

1 **Running head:** ???

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

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12 golden moles, adaptive radiation

¹³ **Abstract**

14 Introduction

15 Phenotypically diverse groups have long attracted the attentions of
16 evolutionary biologists (REFS). Studies which quantify phenotypic variety
17 have important implications for understanding the factors that contribute
18 to high morphological diversity in some groups and not others (REFS).
19 For example...

20 These issues are particularly relevant when it comes to the study of
21 adaptive radiations: "evolutionary divergence of members of a single
22 phylogenetic lineage into a variety of different adaptive forms" (Futuyma
23 1998, cited by Losos, 2010). There are many famous examples of
24 adaptively radiated groups (Gavrilets & Losos, 2009). However, there has
25 also been considerable debate about how adaptive radiations should be
26 defined (Glor, 2010; Losos & Mahler, 2010) based on the relative
27 importance of speciation rate, species richness and morphological
28 diversity. One particular issue is whether it is even meaningful to classify
29 a particular group of species as an adaptive radiation or not since any
30 classification relies on arbitrary distinctions between what is most likely a
31 continua of characteristics which describe the diversity of a particular
32 clade (Olson & ArroyoSantos, 2009).

33 However, despite the controversies and disagreements, there does
34 seem to be a consensus that high morphological diversity is an important
35 criteria for identifying a group of species as belonging to the adaptive
36 radiation scale (Losos & Mahler, 2010; Olson & ArroyoSantos, 2009). One
37 way to test whether a group shows high morphological diversity is
38 through sister taxa comparisons. For example, Losos and Miles 2002 used
39 this approach to demonstrate exceptional diversity in some but not all

40 clades of iguanid lizards. Here we use this approach to test whether
41 tenrecs (Afrosoricida, Tenrecidae) exhibit the high levels of phenotypic
42 diversity which is the expected characteristic of an adaptively radiated
43 clade.

44 The tenrec family is comprised of 34 species, 31 of which are endemic
45 to Madagascar (Olson, 2013). From a single common ancestor (Asher &
46 Hofreiter, 2006), Malagasy tenrecs diversified into a wide variety of
47 descendant species which convergently resemble distantly related
48 insectivore mammals such as shrews (*Microgale* tenrecs), moles
49 (*Oryzorictes* tenrecs) and hedgehogs (*Echinops* and *Setifer* tenrecs)
50 (Eisenberg & Gould, 1969). These convergent resemblances are so great
51 that tenrecs used to be considered part of the general "insectivore" clade
52 and only molecular studies revealed their true phylogenetic relationships
53 with the rest of the Afrotheria clade (Stanhope et al., 1998).

54 Tenrecs are often cited as an example of an adaptively radiated family
55 which exhibits exceptional morphological diversity (Soarimalala &
56 Goodman, 2011; Olson & Goodman, 2003; Eisenberg & Gould, 1969).
57 However, this apparent exceptional diversity is based on subjective
58 comparisons to other groups and it has not been tested. Here we present
59 the first quantitative test of patterns of phenotypic diversity in tenrecs and
60 examine how morphological diversity in tenrecs compares to their closest
61 relatives, the golden moles (Afrosoricida, Chrysochloridae).

62 We use disparity, the diversity of organic form (Foote, 1997; Wills et al.,
63 1994; Erwin, 2007), to measure phenotypic variety within the two families.
64 There is no single definition of disparity and it can be calculated in many
65 ways including measures of morphospace occupation (e.g. Goswami et al.,

2011; Brusatte et al., 2008) and rate-based approaches that assess the amount of directed change away from an ancestor (O'Meara et al., 2006; Price et al., 2013). Here we focus on patterns of phenotypic variety in extant species rather than analysing the rate of diversity accumulation through time. Using the most complete morphological data set of tenrecs and golden moles to date we apply two dimensional geometric morphometrics (Rohlf & Marcus, 1993; Adams et al., 2013) to quantify variation in cranial and mandible morphologies as proxies for phenotypic diversity in the two families.

Our results indicate an overall trend of higher morphological diversity in tenrec compared to golden mole crania. However, most of these differences are not statistically significant, indicating that, with regards to cranial shape, tenrecs are not as phenotypically diverse as they are often though. In contrast, we found significantly greater morphological disparity in golden mole mandibles compared to the diversity within tenrecs. These findings cast doubt over whether the apparent phenotypic diversity within tenrecs should be considered exceptional.

Materials and Methods

Data collection

Morphological data collection

One of us (SF) photographed cranial specimens of tenrecs and golden moles at the Natural History Museum London (NHML), the Smithsonian Institute Natural History Museum (SI), the American Museum of Natural

89 History (AMNH), Harvard's Museum of Comparative Zoology (MCZ)
90 and the Field Museum of Natural History, Chicago (FMNH). We
91 photographed the specimens with a Canon EOS 650D camera fitted with
92 an EF 100mm f/2.8 Macro USM lens using a standardised procedure to
93 minimise potential error (see supplementary material for details).

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

98 In total we collected pictures from 182 skulls in dorsal view (148
99 tenrecs and 34 golden moles) and 181 mandibles in lateral view (147
100 tenrecs and 34 golden moles), representing 31 species of tenrec (out of the
101 total 34 in the family) and 12 species of golden moles (out of a total of 21
102 in the family (Asher et al., 2010)). We used the taxonomy of Wilson and
103 Reeder (2005) supplemented with more recent sources (IUCN, 2012;
104 Olson, 2013) to identify our specimens.

105 We used a combination of both landmarks (type 2 and type 3,
106 (Zelditch et al., 2012)) and semilandmarks to characterise the shapes of
107 our specimens. Our landmarks (points) and semilandmarks (outline
108 curves) used to represent shape variation in the dorsal and ventral skull
109 view are depicted in figures 1 and the landmarks for skulls and mandibles
110 in lateral view are shown in figure 2.

111 Corresponding landmark definitions for each view are in tables

112 We digitised all landmarks and semilandmarks in tpsDIG, version 2.17
113 (Rohlf, 2013).

114 We re-sampled the outlines to the minimum number of evenly spaced

semilandmark points required to represent each outline accurately (MacLeod, 2013, details in supplementary material). We used TPSUtil (Rohlf, 2012) to create sliders files (Zelditch et al., 2012) to define which points were semilandmarks. We conducted all subsequent analyses in R version 3.0.2 (R Development Core Team, 2013) within the geomorph package (Adams et al., 2013). We used the gpagen function to run a general Procrustes alignment (Rohlf & Marcus, 1993) of the landmark coordinates while sliding the semilandmarks by minimising procrustes distance (Bookstein, 1997). We used these Procrustes-aligned coordinates of all species (n=43) 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).

Phylogeny

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

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

140 their respective genera within our data. Therefore we randomly added
141 these species to the common ancestral node (using the findMRCA function
142 in phytools (Revell, 2012)) of all golden moles within each phylogeny.
143 Adding these extra species to the phylogenies created polytomies which
144 we resolved arbitrarily using zero-length branches (Paradis et al., 2004).
145 We calculated pairwise phylogenetic distances among species using the
146 cophenetic function (R Development Core Team, 2013).

147 **Analyses**

148 **Disparity calculations**

149 We calculated morphological disparity separately for golden moles and
150 tenrecs in each of the morphological datasets. We used the PC axes which
151 accounted for 95% of the cumulative variation to calculate four disparity
152 metrics; the sum and product of the range and variance of morphospace
153 occupied by each family (Brusatte et al., 2008; Foth et al., 2012; Ruta et al.,
154 2013). We also calculated morphological disparity directly from the
155 Procrustes-superimposed shape data based on the inter-landmark
156 distances among species pairs (ZelditchMD, Zelditch et al., 2012).

157 We used two approaches to test whether tenrecs have significantly
158 different morphologies compared to golden moles. We compared
159 morphospace occupation between the two groups with non parametric
160 MANOVAs (Anderson, 2001) to test whether tenrecs and golden moles
161 occupy significantly different areas of morphospace (REFS). We used
162 pairwise permutation tests to test our null hypothesis that tenrecs and
163 golden moles have equal disparity. If this hypothesis were true then the

164 designation of each species as belonging to either tenrecs or golden moles
165 should be arbitrary because each group would have the same disparity.
166 Therefore we permuted the data by assigning family identities at
167 random to each specimen and calculated the differences in disparity for
168 each of new family groupings. We repeated these permutations 1000
169 times to generate a distribution of the expected differences in family
170 disparity under the null hypothesis that tenrecs and golden moles have
171 equivalent disparity. We compared our observed (true) measures of the
172 differences in disparity between tenrecs and golden moles to these
173 permuted distributions to test whether the families had significantly
174 different levels of disparity.

175 The majority of tenrecs (19 out of 31 in our data) are members of the
176 *Microgale* (shrew-like) genus which is notable for its relatively low
177 phenotypic diversity (Soarimalala & Goodman, 2011; Jenkins, 2003). The
178 strong similarities among these species may mask signals of higher
179 disparity among other tenrecs. Therefore we repeated our family-level
180 comparisons of disparity with a reduced data set that excluded the
181 *Microgale* so that we could compare disparity within the remaining 12
182 tenrec species to disparity within the 12 species of golden moles.

183 **Results**

184 **Morphological disparity in tenrecs and golden moles**

185 Figures 3 and 4 depict the morphospace plots derived from our principal
186 components analyses of average Procrustes-superimposed shape
187 coordinates for each species in our skull and mandible data respectively.

188 We used the principal components axes which accounted for 95% of the
189 cumulative variation (n = 6 axes for the dorsal skulls analysis and n = 11
190 axes for the mandibles) to calculate the disparity of each family.

191 In the dorsal skulls analysis, tenrecs and golden moles occupy
192 significantly different areas of morphospace (npMANOVA, $F = 59.34$, $R^2 =$
193 0.59 , $p = 0.001$) indicating that the two families have significantly different
194 skull morphologies.

195 For each of the calculated metrics, tenrecs have higher disparity than
196 golden moles but these differences were not significant for the
197 variance-based calculations. Non-*Microgale* tenrecs also higher disparity
198 than golden moles but none of the comparisons were statistically
199 significant .

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

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

Discussion

Our findings provide new insights into phenotypic diversity within the tenrec family. When we compared tenrecs' cranial morphologies to their closest relatives we found a trend towards higher disparity in tenrecs than in golden moles. However, these apparent differences were only significant for some disparity metrics. In contrast, the analyses of the mandibles indicated that golden moles have more diverse mandible shapes than tenrecs.

It is evident that tenrecs are a diverse group, both phenotypically and ecologically. Body sizes of extant tenrecs span three orders of magnitude (2.5 to $> 2,000\text{g}$) which is a greater range than all other Families, and most Orders, of living mammals (Olson & Goodman, 2003). Within this vast size range there is striking morphological diversity, from the spiny *Echinops*, *Setifer* and striking *Hemicentetes* to the shrew-like *Microgale*. Furthermore, tenrecs inhabit a variety of ecological niches and habitats including terrestrial, arboreal, semi-aquatic and semi-fossorial forms (Soarimalala & Goodman, 2011).

Here we have presented the first quantitative investigation of morphological disparity in tenrecs and our results suggest that perhaps phenotypic variation in tenrecs is not as uniformly exceptional as it first appears.

We found an overall pattern of higher disparity in tenrec skull shape than golden moles but only the range and Procrustes distance-based metrics are significant. This is probably because variance and range-based measures describe different aspects of morphospace occupation.

235 Another apparent anomaly in our results is that we found opposite
236 patterns of group dissimilarities in the analyses of skulls and mandibles.
237 Our landmarks and curves for the mandibles (figure 2) include aspects of
238 variation in the dentition but they focus particular attention on the
239 ascending ramus (condyloid, condylar and angular processes). Therefore
240 higher disparity in golden moles could reflect greater morphological
241 variability in these posterior mandible structures. To test this idea we
242 deleted the semi-landmark curves around these structures (curves A, B,
243 and C, table x in supplementary material) and repeated our disparity
244 analyses on all of the specimens. In this case we retrieved the opposite
245 pattern: tenrecs had higher morphological disparity than golden moles
246 (see supplementary material). Therefore, our results indicate that golden
247 moles have greater morphological variation in the posterior structures of
248 their mandibles compared to tenrecs.

249 It proved impossible to position reliable landmarks on the
250 corresponding mandibular articulation areas of the skull in lateral view
251 (see supplementary). Therefore we could not test whether higher
252 morphological disparity in the rami were correlated with associated
253 morphological variety in the articulation areas of the skull.

254 There are certain caveats to consider which could modify the
255 interpretation of our results. Phenotypic variation can evolve for reasons
256 other than adaptive radiation. Therefore, to describe phenotypic
257 divergence as the product of an adaptive radiations requires exceptional
258 morphological diversity in traits which have specific and proven adaptive
259 significance (Losos & Mahler, 2010). The evolution of cranial shape (both
260 upper skull and mandible), particularly dental morphology, has obvious
261 correlations with dietary specialisations (REFS) and occupation of specific

262 ecological niches (REFS).

263 Considering the wide ecological diversity of our study species; the
264 fossorial golden moles and semi-fossorial, arboreal, terrestrial and
265 semi-aquatic tenrecs (REFS) it is reasonable to expect that this variety
266 should be reflected in skull morphology. We assume that variation in
267 cranial shape is an adaptive characteristic which allows the animals to
268 survive in their divergent niches but we have not tested this assumption
269 explicitly.

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

278 However, the results of (Foth et al., 2012) are encouraging. In an
279 analysis of morphological disparity in pterosaurs, they found that
280 disparity calculations based on geometric morphometric characterisation
281 of skull shape yielded broadly similar results compared to analyses of
282 whole-skeleton discrete characters and limb proportion data sets.
283 Therefore the disparity patterns we find here based on geometric
284 morphometric analyses of cranial shape most likely represent
285 approximations of disparity which are accurate for morphological
286 diversity in the clades.

287 These results highlight the importance of applying quantitative

288 methods to testing our assumptions about adaptively radiated groups.

289 These analyses represent the first attempt to find evidence to support
290 the common claim that tenrecs are an adaptive radiation. Future work
291 will develop our results by expanding the analyses to non-cranial
292 morphology and also measures of ecological diversity. However, our
293 current results provide a clear indication that phenotypic variety within
294 tenrecs is perhaps not as exceptional as it first seems and therefore their
295 designation as an adaptive radiation may need to be re-considered.

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List of Figures

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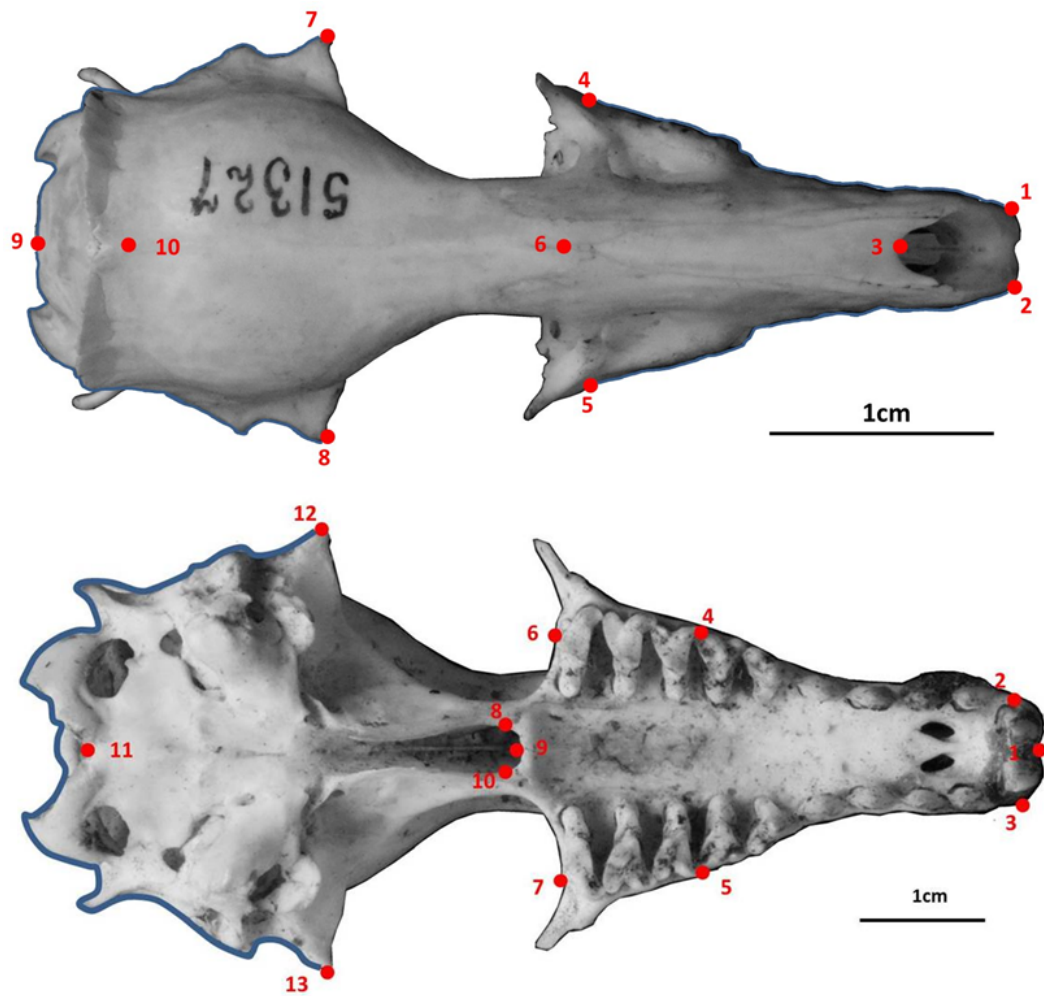


Figure 1: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of skulls in dorsal and ventral views respectively. Curves were re-sampled to the same number of evenly-spaced points. See table X for description of curves and landmarks. The specimens belong to two different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

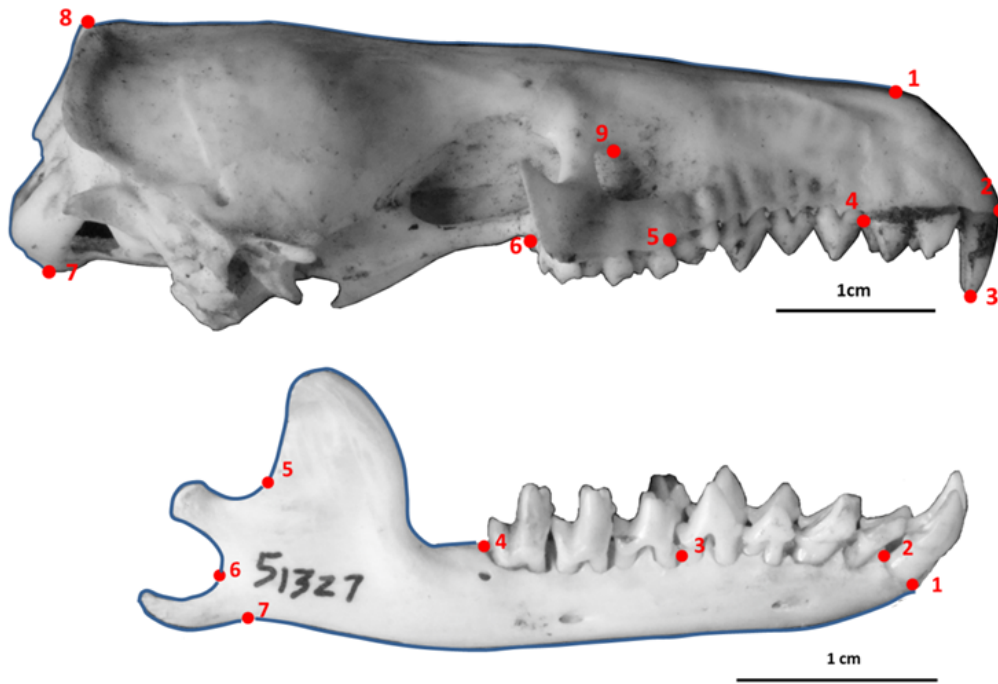


Figure 2: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of lateral views of skulls and mandibles respectively. Curves were re-sampled to the same number of evenly-spaced points. See table X for description of curves and landmarks. The specimens belong to two different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

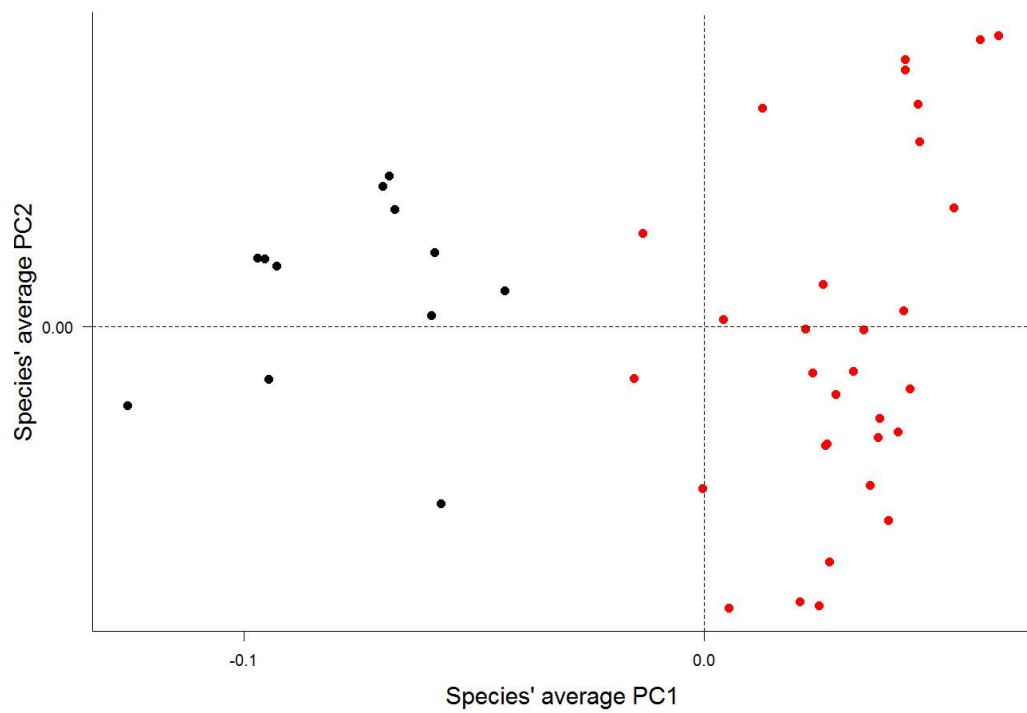


Figure 3: Principal components plot of the dorsal skulls' morphospace occupied by tenrecs (red, $n=31$) and golden moles (black, $n=12$). Axes are PC1 and PC2 of the average scores from a PCA analysis of mean Procrustes shape coordinates for each species.

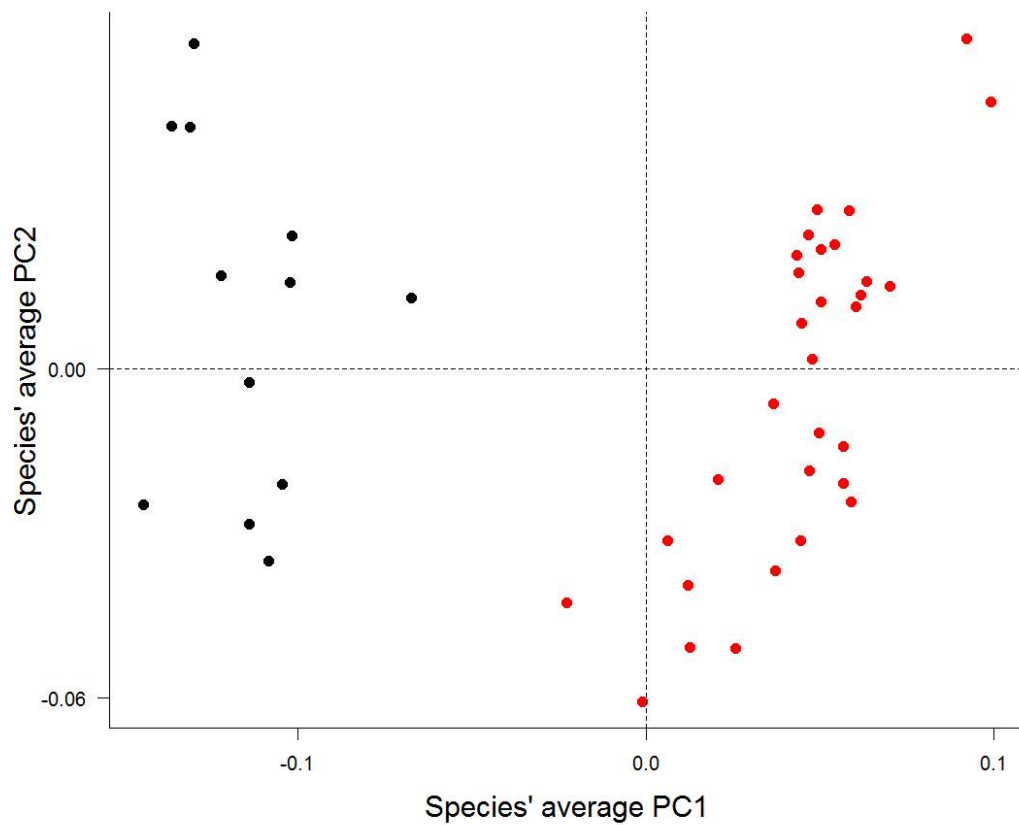


Figure 4: Principal components plot of the mandibles' morphospace occupied by tenrecs (red, n=31) and golden moles (black, n=12). Axes are PC1 and PC2 of the average scores from a PCA analysis of mean Procrustes shape coordinates for each species.