

1 **Running head:** CRANIAL MORPHOLOGICAL DISPARITY IN
2 TENRECS

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

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14 golden moles, adaptive radiation

15 Abstract

16 Understanding why some clades are more phenotypically diverse than
17 others remains a central challenge in evolutionary biology. This issue is
18 particularly relevant when we consider whether a group represents an
19 adaptive radiation. However, we must be able to identify exceptionally
20 diverse clades before we can determine the selective pressures which led
21 to the evolution of their variety. Tenrecs (Afrosoricida, Tenrecidae) are a
22 family of small mammals and are often cited as an example of a
23 phenotypically diverse, adaptively radiated group. However, this
24 assumption has not been tested. Here we use geometric morphometric
25 analyses of cranial and mandible shape to test whether tenrecs show
26 exceptional morphological disparity. We find that tenrecs are no more
27 morphologically diverse than their sister taxa, the golden moles
28 (Afrosoricida, Chrysochloridae), casting doubt over whether tenrecs
29 should be considered to be an exceptionally diverse group.

30 Introduction

31 Phenotypically diverse groups have long attracted the attention of
32 evolutionary biologists, particularly when it comes to the study of
33 adaptive radiations - 'evolutionary divergence of members of a single
34 phylogenetic lineage into a variety of different adaptive forms' (Futuyma
35 1998, cited by Losos, 2010).

36 There are many famous examples of adaptive radiations including
37 Darwin's finches, Caribbean *Anolis* lizards and cichlid fish (Gavrilets &
38 Losos, 2009). However, there has been considerable debate about how
39 adaptive radiations should be defined (Glor, 2010; Losos & Mahler, 2010)
40 based on the relative importance of speciation rates, species richness and
41 morphological diversity. One particular issue is whether it is even
42 meaningful to distinguish a specific group of species as an adaptive
43 radiation or not based on arbitrary statistical thresholds of variety (Olson
44 & Arroyo-Santos, 2009).

45 Despite the controversies and disagreements, there does seem to be a
46 consensus that high morphological diversity is an important criterion for
47 identifying adaptive radiations (Losos & Mahler, 2010; Olson &
48 Arroyo-Santos, 2009). One way to test whether a group shows high
49 morphological diversity is through sister taxa comparisons. For example,
50 Losos and Miles (2002) used this approach to demonstrate exceptional
51 diversity in some but not all clades of iguanid lizards. Here we use
52 sister-taxa comparisons to test whether tenrecs (Afrosoricida, Tenrecidae)
53 exhibit the high levels of phenotypic diversity that are expected of an
54 adaptively radiated clade.

55 The tenrec family contains 34 species, 31 of which are endemic to

56 Madagascar (Olson, 2013). Tenrecs are often cited as an example of an
57 adaptively radiated family which exhibits exceptional morphological
58 diversity (Soarimalala & Goodman, 2011; Olson & Goodman, 2003). For
59 example, there are tenrecs which convergently resemble shrews (*Microgale*
60 tenrecs), moles (*Oryzorictes* tenrecs) and hedgehogs (*Echinops* and *Setifer*
61 tenrecs) (Eisenberg & Gould, 1969) even though they are not closely
62 related to these species (Stanhope et al., 1998).

63 However, evidence for claim that tenrecs are exceptionally diverse has
64 not been tested. Here we present the first quantitative investigation of
65 morphological diversity in tenrecs, and how this compares to their closest
66 relatives, the golden moles (Afrosoricida, Chryscholoridae). We apply two
67 dimensional geometric morphometric techniques (Rohlf & Marcus, 1993;
68 Adams et al., 2013) to create morphospace plots that depict cranial and
69 mandible morphological variation in the two Families. We use these
70 morphospaces to compare the relative morphological disparity (Foote,
71 1997; Wills et al., 1994; Erwin, 2007) within each Family.

72 Our results show an overall trend for higher morphological diversity
73 in tenrec crania compared to those of golden moles. However, these
74 differences are not statistically significant. These findings indicate that,
75 with regards to cranial shape, tenrecs are no more morphologically
76 diverse than their closest relatives.

77 In contrast, we found significantly greater morphological disparity in
78 golden mole mandibles compared to tenrecs. These findings cast doubt
79 over whether the apparent phenotypic diversity within tenrecs should be
80 considered to be truly exceptional.

81 **Materials and Methods**

82 **Morphological data collection**

83 One of us (SF) photographed cranial specimens of tenrecs and golden
84 moles at the Natural History Museum London (BMNH), the Smithsonian
85 Institute Natural History Museum (SI), the American Museum of Natural
86 History (AMNH), Harvard's Museum of Comparative Zoology (MCZ)
87 and the Field Museum of Natural History, Chicago (FMNH). We
88 photographed the specimens with a Canon EOS 650D camera fitted with
89 an EF 100mm f/2.8 Macro USM lens using a standardised procedure to
90 minimise potential error (see supplementary material for details).

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

95 In total we collected pictures from 182 skulls in dorsal view (148
96 tenrecs and 34 golden moles), 173 skulls in ventral view (141 tenrecs and
97 32 golden moles), 171 skulls in lateral view (140 tenrecs and 31 golden
98 moles) and 182 mandibles in lateral view (147 tenrecs and 35 golden
99 moles), representing 31 species of tenrec (out of the total 34 in the family)
100 and 12 species of golden moles (out of a total of 21 in the family (Asher
101 et al., 2010)). We used the taxonomy of Wilson and Reeder (2005)
102 supplemented with more recent sources (IUCN, 2012; Olson, 2013) to
103 identify our specimens.

104 We used a combination of both landmarks (type 2 and type 3,
105 (Zelditch et al., 2012)) and semilandmarks to characterise the shapes of

106 our specimens. Figure 1 shows our landmarks (points) and
107 semilandmarks (outline curves) for the skulls in dorsal and ventral views
108 and figure 2 shows the points and curves we used for lateral views of
109 skulls and mandibles. Corresponding definitions of each of the landmarks
110 can be found in the supplementary material.

111 We digitised all landmarks and semilandmarks in tpsDIG, version 2.17
112 (Rohlf, 2013). We re-sampled the outlines to the minimum number of
113 evenly spaced semilandmark points required to represent each outline
114 accurately (MacLeod, 2013, details in supplementary material). We used
115 TPSUtil (Rohlf, 2012) to create sliders files (Zelditch et al., 2012) to define
116 which points were semilandmarks. We conducted all subsequent analyses
117 in R version 3.0.2 (R Core Team, 2014) within the geomorph package
118 (Adams et al., 2013). We used the gpagen function to run a general
119 Procrustes alignment (Rohlf & Marcus, 1993) of the landmark coordinates
120 while sliding the semilandmarks by minimising Procrustes distance
121 (Bookstein, 1997). We used these Procrustes-aligned coordinates of all
122 species to calculate average shape values for each species ($n = 43$) which
123 we then used for a principal components (PC) analysis with the
124 plotTangentSpace function (Adams et al., 2013).

125 **Disparity calculations**

126 We calculated morphological disparity separately for golden moles and
127 tenrecs in each of the morphological datasets. We used the PC axes which
128 accounted for 95% of the cumulative variation to calculate four disparity
129 metrics; 1) the sum of the range, 2) the product of the range, 3) the sum of
130 the variance and 4) the product of the variance of morphospace occupied

131 by each Family (Brusatte et al., 2008; Foth et al., 2012; Ruta et al., 2013).

132 We used two approaches to test whether tenrecs have significantly
133 different morphologies compared to golden moles. First we compared
134 morphospace occupation between the two groups with non parametric
135 MANOVAs (Anderson, 2001) to test whether tenrecs and golden moles
136 occupy significantly different areas of morphospace (e.g Serb et al., 2011;
137 Ruta et al., 2013).

138 Secondly, we used pairwise permutation tests to test the null
139 hypothesis that tenrecs and golden moles have equal disparity. If this
140 hypothesis was true then the designation of each species as belonging to
141 either tenrecs or golden moles should be arbitrary. Therefore we
142 permuted the data by assigning Family identities at random to each
143 specimen and calculated the differences in disparity for each of the new
144 Family groupings. We repeated these permutations 1000 times to generate
145 a null distribution of the expected differences in Family disparity. We
146 compared our observed (true) measures of the differences in disparity
147 between tenrecs and golden moles to these permuted distributions to test
148 whether the families had significantly different levels of disparity.

149 The majority of tenrec species (19 out of 31 in our dataset) are
150 members of the *Microgale* (shrew-like) Genus which is notable for its
151 relatively low phenotypic diversity (Soarimalala & Goodman, 2011;
152 Jenkins, 2003). The strong similarities among these species may mask
153 signals of higher disparity among other tenrecs. Therefore we repeated
154 our Family-level comparisons of disparity excluding the *Microgale* species
155 so that we could compare disparity within the remaining 12 tenrec species
156 to disparity within the 12 species of golden moles.

Results

Morphological disparity in tenrecs and golden moles

Figure 3 depicts the morphospace plots derived from our principal components analyses of average Procrustes-superimposed shape coordinates for each species in our skull and mandible data respectively. We used the principal components axes which accounted for 95% of the cumulative variation (number of axes: $n = 7$ (dorsal), $n = 8$ (ventral), $n = 8$ (lateral) and $n = 12$ (mandibles)) to calculate the disparity of each Family.

Tenrecs and golden moles clearly have very different cranial and mandible morphologies: in each analysis, the families occupy significantly different areas of morphospace (npMANOVA, table 3). Our comparisons of disparity within each Family yielded different trends for skulls compared to mandibles. In our analyses of the three different views of the skulls, when disparity is calculated from principal components-based metrics there is an overall trend for tenrecs to have higher disparity than golden moles. However, none of these differences are statistically significant (table 1). In contrast, when we calculated disparity based on the squared inter-landmark distances between the average shape of a species and the overall grand mean shape (Zelditch et al., 2012) then golden moles had significantly higher disparity than tenrecs (table 1). These results indicate that golden moles are more distant from the overall mean shape in each of the analyses (farther from the (0,0) points in the PCA plots, see figure 3) which makes intuitive sense given that the overall mean shape in each analysis will necessarily be biased towards the more species-rich tenrec Family.

182 The three curves at the back of the mandibles (figure 2) place a
183 particular emphasis on shape variation in the posterior of the bone; the
184 ramus, coronoid, condylar and angular processes. Therefore, higher
185 disparity in golden mole mandibles compared to tenrecs could be driven
186 by greater morphological variation in these structures. To test this idea,
187 we repeated our morphometric analyses of the mandibles with a reduced
188 dataset of points; just the seven landmark points and one single curve at
189 the base of the jaw between landmarks 1 and 7 (figure 2). When we
190 compared disparity with this reduced data set we found that golden
191 moles no longer had significantly higher disparity than tenrecs in the
192 principal components-based metrics (table 1).

193 **Morphological disparity in non-*Microgale* tenrecs and** 194 **golden moles**

195 We repeated our disparity comparisons with a subset of the tenrec
196 specimens to remove the large and phenotypically similar *Microgale* tenrec
197 Genus. In this case we found that tenrecs have significantly higher
198 disparity than golden moles when the skulls are analysed in lateral view
199 (table 2). However, none of the other comparisons in any of the analyses
200 were significant. Similarly, the trend in the main analysis for golden moles
201 to have significantly higher disparity measured as the sum of squared
202 inter-landmark distances between the average shape of a species and the
203 overall grand mean shape (table 1) was not repeated in this comparison of
204 disparity in non-*Microgale* tenrecs and golden moles (table 2).

Discussion

Our analyses are the first quantitative investigation of morphological disparity in tenrecs. Our results suggest that phenotypic variation in tenrecs is not as exceptional as it first appears.

When we compared tenrec cranial morphologies to their closest relatives we found a trend towards higher disparity in tenrecs compared to golden moles but none of these differences were significant. Even when we removed the phenotypically similar *Microgale* Genus, tenrecs were still no more diverse than golden moles in most of the analyses (table 2). In contrast, our mandible analyses showed that golden moles have more disparate mandibles than tenrecs seemingly due to greater diversity within their posterior-mandible shapes.

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 > 2,000g) which is a greater range than all other Families, and most Orders, of living mammals (Olson & Goodman, 2003). Within this vast size range there is striking phenotypic diversity from the spiny *Echinops*, *Setifer* and *Hemicentetes* to the mole-like *Oryzorictes* and shrew-like *Microgale*.

These diverse forms inhabit a wide variety of ecological niches and habitats including terrestrial, arboreal, semi-aquatic and semi-fossorial environments (Soarimalala & Goodman, 2011). In contrast, although golden moles occupy a wide altitudinal, climatic and vegetational spectrum of habitats (Bronner, 1995), they are all fossorial species which, superficially at least, appear to be less phenotypically diverse than tenrecs.

There is a danger when using sister taxa comparisons that a clade's

231 diversity will be judged to be exceptional just because it is more variable
232 than an exceptionally non-diverse sister taxon (Losos & Miles, 2002).
233 However, we compared an apparently phenotypically diverse clade to a
234 more uniform sister clade yet our results do not indicate that tenrecs are
235 more morphologically diverse than their closest relatives (table 1). These
236 unexpected findings highlight the importance of testing our assumptions
237 about patterns of morphological variety.

238 One apparent anomaly in our results is that we found opposite
239 patterns for disparity among tenrecs and golden moles in the analyses of
240 skulls and mandibles. Our landmarks and curves for the mandibles
241 (figure 2) include aspects of variation in the dentition but they focus
242 particular attention on the ascending ramus (condyloid, condylar and
243 angular processes). Therefore higher disparity in golden moles could
244 reflect greater morphological variability in these posterior mandible
245 structures. To test this idea we deleted the three semi-landmark curves
246 around these structures and repeated our disparity analyses of mandibles
247 using seven landmarks and just one curve at the base of the jaw. In this
248 case we retrieved the opposite pattern: tenrecs had higher morphological
249 disparity than golden moles but not significantly (see supplementary
250 material). Therefore, our results indicate that golden moles have greater
251 morphological variation in the posterior structures of their mandibles
252 compared to tenrecs.

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

258 We focused on variation in cranial morphology which is commonly
259 used to study phenotypic variation within species (Blagojević &
260 Milošević-Zlatanović, 2011; Bornholdt et al., 2008), to delineate species
261 boundaries within a clade (e.g. Panchetti et al., 2008) or for
262 cross-taxonomic comparative studies of phenotypic (dis)similarities (e.g.
263 Ruta et al., 2013; Goswami et al., 2011; Wroe & Milne, 2007). However,
264 studies of morphological disparity are inevitably constrained to measure
265 diversity within specific traits rather than overall phenotypes (Roy &
266 Foote, 1997). Disparity calculations based on skull shape can yield similar
267 results compared to analyses of whole-skeleton discrete characters and
268 limb proportion data sets (Foth et al., 2012). However, we would need to
269 extend our analyses to other morphological proxies of phenotype to test
270 whether the cranial morphological disparity patterns presented here are
271 indicative of overall differences in phenotypic diversity in tenrecs and
272 golden moles

273 Evidence of exceptional morphological diversity is one criterion for
274 designating a clade as an adaptive radiation (Losos & Mahler, 2010) and
275 our analyses are the first measures of morphological diversity within
276 tenrecs, a group which is commonly cited as an example of an adaptive
277 radiation (Olson, 2013). However, describing phenotypic divergence as the
278 product of an adaptive radiation requires exceptional morphological
279 diversity in traits which have specific and proven adaptive significance
280 (Losos & Mahler, 2010).

281 The evolution of cranial shape (both upper skull and mandible),
282 particularly dental morphology, has obvious correlations with dietary
283 specialisations and occupation of specific ecological niches (e.g. Wroe &
284 Milne, 2007). Considering the wide ecological diversity of our study

species; semi-fossorial, arboreal, terrestrial and semi-aquatic (Soarimalala & Goodman, 2011), we think that it is reasonable to expect that this variety should be reflected in skull morphology.

However, we have not included any measures of the ‘adaptiveness’ of cranial shape in our analyses and therefore our analyses should not be considered to be an explicit test of whether or not tenrecs are an adaptive radiation (Losos & Mahler, 2010). Instead we have made the first step towards understanding the apparent phenotypic diversity within tenrecs within a quantitative framework. Future work should focus on explicit measures of the ‘adaptiveness’ and functional importance of tenrec cranial and post-cranial morphologies to understand the significance of morphological diversity within the Family (e.g. Mahler et al., 2010).

We have presented the first quantitative study which tests the common claim that tenrecs are an exceptionally diverse group (Olson, 2013; Soarimalala & Goodman, 2011; Eisenberg & Gould, 1969). Focusing on cranial diversity is only one aspect of morphological variation and further analyses are required to test whether other morphological traits yield similar patterns. However, our current results provide a clear indication that phenotypic variety within tenrecs is perhaps not as exceptional as it first seems.

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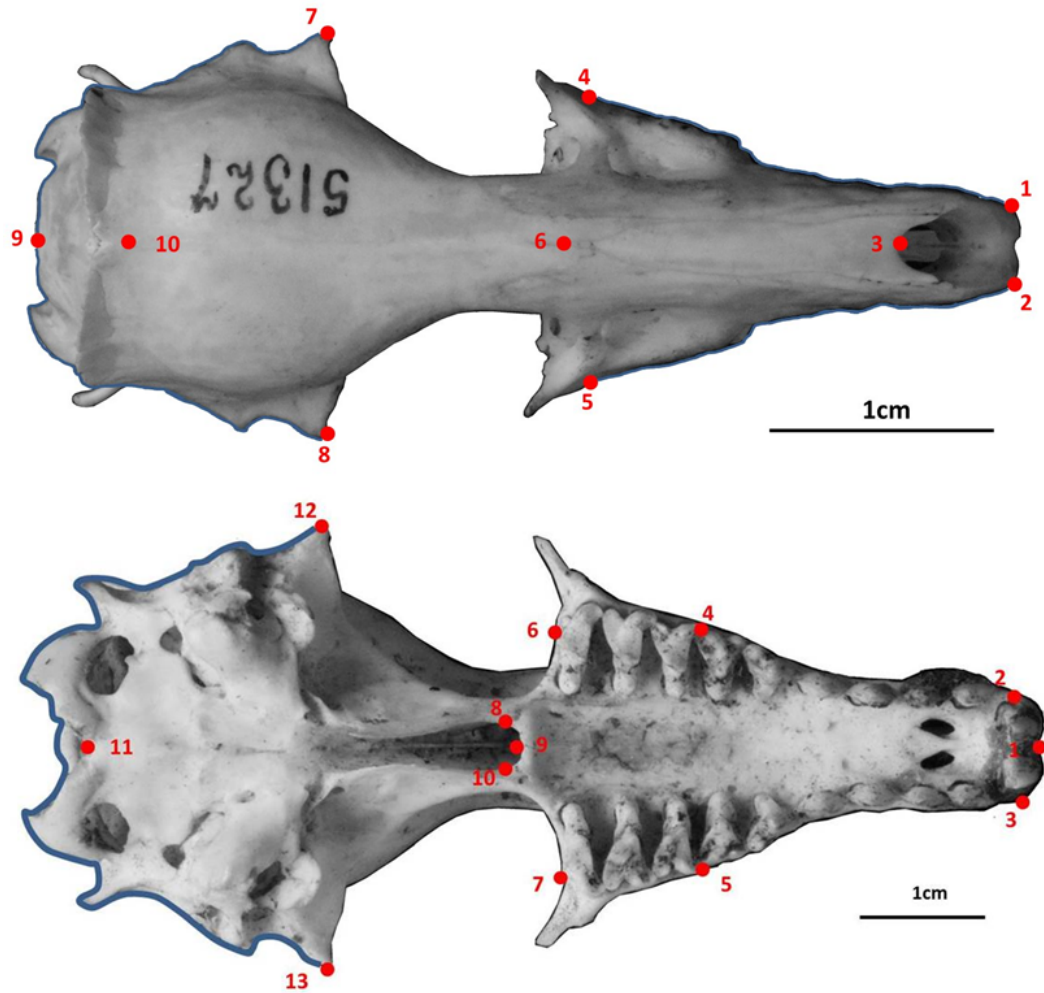


Figure 1: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of skulls in dorsal and ventral views respectively. Curves were re-sampled to the same number of evenly-spaced points. See Supplementary Material for descriptions of the curves and landmarks. The specimens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

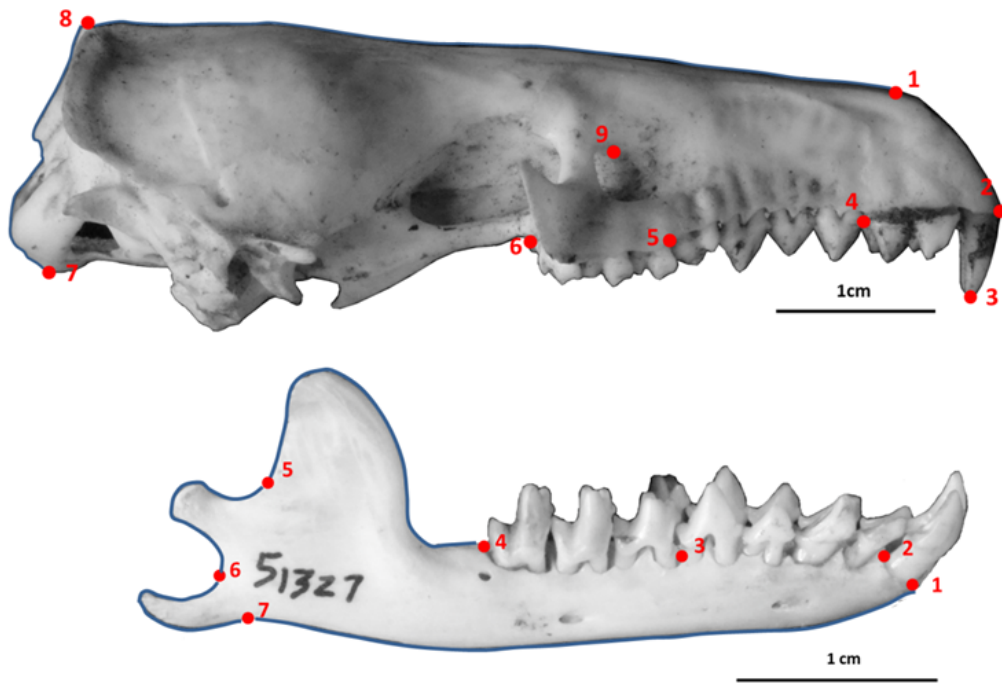


Figure 2: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of lateral views of skulls and mandibles respectively. Curves were re-sampled to the same number of evenly-spaced points. See Supplementary Material for descriptions of the curves and landmarks. The specimens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

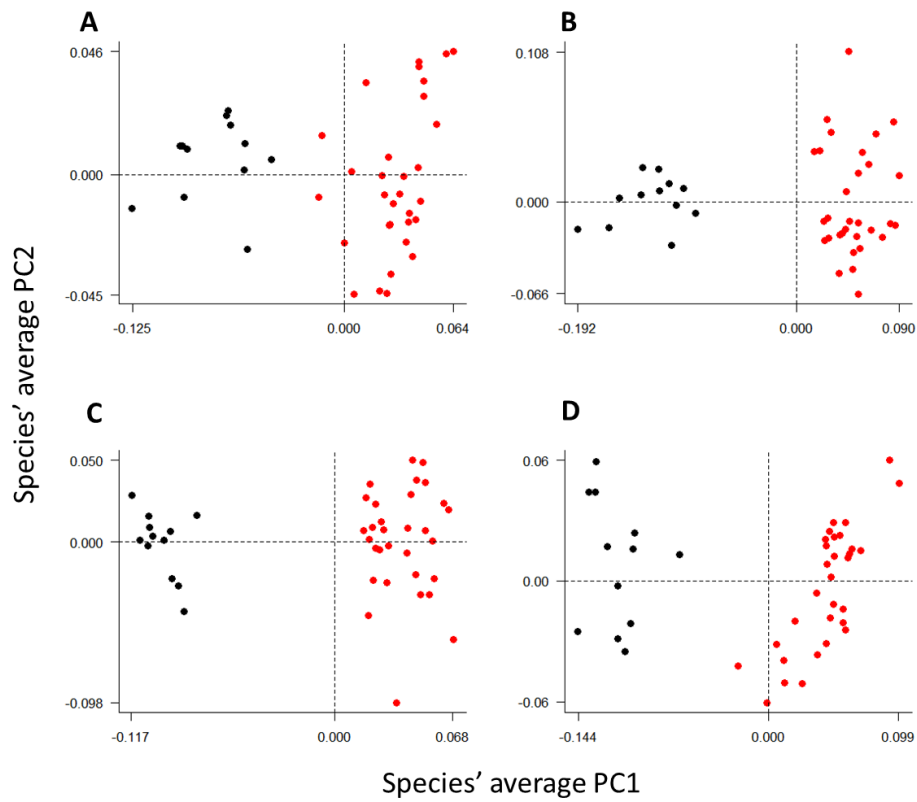


Figure 3: Principal components plots of the morphospaces occupied by tenrecs (red, $n = 31$ species) and golden moles (black, $n = 12$) for the skulls: dorsal (A), ventral (B), lateral (C) and mandibles (D) analyses. Axes are PC1 and PC2 of the average scores from a PCA analysis of mean Procrustes shape coordinates for each species.

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Table 1: Disparity comparisons between tenrecs (T) and golden moles (G) for each of our data sets(rows) and five disparity metrics (columns). ‘Mandibles:one curve’ refers to our shape analysis of mandibles excluding the three curves around the posterior structures of the jaw (figure 2). Significant differences are highlighted in bold with the corresponding p value in brackets. Disparity metrics are: sum of variance, product of variance, sum of ranges, product of ranges and sum of squared distances among species and the overall mean shape.

Disparity metric	SumVar	ProdVar	SumRange	ProdRange
Skulls dorsal	T>G	T>G	T>G	T>G
Skulls lateral	T>G	T>G	T>G	T>G
Skulls ventral	T>G	G>T	T>G	T>G
Mandibles	G>T	G>T* (0.008)	T>G* (0.025)	T>G* (0.009)
Mandibles	G>T	G>T	T>G	T>G

Table 2: Disparity comparisons between non-*Microgale* tenrecs (T) and golden moles (G) for each of our data sets(rows) and five disparity metrics (columns). Significant differences are highlighted in bold with the corresponding p value in brackets. Disparity metrics are; sum of variance, product of variance, sum of ranges, product of ranges and sum of squared distances among species and the overall mean shape.

Disparity metric	SumVar	ProdVar	SumRange	ProdRange
Skulls dorsal	T>G	T>G	T>G	T>G
Skulls lateral	T>G* (0.014)	T>G	T>G* (0.001)	T>G*(0.003)
Skulls ventral	T>G	T>G	T>G	T>G
Mandibles	T>G	G>T	T>G	G>T

Table 3: npMANOVA comparisons of morphospace occupation for tenrecs and golden moles in each of the four analyses (three views of skulls and mandibles). In each case the two families occupy significantly different areas of morphospace.

Analysis	F	R²	p value
Skulls dorsal	66.02	0.62	0.001
Skulls ventral	100.74	0.71	0.001
Skulls lateral	75.07	0.65	0.001
Mandibles	59.34	0.59	0.001