

1 **Pelvis morphology suggests that early Mesozoic birds were too heavy to contact incubate their**
2 **eggs**

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9

10 **Abstract**

11 Numerous new fossils have driven an interest in reproduction of early birds but direct evidence remains
12 elusive. No Mesozoic avian eggs can be unambiguously assigned to a species, which hampers our
13 understanding of the evolution of contact incubation, which is a defining feature of extant birds.
14 Compared to living species eggs of Mesozoic birds are relatively small, but whether the eggs of
15 Mesozoic birds could actually have borne the weight of a breeding adult has not yet been investigated.
16 We estimated maximal egg breadth for a range of Mesozoic avian taxa from the width of the pelvic
17 canal defined by the pubic symphysis. Known elongation ratios of Mesozoic bird eggs allowed us to
18 predict egg mass and hence the load mass an egg could endure before cracking. These values were
19 compared to the predicted body masses of the adult birds based on skeletal remains. Based on 21 fossil
20 species, we show that for non-ornithothoracine birds body mass was 130% of the load mass of the eggs.
21 For Enantiornithes body mass and egg load mass were comparable to extant birds, but some early
22 Cretaceous ornithuromorphs were 110% heavier than their eggs could support. Our indirect approach
23 provides the best evidence yet that early birds could not have sat on their eggs without running the risk
24 of causing damage. We suggest that contact incubation evolved comparatively late in birds.

25

26 **Keywords:** egg size, contact incubation, Mesozoic bird, pelvic canal width, pubis shape

27

28 **Introduction**

29 The evolution of reproductive behaviour of non-avian theropods and early birds remains poorly
30 understood, with the origin of contact incubation being especially contentious (Deeming, 2002a, 2015;
31 Varricchio & Jackson, 2016). Various eggs of Mesozoic birds have been reported (Varricchio &
32 Jackson, 2016; Lawver *et al.*, 2016), but those that contain embryos remain extremely rare (Deeming,
33 2015). Although unattributed to adults of any known species, Mesozoic bird eggs are considered to be
34 relatively small compared with extant species (Dyke & Kaiser, 2010; Varricchio & Jackson, 2016;
35 Chiappe & Meng, 2016) and are more elongated than extant and Cenozoic fossil bird eggs (Deeming
36 & Ruta, 2014). Eggs are invariably attributed to birds on the basis of eggshell structure rather than close
37 association between eggs and skeletal remains, as seen for some non-avian theropods and a pterosaur

38 (Clark *et al.*, 1999; Lü *et al.*, 2011; Wang *et al.*, 2017). The hypothesis that non-avian theropods sitting
39 on clutches of eggs are exhibiting contact incubation (Clark *et al.*, 1999; Varricchio, 2011; Varricchio
40 & Jackson, 2016) is not universally accepted (Deeming, 2002a, 2015; Deeming & Unwin, 2004; Bois
41 & Mullin, 2017) and equivalent fossils do not exist for birds. Although an egg clutch from the Upper
42 Cretaceous of Mongolia has been found in close association with fragmentary hind limb bones
43 (Varricchio & Barta, 2015), there are no examples of articulated skeletal remains with associated eggs.
44 The incomplete fossil record of reproduction in Mesozoic birds is therefore restricting our
45 understanding of reproduction in this important group of vertebrates.

46 In extant birds, egg size is a key element of reproductive performance as it is pivotal in
47 determining clutch size and is related to developmental maturity at hatching (Deeming, 2007), which
48 in turn impacts on the degree of parental care required by the offspring. Egg physiology is attuned to
49 the nesting environment and, in particular, the need for contact incubation by the adults (Deeming,
50 2002b). Eggshells have to withstand the mass of the adult bird during incubation whilst remaining thin
51 enough to allow the young to hatch (Ar *et al.*, 1979; Juang *et al.*, 2017). Generally, the load masses that
52 bird eggshells can tolerate before breaking are much greater than the parents' mass, but in some extinct
53 large and flightless palaeognathous birds disparity between a very high female body mass and load mass
54 resulted in reverse sexual dimorphism in which the smaller males probably incubated the eggs (Birchard
55 & Deeming, 2009; Huynen *et al.*, 2010).

56 The size of fossil bird eggs can be measured directly (Varricchio & Jackson, 2016; Lawver *et*
57 *al.*, 2016) and their elongated symmetrical shape sets them aside from the asymmetrical eggs laid by
58 modern birds (Deeming & Ruta, 2014). Aside from direct fossil evidence, egg size can be predicted
59 from the presumed body mass of the extinct bird using a relationship derived from extant species
60 (Deeming, 2006; Varricchio & Barta, 2015) and generally egg size is relatively small (Varricchio &
61 Jackson, 2016). Unfortunately, the unambiguous association of eggs with identifiable skeletal remains
62 of adult birds inhibits meaningful comparisons across a broader range of taxa.

63 However, pelvic morphology underwent substantial modifications in the course of avian
64 evolution and it has been suggested that pelvic dimensions of Mesozoic birds could also be used to
65 predict the maximum breadth of eggs (Dyke & Kaiser, 2010; Mayr, 2016). Phylogenetically basal birds
66 outside Ornithothoraces, the clade including the sister taxa Enantiornithes and Ornithuromorpha, are
67 characterised by a closed pubic symphysis. In these birds, the opening formed by the symphysis and
68 the synsacrum effectively delimits the space through which an egg would have to pass (Kaiser, 2007;
69 Dyke & Kaiser, 2010; Chiappe & Meng, 2016). Within Ornithothoraces, the tips of the pubes remain
70 connected in most enantiornithines and in basal ornithuromorphs. A consistently open pubic symphysis,
71 with widely separated pubic bones, characterizes the ornithuromorph subclade Ornithurae, to which
72 modern birds belong (Mayr, 2016, 2017).

73 Our hypothesis is that egg breadth is physically constrained by the width of the pelvic canal in
74 extinct birds with fused pubic symphysis, which in turn correlates with egg mass. Additionally, the

75 relationship between egg mass and body mass allows contact incubation behaviour in extant birds.
76 Hence, we can use predicted egg mass for extinct species to explore their incubation behaviour. Here
77 we pursue the novel approach of predicting egg dimensions of Mesozoic birds from their skeletal
78 remains. We use measurements of the maximum width of the pelvic canal of a range of bird species
79 from the Late Jurassic and Early Cretaceous to define the breadth of the egg laid by the bird. Using this
80 value in relationships for modern species we calculate egg mass and the maximum load mass the eggs
81 could bear without breaking. We then compare this value with the predicted body mass of the same
82 individual fossil specimens and with equivalent values for extant birds. Finally, we also examine
83 taxonomic differences in pubis shape for Mesozoic birds.

84

85 **Materials and methods**

86 Data were collected for 21 different species of Mesozoic birds from published reports as listed in
87 Deeming & Mayr (2018). Our taxon sampling includes the Late Jurassic *Archaeopteryx* and Early
88 Cretaceous birds outside Ornithothoraces (e.g., *Confuciusornis*, *Jeholornis* and *Sapeornis*), as well as
89 species of Early Cretaceous Enantiornithes (e.g., *Cathayornis*, *Parapengornis* and *Zhouornis*) and
90 species of Early Cretaceous ornithuromorphs (e.g., *Changzuiornis*, *Gansus* and *Yanornis*).

91 Species were selected on the basis of published images of a specimen that showed an articulated
92 pair of pubes seen from a dorsal or ventral aspect, and also either had a published measurement for
93 femur and humerus lengths and the length of the pubis, or this value could be derived from the published
94 image. The maximum width of the pelvic canal was measured from the image using ImageJ
95 (<https://imagej.nih.gov/ij/>). Semilandmarks were digitally imposed on the pubis in TPSDig2 (Rohlf,
96 2006) to allow for geometric morphometric determination of pubis shape (see Deeming & Mayr [2018]
97 for detailed methodology) (Zelditch *et al.*, 2012).

98 Body mass of the individual specimen was calculated on the basis of femur and humerus lengths
99 based on analysis of data presented by Field *et al.* (2013). Although we appreciate that femur
100 circumference provides a more accurate measure of body mass for most Mesozoic birds such values are
101 not available, or due to crushing of the fossils they are not reliable. Moreover, body mass is going to
102 reflect musculature around both the pectoral and pelvic girdles so calculations that utilise elements of
103 the fore and hind limbs will be more accurate. The original analysis presented by Field *et al.* (2013)
104 was based on measures of skeletal elements of multiple specimens but used a single mean body mass
105 for a species. To correct for this, mean values for femur and humerus lengths were calculated for male
106 and female individuals. Initial analysis showed that sex was not a significant factor affecting body mass
107 predictions from skeletal elements so we averaged any data for a species replicated for both sexes and
108 re-analysed the data. This process reduced the dataset to 315 species (from a sample size of 863 used
109 by Field *et al.*, 2013). A phylogenetic tree was generated using the “Hackett All species” option on
110 Birdtree.org, phylogenetically controlled least squares regression (pglm) was used in R (R Core
111 Development Team, 2012) to predict body mass from Log_{10} -transformed data for femur length, humerus

112 length, or femur and humerus lengths together. Akaike Information Criteria were used to determine the
113 best model. Therefore, body mass (g) of Mesozoic birds was calculated on the basis of the equation:

114
$$\text{Log Body mass} = 1.130 \cdot \text{Log Humerus Length} + 1.356 \cdot \text{Log Femur Length} - 1.690 \text{ (Eq-1)}$$

115 ($R^2 = 0.9256$; $\lambda = 0.941$). Body mass for extant birds were taken from Dunning (2007).

116 Maximum pelvic canal width was assumed to limit the maximum breadth of the egg. However,
117 published data collected for 17 species of chelonians showed that the maximum egg breadth is on
118 average 0.814 of the maximum pelvic aperture (Deeming, 2018). Therefore, in this study maximum egg
119 breath (B, in mm) was calculated by multiplying the maximum pelvic canal width by 0.814. The length
120 of the egg (L, in mm) was then calculated based on a mean egg elongation ratio of 1.757 (SE = 0.060)
121 derived from published values for Mesozoic bird eggs (Varricchio & Jackson, 2016). These values were
122 used to calculate egg mass (in g) using a modified equation from (Hoyt, 1979; Deeming & Ferguson,
123 1990):

124
$$\text{EM} = 0.597 \cdot 1.757 \cdot B^3 \cdot 10^{-3} \quad \text{(Eq-2)}$$

125 where 0.597 is the mean mass constant determined for crocodylian eggs (Deeming & Ferguson, 1990),
126 which better represent the elongated shape of existing Mesozoic bird eggs (mean elongation ratio of 10
127 crocodylians = 1.64; Deeming & Ferguson, 1990). For extant eggs mass was predicted based on
128 published values for breadth and length from Schönwetter (1960-1985) used in the equation:

129
$$\text{EM} = 0.548 \cdot L \cdot B^2 \cdot 10^{-3} \quad \text{(Eq-3)}$$

130 where 0.548 is the mean mass constant determined for bird eggs (Hoyt, 1979).

131 A new relationship was generated for load mass of an eggshell using data for extant species
132 combined from two studies (Ar *et al.*, 1979; Juang *et al.*, 2017) that took into account phylogeny. Our
133 new relationship excluded the outlying data for the ostrich (*Struthio camelus*) egg, which is two orders
134 of magnitude greater than the range of egg sizes in this study and so could have biased our natural Log-
135 transformed regression (Packard *et al.*, 2009). Using a phylogenetic tree generated from the “Hackett
136 All species” option on Birdtree.org, a phylogenetically controlled least squares regression (pglm) was
137 used in R (R Core Development Team, 2012) to predict load mass from calculated egg mass. Therefore,
138 load mass (g) of Mesozoic and extant birds was calculated on the basis of the equation:

139
$$\text{Log Load mass} = 0.835 \cdot \text{Log Egg mass} + 1.861 \text{ (} R^2 = 0.8441; \lambda = 0.734 \text{).} \quad \text{(Eq-4)}$$

140 Statistical analysis involved Log_{10} -transformation of the data before doing analysis of
141 covariance to test for the effect of taxonomic grouping (non-ornithothoracine, Enantiornithes and
142 Ornithuromorpha) whilst controlling for femur length as a covariate. General, and general mixed, linear
143 models were analysed using Minitab (ver. 17) to compare the effects of taxonomic group and the body
144 mass and egg load mass as fixed factors. Non-significant interaction terms were observed and removed
145 in all cases reported. Differences in pelvis shape between the bird types were investigated using Kruskal
146 Wallis tests and general MANOVA on PC1 and PC2 generated by principal component analysis of
147 semi-landmarks along the length of the pubis.

148

149 **Results**

150 Based on femur and humerus lengths, basal non-ornithothoracine birds were heavier than Early
151 Cretaceous members of Ornithothoraces (Table 1). Predicted body masses for Enantiornithes were only
152 about a sixth of the masses predicted for non-ornithothoracine birds and less than half that of the masses
153 predicted for Early Cretaceous Ornithuromorpha (Table 1). Extant species that were similar in the size
154 of the femur to Mesozoic Ornithuromorpha had comparable body masses (Table 1).

155 The maximum width of the pelvic canal delimited by the pubes was typically in an anterior
156 position close to the ischia and ranged between 10 to 26 mm for all species except for a single large
157 species (*Sapeornis chaoyangensis*), which had a pelvic canal width of 42 mm (see Deeming & Mayr,
158 2018). The predicted egg masses for the 21 species of Late Jurassic and Early Cretaceous birds averaged
159 4.7 g (SE of 2.0 with a range of 0.6–10.8 g with an outlier of 41.0 g; Table 1). The largest eggs were
160 laid by non-ornithothoracine birds and the smallest were laid by Enantiornithes (Table 1). This estimate
161 for egg mass is significantly smaller than the value of 28 g calculated from the equation describing the
162 relationship between female body mass and precocial eggs mass in extant birds (Deeming, 2007), which
163 at is approximately seven times greater than that predicted from the pelvic canal dimensions (Table 1).
164 Predicted egg masses as a percentage of predicted body mass were 0.80, 1.71 and 1.01 for non-
165 ornithothoracine birds, Enantiornithes and Mesozoic Ornithuromorpha, respectively. The extant birds lay
166 eggs that average 8.5% of body mass.

167 A general linear mixed model, with species as a random factor, was used to compare the
168 calculated maximum load mass (g) that an egg could endure until breaking with the predicted Mesozoic
169 bird mass. The effects of taxonomic group and category of mass were both significant ($F_{2,20} = 4.67$, P
170 $= 0.023$; $F_{1,20} = 12.61$, $P < 0.001$, respectively; $R^2 = 89.0\%$) but the interaction was not significant and
171 was removed from the model. For non-ornithothoracine birds, body mass was ~87% heavier than load
172 mass, but for the Enantiornithes these values were ~27% lower and for the Ornithuromorpha the
173 predicted body mass was ~79% greater than the load mass (Fig. 1). By contrast, the load mass that
174 extant eggs could support was over three times the body of the birds that laid them (Fig. 1).

175 Geometric morphometric and principal component analysis (Deeming & Ruta, 2014) revealed
176 that PC1 and PC2 values (29) explained ~75% and 15% of the variation in shape, respectively. General
177 MANOVA showed that PC1 and PC2 were significantly affected by taxonomic group (Fig. 2; Wilk's
178 test: $\lambda = 0.552$, $F_{4,34} = 2.9$, $P = 0.035$). This effect was primarily associated with variation in PC2, which
179 was significantly affected by taxonomic group (Kruskal Wallis test: $H = 8.28$, $DF = 2$, $P = 0.014$) but
180 PC1 was not a significant covariate ($H = 3.45$, $DF = 2$, $P = 0.178$). The length of the pubis was
181 approximately three times longer than pelvic canal for non-ornithothoracine birds and Ornithuromorpha
182 but was only 2.3 times longer in the Enantiornithes (Table 1). Quantitatively, non-ornithothoracine had
183 pubes that were relatively straight and formed a V-shaped pelvic canal. In the Ornithuromorpha the
184 pubes were more recurved anteriorly to the pubic symphysis so forming more of a U-shaped pelvic

185 canal. In the Enantiornithes this pattern was exaggerated further by the relatively shorter pubes having
186 to delimit a relatively wide pelvic canal.

187

188 **Discussion**

189 Our analyses suggest that the pubic symphysis delimited a pelvic canal that constrained the
190 physical size of eggs to a mass around 25% of that predicted from data for extant species and is such
191 smaller than other estimates for egg size in Mesozoic birds (Varricchio & Jackson, 2016). Evolutionary
192 changes in early birds affected body size but preserved a minimum size for the pelvic canal. However,
193 the calculated lengths of the eggs fit well within the size of the pelvis delimited by the length of the
194 pubis (see Deeming & Mayr, 2018). Hence, the eggs of the Mesozoic birds in this study were relatively
195 very small and this would have had consequences for the pattern of incubation.

196 The predicted breadth of Early Mesozoic bird eggs is smaller to that of many of the known
197 fossil eggs attributed to birds (Varricchio & Jackson, 2016; Lawver *et al.*, 2016), although we appreciate
198 that there are many examples of larger avian eggs in the fossil record. The range of our egg breadths
199 was 8.6–33.9 mm but all but four species had egg breadths predicted to be <15 mm. Of the 14 values
200 reported by Varricchio and Jackson (2016) only 2 were below 20 mm but all of the values were below
201 41 mm. Likewise, the diameter of enantiornithine eggs from China (Zhou & Zhang, 2004), Mongolia
202 (Balanoff *et al.*, 2008) and Argentina (Schweitzer *et al.*, 2002; Fernández *et al.*, 2013) all lie well within
203 the range of values reported here (20, 22.3 and 27 mm, respectively, from Varricchio & Jackson, 2016).

204 Some eggs attributed to Mesozoic birds are broader than could be laid by the birds included in
205 this study (Varricchio & Jackson, 2016; Lawver *et al.*, 2016). This may reflect the differing temporal
206 and geographical origin of these eggs, which were mainly found in a range of Early and Late Cretaceous
207 locations outside China and not in direct association with comparable articulated skeletal remains.
208 Moreover, assessment of the taxonomic origin of eggs found in isolation can be difficult. For instance,
209 presumed “theropod” eggs from Thailand (Buffetaut *et al.*, 2005) were eventually shown to contain
210 remains of a lizard (Fernandez *et al.*, 2015). Similarly, an egg originally attributed to a neoceratopsian
211 dinosaur has been shown to contain avian remains (Varricchio *et al.* 2015). Avian eggs found in
212 Argentina (Fernández *et al.*, 2013) have been linked by Varricchio and Jackson (2016) with the
213 enantiornithine *Neuquenornis volans* (Clark & Norell, 2001) and it has been suggested that the eggs
214 were 7.5% of the adult body size. However, such a conclusion is unfounded because, firstly, no skeletal
215 element have been found with the eggs, and, secondly, the same strata contain the remains of both
216 *Neuquenornis* and the much larger ornithurine *Patagopteryx* (Fernández *et al.*, 2013), which makes
217 assigning the eggs problematical.

218 Load mass of eggs of extant species is very high compared to body mass, especially in smaller
219 birds (Ar *et al.*, 2017; Juang *et al.*, 2017). Whilst load mass correlates with shell thickness (Ar *et al.*,
220 2017; Juang *et al.*, 2017), it is unclear why bird eggs need to withstand masses much greater than the
221 incubating adult. We acknowledge that eggs of early Mesozoic birds have a different shape and eggshell

222 structure than those of extant birds (see Deeming & Ruta, 2014; Varricchio & Jackson, 2016) and this
223 could impact on our interpretation of the data. However, limited data for the load mass to break a
224 crocodylian egg show that this is equivalent to that of avian eggs of the same mass, despite the different
225 eggshell structure and more elongated shape (Figure S5; Manolis & Webb, personal communication,
226 2017). We, therefore, consider that our approach of applying load mass data of extant birds to the eggs
227 of fossil birds is justified.

228 Predicting egg size from pelvic dimensions is not unrealistic but data from extant species
229 indicates that egg breadth is smaller than the maximal pelvic opening because the bones are surrounded
230 by layers of soft tissue and the gastro-intestinal tract also passes through the pelvic canal. Breadth of
231 turtle eggs averages only 81.4% of the maximal pelvic width and there is a very good relationship
232 between egg breadth and maximal pelvic width (Deeming, 2018). Moreover, the only extant bird
233 species with a closed pubic symphysis, the Ostrich (*Struthio camelus*), has an average egg breadth of
234 12.5 cm and the maximum pelvic aperture is 15 cm (Deeming, personal observations), which is a ratio
235 of 0.833. In female American alligators (*Alligator mississippiensis*) the average egg is only 42 mm
236 (Deeming & Ferguson, 1990), which is 65% of the 65 mm average width of the pelvic aperture (Prieto-
237 Marquez *et al.*, 2007). There is, however, one report of pelvic kinesis in the smallest tortoise *Homopus*
238 *signatus* that lays eggs that are larger than its pelvic aperture (Hofmeyr *et al.*, 2005) but this may be
239 unusual. It is possible that the small Mesozoic birds described in this study exhibited pelvic kinesis
240 allowing laying of a larger egg. However, egg formation takes place in the pelvic girdle and this would
241 limit egg breadth. Whether the pelvic limb musculature would allow for much movement of the pelvic
242 bones is also unclear.

243 The degree of preservation of the birds used in this study is remarkable but whilst many
244 skeletons are articulated all exhibit considerable crushing. This could suggest that our measurements of
245 the articulated pubes may be unrealistic. However, the width of the synsacrum is usually very similar
246 to that of the pelvic canal and in life the articulation of the ilium, ischium and pubis would have
247 delimited the space below the synsacrum. Three-dimensional reconstruction of the pelvis is, therefore,
248 likely to limit the width of the pelvic canal further. This means that our measurements are most likely
249 overestimates, which reduces egg breadth and egg size further.

250 Using the dimensions of the pelvic canal to calculate egg size in Mesozoic birds provides insight
251 into their reproduction despite there being a lack of fossil eggs attributed to these species. Hence, for
252 the species in our study the fact that pubic length scales with body size, whilst pelvic canal width was
253 conserved suggests that there was a maximum egg width for Mesozoic birds that was physically
254 delimited by the pelvic canal. This limitation means, for example, that in Early Cretaceous
255 Enantiornithes the overall reduction in body size (compared to non-ornithothoracine birds) was
256 reflected in a reduction in the length of the pubis but this bone seems to have changed shape to
257 accommodate the maintenance of a minimum pelvic canal width (> 10 mm in these Chinese Mesozoic
258 birds). The length of the pubes has only exhibited a significant reduction for the Enantiornithes, which

259 means that the shapes of the pubes have changed from relatively straight, long bones forming a V-
260 shaped pelvic canal to relatively short bones delimiting a U-shaped pelvic canal.

261 A pelvic canal delimited by a pubic symphysis is a feature of non-avian theropods in general.
262 Whilst a comprehensive review of the dimensions of the pelvic canal in theropods is beyond the scope
263 of our study, Hutchinson (2001) provides scale drawings that show that the pelvic aperture of
264 *Allosaurus* measured ~7cm in breadth for an animal estimated to weigh 1500 kg (Bates *et al.*, 2009).
265 This has profound implications for egg sizes that could be laid by theropods – with an elongation ratio
266 of 2.1 found in some theropods (Deeming & Ruta, 2014) an *Allosaurus* egg is estimated to be ~430 g –
267 only 0.02% of body mass. Data for estimates of body mass and egg mass for four species of theropods
268 (Werner & Griebeler, 2013) suggest that egg mass was very small relative to body mass (0.5-1%) and
269 calculated load masses for eggs were only 20-50% of the predicted. Such values serve to support the
270 view that contact incubation in theropods was very unlikely (Deeming, 2002a; Bois & Mullin, 2017).
271 Clearly, there is a need for further investigation into the size of the pelvic canals of theropods and its
272 implications for egg mass and reproduction in these animals. The concept that non-avian theropods
273 were able to sit on and contact incubate their eggs (Varricchio *et al.*, 2008), which is not universally
274 accepted (Birchard *et al.*, 2013), is not supported by the present study.

275 The disparity between body mass and presumed load mass that could be safely endured by the
276 eggs of the Mesozoic birds as indicated here suggests that these species would find it hard to sit on their
277 eggs in a manner similar to extant breeding birds without causing damage. Analyses of body mass, egg
278 size, and shell thickness in extinct ratites suggests that the relatively small size of the eggs combined
279 with thin eggshells meant that there was a low safety margin for contact incubation leading to reversed
280 sexual dimorphism in some species, e.g., moas (Dinornithiformes) (Birchard & Deeming, 2009;
281 Huynen *et al.*, 2010). Egg sizes are relatively small (< 1.5%) in all of the Mesozoic species here and so
282 are comparable to the relatively small eggs of ratites. Differences in the body mass and the load mass
283 of the eggs would have meant that contact incubation, as exhibited by extant birds (see Deeming,
284 2002c), was most likely precluded in non-ornithothoracines and Early Cretaceous Ornithuromorpha.
285 The difference between eggshell load and bird size in the Enantiornithes is smaller but the scope for
286 egg breakage would still be very high. Only when the pubic symphysis is opened up in the Ornithurae
287 was the restriction on egg size removed allowing birds to lay larger eggs, which can support the body
288 mass and allow evolution of true contact incubation.

289 It is possible that in the Mesozoic the first birds to sit on their eggs were able to achieve this
290 without applying all of their weight. However, extant birds rely on contact incubation between the
291 ventral skin of the body and the top of the eggs and often develop a brood patch to facilitate heat transfer
292 (Lea & Klandorf, 2002). Such a need to intimate bodily contact and the relative smallness of the eggs
293 does make this scenario difficult to envisage. In addition, the limited data for eggs of enantiornithine
294 birds show that these were at least partially deposited in sediment (Deeming, 2006; Fernández *et al.*,

295 2013; Varricchio & Jackson, 2016), which contrasts with a modern-type avian contact incubation, in
296 which the eggs also need to be regularly turned for normal development (Deeming, 2002d).

297 Another possibility is that the shells of the eggs laid by these Mesozoic birds were thicker and
298 so better able to withstand the body mass. We know of no eggs attributed to the species studied here
299 but there are eggs attributed to enantiornithine birds (Lawver *et al.*, 2016). Where available dimensions
300 of these eggs can be used to calculate egg mass and hence predict eggshell thickness from the
301 relationship for extant bird species (Birchard & Deeming, 2009). Comparison of mean (\pm SD) actual
302 and predicted eggshell thicknesses for these fossil eggs showed that actual thickness is \sim 10% greater
303 than predicted but this difference was not significant (actual eggshell thickness: 223.3 ± 100.7 ; predicted
304 eggshell thickness = 200.8 ± 49.6 ; paired t-test $t_5 = -0.69$, $p = 0.523$). This suggests that enantiornithine
305 eggshells would be able to withstand loads masses to comparable extant eggs but future fossil specimens
306 may allow us to test whether this is generally true.

307 This study primarily focusses on Mesozoic birds from China, which exhibit remarkable levels
308 of preservation of articulated skeletons. Avian eggs that contain embryos are rare and they tend to be
309 larger than the apparently small size of the eggs predicted here. This size disparity may reflect the
310 chances of fossilisation or discovery. This study does predict that any avian eggs found from the
311 Mesozoic of China are likely to be very small.

312 Our study has indirectly demonstrated the limitations imposed upon reproduction in Mesozoic
313 birds. As noted above, our values can only over-estimate egg mass based on the maximum pelvic canal,
314 which suggests that differences between bird mass and egg size can only increase. That Mesozoic birds
315 were much heavier than their eggshells could accommodate strongly suggests that contact incubation,
316 as observed in extant birds, probably evolved only after there was an increase in egg width associated
317 with an opening of the pubic symphysis.

318

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324

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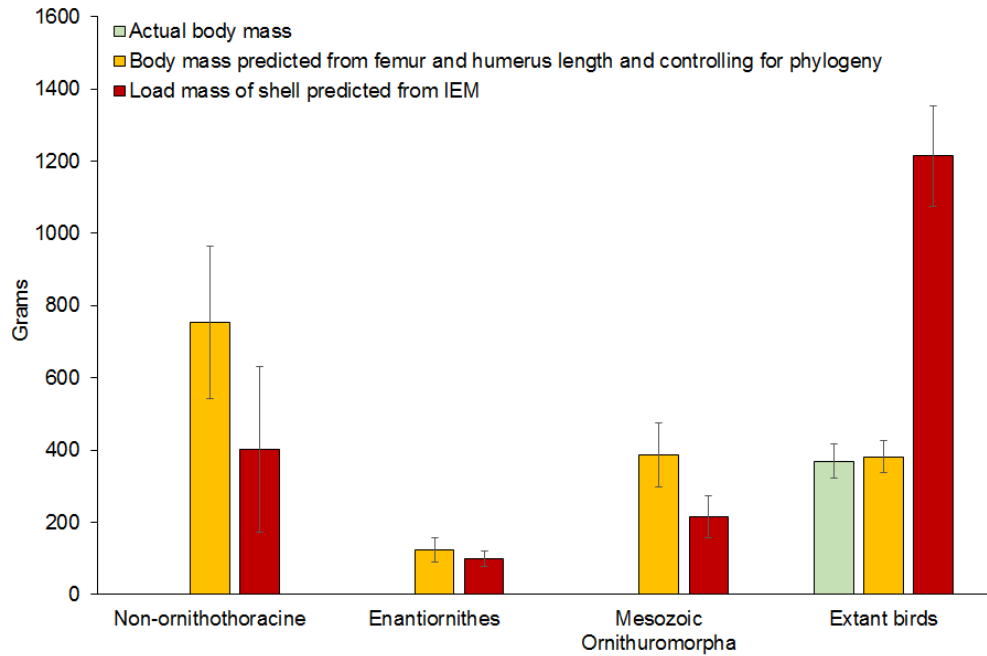
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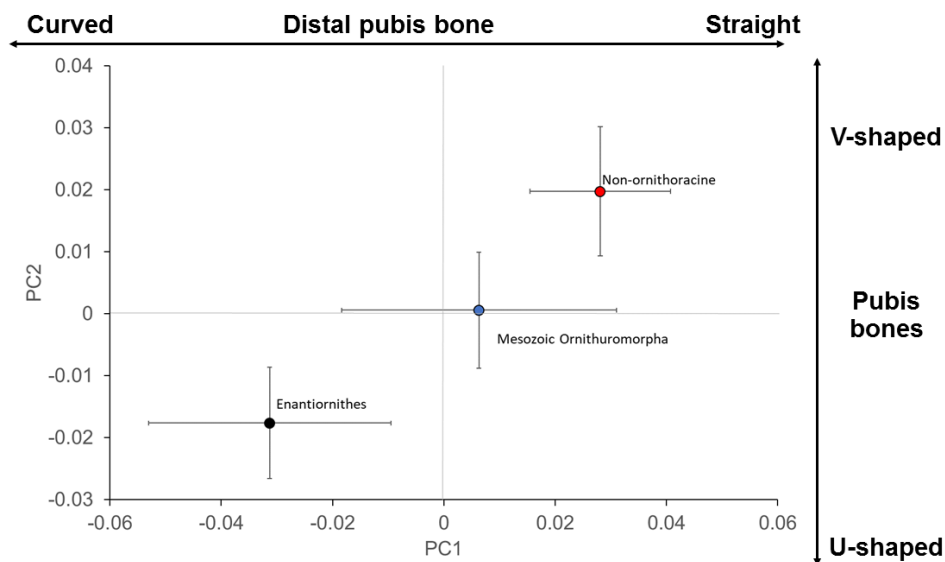
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454 Fig. 1. Mean (\pm SD) values for bird mass predicted from femur and humerus length, and the load mass
 455 required to break an eggshell as calculated from calculated egg mass, for three taxa of Mesozoic birds,
 456 and extant species of a similar size. Mean body mass recorded from adult birds is also included as a
 457 comparison for extant birds.



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 459 Fig. 2. Mean (\pm SE) values for the first two principal components (PC1 and PC2) derived from a semi-
 460 landmark geometric morphometric analysis of pubis shape for the three taxonomic groups of Mesozoic
 461 birds in the dataset.



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