

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 golden moles 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, cichlid fish and Caribbean *Anolis* lizards (Gavrillets & Losos, 2009).
20 These groups exhibit great variety in both species richness and
21 phenotypic diversity. However, taxonomic diversity does not necessarily
22 correlate with phenotypic variety (Ruta et al., 2013; Hopkins, 2013) and
23 clades that have exceptional phenotypic diversity can still be regarded as
24 adaptive radiations even if they are not taxonomically diverse. Therefore,
25 to determine whether a clade has adaptively radiated it is important to
26 test whether it exhibits exceptional (i.e. greater than expected by chance)
27 morphological and ecological diversity (Losos & Mahler, 2010). However,
28 few adaptive radiations have been characterised in this way.

29 Phenotypic diversity is commonly measured as morphological
30 disparity; the diversity of organic form (Foote, 1997; Erwin, 2007)). There
31 is no single definition of disparity and it can be calculated in many ways
32 including measures of morphospace occupation (e.g. Goswami et al., 2011;
33 Brusatte et al., 2008) and rate-based approaches that assess the amount of
34 directed change away from an ancestor (O'Meara et al., 2006; Price et al.,
35 2013). These alternative approaches can be applied to analyses of
36 disparity depending on whether you are interested in current patterns of
37 morphological diversity or the rate at which they accumulate through
38 time. We follow the view of (Losos & Mahler, 2010) and others and

39 Here we investigate morphological disparity in tenrecs (Afrosoricida,

40 Tenrecidae) to determine whether they represent an adaptive radiation
41 sensu (Losos & Mahler, 2010). Tenrecs are comprised of 34 species, 31 of
42 which are endemic to Madagascar (Olson, 2013). From a single common
43 ancestor (Asher & Hofreiter, 2006), Malagasy tenrecs diversified into a
44 wide variety of descendant species which convergently resemble distantly
45 related insectivore mammals such as shrews (*Microgale* tenrecs), moles
46 (*Oryzorictes* tenrecs) and hedgehogs (*Echinops*, *Setifer* tenrecs) (Eisenberg &
47 Gould, 1969).

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

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

65 These findings highlight the vital importance of testing our common,

66 but often erroneous, expectations about patterns of morphological
67 diversity in adaptively radiated groups.

68 **Materials and Methods**

69 **Data collection**

70 **Morphological data collection**

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

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

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

89 Olson, 2013) to identify our specimens.

90 We used a combination of both landmarks (type 2 and type 3,
91 (Zelditch et al., 2012)) and semilandmarks to characterise the shapes of
92 our specimens. Our landmarks (points) and semilandmarks (outline
93 curves) used to represent shape variation in the dorsal skulls and
94 mandibles are in Figures 1 and 2 respectively. Corresponding landmark
95 definitions for each view are in tables 1 and 2.

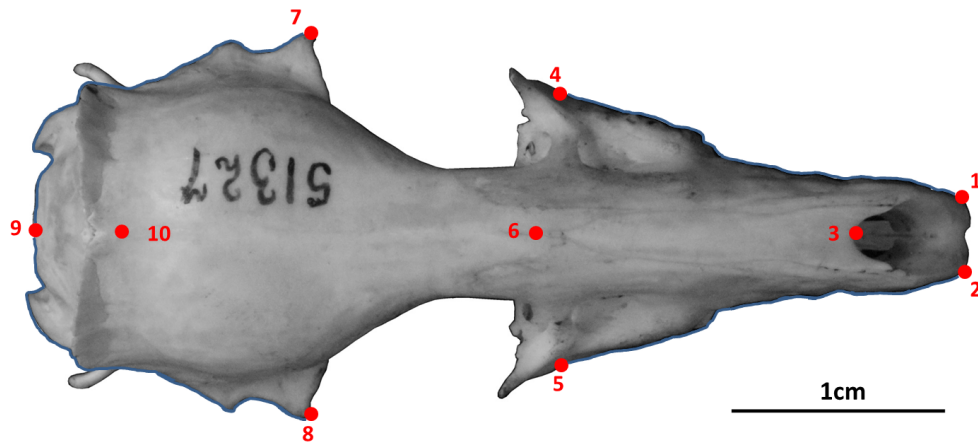


Figure 1: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of skulls in dorsal view. Curves were re-sampled to the same number of evenly-spaced points. See table X for description of curves and landmarks. *Potamogale velox* (Tenrecidae) skull, accession number: AMNH_51327

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)

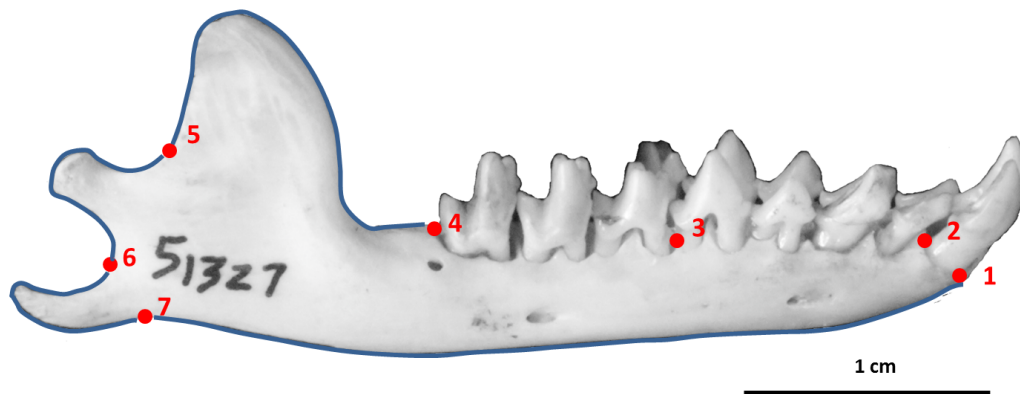


Figure 2: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of mandibles. Curves were re-sampled to the same number of evenly-spaced points. See table X for description of curves and landmarks. *Potamogale velox* (Tenrecidae) mandible, accession number: AMNH_51327

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)

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

We re-sampled the outlines to a standard number of evenly spaced points which were the minimum number 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) which defines which points are semilandmarks. We conducted all subsequent analyses in R version 3.0.2 (R Development Core Team, 2013)

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

114 **Phylogeny**

115 Instead of basing our analyses on individual trees and assuming that their
116 topologies were known without error (e.g. Ruta et al., 2013; Foth et al.,
117 2012; Brusatte et al., 2008; Harmon et al., 2003) we used a distribution of
118 101 pruned phylogenies derived from the randomly resolved mammalian
119 supertrees in (Kuhn et al., 2011).

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

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

134 **Analyses**

135 **Disparity calculations**

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

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

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

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

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

168 **Results**

169 **Morphological disparity in tenrecs**

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

177 Removing the phenotypically similar *Microgale* tenrecs did not

178 qualitatively affect our results; the non-*Microgale* tenrecs still show
179 significantly lower phenotypic disparity than expected by chance
180 (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

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

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

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

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

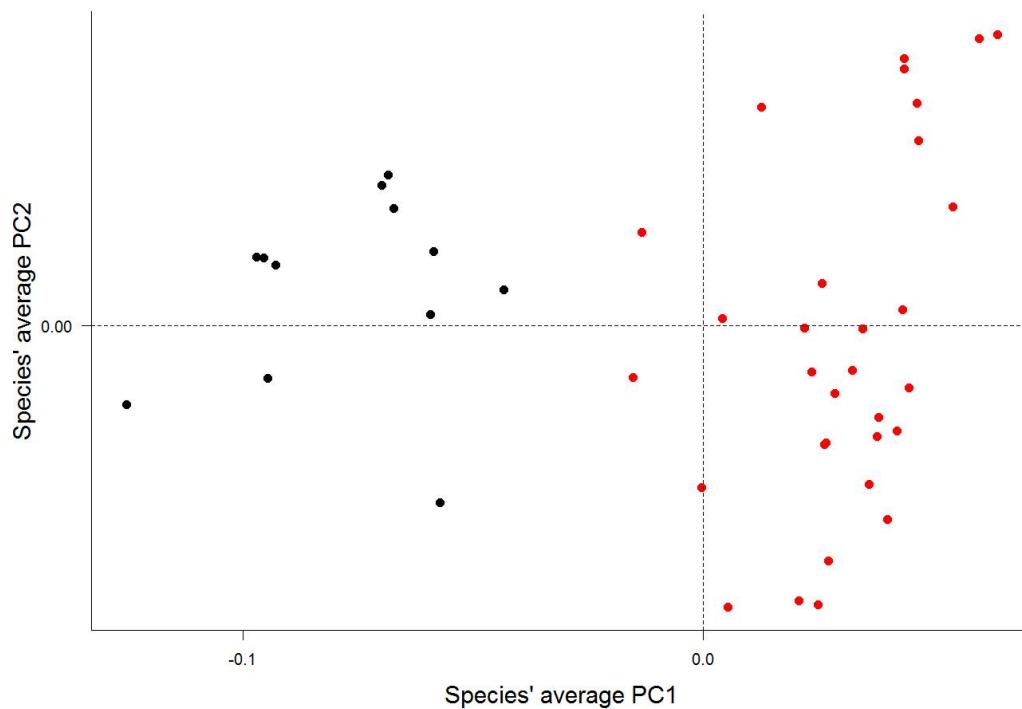


Figure 3: Principal components plot of the dorsal skulls' morphospace occupied by tenrecs (red, $n=31$) and golden moles (black, $n=12$). Axes are PC1 and PC2 of the average scores from a PCA analysis of mean Procrustes shape coordinates for each species.

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

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

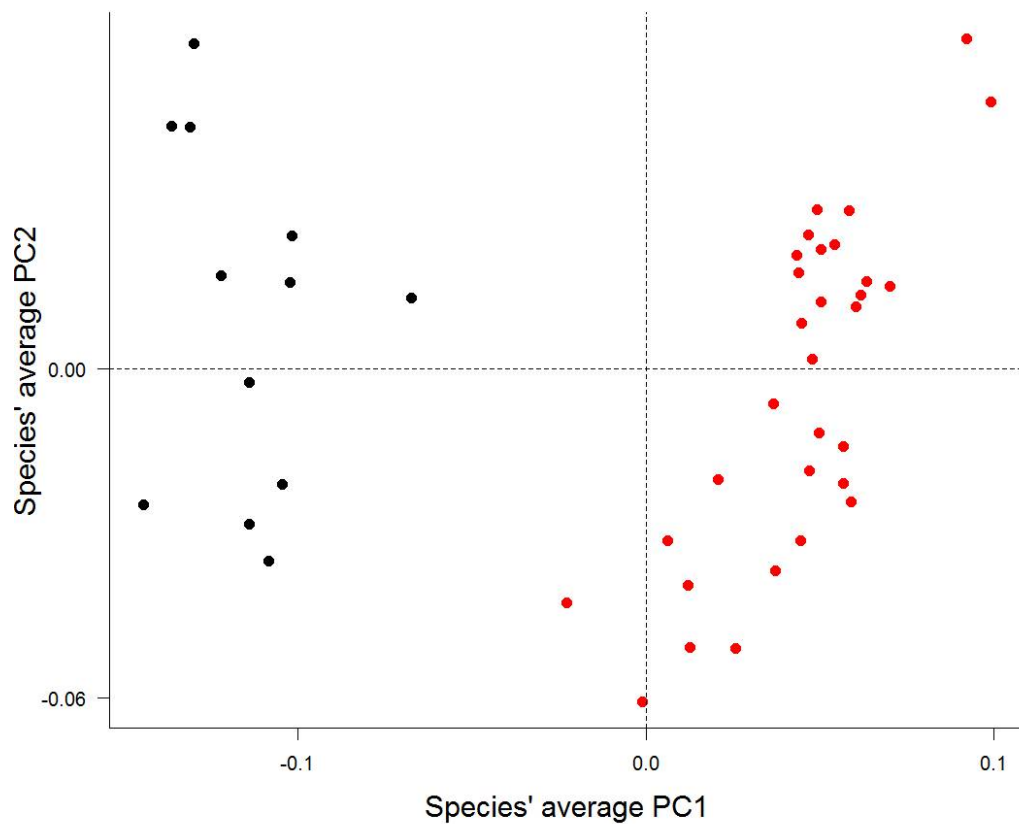


Figure 4: Principal components plot of the mandibles' morphospace occupied by tenrecs (red, $n=31$) and golden moles (black, $n=12$). Axes are PC1 and PC2 of the average scores from a PCA analysis of mean Procrustes shape coordinates for each species.

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

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

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

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

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

233 disparity could reflect derive from factors associated with the modularity
234 of morphological evolution.

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

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

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

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

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

259 an adaptive radiations requires exceptional morphological diversity in
260 traits which have specific and proven adaptive significance (Losos &
261 Mahler, 2010). The evolution of cranial shape (both upper skull and
262 mandible), particularly dental morphology, has obvious correlations with
263 dietary specialisations (REFS) and occupation of specific ecological niches
264 (REFS).

265 Considering the wide ecological diversity of our study species; the
266 fossorial golden moles and semi-fossorial, arboreal, terrestrial and
267 semi-aquatic tenrecs (REFS) it is reasonable to expect that variation in
268 cranial shape should be an adaptive characteristic which allows the
269 animals to survive in their divergent niches. Therefore quantifying the
270 diversity of cranial morphology is a reasonable method of assessing the
271 significance of morphological variety within the context of identifying an
272 adaptive radiation.

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

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

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

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