Why the long face? Comparative shape analysis of miniature, pony, and other horse skulls reveals changes in ontogenetic growth

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Background. Much of the shape variation found in animals is based on allometry and heterochrony. Horses represent an excellent model to investigate patterns of size-shape variation among breeds that were intentionally bred for extreme small and large sizes.

Methods. We tested whether ponies (wither height < 148 cm) have a diverging size-shape relationship in skull shape as compared to regular-sized horse breeds (wither height > 148 cm, here-after called horses) during ontogenetic growth. We used a dataset of 194 specimens from 25 horse and 13 pony breeds, two of which are miniature breeds (wither height < 96.5 cm) – Falabella, Shetland. We applied three-dimensional geometric morphometrics, linear measurements, and multivariate analyses (Procrustes ANOVAs) to quantitatively examine and compare the ontogenetic trajectories between ponies and horse breeds with an emphasis on the miniature breeds as an extreme case of artificial selection on size. Additionally, we tested for juvenile characteristics in adult horse and miniature breeds that could resemble "paedomorphosis" – retention of juvenile characteristics in adult stage; e.g. large eyes, large braincase-to-face-relationship, and large head-to-body relationship.

Results. Allometric regression of size on shape revealed that 42% of shape variation could be explained by variation in size in all breeds. The ontogenetic trajectories of ponies and horses vary in slope and therefore in rate of change per unit size and length. The differences in trajectory lengths and slopes result in ponies having a similar skull shape in an older age stage than horses of the same size in a younger age stage. This pattern could cause the generally perceived "paedomorphic" appearance of ponies. Miniature breeds have larger heads in relation to wither height compared to horses, a non-paedomorphic feature in horses specifically. Also rostra (faces) are longer in adult individuals than in juveniles across all kinds of breeds. This pattern can be explained by the long-face hypothesis for grazing ungulates and could possibly be caused by the mismatch of selection by humans for shorter rostra and the dentition of ruminants.

Conclusions. Miniature breed specimens do not exhibit any of the classical mammalian "paedomorphic" features (large orbits, large heads), except for the adult Falabella that has enlarged orbits, possibly because they are herbivorous ungulates that are affected by functional and metabolic constraints related to low nutrient-food consumption. Instead ponies, including miniature breeds, have faster and shorter ontogenetic growth compared to horses, resulting in adult pony skulls looking in part like juvenile horse skulls.

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15   **Abstract**

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21   here-after called horses) during ontogenetic growth. We used a dataset of 194 specimens from 25

22   horse and 13 pony breeds, two of which are miniature breeds (wither height < 96.5 cm) –

23   Falabella, Shetland. We applied three-dimensional geometric morphometrics, linear

24   measurements, and multivariate analyses (Procrustes ANOVAs) to quantitatively examine and

25   compare the ontogenetic trajectories between ponies and horse breeds with an emphasis on the

26   miniature breeds as an extreme case of artificial selection on size. Additionally, we tested for

27   juvenile characteristics in adult horse and miniature breeds that could resemble

28   "paedomorphosis" – retention of juvenile characteristics in adult stage; e.g. large eyes, large

29   braincase-to-face-relationship, and large head-to-body relationship.

30   **Results**. Allometric regression of size on shape revealed that 42% of shape variation could be

31   explained by variation in size in all breeds. The ontogenetic trajectories of ponies and horses

32   vary in slope and therefore in rate of change per unit size and length. The differences in

33   trajectory lengths and slopes result in ponies having a similar skull shape in an older age stage

34   than horses of the same size in a younger age stage. This pattern could cause the generally

35   perceived "paedomorphic" appearance of ponies. Miniature breeds have larger heads in relation

36   to wither height compared to horses, a non-paedomorphic feature in horses specifically. Also

37   rostra (faces) are longer in adult individuals than in juveniles across all kinds of breeds. This

38   pattern can be explained by the long-face hypothesis for grazing ungulates and could possibly be

39   caused by the mismatch of selection by humans for shorter rostra and the dentition of ruminants.

40   **Conclusions**. Miniature breed specimens do not exhibit any of the classical mammalian

41   "paedomorphic" features (large orbits, large heads), except for the adult Falabella that has

42   enlarged orbits, possibly because they are herbivorous ungulates that are affected by functional

43   and metabolic constraints related to low nutrient-food consumption. Instead ponies, including

44   miniature breeds, have faster and shorter ontogenetic growth compared to horses, resulting in

45   adult pony skulls looking in part like juvenile horse skulls.

46   **Introduction**

47   Allometry, shape change associated with size change, accounts for much of newly generated

48   shape changes (Wilson, 2018). Patterns of shape variation and allometry during ontogeny, that is

49   the size-shape relationship during an organisms growth, have been studied in many domesticated

50   animals such as dogs (Wayne, 1986; Morey, 1992; Goodwin, Bradshaw & Wickens, 1997;

51   Geiger et al., 2017; Werneburg & Geiger, 2017), pigs (Hilzheimer, 1926; Evin et al., 2017),

52   sheep (Geist, 1974), guinea pigs (Kruska & Steffen, 2013), and horses (Radinsky, 1984;

53   Goodwin, Levine & McGreevy, 2008). Recent advances in the study of shape variation,

54   especially through the advancement of statistical methods for the analysis of multivariate

55   geometric morphometric data, have increased our knowledge on how shape variation arises and

56   how variation is patterned (Adams et al., 2004; Adams, Rohlf & Slice, 2013).

57   Horses exhibit a large size range from 84 cm (Falabella) to 178 cm wither height (Shire).

58   Ponies are defined by a wither height less than 148 cm (FEI, 2016). Ponies are derived from

59   selection on larger breeds (Hendricks, 2007). Extremely small ponies, so-called miniature

60   breeds, formally belong to the group of ponies. Miniature breeds are defined as horse breeds with

61   a wither height of less than 96.52 cm (38 in) ("World Class Miniature Horse Registry") and have

62   been purposely bred for extreme small size. The smallest horse breed, the Falabella, originates

63   from Argentina. The breed was first mentioned in the middle of the 19th century when very small

64   individuals of Criollo horses were encountered in the Argentinian Pampa (Hendricks, 2007).

65   After obtaining a few individuals and starting a breeding program with miniature horses, the

66   name giver of the breed, Juan Falabella, added small individuals of English Thoroughbred,

67   Criollo, and the also miniature breed Shetland pony to achieve a harmonious conformation with

68   a wither height lower than 84 cm. The Shetland pony, which was strongly interbred with the

69   Falabella due to its small wither height (max. 106 cm), originates from the Shetland Islands,

70   Scotland. It is among the oldest known horse breeds and was mostly bred locally on the islands

71   for croft works. When an act of British Parliament, however, prohibited child labour in the

72   coalmines in 1847, the demand for these small robust ponies, as a replacement, increased

73   drastically. Over the last century, numerous individuals have been exported, mainly being used

74   for driving or as a first mount for children (Hendricks, 2007).

75   In the following we investigate ontogenetic trajectories of ponies (wither height < 148

76   cm) including two miniature breeds, and regular-sized horse breeds (wither height > 148 cm)

77   using three-dimensional geometric morphometrics (3D GM). We will refer to regular-sized horse

78   breeds as 'horses' for simplicity. If not stated otherwise ponies always include the miniature

79   breeds. We will highlight two miniature breeds – Falabella and Shetland, and their position in

80   morphospace. Osteological samples of the Falabella are so rare that we have quantified skull

81   shape from the only complete skull specimen available in public museum collections. The

82   comparative analysis of these extreme cases of miniaturisation with other breeds will give us

83   insights into differential growth patterns in horses due to artificial selection for size.

84   Further, we aim to shed light on the perceived juvenile appearance of miniature and pony

85   breeds when compared to horses by assessing "paedomorphosis" in its broadest sense – the

86   resemblance of an adult form to a juvenile of a sister group. We are aware that breeds are not

87   individual species, for that reason we do not claim to study paedomorphosis in the strict sense.

88   However, there are certain features in Falabella and Shetland adult skulls that raise the question,

89   whether they have retained juvenile appearance. For example, the adult Falabella skull exhibits a

90   round braincase that can partly be seen in the other miniature breed – the Shetland, but not in the

91   larger Welsh (Fig. 1). Generally, juvenilized phenotypic features are differences in body

92   proportions, e.g. a larger head and shorter limbs (Gould, 1980), and differences in cranial

93   proportions, such as larger eyes, a more prominent and bulging cranium, and a short rostrum in

94   combination with an enlarged braincase (Gould, 1980; Wayne, 1986; Tamagnini, Meloro &

95   Cardini, 2017; Evin et al., 2017). In particular, the shortening of the face portion of the skull in

96   smaller taxa versus the elongation of the face portion in larger related taxa has gained some

97   attention over the past years and has been formalized as the cranial evolutionary allometry

98   hypothesis (CREA) (Tamagnini, Meloro & Cardini, 2017). To approach the quantification of

99   juvenilized shape we use linear measurements derived from the 3D GM dataset for all age

100   classes and all breeds and calculate ratios of length that reflect the typical paedomorphic traits of

101   larger eyes, shorter face, and smaller head to body ratio in ponies.

102   **Materials & Methods**

103   *Specimens analyzed and determination of age classes*

104   A total of 194 juvenile and adult crania were analyzed (Table S1). We examined specimens from

105   the following collections: Museum für Naturkunde Berlin (MfN Berlin, Germany), Institut für

106   Haustierkunde (Christian-Albrechts-Universität of Kiel, Germany), Museum für Haustierkunde

107   „Julius Kühn" (University of Halle, Germany), Naturhistorisches Museum Wien (NHW Vienna,

108   Austria), and Museo de la Plata (MLP La Plata, Argentina). The dataset includes 38 horse

109   breeds, ranging from the smallest (Falabella) to the largest breed (Shire) (Table S1). Of the 38

110   breeds, 13 are considered ponies two of which are miniature breeds as indicated in brackets:

111   Bosnian pony (bos), Exmoor pony (exm), Falabella (fab) (miniature), German Riding pony (grp),

112   Icelandic Horse (ice), Indian pony (ind), Konik (kon), Mongolian (mon), Scottish pony (scp),

113   Shetland pony (she) (miniature), Togo pony (tog), and Welsh (wel). 25 breeds are considered

114   regular-sized breeds or horses: Anglo-Norman (ano), Arab (arb), Birkenfelder (bif), Belgian

115   Draft (blg), Clydesdale (cds), Galician Farm Horse (gbh), Grisons (Graubündner) (grb),

116   Hannoverian (han), Hackney (hny), Holstein (hol), Hungarian (hun), Huzule (huz), Kladrubian

117   (kdr), Kosarian (kos), Lipizzan (lpz), Nonius (nos), Norik (nor), Oldenburgian (odb), Pinzgau

118   (piz), Polish Farm Horse (pll), Seneca Sarajevo (ses), Shire (shi), Styrian (stm), Suffolk (suf),

119   English Thoroughbred (thb), Trakehner (trk).

120   Prior to analyses, each specimen was categorized into an age class from 0 to 6 using an

121   identification key for dental eruption (Habermehl, 1975) with: 0 – dental eruption after birth, 1 –

122   eruption of the first pair of deciduous incisors, 2 – eruption of the second pair of deciduous

123   incisors, 3 – eruption of the third pair of deciduous incisors, 4 – eruption of the first molar, 5 –

124   eruption of the second molar, and 6 – eruption of the third molar (Table S1). Weaning occurs

125   around the end of age class 2 and the beginning of age class 3 (at around six months), while

126   sexual maturity is reached at the beginning of age class 4 (at around one year) and skeletal

127   maturity is reached in age class 6 (around 4 years). Notably, the dataset contains only a single

128   specimen of Falabella, to our knowledge the currently only complete skull from a museum

129   collection to be measured.

130   *Collection of shape data*

131   Cranial shapes were analysed using landmark-based geometric morphometric (GMM)

132   approaches. The crania were measured in three-dimensions (3D) using a MicroScribe ® MLX6

133   (Revware, Inc., Raleigh, North Carolina, USA; accuracy: 0.076 mm) and a total of 60 type I and

134   type II landmarks (Bookstein, 1990) (Table S2, Figure S1) were collected. The dorsal and ventral

135   sides of the crania were measured separately and the landmark datasets were subsequently

136 combined using three reference landmarks (numbered 1, 2, and 33, Figure S1) in the

137 Microscribe® software MUS (Revware, Inc., Raleigh, North Carolina, USA). All subsequent

138 analyses were conducted using R v.3.5.2 (R Core Team, 2016) and related R packages for the

139 analyses of geometric morphometric data: *geomorph* v. 3.1.2 (Adams et al., 2018) and *shapes* v.

140 1.2.4 (Dryden, 2018). The code that was used for the following analyses of 3D GM data can be

141 found as a supplement in Code_and_Results_Falebella_pub.rmd.

142 *3D Geometric morphometric analyses*

143 General Procrustes Analysis (GPA) (Rohlf & Slice, 1990) was performed on the 3D shape data

144 to eliminate the effects of size, orientation, and scaling. GPA translates, rotates, and scales all

145 specimens' coordinates so their centroids coincide and are scaled to unit centroid size, and the

146 squared summed distances between matching landmarks are minimized. Due to its bilateral

147 symmetry, only the symmetric component of the cranium was used in the subsequent analyses

148 (Klingenberg, Barluenga & Meyer, 2002; Kolamunnage & Kent, 2003). We calculated centroid

149 size for each landmark configuration.

150 To visualize morphospace occupation of the age classes of miniature breeds and horses along

151 major axes of variance, we performed a principal component analysis (PCA) using the co-

152 variance matrix of Procrustes scores retained from the GPA. We calculated mean shapes for each

153 age class of horse breeds as well as for the Shetland and Falabella to visualize shape differences

154 with age.

155 *Characterizing cranial ontogenetic shape trajectories of ponies and horses*

156 For subsequent analyses of ontogenetic size-shape co-variation (allometry) between and within

157 pony and horses we performed linear regressions (Procrustes ANOVA) of shape (Procrustes

158 coordinates) on logarithmized centroid size, and a grouping factor, type = H/P, which denotes the

159 group affiliation of each breed to either horse (H) or pony (P) breed as indicated in Table S1 and

160 raw coordinates file. To inspect the inter-specific allometric relationship between pony and horse

161 breeds we used two methods, the regression of shape on size resulting in a plot of regression

162 residuals on log centroid size (Drake & Klingenberg, 2008) and the predicted shape approach

163 (Adams & Nistri, 2010) that plots the first principal component from a regression of predicted

164 shape values on log centroid size. We applied a test for homogeneity of slopes (HOS) when the

165 interaction term of log(size) and type was significant during Procrustes ANOVA (Collyer &

166   Adams, 2013; Collyer, Sekora & Adams, 2015; Adams & Collyer, 2016). The HOS test allowed

167   us to determine whether pony and horse breed ontogenetic allometries differed in slope distance

168   (amount of shape changes with size), slope angles (direction of shape change), or intercept.

169   *Testing features of paedomorphosis in miniature breeds using linear measurements*

170   Additionally, to complement the multivariate statistical analyses for differences in ontogenetic

171   trends between ponies and horses, we aimed to test for features of "paedomorphosis" in the

172   miniature breeds using only linear measurements. We define "paedomorphosis" loosely here, as

173   a general resemblance of adults in miniature breeds to juveniles in all other breeds. Typical

174   phenotypic features of paedomorphosis are differences in body proportions, e.g. a larger head

175   and shorter limbs (Gould, 1980), and differences in cranial proportions including larger eyes, a

176   more prominent and bulging cranium, and a short rostrum in combination with an enlarged

177   braincase (Gould, 1980; Wayne, 1986; Tamagnini, Meloro & Cardini, 2017; Evin et al., 2017).

178   Paedomorphism has been claimed to describe some differences among horse breeds (Budiansky,

179   1997; Goodwin, Levine & McGreevy, 2008), however the long-face hypothesis of grazing

180   ungulates (Spencer, 1995), that postulates that longer faces are observed in smaller forms of

181   grazing ungulates, if also true for horses, could explain lack of signs of paedomorphism in the

182   rostrum. We calculated interlandmark distances (specified below) from the three-dimensional

183   dataset in the R package *geomorph* (Adams et al., 2018) and calculated the ratios for the

184   following three traits:

185   **Larger eyes:** To test whether miniature breeds exhibit larger orbits (eyes) than regular-sized

186   breeds relative to their respective cranial lengths, we calculated the ratio of orbit length to cranial

187   length from measurements of the orbit diameter (LM 15 – 17, Table S2, Figure S1) and total

188   cranial length (LM 37 – 58, Table S2, Figure S1).

189   **Shorter rostrum:** To test for rostral shortening we measured the length of and the angle

190   between palate (LM 37 – 44, Table S2, Figure S1) and basicranium (LM 49 – 58, Table S2,

191   Figure S1). The angle is expected to become smaller the larger the braincase and the shorter the

192   palate becomes.

193   **Smaller head to body ratio:** We inspected the relationship of adult cranial length (LM 33 – 58)

194   (n = 128) and average breed wither height, which we collected from the literature for a subset of

195   11 ponies and 18 horses (breeding guidelines for each breed, Table S3). We calculated the

196 predicted adult cranial length of the miniature breeds as derived from linear regression of adult

197 cranial lengths from horse breeds (Verzani, 2014) and compared it to their actual cranial lengths.

198 The adult cranial length to wither height ratio in relation to breed is used to investigate a possible

199 minimal limit in cranial length in the investigated breeds.

Results

Characterization of cranial shape of miniature and horse breeds

202 We calculated and visualized the mean shape for each age class from Procrustes shape data, as

203 well as that of the adult stage of the two miniature breeds (Fig. 2). A description of the different

204 age classes (0, 3, 6) and the adult crania of the Falabella and Shetland pony are presented in

205 Table 1. The juvenile age classes of horses are characterized by a very broad and short cranium

206 with a bulging anterior-dorsal part of the braincase (Fig. 2). During growth, the cranium

207 elongates (rostrum stronger than the anterior part of the braincase) and the anterior-dorsal part of

208 the cranium flattens. The orbit size decreases in relation to the complete cranium.

Cranial ontogenetic shape change of pony and horse breeds

210 PCA (Fig. 3A) reveals that the ontogenetic stages 0–6 separate in PC1-PC2 space along PC1

211 from adult (PC1 negative) to juvenile age stages (PC1 positive). The first PC accounts for 47.1%

212 of the total shape variation. A gap in the shape space between age classes 0–2 and 3–6 is visible.

213 Also, we can observe that cranial shape among early ontogenetic stages is more similar to each

214 other than cranial shape of the adult stage, where the scatter becomes larger. When comparing

215 the miniature breeds to horses in shape space, it becomes evident that the Shetland specimens

216 align with the respective age classes of larger breeds, but constitute the most 'youthful' cohort of

217 the respective stages (Fig. 3A). The adult skull (age class 6) of the smallest of all horse breeds,

218 the Falabella specimen, clusters most within age stages 3 and 4 of regular-sized breeds (Figs. 3A;

219 4). The same PCA highlighted by group – miniature breeds, ponies, and horses – (Fig.3B)

220 visualizes that horse breeds scatter more along PC2. The contrast of shape change along PC 1

221 (Fig. 3C) demonstrates that the braincase undergoes larger changes than the rostrum.

222 *Analysis of ontogenetic allometry within and between pony and horse breeds*

223 We tested for allometry and differences in allometric growth between ponies and horses

224 performing Procrustes ANOVAs (analyses of variance). Regression of skull shape (Procrustes

225 coordinates) on log centroid size for the entire sample (ponies and horses) shows a strong effect

226 of size on shape ($R^2 = 0.42$, p=0.001). Adding "type" as an additional covariate yielded that

227 mean shapes of ponies and horses (F=9.201, Z=6.488, p=0.001) as well as their allometries

228 (F=3.613, Z=4.141, p=0.001) differ. Specifically, they differ in rate of change (Z=4.125,

229 p=0.001) and slope (angle=21.25 deg, r=0.93, Z=5.28, p=0.001). This result can be visually

230 assessed in Figure 4B. A test of least square (LS) means revealed no difference in intercept (Z=-

231 1.089, p=0.856). Generally, ponies have attained more maturity than horses at the same size,

232 while exhibiting the same skull shape as horses. The position of the adult Falabella (age class 6)

233 skull in the shape-size regression (Fig. 4A) and allometric trend (Fig. 4B) indicate that the

234 Falabella skull shape resembles younger horse breed shapes at the same size.

235 *Testing features of "paedomorphosis" in miniature breeds*

236 During ontogenetic growth of horses we observe that orbits grow smaller in relation to cranial

237 length (Figure 5 A), and the basicranium becomes shorter relative to the length of the rostrum

238 (Figure 5 B). The angle between the basicranium and palate does not differ significantly among

239 the different age stages (Figure 5 C). The growth pattern of Shetland ponies is similar to that of

240 horses and do not show any signs of enlarged orbits or shortened rostra or increased brain case in

241 the adult stage (Figure 5 A -C). The adult Falabella exhibits larger orbits (Figure 5 A) but

242 otherwise no other juvenile features regarding the rostrum or braincase (Figure 5 A-C). The

243 predicted cranial length of the Falabella and Shetland derived from linear regression of adult

244 cranial lengths from horse breeds is 24.6 cm and 31.1 cm respectively, which contrast to their

245 actual lengths of 35.6 cm and about 39 cm, respectively. Both actual cranial lengths fall slightly

246 outside of the 95% prediction interval (Figure 5 D). The cranial length at the upper prediction

247 limit raises the question whether ponies are constrained to have larger crania. Examination of the

248 cranial length to wither height ratio in relation to breed ordered by increasing maximal wither

249 height supports that the adult miniature breeds, Shetland and Falabella, have larger crania

250 relative to wither height than their horse cognates (Figure 5 E).

Discussion

251

252   Horses show allometric cranial growth where the juvenile specimens are significantly

253   different in cranial shape from the adult specimens (Sánchez-Villagra et al., 2017) and this study

254   (42%), as has been attested for other domesticated species (Wilson, 2018) and mammals in

255   general (Porto et al., 2009), The largest shape differences in PC1-PC2 shape space in our sample

256   can be found between the age classes 0-1 and 2-6. The difference between those two age clusters

257   is most likely caused by the low sample size in age class 2 (n = 2) and it is likely that the

258   ontogenetic trajectory for horses and ponies would form a continuum if age class 2 would

259   contain more specimens. To our knowledge, based on our examination of many museum

260   collections, specimens of that age class are rarely available.

261   Ponies and horses show differences in ontogenetic trajectory direction or angle but not in

262   intercept, which indicates that juveniles of all breeds start with a similar skull shape but diverge

263   during ontogenesis. Furthermore, ponies (including miniature breeds) develop faster than

264   regular-sized breeds and stop growth earlier. Therefore, horses develop adult cranial shapes that

265   ponies do not reach during growth. As a result, a younger horse specimen and an older pony

266   specimen can exhibit the same skull shape. This pattern could explain why ponies look like

267   juvenilized adult horses. Only the miniature breed Falabella, but not the Shetland, exhibits a

268   "paedomorphic" feature: enlarged orbits relative to cranial length in its final age state.

269   Given our results, we would like to emphasize that there are likely inter-breed differences

270   in skull shape at birth and possibly prenatally but shape data for those age classes are scarce. We

271   have preliminary evidence that skull shape differences among pony breeds arise prenatally. We

272   compared the ontogenetic trajectories of the Shetland as a miniature breed and the Welsh as a

273   regular pony (Figure S2, not presented in main text due to small sample size). Apart from dogs

274   (Werneburg & Geiger, 2017), this pattern has also been hypothesized in pigs (Evin et al., 2017),

275   and needs to be further investigated in horses including more breeds.

276   We investigated whether ponies, when compared to horses, represent a case of

277   craniofacial evolutionary allometry (CREA) (Cardini & Polly, 2013; Cardini et al., 2015;

278   Tamagnini, Meloro & Cardini, 2017). CREA predicts that larger forms are long-faced and

279   smaller forms short-faced as a sign of paedomorphism. As an approximation for braincase-to-

280   face relationship we calculated the ratio of basicranium-to-palate lengths for miniature and horse

281   breeds. We found no signs of CREA. In contrast, we found that our results are in accordance

282   with the long-face hypothesis for grazing ungulates (Spencer, 1995). The long-face hypothesis

283   does not offer a definite explanation why longer faces are observed in smaller forms of grazing

284   ungulates. In the case of the miniaturized horses, we propose that this could be due to constraints

285   in tooth morphology and the feeding style of grazing. Among veterinarians, it is commonly

286   known that miniature horse breeds have a higher requirement for veterinary dentist procedures,

287   due to their almost regular horse-sized teeth (Wilson, 2012). The same health-related problem

288   has been shown for pet rabbits, which experience a rostral shortening through domestication

289   without a change in dentition (Böhmer & Böhmer, 2017). These functional constraints have been

290   investigated also in humans showing that miniature forms tend to have relatively larger teeth

291   than regular-sized forms (Shea & Gomez, 1988). Since horses and ponies feed on a very nutrient

292   poor diet, they are in need of a highly specialized feeding apparatus to ensure the best energy

293   recovery possible. A strong shortening of the rostrum, as can be found in some dog and pig

294   breeds (Geiger & Haussman, 2016; Evin et al., 2017), is most likely possible due to their energy

295   rich diet (carnivore/omnivore) that can be exploited with fewer, smaller, or differently placed

296   teeth. In cows, which also feed on nutrient poor grass, one case of rostral shortening is known:

297   the Niata breed (Veitschegger et al., 2018); this was likely possible due to the more efficient

298   uptake of nutrients through rumination. There is evidence of rostral shortening in a extinct

299   herbivorous, non-ruminant browsing mammal clade, the short-faced kangaroo subfamily

300   Sthenurinae (Prideaux, 2004). Yet to our knowledge, there is no evidence of the existence of a

301   grazing ungulate with rostral shortening.

302   Large heads and increased head-to-body ratio has been shown to be a paedomorphic

303   feature in other domesticated species, namely dogs and chicken (Alberch et al., 1979; Gould,

304   1980; Wayne, 2001), but does not associate with paedomorphosis in horses as new born foals

305   have shorter rostra than adult individuals because teeth development drives rostral lengthening;

306   as well as foals having relatively longer legs (Habermehl, 1975; van Heel et al., 2006; Goodwin,

307   Levine & McGreevy, 2008) (Table 1). The long legs in horses are a necessity for survival, since

308   new born foals are very precocial and need to keep up with the herd from day one. Our study did

309   not compare the actual limb to head length ratio which has been proposed as a sign for

310   paedomorphism (Goodwin, Levine & McGreevy, 2007, 2008), but used wither height as a proxy

311   for size. We found that the miniature breeds have larger heads relative to body size

312 (approximated by wither height) when compared to horse breeds. So adult miniature breeds do
313 not exhibit the juvenile state of a horse in respect to head-to-body size ratio.
314   Regarding the adult Falabella skull and the case of the Falabella in general, we could not
315 support our first subjective impression that the Falabella must be a "paedomorphic" horse.
316 However, this impression probably derived from the very round anterior-dorsal part of the
317 braincase, whose geometric morphometric quantification by using true landmarks eluded us due
318 to the lack of sutures in that portion of the cranium, but the curvature can be seen in the
319 photograph of the Falabella cranium (Fig. 1A). Additionally, the Falabella does exhibit a less
320 downward curved rostrum than adults of regular-sized breeds (Fig. 1). For a better assessment of
321 a rounded cranium roof, future investigations are advised to use semi-landmarks or polygons
322 (MacLeod, 2013; Collyer, Sekora & Adams, 2015).

323 **Conclusions**

324 We investigated patterns of allometry during ontogeny in horses as a case of directional artificial
325 selection for extreme size differences in domesticated horses. Wither heights range from 84 cm
326 in the Falabella to 178 cm in the Shire horse. We looked at allometric trends between ponies and
327 horses and investigated typical patterns of "paedomorphosis", defined as juvenile appearance in
328 adult stage, with an emphasis on miniature horses as an extreme case of size selection. We found
329 that ponies and horses have shifted ontogenetic trajectories that vary in length but not in
330 direction or angle, with the consequence that ponies exhibit similar skull shapes at older age
331 stages as horses at younger age stages. This pattern is a potential source of the perceived
332 juvenilized skull shape of ponies, additionally to features of the postcranial architecture, namely
333 general small size or short limbs, or behavioral aspects as has been show in dogs (Hare &
334 Woods, 2013), such as the use of body language (Goodwin, Bradshaw & Wickens, 1997) or
335 facial expressions (Waller et al., 2013).
336   Other than the overall shape development of ponies halting earlier than of horses we find
337 no other evidence of "paedomorphic" features, as enlarged orbits, shorter faces, or increased
338 head-to-body ratio, as it is the case in dogs and pigs, except for the adult Falabella skull.
339 Miniature breeds (Falabella and Shetland) have increased skull-to-body ratio when compared to
340 horse breeds. This could be due to the very essence of horses and ponies, that is being a grazing

341 ungulate as postulated in the long-face hypothesis (Spencer, 1995). We propose functional and

342 metabolic constraints rather than flight responses as a potential driver of this pattern.

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Table 1. Description of morphological differences for three age classes of pony and horse breeds (0,3,6) and age class 6 for both miniature breeds (Falabella, Shetland) for the studied sample by module (for a detailed sample composition see Table S1).

1   **Table 1:** Description of morphological differences for three age classes of medium and large breeds (0,3,6) and age class 6 for both
2   miniature breeds (Falabella, Shetland) for the studied sample by module (for a detailed sample composition see Table S1).

	Medium and large breeds			Miniature breeds	
Module	**Age class 0**	**Age class 3**	**Age class 6**	**Falabella (age class 6)**	**Shetland (age class 6)**
Anterior-oral-nasal	Short, very round, and narrow premaxillare; no incisors; maxillare in diastema much narrower as premaxillare; nasale and diastema are straight; diastema is very short	Elongated and broader; Third pair of incisors erupted; elongated diastema; nasale is straight or curved depending on breed; maxillare in diastema almost as broad as premaxillare	Elongated and broader; premaxilla-maxilla suture closed; elongated diastema; nasale is straight or curved depending on breed; maxillare in diastema almost as broad as premaxillare	Short, round, and broad premaxillare; maxillare in diastema almost as broad as premaxillare; all incisors fully erupted; nasale is concave	Elongated and broader; premaxilla-maxilla suture closed; elongated diastema; nasale is slightly convex; maxillare in diastema almost as broad as premaxillare
Orbital	Round or egg-shaped depending on individual; large compared to skull length; post-orbital margin is thin	Round or egg-shaped depending on individual; medium compared to skull length; postorbital margin has thickened	Round or egg-shaped depending on individual; small compared to skull length; postorbital margin is thick	Round or egg-shaped depending on individual; medium compared to skull length; postorbital margin is thick	Round or egg-shaped depending on individual; small compared to skull length; postorbital margin is thickened
Zygomatic-pterygoid	Frontal-zygomatic and temporal-zygomatic suture open; facial crest, zygomatic, and temporal form a straight line in lateral view	Frontal-zygomatic and temporal-zygomatic suture started to close; facial crest, zygomatic, and temporal form a straight line in lateral view	Frontal-zygomatic and temporal-zygomatic suture closed; facial crest and zygomatic form a straight line in lateral view; temporal is curved from lateral view	Frontal-zygomatic and temporal-zygomatic suture started closing; facial crest, zygomatic, and temporal form a curved line in lateral view	Frontal-zygomatic and temporal-zygomatic suture closed; facial crest and zygomatic form a straight line in lateral view; temporal is slightly curved from lateral view
Cranial base	Round; occipital condyle and paracondylar process have a similar length; basisphenoid-presphenoid and basisphenoid-occipital suture open; basillar part of the occipital is broad	Elongated and distinct; basisphenoid-presphenoid started to close and basisphenoid-occipital suture open; basillar part of the occipital is elongated; paracondylar process is slightly longer than paracondylar process	Elongated and very distinct; basisphenoid-presphenoid and basisphenoid-occipital suture closed; basillar part of the occipital is elongated; paracondylar process is much longer than paracondylar process	Short and broad; basisphenoid-presphenoid and basisphenoid-occipital suture closed; basillar part of the occipital is broad; paracondylar process is longer than paracondylar process	Elongated and very distinct; basisphenoid-presphenoid and basisphenoid-occipital suture closed; basillar part of the occipital is elongated; paracondylar process is much longer than paracondylar process

Cranial vault	Occipital is not fused to any other bone; very round; frontal-parietal-occipital doming; occipital crest very small	Frontal-parietal doming; occipital elongated; occipital crest more pronounced; occipital started fusing to surrounding bones	Frontal-parietal-occipital flattened; occipital elongated; occipital crest very pronounced; occipital mostly fused with surrounding bones	Frontal-parietal-occipital doming; occipital elongated; occipital crest very pronounced; occipital mostly fused with surrounding bones	Frontal-parietal-occipital doming; occipital elongated; occipital crest very pronounced; occipital mostly fused with surrounding bones
Age classification	First post-natal stage, before the eruption of the first pair of incisors, up to 1 week old	Time after the eruption of the third pair of incisors until the eruption of the first molar, six month to one year, before sexual maturity; weaning is around 6 month of age	Last age stage after the eruption of the third molar, from 4 years on, skeletal maturity	Adult, age stage 6	Adult, age stage 6

Figure 1

Figure 1: Cranial shape comparison among two miniature breeds and a pony through ontogeny.

Examples of different cranial shapes during ontogeny from lateral view if available for each age class (0-6) for (A) Falabella and (B) Shetland (miniature breeds); and (C) Welsh (pony); each stage is represented by a different individual and all crania are scaled to the same length for comparison. Photographs by Laura Heck.

B

C

Age class

0

A

Falabella

Shetland

Welsh
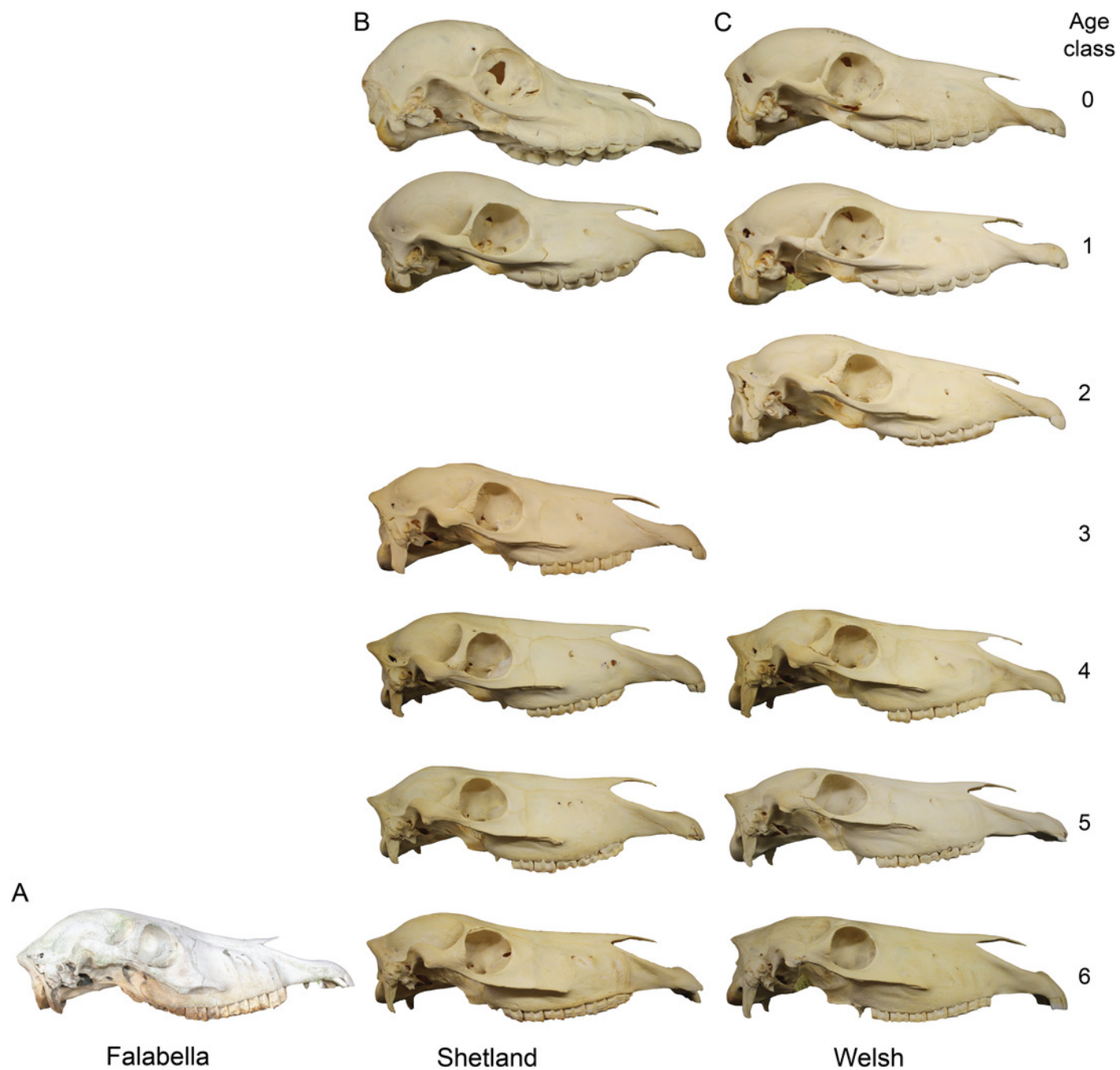
Figure 2

Cranial mean shapes for adult Falabella and Shetland, and for each analyzed age class of horses.

Cranial shapes in A) lateral and B) dorsal view for the average shape of each age class (0-6) of all horse specimens (for detailed sample composition see Table S1), C) lateral and D) dorsal view of adult Falabella and E) lateral and F) dorsal view of the average skull shape of adult Shetland (both miniature breeds); all crania are scaled to the same length for better comparison.
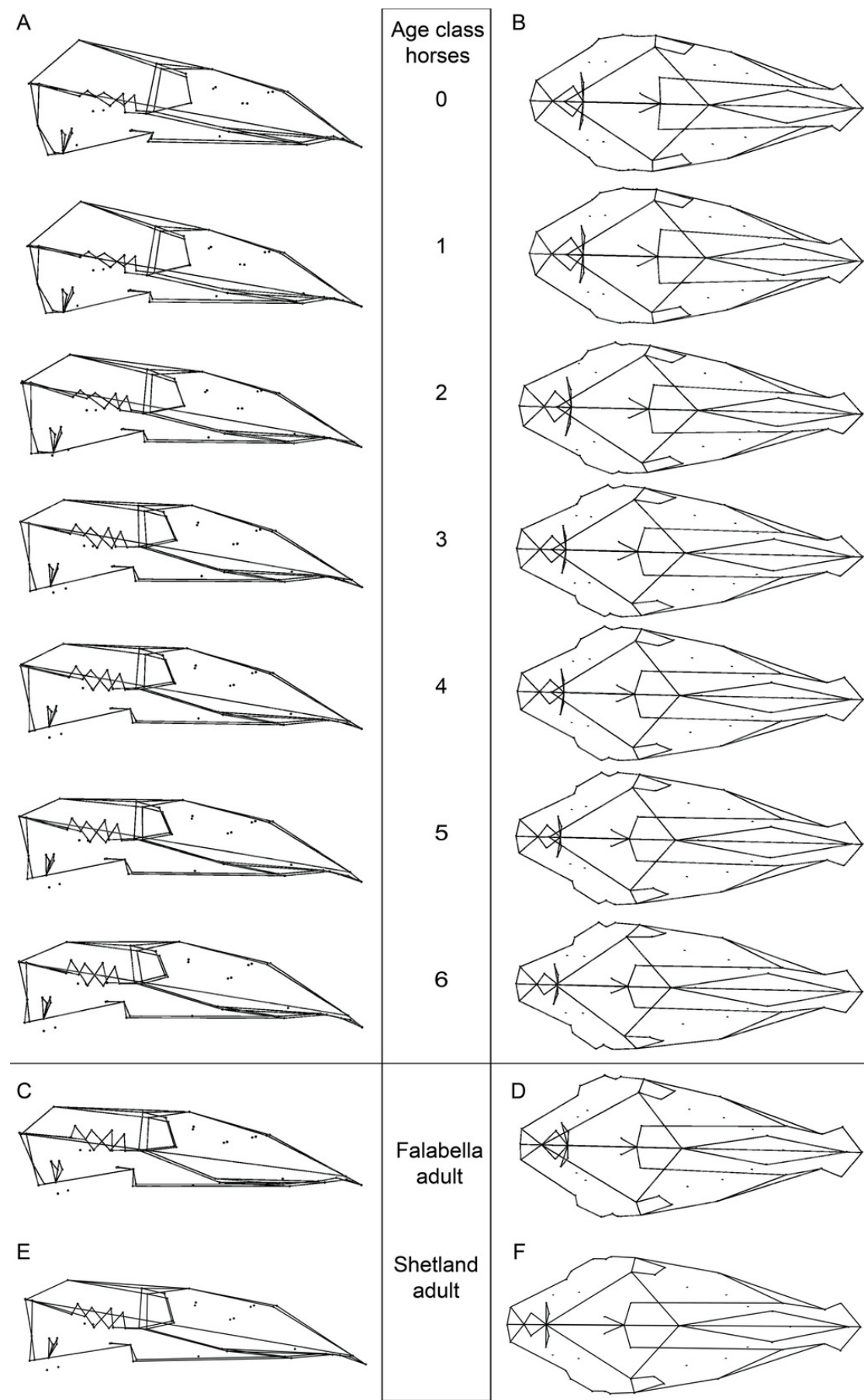
Figure 3

Figure 3. Principal component analysis of 194 specimens of 25 horse and 13 pony breeds, including two miniature breeds.

A) PC1-PC2 scatterplot shows ontogenetic trajectory for all analysed breeds (see Table S1 for details). Miniature breeds, breeds of extreme small size are highlighted with diamond and star shapes. Colours represent age classes. B) PC1-PC2 scatterplot as A) but the three groups – horses (filled black circles), ponies (filled grey diamonds) and miniature breeds (open triangle for Shetland and star for Falabella) are highlighted. C) Dorsal and D) lateral views of the cranium show the shape changes along PC1, adult shape in grey and juvenile shape in black. TPS-grids can be found in Fig S3.
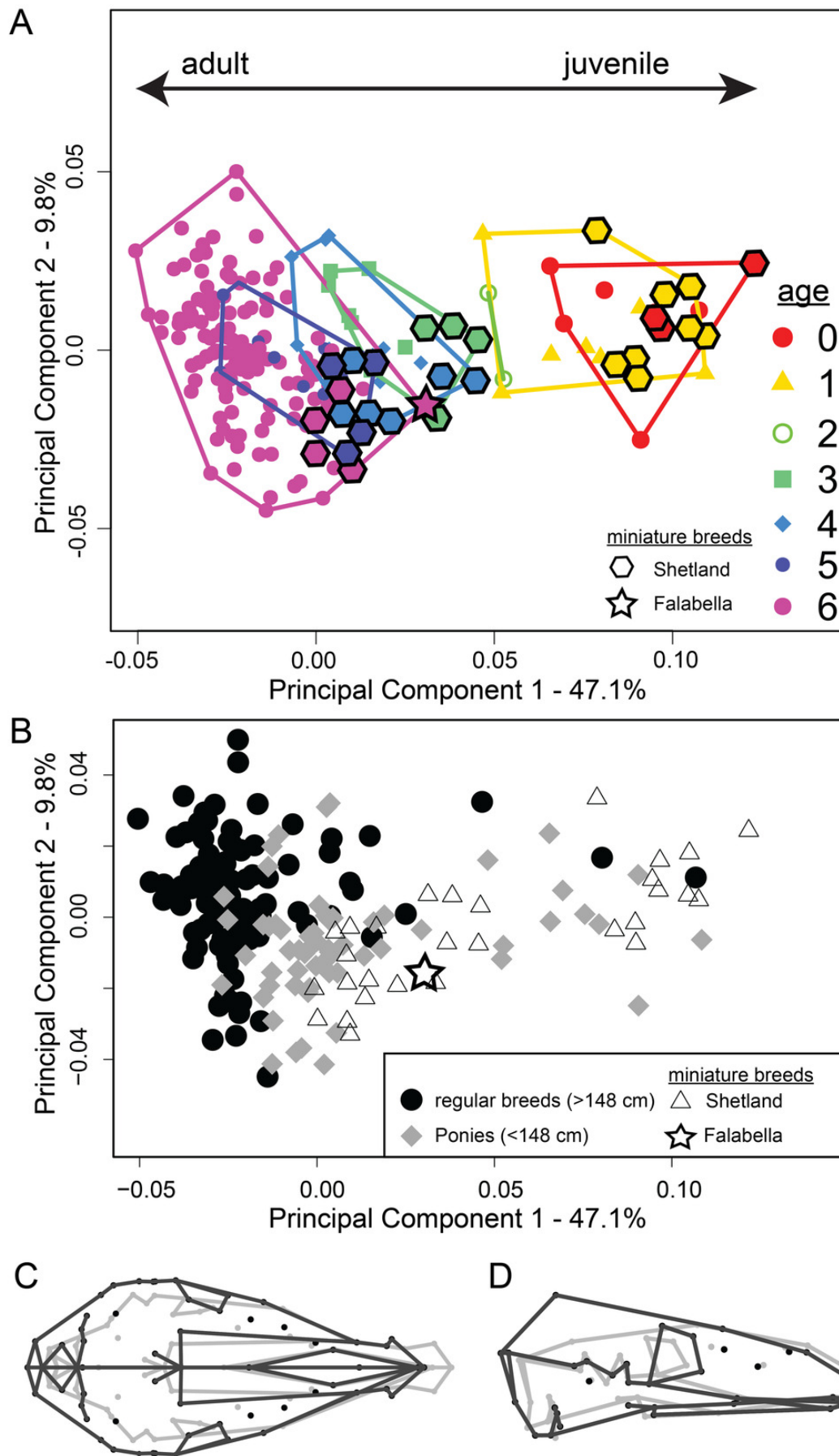
Figure 4

Figure 4. Allometric trend in pony and horse skull shapes.

(A) Regression of shape on log centroid size and (B) predicted shape values from regression of shape on log centroid size. Ponies are shown in stars, horses in open squares. The position of adult Falabella skull is highlighted. Colours correspond to age classes.

A

regular breeds (> 148 cm)
ponies (incl. miniature breeds)
Falabella

age
0
1
2
3
4
5

Regression score

log (centroid size)

B

Predicted skull shape

log (centroid size)
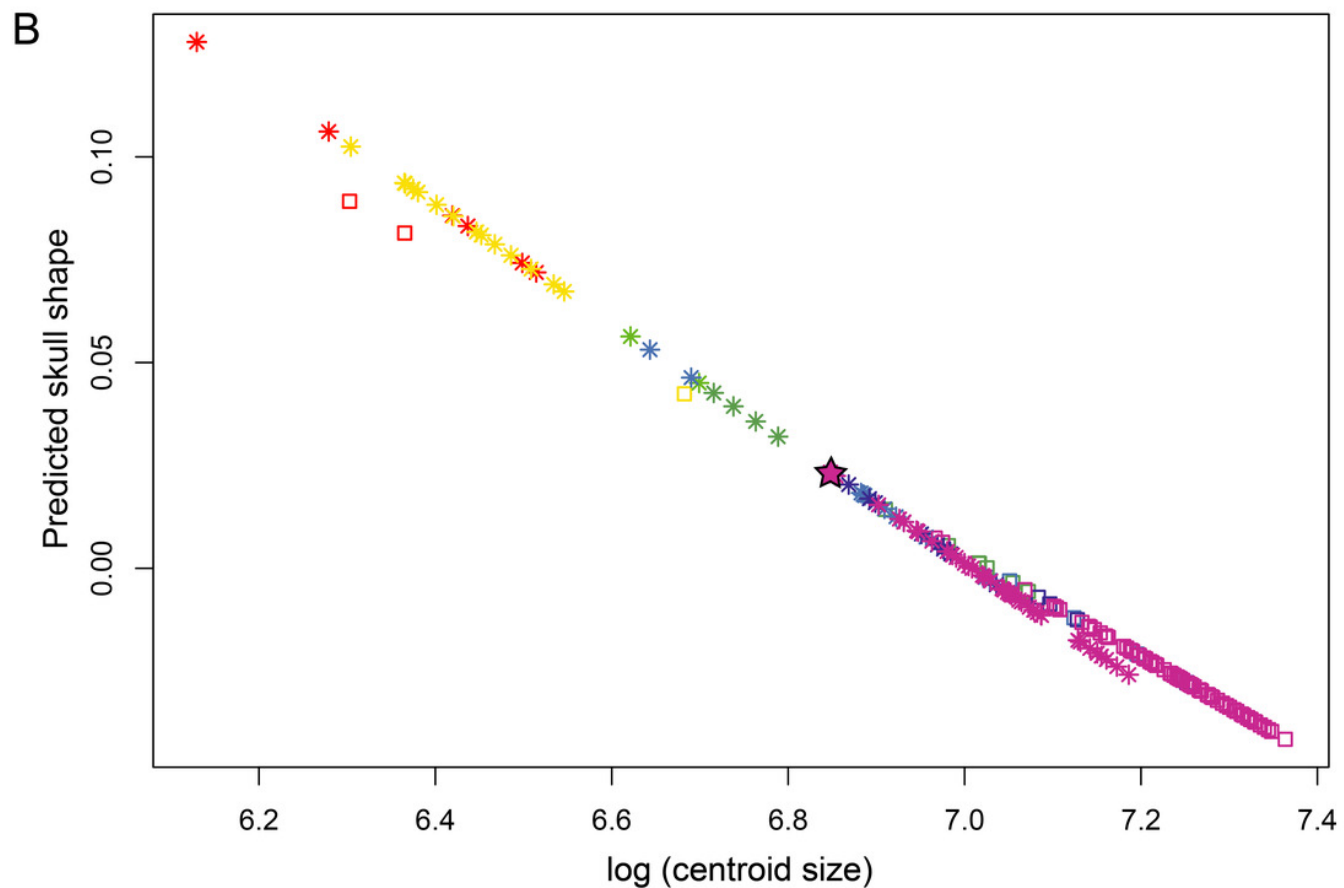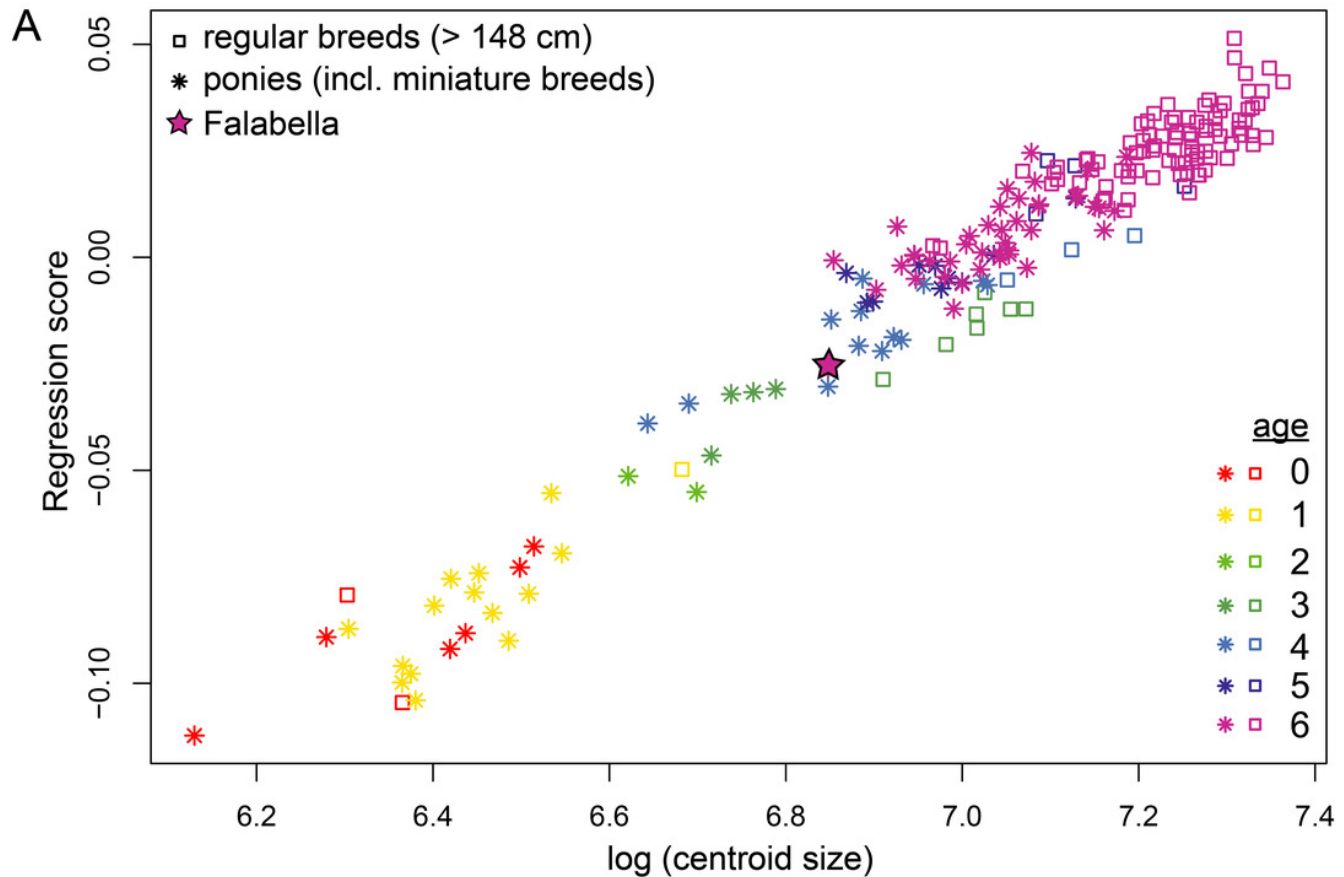
Figure 5

Figure 5. Testing for "paedomorphic" features.

(A-C) Orbit to cranial length ratio, basciranium to palate length ratio, and angle between basicranium and palate, per age category, all breeds except for miniature breeds as boxplots in grey, and Shetland (diamonds) and Falabella (star) as miniature breeds superimposed in black. (D) Adult cranial length in relation to maximal wither height with 95% confidence interval (solid line) and prediction interval (dotted line), and regression line (red). Regression line and 95% prediction curves were extended to smaller wither heights to accommodate the cranial length of the miniature breeds in the same plot. (E) Adult cranial length to wither height ratios were plotted against breed in ascending order from the smallest breed, the Falabella, to the largest breed, the Shire horse. Abbreviations for the breeds: fab: Falabella; she: Shetland; exm: Exmoor pony; wel: Welsch, mon: Mongolian; kon: Konik; bos: Bosnian pony; huz: Huzule; scp: Scottish pony; ice: Icelandic Horse; hny: Hackney; arb: Arab; grp: German Riding pony; grb: Grisons; lpz: Lipizzan; piz: Pinzgau; nor: Norik; ano:Anglo-Norman; thb: English Thoroughbred; hun: Hungarian; trk: Trakehner; han: Hannoverian, odb: Oldenburgian; suf: Suffolk; kdr: Kladrubian; blg: Belgian Draft; hol: Holstein; cds: Clydesdale; shi: Shire; for the ten breeds that were included in 3D GM but not linear analyses, no information on average wither height could be found.