

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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13 **Keywords:** disparity, morphology, geometric morphometrics, tenrecs,
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. This is a good way
52 of assessing the relative diversity of a clade but of course there is also a
53 danger that a focal clade's diversity will be judged to be exceptional just
54 because it is more variable than an exceptionally non-diverse sister taxon
55 (Losos & Miles, 2002).

56 Here we use sister-taxa comparisons to test whether tenrecs
57 (Afrosoricida, Tenrecidae) exhibit the high levels of phenotypic diversity
58 that are expected of an adaptively radiated clade.

59 The tenrec family contains 34 species, 31 of which are endemic to
60 Madagascar (Olson, 2013). Tenrecs are often cited as an example of an
61 adaptively radiated family which exhibits exceptional morphological
62 diversity (Soarimalala & Goodman, 2011; Olson & Goodman, 2003). For
63 example, there are tenrecs which convergently resemble shrews (*Microgale*
64 tenrecs), moles (*Oryzorictes* tenrecs) and hedgehogs (*Echinops* and *Setifer*
65 tenrecs) (Eisenberg & Gould, 1969) even though they are not closely
66 related to these species (Stanhope et al., 1998).

67 However, evidence for claim that tenrecs are exceptionally diverse has
68 not been tested. Here we present the first quantitative investigation of
69 morphological diversity in tenrecs, and how this compares to their closest
70 relatives, the golden moles (Afrosoricida, Chryscholoridae). We apply two
71 dimensional geometric morphometric techniques (Rohlf & Marcus, 1993;
72 Adams et al., 2013) to create morphospace plots that depict cranial and
73 mandible morphological variation in the two Families. We use these
74 morphospaces to compare the relative morphological disparity (Foote,
75 1997; Wills et al., 1994; Erwin, 2007) within each Family.

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

81 In contrast, we found significantly greater morphological disparity in

82 golden mole mandibles compared to tenrecs. These findings cast doubt
83 over whether the apparent phenotypic diversity within tenrecs should be
84 considered to be truly exceptional.

85 **Materials and Methods**

86 **Morphological data collection**

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

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

99 In total we collected pictures from 182 skulls in dorsal view (148
100 tenrecs and 34 golden moles), 173 skulls in ventral view (141 tenrecs and
101 32 golden moles), 171 skulls in lateral view (140 tenrecs and 31 golden
102 moles) and 182 mandibles in lateral view (147 tenrecs and 35 golden
103 moles), representing 31 species of tenrec (out of the total 34 in the family)
104 and 12 species of golden moles (out of a total of 21 in the family (Asher
105 et al., 2010)). We used the taxonomy of Wilson and Reeder (2005)

106 supplemented with more recent sources (IUCN, 2012; Olson, 2013) to
107 identify our specimens.

108 We used a combination of both landmarks (type 2 and type 3,
109 (Zelditch et al., 2012)) and semilandmarks to characterise the shapes of
110 our specimens. Figure 1 shows our landmarks (points) and
111 semilandmarks (outline curves) for the skulls in dorsal and ventral views
112 and figure 2 shows the points and curves we used for lateral views of
113 skulls and mandibles. Corresponding definitions of each of the landmarks
114 can be found in the supplementary material.

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

Disparity calculations

We calculated morphological disparity separately for golden moles and tenrecs in each of the morphological datasets. We used the PC axes which accounted for 95% of the cumulative variation to calculate four disparity metrics; 1) the sum of the range, 2) the product of the range, 3) the sum of the variance and 4) the product of the variance of morphospace occupied by each Family (Brusatte et al., 2008; Foth et al., 2012; Ruta et al., 2013).

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

Secondly, we tested whether tenrecs have significantly higher or lower disparity than golden moles. If the two Families have equal disparity then the designation of each species as being either a tenrec or golden mole should not make any difference to our calculations. Therefore we used pairwise permutation tests to assess whether our data differed from this null hypothesis. We assigned Family identities at random to each specimen and calculated the differences in disparity for these new Family groupings. We repeated these permutations 1000 times to generate a null distribution of the expected differences in Family disparity. We compared our observed (true) measures of the differences in disparity between tenrecs and golden moles to these permuted distributions to test whether the families had significantly different levels of disparity compared to the null hypothesis.

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

163 Results

164 Morphological disparity in tenrecs and golden moles

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

171 Tenrecs and golden moles clearly have very different cranial and
172 mandible morphologies: in each analysis, the families occupy significantly
173 different areas of morphospace (npMANOVA, table 3). Our comparisons
174 of disparity within each Family yielded different trends for skulls
175 compared to mandibles. In our analyses of the three different views of the
176 skulls, there is an overall trend for tenrecs to have higher disparity than
177 golden moles. However, none of these differences are statistically
178 significant (table 1).

179 There is a less clear pattern from our analysis of disparity in
180 mandibles. Three of our four metrics indicate that golden moles have
181 significantly higher disparity in the shape of their mandibles than tenrecs
182 (table 1) although one metric (sum of ranges) indicated the opposite result.

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

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 functionally diverse than tenrecs.

One apparent anomaly in our results is that we found opposite

227 patterns for disparity among tenrecs and golden moles in the analyses of
228 skulls and mandibles. Our landmarks and curves for the mandibles
229 (figure 2) include aspects of variation in the dentition but they focus
230 particular attention on the ascending ramus (condyloid, condylar and
231 angular processes). Therefore higher disparity in golden moles could
232 reflect greater morphological variability in these posterior mandible
233 structures. To test this idea we deleted the three semi-landmark curves
234 around these structures and repeated our disparity analyses of mandibles
235 using seven landmarks and just one curve at the base of the jaw. In this
236 case we retrieved the opposite pattern: tenrecs had higher morphological
237 disparity than golden moles but not significantly (see supplementary
238 material). Therefore, our results indicate that golden moles have greater
239 morphological variation in the posterior structures of their mandibles
240 compared to tenrecs.

241 Given that these posterior structures are predominantly muscle
242 attachment and articulation sites for connections with the upper jaw one
243 might expect that golden moles with highly disparate posterior mandible
244 morphologies should also show high variability in the corresponding
245 mandible articulation areas of the skull. However, we could not locate
246 reliable, homologous points on these areas of the skull pictures in lateral
247 view which could be identified in all of our species. Instead, our
248 landmarks and semilandmark curves for the skulls in lateral view focus
249 attention on morphological variation in the dentition and the overall
250 shape of the top and back of the skulls (figure 2). This may explain why
251 golden mole skulls in lateral view do not show the same pattern of higher
252 disparity compared to tenrecs that we see in our analyses of the
253 mandibles.

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

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

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

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

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

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

301 **Acknowledgements**

302 We thank François Gould, Dean Adams, David Polly, Gary Bronner, Steve
303 Brusatte, Steve Wang, Luke Harmon, Thomas Guillerme and the members
304 of NERD club for insightful discussions and the museum staff and

305 curators for their support and access to collections. Funding was provided
306 by an Irish Research Council EMBARK Initiative Postgraduate Scholarship
307 (SF) and the European Commission CORDIS Seventh Framework
308 Programme (FP7) Marie Curie CIG grant. Proposal number: 321696 (NC)

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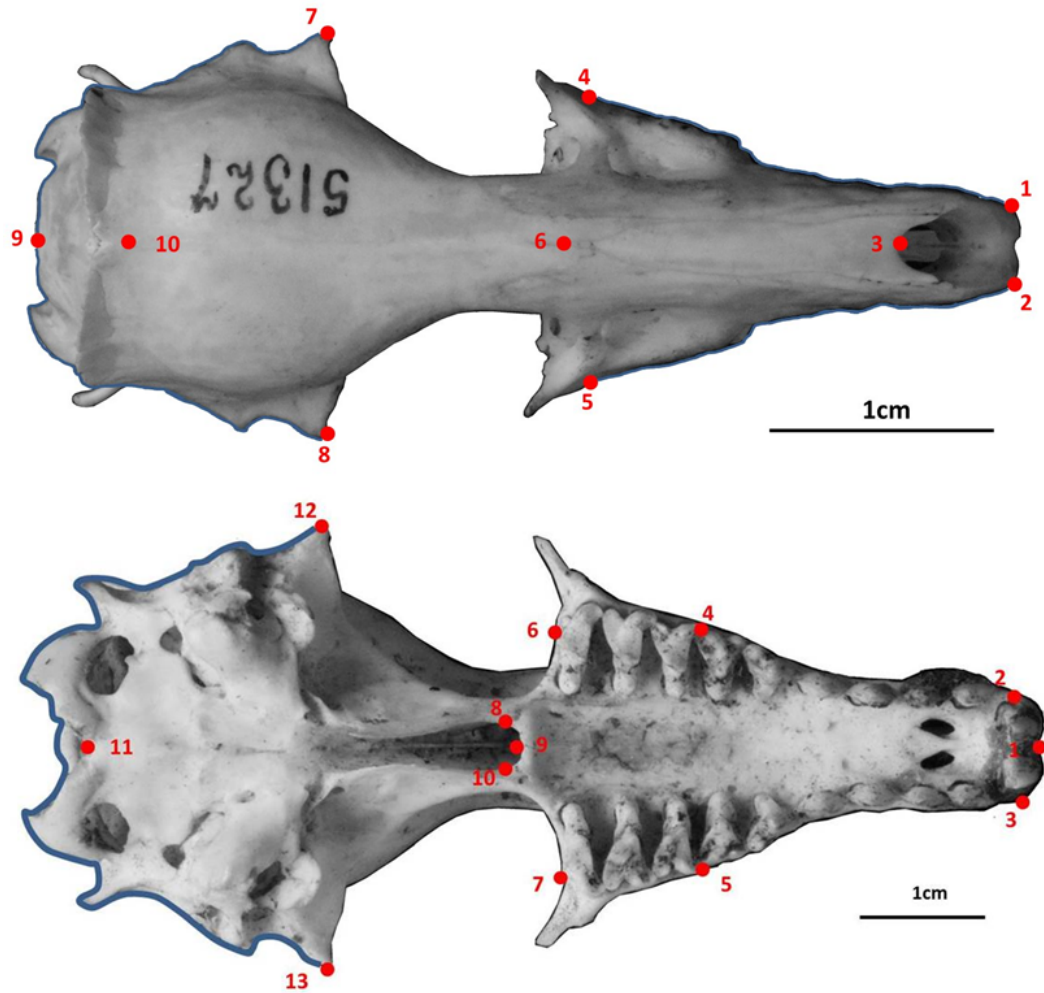


Figure 1: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of skulls in dorsal and ventral views respectively. Curves were re-sampled to the same number of evenly-spaced points. See Supplementary Material for descriptions of the curves and landmarks. The specimens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

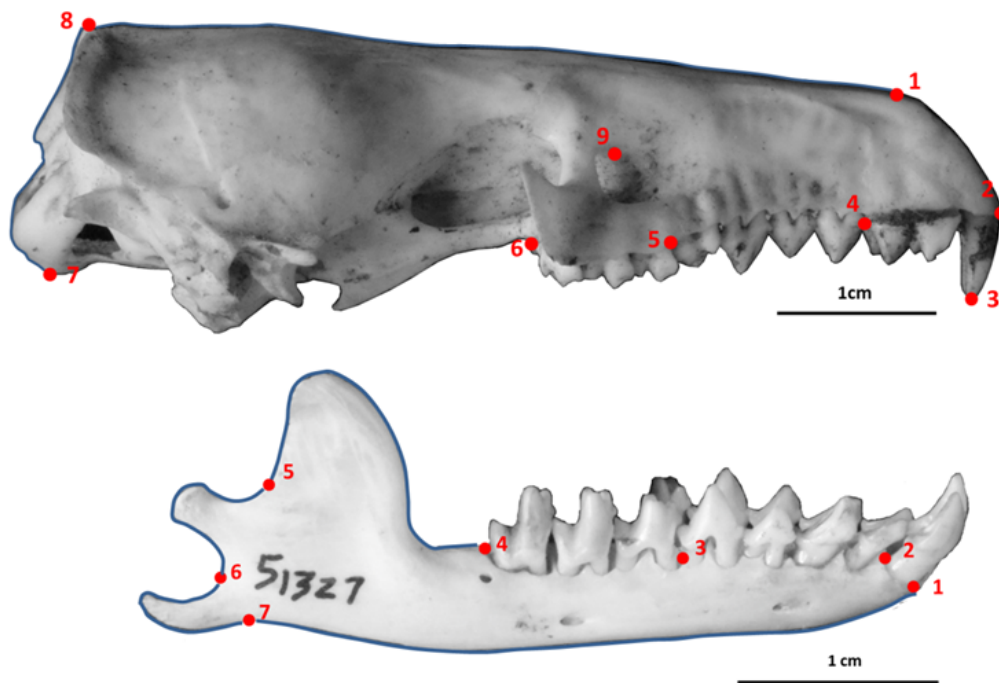


Figure 2: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of lateral views of skulls and mandibles respectively. Curves were re-sampled to the same number of evenly-spaced points. See Supplementary Material for descriptions of the curves and landmarks. The specimens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

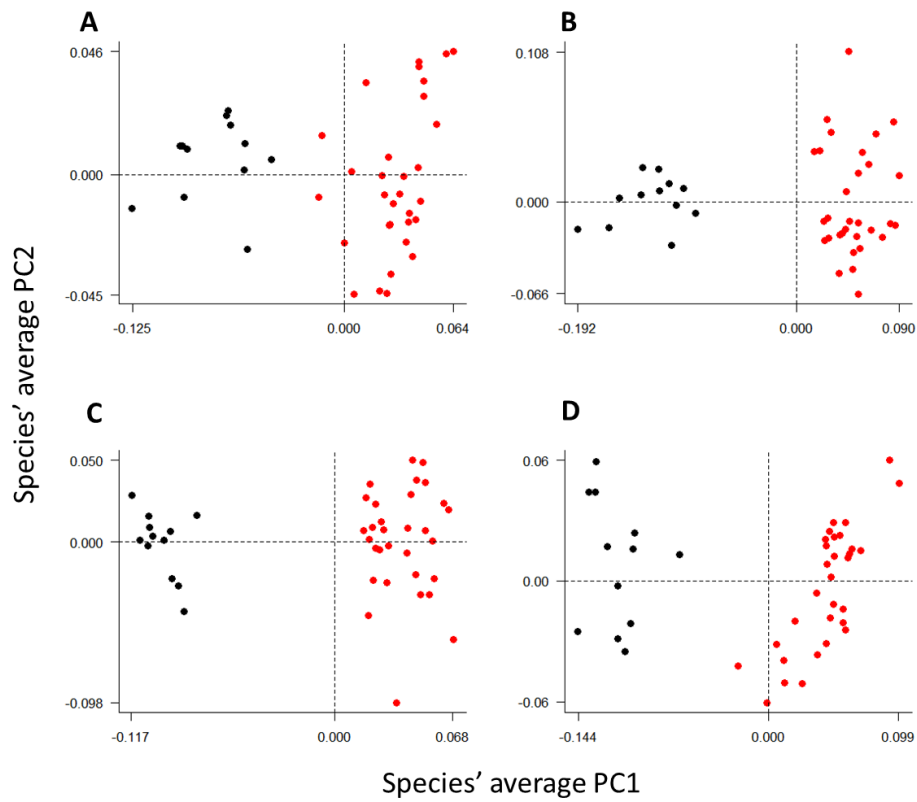


Figure 3: Principal components plots of the morphospaces occupied by tenrecs (red, $n = 31$ species) and golden moles (black, $n = 12$) for the skulls: dorsal (A), ventral (B), lateral (C) and mandibles (D) analyses. Axes are PC1 and PC2 of the average scores from a PCA analysis of mean Procrustes shape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

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 four 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 and product of ranges.

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