

1 **Running head:** ???

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

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12 golden moles, adaptive radiation

¹³ **Abstract**

14 Introduction

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

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

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

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

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

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

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

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

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

Materials and Methods

Data collection

Morphological data collection

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

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

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

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

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

111 Corresponding landmark definitions for each view are in tables

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

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

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

Phylogeny

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

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

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

147 **Analyses**

148 **Disparity calculations**

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

157 We used two approaches to test whether tenrecs have significantly
158 different morphologies compared to golden moles. We compared
159 morphospace occupation between the two groups with non parametric
160 MANOVAs (Anderson, 2001) to test whether tenrecs and golden moles
161 occupy significantly different areas of morphospace (e.g Serb et al., 2011;
162 Ruta et al., 2013). We used pairwise permutation tests to test our null
163 hypothesis that tenrecs and golden moles have equal disparity. If this

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

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

182 **Results**

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

184 Figures 3 depict the morphospace plots derived from our principal
185 components analyses of average Procrustes-superimposed shape
186 coordinates for each species in our skull and mandible data respectively.
187 We used the principal components axes which accounted for 95% of the

188 cumulative variation (n = 7, 8, 8 axes for the dorsal, ventral and lateral
189 skull analyses respectively and n = 12 axes for the mandibles) to calculate
190 the disparity of each family.

191 Tenrecs and golden moles clearly have very different cranial and
192 mandible morphologies: in each analysis, the families occupy significantly
193 different areas of morphospace (npMANOVA, table 2)

194 Discussion

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

202 It is evident that tenrecs are a diverse group, both phenotypically and
203 ecologically. Body sizes of extant tenrecs span three orders of magnitude
204 (2.5 to > 2,000g) which is a greater range than all other Families, and most
205 Orders, of living mammals (Olson & Goodman, 2003). Within this vast
206 size range there is striking morphological diversity, from the spiny
207 *Echinops*, *Setifer* and striking *Hemicentetes* to the shrew-like *Microgale*.
208 Furthermore, tenrecs inhabit a variety of ecological niches and habitats
209 including terrestrial, arboreal, semi-aquatic and semi-fossorial forms
210 (Soarimalala & Goodman, 2011).

211 Here we have presented the first quantitative investigation of

212 morphological disparity in tenrecs and our results suggest that perhaps
213 phenotypic variation in tenrecs is not as uniformly exceptional as it first
214 appears.

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

219 Another apparent anomaly in our results is that we found opposite
220 patterns of group dissimilarities in the analyses of skulls and mandibles.
221 Our landmarks and curves for the mandibles (figure 2) include aspects of
222 variation in the dentition but they focus particular attention on the
223 ascending ramus (condyloid, condylar and angular processes). Therefore
224 higher disparity in golden moles could reflect greater morphological
225 variability in these posterior mandible structures. To test this idea we
226 deleted the semi-landmark curves around these structures (curves A, B,
227 and C, table x in supplementary material) and repeated our disparity
228 analyses on all of the specimens. In this case we retrieved the opposite
229 pattern: tenrecs had higher morphological disparity than golden moles
230 (see supplementary material). Therefore, our results indicate that golden
231 moles have greater morphological variation in the posterior structures of
232 their mandibles compared to tenrecs.

233 It proved impossible to position reliable landmarks on the
234 corresponding mandibular articulation areas of the skull in lateral view
235 (see supplementary). Therefore we could not test whether higher
236 morphological disparity in the rami were correlated with associated
237 morphological variety in the articulation areas of the skull.

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

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

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

262 However, the results of (Foth et al., 2012) are encouraging. In an
263 analysis of morphological disparity in pterosaurs, they found that

264 disparity calculations based on geometric morphometric characterisation
265 of skull shape yielded broadly similar results compared to analyses of
266 whole-skeleton discrete characters and limb proportion data sets.
267 Therefore the disparity patterns we find here based on geometric
268 morphometric analyses of cranial shape most likely represent
269 approximations of disparity which are accurate for morphological
270 diversity in the clades.

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

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

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389 List of Figures

390	1	Landmarks (red points) and curves (blue lines) used to capture the morphological shape of skulls in dorsal and ventral views respectively. Curves were re-sampled to the same number of evenly-spaced points. See table X for description of curves and landmarks. The specimens belong to two different <i>Potamogale velox</i> (Tenrecidae) skulls: accession number AMNH 51327 for the dorsal picture and NHML 1934.6.16.2 for the ventral picture	20
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398	2	Landmarks (red points) and curves (blue lines) used to capture the morphological shape of lateral views of skulls and mandibles respectively. Curves were re-sampled to the same number of evenly-spaced points. See table X for description of curves and landmarks. The specimens belong to two different <i>Potamogale velox</i> (Tenrecidae) skulls: accession number AMNH 51327 for the dorsal picture and NHML 1934.6.16.2 for the ventral picture	21
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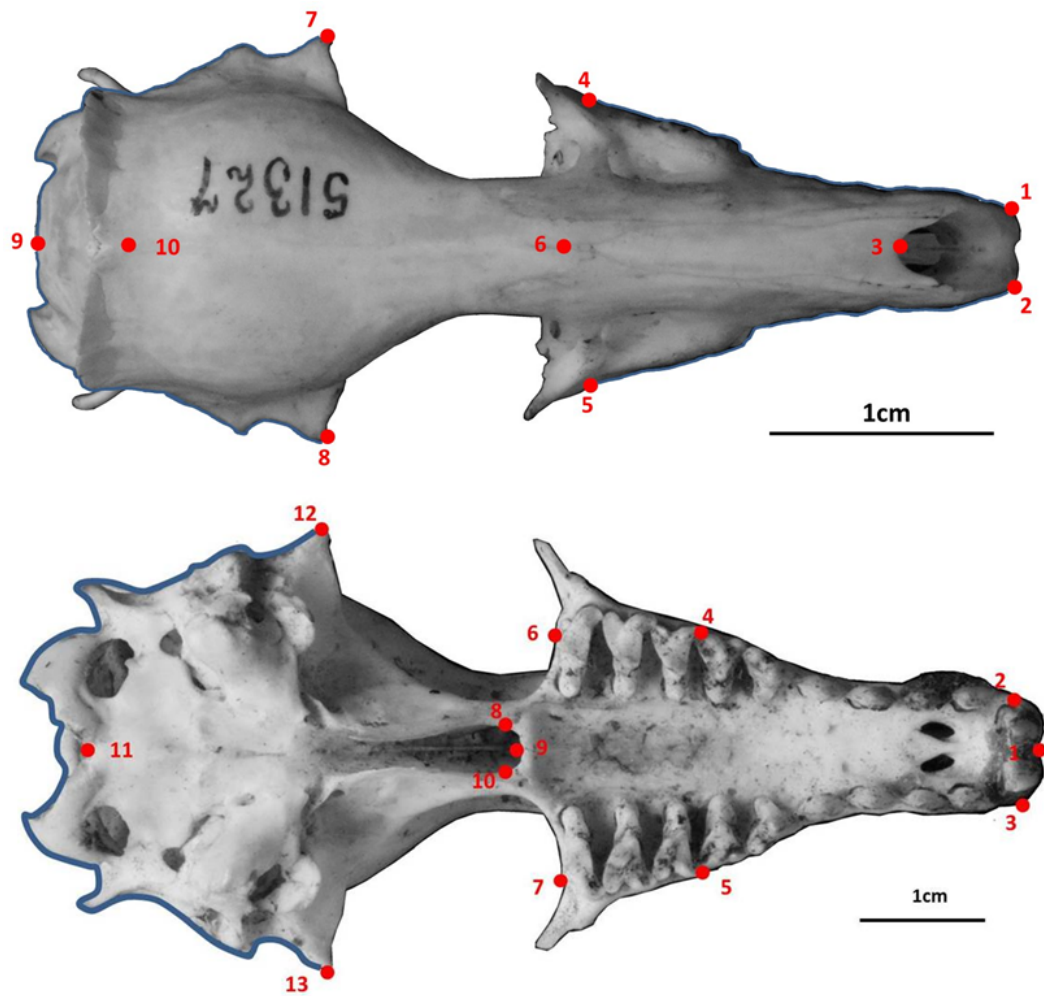


Figure 1: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of skulls in dorsal and ventral views respectively. Curves were re-sampled to the same number of evenly-spaced points. See table X for description of curves and landmarks. The specimens belong to two different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

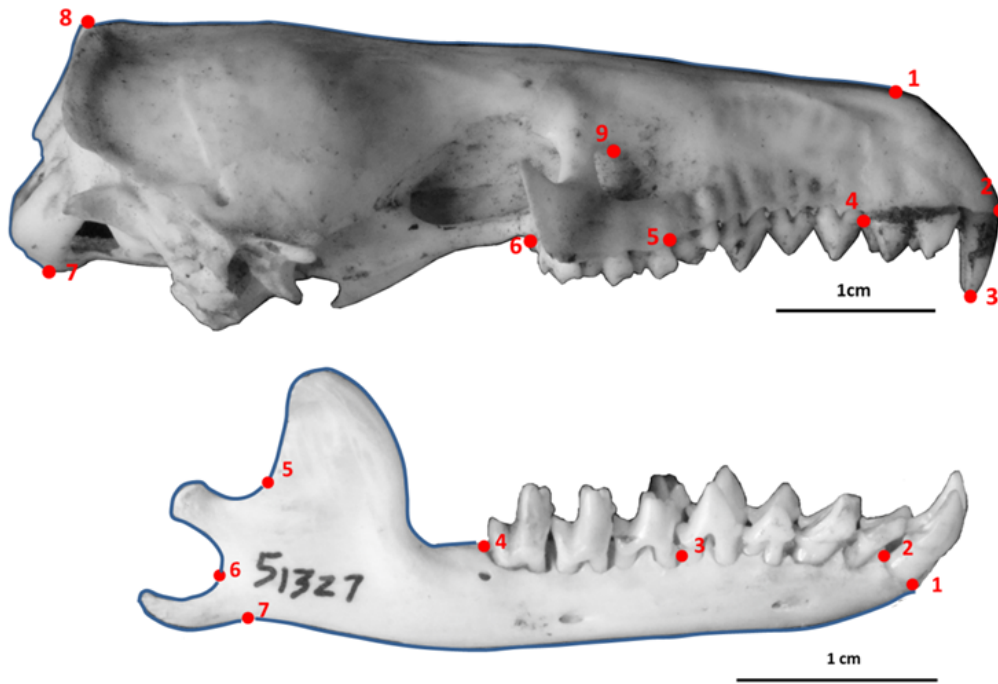


Figure 2: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of lateral views of skulls and mandibles respectively. Curves were re-sampled to the same number of evenly-spaced points. See table X for description of curves and landmarks. The specimens belong to two different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

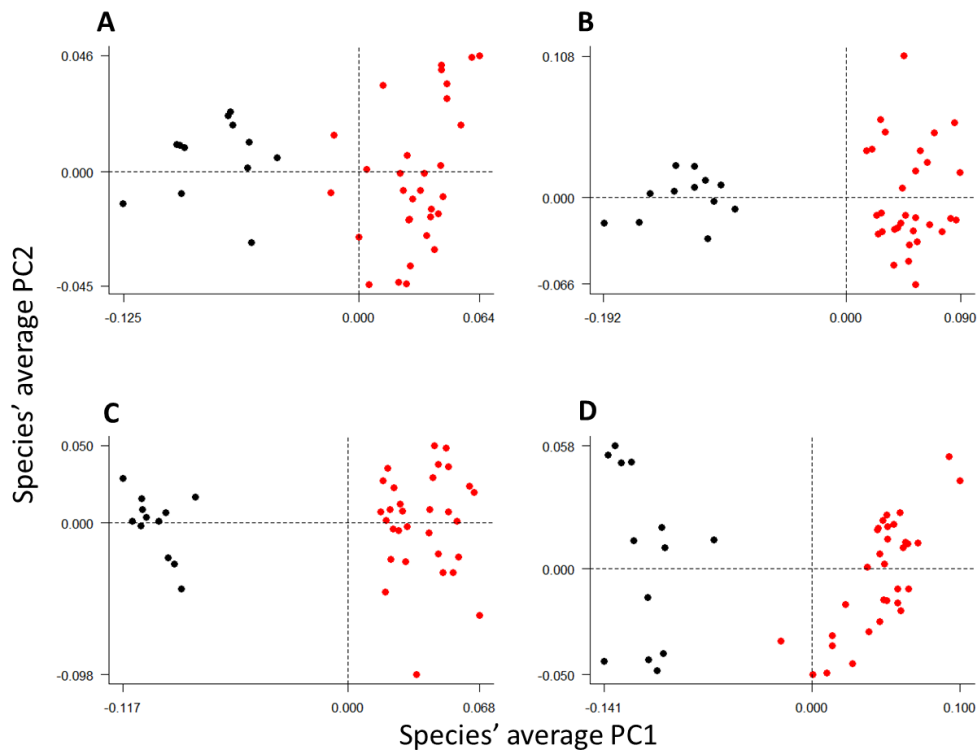


Figure 3: Principal components plots of the morphospaces occupied by tenrecs (red, $n=31$ species) and golden moles (black, $n=12$) for the skulls: dorsal (A), ventral (B), lateral (C) and mandibles (D) analyses. Axes are PC1 and PC2 of the average scores from a PCA analysis of mean Procrustes shape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

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417		ets. Disparity metrics are; sum of variance, product of vari-	
418		ance, sum of ranges, product of ranges and sum of squared	
419		distances among species.	24
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421		occupation for tenrecs and golden moles in each of the four	
422		analyses (three views of skulls and mandibles). In each case	
423		the two families occupy significantly different areas of mor-	
424		phospace.	25

Table 1: Summary of disparity comparisons between tenrecs (T) and golden moles (G) for each of our four 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	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)

Table 2: 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