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1 **Ontogenetic scaling patterns and functional anatomy of the pelvic limb** 2 **musculature in emus (*Dromaius novaehollandiae*)**

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9 10 **Abstract**

11 Emus (*Dromaius novaehollandiae*) are exclusively terrestrial, bipedal and cursorial ratites with some
12 similar biomechanical characteristics to humans. Their growth rates are impressive as their body
13 mass increases eighty-fold from hatching to adulthood whilst maintaining the same mode of
14 locomotion throughout life. These ontogenetic characteristics stimulate biomechanical questions
15 about the strategies that allow emus to cope with their rapid growth and locomotion, which can be
16 partly addressed via scaling (allometric) analysis of morphology. In this study we have collected
17 pelvic limb anatomical data (muscle architecture, tendon length, tendon mass and bone lengths) and
18 calculated muscle physiological cross sectional area (PCSA) and average tendon cross sectional area
19 from emus across three ontogenetic stages (n=17, body masses from 3.6 to 42 kg). The data were
20 analysed by reduced major axis regression to determine how these biomechanically relevant aspects
21 of morphology scaled with body mass. Muscle mass and PCSA showed a marked trend towards
22 positive allometry (26 and 27 out of 34 muscles respectively) and fascicle length showed a more
23 mixed scaling pattern. The long tendons of the main digital flexors scaled with positive allometry for
24 all characteristics whilst other tendons demonstrated a less clear scaling pattern. Finally, the two
25 longer bones of the limb (tibiotarsus and tarsometatarsus) also exhibited positive allometry for
26 length and the two others (femur and first phalanx of digit III) had trends towards isometry. These
27 results indicate that emus experience a relative increase in their muscle force-generating capacities,
28 as well as potentially increasing the force-sustaining capacities of their tendons, as they grow.
29 Furthermore, we have clarified anatomical descriptions and provided illustrations of the pelvic limb
30 muscle-tendon units in emus.

31 Introduction

32 Scaling studies (relating animal body mass to other biological parameters) have broadly elucidated
33 locomotor adaptations across a wide range of body sizes. These studies have also described
34 important size-related biomechanical (Alexander et al. 1979; Bertram & Biewener 1990; Biewener
35 1982; Gatesy & Biewener 1991; LaBarbera 1989; Maloiy et al. 1979; McMahon 1975) and metabolic
36 (Gillooly et al. 2001; Hemmingsen 1960; Hokkanen 1986; Kleiber 1932; Schmidt-Nielsen 1984; Taylor
37 et al. 1981) constraints across species. Intraspecific scaling studies are less common (Allen et al.
38 2010,2014; Carrier & Leon 1990; Carrier 1983; Dial & Jackson 2011; Main & Biewener 2007; Miller et
39 al. 2008; Picasso 2012a; Smith & Wilson 2013; Young 2009, Picasso 2014) These ontogenetic
40 approaches yield valuable insights into musculoskeletal adaptations to growth and potentially to
41 identify size-related constraints on mechanical function within a species. Furthermore, studies of
42 species where the mode of locomotion and basic anatomy remains similar during development
43 contribute to the understanding of strategies and trade-offs that occur during growth. Such
44 information can, for example, be used to comprehend developmental abnormalities and study
45 intervention strategies to manage them.

46 Ratites are large flightless birds with cursorial morphology (e.g., Smith et al. 2010; Smith & Wilson
47 2013) that makes them attractive subjects for studies of terrestrial locomotion and bipedalism
48 (Abourachid, 2000). Certain characteristics make emus (*Dromaius novaehollandiae*) particularly
49 useful: they have some anatomical and functional similarities to other bipedal animals, including
50 purportedly humans (Goetz et al. 2008). Compared to ostriches, they are generally easier to handle
51 and train in experimental settings due to their smaller size and calmer temperament. Finally, their
52 growth rate is impressive, as they multiply their body weight ~80 times in the first 18 months of life
53 (Minnaar & Minnaar 1998) whilst maintaining the same cursorial mode of locomotion. Despite this
54 interest there are still some discrepancies in published anatomical descriptions and depictions of the
55 pelvic limb musculature of emus (Haughton 1867; Patak & Baldwin 1998; Vanden Berge & Zweers
56 1993), and clear visual anatomical aids are lacking in the literature.

57 Some of the biomechanical changes in the hindlimb occurring during the growth in emus have been
58 described . Main and Biewener (2007) measured the skeletal strain patterns on the surfaces of the
59 femur and the tibiotarsus (TBT) in running emus, demonstrating a significant increase in the
60 magnitude of cranial and caudal femoral and caudal tibiotarsal strains during ontogeny, despite the
61 enlargement and strengthening of those bones via positive allometric scaling of the second moment
62 of area. Muscles have been shown to influence the strain patterns of bones (Yoshikawa et al. 1994),
63 and although other factors are likely to be involved in the changes in peak bone strains reported
64 across ontogeny (Main & Biewener 2007), allometric scaling of the musculature could also play a
65 role in these differences in bone tissue loading. The strains induced by muscle contraction will be
66 proportional to the muscle forces acting on the bone; therefore by estimating muscle forces (e.g.,
67 maximal force capacity based upon anatomy), associations between these two findings would be
68 possible.

69 In order to build on already available biomechanical data for emus (Goetz et al. 2008; Main &
70 Biewener 2007), we aim here to quantify the ontogenetic scaling patterns of four pelvic limb bones,
71 pelvic limb muscles and their tendons and in the process describe and compare the functional and
72 descriptive anatomy of the pelvic limb musculature of emus. We use regression analysis to
73 determine the relationship of muscle architectural properties with body mass in an ontogenetic
74 series of emus and then examine the implications of these findings for the locomotor ontogeny of
75 emus, other ratites as well as extinct theropod dinosaurs.

76 Materials and methods

77 *Animal subjects and care: UK group*

78 We dissected 17 emus for this study, obtained from our ongoing research examining emu
79 ontogenetic biomechanics (conducted with ethical approval under a UK Home Office license). The
80 emus were divided in three groups of animals according to their age: Group 1: Five individuals at 4-6
81 weeks old; Group 2: Six 24-28 weeks (6 months) old individuals; and Group 3: Six 64-68 weeks (16
82 months) old individuals. All birds had been used as experimental animals and kept in a small pen
83 (7x7m) for the first six weeks of life, after which they were moved to an outdoor larger enclosure
84 with grass footing (40mx15m) until they were six months old; after this they were moved to a large
85 (1.6 hectares) grass field (maximal animal density at one time was 8 birds/ha). The birds were all
86 born in three consecutive yearly breeding seasons. Only the birds in Group 3 were from the same
87 breeding season but not necessarily the same progenitors; birds from the other two Groups were
88 from two different seasons.

89
90 All animals were hatched at a commercial breeding farm in the UK and raised from four weeks of age
91 at the Royal Veterinary College. They were fed a commercial ostrich pelleted diet supplemented
92 with grass and from six weeks of age were kept with free access to commercial food and grass. At 24
93 weeks, their diet changed from an ostrich grower diet to adult ostrich pelleted food (Dodson and
94 Horrel Ltd., Kettering, Northamptonshire, UK). There were no restrictions or enforcements on the
95 animals' regular exercise regime and all animals were allowed the same area and conditions to
96 exercise during their development. All animals were euthanized after other experimental procedures
97 were completed, by lethal intravenous injection of a barbiturate following induction of deep
98 terminal general anaesthesia by intramuscular injection of ketamine and xylazine. Carcasses were
99 kept frozen in a -20°C freezer for up to 2 years before dissection. Thawing was allowed at variable
100 ambient temperatures and for variable amounts of time depending on the size of the animal, and
101 dissection started no longer than 4 days after removal from the freezer. All dissections were
102 performed within a six week period and led by the same individual (L.P.L.).

103 *USA group of emus*

104 Unpublished raw data of muscle masses from a different group of 29 emus (0.74 to 51.7 kg body
105 mass) used for similar purposes as those described for the UK group were also included in this study.
106 This group was bred and reared in the USA (Concord Field Station, Harvard University) under the
107 care of another investigator (R.P.M.) who led all dissections for this group. The size and age
108 composition for this group was more heterogeneous, and only body masses and muscle masses
109 were available for analysis. Because the purpose of the dissections in the group was not a systematic
110 ontogenetic musculoskeletal scaling study, the number of muscles dissected per animal varied.
111

112 *Bone measurements*

113 Maximal interarticular lengths of the femur, tibiotarsus (TBT), tarsometatarsus (TMT) and first
114 phalanx of the middle (third) digit were measured using an ordinary flexible measuring tape (± 1 mm)
115 once they were cleared of all soft tissues.

117 *Myology and muscle architecture*

118 We identified muscles of emus using four separate literature sources (Haughton 1867; Patak &
119 Baldwin 1998; Smith et al. 2007; Vanden Berge & Zweers 1993); when our observations differed
120 from these, we described the anatomical landmarks and attachments in detail according to our
121 observations. General main actions of the muscle were defined based on these publications and
122 confirmed by identifying the muscle attachments and paths and then mimicking the muscle action
123 by applying tension on the muscle during dissection. We used additional reference to a
124 biomechanical model of an ostrich (Hutchinson et al. 2014) to refine the three-dimensional actions
125 of the hip muscles, as those actions are difficult to accurately ascertain from visual inspection and
126 manipulation. Table 1 shows our simplified description of the anatomy, abbreviations used

127 throughout this study, and inferred muscle actions. Figures 1 to 3 show schematic anatomical
128 representations of the muscle anatomy.

129

130 To avoid freeze drying of the carcasses, we ensured all animals were frozen soon after euthanasia
131 kept in sealed bags, and were not thawed and refrozen before dissection. The carcasses showed
132 minimal autolysis and therefore an easier and better dissection during which muscle actions could
133 be approximated without damaging their structure and attachments.

134 Dissection of the right pelvic limb muscles was performed in all specimens apart from the first two
135 subjects in the 4-6 week old group, in which the muscles of the left limb were dissected first to
136 standardise the technique. Measurements taken from the muscles of the left limb were not used
137 (avoiding duplication of information), with the exception of when there were unidentified/damaged
138 muscles from the right limb of the same specimen, in order to create a complete set of muscles for
139 each specimen.

140 After identification of each muscle, we performed complete dissection and removal of it by
141 transection at its origin and insertion(s). Next, the muscle was laid flat on a table and we took four
142 muscle architectural measurements in a standard protocol: muscle mass (M_m), fascicle length (L_f),
143 muscle belly length and pennation angle (Θ). Muscle mass was measured on an electronic scale (\pm
144 0.01 g) after removal of tendons, fat and aponeuroses. Fascicle length was measured from at least
145 five random sites within the muscle belly using digital callipers (\pm 0.1 mm). Muscle belly length was
146 measured as the length (\pm 1 mm) from the origin of the most proximal muscle fascicles to the
147 insertion of the most distal fascicles into the distal tendon or aponeurosis. The pennation angle was
148 measured at least five times using a goniometer ($\pm 5^\circ$) with the mean of the latter measurements
149 was taken as the pennation angle for the muscle. The repeated measurements were taken from
150 multiple cuts into the muscle to expose different anatomical orientations of the fascicles with the
151 same muscle. This methodology minimises the differences that may be seen across an individual
152 muscle and ensures mean values used for further calculations are representative of the overall
153 architecture of the muscle. We calculated total limb muscle mass by adding the individual masses of
154 the muscle bellies. Our approach was straightforward for most muscles, apart from three smaller
155 muscles of the limb: IFI, ISF and FPPDII (Table 1), where minor dissection mistakes might have
156 impaired estimates of their masses and architectural properties.

157 Muscle volume was calculated by dividing muscle mass by estimated muscle density of vertebrates
158 (1.06 g cm^{-3} ; (Brown et al. 2003; Hutchinson et al. 2014; Mendez & Keys 1960)). From these data we
159 calculated physiological cross-sectional area (PCSA) for each muscle via the standard formula (Powell
160 et al. 1984; Sacks & Roy 1982) (Equation 1):

$$PCSA = \left(\frac{V_{muscle}}{L_{fascicle}} \right) \cos\theta$$

161 When a tendon was present it was dissected down to its insertion onto the bone together with the
162 muscle. The tendon was then transected at the musculotendinous junction when a clear separation
163 became apparent and stretched on a flat surface. We then measured lengths with a standard ruler
164 or flexible measuring tape ($\pm 1\text{mm}$), and tendon mass was also measured using the same
165 instrumentation as for the muscles.

166 Tendon cross-sectional area (TCSA) was calculated using tendon length (L_{ten}); from muscle origin to
167 bony insertion; and tendon mass (M_{ten}) as follows (Equation 2):

$$TCSA = \frac{M_{ten}}{1120L_{ten}}$$

168 Where 1120 kg m^{-3} is assumed as the density of tendon (Hutchinson et al. 2014; Ker 1981).

169 *Statistical analysis*

170 Ontogenetic scaling relationships of (non-normalized) muscle properties were analysed using
171 reduced major axis ("Model II") regression for \log_{10} of each property vs \log_{10} body mass using
172 custom-designed R software code (R Development Core Team 2010) code. A Shapiro-Wilk test was
173 performed to assess normality of distribution of the residuals, and the p value for significance was
174 set to <0.05 . The inclusion criteria for data presented were: Datasets first had to have a p value
175 <0.05 in the above described Shapiro-Wilk test. If this p was >0.05 , the data were then tested for the
176 presence of outliers (which were set at ± 2 standard deviations [SD] from the mean) and outliers
177 removed. The RMA linear regression was performed again using this dataset and again, data were
178 only presented if the p value for distribution of residuals was <0.05 . Once the datasets were defined,
179 R^2 correlation values and upper and lower bounds of the 95% confidence interval (CI) were
180 calculated to assess the spread of data points around each regression line.

181

182 In order to obtain relative values to compare results from individuals of different size, muscle mass,
183 PCSA and F_{length} were normalized to body mass (BM) by dividing each value by the subject's BM,
184 $BM^{0.67}$ and $BM^{0.33}$ respectively. We used body mass (BM) as our independent variable and the target
185 architectural parameter as our dependant variable. Overall, we followed a similar approach as that
186 described by Allen et al. (2010,2014).

187 Briefly, for two objects to be considered geometrically similar (and thus for an isometric scaling
188 pattern to be inferred), areas should scale to the square product of lengths and volumes to the cube
189 of lengths. Because mass is a volumetric property, the dependant variable is considered to scale
190 isometrically if the mass of the structure scales with BM^1 , areal properties (PCSA, TCSA) scale to
191 $BM^{0.67}$ and lengths scale to $BM^{0.33}$, whereas angles and other non-dimensional variables should scale
192 as BM^0 .

193

194 **Results**

195 We obtained 6524 measurements of seven different muscle-tendon architectural parameters from
196 34 pelvic limb muscles and four pelvic limb bones in 17 emus from 3.6 to 42 kg of body mass. We
197 found strong evidence for positive allometric scaling for many of these architectural parameters, as
198 described below. To aid interpretation of our results, we have divided the muscles of the limb into
199 proximal (those acting mostly on the hip and knee joints) and distal (those acting on the ankle, foot
200 and digits) groups and have used this division to compare trends between the two regions.

201 *Bone lengths*

202 The lengths of the four bones scaled with moderate positive allometry (expected slope representing
203 isometry would be 0.33). The femur had the least marked allometric exponent (0.38), whilst the
204 tarsometatarsus the greatest (0.44), the tibiotarsus had a slope value of 0.41 and for the 1st phalanx
205 of the second digit (P1) the value was 0.39 (for full results see Table 2).

206

207 *Myology, architectural characteristics of muscles and functional interpretation*

208 We classified a total of 34 muscles in Table 1. As noted by Regnault et al. (2014), there is no patellar
209 ossification in the knee joint of emus, unlike ostriches and some other palaeognaths as well as most
210 extant birds. Although muscle origins, insertions and paths were generally found to agree with
211 previous publications (Haughton 1867; Patak & Baldwin 1998; Vanden Berge & Zweers 1993) and
212 hence detailed re-description is unnecessary, there were a few muscles for which we have found
213 some differences worth noting, or for which we needed to use methodological simplifications:

214

215 M. iliotibialis lateralis pars postacetabularis (IL): The distal fusion and similar actions of both parts of
216 the IL muscle (Fig.1) meant that, in order to avoid dissection errors when finding the division
217 between the cranial and caudal parts of the muscle, we measured and presented them together.

218 M. ilioprochantericus cranialis (ITCR): Although this was a clear, separate muscle in most specimens
219 (Fig. 2), it was found to be fused with the ITM in two specimens of body mass ~20 kg, which is a
220 common finding in birds (Gangl et al. 2004)

221 M. ischiofemoralis (ISF): This small muscle is difficult to detect and dissect, which is likely to have
222 affected the accuracy of the data obtained from it (leading to lower R² values and wider 95% CI
223 ranges). Its action is likely to involve fine motor control, proprioception and stabilisation of the hip
224 joint, given its very small size. Some studies have considered this muscle to be absent (or fused with
225 other muscles; e.g., CFP) in emus (Haughton 1867; Patak & Baldwin 1998), which would be unusual
226 for any birds. The origin and insertion of the muscle that we label the ISF (Fig. 3) is best interpreted
227 as a reduced -- but still present -- muscle, similar to that in ostriches (Gangl et al. 2004; Zinoviev
228 2006).

229 M. caudofemoralis pars pelvica (CFP): We consider, contrary to other reports (Haughton 1867; Patak
230 & Baldwin 1998), that this muscle is present in emus (Fig. 2). Prior studies classified this muscle as
231 the "iliofemoralis" but we agree with the *Nomina Anatomica Avium* (Vanden Berge & Zweers 1993)
232 and other reports (Gangl et al. 2004; Hutchinson 2004a; Hutchinson et al. 2014; Zinoviev 2006) that
233 it is present in ratites, related to a reduced portion of the large caudofemoralis muscle that is
234 ancestrally present in tailed reptiles (Gatesy 1999). There is no evidence of a caudalis part to the M.
235 caudofemoralis in emus, unlike in ostriches (Gangl et al. 2004) and some other ratites, so this sub-
236 division of the CFP is either fused to the CFP or lost.

237 M. ambiens (AMB): We found this muscle to have two insertions, previously unnoticed: a tendinous
238 one onto the tibia and a fleshy one onto the distal femur. Unusual modifications of this muscle seem
239 common in ratite birds (Hutchinson et al. 2014)

240 M. popliteus: This is a short, deeply positioned, fleshy muscle with multiple fibrous planes within it,
241 originating on the caudolateral, proximal aspect of the tibiotarsus and inserting onto the medial side
242 of the proximal fibula (Fig. 3). It is likely a stabiliser or pronator/supinator of the fibula, as in
243 ostriches (Fuss 1996), and may act as a proprioceptive or ligament-like structure.

244 *Normalized data for individual muscles*

245 To allow relative comparisons between muscle measurements, we normalized data from only the 16
246 month old (Group 3, adult birds) emus. Data are only presented for adult emus so as not to influence
247 the relative proportions due to ontogenetic allometry. The entire ontogenetic data set was analysed
248 similarly with negligible differences found, indicating that the relative patterns seen between
249 muscles for adults are present in very young birds as well. Data for muscle mass, fascicle length and
250 PCSA are presented in Figure 4. The largest relative muscles with regards to mass were three
251 proximal (ILPO, ILFB and IC) and three distal muscles (GM, FL and GL). This order changes when
252 muscles are ranked according to PCSA because parallel-fibred muscles tend to drop down the list,
253 with the large ILPO being the only parallel-fibred muscle seen in the top 10 of a list that is otherwise
254 dominated by distal muscles (FL, GM, GL and FPDIII). On the other hand, when fascicle length is
255 compared, the three parts of the gastrocnemius (GIM, GM and GL) are the only distal muscles listed
256 amongst the 10 muscles with the longest fascicles. . The four muscles with the longest fascicles are
257 the FCLP, IC, ILFB and ILPO.

258 *Limb muscle masses*

259 Total mass values of the hindlimb musculature represented a mean of 13.4±3% of BM, with the
260 proximal limb musculature (PLM) representing 61±2% of limb muscle mass and the distal limb
261

262 muscles (DLM) accounting for the remaining 39±2%. However, if only values for the six largest birds
263 (adults) are analysed, limb muscle mass accounts for 15±1% of BM. The limb muscle mass is only
264 11±3% of body mass in the five birds that were 4-6 weeks old.

265

266 *Scaling regression analysis*

267 The slopes of the reduced major axis regression lines for muscle properties vs. body mass are shown
268 in Tables 3 and 4, with R^2 and 95% CIs, as well as represented in Figures 5 (A and B) and 6. Ranges of
269 the slope and amplitudes of the CIs referred to below are the upper and lower bounds of the 95%
270 CIs for the regression slopes. Scaling exponents and CIs are presented in Table 3. Scaling exponents
271 and lines representing isometry are plotted in Figure 5A and 5B (M_m , L_f and PCSA) and Figure 7 (M_{ten} ,
272 L_{ten} and TCSA). In summary, there was strong positive allometry of muscle mass and mild positive
273 allometry or isometry of fascicle length, leading to a marked positive allometry of PCSA.

274

275 *Scaling of limb muscle masses*

276 We found limb muscle mass as well as the masses of proximal (PLM) and distal limb muscles (DLM)
277 to be tightly correlated with body mass across all three groups. The regression slope of limb muscle
278 mass vs. BM was 1.16 (1.05<CI<1.29, $R^2=0.96$), whilst PLM had a value of 1.14 (1.02<CI<1.27,
279 $R^2=0.96$) and DLM exhibited a slope of 1.20 (1.09<CI<1.32, $R^2=0.97$).

280

281 Consistent with the trends for the hindlimb more broadly, the individual muscles also generally
282 showed positive ontogenetic allometry. Out of 34 muscles, 26 had slopes for M_m vs. BM with their
283 lower CI limit >1 (consistent with positive allometry), and only eight (ITCr, ITM, IFI, ISF, FCLA, FMTL,
284 AMB and FPPDII) had a lower CI boundary for the regression slope lower than 1 (indicating potential
285 negative allometry). Of the 26 muscles showing positive allometry of M_m , we found strong positive
286 allometry (regression slopes with the lower boundary of the CI greater than 1.1) in 18/34.

287

288 Similarly, scaling patterns of the muscle masses for the USA group of emus (Figure 6), showed similar
289 scaling patterns to the UK group, with only five muscles having a lower CI boundary <1 (POP, ILPO,
290 FPDIV, OBTII and FPDII) and the remaining having their CIs entirely within positive allometry values.

291

292 *Scaling of muscle fascicle length*

293 In general, fascicle length (L_f) was only moderately well correlated with body mass due to substantial
294 variation in the data (a combination of inevitable measurement errors, sampling bias and true
295 biological variation, as usual for muscle fascicle measurements (e.g., Allen et al. [2010,2014]) The
296 datasets for four muscles (ISF, PIFLM, FPDII and FPPDII) had a p value>0.05, so these are not
297 presented (Table 3). Of the remaining 30 muscles, only 16/30 had R^2 values >0.5. Scaling of L_f vs. BM
298 showed a trend towards positive allometry for 18/30 muscles (lower limit of the slope's CI >0.33),
299 and for the remaining 12 muscles a slope of 0.33 was included in the CIs, so isometry could not be
300 ruled out.

301

302 *Scaling of muscle PCSA*

303 The lower boundary of the CIs of the scaling slope was greater than 0.66 (i.e., exhibiting positive
304 allometry) for 27 muscles and a value <0.66 (suggesting a potential negative allometry of muscle
305 PCSA in emus) was obtained for eight muscles (ITM, ITC, IFI, FMTL, AMB, TC and FPPDII) (Table 3).

306

307 *Scaling of tendon mass*

308 We recorded tendon characteristics for 28 muscles (Table 4); the six muscles excluded did not have a
309 discrete tendon at either of their attachments (CFP, FCLA, FCLP, IC, PIFLM, POP). We encountered
310 difficulties in achieving a consistent method for tendon dissection and measurement of muscles with
311 thin (IFE, AMB), very short (ISF and IFI) or multiple tendons (FMTM, FMTIM), which lead us to
312 exclude data from these as well. The tendon of the GIM was included with the GM tendon, and the

313 FMTL tendon was not measured because the muscle was transected at the proximal aspect of the
314 large patellar tendon for studies of patellar tendon morphology by Regnault et al. (2014). Thus data
315 are presented for the tendons of 20 muscles. The major gastrocnemius tendon resulting from the
316 fusion of the tendons of the three gastrocnemius muscles was dissected by transecting the tendon
317 of the GL at the site of fusion onto the common tendon; therefore the GM remained with the
318 extensive common portion of the tendon, which distally was transected at its insertion onto the
319 fibrous scutum at the level of the ankle joint.

320

321 The scaling slopes for tendon mass indicate positive allometry in 10 out of 20 tendons (lower CI
322 boundary >1) across emu ontogeny. The masses for the remaining ten tendons scaled with isometry
323 (lower CI<1.0, upper CI>1.2)..

324 *Scaling of tendon length*

325 We measured L_{ten} for the same 20 muscles for which we obtained tendon masses (Table 4), from
326 the end of the muscle belly to the insertion. Statistical analysis of one muscle (ITCr) led to exclusion
327 of this muscle because the p value was >0.05. For the other 19 tendons, the general scaling trend
328 was towards strong positive allometry, with 16 muscles having the lower limit of the CI >0.33. In
329 three muscles (FCM, GM, FL), the lower CI for tendon length was <0.33, indicating isometry for
330 length in these tendons. Given these patterns, we infer a general trend for positive allometry of
331 tendon length in growing emus.

332

333 *Scaling of tendon cross-sectional area*

334 Average TCSA was calculated for the same 20 tendons as above (Table 4). The dataset for ILPO had a
335 p value >0.05 and was excluded. Of the 19 remaining tendons, 10 showed a lower CI limit of the
336 slope consistent with positive allometry (>0.66). The remaining nine tendons showed ontogenetic
337 isometry for TCSA.

338

339

340 **Discussion**

341 Emus, like other ratites and other precocial birds, must have locomotor independence from hatching
342 and develop into large, running adult birds within 16-18 months (Davies & Bamford 2002). Taking
343 into consideration their initial development within the egg, their ontogeny poses interesting
344 questions about their locomotor development, related to our study's aims, such as: How do muscle
345 structure and anatomy change to accommodate precocial development in emus? What are the
346 strategies that growing emus use to maintain tissue mechanical safety factors during rapid
347 development of cursorial morphology and high-speed locomotor abilities? Our data suggest some
348 answers to these questions, as follows.

349

350 *Scaling patterns across ontogeny*

351 We found positive allometry of emu pelvic limb muscle masses, indicating that most muscles get
352 become significantly more powerful (in relative and absolute terms) as the animals grow. However,
353 the functional relevance of this observation is slightly mitigated by a less marked positive allometry
354 of PCSA (and therefore maximal muscle force), driven by a trend for fascicle length that is closer to
355 isometry (i.e., preserving geometric similarity).

356 In the proximal part of the pelvic limb of emus, the developmental and functional mechanics appear
357 to rely on the arrangement of large and metabolically expensive muscles (ILPO, ILFB, IC, FCLP and
358 FMTL) to provide the wide range of motion of the knee joint (and hip, during faster running) in
359 combination with a relatively short femur that scales close to isometry. This arrangement also leads
360 to a proximal to distal gradient of muscle mass, which has been previously reported for other birds
361 (Paxton et al. 2010; Smith et al. 2006) and has long been thought to favour energy-savings by

362 keeping the distal end of the limb light and its muscles dependent on springy tendons. The proximal-
363 distal gradient also concentrates large, power-generating muscles in the proximal limb (Alexander
364 1974; Alexander 1991) with large moment arms (Hutchinson et al. 2014; Smith et al. 2007) and thus
365 the ability to produce the considerable joint moments needed for high-speed running (Hutchinson
366 2004a,b).

367 The distal limb, on the other hand, is heavily dependent on the triad of *M. gastrocnemius* (GL, GIM
368 and GM) along with *M. fibularis longus* (FL); both ankle extensors; as well as *M. tibialis cranialis* (TC)
369 and *M. extensor digitorum longus* (EDL); both ankle flexors. Combined, these muscles constitute
370 80% of the muscle mass and 60% of the force-generating capacity (PCSA) of this portion of the limb.
371 The unusual proportion of body mass taken up by the ankle extensors has been noted before
372 (Hutchinson 2004a) and is likely an ancestral characteristic of birds (e.g., Paxton et al. 2010) but is
373 taken to an extreme in large ratites (e.g., Smith et al. 2006).

374 Further distally, the long and slender tarsometatarsus bone lends itself well as a support for the long
375 tendons of the digital flexor muscles which in turn provide essential springs used in support and
376 propulsion of the limbs and body. The relatively small muscles and long tendons of the digital flexors
377 make them likely to operate mainly as energy storage devices at faster speeds, as seen in other
378 species like horses and smaller running birds (Biewener 1998; Daley & Biewener 2011). The positive
379 allometry of many tendon properties in emus is in line with this increase in force-generating capacity
380 seen during ontogeny. As in most other birds, the tendons running along the tarsometatarsus are
381 almost exclusively on the cranial and caudal (dorsal/plantar) side. It would also be interesting to
382 know the effect on bone strains from this “bow and arrow” anatomical arrangement between the
383 tarsometatarsus and the dorsal/plantar tendons to see if it influences the predominantly torsional
384 loads experienced by the two proximal pelvic limb bones (Main & Biewener 2007).

385 For these spring-like tendons, a trade-off between muscle force and tendon elasticity does not seem
386 to occur in emus. This lack of a trade-off is indicated by the similar scaling patterns of the cross-
387 sectional areas of the digital flexor muscles and tendons, both of which trend towards positive
388 allometry across emu ontogeny. As seen in other species (Ker et al. 1988), the relative increases in
389 the cross-sectional areas of tendons might maintain tendon safety factors (maximal stresses before
390 failure vs. *in vivo* maximal stress) as emus increase in size. However, tendons might also change their
391 biomechanical properties (Young’s modulus) with age, as seen in other species (Shadwick 1990;
392 Thorpe et al. 2014), therefore influencing biomechanical interpretations of the data presented here.
393 Without measuring tendon elastic modulus with age, it is difficult to interpret how tendon stiffness
394 and safety factor might change with age in emus.

395 To complement data from a prior study showing the scaling patterns of the cross-sectional areas of
396 the femur and tibiotarsus of emus to be close to isometry (Main & Biewener 2007), here we
397 analysed the scaling patterns of the lengths of the three longest limb bones and the first phalanx of
398 the third toe. Our data indicate positive allometry of the two longer bones, the tibiotarsus (lower CI
399 limit=0.37) and tarsometatarsus (lower CI limit=0.39), but a less marked positively allometric scaling
400 trend for the femur (lower limit of CI=0.34) and for the first phalanx of digit III (lower CI limit=0.33).
401 These results differ from those reported for another ratite, the greater rhea (*Rhea americana*), in
402 which only the tarsometatarsus showed positive allometry (Picasso 2012a) but interestingly are in line
403 with general interspecific scaling exponents found for pelvic limb bone lengths across different
404 species of palaeognaths (Cubo & Casinos, 1996). Considering our results, if similar cross-sectional
405 geometry is assumed along the length of the bone shafts, this would lead to an increase in strains (at
406 least in bending, due to larger moments) at the mid-shaft with increasing body mass. However,
407 changes in cross-sectional areal geometry have been shown to lead to slight positive allometry of
408 the cross-sectional geometry of avian limb bones across species (Doube et al. 2012) and
409 ontogenetically (Main & Biewener 2007). As these geometrical changes might not suffice to explain

410 the increases in strain magnitudes seen during ontogeny, they leave unexplained the role of internal
411 forces (of soft tissues) on bone mechanics and consequently their influence on bone morphology
412 during growth.

413 Although there are very limited data on the ontogeny of skeletal muscle physiology, experiments in
414 mice and cats (Close 1964; Close & Hoh 1967) demonstrate that although muscle force: velocity
415 parameters change from newborns to adults, these changes appear to occur in a relatively short
416 period and therefore newborn muscle, after the first few days of life, becomes similar to that of
417 adults. However, mice and cats, like many other mammals, are born with neuromotor immaturity
418 (Muir 2000), in contrast to emus. It is therefore reasonable to speculate that, like other birds (Gaunt
419 & Gans 1990), emus are unlikely to have appreciable changes in muscle physiology during growth.
420 Thus changes in functional (e.g., maximal force-generating capacity) and biomechanical parameters
421 should be detectable by anatomical studies such as ours.

422 Few studies have quantified the ontogenetic scaling patterns of limb musculature in birds (Carrier &
423 Leon 1990; Dial & Carrier 2012; Paxton et al. 2014; 2012b; Picasso 2014), but positive allometry
424 predominates in the muscle masses involved in the major adult mode of locomotion (flying vs.
425 cursorial). In the Californian gull, the *M. gastrocnemius* scaled isometrically but the *M. pectoralis* had
426 strong positive allometry with an inflection point when the fledglings started exercising their wings
427 (Carrier & Leon 1990). Paxton et al. (2014; also 2010) recently reported the ontogenetic scaling
428 patterns of the musculature of a highly modified galliform, the broiler chicken. These birds,
429 unsurprisingly due to their selective breeding, were found to have positive allometry of muscle
430 masses of the main pelvic limb muscles but isometry of the fascicle lengths (Paxton et al. 2014), a
431 pattern that is nonetheless similar to our findings. Picasso et al. (2012b) found quite similar scaling
432 patterns across rhea ontogeny: an average 64-fold increase in pelvic limb muscle mass from 1 month
433 of age to adulthood whilst only a 34-fold increase in body mass. In a later study, where scaling
434 exponents were calculated, a more generalised positively allometric scaling was found in these
435 South American ratites compared to emus: with all muscle masses but two (where isometry was
436 evident) scaling with positive allometry (slopes ~ 1.3). Total limb muscle mass of rheas scaled with an
437 exponent of 1.18 (Picasso 2014), which is similar to our value of 1.16. Together, these data suggest
438 that positive allometry prevails across ontogeny for leg muscles in extant birds with precocial
439 development; potentially a homologous feature of their development that is quite unlike the
440 isometry prevailing in their closest extant relatives, Crocodylia (Allen et al., 2010, 2014).

441 Dial and Carrier (2012) suggested that birds must optimise their energy consumption to achieve their
442 ultimate functional gait whilst channelling resources to their precocial gait (Dial & Carrier 2012)
443 (running vs. swimming or flying). Ratites are unusual for birds in that they solely have terrestrial gaits
444 throughout their life and, in the case of emus, their wings have atrophied to such an extent that they
445 should not present much metabolic competition to hindlimb development. Considering the
446 approximately isometric overall scaling of kinematic parameters (e.g., stride lengths, stride
447 frequencies, duty factors) seen in ratites (Main & Biewener 2007; Smith et al. 2010), it is likely that
448 this increase in muscle masses will lead to a limb that is adapted for power production and perhaps
449 (considering our less allometric tendon results) elastic energy storage/return. The former is also
450 supported by metabolic studies which found a predominance of fast fibres in the *M. gastrocnemius*
451 of adult emus (Patak 1993), although more studies of muscle physiology in emus and other ratites
452 would be valuable.

453 The need for locomotor independence and high performance in vulnerable, young, precocial and
454 cursorial birds might favour allometry of muscle architecture (Carrier 1996). If so, could adult muscle
455 phenotypes be a reflection of the locomotor needs during early development and therefore be
456 overdesigned for their demands? Alternatively, negative allometric scaling in the musculoskeletal
457 system may occur as seen in goats (Main & Biewener 2004) and jackrabbits (Carrier 1983). It is hard

458 to draw an inference from our data, because the overall positive allometry seen in the pelvic limb
459 musculature could indicate a necessity to grow faster and stronger to adulthood to compensate for a
460 juvenile disadvantage or could reflect selective pressures on the locomotor ontogeny of emus in
461 which muscles congenitally primed for fast growth during adolescence could lead to continued
462 growth past an optimum in adulthood. Although direct measurements of maximal performance of
463 complex locomotor systems is problematic, a modelling approach using the data presented here
464 could be a valid approach to answer this question.

465 *How well are farmed emus representative of the species overall?*

466 Although emu farming is relatively common, its goal is to extract meat, oil and skin and therefore
467 these birds are not bred in captivity for their locomotor behaviour, nor do they suffer strong
468 predatory pressures on it. The diet of captive bred birds as well as their relative sedentary regime
469 when compared to wild animals is likely to influence tissue development and distribution. However,
470 as farming of these birds is a recent activity and it is not a highly specialised or intense process as
471 with other domesticated species (Goonewardene et al. 2003), it is unlikely that heritable traits of the
472 emu musculoskeletal system have been significantly altered. Therefore, we expect the muscle
473 distribution and scaling patterns of our emus to be similar to wild emus.

474
475 By presenting muscle mass data from two distinct groups of birds (UK and USA groups), we
476 established that these groups at least have similar scaling patterns, ruling out any potential bias
477 imposed by different breeding regimes. With regards to diet, it was apparent that our birds were
478 carrying a significant amount of subcutaneous and peritoneal fat; likely encouraged by their *ad*
479 *libitum* access to a commercial pelleted diet. The influence of body fat on our scaling results is hard
480 to test with the available data, but Hutchinson et al. (2014) noted a possible reduction in relative
481 muscle masses in wild vs. captive bred ostriches, which could also apply to emus. Regardless, it is
482 less certain that the scaling patterns for muscle/tendon architecture observed here would differ in
483 wild vs. captive emus.
484

485 *Conclusions*

486 We have provided a new dataset on the ontogenetic scaling of pelvic limb anatomy and muscle
487 architectural properties of a cursorial bird (the first complete architectural dataset of its kind), and
488 we have done this using a group of 17 emus across a tenfold increase in body mass. A marked trend
489 of positive allometry of muscle masses and PCSAs is accompanied by less marked positive allometry
490 of fascicle lengths. Tendons, specially the long digital flexors, also demonstrate positive allometry of
491 their lengths, as do the two longer limb bones (tibiotarsus and tarsometatarsus). We have
492 illuminated the ontogenetic adaptation of the musculoskeletal system in an extreme example of size
493 variation during rapid growth. Our dissections refined the myology of the pelvic limb in emus (Table
494 1 and Figures 1-3) and found some anatomical aspects that were previously misunderstood. This is
495 important, as functional studies depending on inaccurate anatomical accounts of the myology could
496 obtain unrealistic results from biomechanical models using such data (Goetz et al. 2008; Hutchinson
497 et al. 2014). This work should be a valuable resource for future functional, comparative and
498 evolutionary studies of emus, other birds and extinct related animals.
499

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507 manuscript.

508 Tables and table captions

509 Table 1. Pelvic limb muscles of emus and their apparent actions.

Muscle	Abbreviation	Origin	Insertion	Action
<i>M. iliotibialis cranialis</i>	IC	Dorsal edge of preacetabular ilium	Insertion on the medial aspect of the proximal tibiotarsus	Main: Hip flexion; knee extension/flexion Other: Hip medial rotation, adduction
<i>M. iliotibialis lateralis</i> (cranial and caudal portions)	ILPO	Lateral edge of acetabular ala	Cranio-lateral proximal tibiotarsus (cranial and lateral cristae cnemiales) via aponeurosis (combined with FMTL)	Main: Hip extension, abduction; knee extension Other: Hip medial/lateral rotation
<i>M. iliotrochantericus cranialis</i>	ITCr	Cranial surface of preacetabular ilium	Lateral aspect of the femoral trochanteric crest (distal to IFE insertion)	Main: Hip flexion, medial rotation Other: Hip abduction/adduction
<i>M. iliotrochantericus medialis</i>	ITM	Craniodorsal surface of preacetabular ilium	Lateral aspect of the femoral trochanteric crest (proximal to IFE insertion)	Main: Hip flexion, medial rotation Other: Hip abduction/adduction
<i>M. iliotrochantericus caudalis</i>	ITC	Ala preacetabularis ilii: fossa iliaca dorsalis	Lateral aspect of the femoral trochanteric crest	Main: Hip flexion, medial rotation Other: Hip abduction/adduction
<i>M. iliofibularis</i>	ILFB	Ala postacetabularis ilii: facies lateralis	Proximal third of the corpus fibulae	Main: Knee flexion, hip extension Other: Hip abduction
<i>M. iliofemoralis externus</i>	IFE	Crista iliaca dorsalis, dorsal to foramen acetabulum	Lateral side of femoral trochanteric crest (between ITC and ITM insertions)	Main: Hip flexion, abduction Other: Hip medial/lateral rotation
<i>M. iliofemoralis internus</i>	IFI	Ventral preacetabular ilium	Medial side of proximal femoral shaft; tubercle	Main: Hip flexion, adduction Other: Hip medial/lateral rotation
<i>M. ischiofemoralis</i>	ISF	Cranial margin of the foramen ilioischadicum	Proximal caudal femur under origin of FMTL	Main: Hip abduction, lateral rotation Other: Hip flexion/extension
<i>M. caudofemoralis p. pelvica</i>	CFP	Caudolateral ilium and ischium	Proximal caudomedial femur	Main: Hip extension Other: Hip lateral rotation, abduction
<i>M. flexor cruris lateralis pars pelvica</i>	FCLP	Caudolateral corner of pelvis	Proximal craniomedial tibiotarsus	Main: Hip extension, abduction Other: Medial rotation of hip and knee; knee flexion
<i>M. flexor cruris lateralis pars accessoria</i>	FCLA	By a raphe from the distal third of the FCLP	Caudomedial femoral shaft	Main: Hip extension, abduction Other: Hip medial rotation
<i>M. flexor cruris medialis</i>	FCM	Caudolateral extremes of ischium and pubis	Via split cranial aponeurosis: on the caudal femoral shaft, and on the caudoproximal	Main: Hip extension, abduction; knee flexion Other: Hip medial rotation

			tibiotarsus, caudodistally to the insertion of the FCLP.	
<i>M. puboischiofemoralis p. lateralis and p. medialis</i>	PIFLM	Along the length of the lateral ischium	Via thin tendinous insertion onto the caudal aspect of the femoral shaft	Main: Hip extension, abduction Other: Hip lateral rotation
<i>M. femorotibialis lateralis (Cranial, intermediate and caudal portions)</i>	FMTL	Caudolateral surface of femoral shaft. With 3 fused parts: cranial, intermediate and caudal	Crista cnemalis of tibiotarsus via a thick patellar tendon (no ossified patella) with ILPO	Knee extension
<i>M. femorotibialis intermedialis</i>	FMTIM	Cranial surface of the proximal femoral shaft	Medial side of crista cnemalis cranialis of tibiotarsus	Knee extension
<i>M. femorotibialis medialis</i>	FMTM	3 distinct heads originating from the medial surface of the femur, cranial and caudal portions on the proximal third and distal portion on the distal third	Proximo-medial extremity of tibiotarsus	Knee flexion, adduction
<i>M. obturatorius medialis (Ilium – Ischium part)</i>	OMII	Surface of fenestra ilioischium	Long tendon that passes through the foramen ilioischadicum and inserts onto the lateral side of the femoral trochanteric crest	Main: Hip lateral rotation Other: Hip flexion, adduction
<i>M. obturatorius medialis (Ischium – pubis part)</i>	OMIP	Surface of fenestra ischiopubica	As OMII	Main: Hip lateral rotation Other: Hip flexion, adduction
<i>M. ambiens</i>	AMB	Cranial pubic rim (preacetabular process)	Two insertions on the medial knee ligaments, one tendinous and the other one fleshy	Main: Hip adduction; knee flexion Other: Hip medial rotation
<i>M. gastrocnemius lateralis</i>	GL	Lateral condyle of femur, aponeurosis of M. Iliotibialis and tendon from cranial fibula	Tendons fusing to form a thick fibrous calcaneal pad, onto caudal side of tarsometatarsus (Calcaneal scutum)	Main: Ankle extension; knee flexion
<i>M. gastrocnemius medialis</i>	GM	Aponeurosis of M. Iliotibialis and facies gastrocnemialis, connecting to the medial surface of the proximal tibia	As GL	Main: Ankle extension; knee flexion
<i>M. gastrocnemius Intermedius</i>	GIM	Craniolateral femur, adjacent of the origin of FHL muscle	As GL and GIM	Main: Ankle extension; knee flexion
<i>M. fibularis longus</i>	FL	Proximal origin from medial distal patellar ligament and craniolaterally onto proximal tibiotarsus.	Two tendinous insertions: Plantar calcaneal scutum and joining the tendon of FPDIII	Main: Ankle extension Other: Knee flexion; toe flexion via FPDIII tendon
<i>M. tibialis cranialis c. tibiale and c. femorale</i>	TC	2 heads: A fleshy one onto the proximal cranial tibiotarsus, and via a thick tendon onto the cranial aspect of the lateral trochlear ridge of the femur	Cranial side of proximal tarsometatarsus	Main: Ankle flexion Other: Knee extension (femoral head)
<i>M. popliteus</i>	POP	Medial side of proximal fibula	Caudal side of proximal tibiotarsus	Main: Fibular rotation
<i>M. flexor perforatus digiti II</i>	FPDII	Via origin of FPDIII	Splits into 2 branches at level of proximal phalanx to insert on either side of middle	Main: Digit II flexion Other: Ankle extension

			phalanx, ventrally	
<i>M. flexor perforatus digiti III</i>	FPDIII	2 tendons: Cranial fibula and medial side of the medial condyle of the femur	Proximal phalanx, small portion fused to FPPDII tendon in some specimens, ventrally	Main: Digit III flexion Other: Ankle extension
<i>M. flexor perforans et perforatus digiti II</i>	FPPDII	Deep fibular tendon of GL muscle	Middle phalanx of digit II, ventrally	Main: Digit II flexion Other: Ankle extension
<i>M. flexor perforans et perforatus digiti III</i>	FPPDIII	Lateral knee ligaments and FPDIV origin	Middle phalanx of digit III, ventrally	Main: Digit III flexion Other: Ankle extension
<i>M. flexor perforatus digiti IV</i>	FPDIV	Superficial side of FPDIII origin	Proximal and middle phalanges of digit IV, ventrally	Main: Digit IV flexion Other: Ankle extension
<i>M. flexor hallucis longus</i>	FHL	2 heads: lateral and caudal aspects of distal femur near condyles	Fuses with FDL tendon	Main: Ankle extension; knee flexion
<i>M. flexor digitorum longus</i>	FDL	2 heads: proximal tibiotarsus and distal third of fibula (3/4 of length)	Splits into 3 parts above MTP joint to insert onto the distal, ventral phalanx of each toe	Main: Digits II, III and IV flexion Other: Ankle extension
<i>M. extensor digitorum longus</i>	EDL	Cranial proximal tibiotarsus	Dorsal surface of each phalanx	Main: Digits II, III and IV extension; ankle flexion

510

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Bone	Scaling exponent	Lower 95% CI	Upper 95% CI	R ²
Femur	0.38	0.34	0.42	0.96
Tibiotarsus	0.41	0.38	0.45	0.97
Tarsometatarsus	0.44	0.39	0.49	0.96
First Phalanx (Dig III)	0.39	0.33	0.46	0.91

511 **Table 2.** Regression analysis results for the lengths of the four limb bones. The lower 95% boundary
512 (>0.33) demonstrates positive allometry of the tibiotarsus and the tarsometatarsus but results are
513 closer to isometry for the femur and first phalanx of digit III.

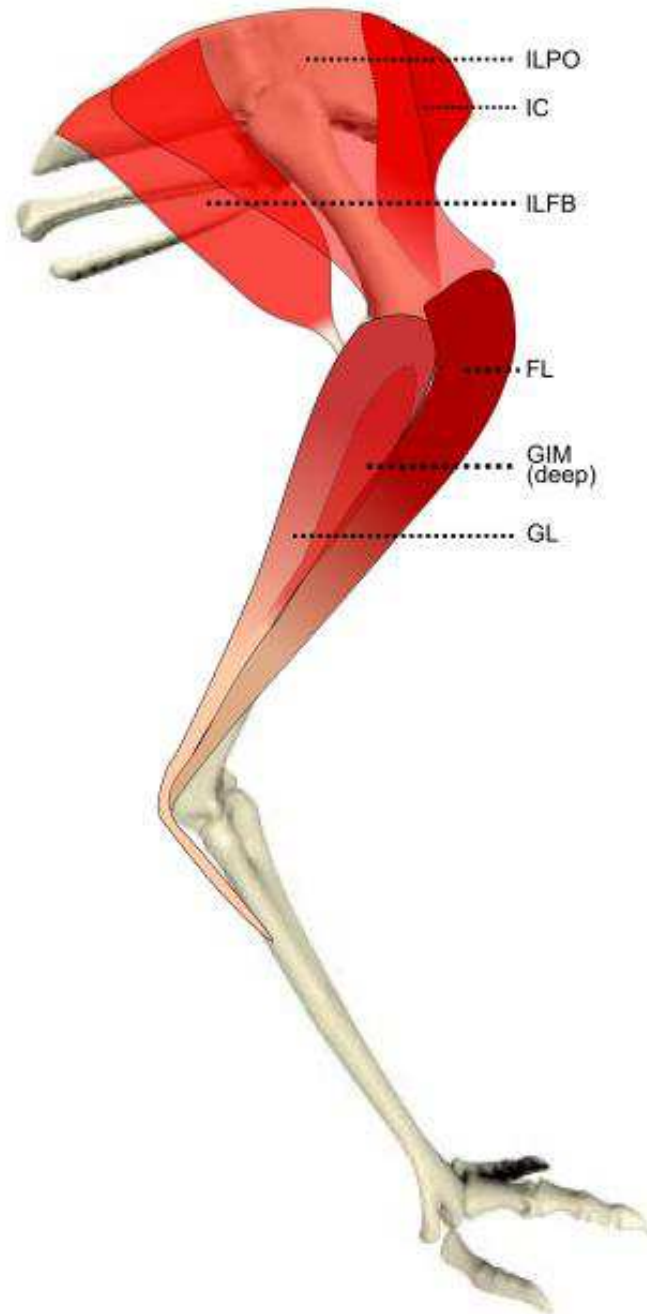
514

Muscle	M_m vs BM					L_f vs BM					$PCSA$ vs BM				
	Outliers	Slope	Lower 95% CI	Upper 95% CI	R^2	Outliers	Slope	Lower 95% CI	Upper 95% CI	R^2	Outliers	Slope	Lower 95% CI	Upper 95% CI	R^2
AMB	0	1.08	0.96	1.21	0.96	0	0.42	0.31	0.57	0.67	0	0.81	0.64	1.03	0.81
CFP	0	1.18	1.09	1.28	0.98	0	0.48	0.31	0.73	0.36	0	0.94	0.78	1.13	0.89
EDL	0	1.25	1.10	1.41	0.95	0	0.54	0.39	0.75	0.64	0	0.82	0.67	1.01	0.86
FCLA	1	1.16	0.95	1.43	0.87	1	0.36	0.24	0.53	0.51	1	0.89	0.73	1.09	0.87
FCLP	0	1.26	1.16	1.36	0.98	0	0.33	0.24	0.44	0.69	0	0.99	0.89	1.09	0.97
FCM	1	1.31	1.16	1.48	0.95	1	0.60	0.39	0.91	0.42	1	0.95	0.75	1.20	0.83
FDL	1	1.29	1.15	1.44	0.96	1	0.58	0.37	0.90	0.36	1	0.93	0.76	1.15	0.86
FHL	1	1.22	1.04	1.42	0.93	1	0.66	0.42	1.04	0.34	1	0.98	0.70	1.37	0.64
FL	0	1.32	1.23	1.42	0.98	0	0.44	0.33	0.58	0.73	0	0.98	0.84	1.16	0.91
FMTIM	0	1.24	1.05	1.48	0.90	0	0.64	0.43	0.97	0.40	0	0.99	0.70	1.41	0.57
FMTL	0	1.19	0.95	1.49	0.83	0	0.43	0.31	0.60	0.64	0	0.86	0.65	1.14	0.73
FMTM	0	1.29	1.05	1.59	0.86	0	0.45	0.29	0.70	0.31	0	0.99	0.80	1.22	0.85
FPDII	0	1.45	1.26	1.67	0.93	-	-	-	-	-	0	1.40	1.06	1.84	0.74
FPDIII	0	1.34	1.19	1.51	0.95	0	0.60	0.41	0.88	0.47	0	1.03	0.78	1.36	0.74
FPDIV	0	1.20	1.09	1.32	0.97	0	0.43	0.28	0.65	0.38	0	0.99	0.80	1.22	0.85
FPPDII	0	0.75	0.59	0.95	0.81	0	0.74	0.49	1.14	0.37	0	0.68	0.44	1.07	0.29
FPPDIII	0	1.29	1.15	1.45	0.96	-	-	-	-	-	0	0.98	0.72	1.34	0.67
GIM	0	1.32	1.01	1.73	0.75	0	0.46	0.34	0.63	0.69	0	1.03	0.72	1.48	0.54
GL	0	1.30	1.19	1.43	0.97	0	0.51	0.40	0.67	0.77	0	0.88	0.76	1.01	0.93
GM	0	1.24	1.14	1.33	0.98	0	0.34	0.26	0.43	0.77	0	0.93	0.82	1.06	0.95
IC	0	1.27	1.15	1.40	0.97	0	0.31	0.24	0.39	0.81	0	1.00	0.88	1.13	0.95
IFE	0	1.26	1.11	1.42	0.95	0	0.56	0.42	0.75	0.72	0	0.79	0.66	0.93	0.91
IFI	2	1.22	0.97	1.54	0.85	2	0.49	0.33	0.72	0.57	2	0.92	0.66	1.28	0.68
IB	0	1.32	1.22	1.42	0.98	0	0.36	0.30	0.44	0.89	0	0.98	0.89	1.07	0.97
ILPO	0	1.29	1.16	1.43	0.96	0	0.31	0.21	0.46	0.50	0	1.08	0.92	1.26	0.92
ISF	3	1.10	0.93	1.32	0.92	-	-	-	-	--	3	1.06	0.73	1.54	0.63
ITC	2	1.26	1.14	1.39	0.97	2	0.76	0.61	0.95	0.86	2	0.64	0.50	0.81	0.84
ITCr	0	1.16	0.99	1.36	0.92	0	0.37	0.27	0.50	0.68	0	0.89	0.70	1.13	0.80
ITM	2	1.12	0.83	1.51	0.75	2	0.78	0.49	1.23	0.39	2	0.89	0.55	1.45	0.29
OMII	0	1.23	1.10	1.39	0.95	0	0.73	0.46	1.15	0.27	0	1.05	0.76	1.45	0.65
OMIP	0	1.23	1.11	1.36	0.97	0	0.53	0.36	0.77	0.49	0	0.94	0.77	1.15	0.87
PIFLM	0	1.24	1.13	1.36	0.97	-	-	-	-	-	0	1.11	0.89	1.39	0.83
POP	2	1.44	1.17	1.76	0.88	2	0.68	0.41	1.13	0.22	2	1.15	0.88	1.51	0.79
TC	0	1.20	1.08	1.33	0.97	0	0.68	0.50	0.93	0.67	0	0.77	0.55	1.07	0.63

515 **Table 3.** Results of RMA linear regression of muscle architecture vs. body mass (BM) for the pelvic limb of *Dromaius novaehollandiae*, across ontogeny. M_m ,
516 muscle mass (kg); L_f , fascicle length (m), $PCSA$, physiological cross-sectional area (m²).

Tendon	M_{ten} vs BM					L_{ten} vs BM					TCSA vs BM				
	Outliers	Slope	Lower 95% CI	Upper 95% CI	R^2	Outliers	Slope	Lower 95% CI	Upper 95% CI	R^2	Outliers	Slope	Lower 95% CI	Upper 95% CI	R^2
EDL	0	1.26	1.10	1.44	0.94	1	-0.81	-1.07	-0.61	0.75	0	0.86	0.61	1.22	0.58
FCM	0	1.31	1.01	1.69	0.86	0	0.46	0.27	0.79	0.34	0	1.05	0.78	1.43	0.81
FDL	1	1.22	1.08	1.39	0.95	1	0.43	0.36	0.51	0.91	1	0.81	0.70	0.93	0.94
FHL	1	1.29	1.09	1.53	0.91	1	0.45	0.34	0.60	0.74	1	0.87	0.75	1.01	0.93
FL	0	1.33	1.15	1.52	0.94	0	0.39	0.31	0.50	0.81	0	0.99	0.82	1.20	0.88
FPDII	0	1.26	1.03	1.53	0.87	0	0.63	0.40	0.97	0.32	0	1.09	0.76	1.57	0.56
FPDIII	0	1.38	1.21	1.58	0.94	0	0.43	0.36	0.52	0.88	0	1.01	0.82	1.24	0.86
FPDIV	0	1.17	1.05	1.31	0.96	0	0.42	0.37	0.48	0.95	0	0.76	0.67	0.86	0.95
FPPDII	0	1.34	0.95	1.88	0.60	0	0.78	0.58	1.06	0.69	0	0.80	0.50	1.27	0.24
FPPDIII	0	1.24	1.06	1.44	0.92	0	0.43	0.38	0.49	0.95	0	0.83	0.68	1.03	0.85
GL	0	1.63	1.19	2.23	0.66	0	0.89	0.59	1.36	0.38	0	0.95	0.69	1.30	0.66
GM	0	0.98	0.78	1.23	0.83	0	0.28	0.18	0.43	0.37	0	0.79	0.64	0.97	0.85
IB	1	1.03	0.79	1.33	0.79	1	0.51	0.35	0.73	0.57	1	0.81	0.53	1.23	0.43
ILPO	2	1.38	0.99	1.93	0.68	2	1.04	0.69	1.56	0.51	-	-	-	-	-
ITC	3	1.04	0.81	1.33	0.84	3	0.61	0.44	0.83	0.74	3	0.75	0.46	1.22	0.34
ITCr	1	1.02	0.76	1.36	0.73	-	-	-	-	-	1	1.18	0.80	1.74	0.52
ITM	7	1.37	0.76	2.46	0.43	6	0.72	0.37	1.42	0.09	7	1.19	0.61	2.33	0.21
OMII	0	1.26	0.98	1.62	0.79	0	0.71	0.53	0.94	0.72	0	0.75	0.51	1.10	0.48
OMIP	0	0.99	0.74	1.33	0.70	1	0.48	0.36	0.65	0.71	1	0.67	0.44	1.02	0.43
TC	0	1.06	0.85	1.30	0.85	0	0.50	0.34	0.73	0.47	0	0.75	0.56	1.00	0.71

518 **Table 4.** Results of RMA linear regression of tendon dimensions vs. body mass (BM) for the pelvic limb of *Dromaius novaehollandiae*, across ontogeny. M_{ten} ,
519 tendon mass (kg); L_{ten} , tendon length (m); TCSA, tendon cross-sectional area (m²).



522

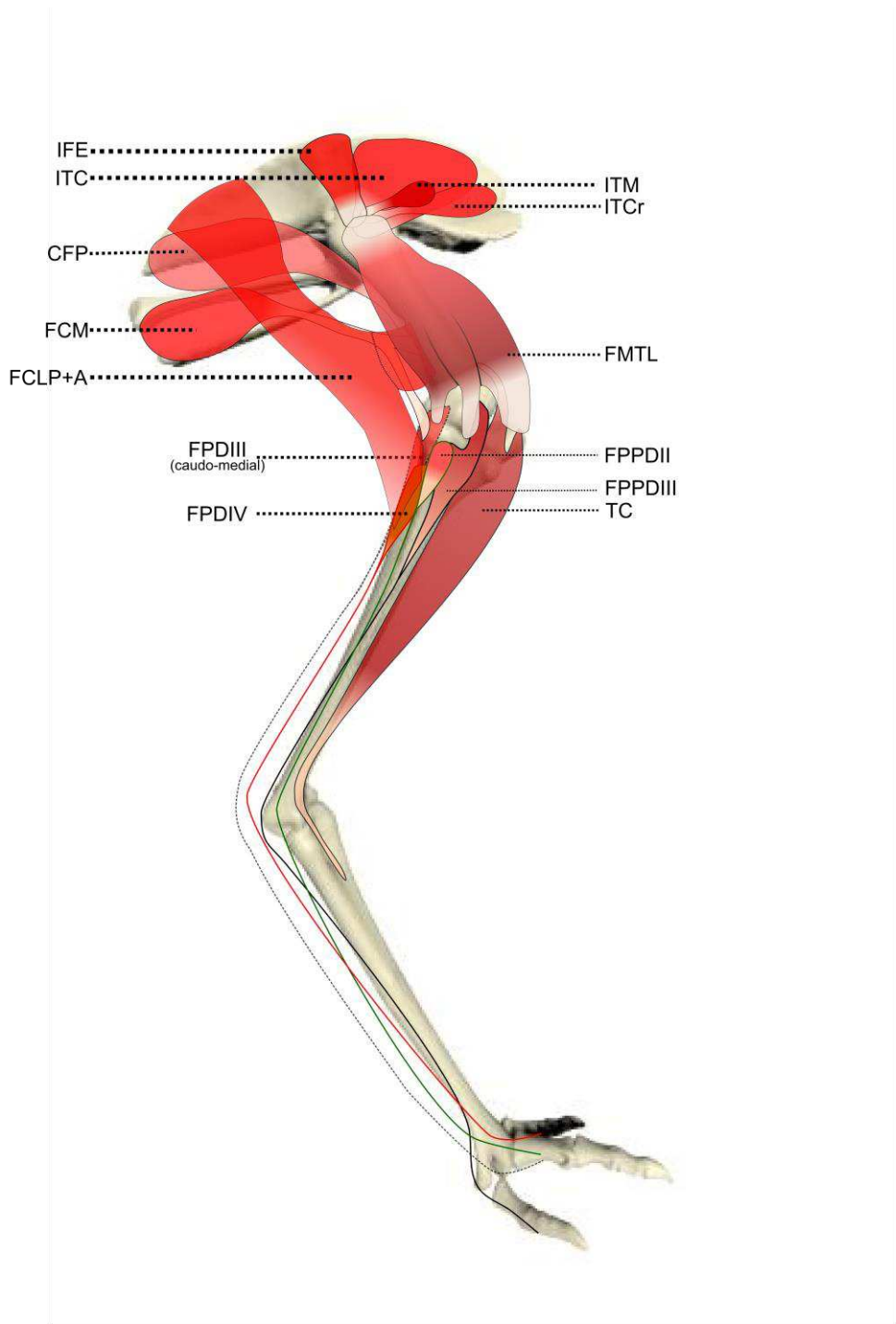
523 **Figure 1** Schematic anatomical representation of the most superficial layer of muscles, in lateral
524 view, of the pelvic limb of an adult emu.

525

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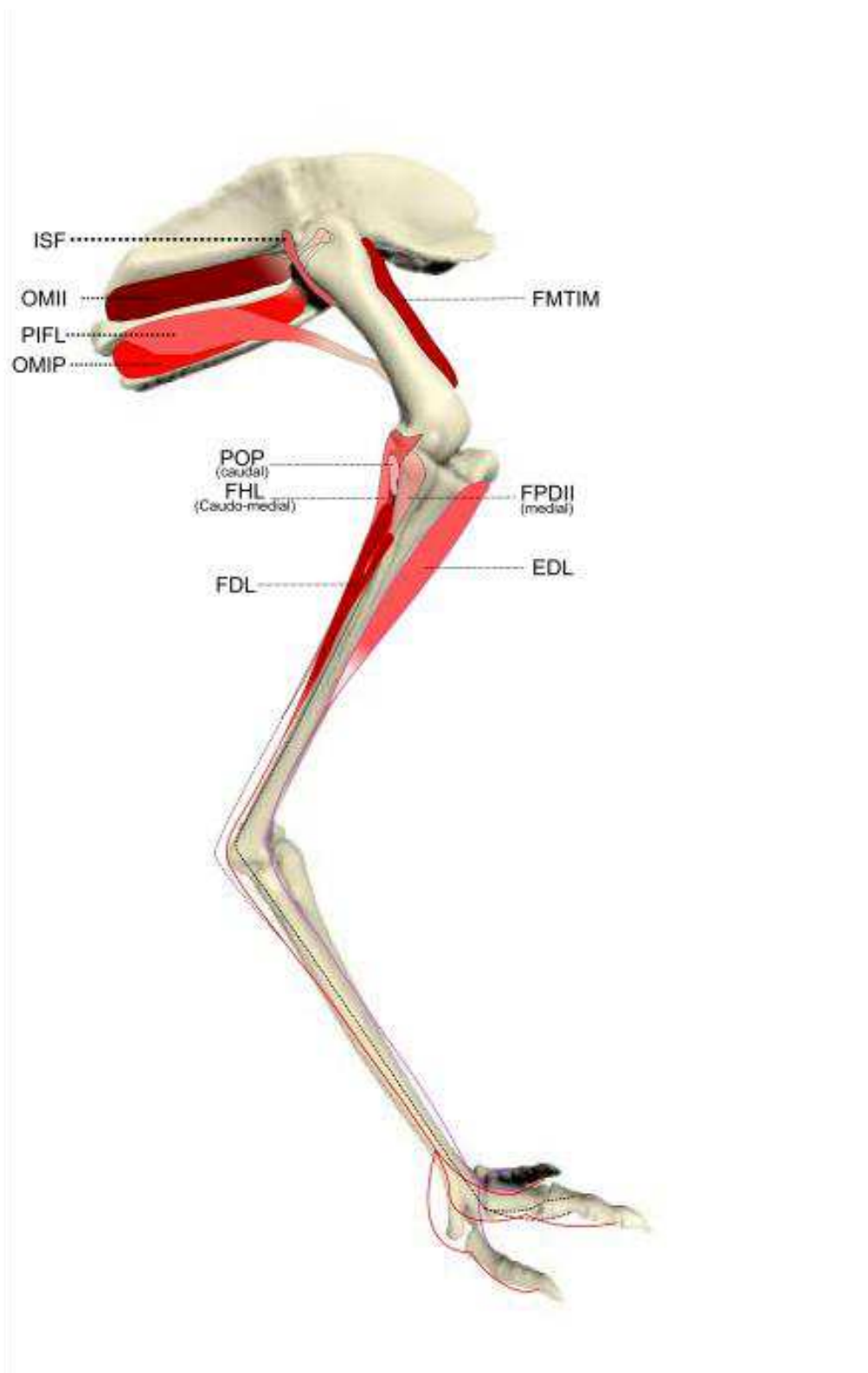
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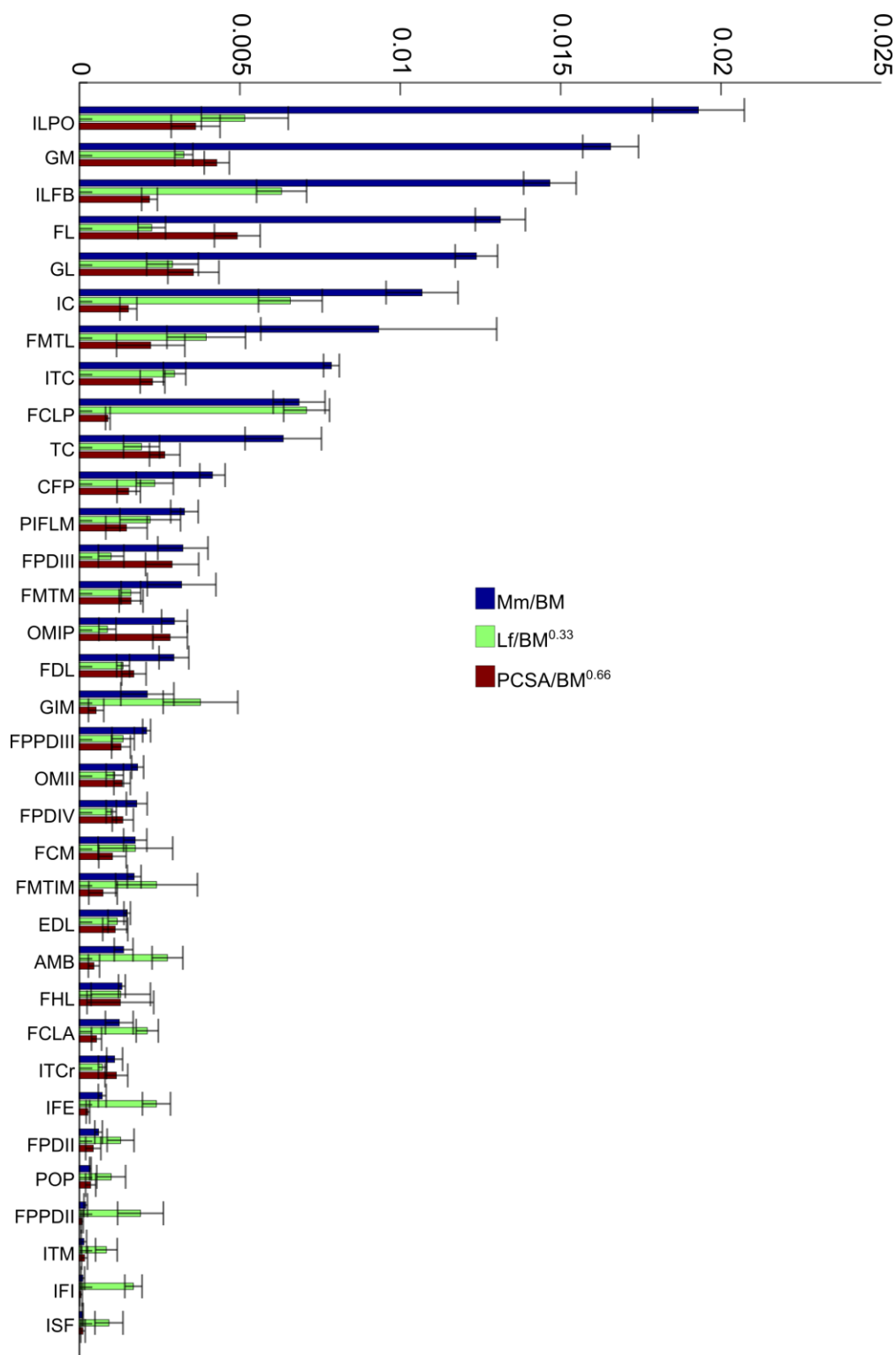
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530 **Figure 2.** Schematic anatomical representation of the intermediate layer of muscles, from a lateral
531 view, of the pelvic limb of an adult emu.



532

533 **Figure 3.** Schematic anatomical representation of the deeper layer of muscles, from a lateral view, of
534 the pelvic limb of an adult emu.

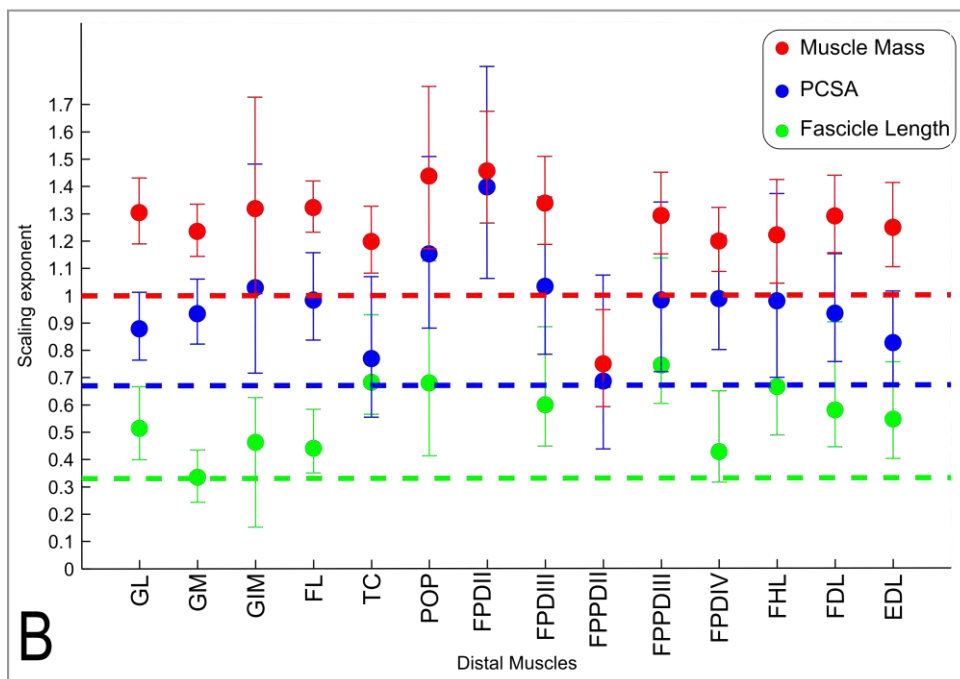
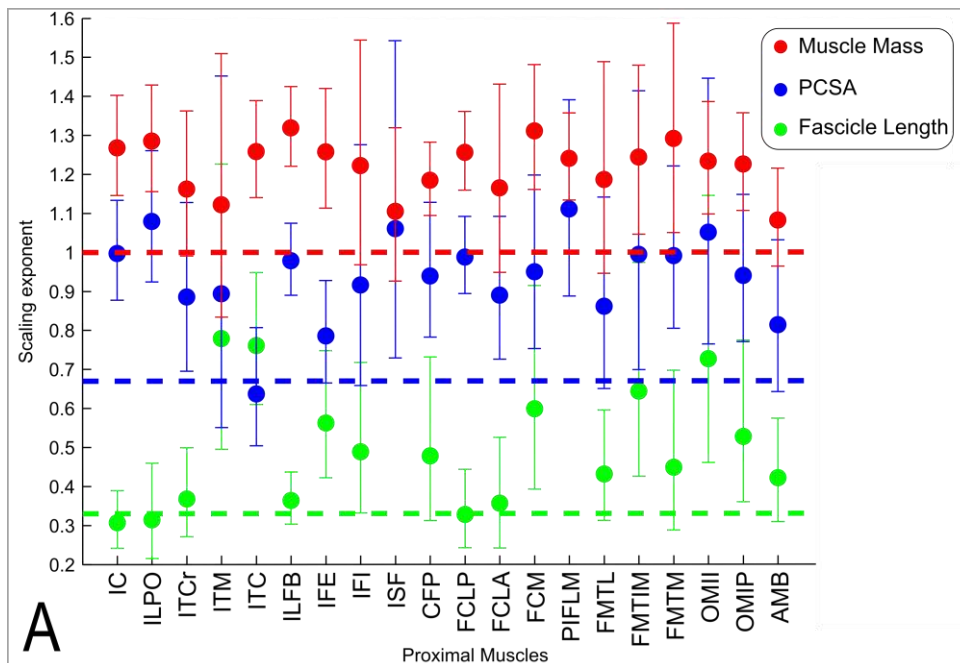


535

536 **Figure 4.** Normalized relative muscle parameters for individual muscles in emu pelvic limbs of the 16
 537 month old birds only (Group 3; mean body mass 38.5 kg); mean values (error bars showing ± 1 S.D.)
 538 are shown. Abbreviations for muscles are in Table 1. The key on the right side of the figure shows
 539 how muscle mass (M_m), physiological cross-sectional area (PCSA), and fascicle length (L_f) were
 540 normalized. L_f values were adjusted to be 1/10 of the actual results in order to be of similar
 541 magnitude to the others. Muscles are organised from top to bottom in decreasing order of muscle
 542 mass.

543

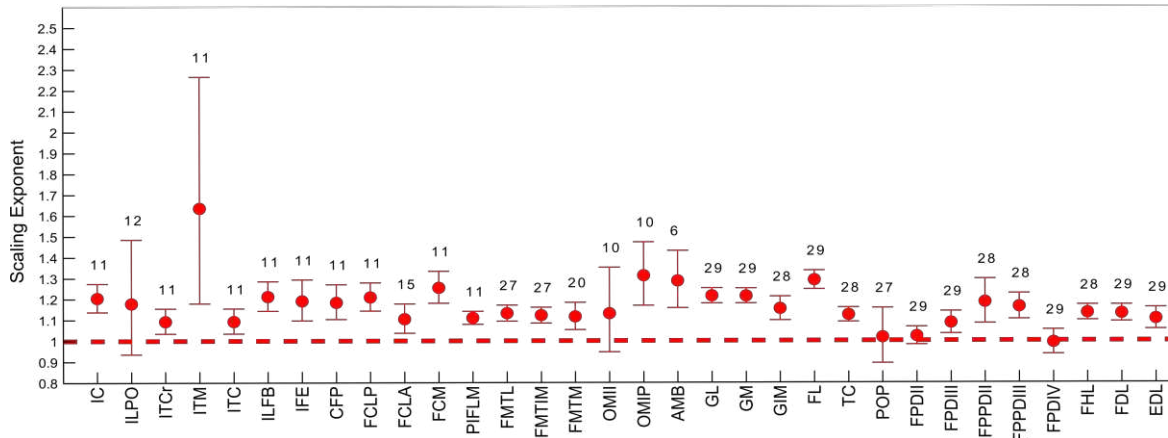
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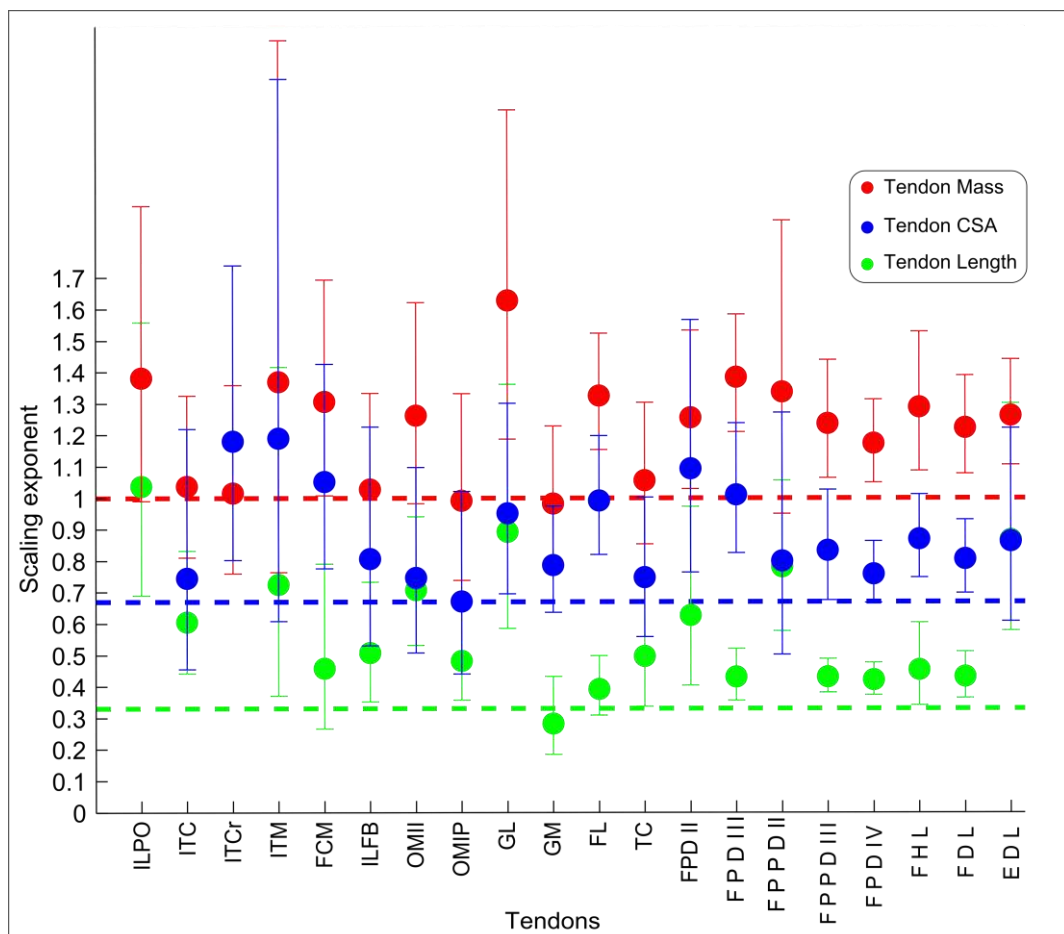
546

547 **Figure 5.** Ontogenetic scaling exponents and 95% confidence intervals (shown as error bars around
 548 mean exponent) for muscle mass (red), PCSA (blue) and fascicle length (green) for individual muscles
 549 in emu pelvic limbs. Abbreviations for muscles are in Table 1. Dashed lines indicate the expected
 550 isometric scaling exponent for each parameter. Data are for **A)** proximal limb muscles and **B)** distal
 551 limb muscles.



552
 553 **Figure 6.** Ontogenetic scaling exponents and 95% confidence intervals for masses of individual
 554 muscles in emu pelvic limbs, from the USA group. Abbreviations for muscles are in Table 1. Dashed
 555 line indicates the expected isometric scaling exponent (1.0), and the number above each parameter
 556 indicates the number of muscles included in each regression analysis.

557



558
 559 **Figure 7.** Ontogenetic scaling exponents and 95% confidence intervals for tendon mass (red),
 560 average cross-sectional area (blue) and length (green) for 20 individual muscles in emu pelvic limbs.
 561 Abbreviations for muscles are in Table 1. Dashed lines indicate the expected isometric scaling
 562 exponent for each parameter.

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