

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 that, on average, tenrec crania are more phenotypically diverse than golden mole skulls. However, we recover the opposite pattern in our analyses of mandible shape; golden moles appear to have greater phenotypic diversity in their mandibles than tenrecs. Therefore, these findings support the designation of tenrecs as an exceptionally diverse group but also highlight how our understanding of patterns of phenotypic diversity changes depending on the morphological proxies which we use.

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 History (AMNH), Harvard's Museum of Comparative Zoology (MCZ)

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

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

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

104 We used a combination of both landmarks (type 2 and type 3,
105 (Zelditch et al., 2012)) and semilandmarks to characterise the shapes of
106 our specimens. Our landmarks (points) and semilandmarks (outline
107 curves) used to represent shape variation in the dorsal skulls and
108 mandibles are depicted in Figures 1 and 2 respectively. Corresponding
109 landmark definitions for each view are in tables 1 and 2. We also placed
110 landmarks and semilandmarks on photographs of ventral and lateral skull
111 views, details can be found in the supplementary material. We digitised
112 all landmarks and semilandmarks in tpsDIG, version 2.17 (Rohlf, 2013).

113 We re-sampled the outlines to the minimum number of evenly spaced
114 semilandmark points required to represent each outline accurately

115 (MacLeod, 2013, details in supplementary material). We used TPSUtil
116 (Rohlf, 2012) to create sliders files (Zelditch et al., 2012) to define which
117 points were semilandmarks. We conducted all subsequent analyses in R
118 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 inter-landmark
155 distances among species pairs (ZelditchMD, Zelditch et al., 2012). We used

156 To test whether tenrecs have significantly different morphologies than
157 golden moles, we used a non parametric MANOVA (Anderson, 2001) to
158 compare morphospace occupation between the two groups and pairwise
159 permutation tests to assess the evidence for significant differences in each
160 disparity metric.

161 Sister taxon comparisons are inadequate on their own to determine
162 whether a clade is exceptionally diverse (Losos & Miles, 2002). Therefore
163 we repeated our morphometric analyses with a larger data set that

164 included other small mammal species to which tenrecs are considered to
165 be convergent. We added specimens from hedgehogs (Erinaceidae, x
166 specimens of x species), moles (Talpidae, x specimens of x species), shrews
167 (Soricidae, x specimens of x species) and Solenodons (Solenodontidae, x
168 specimens of 2 species).

169 Results

170 Morphological disparity in tenrecs and golden moles

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

177 In the dorsal skulls analysis, tenrecs and golden moles occupy
178 significantly different areas of morphospace (npMANOVA, $F = 59.34$, $R^2 =$
179 0.59 , $p = 0.001$) indicating that the two families have significantly different
180 skull morphologies.

181 For each of the calculated metrics, tenrecs have higher disparity than
182 golden moles but these differences were not significant for the
183 variance-based calculations. Non-*Microgale* tenrecs also higher disparity
184 than golden moles but none of the comparisons were statistically
185 significant .

186 Tenrecs and golden moles have significantly different mandible shapes

187 (npMANOVA $F = 59.34$, $R^2 = 0.59$, $p = 0.001$). However, unexpectedly,
188 golden moles appear to have higher disparity than tenrecs in the shape of
189 their mandibles (although these differences are only significant when
190 disparity is calculated as product of variance or ZelditchMD).

191 We tested whether these results may be artefacts of relatively low
192 phenotypic diversity within *Microgale* tenrecs. However, although golden
193 moles and non-*Microgale* tenrecs occupy significantly different areas of
194 morphospace (npMANOVA $F = 31.6$, $R^2 = 0.59$, $p = 0.001$), there is no
195 significant difference between the two groups for any metrics of disparity.

196 Discussion

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

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

211 including terrestrial, arboreal, semi-aquatic and semi-fossorial forms
212 (REFS). However, our results cast doubt over whether the evident
213 diversity within the tenrec family should be considered to be a true
214 adaptive radiation.

215 Phenotypic and ecological divergences within a clade are not
216 surprising; most clades have at least small levels of disparity so, when it
217 comes to identifying adaptive radiations, it's important to identify clades
218 which are exceptional in their diversity (Losos & Mahler, 2010). Here we
219 have presented the first quantitative investigation of morphological
220 disparity in tenrecs and our results suggest that perhaps phenotypic
221 variation in tenrecs is not the product of an adaptive radiation in the strict
222 sense of its definition.

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

227 Another apparent anomaly in our results is that we found opposite
228 patterns of group dissimilarities in the analyses of skulls and mandibles.
229 The discrepancies could arise from factors associated with the modularity
230 of morphological evolution.

231 There is strong evidence that morphological variation in skulls and
232 mandibles is derived from differential evolution of integrated
233 developmental modules (reviewed by Klingenberg, 2013). For example,
234 there seems to be two primary modules in the mouse mandible; an
235 alveolar part which holds the teeth and the ascending ramus for muscle
236 attachment and which articulates with the skull (Klingenberg, 2008).

237 Geometric shape covariation is stronger within rather than between these
238 modules.

239 Our landmarks and curves for the mandibles (figure 2, table 2) include
240 aspects of variation in the dentition but they focus particular attention on
241 the ascending ramus (condyloid, condylar and angular processes).

242 Therefore the higher morphological disparity in golden mole mandibles
243 most likely reflects greater variation in the shape of the muscle attachment
244 areas of the mandible. It proved impossible to position reliable landmarks
245 on the corresponding mandibular articulation areas of the skull in lateral
246 view (see supplementary). Therefore we could not test whether higher
247 morphological disparity in the rami were correlated with associated
248 morphological variety in the articulation areas of the skull.

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 this variety
266 should be reflected in skull morphology. We assume that variation in
267 cranial shape is an adaptive characteristic which allows the animals to
268 survive in their divergent niches but we have not tested this assumption
269 explicitly.

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

278 However, the results of (Foth et al., 2012) are encouraging. In an
279 analysis of morphological disparity in pterosaurs, they found that
280 disparity calculations based on geometric morphometric characterisation
281 of skull shape yielded broadly similar results compared to analyses of
282 whole-skeleton discrete characters and limb proportion data sets.
283 Therefore the disparity patterns we find here based on geometric
284 morphometric analyses of cranial shape most likely represent
285 approximations of disparity which are accurate for morphological
286 diversity in the clades.

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

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

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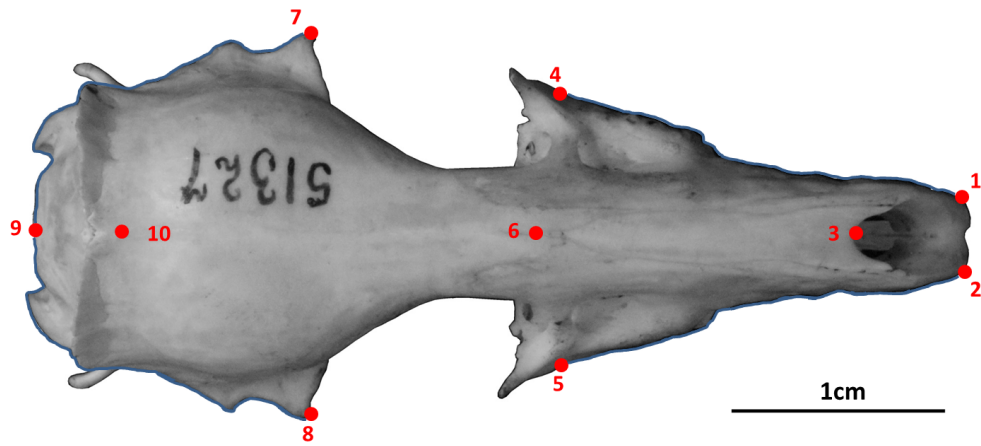


Figure 1: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of skulls in dorsal view. Curves were re-sampled to the same number of evenly-spaced points. See table X for description of curves and landmarks. *Potamogale velox* (Tenrecidae) skull, accession number: AMNH_51327

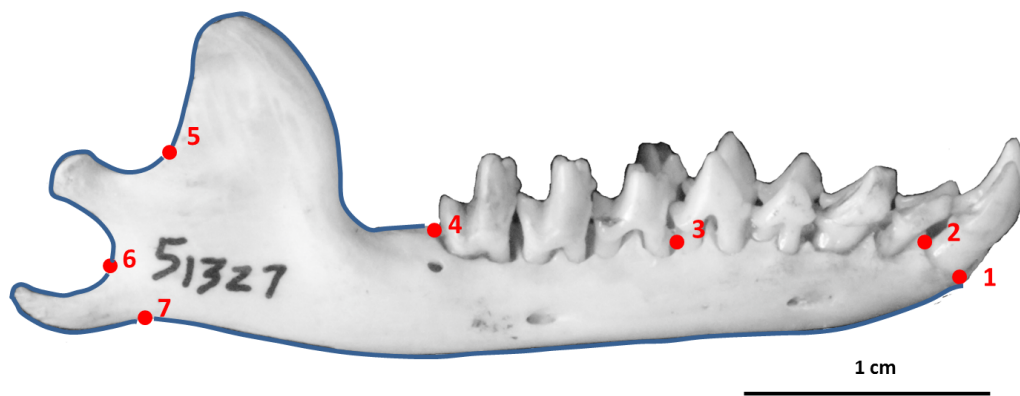


Figure 2: Landmarks (red points) and curves (blue lines) used to capture the morphological shape of mandibles. Curves were re-sampled to the same number of evenly-spaced points. See table X for description of curves and landmarks. *Potamogale velox* (Tenrecidae) mandible, accession number: AMNH_51327

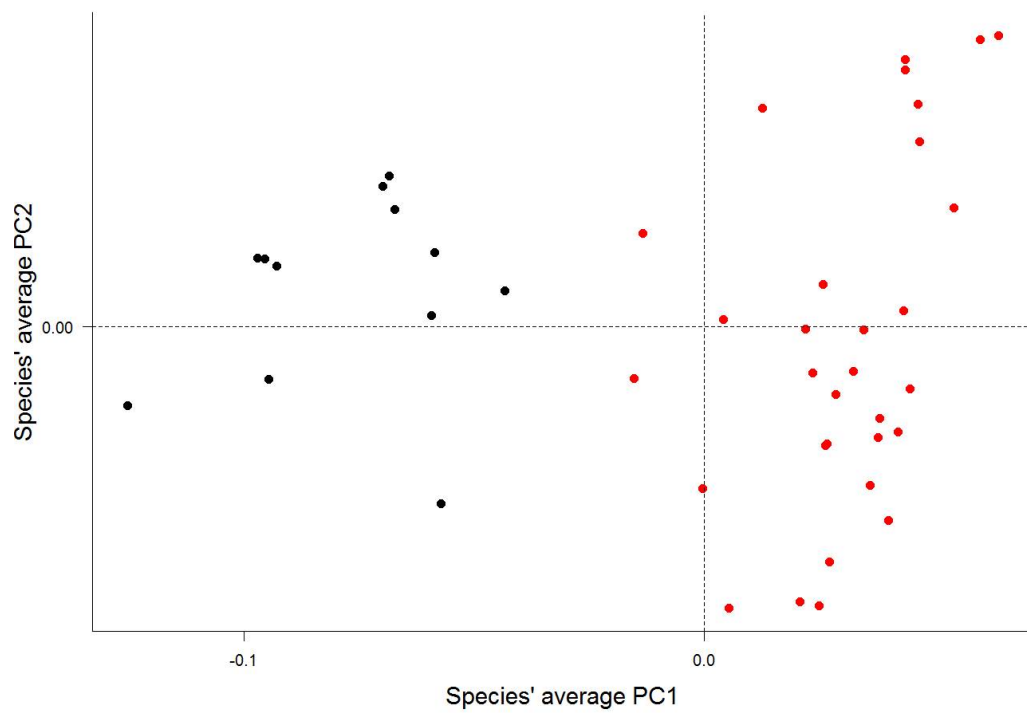


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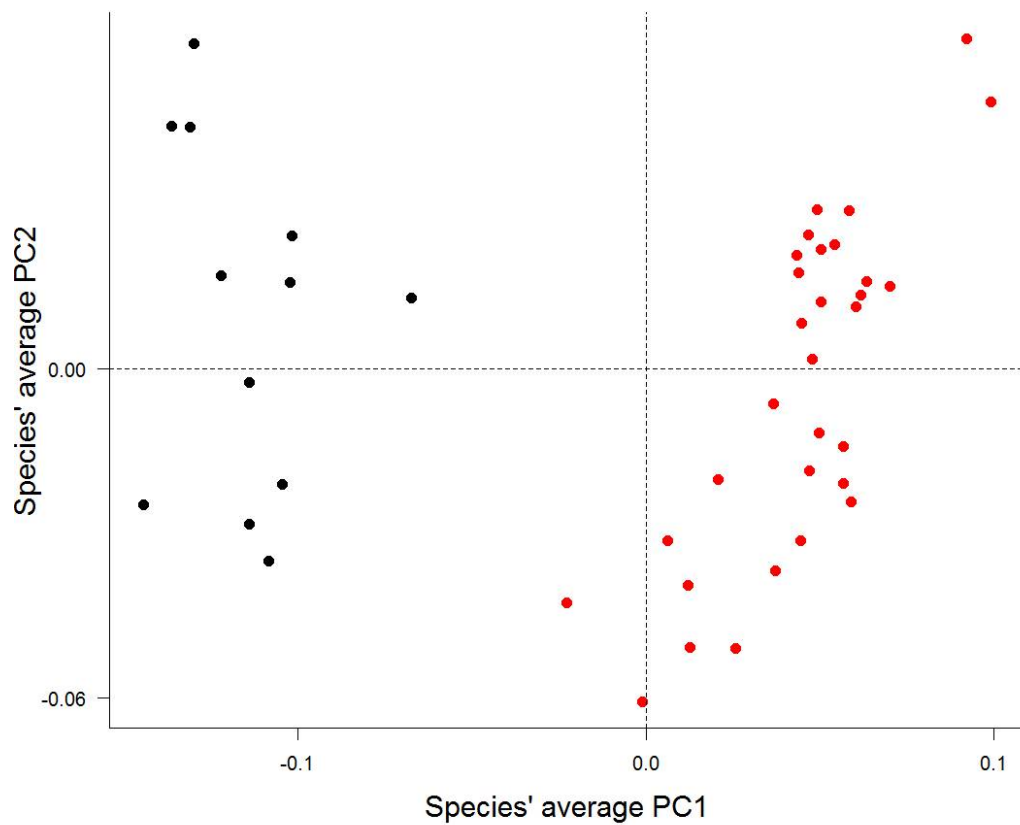


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430		landmarks) for the mandibles in lateral (buccal) view (see	
431		figure 2)	27

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 saggital and parietal sutures
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 landamarks 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 landamarks 5 and 2 (outline of the rostrum only, not the shape of the teeth)

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
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)