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1 **Skull morphological variation in a British stranded population**
2 **of false killer whale (*Pseudorca crassidens*, Owen 1846): a 3D**
3 **geometric morphometric approach**

4
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24 **Running heading: False killer whale skull morphology**

27 **Abstract**

28 The false killer whale *Pseudorca crassidens* (Owen, 1846) is a globally distributed delphinid,
29 that shows geographical differentiation in its skull morphology. We explored cranial
30 morphological variation in a sample of 85 skulls belonging to a mixed sex population stranded
31 in the Moray Firth, Scotland in 1927. Microscribe 3D 2GX was used to record 37 anatomical
32 landmarks on the cranium and 25 on the mandible in order to investigate size and shape
33 variation and to explore sexual dimorphism using geometric morphometric. Males showed
34 greater overall skull size than females whilst no sexual dimorphism could be identified in
35 cranial and mandibular shape. Allometric skull changes occurred in parallel for both males and
36 females supporting the lack of sexual shape dimorphism for this particular sample. Also,
37 fluctuating asymmetry did not differ between crania of males and females. This study confirms
38 the absence of sexual shape dimorphism and the presence of a sexual size dimorphism in this
39 false killer whale population.

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44 **Keywords:** toothed whale, morphology, asymmetry, partial least squares, false killer whale.

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54 **Introduction**

55 The false killer whale, *Pseudorca crassidens* (Owen, 1846) is a large cetacean with a
56 cosmopolitan distribution that ranges mainly between 50°N and 50°S in latitude (Baird 2009a).
57 Adults can reach total body lengths (TBL) of 5m (females) to 6m (males), making this species
58 one of the largest members of the Delphinidae family (Baird 2009a). Together with the true
59 killer whale (*Orcinus orca*), *P. crassidens* shows an occasional tendency to eat marine
60 mammals such as small and large cetaceans (Alonso et al. 1999; Odell and McClune 1999;
61 Baird 2009a) although their main prey is squid and fish (Alonso et al. 1999; Baird 2009a).

62 Morphological variation in the false killer whale is poorly understood and there have been few
63 studies on the skull morphology of this large odontocete. The skull has conical and large teeth,
64 and the tooth count is 7-11 for each of the upper jaws and 8-12 for the lower jaws (Yamada
65 1956; Baird 2009a). A previous analysis from a stranded false killer whale population
66 described a degree of sexual dimorphism in body size with males generally larger in overall
67 body length and weight (Baird 2009a). Mead (1975) and Baird (2009a) also reported
68 differences in the shape of the head due to the melon that is generally more pronounced in
69 males than in females. Since the melon is an organ of sound production and transmission it is
70 likely that this is associated with sexual differences in false killer whale echolocation.

71 Skull shape can be a good proxy for understanding factors which influence variation (sexual
72 or ecogeographical) in the false killer whale as demonstrated for other cetacean species (see:
73 del Castillo et al. 2014, 2016, 2017). To date, only one study has identified skull sexual
74 dimorphism and population differences in *P. crassidens* based on specimens from South Africa
75 and Scotland (Kitchener et al. 1990). The authors detected significant sexual differences in the
76 length of the rostrum, the ventral cranium and the temporal fossa. Another study on growth
77 pattern in Japanese and South African false killer whales identified that at sexual maturity,
78 South African whales were smaller than Japanese whales, and males from both populations
79 were larger than females (Ferreira et al. 2014). Scottish individuals measured by Kitchener et
80 al. (1990) were generally larger than the South African individuals and closer in body size to
81 the Japanese population (Ferreira, 2009). No other published study has described skull size and
82 shape variation in this species.

83 Geometric morphometrics (Rohlf and Marcus 1993) can be a useful tool for studying skull
84 morphological variation (Marcus et al. 2000). This method quantifies size and shape variation
85 via the digitisation of spatial coordinates belonging to a set of anatomically and/or

86 geometrically defined homologous landmarks (2D/3D) on biological specimens (Adams et al.
87 2004; Adams and Otárola-Castillo 2013). Previous geometric morphometric approaches on
88 cetaceans have successfully separated geographic populations, ontogenetic groups, sexes and
89 species in many odontocetes (Monteiro-Filho et al. 2002; Westgate 2007; Nicolosi and Loy
90 2010; Loy et al. 2011; Wiig et al. 2012; del Castillo et al. 2014) and so it stands to reason that
91 these methods can successfully identify size and/or shape affinities/disparities between male
92 and female false killer whales.

93 Using geometric morphometrics, this study aims to address the following research questions
94 pertinent to *P. crassidens*:

95 1. To what extent does a single population display intraspecific morphological variation in the
96 skull? Are skull size and skull shape sexually dimorphic? It is expected that skull sizes of false
97 killer whales will exhibit a significant degree of sexual dimorphism (Kitchener et al. 1990;
98 Ferreira et al., 2014), whilst dimorphism in skull shape might be subtle and difficult to identify
99 (Loy et al. 2011).

100 2. Do males and females show differences in the degree of cranial asymmetry? Previous
101 morphological studies on toothed whales showed differences in the degree of directional
102 asymmetry (Fahlke and Hampe 2015; Coombs et al., 2020), related to prey size (MacLeod et
103 al. 2007; McCurry et al. 2017) and suction feeding abilities (del Castillo et al. 2017).
104 Differences between sexes have been found in the nasal area of the pontoporiid *Pontoporia*
105 *blainvillei* (del Castillo et al., 2014), which might be related to their vocalization abilities.
106 Based on this, we might expect a difference in the degree of cranial asymmetry between males
107 and females of *Pseudorca crassidens*.

108 3. Do males and females show differences in the degree of skull integration (Klingenberg
109 2009)? It is predicted that integration/modularity between crania and mandibles should occur
110 in both sexes. Previous morphological studies on mammals (Zelditch and Carmichael 1989;
111 Marroig and Cheverud 2001; Hallgrímsson et al. 2002; Klingenberg et al. 2003; Klingenberg
112 2008; Willmore et al. 2009; Figueirido et al. 2013; Veneziano et al. 2018) showed a significant
113 degree of association between cranial and mandibular morphology at both intra and
114 interspecific scales. However, not many studies have yet explored patterns of integration in
115 cetaceans (Churchill et al. 2019). Since they do not chew their food extensively and their
116 mandibles are also involved in sound reception (Cranford et al. 2008, 2015; Cranford and Krysl
117 2018), different levels of integration are expected, compared with other mammal groups.
118 Additionally, if diet and sound reception differ between sexes it might be possible that the level

119 of integration also shows some degree of differentiation between sexes. Alternatively, these
120 similarities might indicate a similar specialization through feeding adaptations.

121

122 **Materials and Methods**

123 *Samples-* We examined 85 crania (♂=37; ♀=39; No Data available – ND = 9; (**Appendix 1**);
124 and 29 complete skulls (combined cranium and mandibles; ♂=12; ♀=17) of *Pseudorca*
125 *crassidens* housed at the Natural History Museum, London, UK (**Appendix 1**). Though these
126 specimens have two different groups of catalogue numbers – 1961 and 1992, all are considered
127 related to a mass-stranding event which took place in October 1927 at the Dornoch Firth,
128 Scotland. Specimens labelled 1992 were collected from Ardgay Bay and along the Kyle (a
129 narrow sea channel) beyond Bonar Bridge to Invershin. Dornoch Firth is part of the larger
130 Moray Firth embayment located on the east coast of the Highlands in the north of Scotland.
131 Information regarding the gender of all six specimens with the catalogue number 1992 and the
132 two within the sample with catalogue number 1961 are missing (see **Appendix 1**). The majority
133 of the samples were considered as adults, but we identified two as subadults because the
134 maxillary bones did not reach the nuchal crest caudally and the frontal bones were visible in
135 dorsal view (Cozzi et al. 2016).

136 *Sampling-* Three dimensional (3D) coordinates of 37 anatomically-defined homologous
137 landmarks were placed on 85 crania (**Figure 1; Table 1**), and twenty-five landmarks were
138 placed on 29 mandibles (**Figure 1; Table 2**) using Microscribe G2X at an accuracy of 0.23
139 mm (Immersion Corp., San Jose CA, USA). Due to the large size of the specimens two
140 landmarking sessions for each specimen were recorded by the same researcher (DV) on the
141 cranium in order to cover both dorsal and ventral parts. These were then merged using DVLR
142 software (Dorsal-Ventral-Left-Right fitting, <http://www.nycep.org/nmg>). Coordinates on
143 mandibles were captured in a single landmarking session by the same researcher (DV).
144 Landmarks were imported into Morphueus 20140704 (Slice 2014) and MorphoJ 1.06d
145 (Klingenberg 2011) to ensure that all the 3D spatial coordinates were captured in an identical,
146 sequential order.

147 *Measurement error-* To explore the degree of measurement error introduced by the 3D
148 landmarking, linear measurements between selected anatomical landmarks were taken with a
149 measuring tape on crania (accuracy of 0.1 mm), and successively compared with inter-
150 landmark distances taken on the dorsal and ventral views and on the combined landmarks

151 configurations with DVL. To test the Microscribe degree of accuracy during the data
152 collection, the spatial position of 18 equally distant (=1 cm) points along a scale bar 5cm by
153 3cm were taken right before the beginning of each landmarking session on crania. The
154 distances between the selected 18 points were checked to ensure accuracy of the spatial
155 coordinates. In all cases the distances obtained using the microscribe showed an error of <5%
156 compared to the values of the scale bar. To evaluate the reliability of the landmark
157 configuration, a repeatability index (R) was calculated on 85 crania using the Procrustes
158 ANOVA (analyses of shape variance) in MorphoJ 1.06d. The operator (DV) digitized each
159 cranium twice and followed standard protocol procedures and analyses described in Fruciano
160 (2016), and Cardini (2014) in order to ensure that the shape variance explained by the replica
161 was significantly smaller than that exhibited by individuals. This was accomplished using a
162 Procrustes ANOVA in MorphoJ 1.06d (Klingenberg 2011), a method adapted for the study of
163 shape variation (Klingenberg and McIntyre 1998; Klingenberg et al. 2002) equivalent to a two-
164 way ANOVA (Palmer and Strobeck 1986) with individuals and replicas as factors, and shape
165 coordinates (see next section) as dependent variable. The repeatability index R , which varies
166 between 0 (not repeatable) and 1 (perfectly repeatable), was equally computed based on the
167 comparison of shape variation between the first and the second landmarking session following
168 Fruciano (2016).

169 *Geometric Morphometrics (GM)*- Landmarks of crania and mandible were separately
170 superimposed using a Generalised Procrustes Analysis (GPA) which removes the effects of
171 differences in size, position, and orientation from the 3D spatial coordinates (Rohlf and Marcus
172 1993). This is an iterative procedure where variation in size is first removed by scaling each
173 configuration so that it has a centroid size (CS = the square root of the sum of squared distances
174 between each landmark and the centroid) equal to 1.0; rotation and translation are taken into
175 account by centring and rotating the landmark configuration in order to obtain an optimal
176 solution that minimizes the quadratic distances between homologous points (Bookstein 1997).
177 After GPA, a new set of coordinates (named Procrustes) are created and then used as a proxy
178 for shape variables to explore the potential for differences in cranial and mandibular
179 morphology between sexes, separately.

180 *Data analyses on 3D crania and mandibles*- GM permits partitioning of the asymmetric and
181 symmetric components of shape variation (Klingenberg et al. 2002). As many species of
182 odontocetes show a high degree of directional asymmetry in their crania (MacLeod 2002;
183 Fahlke et al. 2011; Fahlke and Hampe 2015; Huggenberger et al. 2017; Churchill et al. 2019),

184 and the asymmetric component is relevant for the aim of the study, these variables were
185 partitioned following the guidelines of Klingenberg et al. (2002).

186 Procrustes ANOVA (analysis of shape variance) was performed on 85 crania replicates to
187 investigate the presence of Directional (DA) and Fluctuating Asymmetry (FA) in cranium
188 shape using MorphoJ 1.06d (Klingenberg 2011). DA is defined as a deviation from symmetry
189 showed in most of the individuals belonging to the same species (MacLeod et al. 2007). FA
190 can be defined as the difference in mean absolute value of left and right sides in the same
191 individual (Klingenberg et al. 2002). When the mean value is close to zero, it means that the
192 structure shows an almost perfect symmetry (Tomkins and Kotiaho 2001). FA scores were
193 quantified in each individual in units of Procrustes and Mahalanobis distances. While FA
194 Procrustes distances are calculated as individual deviation from the mean asymmetry to the
195 absolute shape, Mahalanobis distances are quantified as individual deviation from the mean
196 asymmetry in the sample (Klingenberg and Monteiro 2005). A two-independent-sample *t*-test
197 was performed to assess possible sexual differences in FA scores of the crania. Because
198 odontocete mandibles are generally considered symmetrical (Barroso et al. 2012), the full
199 shape of the mandible was captured without separating symmetric from the asymmetric
200 component.

201 To explore the degree of intraspecific asymmetric and symmetric shape variation in the 85
202 crania and full shape variation in the 29 mandibles, Principal Component Analysis (PCA) was
203 performed separately for crania and mandibles using the functions `bilat.symmetry` and
204 `plotTangentSpace`, respectively in the `geomorph` 3.1.2 package (Adams et al. 2016) within R
205 3.5.2 (R Core Team 2018). To aid identification of different skull shapes within sexes, a
206 permutation test (1,000 permutations) on Procrustes distances and a Discriminant Function
207 Analysis (DFA) were also performed in MorphoJ 1.06d (Klingenberg 2011) for the mandibles
208 and crania datasets separately. This analysis uses the differences between means of Procrustes
209 and Mahalanobis distances to classify the specimens in two groups (males and females); a
210 significant *p*-value will be associated with a significant degree of sexual dimorphism in shape.

211 ANOVA and Procrustes ANOVA (using the function `procD.lm` of `geomorph` 3.1.2) were
212 additionally performed on the 74 sexed crania and 29 sexed mandibles to test for sexual
213 dimorphism in skull size (SSD) and shape, respectively. The same function was employed to
214 test allometry (the impact of size on shape variation) with log transformed CS as *X* and
215 symmetric shape component as *Y*. Slope differences between sexes were explored adding sex

216 as a factor in the model ‘shape~size’ and testing the interaction term ‘size*sex’. Analyses on
217 the sexed crania were run after the exclusion of two subadult (male) specimens. This was done
218 to give the same range of size for both sexes as this dataset did not include female subadults.
219 In the case of common allometric patterns being found between the sexes, residuals (or size
220 free variables) were used for further analyses of sexual dimorphism. Additionally, a between-
221 sex ANOVA was also performed on Total Body Length (TBL) – information collected after
222 stranding and stored in the NHM database – as comparison with CS values from the skull. CS
223 and TBL were summarized using boxplots and the significance of differences between sexes
224 was tested using *t*-tests against the null hypothesis of being no difference between means for
225 either variable.

226 Patterns of covariation between cranium and mandibular shape were examined using two-
227 blocks Partial Least Squares (2B-PLS) analysis (Zelditch et al. 2012, 2013) pooled within sexes
228 in a dataset of 29 complete skulls (the combined cranium and mandible). PLS is a useful
229 method for studies investigating integration/modularity between two different blocks of
230 variables (Klingenberg 2009; Zelditch et al. 2012; Klingenberg and Marugán-Lobón 2013),
231 such as the mandible and cranium shape in this instance. Unlike the PCA, the PLS method uses
232 singular value decomposition (SDV) to identify vectors called singular axes (SAs; Zelditch et
233 al. 2012), which explains covariance in the same way that PCA explains variance. Unlike the
234 PCs, SAs are paired, and each SA score accounts for the covariance between blocks
235 (Klingenberg 2009; Zelditch et al. 2012). Differences in covariation trajectories between sexes
236 were tested using angular comparison of the PLS vectors in MorphoJ 1.06d (Klingenberg 2011;
237 Klingenberg and Marugán-Lobón 2013) against the null hypothesis of no difference from two
238 random orthogonal vectors (90 degrees). Therefore, a significant *p*-value will reflect a
239 statistically more similar shape variation than two random vectors. In contrast, a non-
240 significant *p*-value will indicate different directionalities in shape between sexes. PLS analyses
241 were applied to male and female datasets separately, and the angle between each PLS of each
242 dataset was calculated. Like the PCs, SAs can be described by deformation along axes, which
243 helps with the interpretation of the results (Zelditch et al. 2012). The null hypothesis of no
244 covariation between cranium and mandible was tested with 1,000 resamples. (Zelditch et al.
245 2012, 2013). Unlike the angular comparison between PCs in between sexes, differences in
246 directionalities of PLS vectors are not indicative of different shapes but of different patterns of
247 integration between sexes.

248 **Results**

249 Cranial dataset

250 *Measurement error*- The Procrustes ANOVA (**Table 3**) showed significant effects of
251 individuals on shape as well as side, representing Directional Asymmetry (DA), and the
252 interaction between individual and side, representing Fluctuating Asymmetry (FA). Sum of
253 squares (SS) was greater in DA and smaller in the landmarking error, suggesting a negligible
254 impact of landmarking on shape variation. This was equally confirmed by the Repeatability
255 (*R*) score for shape that was 0.95.

256 *Asymmetric component*- In the PCA of the asymmetric component of shape, PC1 summarized
257 29.4% of the variation (**Figure 2A**). Along this axis, individuals that are located towards the
258 negative region show an accentuation of DA, while those in the positive region of the axis have
259 less asymmetrical crania. Males and females showed no differences in the average of FA scores
260 no matter whether Mahalanobis ($p=0.2451$) or Procrustes FA scores ($p=0.9847$) were
261 considered (**Figure 3**).

262

263 *Symmetric component*- PC1 and PC2 (**Figure 2B**) on the symmetric component of shape
264 accounted for 19% and 12% of variance, respectively (**Appendix 2**). PC1 positive scores
265 correspond to a more laterally compressed facial region, an area bounded posteriorly by the
266 dorsal apex of the nuchal crest defined by landmark 10. PC1 negative scores represent a shorter
267 rostrum and a transverse widening of the neurocranium, resulting in a more tapered skull shape.
268 For the area of the occipital condyles described by seven landmarks (LM 15, 16, 17, 18, 19,
269 20, 21), negative PC scores represent a wider shape together with an enlargement of the medial
270 wall of the temporal fossa formed by a small portion of the squamosal (squamosal plate) and
271 by the parietal described by three landmarks (LM 12, 14, 27). The PC2 axis describes changes
272 in the curvature of the rostrum profile and the position of the neurocranium relative to the
273 rostrum. PC2 negative scores reflect a high degree of curvature in the skull profile and a wider
274 neurocranium with the displacement of landmarks 10, 11, and 12. Landmarks 10 and 7 are
275 further apart compared to PC2 positive scores. The plot of PC1 against PC2 (**Figure 2A**)
276 indicated considerable male-female overlap in the morphospace. When distances between
277 groups were compared by a linear DFA, there was no significant distance between sexes ($p=$
278 0.23). Equally, Procrustes ANOVA highlighted no significant ($p=0.132$) difference in cranium
279 shape between males and females (**Table 4**).

280 *Allometry*-The regression of Procrustes coordinates versus CS revealed a significant ($p=0.001$)
281 allometric component in cranium shape, with size explaining 44% of variance (**Table 5**) of the
282 pooled sample. Procrustes ANOVA revealed no difference between sex allometric slopes for
283 CS ($F_{2,74}=1.1692$, $p=0.259$; **Table 5**) or TBL ($F_{2,74}=0.8252$, $p= 0.661$; **Table 5**). When
284 allometric trajectories were individually analysed for males and females it was possible to note
285 a significant impact of size on shape that explained 16.34% of variance in males ($n = 37$; $p <$
286 0.001), and 12.59% of variance in females ($n= 39$, $p < 0.001$). The angle vector was 26.13°
287 with $p < 0.001$, meaning that the two vectors are pointing in the same direction, and they have
288 similar allometric trajectories. A test for differences between sexes using cranial and residuals
289 shape variables of allometry confirmed no difference in shape between males and females ($p=$
290 0.057 , **Table 4**). On the other hand, a boxplot showed greater values for cranium CS and TBL
291 in male specimens confirmed by t -tests (CS: $p=0.007$; TBL: $p= 0.05$) (**Figure 4A-B**).

292 3D Mandibles dataset

293 *Shape analyses*- PC1 and PC2 accounted for 42.8% of the total variance (**Figure 5; Appendix**
294 **3**) and showed mixed scores belonging to male and female specimens. Positive scores on PC1
295 describe a lengthened mandible, represented by a forward shift of landmarks 6 and 7 that
296 represent the most anterior point of the mandibular foramen on the medial side or the acoustic
297 window on the lateral side (Mead and Fordyce 2009). The right and left sides of the mandibular
298 foramen show a different angle compared to PC1 negative values. The hemi-mandibles create
299 a more obtuse angle on PC1 positive values, and the mandible appears more elongated (**Figure**
300 **5**, wireframe in occipital, ventral and lateral view). Also, positive values on PC1 represent a
301 backward shift in the space of the landmarks 4 and 5 describing the posterior end of the dental
302 groove on the alveolar border of the mandible, while landmarks 12 and 13 (the coronoid
303 process) shift upward. PC2 describes the curvature of the mandible, with negative values
304 showing a more convex dorsal margin and larger mandibular body. A permutation test based
305 on Procrustes distances highlighted no differences in mandible shape between males and
306 females ($p = 0.9864$). This was equally confirmed by DFA ($p = 0.8962$). Procrustes ANOVA
307 on the total sample of 29 specimens showed that size explained 5.8% of total mandible shape
308 variance (**Table 6**), although this was not significant and a significant effect was neither
309 detected for sex (**Table 6**). If TBL was considered as a factor against mandibular shape, rather
310 than CS, the result was unaffected (**Table 6**). Both CS and TBL demonstrated that males were
311 generally larger than females (**Figure 4C-D**; CS: $p=0.007$; TBL: $p=0.01$).

312 *Cranial and Mandibular Integration*

313 The 2B-PLS analysis is shown in **Figure 6**. The first pair of SAs account for 62.52% of the
314 total squared covariance between cranium and mandible. Although high ($r = 0.795$), the
315 strength of association between scores of cranium and mandible shape was not significant ($p =$
316 0.081).

317 2B-PLS for females ($n=18?$) showed a significant ($p = 0.0014$) correlation (RV= 0.5093)
318 between cranium and mandible shape, while in males ($n = 11$) the correlation between these
319 two anatomical units was non-significant ($p = 0.0799$) even if the correlation coefficient was
320 higher (RV= 0.6336). Comparing the cranium axis of males and females, PLS1 showed an
321 angle of 56.937° , and PLS2 an angle of 57.603° , and both were significant ($p < 0.00002$; $p =$
322 0.00003 ; **Table 7**). Similar results were obtained for the mandible, with PLS1 showing an angle
323 of 38.785° , and PLS2 an angle of 60.013° ($p < 0.00001$; $p = 0.00223$; **Table 7**).

324 **Discussion**

325 The investigation of sexual dimorphism in the morphology of cetaceans might give insights
326 into their social structure, breeding behaviours and foraging. In this study, we identified a
327 significant level of sexual dimorphism in the general size of the body, cranium, and mandible
328 of the large delphinid *Pseudorca crassidens*. On the other hand, the shape traits separately
329 investigated for the cranium and the mandible showed no difference between males and
330 females, and the two groups appear to have similar allometric trajectories.

331 These results are consistent with Kitchener et al. (1990), who found that males of *P. crassidens*
332 were characterised by larger crania and mandibles compared to females. Equally, fieldwork
333 data support our findings on total body length, but not on cranial shape considering that
334 significant sexual differences in the external head shape (including soft tissues) of *P. crassidens*
335 have been described (Stacey et al. 1994). The absence of skull shape sexual dimorphism seems
336 to be common in cetacean species that live in large monospecific groups (de Francesco and
337 Loy 2016). This might be partly related to the conservative social structure that both males and
338 females maintain for niche partitioning during aquatic foraging or could instead be related to
339 food sharing within the group (Baird 2009a; Ralls and Mesnick 2009). Adult specimens
340 generally show an enlargement of the area of the temporal fossa (formed by the alisphenoid,
341 frontal, parietal and squamosal bones). Having a large temporal area allows for a larger
342 attachment surface of the temporalis muscle (Cozzi et al. 2016), associated to the production
343 of stronger bite forces. A reduction in the size of this area would cause the mouth to close faster

344 (i.e. in subadults specimens) at the expense of the bite force, because force and velocity are
345 inversely proportional with a well-established trade-off (Marshall 2009). The temporal muscle
346 is inserted along the dorsal ridge of the mandible, with a stronger and somewhat tendinous
347 attachment over the coronoid process (landmarks 12 and 13) and a weaker attachment
348 anteriorly along the dorsal margin of the mandibular foramen (Seagers 1982). The area of the
349 temporal fossa can be used to predict prey size, bite strength, and grip and tear feeding mode
350 (Marshall 2009; Galatius et al. 2020). If this area had been greater in males, it may have testified
351 for a male-male aggression character related to sexual dimorphism (Cozzi et al. 2016).

352 To date little is known about male and female *P. crassidens* social behaviour. In general, males
353 and females share the same diet and exhibit high fidelity to the natal group (Martien et al.
354 2011). They feed on a variety of squid, fish, and occasionally mammals such as the sperm
355 whale and delphinids (Stacey et al. 1994; Palacios and Mate 1996; Odell and McClune 1999;
356 Baird 2009a). They catch their food mostly during the day, exceeding then dive depths of 200m,
357 and tend to remain at shallow depths during the night (Baird 2009b; Minamikawa et al. 2013).
358 Prey specialisation has also been suggested in different populations (Ferreira 2008; Botta et al.
359 2012).

360 The absence of sexual shape dimorphism or monomorphism in *P. crassidens* might be due to
361 their ability to socialize and share food resources within the pod (Stacey et al. 1994; Odell and
362 McClune 1999; Baird 2009a). This has been confirmed by stable isotope studies (Botta et al.
363 2012; Riccialdelli and Goodall 2015). Similar to the results presented here, previous studies on
364 other, smaller delphinids such as *Cephalorhynchus commersoni*, *Tursiops truncatus*, *Delphinus*
365 *delphis*, *Stenella coeruleoalba* and *S. attenuata* (Clark and Odell 1999; Wilson et al. 1999;
366 Sanvicente-Añorve et al. 2004; Murphy and Rogan 2006; Amaral et al. 2009; Parés-Casanova
367 and Fabre 2013; del Castillo et al. 2016) found no sexual dimorphism in skull shape, suggesting
368 that males and females might have similar feeding behaviours (MacLeod et al. 2006).

369 *Asymmetry* - In this study the percentage of variance explained by DA was greater than FA. As
370 the odontocete cranium shows asymmetry related to the production of echolocation high
371 frequency sounds (Cranford et al. 1996; Fahlke and Hampe 2015; Cozzi et al. 2016; Coombs
372 et al. 2020), these results agree with expectations based on previous studies (del Castillo et al.
373 2014, 2016, 2017). The DA accounted for 25% and the FA for 10% of total shape variation in
374 *P. crassidens* (**Table 3**). Similar results for FA were found for *Lagenorhynchus australis*
375 (8.5%; del Castillo et al. 2017), *Lagenorhynchus obscurus* (9.5%; del Castillo et al. 2017), and

376 *Cephalorhynchus commersoni* (10%; del Castillo et al. 2016). Also, in these species the DA
377 accounted for 43%, 25%, and 34% respectively (del Castillo et al. 2017); *P. crassidens* shows
378 a variation similar to *L. obscurus* but lower variation compared to *L. australis* and *C.*
379 *commersoni*. Therefore, the DA can be argued to be functionally linked to both echolocation
380 (Fahlke and Hampe 2015) and prey size (MacLeod et al. 2007; McCurry et al. 2017). In fact,
381 the two sympatric species *L. osburus* and *L. australis* showed a different degree of DA and
382 different suction feeding abilities (del Castillo et al. 2017). In Lissodelphininae there is
383 variation in the magnitude of directional asymmetry between species, and this variation is
384 related to ecological partitioning (Galatius and Goodall 2016; del Castillo et al. 2017). The
385 nasal area is the most affected area by the asymmetric component (**Figure 2B**) in both males
386 and females of *P. crassidens*. This is in line with the pontoporiid *Pontoporia blainvillei* which
387 showed DA differences in the bony nares region between sexes, probably due to a different
388 vocalization (del Castillo et al. 2014). Different fluctuating asymmetry scores have not been
389 detected in false killer whale females and males (**Figure 5**). For this reason, differences in the
390 shape of the head between sexes are most likely related to the shape of soft tissues, such as the
391 melon, involved in emission beam production, although this cannot be tested with our dataset.

392 *Sexual size dimorphism (SSD)*- Sexual size dimorphism can be described as the difference
393 between features such as body size between males and females (Ralls and Mesnick 2009). SSD
394 can evolve for different reasons and can be explained by factors such as age at sexual maturity,
395 mating system, contest competition, female choice, and sound production.

396 Size explained a significant part of the total variation in cranial shape (4 %); this is a lower
397 percentage if compared with other toothed whales (i.e *Cephalorhynchus commersoni*; 5.7%;
398 del Castillo et al. 2016; *P. blainvillei*; 54.1% del Castillo et al., 2014). Considering that our
399 sample did not include ontogenetic groups, the obtained result is not surprising and in line with
400 other studies that explored allometric variation only in adults (De Francesco and Loy, 2016).
401 Female false killer whales in Scotland attain sexual maturity earlier than males (Purves and
402 Pilleri 1978). Whilst males reach maturity when their body length is 396-457 cm, roughly
403 around the age of 11-18 (Kitchener et al. 1990; Stacey et al. 1994), females reach maturity
404 between the ages of 8-11 (Ferreira et al. 2014) and 336 cm of body length (Stacey et al. 1994).
405 Their breeding age range is similar to *Orcinus orca* (Ottensmeyer and Whitehead 2003): males
406 stop growing after 15 years of age (Duffield 1988) and females reach reproductive age earlier
407 than males. Males might not provide parental care for calves and, instead, invest that energy in
408 growth (Nowak and Walker 1999). In addition, having males with a larger body size can

409 increase their ability to dive to greater depths (Beck et al. 2003; Baird et al. 2005; Piscitelli et
410 al. 2010; Riccialdelli and Goodall 2015; Goldbogen et al. 2019). In cetaceans, this delay in
411 male maturation is also related to a polygynous mating system (some males with multiple
412 partners), while the absence of sexual dimorphism is related to a polygynandrous mating
413 system (males and females have multiple partners) (Mesnick and Ralls 2018; Murphy et al.
414 2005). Both strategies are associated with male sperm competition (Mesnick and Rall 2018),
415 and are interpreted as a way to increase fitness and genetic variability through the offspring
416 (Stockley, 2004).

417 Food intake in two females and one male of false killer whales in captivity indicates an increase
418 in annual food consumption for the male from the fourth to the sixth years of age (Kastelein et
419 al. 2000). This might confirm the hypothesis that males use the energy to grow and increase
420 their body size, whilst females use the energy to take care of the offspring. Sexual size
421 dimorphism with males larger than females has also been observed in *Lagenorhynchus* spp.
422 (Reeves et al. 1999; Galatius 2010; del Castillo et al. 2017), *Lissodelphis borealis* (Mesnick
423 and Ralls 2018), *Tursiops truncatus* (Tolley et al. 1995; Amaral et al. 2009; Parés-Casanova
424 and Fabre 2013), *Orcinus orca*, *Globecephala* spp. (Mesnick and Ralls 2018), among the other
425 delphinids, in the monodontids *Delphinapterus leucas* (Mesnick and Ralls 2018) and *Monodon*
426 *monoceros* (Garde et al. 2007; Mesnick and Ralls 2018), in the ziphiid *Mesoplodon*
427 *densirostris*, in the physeterid *Physeter macrocephalus* (Mesnick and Ralls 2018), and in the
428 iniid *Inia geoffrensis* (Mesnick and Ralls 2018). Instead, a reversed sexual dimorphism, with
429 females being larger than males, has been observed in *Cephalorhynchus* spp. (del Castillo et
430 al. 2016; Mesnick and Ralls 2018) among the other delphinids, in the phocoenids *Phocoena*
431 *phocoena* and *P. sinus* (Mesnick and Ralls 2018), in the pontoporiid *Pontoporia blainvillei*
432 (Ramos et al. 2002; del Castillo et al. 2014; Mesnick and Ralls 2018), in the ziphiid *Berardius*
433 *spp.* (Mesnick and Ralls 2018), in the recently extinct *Lipotes vexillifer* (Mesnick and Ralls
434 2018), and also in 13 mysticete species (Ralls and Mesnick 2009). In *P. phocoena*, females are
435 larger than males, which provides to the former a higher reproducibility potential for annual
436 reproduction (Read and Gaskin 1990; Galatius 2010; Gol'din and Vishnyakova 2016). Females
437 of *P. phocoena* reach sexual maturity later than males (Sørensen and Kinze 1994; McLellan et
438 al. 2002; Lockyer 2003; Lockyer et al. 2003; Marino et al. 2004), can better compete for
439 resources, and their calves have a more adequate size to maintain body temperature (Ralls
440 1976).

441 Body size changes can also be related to biosonar types (Jensen et al. 2018) and communication
442 sounds, with sexual dimorphism being observed for calls , such as in *Globicephala melas*
443 (Ralls and Mesnick 2018), or on emission beam patterns (Au et al. 1995; Kloepper et al. 2012).
444 Most of the largest odontocete species were recognized as having the greatest degree of SSD:
445 *Physeter macrocephalus*, *Orcinus orca*, *Hyperoodon* spp., *Monodon monoceros*,
446 *Delphinapterus leucas*, *Globicephala* spp., *Berardius bairdii*, *Ziphius cavirostris*, and
447 *Mesoplodon* spp. (Cranford 1999; MacLeod and MacLeod 2009; Ralls and Mesnick 2009;
448 MacLeod 2010; Goldbogen et al. 2019). A known trend is that the larger the animal, the louder
449 sound it will produce (Ralls and Mesnick 2009). False killer whales are extremely vocal
450 (Murray et al. 1998) and differences in vocalization were recorded between populations but
451 not between sexes (Rendell et al. 1999; Oswald et al. 2003; Sanino and Fowle 2006; Barkley
452 et al. 2019).

453 The allometric parallel slopes observed for males and females showed that the directions of
454 shape changes in the cranium are conserved among sexes. As morphological changes can also
455 be associated with phylogenetic differences (Galatius et al., 2020) in size within Delphinidae
456 (evolutionary allometry), allometric trajectories should be analysed in the whole context of
457 toothed whale evolution to understand if those trajectories tend to differ along with the
458 increasing of the divergence time between different species of delphinids/odontocetes.
459 Describing these patterns will deepen our knowledge of the underlying macroevolutionary
460 processes in Delphinidae and Odontoceti.

461 **Conclusion**

462 In conclusion, although false killer whales are sexually dimorphic in the external shape of the
463 head (Stacey et al. 1994), this study showed sexual size dimorphism but no sexual skull shape
464 dimorphism. Combining the results and the interpretations above, it is likely that false killer
465 whales are polygynandrous (Nowak and Walker 1999; Shirihai 2006), with males being larger
466 than females, but both sexes sharing food resources (Botta et al. 2012; Riccialdelli and Goodall
467 2015). Using isometric-free 3D variables, this study provides new insights into cranial
468 asymmetry in individuals belonging to the same population. In addition, exploring FA proxies
469 and the related skull traits between populations might prove an important area for future
470 research. Moreover, further studies using stable isotopes and DNA analyses from these
471 specimens might further improve our understanding of the ecology and genetics of false killer
472 whale populations.

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479 **Author contributions**

480 D.V. collected the data and performed the statistical analyses. D.V. together with C.M., R.S.,
481 O.L., G.B., R.P.B. wrote and revised the manuscript. R.C.S. helped D.V. during data collection
482 at NHM. C.M. supervised the project.

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823 **Tables and captions**

824 **Table 1** Description of 37 landmarks taken on *Pseudorca crassidens* 3D cranium skull used in
 825 the Geometric Morphometric analysis

	Landmarks homologous on the cranium
1-2	Tip of the rostrum
3-4	Anteriormost point of the premaxillary foramen
5-6	Posteriormedial point of the premaxilla
7	Anteriormost point of the medial suture between the nasal bones
8-9	Sutural triple-junction between nasal, frontal and maxilla
10	External occipital protuberance or lambdoid crest
11-12	Sutural triple-junction between supraoccipital, frontal and parietal
13-14	Posteriormost point on the temporal crest
15	<i>Opisthion</i> ; middle point of the dorsal border of the <i>foramen magnum</i> on the intercondyloid notch
16-17	Dorsal tip of the occipital condyle
18-19	Lateral tip of the occipital condyle
20-21	Ventral tip of the occipital condyle
22-23	Medial tip of the paraoccipital process; ventralmost point of the paraoccipital process
24-25	Suture of pterygoid and basioccipital at the junction between pharyngeal crest and basioccipital crest
26-27	Posteroventral point of the postorbital process
28-29	Anteroventral point of the preorbital process
30-31	Anterior tip of lacrimal bone
32-33	Posteriormost point of the antorbital notch

34-35	Anteriormost point of the palatine
36-37	Posteriormost point of the upper alveolar groove

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846 **Table 2** Description of 25 landmarks taken on *Pseudorca crassidens* 3D mandibles used in
 847 Geometric Morphometric analysis.

	Landmarks homologous on mandible
1-2	<i>Pogonion</i> ; Tip of the mandible
3	<i>Gnathion</i> , the lowest point along the midline of the mandibular symphysis
4-5	Posterior end of the alveolar groove
6-7	Anteriormost point of the mandibular foramen
8-9	Posteroventral point of the mandibular foramen
10-11	Posterodorsal point of the mandibular foramen
12-13	Dorsal tip of the coronoid process
14-15	Most anterior point of the mandibular notch
16-17	Innermost point of the condyle
18-19	Outer point of the condyle
20-21	Medialmost point of the condyle
22-23	Ventralmost extreme point of the condylar process
24-25	Posteroventral tip of the angular process

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855 **Table 3** Procrustes ANOVA on 85 specimens (crania) of *Pseudorca crassidens* to evaluate
856 Repeatability index (*R*) as well as Fluctuating (FA) and Directional Asymmetry (DA).

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Effect	SS	MS	df	<i>F</i>	<i>p</i>	<i>R</i>
Individual	0.26783	6.65E-05	4028	5.36	<0.0001	0.95
Side (DA)	0.12401	0.00243	51	195.88	<0.0001	
Ind*Side(FA)	0.04811	1.24E-05	3876	2.1	<0.0001	
Err (Rep)	0.04729	5.91E-06	8008			

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875 **Table 4** Procrustes ANOVA to test for shape differences between sexes on crania A) shape B)
 876 and residuals of allometry of 74 *Pseudorca crassidens* specimens.

Shape ~	df	SS	MS	R ²	F	Z	p
A Sex	1	0.0024	0.0024	0.0193	1.4202	1.1327	0.132
Residuals	72	0.1223	0.0016	0.9806			
Total	73	0.1247					
B Sex	1	0.0026	0.0026	0.0224	1.6507	1.5929	0.057
Residuals	72	0.1169	0.0016	0.9775			
Total	73	0.1196					

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894 **Table 5** Procrustes ANOVA to test for slopes allometry of sexes on crania log Centroid Size
 895 (CS), Total Body Length (TBL), and shape of 74 *Pseudorca crassidens* specimens.
 896 Significance is highlighted in bold.

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Shape ~	df	SS	MS	R ²	F	Z	p
CS	1	0.00517	0.00517	0.04132	3.1459	3.4733	0.001
Sex	1	0.00298	0.00298	0.02382	1.8135	1.8652	0.028
CS:Sex	1	0.00192	0.00192	0.01536	1.1692	0.6291	0.259
Residuals	70	0.11505	0.00164	0.9195			
Total	73	0.12512					
TBL	1	0.00749	0.00749	0.05988	4.6288	4.4575	0.001
Sex	1	0.00299	0.00299	0.02388	1.8459	1.932	0.025
TBL:Sex	1	0.00134	0.00134	0.01068	0.8252	-0.419	0.661
Residuals	70	0.1133	0.00162	0.90556			
Total	73	0.12512					

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911 **Table 6** Procrustes ANOVA to test for slopes allometry of sexes on mandibles log Centroid
 912 Size (CS), Total Body Length (TBL), and shape of 29 *Pseudorca crassidens* specimens.

Shape ~	df	SS	MS	R^2	F	Z	p
CS	1	0.00322	0.00322	0.05842	1.7004	1.4716	0.071
Sex	1	0.00175	0.00175	0.03174	0.9238	0.01438	0.474
CS:Sex	1	0.0028	0.0028	0.05091	1.4817	1.0704	0.144
Residuals	25	0.0473	0.00189	0.85893			
Total	28	0.05507					
TBL	1	0.00281	0.00281	0.0511	1.4803	1.163	0.128
Sex	1	0.00242	0.00242	0.04399	1.2743	0.75185	0.201
TBL:Sex	1	0.00231	0.00231	0.04199	1.2166	0.63567	0.262
Residuals	25	0.04752	0.0019	0.86292			
Total	28	0.05507					

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938 **Table 7** Angular comparison of Partial Least Square (PLS) vectors of block 1 (cranium) and 2
 939 (mandible) between sexes. Significant *p*-values of these blocks of covariation trajectories
 940 between sexes are in highlighted in bold. They reflect a statistically more similar shape
 941 variation than two random vectors.

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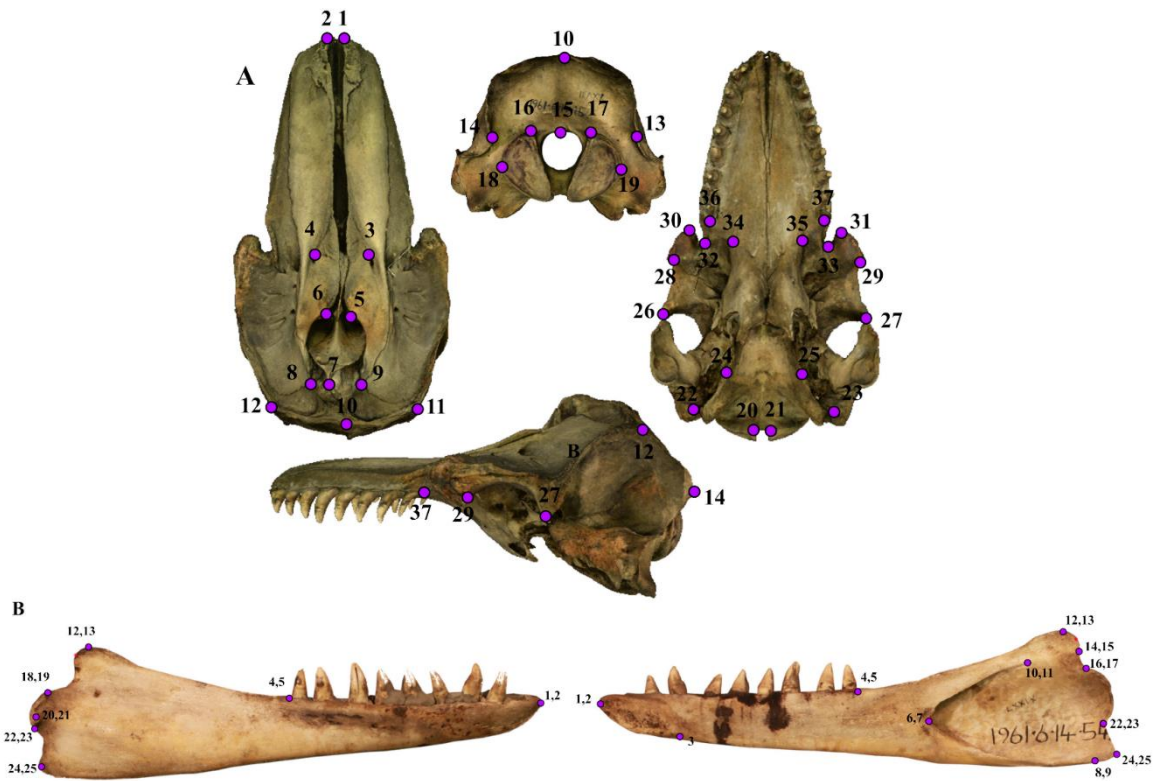
Block1	PLS1	PLS2	PLS3	PLS4
PLS1	56.937	81.210	85.647	84.240
	<0.00002	0.26994	0.47022	0.05357
PLS2	85.928	57.603	81.735	83.487
	0.60988	0.00003	0.29971	0.41415
PLS3	89.520	75.890	84.475	88.435
	0.95204	0.07566	0.48862	0.84457
PLS4	85.119	85.692	84.561	77.145
	0.54074	0.58927	0.49541	0.10587
Block2	PLS1	PLS2	PLS3	PLS4
PLS1	38.785	76.449	86.124	82.989
	<0.00001	0.17549	0.69965	0.48487
PLS2	77.996	60.013	88.798	81.081
	0.23058	0.00223	0.90479	0.37383
PLS3	67.504	79.592	88.326	89.520
	0.02330	0.29902	0.86768	0.96187
PLS4	86.546	88.328	62.253	58.737
	0.73099	0.86788	0.00483	0.00140

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965 **Figure 1** Landmark configuration on the A) cranium photogrammetric-based 3D model of the
 966 specimen (*Pseudorca crassidens* 1961.6.14.15 NHM, London) in dorsal, ventral, left lateral,
 967 and occipital views and B) right hemi-mandible of the specimen *Pseudorca crassidens*
 968 1961.6.14.54 NHM, London, in labial and lingual views. See Table 1 and Table 2 for
 969 description.

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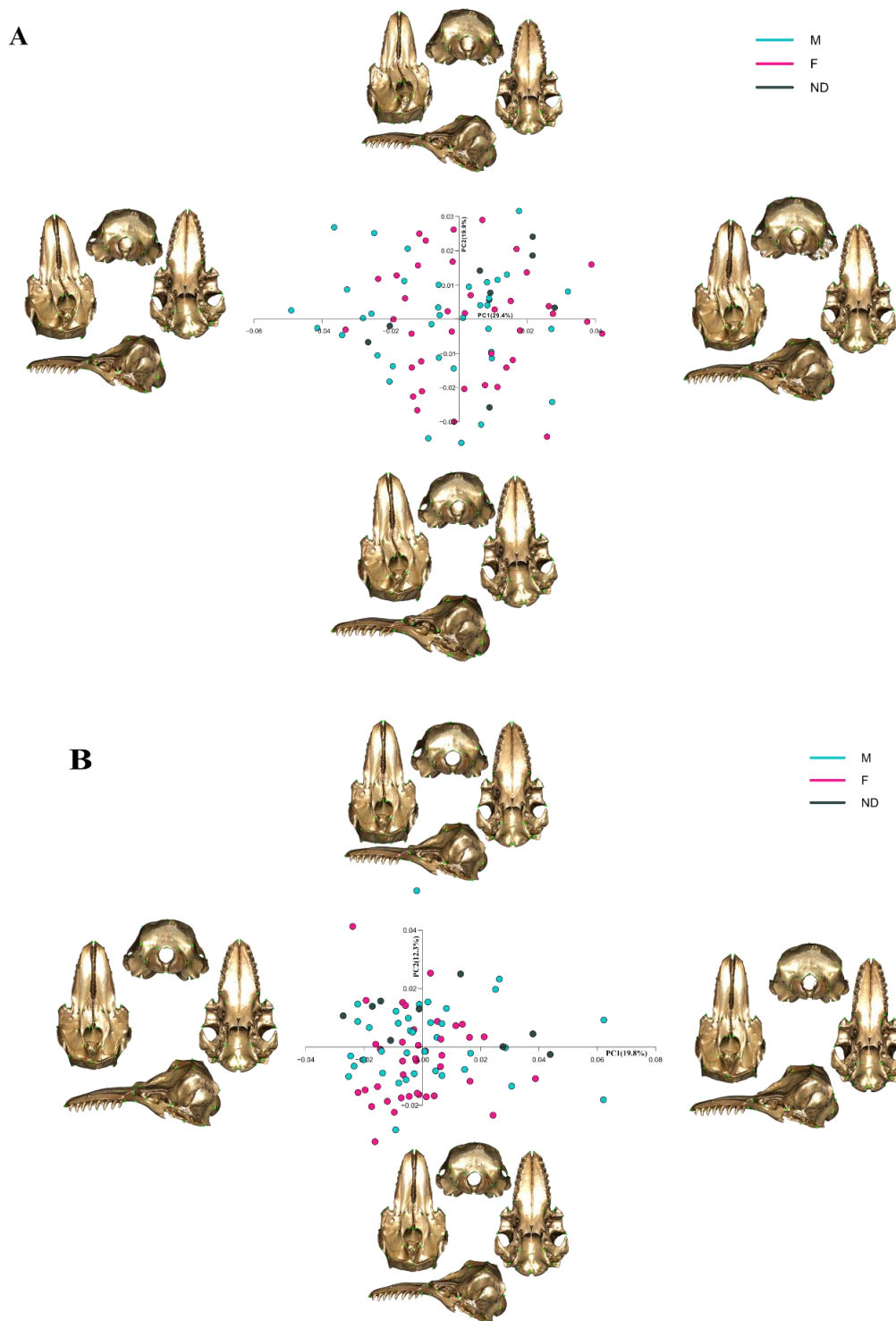
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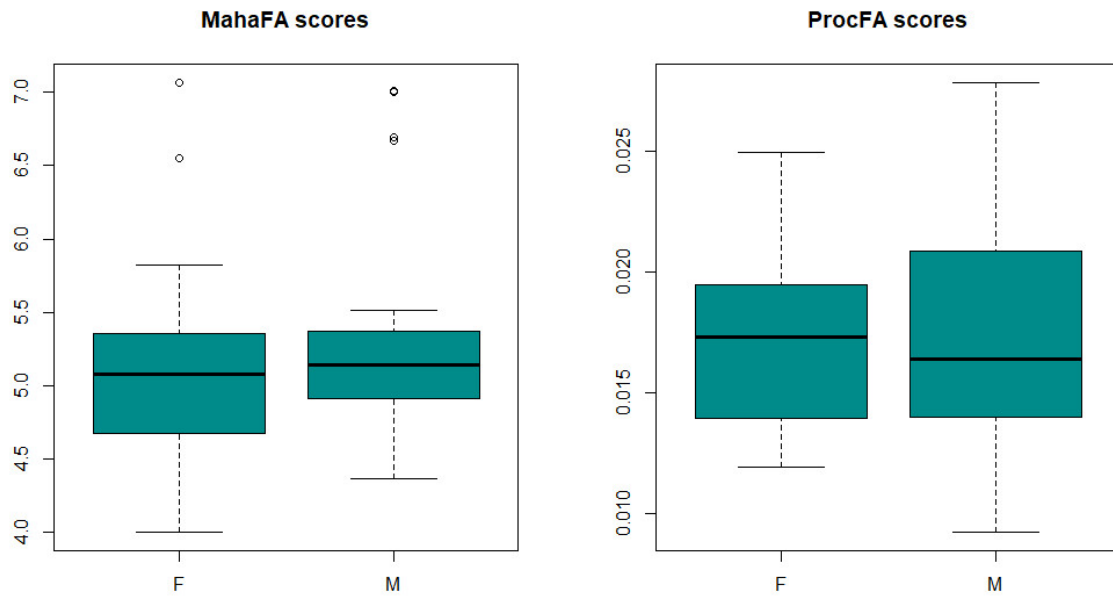
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979 **Figure 2** Principal component plot of the asymmetric (A) and symmetric (B) component of
 980 shape for 3D skull dataset. Greyscale has been used to indicate sex categories (F=females,
 981 M=males, ND= no data). Shape differences along the axis of the PC1 and PC2 are visualised
 982 with warping of the crania 3D models.



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986 **Figure 3** Boxplots of Mahalanobis and Procrustes FA scores among female and male
 987 specimens.

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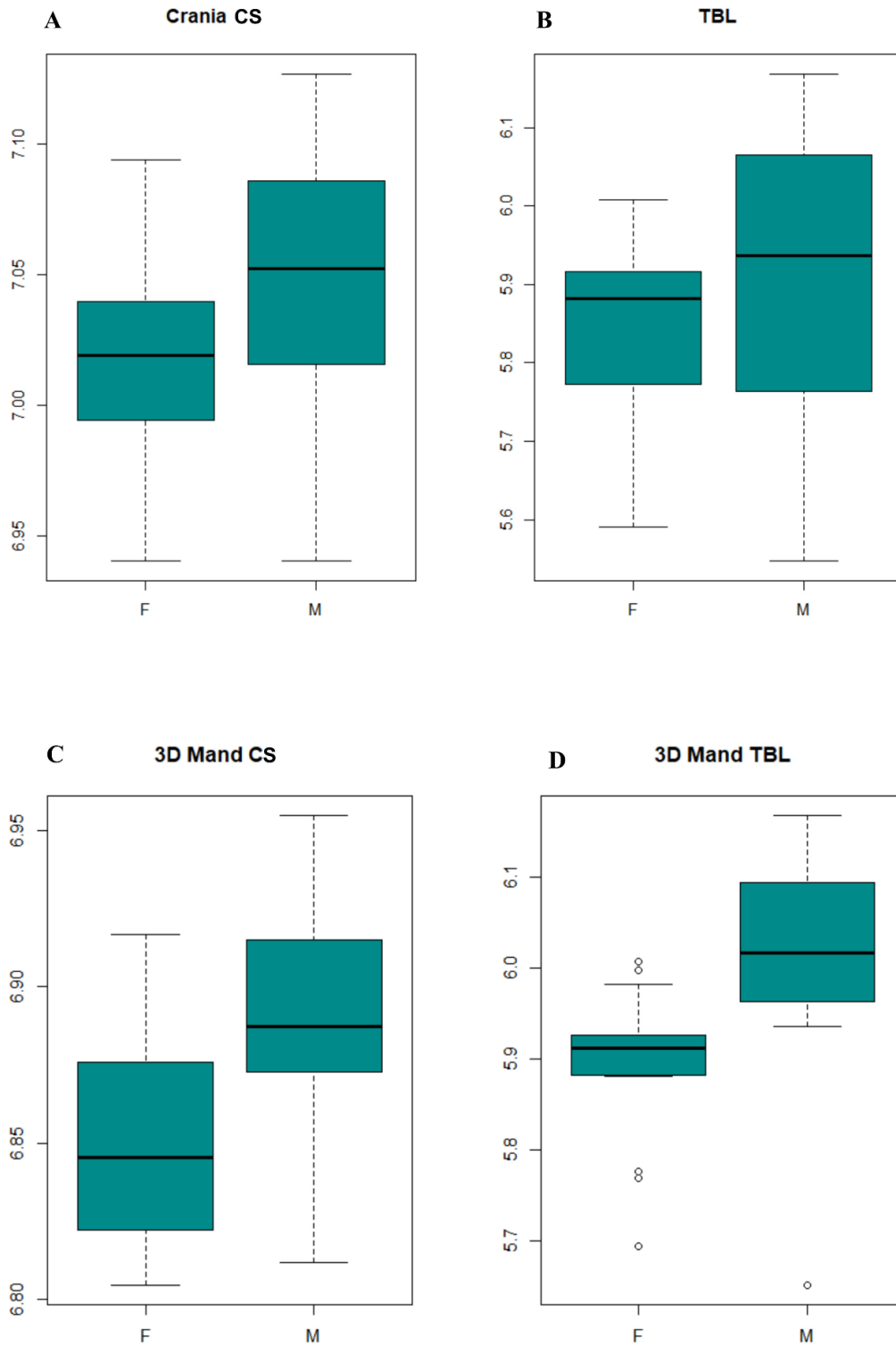
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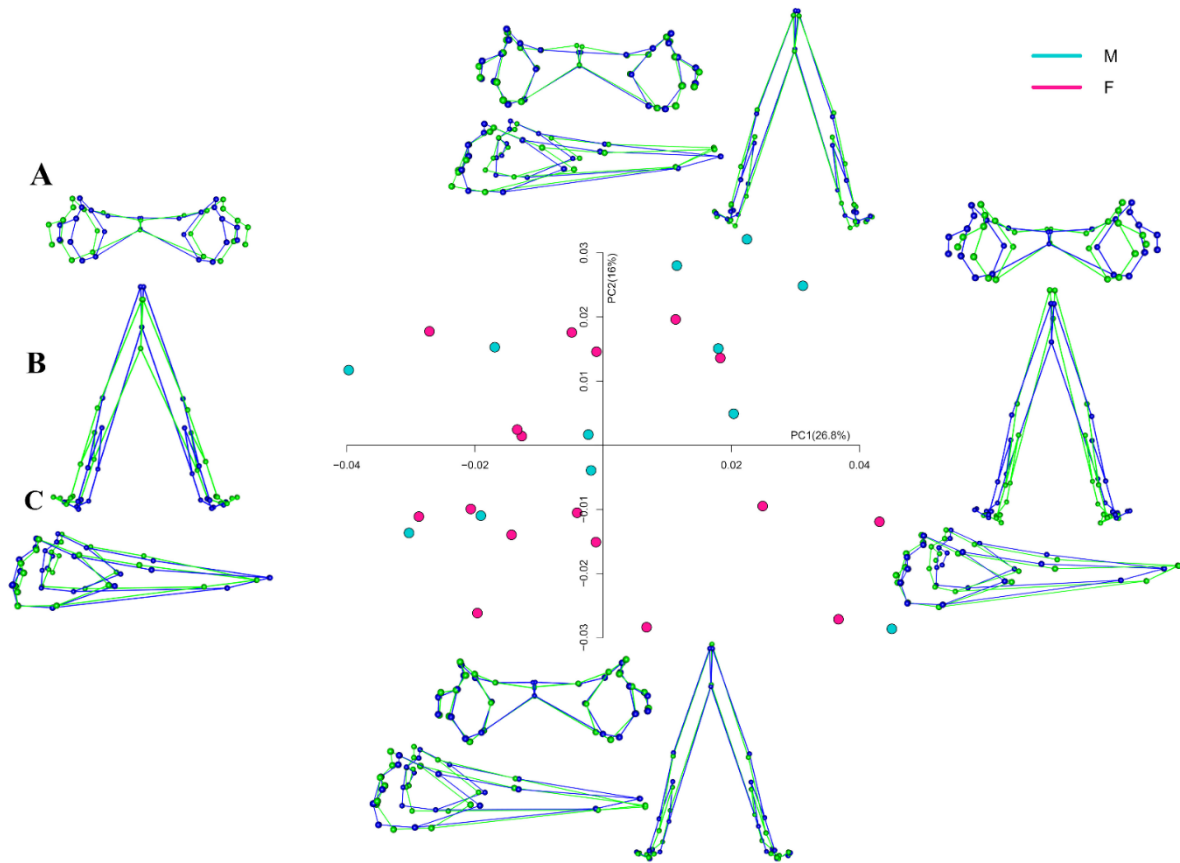
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1000 **Figure 4** Box-whisker plots of crania dataset ($n=74$) log[CS] (A) and TBL (B) and mandibles
 1001 dataset ($n=29$) log[CS] (C) and TBL (D) of females (F) and males (M) false killer whales.

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1004 **Figure 5** Principal component plot of the symmetric component of shape for 3D mandible
 1005 dataset, in R. Greyscale has been used to indicate sex categories (light
 1006 grey F=females, dark grey M=males). Shape differences along the axis of the PC1 and PC2
 1007 can be viewed by wireframe in A) occipital, B) dental, and C) lateral view. The dark colour
 1008 refers to the mean shape of the individuals while the light colour refers to the extreme individual
 1009 on the negative and positive PC axes.

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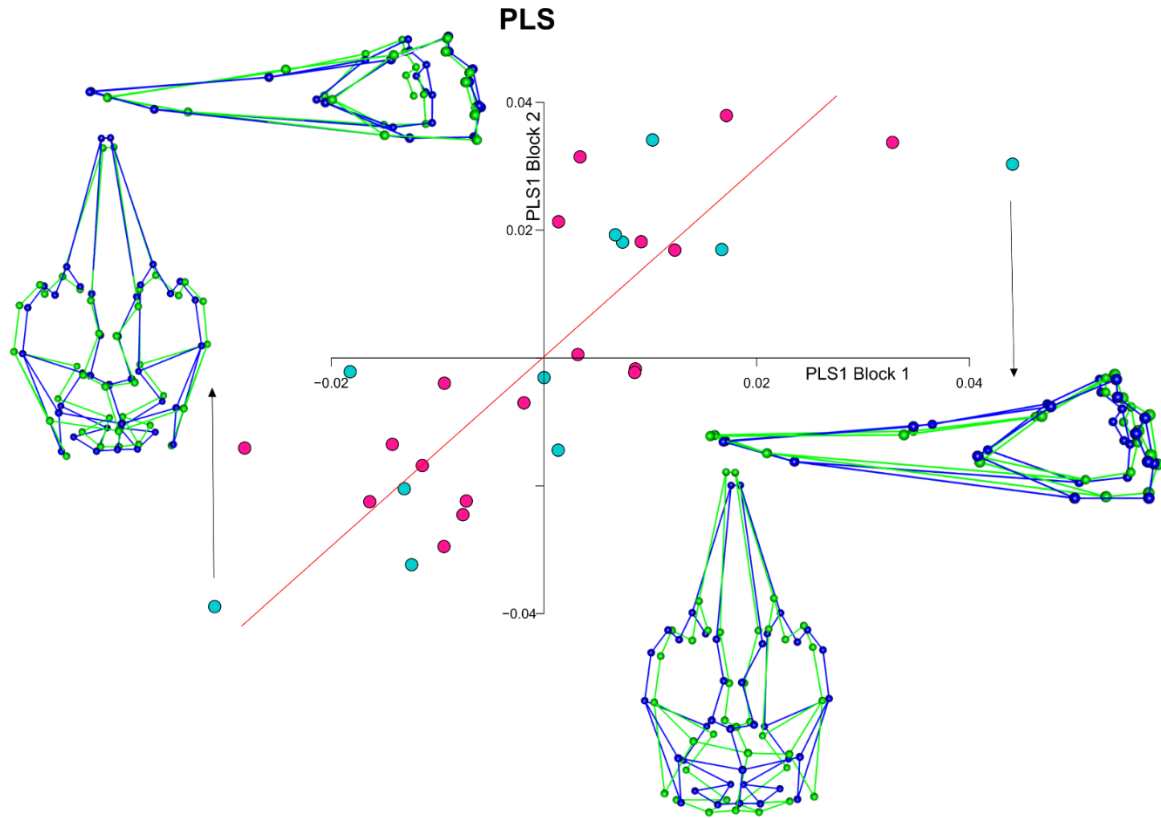
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1019 **Figure 6** Scatter plot of the PLS1 of block1 (Cranium) and block2 (Mandible). Shape
 1020 differences can be viewed by wireframe. The dark colour refers to the mean shape of the
 1021 individuals while the light colour refers to extreme most individual on the PLS1 axes.
 1022 Greyscale has been used to indicates sex categories (light grey F=females, dark grey M=males).

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