

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 & Arroyo-Santos, 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 & Arroyo-Santos, 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 Core Team, 2014) within the geomorph package
119 (Adams et al., 2013). We used the gpagen function to run a general
120 Procrustes alignment (Rohlf & Marcus, 1993) of the landmark coordinates
121 while sliding the semilandmarks by minimising procrustes distance
122 (Bookstein, 1997). We used these Procrustes-aligned coordinates of all
123 species to calculate average shape values for each species (n=43) which we
124 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 (SSqDist, Zelditch et al.,
135 2012).

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

141 Serb et al., 2011; Ruta et al., 2013).

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

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

Results

Morphological disparity in tenrecs and golden moles

Figures 3 depict 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 ($n = 7, 8, 8$ axes for the dorsal, ventral and lateral skull analyses respectively and $n = 12$ axes for the 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 levels within each family yielded different trends for the skulls compared to the mandible analyses.

In our analyses of the three different views of the skulls, when disparity is calculated from principal component - 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 sum of squared interlandmark differences between species pairs (Zelditch et al., 2012) then golden moles had significantly higher levels of disparity than tenrecs (table 1).

There is a less clear pattern from our analysis of disparity in the mandibles. Three of our five metrics indicate that golden moles have significantly higher disparity in the shape of their mandibles than tenrecs

187 (table 1) although one metric (sum of ranges) indicated the opposite result.

188 The three curves that we placed at the back of the mandibles (figure 2)
189 place a particular emphasis on shape variation in the posterior of the
190 bone; the ramus, coronoid, condylar and angular processes. Therefore,
191 higher disparity in golden mole mandibles compared to tenrecs could be
192 driven by greater morphological variation in these structures. To test this
193 idea, we repeated our morphometric analyses of the mandibles with a
194 reduced data set of points; just the seven landmark points and one single
195 curve at the base of the jaw between landmarks 1 and 7 (figure 2). When
196 we compared familial disparity levels with this reduced data set we found
197 that golden moles no longer had significantly higher disparity than tenrecs
198 but rather there were some indications that the opposite was true (table 1).

199 **Morphological disparity in non-*Microgale* tenrecs and** 200 **golden moles**

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

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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398 **List of Figures**

399	1	Diagram of the landmarks and curves for the skulls in dorsal	
400		and ventral views	20
401	2	Diagrams of the landmarks and curves used for lateral views	
402		of skulls and mandibles	21
403	3	Principal components plots of the morphospaces occupied	
404		by tenrecs and golden moles	22

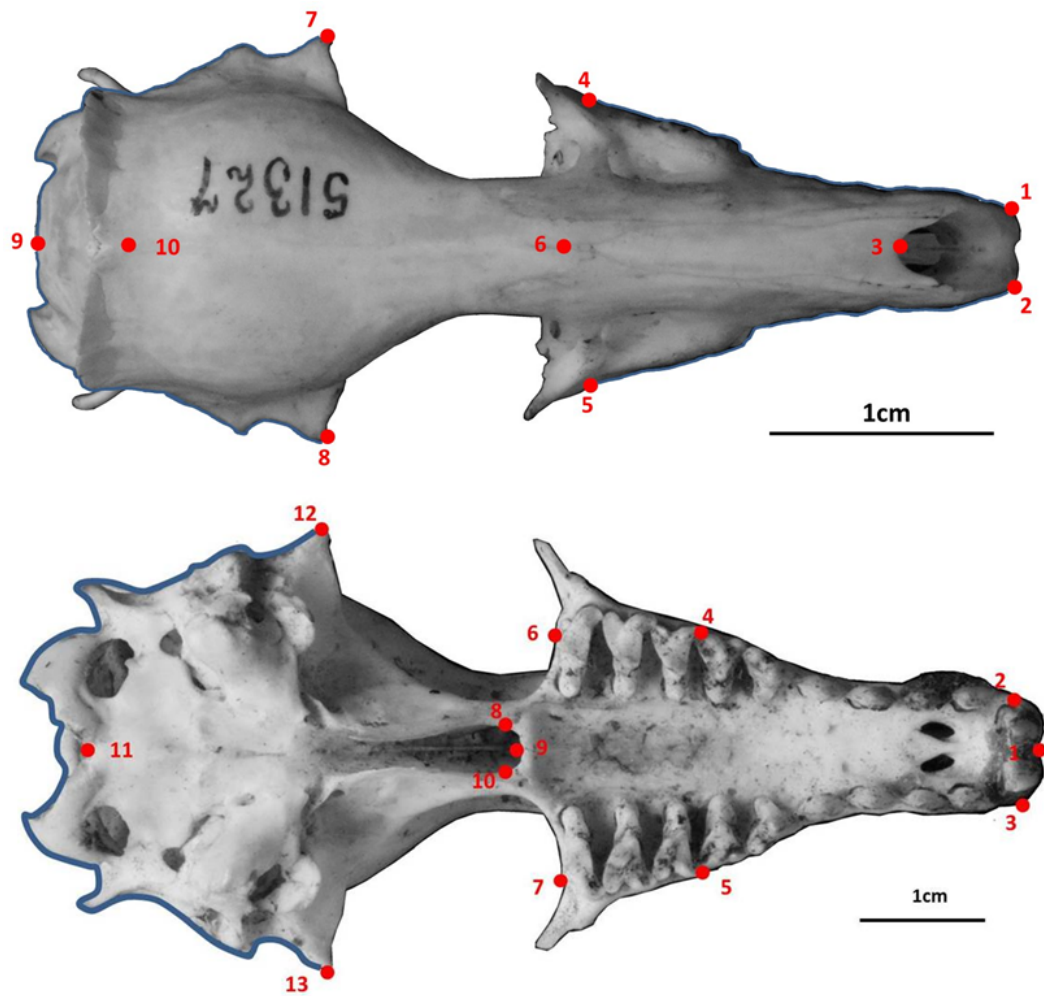


Figure 1: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of skulls in dorsal and ventral views respectively. Curves were re-sampled to the same number of evenly-spaced points. Descriptions of the curves and landmarks are in the supplementary material. The specimens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

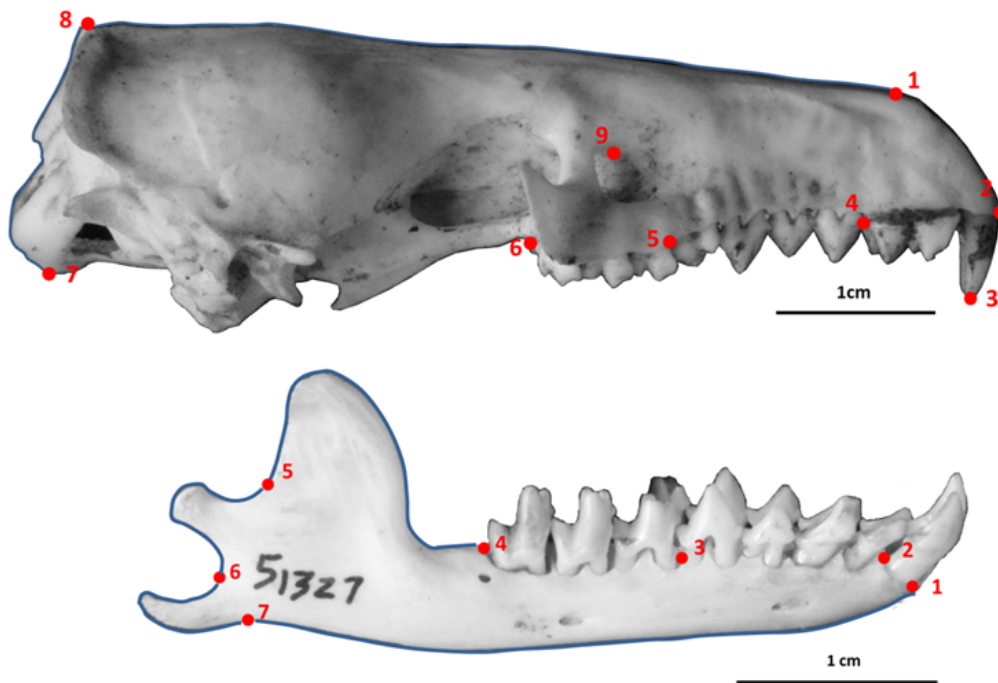


Figure 2: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of lateral views of skulls and mandibles respectively. Curves were re-sampled to the same number of evenly-spaced points. Descriptions of the curves and landmarks are in the supplementary material. The specimens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

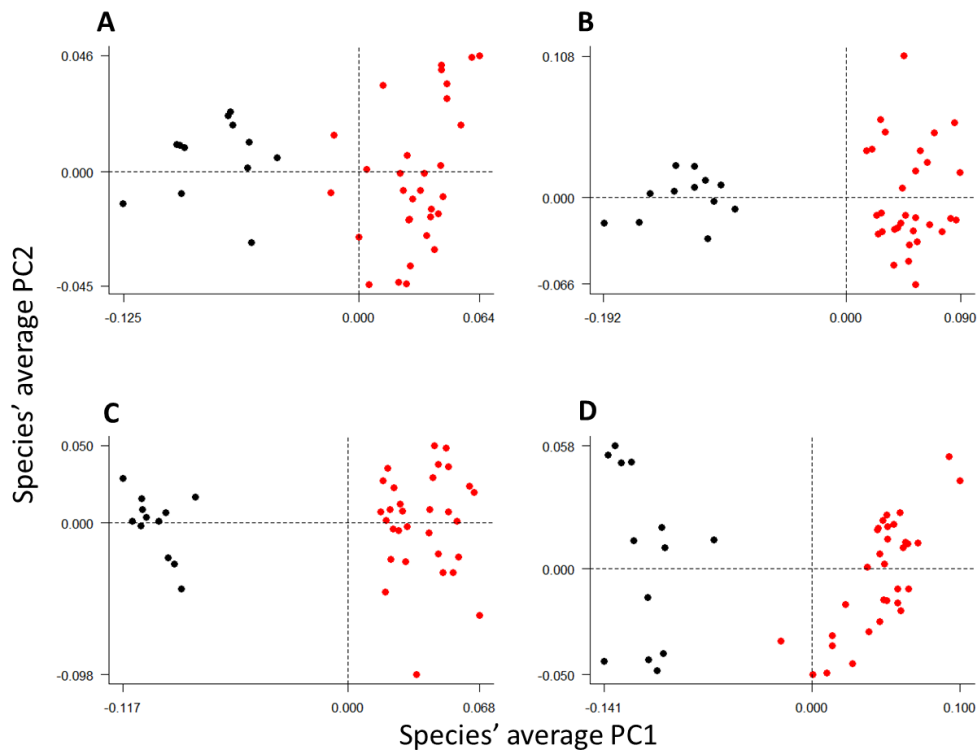


Figure 3: Principal components plots of the morphospaces occupied by tenrecs (red, n=31 species) and golden moles (black, n=12) for the skulls: dorsal (A), ventral (B), lateral (C) and mandibles (D) analyses. Axes are PC1 and PC2 of the average scores from a PCA analysis of mean Procrustes shape coordinates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

405 List of Tables

406	1	Summary of disparity comparisons between tenrecs and golden	
407		moles	24
408	2	Summary of disparity comparisons between non- <i>Microgale</i>	
409		tenrecs and golden moles	25
410	3	Summary of npMANOVA comparisons of morphospace oc-	
411		cupation for tenrecs and golden moles	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	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