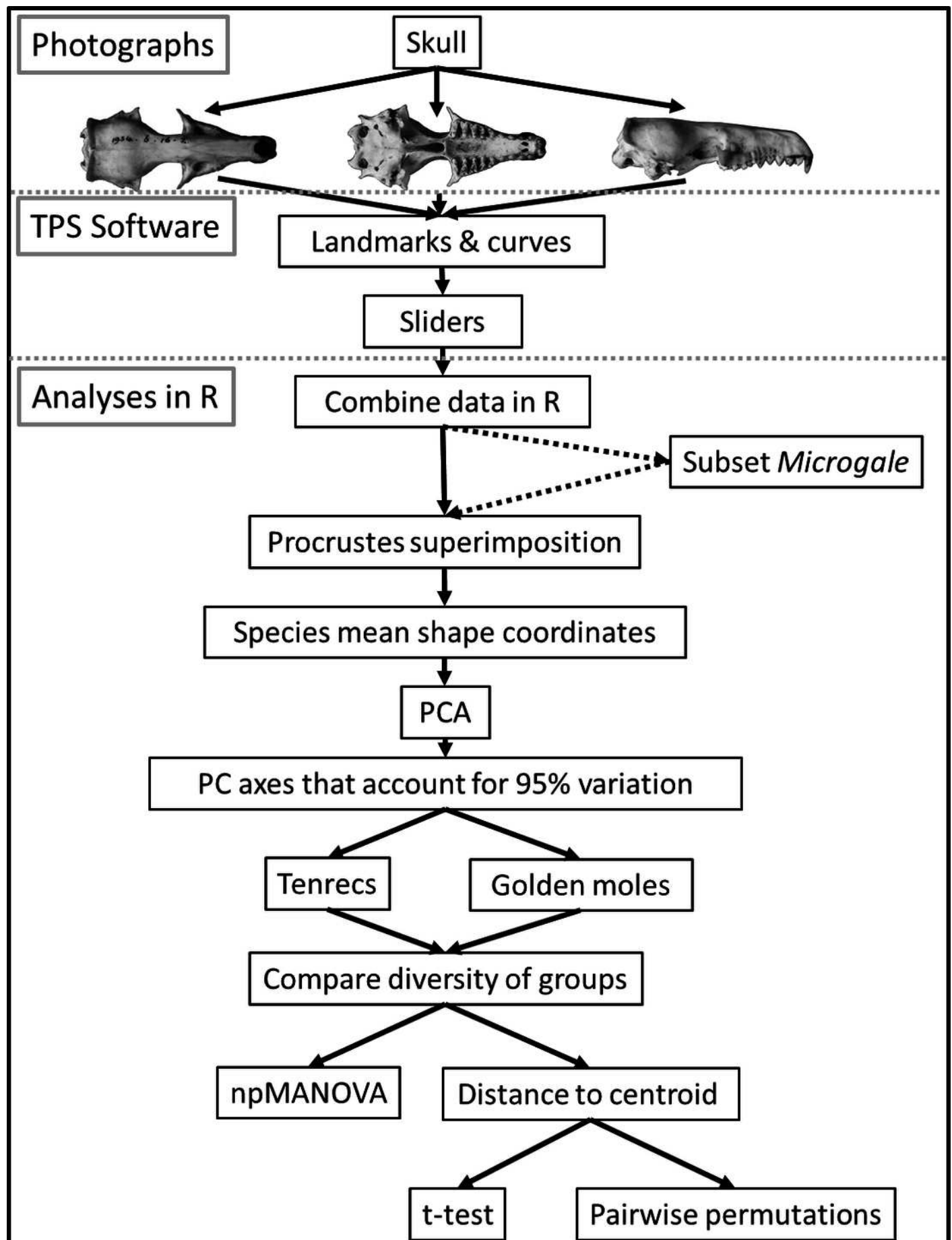
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1

Flowchart diagram of data collection and analysis

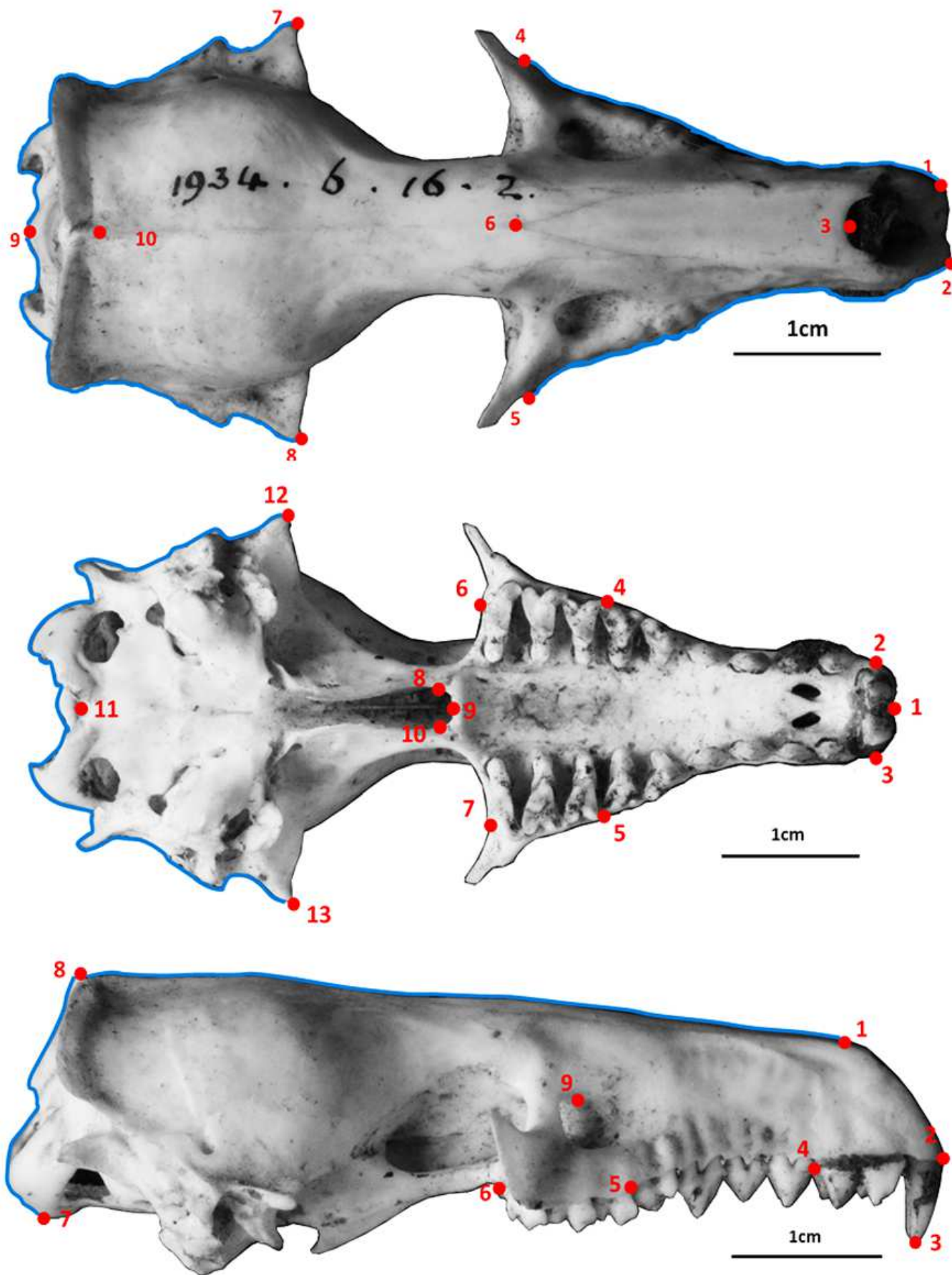
Summary of the main steps in our data collection, processing and analysis protocol. Note that the analyses were repeated separately for each set of photographs: skulls in dorsal, ventral and lateral views. The dashed arrows refer to the stage at which we selected a subsample of the tenrecs (including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



2

Skulls: dorsal, ventral and lateral landmarks

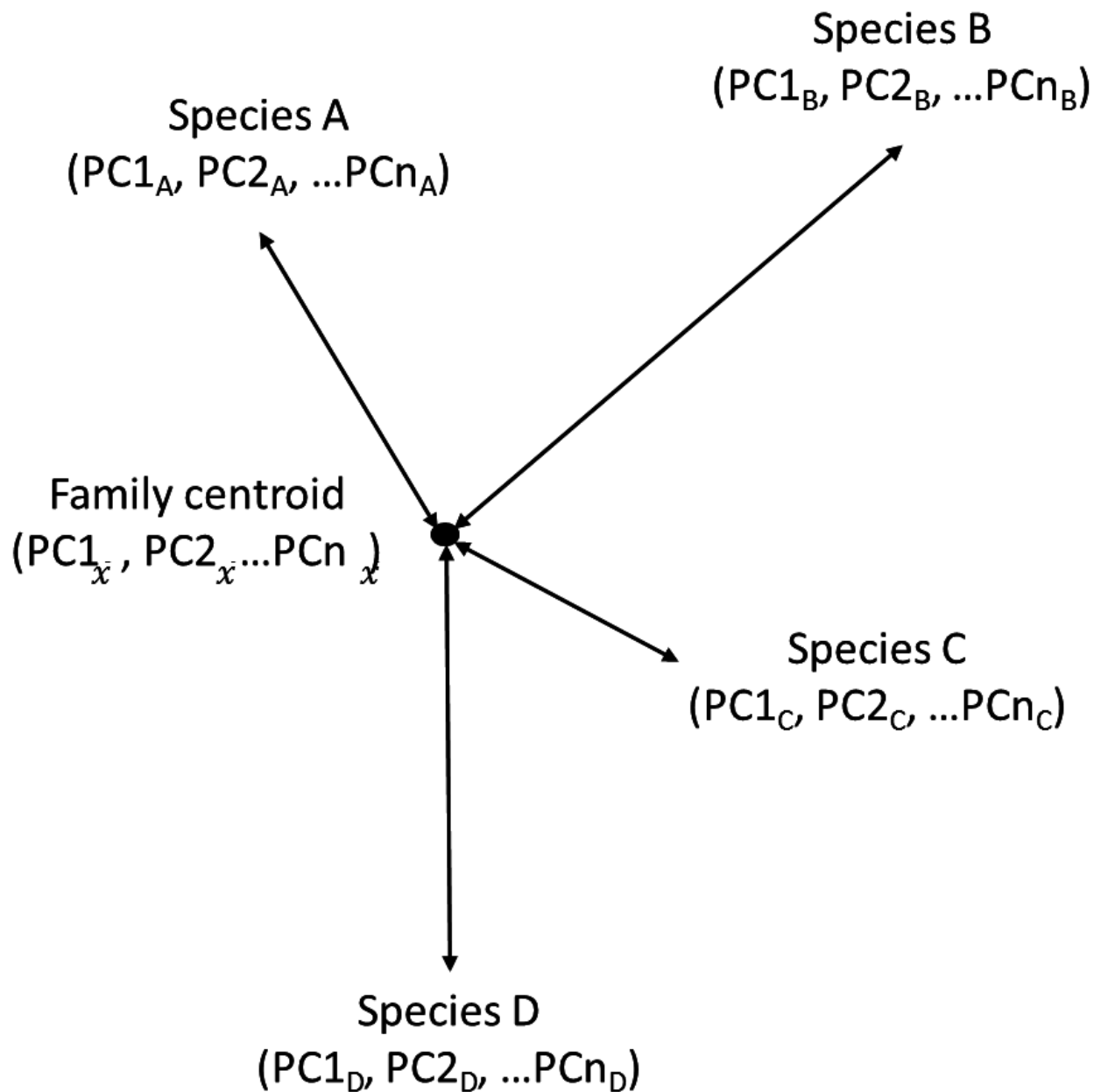
Landmarks (numbered points) and curves (outlines) for the skulls in dorsal, ventral and lateral view. See the supplementary material for detailed landmark descriptions. The skulls are an example of a *Potamogale velox* (otter shrew tenrec), museum accession number BMNH 1934.6.16.2.



3

Calculating diversity as mean Euclidean distance to Family centroid.

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 PC scores for the entire Family). Morphological diversity of the Family is the average value of these Euclidean distances.



4

Morphospace (principal components) plot of morphological diversity in tenrec and golden mole skulls.

Principal components plots of the morphospaces occupied by tenrecs (triangles, n=31 species) and golden moles (circles, n=12 species) for 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.

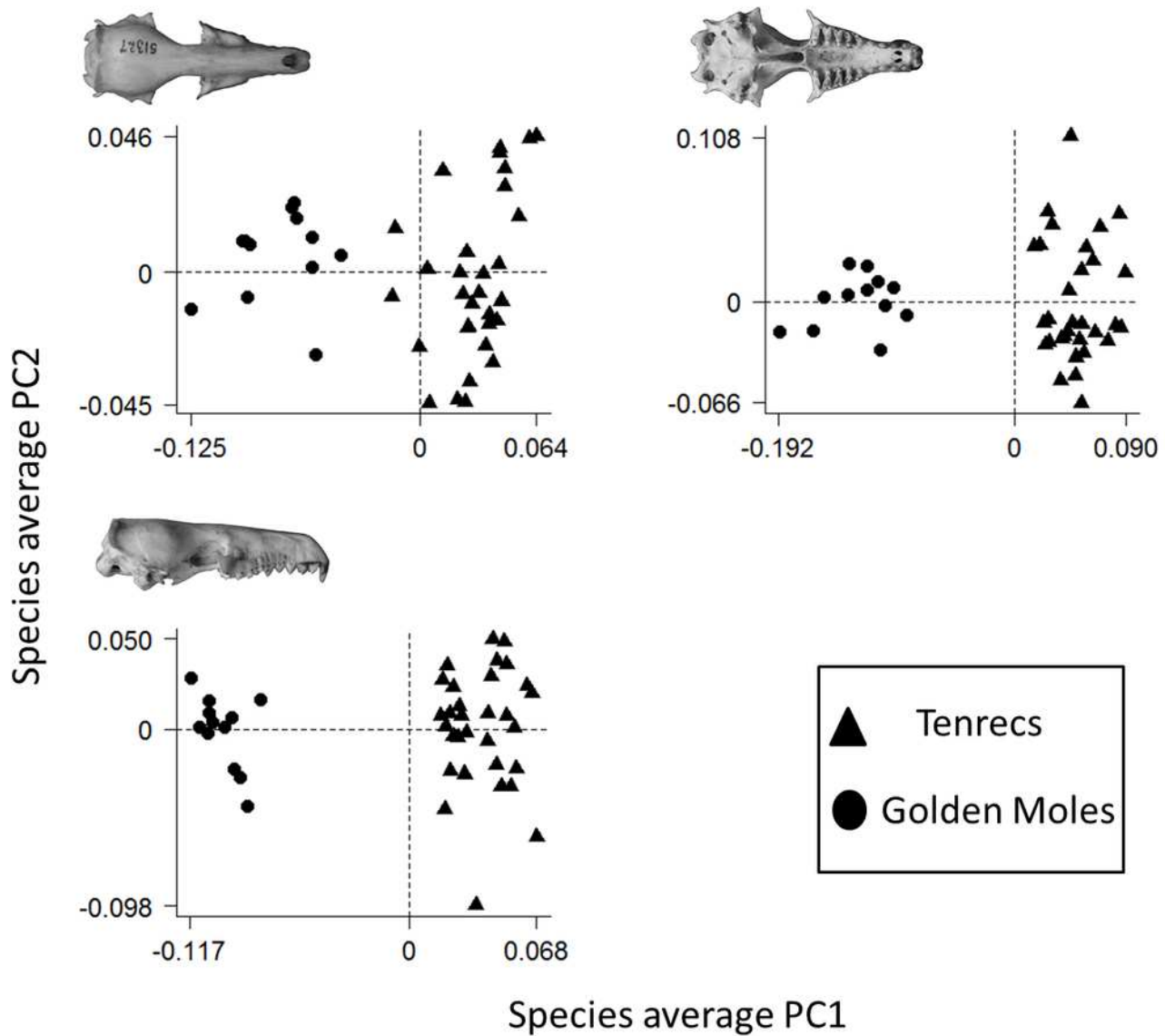


Table 1 (on next page)

Comparing morphological diversity in tenrecs and golden moles

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 $\pm$ s.e)	(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 (on next page)

Results of the permutation tests

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.

1

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