

1 **Running head:** ???

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

6 Sive Finlay^{1,2,*} and Natalie Cooper^{1,2}

7 ¹ School of Natural Sciences, Trinity College Dublin, Dublin 2, Ireland.

8 ² Trinity Centre for Biodiversity Research, Trinity College Dublin, Dublin 2, Ireland.

9 *sfinlay@tcd.ie; Zoology Building, Trinity College Dublin, Dublin 2, Ireland.

10 Fax: +353 1 6778094; Tel: +353 1 896 2571.

11 **Keywords:** disparity, morphology, geometric morphometrics, tenrecs,
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. Corresponding definitions of each of
111 the landmarks can be found in the supplementary material.

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

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

126 **Phylogeny**

127 Instead of basing our analyses on individual trees and assuming that their
128 topologies were known without error (e.g. Ruta et al., 2013; Foth et al.,
129 2012; Brusatte et al., 2008; Harmon et al., 2003) we used a distribution of
130 101 pruned phylogenies derived from the randomly resolved mammalian
131 supertrees in (Kuhn et al., 2011).

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

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

146 **Analyses**

147 **Disparity calculations**

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

196 In our analyses of the three different views of the skulls, when
197 disparity is calculated from principal component - based metrics there is
198 there is an overall trend for tenrecs to have higher disparity than golden
199 moles. However, none of these differences are statistically significant
200 (table 1). In contrast, when we calculated disparity based on the sum of
201 squared interlandmark differences between species pairs (Zelditch et al.,
202 2012) then golden moles had significantly higher levels of disparity than
203 tenrecs (table 1).

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

208 The three curves that we placed at the back of the mandibles (figure 2)
209 place a particular emphasis on shape variation in the posterior of the
210 bone; the ramus, coronoid, condylar and angular processes. Therefore,
211 higher disparity in golden mole mandibles compared to tenrecs could be
212 driven by greater morphological variation in these structures. To test this
213 idea, we repeated our morphometric analyses of the mandibles with a

214 reduced data set of points; just the seven landmark points and one single
215 curve at the base of the jaw between landmarks 1 and 7 (figure 2). When
216 we compared familial disparity levels with this reduced data set we found
217 that golden moles no longer had significantly higher disparity than tenrecs
218 but rather there were some indications that the opposite was true (table 1).

219 **Morphological disparity in non-*Microgale* tenrecs and** 220 **golden moles**

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

230 **Discussion**

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

237 shapes than tenrecs.

238 It is evident that tenrecs are a diverse group, both phenotypically and
239 ecologically. Body sizes of extant tenrecs span three orders of magnitude
240 (2.5 to $> 2,000\text{g}$) which is a greater range than all other Families, and most
241 Orders, of living mammals (Olson & Goodman, 2003). Within this vast
242 size range there is striking morphological diversity, from the spiny
243 *Echinops*, *Setifer* and striking *Hemicentetes* to the shrew-like *Microgale*.
244 Furthermore, tenrecs inhabit a variety of ecological niches and habitats
245 including terrestrial, arboreal, semi-aquatic and semi-fossorial forms
246 (Soarimalala & Goodman, 2011).

247 Here we have presented the first quantitative investigation of
248 morphological disparity in tenrecs and our results suggest that perhaps
249 phenotypic variation in tenrecs is not as uniformly exceptional as it first
250 appears.

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

255 Another apparent anomaly in our results is that we found opposite
256 patterns of group dissimilarities in the analyses of skulls and mandibles.
257 Our landmarks and curves for the mandibles (figure 2) include aspects of
258 variation in the dentition but they focus particular attention on the
259 ascending ramus (condyloid, condylar and angular processes). Therefore
260 higher disparity in golden moles could reflect greater morphological
261 variability in these posterior mandible structures. To test this idea we
262 deleted the semi-landmark curves around these structures (curves A, B,

263 and C, table x in supplementary material) and repeated our disparity
264 analyses on all of the specimens. In this case we retrieved the opposite
265 pattern: tenrecs had higher morphological disparity than golden moles
266 (see supplementary material). Therefore, our results indicate that golden
267 moles have greater morphological variation in the posterior structures of
268 their mandibles compared to tenrecs.

269 It proved impossible to position reliable landmarks on the
270 corresponding mandibular articulation areas of the skull in lateral view
271 (see supplementary). Therefore we could not test whether higher
272 morphological disparity in the rami were correlated with associated
273 morphological variety in the articulation areas of the skull.

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

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

289 explicitly.

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

298 However, the results of (Foth et al., 2012) are encouraging. In an
299 analysis of morphological disparity in pterosaurs, they found that
300 disparity calculations based on geometric morphometric characterisation
301 of skull shape yielded broadly similar results compared to analyses of
302 whole-skeleton discrete characters and limb proportion data sets.
303 Therefore the disparity patterns we find here based on geometric
304 morphometric analyses of cranial shape most likely represent
305 approximations of disparity which are accurate for morphological
306 diversity in the clades.

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

309 These analyses represent the first attempt to find evidence to support
310 the common claim that tenrecs are an adaptive radiation. Future work
311 will develop our results by expanding the analyses to non-cranial
312 morphology and also measures of ecological diversity. However, our
313 current results provide a clear indication that phenotypic variety within
314 tenrecs is perhaps not as exceptional as it first seems and therefore their

315 designation as an adaptive radiation may need to be re-considered.

316 **Acknowledgements**

317 We thank François Gould, Dean Adams, David Polly, Gary Bronner, Steve
318 Brusatte, Steve Wang, Luke Harmon, Thomas Guillaume and the members
319 of NERD club for insightful discussions and the museum staff and
320 curators for their support and access to collections. Funding was provided
321 by an Irish Research Council EMBARK Initiative Postgraduate
322 Scholarship (SF) and the European Commission CORDIS Seventh
323 Framework Programme (FP7) Marie Curie CIG grant. Proposal number:
324 321696 (NC, SF)

325 **References**

- 326 Adams, D., Otárola-Castillo, E. & Paradis, E. 2013. geomorph: an R
327 package for the collection and analysis of geometric morphometric
328 shape data. *Methods in Ecology and Evolution* **4**: 393–399.
- 329 Anderson, M. 2001. A new method for non-parametric multivariate
330 analysis of variance. *Austral Ecology* **26**: 32–46.
- 331 Asher, R. & Hofreiter, M. 2006. Tenrec phylogeny and the noninvasive
332 extraction of nuclear DNA. *Systematic Biology* **55**: 181–194.
- 333 Asher, R.J., Maree, S., Bronner, G., Bennett, N., Bloomer, P., Czechowski,
334 P., Meyer, M. & Hofreiter, M. 2010. A phylogenetic estimate for golden
335 moles (Mammalia, Afrotheria, Chrysochloridae). *BMC Evolutionary*
336 *Biology* **10**: 1–13.

- 337 Bookstein, F. 1997. Landmark methods for forms without landmarks:
338 morphometrics of group differences in outline shape. *Medical image*
339 *analysis* **1**: 225–243.
- 340 Brusatte, S., Benton, M., Ruta, M. & Lloyd, G. 2008. Superiority,
341 competition and opportunism in the evolutionary radiation of
342 dinosaurs. *Science* **321**: 1485–1488.
- 343 Eisenberg, J.F. & Gould, E. 1969. The Tenrecs: A Study in Mammalian
344 Behaviour and Evolution. *Smithsonian Contributions to Zoology* **27**: 1–152.
- 345 Erwin, D. 2007. Disparity: morphological pattern and developmental
346 context. *Palaeontology* **50**: 57–73.
- 347 Foote, M. 1997. The evolution of morphological diversity. *Annual Review of*
348 *Ecology and Systematics* **28**: 129–152.
- 349 Foth, C., Brusatte, S. & Butler, R. 2012. Do different disparity proxies
350 converge on a common signal? Insights from the cranial morphometrics
351 and evolutionary history of *Pterosauria* (Diapsida: Archosauria). *Journal*
352 *of Evolutionary Biology* **25**: 904–915.
- 353 Gavrillets, S. & Losos, J. 2009. Adaptive radiation: contrasting theory with
354 data. *Science* **323**: 732–736.
- 355 Glor, R. 2010. Phylogenetic insights on adaptive radiation. *Annual Review*
356 *of Ecology, Evolution, and Systematics* **41**: 251–270.
- 357 Goswami, A., Milne, N. & Wroe, S. 2011. Biting through constraints:
358 cranial morphology, disparity and convergence across living and fossil
359 carnivorous mammals. *Proceedings of the Royal Society B: Biological*
360 *Sciences* **278**: 1831–1839.

- 361 Harmon, L., Schulte, J., Larson, A. & Losos, J.B. 2003. Tempo and mode of
362 evolutionary radiation in iguanian lizards. *Science* **301**: 961–964.
- 363 IUCN 2012. International Union for Conservation of Nature.
- 364 Jenkins, P. 2003. *Microgale, shrew tenrecs*, pp. 1273–1278. The University of
365 Chicago Press, Chicago.
- 366 Kuhn, T., Mooers, A. & Thomas, G. 2011. A simple polytomy resolver for
367 dated phylogenies. *Methods in Ecology and Evolution* **2**: 427–436.
- 368 Losos, J. 2010. Adaptive radiation, ecological opportunity, and
369 evolutionary determinism. American Society of Naturalists E. O. Wilson
370 Award Address. *The American Naturalist* **175**: 623–639. 10.1086/652433.
- 371 Losos, J. & Miles, D. 2002. Testing the hypothesis that a clade has
372 adaptively radiated: Iguanid lizards as a case study. *The American*
373 *Naturalist* **160**: 147–157.
- 374 Losos, J.B. & Mahler, D. 2010. *Adaptive radiation: the interaction of ecological*
375 *opportunity, adaptation and speciation*, chap. 15, pp. 381–420. Sinauer
376 Association, Sunderland, MA.
- 377 MacLeod, N. 2013. Landmarks and semilandmarks: Difference without
378 meaning and meaning without difference.
- 379 Olson, L. & Goodman, S. 2003. *Phylogeny and biogeography of tenrecs*, pp.
380 1235–1242. The University of Chicago Press, Chicago.
- 381 Olson, L.E. 2013. Tenrecs. *Current Biology* **23**: R5–R8.
- 382 Olson, M.E. & ArroyoSantos, A. 2009. Thinking in continua: beyond the
383 adaptive radiation metaphor. *BioEssays* **31**: 1337–1346.

- 384 O'Meara, B., Ané, C., Sanderson, M. & Wainwright, P. 2006. Testing for
385 different rates of continuous trait evolution using likelihood. *Evolution*
386 **60**: 922–933.
- 387 Paradis, E., Claude, J. & Strimmer, K. 2004. Ape: Analyses of
388 Phylogenetics and Evolution in R language. *Bioinformatics* **20**: 289–290.
- 389 Price, S., Tavera, J., Near, T. & Wainwright, P. 2013. Elevated rates of
390 morphological and functional diversification in reef-dwelling haemulid
391 fishes. *Evolution* **67**: 417–428.
- 392 Revell, L. 2012. phytools: an R package for phylogenetic comparative
393 biology (and other things). *Methods in Ecology and Evolution* **3**: 217–223.
- 394 Rohlf, F. 2012. Tpsutil.
- 395 Rohlf, F. 2013. Tpsdig2 ver 2.17.
- 396 Rohlf, J. & Marcus, L. 1993. A revolution in morphometrics. *Trends in*
397 *Ecology & Evolution* **8**: 129–132.
- 398 Roy, K. & Foote, M. 1997. Morphological approaches to measuring
399 biodiversity. *Trends in Ecology & Evolution* **12**: 277–281.
- 400 Ruta, M., Angielczyk, K., Fröbisch, J. & Benton, M. 2013. Decoupling of
401 morphological disparity and taxic diversity during the adaptive
402 radiation of anomodont therapsids. *Proceedings of the Royal Society B:*
403 *Biological Sciences* **280**: 20131071.
- 404 Serb, J., Alejandrino, A., Otárola-Castillo, E. & Adams, D. 2011.
405 Morphological convergence of shell shape in distantly related scallop
406 species (mollusca: Pectinidae). *Zoological Journal of the Linnean Society*
407 **163**: 571–584.

- 408 Soarimalala, V. & Goodman, S. 2011. *Les petits mammifères de Madagascar*.
 409 Guides sur la diversité biologique de Madagascar. Association Vahatra,
 410 Antananarivo, Madagascar.
- 411 Stanhope, M., Waddell, V., Madsen, O., de Jong, W., Hedges, S., Cleven,
 412 G., Kao, D. & Springer, M. 1998. Molecular evidence for multiple
 413 origins of insectivora and for a new order of endemic african insectivore
 414 mammals. *Proceedings of the National Academy of Sciences* **95**: 9967–9972.
- 415 Team, R.D.C. 2013. R: A language and environment for statistical
 416 computing.
- 417 Wills, A., Briggs, D. & Fortey, R. 1994. Disparity as an evolutionary index:
 418 A comparison of Cambrian and recent arthropods. *Paleontological Society*
 419 **20**: 93–130.
- 420 Wilson, D. & Reeder, D. 2005. *Mammal species of the world. A taxonomic and*
 421 *geographic reference (3rd ed)*. Johns Hopkins University Press.
- 422 Zelditch, M., Swiderski, D. & Sheets, D. 2012. *Geometric Morphometrics for*
 423 *Biologists, second edition*. Academic Press, Elsevier, United States of
 424 America.

List of Figures

426	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 <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
427			
428			
429			
430			
431			
432			
433			
434	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 <i>Potamogale velox</i> (Tenrecidae) skulls: accession number AMNH 51327 for the dorsal picture and NHML 1934.6.16.2 for the ventral picture	22
435			
436			
437			
438			
439			
440			
441			
442	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.	23
443			
444			
445			
446			
447			

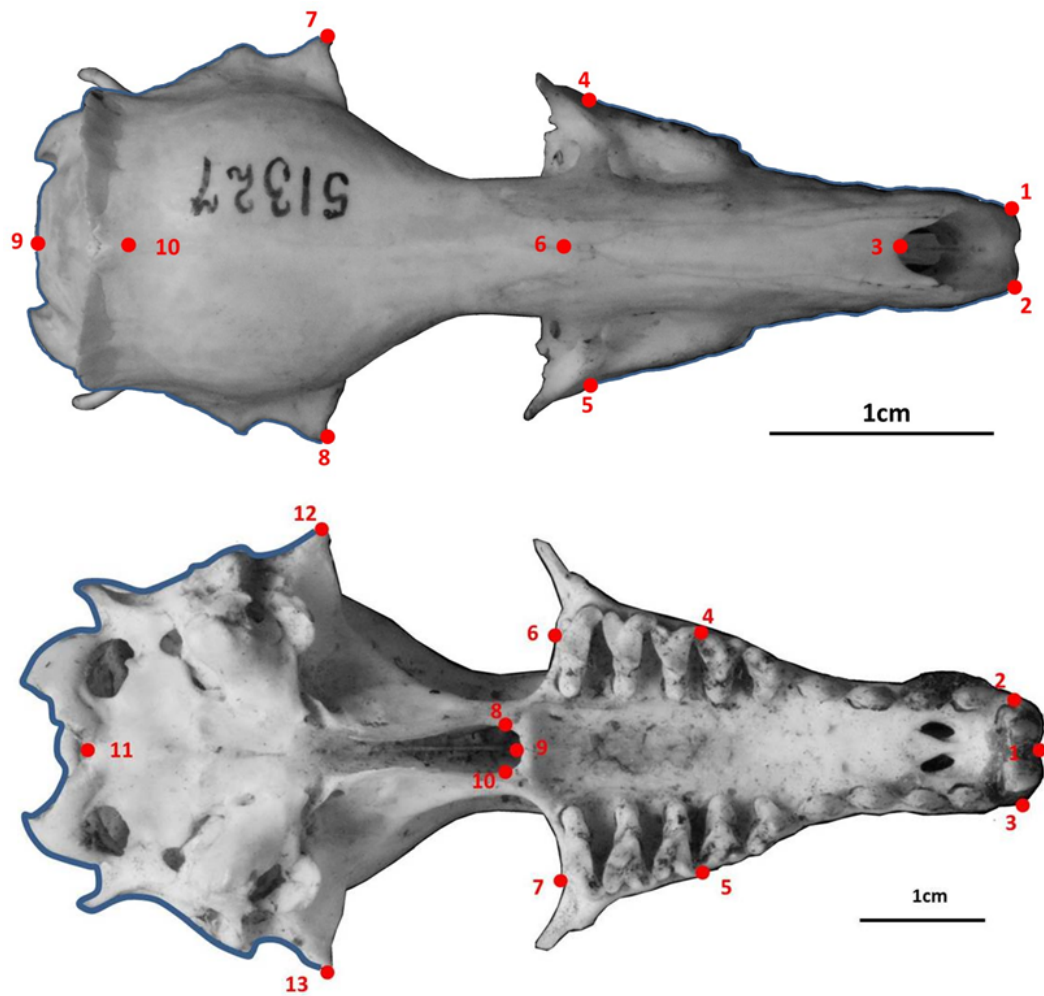


Figure 1: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of skulls in dorsal and ventral views respectively. Curves were re-sampled to the same number of evenly-spaced points. Descriptions of the curves and landmarks are in the supplementary material. The specimens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

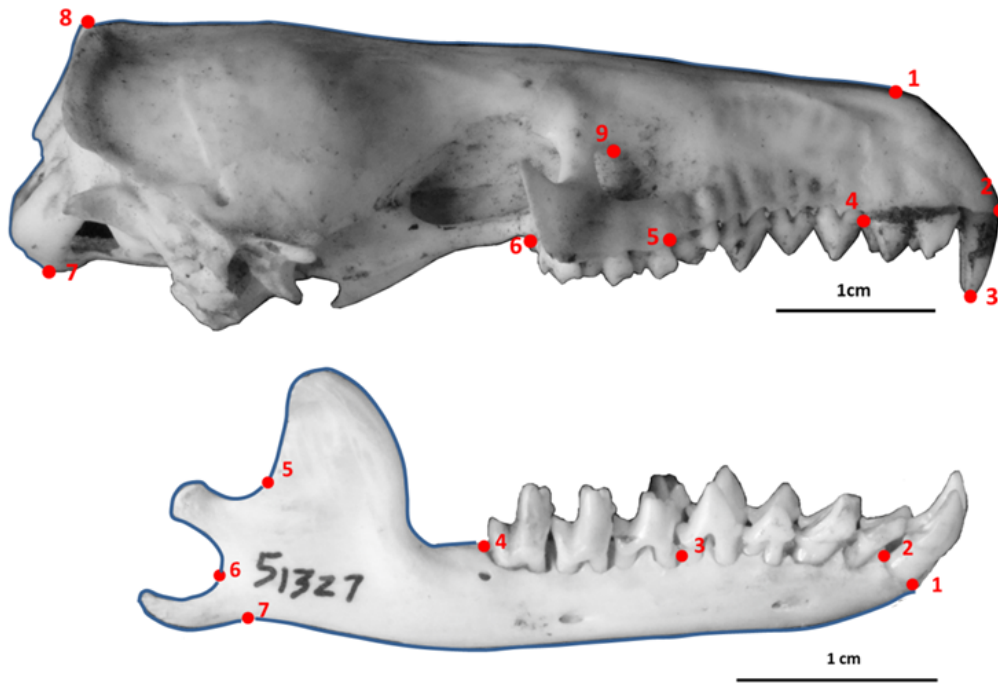


Figure 2: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of lateral views of skulls and mandibles respectively. Curves were re-sampled to the same number of evenly-spaced points. Descriptions of the curves and landmarks are in the supplementary material. The specimens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

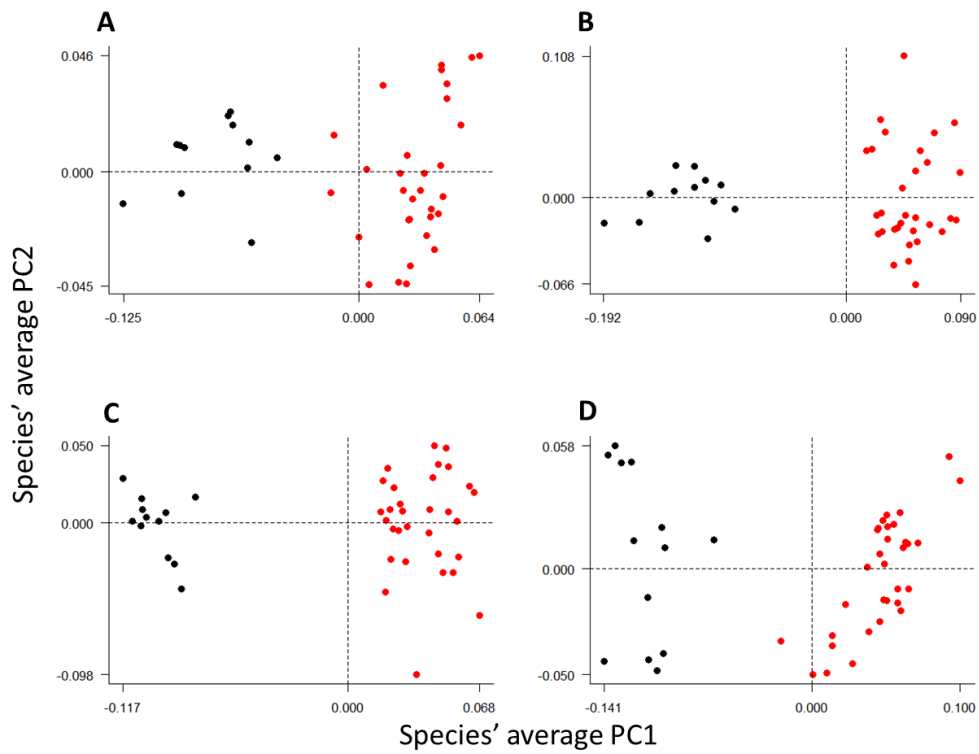


Figure 3: Principal components plots of the morphospaces occupied by tenrecs (red, $n=31$ species) and golden moles (black, $n=12$) for the skulls: dorsal (A), ventral (B), lateral (C) and mandibles (D) analyses. Axes are PC1 and PC2 of the average scores from a PCA analysis of mean Procrustes shape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

448 List of Tables

449	1	Summary of disparity comparisons between tenrecs (T) and	
450		golden moles (G) for each of our data sets(rows) and five	
451		disparity metrics (columns). "Mandibles:one curve" refers to	
452		our shape analysis of mandibles excluding the three curves	
453		around the posterior structures of jaw (figure 2). Significant	
454		differences are highlighted in bold with the corresponding	
455		p value in brackets. Disparity metrics are; sum of variance,	
456		product of variance, sum of ranges, product of ranges and	
457		sum of squared distances among species.	25
458	2	Summary of disparity comparisons between non- <i>Microgale</i>	
459		tenrecs (T) and golden moles (G) for each of our data sets(rows)	
460		and five disparity metrics (columns). Significant differences	
461		are highlighted in bold with the corresponding p value in	
462		brackets. Disparity metrics are; sum of variance, product	
463		of variance, sum of ranges, product of ranges and sum of	
464		squared distances among species.	26
465	3	Summary of the npMANOVA comparisons of morphospace	
466		occupation for tenrecs and golden moles in each of the four	
467		analyses (three views of skulls and mandibles). In each case	
468		the two families occupy significantly different areas of mor-	
469		phospace.	27

Table 1: Summary of disparity comparisons between tenrecs (T) and golden moles (G) for each of our data sets(rows) and five disparity metrics (columns). "Mandibles:one curve" refers to our shape analysis of mandibles excluding the three curves around the posterior structures of jaw (figure 2). Significant differences are highlighted in bold with the corresponding p value in brackets. Disparity metrics are; sum of variance, product of variance, sum of ranges, product of ranges and sum of squared distances among species.

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

Table 2: Summary of disparity comparisons between non-*Microgale* tenrecs (T) and golden moles (G) for each of our data sets(rows) and five disparity metrics (columns). Significant differences are highlighted in bold with the corresponding p value in brackets. Disparity metrics are; sum of variance, product of variance, sum of ranges, product of ranges and sum of squared distances among species.

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

Table 3: Summary of the npMANOVA comparisons of morphospace occupation for tenrecs and golden moles in each of the four analyses (three views of skulls and mandibles). In each case the two families occupy significantly different areas of morphospace.

Analysis	F	R²	p value
Skulls dorsal	66.02	0.62	0.001
Skulls ventral	100.74	0.71	0.001
Skulls lateral	75.07	0.65	0.001
Mandibles	59.34	0.59	0.001