

1 **Running head:** ???

2 Cranial morphological disparity within the
3 adaptive radiation of tenrecs (Afrosoricida,
4 Tenrecidae) is no greater than expected by
5 chance

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12 adaptive radiation

¹³ Abstract

14 Introduction

15 Adaptive radiations, "evolutionary divergence of members of a single
16 phylogenetic lineage into a variety of different adaptive forms" (Futuyma
17 1998, cited by Losos, 2010) have long-attracted the interests and attentions
18 of naturalists. Some of the most famous examples include Darwin's
19 finches (REF), cichlid fish (REF), Caribbean *Anolis* lizards (REF) and
20 Hawaiian *Drosophila* (REF). These groups exhibit great variety in both
21 species richness and phenotypic diversity. However, taxonomic diversity
22 does not necessarily correlate with phenotypic variety (Ruta et al., 2013;
23 Hopkins, 2013) and clades that have exceptional phenotypic diversity can
24 still be regarded as adaptive radiations even if they are not taxonomically
25 diverse. Therefore, to determine whether a clade has adaptively radiated
26 it is important to test whether there it exhibits exceptional (i.e. greater
27 than expected by chance) morphological and ecological diversity (Losos &
28 Mahler, 2010). However, few adaptive radiations have been characterised
29 in this way.

30 Phenotypic diversity is commonly measured as morphological
31 disparity; the diversity of organic form (Foote, 1997; Erwin, 2007)). There
32 is no single definition of disparity and it can be calculated in many ways
33 including measures of morphospace occupation (e.g. Goswami et al., 2011;
34 Brusatte et al., 2008) and rate-based approaches that assess the amount of
35 directed change away from an ancestor (O'Meara et al., 2006; Price et al.,
36 2013).

37 Here we investigate morphological disparity in tenrecs (Afrosoricida,
38 Tenrecidae) to determine whether they represent an adaptive radiation
39 sensu (Losos & Mahler, 2010). Tenrecs are comprised of 34 species, 31 of

40 which are endemic to Madagascar (Olson, 2013). From a single common
41 ancestor (Asher & Hofreiter, 2006), Malagasy tenrecs diversified into a
42 wide variety of descendant species which convergently resemble distantly
43 related insectivore mammals such as shrews (*Microgale* tenrecs), moles
44 (*Oryzorictes* tenrecs) and hedgehogs (*Echinops*, *Setifer* tenrecs) (Eisenberg &
45 Gould, 1969).

46 Tenrecs are often cited as an example of an adaptively radiated family
47 which exhibits exceptional morphological diversity (Soarimalala &
48 Goodman, 2011; Olson & Goodman, 2003; Eisenberg & Gould, 1969).
49 However, this apparent exceptional diversity is based on subjective
50 comparisons to other groups and it has not been tested quantitatively. If
51 tenrecs are exceptionally morphologically diverse then there are two
52 predictions; tenrecs are more morphologically disparate than expected by
53 chance and they are significantly more diverse than their nearest relatives,
54 the golden moles (Afrosoricida, Chrysochloridae).

55 Using the most complete morphological data set of tenrecs and golden
56 moles to date we apply geometric morphometric analyses (Rohlf &
57 Marcus, 1993; Zelditch et al., 2012) to quantify morphological disparity
58 among our species. Our results indicate that, on average, tenrecs are more
59 phenotypically diverse than their closest relatives but their morphological
60 diversity is no greater than that which is expected to evolve by chance.
61 Therefore, under strict definitions, their designation as an exceptional
62 adaptive radiation may need to be reconsidered.

63 These findings highlight the vital importance of testing our common,
64 but often erroneous, expectations about patterns of morphological
65 diversity in adaptively radiated groups.

66 **Materials and Methods**

67 **Data collection**

68 **Morphological data collection**

69 One of us (SF) photographed cranial specimens of tenrecs and golden
70 moles at the Natural History Museum London (BMNH), the Smithsonian
71 Institute Natural History Museum (SI), the American Museum of Natural
72 History (AMNH), Harvard's Museum of Comparative Zoology (MCZ)
73 and the Field Museum of Natural History, Chicago (FMNH). We
74 photographed the specimens with a Canon EOS 650D camera fitted with
75 an EF 100mm f/2.8 Macro USM lens using a standardised procedure to
76 minimise potential error (see Supplementary Material for details).

77 We collected pictures of the skulls in dorsal, ventral and lateral views
78 (right side of the skull) and of the outer (buccal) side of the right
79 mandibles. A full list of museum accession numbers and access to the
80 images can be found in the Supplementary Material.

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

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

90 our specimens. Our landmarks (points) and semilandmarks (outline
91 curves) used to represent shape variation in the dorsal skulls and
92 mandibles are in Figures 1 and 2 respectively. Corresponding landmark
93 definitions for each view are in tables 1 and 2.

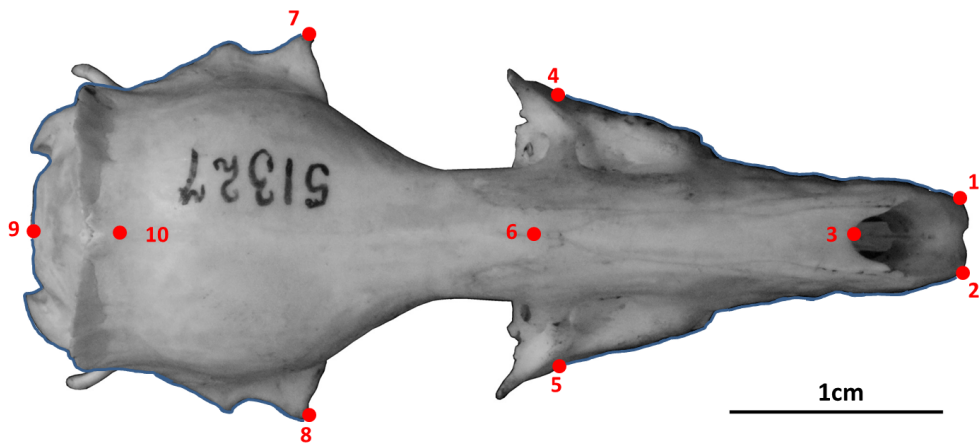


Figure 1: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of skulls in dorsal view. Curves were re-sampled to the same number of evenly-spaced points. See table X for description of curves and landmarks. *Potamogale velox* (Tenrecidae) skull, accession number: AMNH_51327

Table 1: Descriptions of the landmarks (points) and curves (semilandmarks) for the skulls in dorsal view (see Figure 1).

Landmark	Description
1 + 2	Left (1) and right (2) anterior points of the premaxilla
3	Anterior of the nasal bones in the midline
4 + 5	Maximum width of the palate (maxillary) on the left (4) and right (5)
6	Midline intersection between nasal and frontal bones
7 + 8	Widest point of the skull on the left (7) and right (8)
9	Posterior of the skull in the midline
10	Posterior intersection between sagittal and parietal sutures
Curves	Description
Curve A (12 points)	Outline of the braincase on the left side, between landmarks 9 and 7 (does not include visible features from the lower (ventral) side of the skull)
Curve B (10 points)	Outline of the palate on the left side, between landmarks 4 and 1 (outline of the rostrum only, not the shape of the teeth)
Curve C (12 points)	Outline of the braincase on the right side, between landmarks 9 and 8 (does not include visible features from the lower (ventral) side of the skull)
Curve D (10 points)	Outline of the palate on the right side, between landmarks 5 and 2 (outline of the rostrum only, not the shape of the teeth)

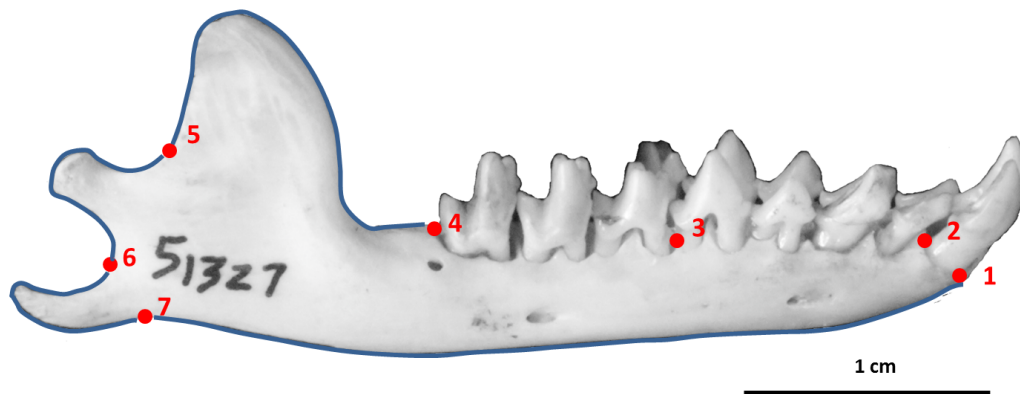


Figure 2: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of mandibles. Curves were re-sampled to the same number of evenly-spaced points. See table X for description of curves and landmarks. *Potamogale velox* (Tenrecidae) mandible, accession number: AMNH_51327

Table 2: Descriptions of the landmarks (points) and curves (semilandmarks) for the mandibles in lateral (buccal) view (see figure 2)

Landmark	Description
1	Anterior of the alveolus of the first incisor
2	Posterior of the alveolus of the first incisor
3	Anterior of the alveolus of the first molar
4	Posterior of the alveolus of the last molar
5	Maximum curvature between the coronoid and condylar processes
6	Maximum curvature between the condylar and angular processes
7	Maximum curvature between the angular process and the horizontal ramus
Curves	Description
Curve A	Condylar process (between landmarks 4 and 5, 15 points)
Curve B	Condylar process (between landmarks 5 and 6, 15 points)
Curve C	Angular process (between landmarks 6 and 7, 15 points)
Curve D	Base of the jaw (between landmarks 7 and 1, 12 points)

94 Our analyses of ventral and lateral skull views yielded similar patterns
95 in our disparity analyses (see results), details can be found in the
96 Supplementary Material. We digitised all landmarks and semilandmarks
97 in tpsDIG, version 2.17 (Rohlf, 2013).

98 We re-sampled the outlines to a standard number of evenly spaced
99 points which were the minimum number required to represent each
100 outline accurately (MacLeod, 2013, details in Supplementary Material).
101 We used TPSUtil (Rohlf, 2012) to create sliders files (Zelditch et al., 2012)
102 which defines which points are semilandmarks. We conducted all
103 subsequent analyses in R version 3.0.2 (R Development Core Team, 2013)

104 within the geomorph package (Adams et al., 2013). We used the gpagen
105 function to run a general Procrustes alignment (REFS) of the landmark
106 coordinates while sliding the semilandmarks by minimising procrustes
107 distance rather than bending energy (REFS). We used these
108 Procrustes-aligned coordinates of all species (n=43) to calculate average
109 shape values for each species which we then used for a principal
110 components (PC) analysis (REFS) with the plotTangentSpace function
111 (Adams et al., 2013).

112 **Phylogeny**

113 Instead of basing our analyses on individual trees and assuming that their
114 topologies were known without error (e.g. Ruta et al., 2013; Foth et al.,
115 2012; Brusatte et al., 2008; Harmon et al., 2003) we used a distribution of
116 101 pruned phylogenies derived from the randomly resolved mammalian
117 supertrees in (Kuhn et al., 2011).

118 Eight species (six *Microgale* tenrecs and two golden moles) in our
119 morphological data were not in the phylogenies. Phylogenetic
120 relationships among the *Microgale* have not been resolved more recently
121 than the (Kuhn et al., 2011) analysis, therefore we added the additional
122 *Microgale* species at random to the *Microgale* genus within each phylogeny
123 (Revell, 2012). We could not use the same approach to add the two
124 missing golden mole species because they were the only representatives of
125 their respective genera within our data. Therefore we randomly added
126 these species to the common ancestral node (using the findMRCA function
127 in phytools (Revell, 2012)) of all golden moles within each phylogeny.
128 Adding these extra species to the phylogenies created polytomies which

129 we resolved arbitrarily using zero-length branches (Paradis et al., 2004).
130 We calculated pairwise phylogenetic distances among species using the
131 cophenetic function (R Development Core Team, 2013).

132 **Analyses**

133 **Disparity calculations**

134 We calculated morphological disparity separately for golden moles and
135 tenrecs in each of the morphological datasets. We used the PC axes which
136 accounted for 95% of the cumulative variation to calculate four disparity
137 metrics; the sum and product of the range and variance of morphospace
138 occupied by each family (Brusatte et al., 2008; Foth et al., 2012; Ruta et al.,
139 2013). We also calculated morphological disparity directly from the
140 Procrustes-superimposed shape data (Zelditch et al., 2012). Disparity is
141 expected to be higher in larger groups (REFS). Therefore we repeated our
142 disparity comparisons between the two families using rarefaction (see
143 Supplementary Material) to confirm that observed differences in disparity
144 between the two groups were not artefacts of differences in sample size.

145 To test whether tenrecs are more morphologically disparate than
146 expected by chance, we simulated shape evolution (Harmon et al., 2008) of
147 the species-average, Procrustes-superimposed shape coordinates of each
148 tenrec species across our distribution of phylogenies under a Brownian
149 Motion (BM) model (1000 simulations on each of 101 phylogenies pruned
150 to include tenrec species only). We ran a principal components analysis on
151 each of the simulations and used the PC axes which accounted for 95% of
152 the cumulative variation to calculate disparity metrics.

153 We compared the observed disparity measure to the corresponding
154 distribution of values and used a two-tailed test to determine whether the
155 observed (true) disparity measures were more or less than expected by
156 chance.

157 The majority of tenrecs (19 out of 31 in our data) are members of the
158 *Microgale* (shrew-like) genus which is notable for its relatively low
159 phenotypic diversity (Soarimalala & Goodman, 2011; Jenkins, 2003) and
160 may mask signals of high disparity among other tenrecs. To test this we
161 repeated our simulations of shape evolution excluding *Microgale* species.
162 This reduced our data from 31 to 12 species.

163 To test whether tenrecs are more disparate than their nearest relatives,
164 we used a non parametric MANOVA (Anderson, 2001) to compare
165 morphospace occupation between the two groups (REFS?).

166 **Results**

167 **Morphological disparity in tenrecs**

168 We compared observed disparity to calculations of disparity from BM
169 simulations of shape data (101,000 simulations across 101 phylogenies).
170 For each metric of disparity in both the dorsal skulls (table 3) and
171 mandibles (table 4), the true (observed) values were significantly lower
172 than expected compared to the distribution of simulated values. We also
173 found significantly lower disparity than expected by chance in both the
174 ventral and lateral skull views (Supplementary Material).

175 Removing the phenotypically similar *Microgale* tenrecs did not

176 qualitatively affect our results; the non-*Microgale* tenrecs still show
 177 significantly lower phenotypic disparity than expected by chance
 178 (simulation results in the supplementary material).

Table 3: Comparison of observed and simulated disparity measures for the dorsal skulls analysis; observed (true) disparity measures, minimum simulated value (sim.min), maximum simulated value (sim.max), standard deviation of the simulated values (sdev.sim) and p value comparing the observed disparity measures to the distribution of simulated values)

Disparity metric	Observed	Sim.min	Sim.max	Sdev.sim	p value
Sum of Variance	0.0017	24742.44	286028.06	20878.99	0
Product of Variance	0.00013	1306.57	286028.06	3518.66	0
Sum of Ranges	0.38	1224.51	2934.11	167.54	0
Product of Ranges	0.047	148.62	1627.71	60.48	0

Table 4: Comparison of observed and simulated disparity measures for the mandibles analysis; observed (true) disparity measures, minimum simulated value (sim.min), maximum simulated value (sim.max), standard deviation of the simulated values (sdev.sim) and p value comparing the observed disparity measures to the distribution of simulated values)

Disparity metric	Observed	Sim.min	Sim.max	Sdev.sim	p value
Sum of Variance	0.0032	23459.28	286827.19	20915.32	0
Product of Variance	0.000189	1173.95	286827.19	3346.28	0
Sum of Ranges	0.676	1212.44	2996.77	170.86	0
Product of Ranges	0.0639	151.54	1520.68	60.51	0

179 **Morphological disparity in tenrec and golden moles**

180 Figures 3 and 4 depict the morphospace plots derived from our principal
181 components analyses of average Procrustes-superimposed shape
182 coordinates for each species in our skull and mandible data respectively.
183 We used the principal components axes which accounted for 95% of the
184 cumulative variation ($n = 6$ axes for the dorsal skulls analysis and $n = 11$
185 axes for the mandibles) to calculate the disparity of each family.

186 There was agreement among all of our disparity metrics that tenrecs
187 have more diverse dorsal skull shapes than golden moles and the two
188 families occupy significantly different areas of morphospace.

189 Non-*Microgale* tenrecs also have higher disparity than golden moles
190 and we found the same results in our analyses of ventral and lateral skull
191 shapes (see Supplementary Material).

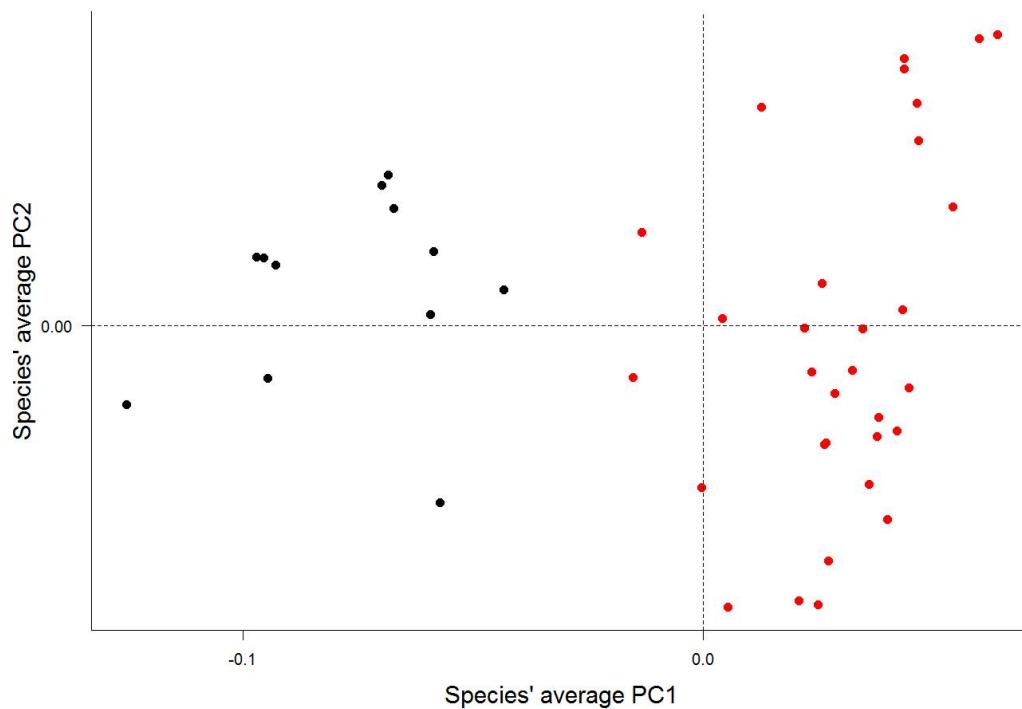


Figure 3: Principal components plot of the dorsal skulls' morphospace occupied by tenrecs (red, $n=31$) and golden moles (black, $n=12$). Axes are PC1 and PC2 of the average scores from a PCA analysis of mean Procrustes shape coordinates for each species.

192 Surprisingly, our analyses of disparity in mandible shape yielded the
 193 opposite result; golden moles have significantly higher diversity in the
 194 shape of their mandibles than tenrecs. Again, this result is not an artifact
 195 of the relatively low phenotypic diversity within *Microgale* tenrecs;
 196 non-*Microgale* tenrecs still have significantly lower disparity in the shape
 197 of their mandibles than golden moles.

198 Rarefaction analyses confirmed that our findings were not the result of
 199 differences in sample size (see supplementary material).

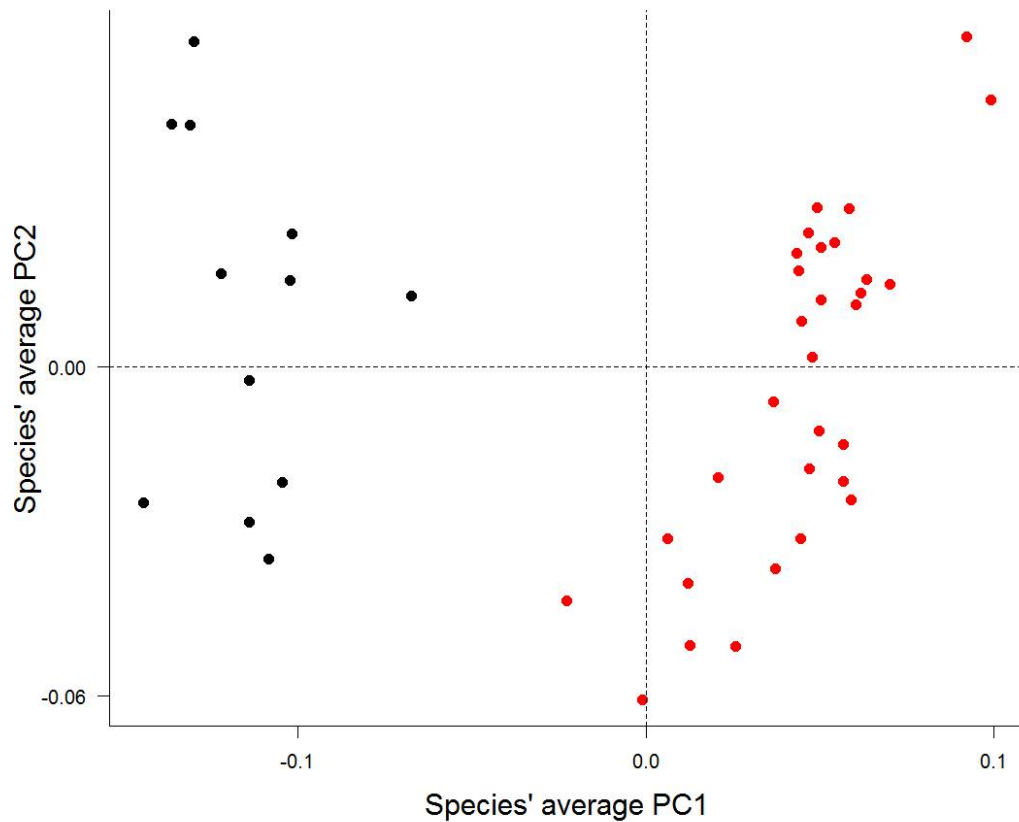


Figure 4: Principal components plot of the mandibles' morphospace occupied by tenrecs (red, n=31) and golden moles (black, n=12). Axes are PC1 and PC2 of the average scores from a PCA analysis of mean Procrustes shape coordinates for each species.

Discussion

Our findings provide new insights into phenotypic diversity within the tenrec family. Contrary to previous suggestions (e.g. Eisenberg & Gould, 1969; Olson, 2013), tenrecs do not appear to be exceptional in their morphological diversity. They do seem to be more morphologically

205 disparate than their closest relatives but only in skull morphology; the
206 opposite is true when we look at mandible morphology (figure 4). Our
207 results illustrate the vital importance of applying quantitative methods to
208 test assumptions about morphological diversity.

209 Tenrecs are evidently a diverse group, both phenotypically and
210 ecologically. Body sizes of extant tenrecs span three orders of magnitude
211 (2.5 to >2,000g) which is a greater range than all other Families, and most
212 Orders, of living mammals (Olson & Goodman, 2003). Within this vast
213 size range there is striking morphological diversity, from the spiny
214 *Echinops*, *Setifer* and striking *Hemicentetes* to the shrew-like *Microgale*.
215 Furthermore, tenrecs inhabit a variety of ecological niches and habitats
216 including terrestrial, arboreal, semi-aquatic and semi-fossorial forms
217 (REFS).

218 However, our results cast doubt over whether the evident diversity
219 within the tenrec family should be considered to be an adaptive radiation.
220 Phenotypic and ecological divergences within a clade are not surprising;
221 most clades have at least small levels of disparity so, when it comes to
222 identifying adaptive radiations, it's important to identify clades which are
223 exceptional in their diversity (Losos & Mahler, 2010). Here we have
224 presented the first quantitative investigation of morphological disparity in
225 tenrecs and our results suggest that perhaps phenotypic variation in
226 tenrecs is not the product of an adaptive radiation in the strict sense of its
227 definition.

228 Although tenrecs are not more morphologically diverse than expected
229 by chance, they do show greater cranial disparity than their nearest
230 relatives. The discrepancies between our analyses of cranial and mandible

231 disparity could reflect derive from factors associated with the modularity
232 of morphological evolution.

233 There is strong evidence that morphological variation in skulls and
234 mandibles is derived from differential evolution of integrated
235 developmental modules (reviewed by Klingenberg, 2013). For example,
236 there seems to be two primary modules in the mouse mandible; an
237 alveolar part which holds the teeth and the ascending ramus for muscle
238 attachment and which articulates with the skull (Klingenberg, 2008).
239 Geometric shape covariation is stronger within rather than between these
240 modules.

241 Our landmarks and curves for the mandibles (figure 2, table 2) include
242 aspects of variation in the dentition but they focus particular attention on
243 the ascending ramus (condyloid, condylar and angular processes).
244 Therefore the higher morphological disparity in golden mole mandibles
245 most likely reflects greater variation in the shape of the muscle attachment
246 areas of the mandible. In contrast it proved impossible to position reliable
247 landmarks on the corresponding articulation areas of the skull in lateral
248 view (see Supplementary).

249 If variation in muscle attachment/articulation sites is driving
250 morphological disparity in mandibles, it is not clear why golden moles
251 should have more disparate articular rami than tenrecs.

252 While our findings cast doubt on the designation of tenrecs as an
253 adaptive radiation sensu (Losos & Mahler, 2010), there are certain caveats
254 to consider which could modify the interpretation of our results.

255 Phenotypic variation can evolve for reasons other than adaptive
256 radiation. Therefore, to describe phenotypic divergence as the product of

257 an adaptive radiations requires exceptional morphological diversity in
258 traits which have specific and proven adaptive significance (Losos &
259 Mahler, 2010). The evolution of cranial shape (both upper skull and
260 mandible), particularly dental morphology, has obvious correlations with
261 dietary specialisations (REFS) and occupation of specific ecological niches
262 (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 variation in
266 cranial shape should be an adaptive characteristic which allows the
267 animals to survive in their divergent niches. Therefore quantifying the
268 diversity of cranial morphology is a reasonable method of assessing the
269 significance of morphological variety within the context of identifying an
270 adaptive radiation.

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

279 However, the results of (Foth et al., 2012) are encouraging. In an
280 analysis of morphological disparity in pterosaurs, they found that
281 disparity calculations based on geometric morphometric characterisation
282 of skull shape yielded broadly similar results compared to analyses of

283 whole-skeleton discrete characters and limb proportion data sets.
284 Therefore the disparity patterns we find here based on geometric
285 morphometric analyses of cranial shape most likely represent
286 approximations of disparity which are accurate for morphological
287 diversity in the clades.

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