

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)
39 used this approach to demonstrate exceptional diversity in some but not

all clades of iguanid lizards. Here we test whether tenrecs (Afrosoricida, Tenrecidae) exhibit the high levels of phenotypic diversity which is the expected characteristic of an adaptively radiated clade.

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

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

We use disparity, the diversity of organic form (Foote, 1997; Wills et al., 1994; Erwin, 2007), to measure phenotypic variety within the two families. There is no single definition of disparity and it can be calculated in many ways including measures of morphospace occupation (e.g. Goswami et al., 2011; Brusatte et al., 2008) and rate-based approaches that assess the

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

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

82 **Materials and Methods**

83 **Morphological data collection**

84 One of us (SF) photographed cranial specimens of tenrecs and golden
85 moles at the Natural History Museum London (NHML), the Smithsonian
86 Institute Natural History Museum (SI), the American Museum of Natural
87 History (AMNH), Harvard's Museum of Comparative Zoology (MCZ)
88 and the Field Museum of Natural History, Chicago (FMNH). We
89 photographed the specimens with a Canon EOS 650D camera fitted with

90 an EF 100mm f/2.8 Macro USM lens using a standardised procedure to
91 minimise potential error (see supplementary material for details).

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

96 In total we collected pictures from 182 skulls in dorsal view (148
97 tenrecs and 34 golden moles), 173 skulls in ventral view (141 tenrecs and
98 32 golden moles), 171 skulls in lateral view (140 tenrecs and 31 golden
99 moles) and 182 mandibles in lateral view (147 tenrecs and 35 golden
100 moles), representing 31 species of tenrec (out of the total 34 in the family)
101 and 12 species of golden moles (out of a total of 21 in the family (Asher
102 et al., 2010)). We used the taxonomy of Wilson and Reeder (2005)
103 supplemented with more recent sources (IUCN, 2012; Olson, 2013) to
104 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. Figure 1 shows our landmarks (points) and
108 semilandmarks (outline curves) for the skulls in dorsal and ventral views
109 and the figure 2 shows the points and curves we used for lateral views of
110 skulls and mandibles. Corresponding definitions of each of the landmarks
111 can be found in the supplementary material.

112 We digitised all landmarks and semilandmarks in tpsDIG, version 2.17
113 (Rohlf, 2013). We re-sampled the outlines to the minimum number of
114 evenly spaced semilandmark points required to represent each outline
115 accurately (MacLeod, 2013, details in supplementary material). We used

116 TPSUtil (Rohlf, 2012) to create sliders files (Zelditch et al., 2012) to define
117 which points were semilandmarks. We conducted all subsequent analyses
118 in R version 3.0.2 (R Development Core Team, 2013) within the geomorph
119 package (Adams et al., 2013). We used the gpagen function to run a
120 general Procrustes alignment (Rohlf & Marcus, 1993) of the landmark
121 coordinates while sliding the semilandmarks by minimising procrustes
122 distance (Bookstein, 1997). We used these Procrustes-aligned coordinates
123 of all species (n=43) to calculate average shape values for each species
124 which we then used for a principal components (PC) analysis with the
125 plotTangentSpace function (Adams et al., 2013).

126 **Disparity calculations**

127 We calculated morphological disparity separately for golden moles and
128 tenrecs in each of the morphological datasets. We used the PC axes which
129 accounted for 95% of the cumulative variation to calculate four disparity
130 metrics; the sum and product of the range and variance of morphospace
131 occupied by each family (Brusatte et al., 2008; Foth et al., 2012; Ruta et al.,
132 2013). We also calculated morphological disparity directly from the
133 Procrustes-superimposed shape data based on the sum of the squared
134 inter-landmark distances among species pairs (ZelditchMD, Zelditch
135 et al., 2012).

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

141 Ruta et al., 2013). We used pairwise permutation tests to test our null
142 hypothesis that tenrecs and golden moles have equal disparity. If this
143 hypothesis were true then the designation of each species as belonging to
144 either tenrecs or golden moles should be arbitrary because each group
145 would have the same disparity. Therefore we permuted the data by
146 assigning family identities at random to each specimen and calculated the
147 differences in disparity for each of the new family groupings. We repeated
148 these permutations 1000 times to generate a null distribution of the
149 expected differences in family disparity. We compared our observed (true)
150 measures of the differences in disparity between tenrecs and golden moles
151 to these permuted distributions to test whether the families had
152 significantly different levels of disparity.

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

161 **Results**

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

163 Figures 3 depict the morphospace plots derived from our principal
164 components analyses of average Procrustes-superimposed shape

165 coordinates for each species in our skull and mandible data respectively.
166 We used the principal components axes which accounted for 95% of the
167 cumulative variation ($n = 7, 8, 8$ axes for the dorsal, ventral and lateral
168 skull analyses respectively and $n = 12$ axes for the mandibles) to calculate
169 the disparity of each family.

170 Tenrecs and golden moles clearly have very different cranial and
171 mandible morphologies: in each analysis, the families occupy significantly
172 different areas of morphospace (npMANOVA, table 3). Our comparisons
173 of disparity levels within each family yielded different trends for the
174 skulls compared to the mandible analyses.

175 In our analyses of the three different views of the skulls, when
176 disparity is calculated from principal component - based metrics there is
177 there is an overall trend for tenrecs to have higher disparity than golden
178 moles. However, none of these differences are statistically significant
179 (table 1). In contrast, when we calculated disparity based on the sum of
180 squared interlandmark differences between species pairs (Zelditch et al.,
181 2012) then golden moles had significantly higher levels of disparity than
182 tenrecs (table 1).

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

187 The three curves that we placed at the back of the mandibles (figure 2)
188 place a particular emphasis on shape variation in the posterior of the
189 bone; the ramus, coronoid, condylar and angular processes. Therefore,
190 higher disparity in golden mole mandibles compared to tenrecs could be

191 driven by greater morphological variation in these structures. To test this
192 idea, we repeated our morphometric analyses of the mandibles with a
193 reduced data set of points; just the seven landmark points and one single
194 curve at the base of the jaw between landmarks 1 and 7 (figure 2). When
195 we compared familial disparity levels with this reduced data set we found
196 that golden moles no longer had significantly higher disparity than tenrecs
197 but rather there were some indications that the opposite was true (table 1).

198 **Morphological disparity in non-*Microgale* tenrecs and** 199 **golden moles**

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

209 **Discussion**

210 Our findings provide new insights into phenotypic diversity within the
211 tenrec family. When we compared tenrecs' cranial morphologies to their
212 closest relatives we found a trend towards higher disparity in tenrecs than
213 in golden moles. However, these apparent differences were only

214 significant for some disparity metrics. In contrast, the analyses of the
215 mandibles indicated that golden moles have more diverse mandible
216 shapes than tenrecs.

217 It is evident that tenrecs are a diverse group, both phenotypically and
218 ecologically. Body sizes of extant tenrecs span three orders of magnitude
219 (2.5 to > 2,000g) which is a greater range than all other Families, and most
220 Orders, of living mammals (Olson & Goodman, 2003). Within this vast
221 size range there is striking morphological diversity, from the spiny
222 *Echinops*, *Setifer* and striking *Hemicentetes* to the shrew-like *Microgale*.
223 Furthermore, tenrecs inhabit a variety of ecological niches and habitats
224 including terrestrial, arboreal, semi-aquatic and semi-fossorial forms
225 (Soarimalala & Goodman, 2011).

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

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

234 Another apparent anomaly in our results is that we found opposite
235 patterns of group dissimilarities in the analyses of skulls and mandibles.
236 Our landmarks and curves for the mandibles (figure 2) include aspects of
237 variation in the dentition but they focus particular attention on the
238 ascending ramus (condyloid, condylar and angular processes). Therefore
239 higher disparity in golden moles could reflect greater morphological

240 variability in these posterior mandible structures. To test this idea we
241 deleted the semi-landmark curves around these structures (curves A, B,
242 and C, table x in supplementary material) and repeated our disparity
243 analyses on all of the specimens. In this case we retrieved the opposite
244 pattern: tenrecs had higher morphological disparity than golden moles
245 (see supplementary material). Therefore, our results indicate that golden
246 moles have greater morphological variation in the posterior structures of
247 their mandibles compared to tenrecs.

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

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

262 Considering the wide ecological diversity of our study species; the
263 fossorial golden moles and semi-fossorial, arboreal, terrestrial and
264 semi-aquatic tenrecs (REFS) it is reasonable to expect that this variety
265 should be reflected in skull morphology. We assume that variation in

266 cranial shape is an adaptive characteristic which allows the animals to
267 survive in their divergent niches but we have not tested this assumption
268 explicitly.

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

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

286 These results highlight the importance of applying quantitative
287 methods to testing our assumptions about adaptively radiated groups.

288 These analyses represent the first attempt to find evidence to support
289 the common claim that tenrecs are an adaptive radiation. Future work
290 will develop our results by expanding the analyses to non-cranial
291 morphology and also measures of ecological diversity. However, our

current results provide a clear indication that phenotypic variety within
tenrecs is perhaps not as exceptional as it first seems and therefore their
designation as an adaptive radiation may need to be re-considered.

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List of Figures

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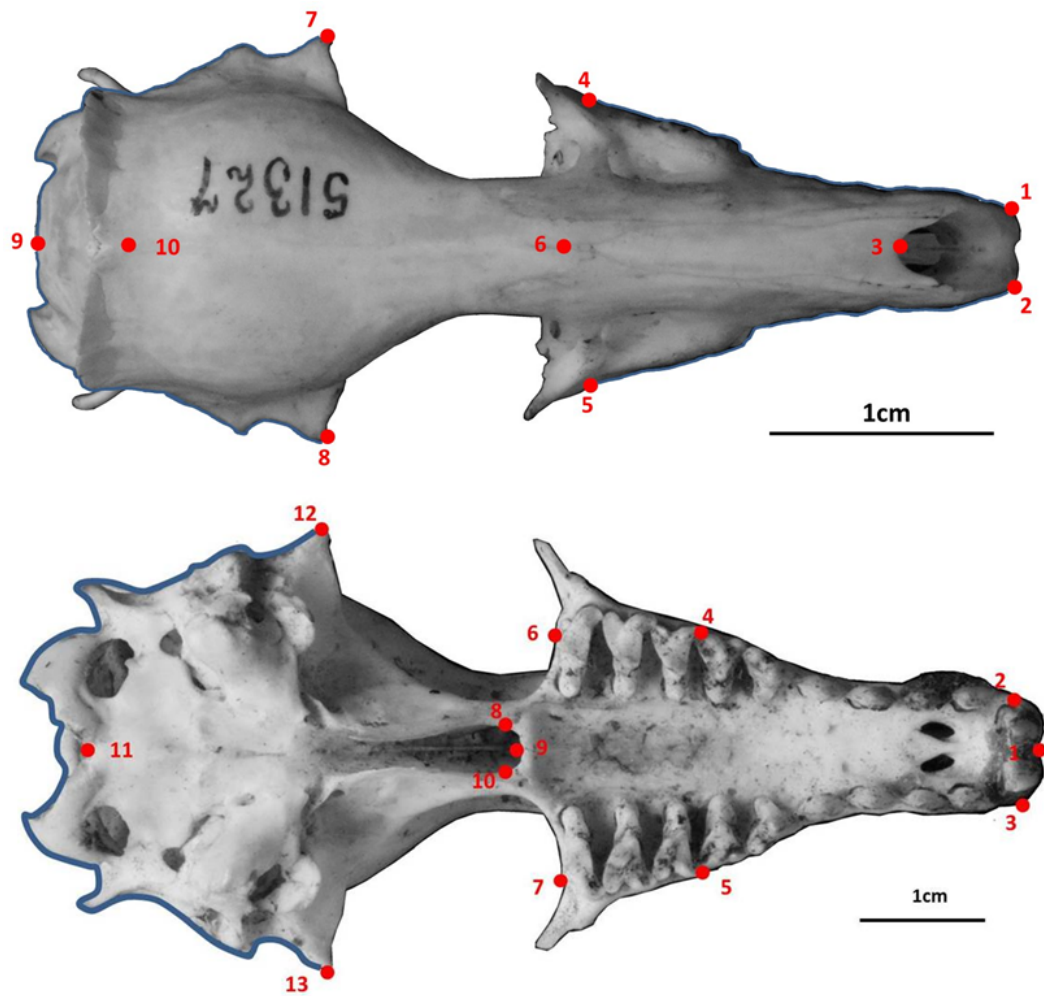


Figure 1: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of skulls in dorsal and ventral views respectively. Curves were re-sampled to the same number of evenly-spaced points. Descriptions of the curves and landmarks are in the supplementary material. The specimens 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

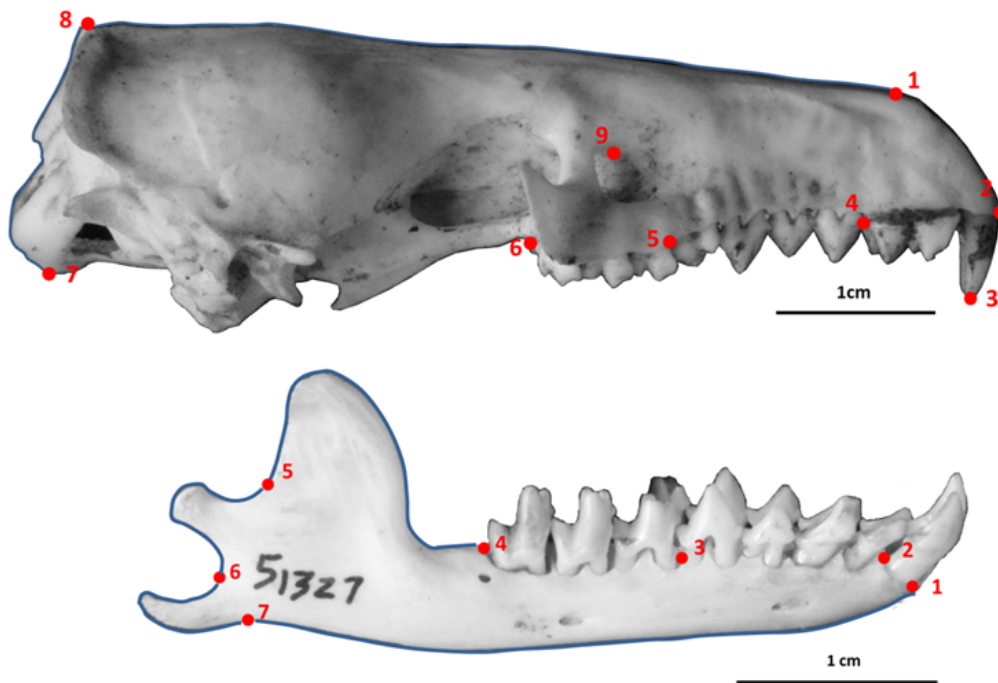


Figure 2: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of lateral views of skulls and mandibles respectively. Curves were re-sampled to the same number of evenly-spaced points. Descriptions of the curves and landmarks are in the supplementary material. The specimens 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

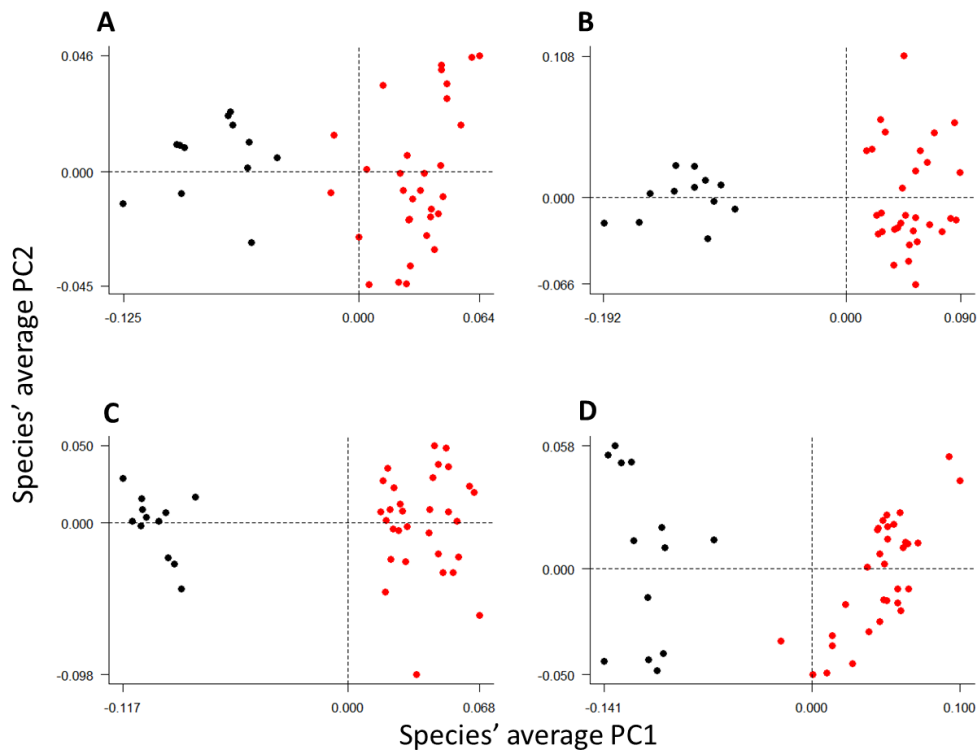


Figure 3: Principal components plots of the morphospaces occupied by tenrecs (red, $n=31$ species) and golden moles (black, $n=12$) for the skulls: dorsal (A), ventral (B), lateral (C) and mandibles (D) analyses. Axes are PC1 and PC2 of the average scores from a PCA analysis of mean Procrustes shape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

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431		our shape analysis of mandibles excluding the three curves	
432		around the posterior structures of jaw (figure 2). Significant	
433		differences are highlighted in bold with the corresponding	
434		p value in brackets. Disparity metrics are; sum of variance,	
435		product of variance, sum of ranges, product of ranges and	
436		sum of squared distances among species.	24
437	2	Summary of disparity comparisons between non- <i>Microgale</i>	
438		tenrecs (T) and golden moles (G) for each of our data sets(rows)	
439		and five disparity metrics (columns). Significant differences	
440		are highlighted in bold with the corresponding p value in	
441		brackets. Disparity metrics are; sum of variance, product	
442		of variance, sum of ranges, product of ranges and sum of	
443		squared distances among species.	25
444	3	Summary of the npMANOVA comparisons of morphospace	
445		occupation for tenrecs and golden moles in each of the four	
446		analyses (three views of skulls and mandibles). In each case	
447		the two families occupy significantly different areas of mor-	
448		phospace.	26

Table 1: Summary of 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 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.

Disparity metric	SumVar	ProdVar	SumRange	ProdRange	SSqDist
Skulls dorsal	T>G	T>G	T>G	T>G	G>T* (0)
Skulls lateral	T>G	T>G	T>G	T>G	G>T* (0)
Skulls ventral	T>G	G>T	T>G	T>G	G>T* (0)
Mandibles	G>T	G>T* (0.008)	T>G* (0.025)	T>G* (0.009)	T>G* (0)
Mandibles: one curve	G>T	G>T	T>G	T>G	T>G* (0)

Table 2: Summary of 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.

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

Table 3: Summary of the 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