Skeletal variation in bird domestication: limb proportions and sternum in chicken, with comparisons to mallard ducks and Muscovy ducks

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Abstract

Background. Domestication, including selective breeding, can lead to morphological changes of biomechanical relevance. In birds, limbs proportion and sternum characteristics are of great importance and have been studied in the past for its relation with flight, terrestrial loccomotion and animal welfare. In this work we studied the effects of domestication and breed formation in limb proportions in chicken, mallard ducks and Muscovy ducks.

Methods. Here we analysed the scaling of limb proportions. First, we quantified the proportional length of three long bones of forelimb (humerus, radius and carpometacarpus) and hind limb (femur, tibiotarsus and tarsometatarsus) of red jungle fowl and its domestic counterpart, chickens (*Gallus gallus*), and of analogous comparisons for mallard duck (*Anas plathyrhynchos*) and

30   Muscovy duck (*Cairina moschata*). We compared sternum characteristics in red jungle fowl and

31   9 chicken breeds.

32   **Results.** We found a lack of significant change in the proportions of long bones of chicken and

33   Muscovy duck due to domestication, but significant differences in the case of mallard ducks.

34   Variation of evolvability, allometric scaling, and heterochrony may serve to describe some of the

35   patterns of change we report. Flight capacity loss in malard ducks resulting from domestication

36   may have a relation with the difference in proportions. The lack of variation in proportions that

37   could distinguish domestic from wild forms of chicken and Muscovy ducks may reflect less

38   intensive selection for flight capacity. In chicken, some of the differences identified in the traits

39   discussed are breed-dependent. The study of the sternum revealed a higher frequency of notched

40   carina sterni in the red junglefowl compared to domestic chicken. The condition of crooked keel,

41   however, is not unique to chicken. Despite some similar morphological changes identified across

42   species, this study highlights the lack of universal patterns in domestication and breed formation.

Introduction

45   Through domestication, much morphological diversity has been generated (Darwin, 1868; Herre

46   & Röhrs, 1990). Domesticated animals exhibit phenotypic changes compared to their wild

47   counterparts (Clutton-Brock, 1999). This is the case in domestic birds, as in recent works on the

48   skulls of pigeons and chickens (Young, et al., 2017; Stange, et al., 2018) and the integument in

49   chickens (Núñez-León, et al., 2019). In contrast, postcranial anatomy, including limb bones, has

50   rarely been dealt with analytically and globally in domesticated species (see Wayne 1986 for

51   dogs; van Grouw 2018 for an overview for many species), despite having been widely studied in

52   ‑‑   bird evolutionary biology (Middleton & Gatesy, 2000; Dyke & Nudds, 2009; Nudds, et al.,

53   2013). Mentioned in Darwin's 1868 'Variation in Animals and Plants Under Domestication',

54   changes in limb length (or lack thereof) in domestic birds can be observed. Especially notable is

55   the reduction of wing length of the mallard duck after domestication (Darwin, 1868).

56   Limb proportions can be of importance in biomechanical processes such as flight ability.

57   Middleton and Gatesy (2000) highlighted the humerus relative proportion in the forelimb, where

58   flightless birds have relatively longer humeri while flight manoeuvrability is being linked to

59   shorter humeri. The selective pressure for flight is thus expected to influence the relative

60   proportion of the different bones in the forelimb (Mason, 1984). Chickens are considered short-

61 distance non-migrant flyers, however their flight capability is breed-dependent (Schippers, et al.,

62 2013). Although certain breeds are known to have completely lost their flight capacity (e.g.

63 Ukokkei and Polish breeds) this is largely attributed to the unfitness of their plumage for such

64 task (Ekarius, 2007; Smith, 2018). Other breeds are short-distance flyers, including the wild type

65 red junglefowl (RJF), but differences in flight capacity have been reported depending on the

66 weight of the breed: the heavier, the less prone to sustained flight (Darwin, 1868; Schippers, et

67 al., 2013).

68 It is generally agreed that domestic mallard ducks have lost their flight capacity when compared

69 to their wild counterpart, which in contrast to chickens, are long distance migratory birds

70 (Accordi & Barcellos, 2006). This change has been attributed to a gain in weight and reduction

71 in the proportional wing length (Darwin, 1868; Cnotka, 2006). Because domestic Muscovy

72 ducks can fly (Anon., 2016; Anon., 2017), their feathers are trimmed or clipped to discourage

73 flight in breeding farm (Smith, 2007). Unlike the case of differences in wing length between

74 domestic and wild mallards, finding osteological differences between domestic and wild

75 Muscovy ducks has proven more difficult (Angulo, 1998; Stahl, et al., 2006).

76 Another skeletal element of biomechanical importance in birds is the sternum, the site of

77 attachment of the pectoralis muscle, important for producing mechanical work during

78 downstroke and pronating the wing, and the supracoracoideus muscle, which elevates and

79 supinates the wing during upstroke (Biewener, 2011). This element varies in shape and

80 proportions and is a source of intensive study in poultry research concerned with welfare due to

81 widespread reports of damage ranging between 30 and 100% of commercial hens (Fleming, et

82 al., 2004; Harlander-Matauschek, et al., 2015; Toscano, et al., 2020). Keel damage may include

83 crookedness or bending, as well as fractures (Casey-Trott, et al., 2015). The problem appears

84 somewhat historical as it was referred to by Darwin (1868, p. 282) as 'generally so much

85 deformed that it is scarcely possible to compare its form strictly in the several breeds'. The

86 crookedness of the keel has been largely studied in the context of its causes, its relation with

87 animal welfare, and its effect on productivity (Blount, 1933; Warren, 1937; Waters, 1949;

88 Fleming, et al., 2004) and the market value of the domestic chicken (Hyre, 1995). Keel

89 crookedness has been reported to have environmental and genetic origins, appearing mostly

90 when chickens are given the opportunity to perch (Blount, 1933; Warren, 1937; Waters, 1949).

91 However, whether crookedness of the keel is associated with domestication in its initial, less

92   intense phase (Vigne, 2011), or if it appeared only with breed formation and improvement has

93   not been determined. Deformations of the keel can be divided into two types: fractures, defined

94   as sharp bends, fragmented sections or shearing of the keel; and deviations, defined as

95   abnormally shaped bone containing section(s) that vary from an ideally perfect two-dimensional

96   straight plane that has not resulted from fracture (Casey-Trott, et al., 2015). Here we use the term

97   'crookedness' to denote exclusively the deviations, not fractures, of the keel, as defined in

98   Casey-Trott et al. (2015).

99   In this study, we analysed the limb proportions of three domestic species: chicken (*Gallus*

100   *gallus*), mallard duck (*Anas plathyrhynchos*) and Muscovy duck (*Cairina moschata*) in order to

101   determine whether there has been changes due to domestication and breed formation. We

102   examined this matter in the context of evolvability, allometry, heterochrony, and selective

103   pressures (artificial selection) that affect flight capacity. In the case of chickens, we examined

104   these changes also among a diversity of breeds. Further, we investigated variation in the sternum

105   by coding discrete features that characterize its variation between fowl and chicken in order to

106   study differences among breeds. Specifically, we examined the crookedness of the keel,

107   extensively studied in the past but never comparing breeds (Blount, 1933; Warren, 1937; Waters,

108   1949; Hyre, 1995; Fleming, et al., 2004; Kittelsen, et al., 2020), plus three other features:

109   presence of a notch on the ventral margin of the carina sterni, sponginess or smoothness of the

110   foramen pneumaticum and pars cardiaca and shape of the caudal end of the trabecula mediana.

111

Materials & Methods

113   **Measurements.** We took measurements of the length of the humerus, radius and

114   carpometacarpus of the forelimb and length of the femur, tibiotarsus and tarsometatarsus and of

115   the hind limb. For each bone, we measured the length as the maximum length of the bone

116   parallel to the measuring device (using digital calipers to the nearest tenth of a mm), coinciding

117   with the anatomical structures shown in *Fig.1*.

118   We considered the proportion of a bone to be the proportion of that bone with respect to the total

119   length of the limb. The total length of the forelimb was taken as the sum of the lengths of the

120   carpometacarpus, radius and humerus, while the total length of the hind limb was taken as the

121   sum of the lengths of the tarsometatarsus, tibiotarsus and femur (*Fig.2*).

122   **Specimens.** We compared proportions between the wild and domestic forms of different bird

123   species: *Gallus gallus*, *Anas platyrhynchos* and *Cairina moschata* (*Table 1*). We chose these

124   three species for their historical importance in bird domestication and wide availability in

125   osteological collections where the labelling as wild and domestic forms is reliable. We only

126   considered adult skeletally mature specimens for this work, with individuals considered adults

127   when the epiphyses of all long bones were externally completely fused to the diaphyses.

128   As the wild forebearer of the chicken we used the RJF (Al-Nasser, et al., 2007; Lawal, et al.,

129   2020) although there has been introgression of grey junglefowl. (Eriksson, et al., 2008; Lawal, et

130   al., 2020). For the mallard duck and the Muscovy duck, we have used their wild counterparts

131   available in the visited museum osteological collections.

132   In *Gallus gallus*, we measured 29 RJFs and 103 domestic chickens for the forelimb and 28 RJFs

133   and 99 chickens for the hind limb (*Table 2*). We excluded the modern meat lines (broilers) due to

134   their short life span, resulting in an insufficient osteological maturation to be considered valid as

135   adult specimens with the criterion used in this work, since the epiphyses of their long bones are

136   not completely fused to the diaphyses (Zuidhof, et al., 2014; Bennett, et al., 2018). In *Anas*

137   *platyrhynchos*, 56 wild and 32 domestic specimens were measured. Of the 32 domestic mallards,

138   seven were from known breeds (four Aylesbury, two Black Labrador or Buenos Aires Drake and

139   one Khaki Campbell). Given the low number of labelled breeds, we only made the distinction

140   between wild and domestic mallards. In *Cairina moschata*, 39 wild and 17 domestic specimens

141   were measured.

142   The specimens used for this study are housed in the Paläontologisches Institut und Museum,

143   Universität Zürich (Switzerland), Naturmuseum Senckenberg (Germany), Staatssammlung für

144   Anthropologie und Paläoanatomie München (Germany), Zoologisches

145   Institut/Populationsgenetik (former Institut für Haustierkunde), Christian-Albrechts-Universität

146   zu Kiel (Germany), Natural History Museum at Tring, Bird Collection, General and Darwin

147   collection (United Kingdom).

148   **Analyses.** We performed independent two-tailed student's t-tests to check for differences in the

149   limb bones proportions in their respective limb between wild and domestic forms for all species.

150   Further, we performed independent two-tailed student's t-tests to check for differences in limb

151   length, as a proxy for body size, between domestic and wild forms of the three species in this

152   study (*Fig.3*). In the case of *Gallus gallus*, we also tested if there are significant differences in

153   the proportions among breeds (*Table 3*). For this, we used only domestic breeds with sample size

154   greater than four, namely Araucana, bantam, Chabo, cochin, Ukokkei, 'Italiener', Kömpfer,

155   Shamo and Polish as well as the RJF. Due to violation of assumptions of normality and

156   homoscedasticity (*Table S1* and *Table S2* in supplementary materials), we performed non-

157   parametric Kruskal-Wallis tests.

158   In order to determine the explanatory power of body size on long bone proportions in *Gallus*

159   *gallus, Anas plathyrhynchos*, and *Cairina moschata*, we performed linear regressions using hind

160   limb and forelimb total length as a proxy of body size, respectively. We contrasted the log-

161   transformed values of each bone with the log-transformed values of the total length of the

162   correspondent limb. Total limb length is the best approximation available, since the age of the

163   used specimen might be variable, even though all were skeletally mature, and using the mean

164   breed weight or size could be more problematic. To determine if the regression slopes were equal

165   to 1 (null hypothesis of isometry), we determined if the 95% confidence intervals of the slopes

166   included 1.0. We assumed positive or negative allometry to best explain a given scaling

167   relationship if the confidence interval of the regression did not include 1, with a slope of > 1.0 or

168   < 1.0, respectively. Similar as for the adult sample described here, we extracted data about limb

169   bone dimensions of chicken embryos and juveniles from the literature and determined allometric

170   growth patterns as described for the adult sample. In order to illustrate the distribution of

171   proportions of the hind limb bones in the morphospace of *Gallus gallus* during pre-hatching

172   development, data were taken from Thomas, (2014) and Faux and Field (2017) and we

173   performed the same analyses as for the regression slopes of the three species previously

174   mentioned. The results are displayed in *Fig.4* and *Table 4*.

175   In the following summary of feature variations, we account for five characters of the sternum of

176   *Gallus gallus* across nine different domestic breeds and the RJF as their wild counterpart.

177   Sternum characters were coded in 63 *Gallus gallus* specimens from which 12 were RJF and the

178   rest belonged to domestic breeds.

179   **Description of character states.**

180   •   Carina sterni is defined as 'straight' when the direction of growth is maintained in a

181   straight line, as opposed to 'crooked', in which the growth is tortuous with one or multiple

182   pronounced torsions (*Fig.5a*).

183 • Carina sterni is defined as 'notched' when the direction of the lower margin of the carina

184 in lateral view changes direction, creating a notch. It is defined as 'non notched' if this does not

185 happen (*Fig.5b*).

186 • Pars cardiaca (PC) and Foramen pneumaticum (FP) are described as 'spongy' or

187 'smooth' depending on the type of external appearance, either porous or flat respectively

188 (*Fig.5c*).

189 • The caudal end of the trabecula mediana of the sternum is differentiated between

190 'fanned' (end wider than the rest of the trabecula in dorsal view) and 'straight' (end as wide as

191 the rest of the trabecula in dorsal view; *Fig.5d*).

192

193 **Results**

194 The two-tailed, independent t-test for the proportion of long bones of the forelimbs and hind

195 limbs performed comparing wild versus domestic in three species: *Gallus gallus*, *Anas*

196 *plathyrhynchos* and *Cairina moschata* show that significant differences in limb proportions only

197 occur in *Anas plathyrhynchos* (*Table2*). Domestic mallard ducks, compared to their wild

198 counterpart, have proportionally longer humeri and shorter radii and carpometacarpi in the case

199 of the wing, and proportionally longer tarsometatarsi and shorter femurs in the case of the hind

200 limb (*Fig.6*).

201 The Kruskal-Wallis test comparing limb proportions among chicken breeds revealed significant

202 differences in the selected breeds (*Table 3*). The detailed pairwise comparison is shown in *Fig.7*

203 and the supplementary materials for breeds with sample size equal or greater than five (*Table*

204 *S3*).

205 A brief comparison of the total forelimb length, showing the substantial size variation, in

206 different breeds of *Gallus gallus* is provided in *Table 5*. The lengths of the long bones are

207 strongly and significantly correlated with the total size of the corresponding limb as a proxy for

208 body size in chicken, mallard ducks, and Muscovy ducks (*Fig.8, Table 6)*. Pairwise comparisons

209 of total limb length between wild and domestic forms in each species, as a proxy for body size,

210 show that the domestic varieties are larger than the wild ones in *Gallus gallus* and *Anas*

211 *plathyrhynchos* but no significant differences were observed in *Cairina moschata* (*Fig.3*). Our

212 observations on the characters of the sternum are summed up in *Table 7*.

213

Discussion

214

215 Given the previous studies on differences between wild and domestic animals and the

216 importance in locomotion of forelimb and hind limb proportions and sternum characteristics, we

217 aimed to determine whether differences exist between wild and domestic forms of three bird

218 species and to shed light on the possible underlying mechanisms.

219 We observed no evidence of significant differences between wild and domestic forms of *Gallus*

220 *gallus* in the proportional length of the long bones of the forelimbs (humerus, radius and

221 carpometacarpus) and hind limbs (femur, tibiotarsus and tarsometatarsus; *Table 1*). However,

222 when the RJF and breeds of domestic chicken were analysed as individual groups, significant

223 differences were detected (*Fig.7, Table S3*). One possible interpretation is for diversification to

224 have taken multiple directions in the case of the limb proportions in domestic birds, but selection

225 has not provoked a unique directionality, maintaining the same mean proportions between

226 domestic and wild forms in all bones. The most notable case of breed-specific specialisation is

227 the Chabo, also known as Japanese bantam. Chabo is a true bantam breed (i.e. it does not present

228 a large variant) with characteristically short legs (Roberts, 2008). The short leg trait is associated

229 with a dominant allele of gene *Cp*, which is lethal in homozygosis (Shibuya, et al., 1972;

230 Shibuya & Kuroda, 1973) and is selected as a distinct characteristic of the breed (Van Grouw,

231 2018). The *Cp* gene accelerates differentiation of chondrocytes accompanied by suppression of

232 their proliferation, leading to stunted limb long bone growth (Shibuya, et al., 1972). Similar

233 phenotypes are also known in domestic dogs (e.g. Dachshund, Corgi) and cats, and represent

234 cases of specialisation in breed formation (Rimbault & Ostrander, 2012).

235 Our results further show that proportions of the bones in *Anas plathyrhynchos* vary significantly

236 when comparing wild and domestic forms (*Table 1*; *Fig.6*). Unlike wild and domestic *Gallus*

237 *gallus*, domestic forms of the mallard duck thus show a set of proportions in the long bones that

238 is significantly different from the wild form. Since body size differences were marked between

239 the wild and domestic forms of the three investigated species, with the domestic forms being on

240 average larger than their wild relatives in *Gallus gallus* and *Anas playrhinchos* (*Fig.3*), we

241 compared the log-transformed length of the long bones with the log-transformed total length of

242 the limb as a proxy for body size to investigate the influence of allometric scaling on limb size

243 proportions (*Fig.8, Table 6*). Limb proportions were found to scale with size in an inconsistent

244 way in the different species (*Table 6*). The observed difference of limb proportions in wild and

245   domestic mallards (*Table 1*; *Fig.6*) could thus be interpreted as the result of allometric scaling

246   due to particularly pronounced size differences in the wild vs. the domestic sample (*Fig.3*).

247   Specifically, in the case of the mallard's forelimb, the humerus scales positively allometrically,

248   the radius isometrically, and the carpometacarpus negatively allometrically, leading to

249   proportionally longer humeri and shorter radii in larger specimens (*Fig.2, Fig.8, Table 6*).

250   Although no ontogenetic study is available for mallard ducks so far as a comparison, this same

251   tendency for allometric scaling of the limb bones can be extracted from the data available in the

252   literature regarding embryological growth of *Gallus gallus* (Faux & Field, 2017) and ontogenetic

253   development after hatching (Thomas, et al., 2016; Jackson & Diamond, 1996) (*Fig.4A* and

254   *Fig.4B*). As the body size of the embryo and hatched birds increases, their limb proportions

255   change in a similar tendency (except tibiotarsus and tarsometatarsus in post-hatching growth,

256   *Fig.4*, *Table 4*) as we observe in differently sized adult chickens (*Fig.8a,b, Table 6*). This can

257   also be observed for wing growth in *Larus californicus*, which shows a progressive decrease in

258   the humerus length relative to the radius and carpometacarpus (Middleton & Gatesy, 2000). This

259   suggests that the differences in proportions of the limbs among adult chickens might be at least

260   partially related to allometric scaling during development and growth. Differences in limb

261   proportions among breeds could thus be related to different sizes of breeds.

262   As differences in limb proportions between the wild and the domestic groups are not apparent in

263   chicken and Muscovy ducks (*Fig.6*, *Table 1*), although allometric scaling of limb bones was

264   observed (*Fig.8, Table 6*), a lack of pronounced size differences (*Fig.3*) between wild and

265   domestic could explain the lack of proportional differences.

266   The literature shows implications of different allometries in limbs. An apparent inverse

267   correlation of the proportion of the humerus in the wing with aerial maneuverability in birds has

268   been proposed in the past (Middleton & Gatesy, 2000). Moreover, flightlessness is reportedly

269   linked to a proportionally long humerus compared to the rest of the long bones of the wing in

270   theropods (Middleton & Gatesy, 2000) and steamer ducks (Tachyeres) (Livezey & Humphrey,

271   1986).

272   Experiments on the domestication of the wild mallard resulted in bigger body sizes and rapid

273   loss (after three generations) of the ability to fly (Darwin, 1868). Mason (1984) proposed that

274   this loss of flight capacity might be due to the loss of positive selection for flying ability: under

275   the care of humans, mallards are usually granted access to a reliable source of food at a specific

276   location, thus flight becomes less essential for survival. An alternative explanation could be that

277   the selection of the species for specific traits could have pleiotropic effects that lead to a

278   reduction of flight capacity. These hypotheses remain to be tested in future work. The loss of the

279   capacity to fly may be related to the proportion of the limbs, which upon less selection due to

280   lack of necessity to fly may have become significantly different from their wild counterpart

281   (*Table S2*). Other skeletal, muscular and perhaps neurological changes may also be related to the

282   loss of flight capacity. In the case of the hind limb, we observed in domestic forms of the mallard

283   duck a relative shortening of the femur and elongation of the tarsometatarsus. Gatesy and

284   Middleton (1997) reported an apparent gradient of cursoriality increasing with tarsometatarsal

285   proportion among theropod species with similar Tibiotarsus/Femur ratios. The pattern we

286   observe in the domestic mallard duck, together with a decrease in flight adaptations (above), is

287   consistent with a more terrestrial, although not necessarily highly cursorial, lifestyle of the

288   domesticated vs. the wild form.

289   Changes in limb proportions are not observed in *Cairina moschata*. Its proportions remain

290   indistinguishable from the wild form, as opposed to *Anas plathyrhynchos* (*Table 1*). Changes in

291   flight habits might not have been similar between the wild and domestic forms of mallard ducks

292   and Muscovy ducks. While some populations of wild mallard ducks are migratory (Bellerose &

293   Crompton, 1970), domestic mallards rarely fly as much and many breeds lack flight capacity

294   entirely (Smith, et al., 1989). Muscovy ducks, on the other hand, although non-migratory birds

295   (Accordi & Barcellos, 2006), have been reported to fly frequently (Anon., 2016; Anon., 2017).

296   This suggesting that their flight habits might not have changed so markedly as to produce a

297   different morphology. Alternatively, and related to the allometric scaling relationships

298   considered above, it is noteworthy that in contrast to the other two species, limb bones of the

299   forelimb were found to consistently scale isometrically in the Muscovy duck, suggesting

300   restricted evolvability concerning forelimb proportions in this species. An analogous conclusion

301   was reached when postulating lower evolvability in cats versus dogs when reporting largely

302   isometric versus allometric in the skulls, respectively (Sánchez-Villagra, et al., 2017).

303   The variations on the sternum of *Gallus gallus* (*Table 7*) show that the RJF generally possesses a

304   notched carina sterni, a smooth surface of the pars cardiaca and foramen pneumaticum and a

305   fanned caudal end of the trabecula mediana. The RJF develops a crooked keel in half of our

306   observed specimens (*Table 7*). The crookedness of the keel has been shown to be hereditary and

307   influenced by early roosting conditions (Blount, 1933; Warren, 1937; Waters, 1949). Our

308   observations reveal that this is not a feature unique to domestic varieties, as has been previously

309   reported (Kittelsen, et al., 2020).

310   Most domestic variants exhibit straight carina sterni, with the notable exception of the Chabo and

311   Ukokkei breeds. One possible explanation might be that the shortness of the legs in the Chabo

312   and the inability to fly of the Ukokkei are responsible for a more direct contact with higher

313   pressure on the keel with the perching structure of their environments, as it has been shown to be

314   a determinant factor for its appearance (Blount, 1933; Warren, 1937; Waters, 1949; Pickel, et al.,

315   2011; Casey-Trott, et al., 2015). Behaviour, especially flying and perching, could be an

316   important factor distinguishing breeds but could not be assessed in this study.

317   The notch in the carina sterni seems to be a rare condition in domestic breeds, while it is the most

318   common condition in the wild form, contrary to the other features observed with a more general

319   distribution. The sponginess of the pars cardiaca and foramen pneumaticum is a rare condition in

320   most breeds except for the case of the Araucana breed. Most breeds show a fanned end of the

321   sternum as is the case of the wild form. In summary, these results reveal that the crookedness of

322   the keel is not unique to domestic forms and, while the prevalence of the notch in the carina

323   sterni can be distinguishing between the wild and domestic forms, the variation of the different

324   characters are not segregated among the breeds.

325

326   Conclusions

327   This study shows how the allometric growth of *Gallus gallus* can help us understand the

328   variation in limb proportions of differently sized breeds. Furthermore, we show that significant

329   differences in the proportions of limb bones of wild and domestic *Anas plathyrhynchos* exist,

330   whereas no significant differences between wild and domestic forms of *Gallus gallus* and

331   *Cairina moschata* were found. We offer possible explanations for these differences such as an

332   extension of the allometric growth of domestic Mallard ducks, loss of positive selection for

333   flying ability, and/or pleiotropic effects or evolvability constraints, which could inspire future

334   research. Furthermore, we observed that the condition of crooked keel is not unique to domestic

335   forms of *Gallus gallus* and a higher number of cases of notched carina sterni can be found in

336   RJF. These findings add new observations to the study of keel characteristics that can be added

337   to the body of knowledge of domestication and poultry welfare.

338

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352

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Results of two-tailed, independent t-test for the lengths of long bones of the forelimbs and hind limbs of domestic and wild forms of *Gallus gallus*, *Anas plathyrhynchos* and *Cairina moschata.*

*: the number of degrees of freedom is approximated by the Welch-Satterthwaite formula.

Bold: null hypothesis of equality of means rejected. Df = degrees of freedom.

Species	Bone	Df	T	p-value
Gallus gallus	Humerus	70.893*	-0.746	0.4584
	Radius	140	1.674	0.0963
	Carpometacarpus	140	-1.603	0.1112
	Femur	133	1.477	0.1420
	Tibiotarsus	135	-1.111	0.2685
	Tarsometatarsus	135	-0.982	0.3279
Anas plathyrhynchos	Humerus	86	5.212	**< 0.0001**
	Radius	45.049*	-2.520	**0.0154**
	Carpometacarpus	43.519*	-3.166	**0.0028**
	Femur	86	-1.989	**0.0498**
	Tibiotarsus	45.171*	-1.001	0.3222
	Tarsometatarsus	86	3.042	**0.0031**
Cairina mostacha	Humerus	54	-0.199	0.8430
	Radius	54	1.390	0.1701
	Carpometacarpus	54	-0.899	0.3728
	Femur	54	0.730	0.4684
	Tibiotarsus	54	-0.408	0.6849
	Tarsometatarsus	54	-0.271	0.7873

Breeds of chicken (*Gallus gallus)* and number of specimens measured in this study.

balanced

Breed	$N_{Forelimb}$	$N_{Hind\ limb}$	Breed	$N_{Forelimb}$	$N_{Hind\ limb}$
RJF	29	28	Pennsylvania Naked Neck	2	2
'African cock'	1	1	Rhode Island	1	0
Appenzeller Barthuhn	3	3	Rumpless fowl	1	1
Appenzeller Spitzhaubenhuhn	5	5	Seidenhuhn	5	5
Araucana	13	13	Shamo	8	8
Bantam	7	8	Silver pencil hamburgh hen	1	0
Brahmahuhn	1	1	Polish	5	5
Burmese Bantam	1	1	Spanish cock	2	2
Chabo	16	16	Sultan	2	1
Cochin	6	6	Tail-Less Bantam	1	1
Dorking cock	1	1	Ukokkei	10	10
Game	1	1	Welsumer	3	2
Gold spangle Polish	1	1	White crested rumpless Turkish fowl	1	1
Golden pencil hamburgh	1	1	White dorkinghen	1	1
Italiener	2	2	White Leghorn	4	4
Kulm	1	1	Zwergwelsumer	2	2
Light sussex	3	2			

Results of Kruskal-Wallis tests for comparison among breeds of *Gallus gallus*.

Kruskal-Wallis rank sum test				
Limb	**Bone**	**Chi-squared**	**df**	**p-value**
Forelimb	Humerus	47	7	6.84E-08
	Radius	37	7	5.58E-06
	Carpometacarpus	16	7	0.02805
Hind limb	Femur	37	7	4.64E-06
	Tibiotarsus	23	7	0.001848
	Tarsometatarsus	33	7	2.63E-05

Results of linear regressions of long bone lengths vs. total limb length of embryological development (data taken from Faux and Field, 2017) and ontogeny (data taken from Thomas, 2014).

a = regression slope with corresponding 95% confidence interval (ci); scaling pattern = interpretation of isometry (ci including 1, a=1), negative allometry (ci not including 1, a<1)), or positive allometry (ci not including 1, a>1)); r2 = coefficient of determination; F = F statistic with associated degrees of freedom (df); p = p-value.

Study	Bone	a (ci)	Scaling pattern	r^2	F (df)	p
Faux and Field (2017)	Femur	0.963 (0.928, 0.998)	Negative allometry	0.9628	$3.242*10^3$ (1, 23)	$<2.2* 10^{-16}$
	Tibiotarsus	1.005 (0.958, 1.051)	Isometry	0.9886	$1.993*10^3$ (1, 23)	$<2.2* 10^{-16}$
	Tarsometatarsus	1.033 (1.001, 1.065)	Positive allometry	0.9948	$4,403*10^3$ (1, 23)	$<2.2* 10^{-16}$
Thomas (2014)	Femur	0.930 (0.909, 0.952)	Negative allometry	0.9943	$7.549*10^3$ (1, 43)	$<2.2* 10^{-16}$
	Tibiotarsus	1.040 (1.027, 1.053)	Positive allometry	0.9983	$2.5*10^4$ (1,43)	$<2.2* 10^{-16}$
	Tarsometatarsus	1.016 (0.994, 1.038)	Isometry	0.9951	$8.788*10^3$ (1,43)	$<2.2* 10^{-16}$

Mean length of the forelimb and hind limb of the different chicken breeds in mm.

Measurements belonging to RJF are shown in bold.

	Bantam	Chabo	Red junglefowl	Ukokkei	Polish	White Leghorn	Appenzeller Spitzhaubenhuhn	Araucana	Shamo
Forelimb length (mm)	115,47	123,5719	158,8323	175,508	179,2575	192,5175	197,032	202,0969	231,7588
Hind limb length (mm)	175,915	172,9388	241,4441	263,119	269,7775	297,655	307,306	312,8046	365,585

Results of linear regressions of long bone lengths vs. total limb length in *Gallus gallus*, *Anas plathyrhynchos* and *Cairina moschata*.

a = regression slope with corresponding 95% confidence interval (ci); scaling pattern = interpretation of isometry (ci including 1, a=1), negative allometry (ci not including 1, a<1)), or positive allometry (ci not including 1, a>1)); r2 = coefficient of determination; F = F statistic with associated degrees of freedom (df); p = p-value.

Species	Bone	a (ci)	Scaling pattern	r^2	F (df)	p
Gallus gallus	Humerus	0.937 (0.926, 0.948)	Negative allometry	0.9954	$3.002*10^4$ (1, 140)	$<2.2*10^{-16}$
	Radius	1.069 (1.054, 1.085)	Positive allometry	0.9923	$1.809*10^4$ (1, 140)	$<2.2*10^{-16}$
	Carpometacarpus	1.004 (0.981, 1.027)	Isometry	0.9813	$7.342*10^3$ (1, 140)	$<2.2*10^{-16}$
	Femur	0.896 (0.881, 0.911)	Negative allometry	0.9903	$1.38*10^4$ (1, 135)	$<2.2*10^{-16}$
	Tibiotarsus	1.005 (0.998, 1.013)	Isometry	0.998	$6.822*10^4$ (1, 135)	$<2.2*10^{-16}$
	Tarsometatarsus	1.105 (1.088, 1.122)	Positive allometry	0.9918	$1.636*10^4$ (1, 135)	$<2.2*10^{-16}$
Anas plathyrhynchos	Humerus	1.038 (1.016, 1.061)	Positive allometry	0.9898	$8.336*10^3$ (1, 86)	$<2.2*10^{-16}$
	Radius	0.985 (0.965, 1.006)	Isometry	0.9907	$9.137*10^3$ (1, 86)	$<2.2*10^{-16}$
	Carpometacarpus	0.956 (0.926, 0.986)	Negative allometry	0.9791	$9.903*10^3$ (1, 86)	$<2.2*10^{-16}$
	Femur	0.977 (0.941, 0.996)	Negative allometry	0.9844	$5.423*10^3$ (1, 86)	$<2.2*10^{-16}$
	Tibiotarsus	0.99 (0.973, 1.008)	Isometry	0.9933	$1.268*10^4$ (1, 86)	$<2.2*10^{-16}$
	Tarsometatarsus	1.054 (1.023, 1.085)	Positive allometry	0.9819	$4.677*10^3$ (1, 86)	$<2.2*10^{-16}$
Cairina moschata	Humerus	0.992 (0.971, 1.013)	Isometry	0.9941	$9.336*10^3$ (1, 54)	$<2.2*10^{-16}$
	Radius	0.987 (0.954, 1.021)	Isometry	0.9849	$3.513*10^3$ (1, 54)	$<2.2*10^{-16}$
	Carpometacarpus	1.026 (0.968, 1.083)	Isometry	0.9595	$1.28*10^3$ (1, 54)	$<2.2*10^{-16}$
	Femur	0.988 (0.954, 1.022)	Isometry	0.9846	$3.455*10^3$ (1, 54)	$<2.2*10^{-16}$
	Tibiotarsus	0.97 (0.95, 0.99)	Negative allometry	0.9944	$9.641*10^3$ (1, 54)	$<2.2*10^{-16}$
	Tarsometatarsus	1.068 (1.029, 1.108)	Positive allometry	0.9819	$2.933*10^3$ (1, 54)	$<2.2*10^{-16}$

Table of characters and character states by breed.

Characters and character states: carina sterni (straight or crooked), carina sterni (notched or non-notched), pars cardiaca (PC) and foramen pneumaticum (FP) (spongy or smooth), trabecula mediana: (fanned or straight). Numbers in the table indicate the number of specimens per character state.

Breed	Carina sterni		Carina sterni		PC and FP		Trabecula mediana	
	Crooked	Straight	Notched	Non-notched	Spongy	Smooth	Fanned	Straight
Araucana	1	6	1	6	4	3	3	2
Bantam	0	7	2	5	2	5	7	0
Chabo	8	8	3	13	6	10	11	5
Cochin	1	3	0	4	1	3	1	3
Ukokkei	3	0	1	2	1	2	2	1
Italiener	2	1	0	3	1	2	1	2
Kömpfer	0	1	0	1	0	1	1	0
RJF	6	6	9	3	0	12	10	2
Shamo	2	4	2	4	2	4	2	3
Polish	3	1	1	3	3	1	2	2
TOTAL	26	37	19	44	20	43	40	20

Figure 1

Anatomical structures used to define measurements parallel to the longitudinal axis of the limb bones (indicated with red dots).

Humerus (A): caput humeri (B) and cotylus ventralis (C); Radius (D): cotyla humeralis (E) and facies articularis radiocarpalis (F); Carpometacarpus (G): trochlea carpalis (H) and facies articularis digitalis minor (I); Femur (J): trochanter femoris (K) and condylus lateralis (L); Tibiotarsus (M): crista cnemialis cranialis (N) and epicondylus lateralis (O); Tarsometatarsus (P): crista medialis hypotarsi (Q) and trochlea metatarsi III (R) Shown bones belonging to domestic chicken (*Gallus gallus*, Araucana)

A

B

C

D

E

F

G

H

I

J

K

L

M

N

O

P

Q

R
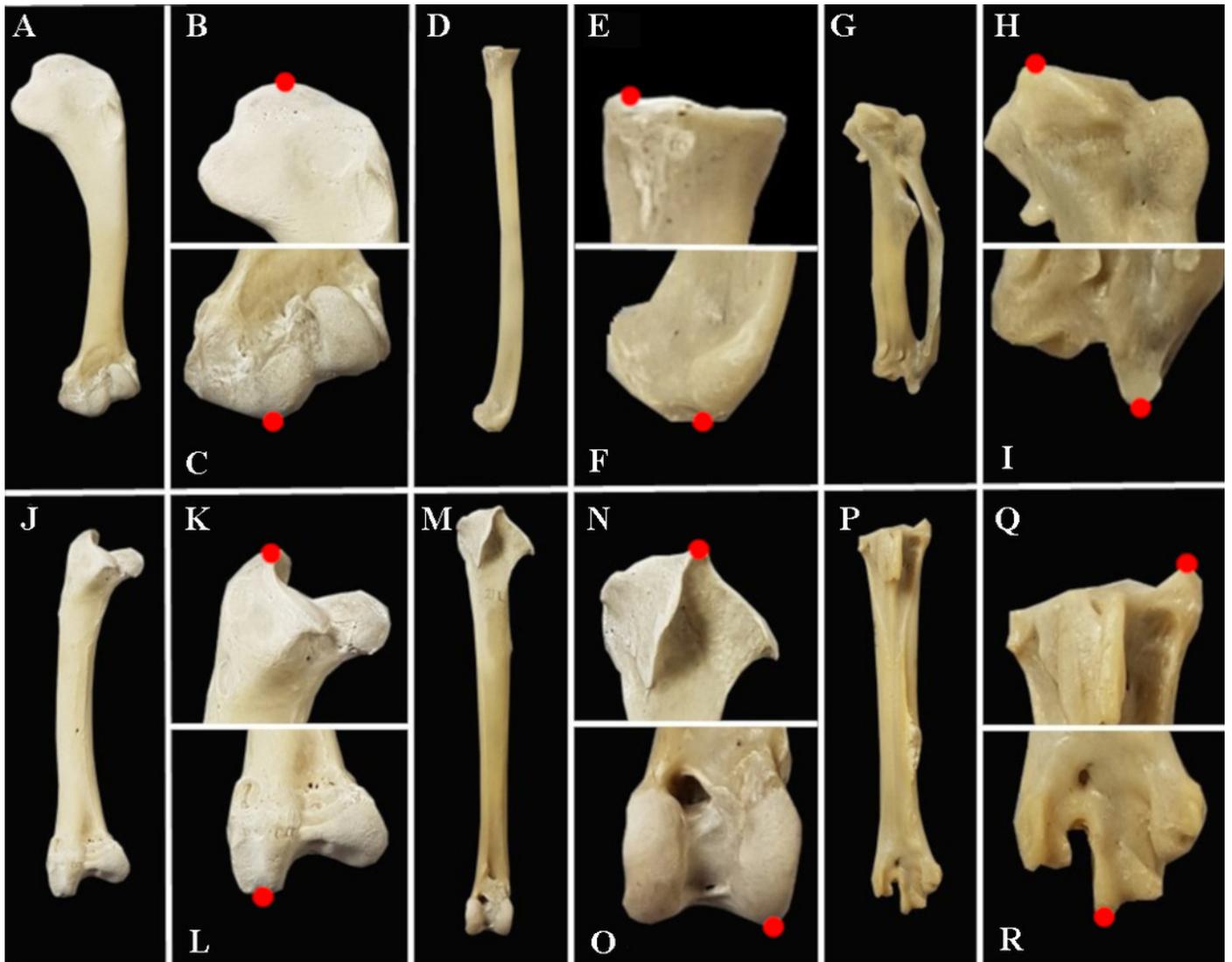
Figure 2

Forelimb and hind limb proportions of the three bones in each limb represented graphically in a ternary plot.

For the hind limb (A), the considered bones are femur (black), tibiotarsus (red) and tarsometatarsus (blue); for the forelimb (B), the considered bones are humerus (black), radius (red) and carpometacarpus (blue); a ternary plot is used to show the proportions for each limb (C).
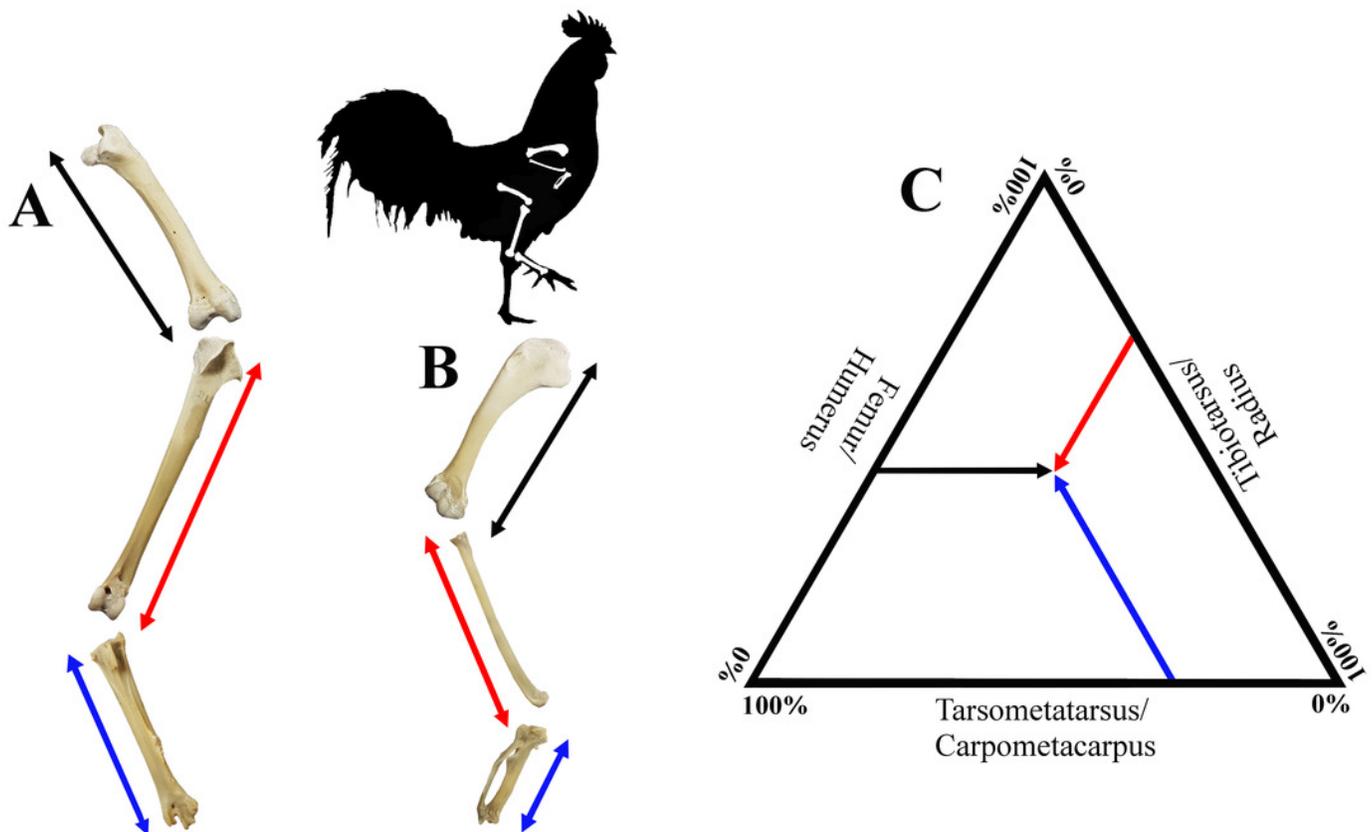
Figure 3

Boxplots comparing limb length between wild and domestic forms.

(A and B) For chicken; (C and D) for Mallard ducks and (E and F) for Muscovy ducks. T test results are included and show t statistic (t) with associated degrees of freedom (df); p = p-value.

A

Length of forelimb (mm)

t=3.13, df=108.24
p-value=2.25*10^{-3}

Domestic   Wild

B

Length of hind limb (mm)

t=2.34, df=86.14
p-value=2.17*10^{-2}

Domestic   Wild

C

Length of forelimb (mm)

t=8.27, df=37.62
p-value=5.531*10^{-10}

Domestic   Wild

D

Length of hind limb (mm)

t=10.71, df=37.71
p-value=5.392*10^{-13}

Domestic   Wild

E

Length of forelimb (mm)

t=-0.03, df=32.41
p-value=9.71*10^{-1}

Domestic   Wild

F

Length of hind limb (mm)

t=0.27, df=33.02
p-value=7.89*10^{-1}

Domestic   Wild
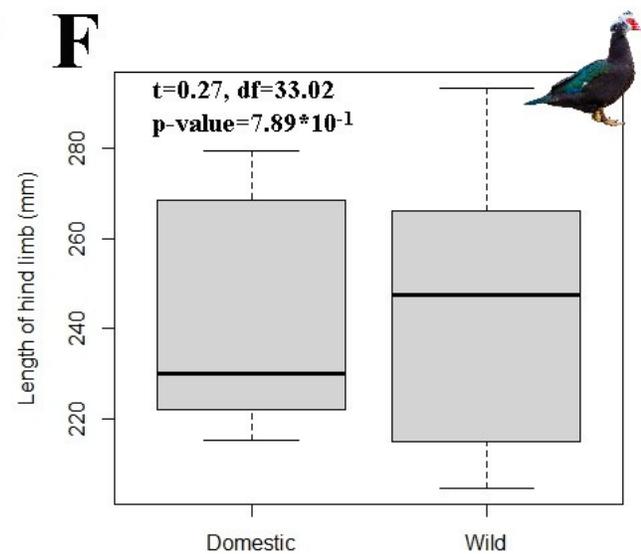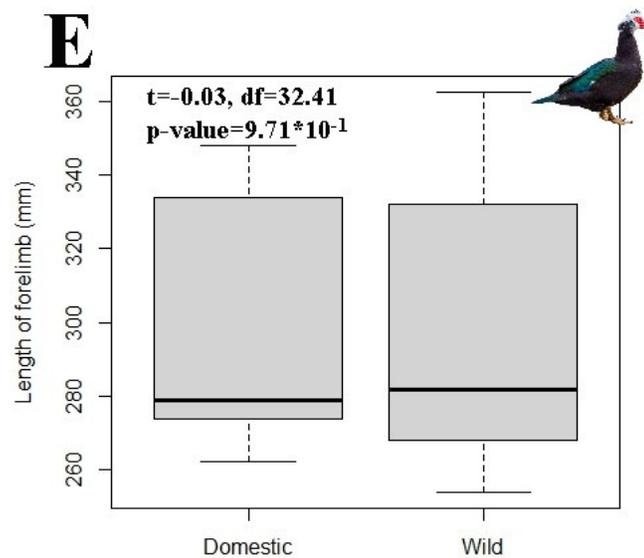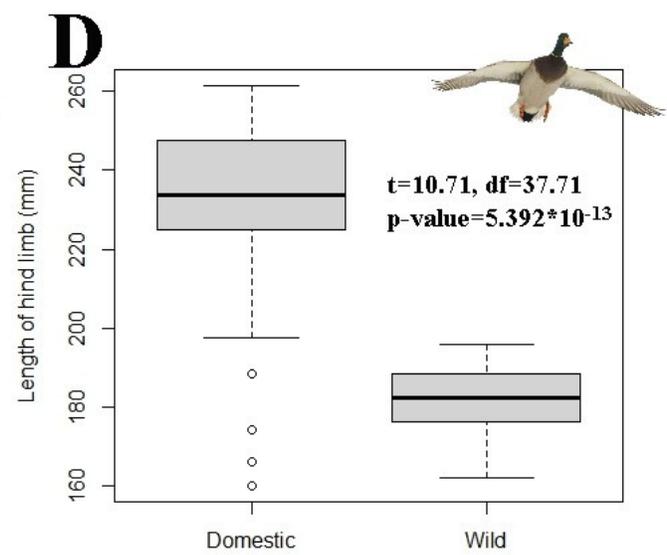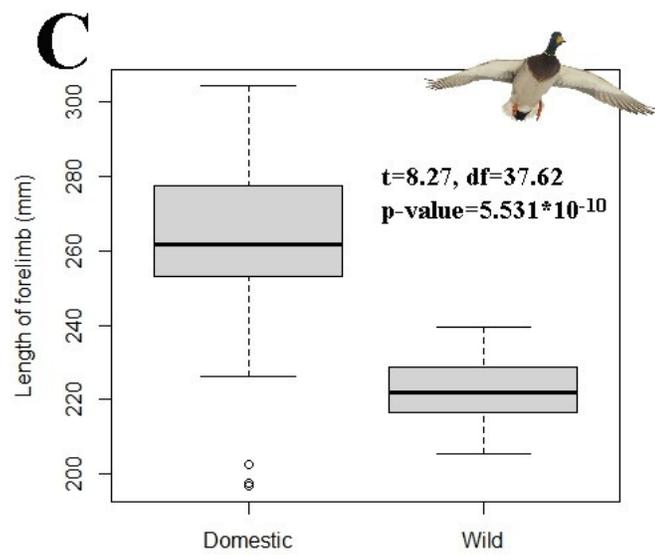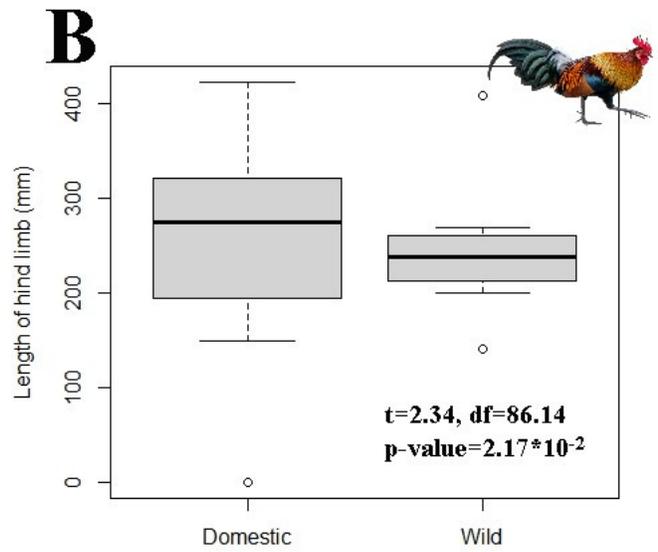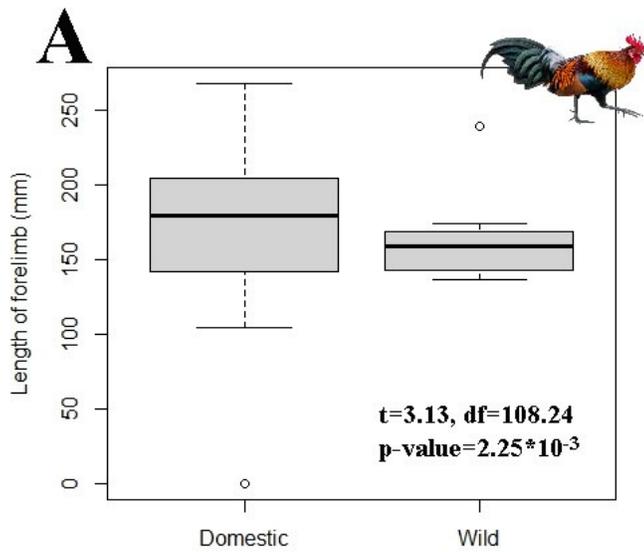
Figure 4

Bivariate plots reflecting the allometric scaling in hind limb of embryological and adult *Gallus gallus*.

(A) Measurements taken from embryos at day 7 of incubation to day 17 (data taken from Faux and Field, 2017). (B) Measurements taken from juveniles from 1 week after hatching to week 36 (data taken from Thomas, 2014). (C) Variation of proportions of adults of chicken breeds and RJF sampled in this study.
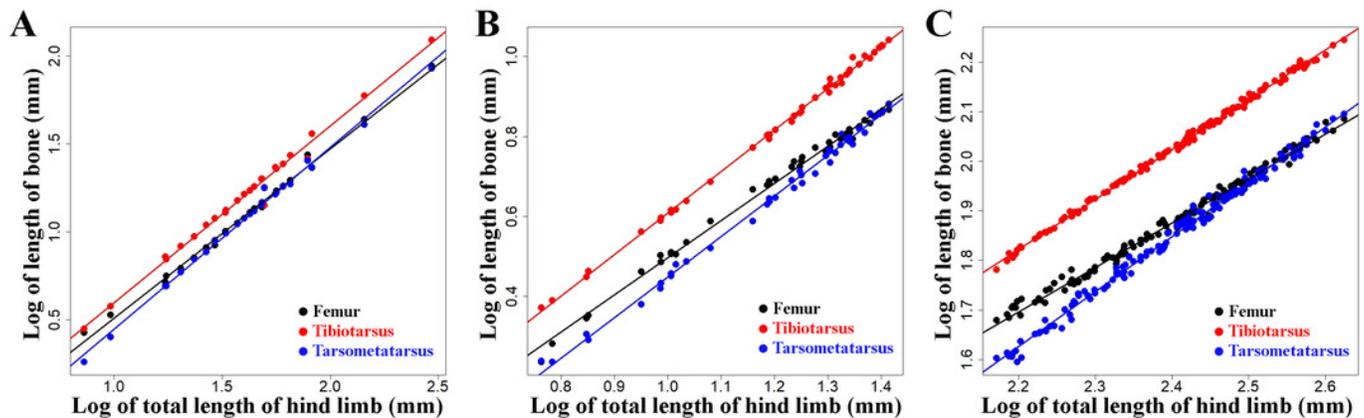
Figure 5

Characters and character states of the sternum in *Gallus gallus*.

(A) Straight carina sterni (CS) (Araucana SAPM-AV-05259), (B) crooked carina sterni (RJF SAPM-AV-05218), (C) non-notched carina sterni (Araucana SAPM-AV-05274), (D) notched carina sterni (RJF SAPM-AV-05218) where notch is indicated by the red arrow, (E) smooth surface and poorly defined concavities of PC and FP (RJF SAPM-AV-05234), (F) spongy well-defined concavities of PC and FP (Araucana SAPM-AV-05259)), (G) Straight end of the trabecula mediana (TM) in dorsal view (Araucana SAPM-AV-05264), (H) fanned end of the trabecula mediana (TM) in dorsal view (RJF SAPM-AV-05266). Specimens are form the Staatssammlung für Anthropologie und Paläoanatomie München. Scale = 1cm.
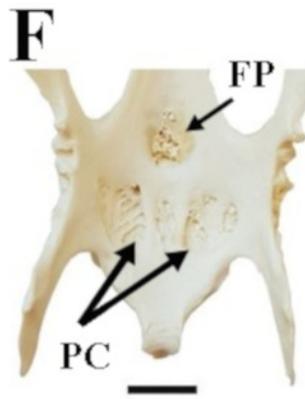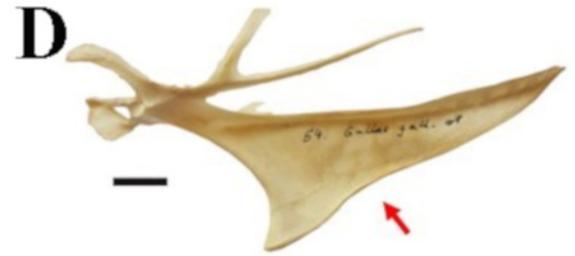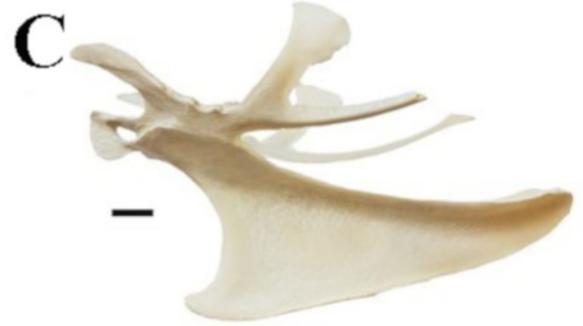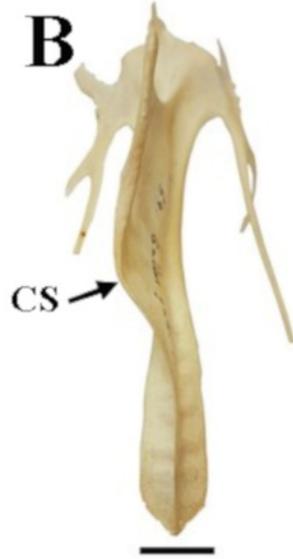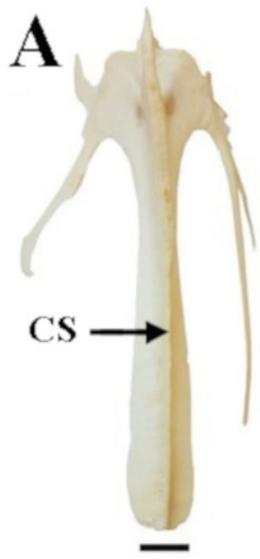
Figure 6

Ternary plots illustrating the proportions in *Gallus gallus* (red), *Anas plathyrhynchos* (blue) and *Cairina moschata* (green)

Axes representing the proportions of each bone in the limb as a percentage. (A) for forelimb, (B) for hind limb. Each plot is accompanied with zoomed in areas correspondent to each species differentiating wild forms (red dots) and domesticated forms (black dots). Circles in zoomed areas capture where most points for wild or domestic forms fall. (For statistical comparison of proportions see *Table 1*).
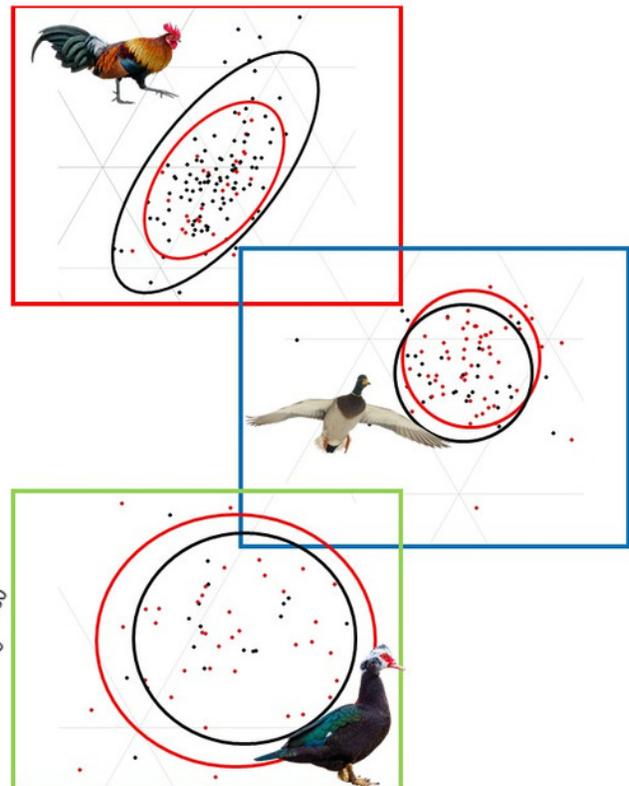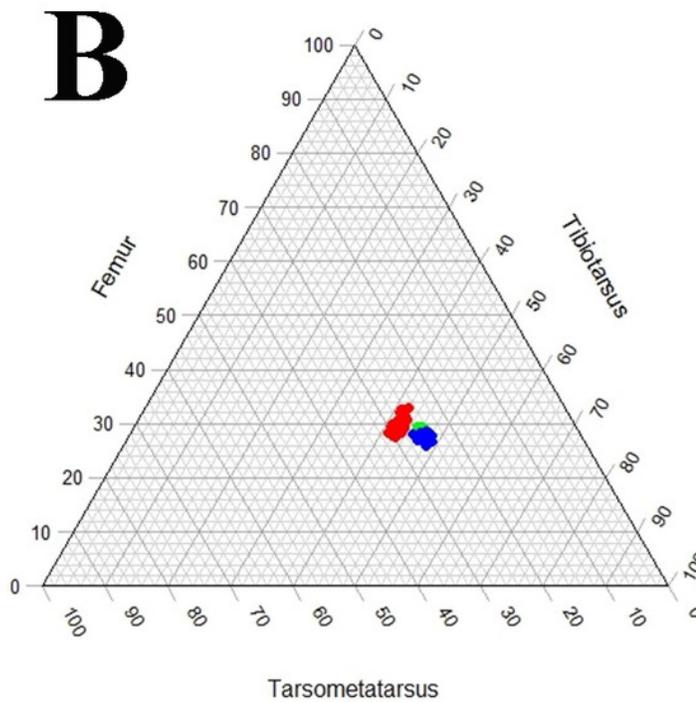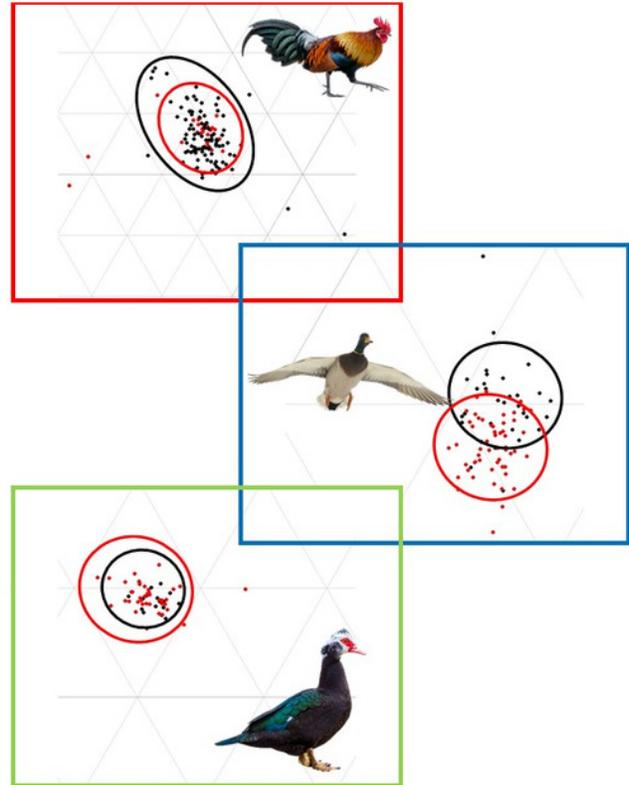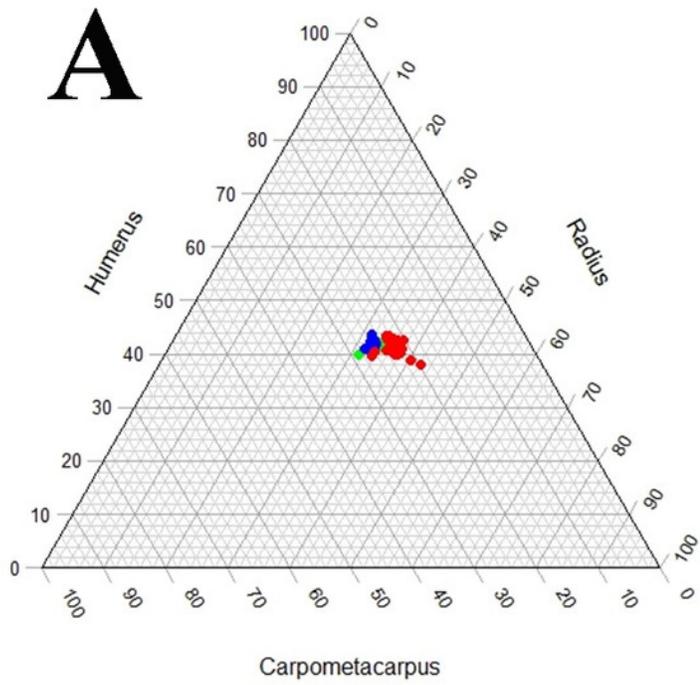
Figure 7

Comparison of limb bones proportions among breeds of chicken.

Each figure depicts the proportion of one bone in its limb (forelimb bones shown on the left panels, hind limb bones on the right panels). On the vertical axis, the proportion of the bone in the limb. On the horizontal axis, the name of the breed to which the above distribution belongs. RJF is highlighted in red.
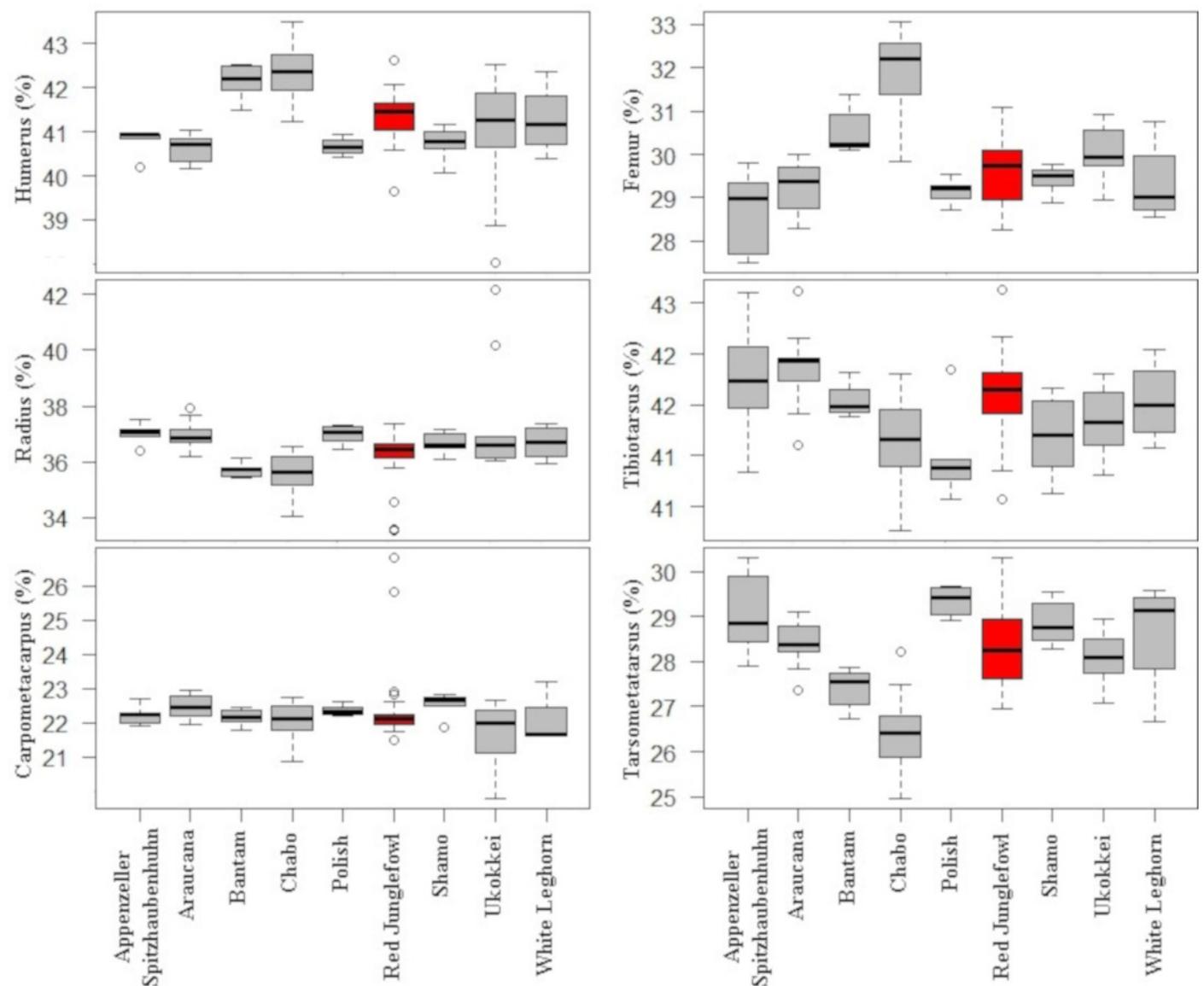
Figure 8

Log-transformed length of individual bone of the forelimb and hind limb vs. log-transformed length of the respective limb as a proxy for body size.

(A and B) for *Gallus gallus*, (C and D) for *Anas plathyrhynchos,* (E and F) for *Cairina moschata*. Domestic breeds are represented with a hollow circle and wild forms are represented with a filled dot. Included are regression equations, regression lines, R squared values, F statistics including degrees of freedom in brackets, and the p-values. Measurements in centimetres.