

A peer-reviewed version of this preprint was published in PeerJ on 23 December 2014.

[View the peer-reviewed version](https://peerj.com/articles/706) (peerj.com/articles/706), which is the preferred citable publication unless you specifically need to cite this preprint.

Chadwick KP, Regnault S, Allen V, Hutchinson JR. 2014. Three-dimensional anatomy of the ostrich (*Struthio camelus*) knee joint. PeerJ 2:e706 <https://doi.org/10.7717/peerj.706>

Three-dimensional anatomy of the knee joint of ostriches (*Struthio camelus*)

The three-dimensional anatomy of the ostrich (*Struthio camelus*) knee (femorotibial, femorofibular, and femoropatellar) joint has scarcely been studied, and could elucidate certain mechanobiological properties of sesamoid bones. The adult ostrich is unique in that it has double patellae, while another similar ratite bird, the emu, has none. Understanding why these patellae form and what purpose they may serve is dually important for future studies on ratites as well as understanding mechanobiological characteristics of sesamoid bone development. For this purpose, we present a three-dimensional anatomical study of the ostrich knee joint, detailing osteology, ligaments and menisci, and myology. We have identified seven muscles which connect to the two patellae and compare our findings to past descriptions. These descriptions can be used to further study the biomechanical loading and implications of the double patella in the ostrich.

1 **Three-dimensional anatomy of the knee joint of ostriches (*Struthio camelus*)**

2

3 Kyle P. Chadwick, Sophie Regnault, Vivian Allen, John R. Hutchinson

4 Structure & Motion Lab, Department of Comparative Biomedical Sciences, The Royal
5 Veterinary College, Hawkshead Lane, Hatfield AL9 7TA, United Kingdom

6 Contact: kchadwick@rvc.ac.uk

7

8 Introduction

9
10 Ostriches (*Struthio camelus*) are well known for their exceptional bipedal running
11 abilities (e.g., Alexander et al. 1979). Their muscular, three-dimensionally mobile legs
12 (Rubenson et al., 2007) are attractive subjects for studies of mechanical forces in the knee
13 because they are able to accommodate large dynamic loads (Rubenson et al., 2010;
14 Hutchinson et al., 2014). The pelvic limbs of ostriches raise questions of how much support
15 is active (i.e. muscular) vs. passive (skeletal, ligamentous, etc.) and the relative roles of the
16 many structures in the knee region.

17 The knee joint sesamoid bones (kneecaps or patellae) in ostriches are of particular
18 interest, because – unusually for birds and indeed all other animals – they are present as
19 double (proximal and distal) rather than single bones. This has been recognized for at least
20 a century and a half (Macalister, 1864; Houghton, 1864), however, until recently the double
21 patellar sesamoids of ostriches have been overlooked in a comparative context. Regnault et
22 al. (2014) showed that ostriches are unusual among ratite (Palaeognathae) birds in having
23 these two patellae—emus and potentially other ratites (e.g. cassowaries, extinct moa)
24 appear to have lost the patella completely, whereas kiwis and tinamous have retained a
25 plesiomorphically small patella. The condition in other species is uncertain, and although
26 Stannius (1850) and de Vriese (1909) hint tantalisingly of a double patella in *Rhea*, evidence
27 so far suggests that that they have evolved only once within the lineage leading to *Struthio*.

28 All bones develop under a combination of genetic and epigenetic (mechanical)
29 inputs, but sesamoid bones including the patella appear to be particularly dependent on
30 early biomechanical influences (Sarin et al., 1999), with poor formation or complete
31 developmental failure in embryonic immobilisation studies (Mikic et al., 2000; Osborne et al.,
32 2002; Kim et al., 2009). Although the relative importance of biomechanical stimulation seems
33 to vary amongst species and sesamoids (Vickaryous and Olson, 2007, Kim et al., 2009), it is
34 clear that some aspect of normal embryonic movement is vital for sesamoid formation.
35 Through the use of 3D models and finite element analysis, previous researchers have found
36 that sesamoid ossification centres occur in regions of high tissue stress (Roddy, 2011).
37 Moreover, it seems that the type of stress is key; high octahedral shear (i.e., pure shear)
38 stresses appear to promote sesamoid ossification whereas hydrostatic (i.e., pure normal)
39 stresses inhibit it (Sarin & Carter, 2000; Giori, 1993).

40 Multiple studies of real tissue *in* and *ex vivo* corroborate these ideas, and have found
41 regions of fibrocartilage and bone proliferation corresponding with areas of compressional
42 loading (Scapinelli & Little, 1970; Benjamin & Ralphs, 1997; Vogel & Peters, 2005). Potential
43 mechanosensitive genes involved in the regulation of embryonic ossification have been
44 identified (Nowlan et al., 2008), though investigation of the role of genetics in sesamoid
45 formation is complex and ongoing. Most researchers conclude that both mechanical and
46 genetic factors interact and play complementary parts in creating sesamoid bones. In
47 studying long bones, Carter et al. (1998) hypothesised that the relative rate of perichondral
48 vs. endochondral ossification (controlled by genetics) in turn creates a biomechanical
49 environment favourable (if the two occur simultaneously) or unfavourable (if perichondral
50 precedes endochondral ossification) to the formation of secondary centres. Carter (1987)
51 postulated that variations in genotype, favoured over time by natural selection, work in
52 concert with mechanical stimuli through ontogeny to create mechanically efficient designs in
53 vertebrate skeletons.

54 The aforementioned studies provide plausible explanations for the large variation of
55 sesamoids across vertebrate taxa, even amongst those with grossly similar mechanical
56 loading (e.g. birds; Regnault et al., 2014). However, more case studies are needed about the
57 biomechanical function(s) that sesamoids perform in an individual at any one time, how
58 those roles are moulded during ontogeny, and how the form and function of sesamoids
59 evolve. In particular, it is not yet clear how much the sensitivity of sesamoids to their
60 mechanical environment varies—are some, such as the patella, more developmentally
61 plastic in some taxa (e.g. birds) than others (e.g. mammals) (Barnett & Lewis, 1958)? If so,
62 has any differential plasticity of sesamoid development played an important role in evolution,

63 such as undergoing genetic assimilation (Sarin et al., 1999), or indicating key changes in
64 locomotor function that correspond to altered loads on sesamoids (Hutchinson, 2002)?

65 We are interested in questions such as, how are the patellae of an ostrich loaded and
66 how do they develop in response to these loads? We aim to investigate these questions
67 using a three-dimensional (3D) model of knee joint morphology, which this study provides
68 the basis for. To do this, we scanned and digitally segmented the ostrich knee structures
69 (muscles, ligaments, and bones) into discrete elements, allowing connecting tissues and
70 muscles to be described and measured. We present an anatomical description of the
71 morphology of the knee joint of ostriches, with a focus on features that are most relevant to
72 the mechanics of the two patellae. Anatomy of the knee region has been characterized in
73 numerous birds (Haines, 1942; Cracraft, 1971; Abourachid, 1991; Fuss & Gasser, 1992),
74 and several studies contain descriptions of knee tissues in ostriches (Macalister, 1864;
75 Haughton, 1864; De Vriese, 1909; Fowler, 1991; Bezuidenhout, 1999; Gangl, 2004; Wagner,
76 2004; Zinoviev, 2006; Smith, 2006). None of these studies focus directly on the two patellae
77 and their interaction with surrounding tissues. The anatomy is not simple and is best
78 understood with a full three-dimensional perspective; therefore we present an interactive 3D
79 representation of a representative knee in a mature ostrich.

81 **Materials and methods**

82
83 Our 3D model is based on the right leg of a skeletally mature adult (unknown age)
84 male ostrich, body mass 71.3kg. It was imaged with digital radiography (Figure 1; Philips MX
85 8000 IDT 16 scanner, 16 bit images, ~428x352 mm images at 10 pixels mm⁻¹ resolution,
86 varying kV and mAs), computed tomography (CT; Philips MX 8000 IDT 16 scanner, 120 kV,
87 100 mAs, 0.8mm slice thickness), and magnetic resonance imaging (MRI; Philips Medical
88 Systems Intera scanner, TR: 3596ms, TE: 120ms, α :90°, 3mm slice thickness). Following
89 this the leg was dissected to qualitatively study the anatomy, and these observations
90 validated through dissections of three other individuals (adults of unknown age, 65.3 and
91 130 kg body mass at death), CT imaging of six individuals (settings similar to those above),
92 comparative studies of museum specimens (Table 1 and 15 others from various collections),
93 and consultation of the relevant literature (cited above), to ensure that our observations on
94 this individual were as representative as possible.

95 To construct the model, we segmented the resulting DICOM images from CT and
96 MRI for our representative ostrich specimen (and select comparative specimens) in Mimics
97 (Materialise Inc., Leuven, Belgium) software. Bones were segmented from CT images and
98 muscles were segmented from MRI images. The segmentations were individually and semi-
99 automatically rendered into 3D objects. The 3D images of the bones were co-registered with
100 the muscle MRI files and manually aligned to fit the limb posture from the MRI scan. This
101 allowed 3D objects representing all relevant bones and muscles to fit together into a single
102 model.

104 **Results**

106 *Osteology*

107 The knee joint of an adult ostrich has five component bones: the distal femur, the
108 proximal tibia and fibula, and the proximal and distal patella (Figure 2b). The femur has
109 asymmetric condyles, the lateral being appreciably larger than the medial. This is unusual
110 compared to humans (Rehder, 1983); however, numerous other species have asymmetric
111 condyles as well (e.g. Rewcastle, 1983). There is also a large lateral femoral epicondyle
112 lateral to the lateral femoral condyle, forming a fibular trochlea. The tibiotarsus has lateral
113 and cranial tibial crests extending from those two aspects of the proximal tibia.

114 The proximal patella lies high on the lateral femoral condyle, dipping slightly into the
115 large sulcus in the position the specimen was scanned in (similar to that in three other
116 specimens scanned). The proximal patella therefore topologically corresponds to the single

117 patella of other birds, which occupies a position within or slightly above the sulcus (Shufeldt,
118 1884; Haines, 1942; Cracraft, 1971), and its flattened morphology likewise is similar.

119 The distal patella, which has only been briefly mentioned in literature (Macalister,
120 1964; De Vriese, 1909; Walker, 1890; Bezuidenhout, 1999; Gangl, 2004; Wagner, 2004), is
121 75.7mm long in our subject (ossified portion; Table 1) and sits in front of the lateral femoral
122 condyle. There was considerable variability in the distal patella lengths we observed in our
123 dissected and museum specimens, however the length does roughly correlate with femur
124 length (Table 1), which suggests a correlation with age. The distal patella extends down to
125 just above the tip of the tibial crest, where it is connected by a short band of connective
126 tissue (~3mm), apparently corresponding to a distal remnant of the patellar tendon. This
127 distal-most sesamoid appears almost as an extension of the tibial crest, similar to the
128 position of the extended tibial crest in some diving species (Shufeldt, 1883, 1884; Walker,
129 1890). Both patellae are enveloped by a thick, fibrous facial sheet to which many tendons
130 contribute. While neither patella articulates directly with any other bone in the knee (through
131 an articular cartilage interface), the layer of fibrous tissue between the femur and proximal
132 patella is thin and may allow transmission of contact forces in some poses or loading
133 regimes.

134 135 *Ligaments and Menisci*

136 There are four primary ligaments which provide stability and alignment in the knee
137 joint of ostriches, as in many other tetrapods (Figure 2a; Fuss, 1989, 1991, 1996). A wide,
138 flat collateral ligament spans the femorotibial joint space on either side, laterally and
139 medially. The medial collateral ligament (MedCL) connects the medial femoral condyle to the
140 tibiotarsus. It originates within a small fossa on the distal medial side of the medial femoral
141 condyle and inserts distally to the tibial plateau on the medial edge of the proximal tibia. The
142 lateral collateral ligament (LatCL) originates on the distal part of the lateral femoral
143 epicondyle, and inserts onto the fibula, on the posterior-distal corner of the lateral side of the
144 bulbous epiphysis, as well as the lateral meniscus, on the lateral side of the large, pointed
145 cranial extension of the meniscus. There is additionally a larger lateral collateral ligament
146 (LatCL_2) which originates at the very top of the lateral femoral condyle, inserts on the shaft
147 of the fibula, and also connects cranially to the meniscus. The cranial cruciate ligament
148 (CranCL) is round in cross-section, originates caudally (in the popliteal fossa) between the
149 femoral condyles and inserts cranially on the tibial plateau (Figure 3a). The caudal cruciate
150 ligament (CaudCL) is thicker and flatter. It originates from a small impression on the medial
151 side of the lateral femoral condyle, crosses over the top of the CranCL, and inserts on the
152 caudomedial corner of the tibial plateau (Figure 3a). We found slight differences in size and
153 shape of attachments, particularly on the tibial head, from previous descriptions (Fuss &
154 Gasser, 1992), however the general location agreed (Figure 3b).

155 The medial meniscus sits between the medial femoral condyle and the tibial plateau.
156 It is circular, thickest on its outermost aspect and thinner towards the incomplete centre, so
157 that it forms a triangular wedge in cross section. Cranially, the medial meniscus connects to
158 the lateral meniscus. The lateral meniscus is smaller than the medial meniscus and is longer
159 (craniocaudally) than it is wide (mediolaterally). It sits primarily in the gap between the
160 tibiotarsus and the fibula and extends cranially up the lateral femoral condyle. The femoral
161 meniscal ligament attachments match well with Fuss and Gasser's (1992) descriptions,
162 however the tibial attachments differ in size and two meniscal attachments on the fibula were
163 found, which were not previously noted (Figure 3b).

164 165 *Myology*

166 From our MRI scan and dissections of the knee region, there were 12 distinct
167 muscles identified that cross the knee joint near the patellae (see Hutchinson et al., 2014 for
168 details on anatomical nomenclature): M. ambiens part 1 (AMB1), M. femorotibialis
169 intermedius (FMTIM), M. femorotibialis lateralis pars distalis (FMTLD), M. femorotibialis
170 lateralis pars proximalis (FMTLP), M. femorotibialis medialis (FMTM), M. fibularis longus
171 (FL), M. gastrocnemius intermedius (GIM), M. gastrocnemius lateralis (GL), M.

172 gastrocnemius medialis (GM), M. iliotibialis cranialis (IC), M. tibialis cranialis- femoral head
173 (TCfem), and M. tibialis cranialis- tibial head (TCtib). Seven of these muscles are directly
174 connected by tendons to the patellae: the IC, GL, FL, GM, FMTIM, FMTLD, and FMTLP
175 (Figure 4). The IC, FMTIM, FMTLD, and FMTLP muscle bellies lie proximal to the patellae,
176 whereas the GL, FL and GM muscle bellies lie distally.

177 The knee extensors have major insertions around the patella. The IC originates on
178 the cranial end of the ilium and inserts into the superficial tendofascial sheet as well as the
179 medial side of the tibial head. The origin of the FMTLD is along the entire lateral femoral
180 shaft and it inserts onto the deep tendofascial sheet above the lateral femoral condyle. The
181 FMTLP origin occurs laterally on the femoral trochanter, and laterally on the proximal
182 femoral shaft (Gangl et al., 2004), and inserts into the deep tendofascial sheet near the
183 proximal patella. The FMTIM arises from the Crista trochanteris and proximal three-quarters
184 of the cranial femoral shaft (Gangl et al., 2004), and inserts on the deep tendofascial sheet,
185 near the proximal patella and directly above the medial femoral condyle. A third femorotibial
186 muscle, M. femorotibialis medialis, crosses the knee joint from the medial femoral shaft to
187 the medial surface of the proximal tibia but does not interact with the patellar tissues and
188 thus is not further described here (but see Zinoviev, 2006 for an accurate account; and
189 Hutchinson et al., 2014 for some explanation of confusion surrounding these femorotibial
190 muscles' identities in other literature).

191 The thin, round tendon of the AMB1, which originates from the pectineal
192 (preacetabular) process of the pubis, runs through the tendofascial sheet and directly behind
193 the distal patella in a distolateral direction, toward its fusion with the tendinous origin of M.
194 flexor perforates digiti III, distal to the fibular head (Gangl et al., 2004). We observed that
195 there were no direct tissue connections between the AMB1 tendon and the patellae. The
196 tendon was free to slip and move independently within the tendofascial sheet, behind the
197 distal patella, unlike in many other (neognath) birds in which the AMB1 tendon perforates or
198 grooves the front of the patella (e.g. Shufeldt, 1884). However, we describe it here as it does
199 run close to the patellae. The second head of M. ambiens, which is unique to ostriches,
200 originates dorsal to the other from the cranioventral iliac rim and inserts on the medial
201 surface of the proximal tibia (Hutchinson et al., 2014). However, it does not come near the
202 patellae and so is not described further.

203 The lower limb muscles of ostriches also have associations with the patella. The GL
204 originates on the proximolateral side of the distal patella and superficial tendofascial sheet,
205 joining with the GM and GIM into a single gastrocnemius end-tendon distally, and inserting
206 onto the tarsometatarsus after wrapping around the intertarsal joint. The FL attaches to the
207 distolateral side of the distal patella and splits into two tendons of insertion proximal to the
208 intertarsal joint, Tendo lateralis and Tendo caudalis. Tendo lateralis inserts on the tendon of
209 the M. flexor perforates digiti III, distal to the intertarsal joint, and the Tendo caudalis inserts
210 on the lateral tibial condyle (Gangl et al., 2004). The GM takes its origin from the superficial
211 tendofascial sheet and the medial side of the distal patella, and joins the gastrocnemius end-
212 tendon before the intertarsal joint. Other lower limb muscles such as M. tibialis cranialis, M.
213 popliteus and the many digital flexors do not originate near the patellae and are well
214 described in the literature (Gangl et al., 2004; Zinoviev, 2006), so we do not discuss them
215 here.

216
217

218 Discussion

219 We scanned, modelled, and dissected an ostrich knee and found previously
220 undescribed or unclear morphology which may be crucial in ostrich knee function. Literature
221 and other specimens bolstered our findings. From the detailed, three-dimensional
222 anatomical data that we collected, we are able to confidently describe the functional
223 attachments of muscles to the tendofascial sheets containing the two patellae, suggest
224 mechanical implications of these attachments in a dynamic limb, and compare our findings
225 to previous anatomical descriptions.

226
227
228
229
230
231
232
233
234
235
236
237
238
239
240
241
242
243
244
245
246
247
248
249
250
251
252
253
254
255
256
257
258
259
260
261
262
263
264
265
266
267
268
269
270
271
272
273
274
275
276
277
278
279
280

Functional Attachments

To understand the loading across the knee joint of ostriches, identification and description of the tissues which directly interact with the two sesamoid bones is essential (Figures 2-4). The two sesamoids are embedded in sheets of tendofascial tissue that bond together at the proximal edge of the distal patella. The sheets are the origins and insertions of various leg muscles. The proximal sesamoid constitutes the insertion of the FMTIM tendon proximal-medially and the FMTLP tendon proximal-laterally. Distally, the sheath attaches to the distal sesamoid. The distal sesamoid forms the insertion for the FMTLD tendon proximal-laterally and the IC tendon proximally. The distal sesamoid also is part of the muscle origins of the GL proximal-laterally, the FL distal-laterally, and the GM medially.

Based on our anatomical observations, we hypothesize that all seven of the muscles attached to the patellae would induce a compressive (into the joint) stress on the patellae. The GL, FL, and GM would also induce a tensile force component in the distal direction while the IC, FTIM, FMTLP, and FMTLD would exert a tensile force component in the proximal direction. This could create areas of large compressive and shear loading near the joint as the tissues wrap around the femoral condyles. In addition to the proximal-distal loading, additional mediolateral loads may occur as a result of the tissues wrapping around the distal femur where there is a complex surface between the large lateral condyle and deep sulcus. This variegated surface may induce higher stress concentrations in areas where the surface geometry is most irregular.

Patellar anatomy and connections

The first two (in 1894) mentions of ostriches having a second patella described it not as a true patella, but as an “ossified ligamentum patellae” (Macalister, 1964; Houghton, 1864). Since then there have been several other descriptions. Walker (1890) mentioned a small double patella in ostrich while De Vriese (1909) described the patellae as large, consisting of two successive parts which connected to the tibia by a short ligament. Fowler (1991) claimed that ostriches only had a single ossified bone in the tendon which inserted onto the cnemial crest. We found this to be untrue of our adult subjects. In a juvenile ostrich hindlimb we observed joints which were not fully ossified and no patellae were detected, but it is still unclear when in ontogeny each patella ossifies.

In more modern literature, there have been two primary papers providing thorough descriptions of the patellae and related ostrich knee anatomy (Bezuidenhout, 1999; Gangl et al., 2004). Bezuidenhout (1999) describes a primary patella with medial and lateral articular surfaces, and a “second patella” distal to the patella. The “second patella” is described as a long bony column extending from the medial bottom edge of the patella to the tibial crest. This account was also the first to detail muscle attachments to the two patellae. Muscles described in association with the patellae were the M. femorotibialis medius (inserts laterally on the patella), the M. femorotibialis accessorius (inserts proximally on the patella), the M. femorotibialis internus (inserts medially on the patella), and the M. gastrocnemius (one of four heads originates from the patella). We consider the three M. femorotibialis to be what we describe as FMTLP and FMTIM (two muscle bellies, *vide* Zinoviev, 2006; Hutchinson et al. 2014). Gangl et al. (2004) first described what we consider another very important aspect of the double patellae, which is the tendofascial sheet in which they are embedded, connecting multiple muscles and inserting on the Crista cnemialis cranialis. The authors also detailed additional muscles which surround and attach to this tendofascial sheet. The muscles which Gangl et al. (2004) described as inserting onto the tendofascial sheet are the M. iliobtibialis cranialis and the M. femorotibialis accessorius – caput mediale (what we describe as FMTIM). The tendon of the M. ambiens (here AMB1) was described as running medially to the proximal patella and caudally to the distal patella through the tendofascial sheet of the knee within its own channel. The M. fibularis longus and the M. gastrocnemius pars medialis were both described as having their origins on the distal patella.

Additional modern studies have also shed light on the patellae through both osteological (Wagner, 2004) and myological (Zinoviev, 2006; Smith, 2006) descriptions.

281 Wagner (2004) added a description of the occurrence and shape of the proximal and distal
282 patella at various ages of ostrich, as well as describing the fascia formed by the ends of
283 multiple tendons which the two patellae are embedded. Zinoviev (2006) described the
284 proximal patella as being embedded within the distal extension of the tendon of the M.
285 femorotibialis medius pars distalis (what we describe as FMTIM), while Smith et al. (2006)
286 described the patella to be within the flat tendon of insertion of the M. femorotibialis medius,
287 externus, and accessorius (what we describe as FMTLP, FMTLD, and FMTIM, respectively).
288

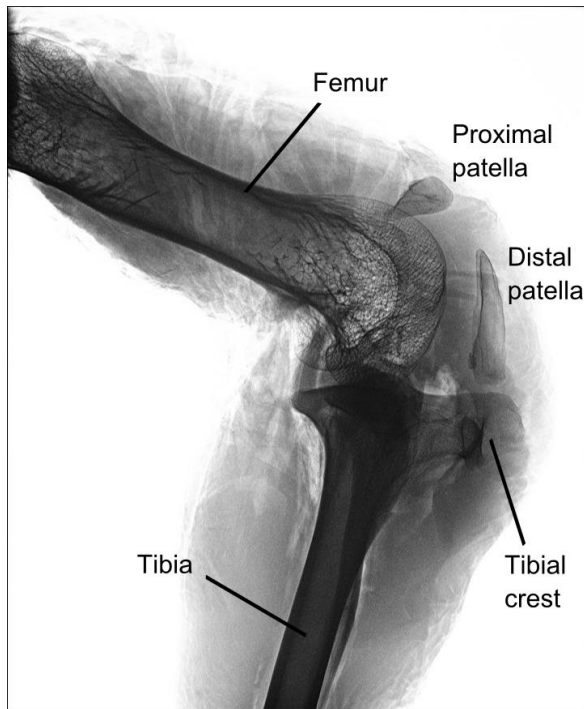
289 **Conclusion**

291
292 In this study we have identified and described the tissues surrounding the knee joint in the
293 ostrich and compared our findings to the previous literature. We have also speculated on the
294 mechanics and function of the anatomical features which directly interact with the patellae. It
295 is still not clear why the double patellae develop in the ostrich, and if particular mechanical
296 factors play a primary role in determining their shape and location. In future work, we intend
297 to address these questions through modelling methods such as finite element analysis.
298

299 **Acknowledgments**

301
302 We thank Richard Lam and Renate Weller for their assistance with all of the scans. We also
303 thank Jeff Rankin and Luis Lamas for sharing their expertise in ratite anatomy. Additionally,
304 Joanne Cooper, Judith White and Hein Van Grouw at the NHM were very helpful in assisting
305 our accessing of specimens.
306

307



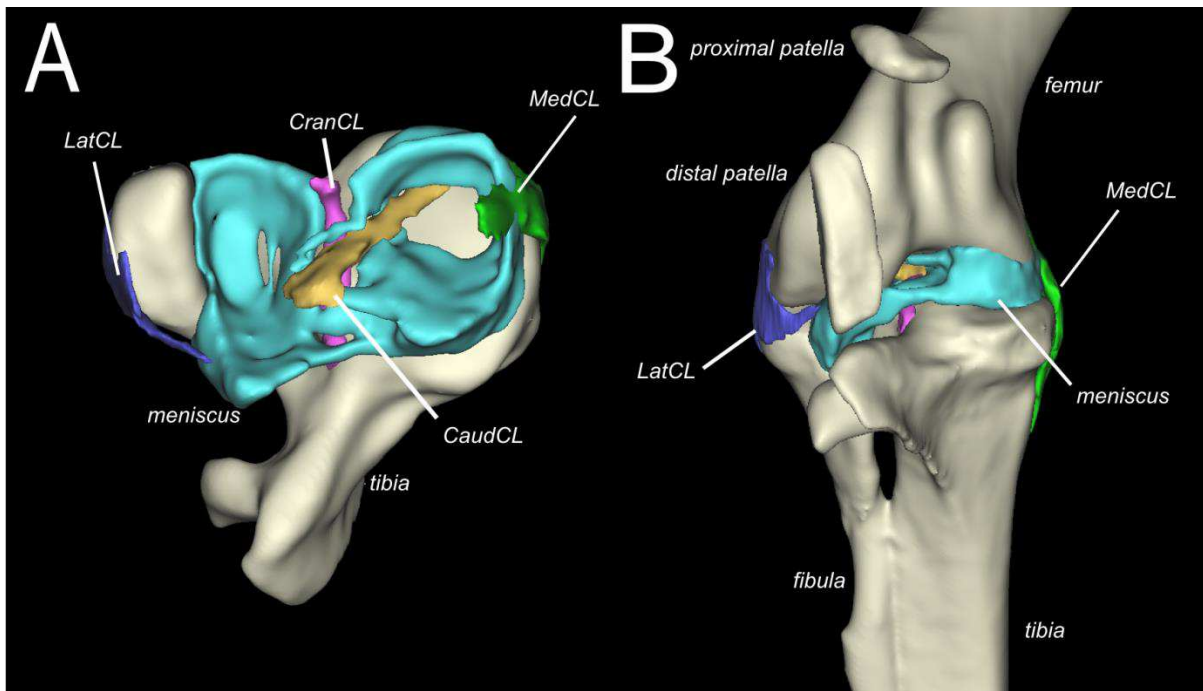
308 **Figure 1: Digital radiograph of the ostrich knee joint showing sagittal plane locations of the**
 309 **two patellae.**
 310
 311

Subject	Distal patella length (mm)	Femur length (mm)	Ratio
NHMUK (1888.3.15.1)	39.5	277.0	0.143
NHMUK (1857.2.24.10)*	64.9	292.5	0.222
NHMUK (1895.10.14.1)	57.7	306.0	0.189
NHMUK (1925.5.12.1)	57.7	312.0	0.185
NHMUK (1915.3.29.1)*	51.2	272.0	0.188
NHMUK (1894.3.17.1)*	62.5	314.0	0.199
NHMUK (1954.5.1)*	61.7	292.5	0.211
NHMUK (1972.1.2)	44.9	284.0	0.158
RVC1	33.1	306.0	0.108
<i>RVC2</i>	75.7	317.0	0.239
RVC3	67.2	307.2	0.219
Average	56.0	298.2	0.187
Standard deviation	8.4	14.8	0.024

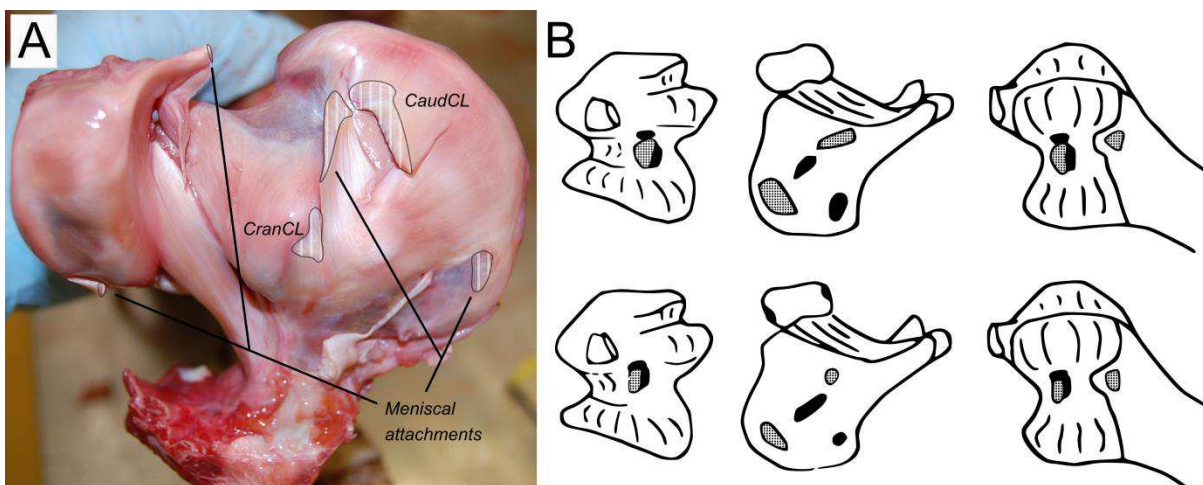
308
 309
 310
 311

312
 313
 314
 315
 316
 317
 318

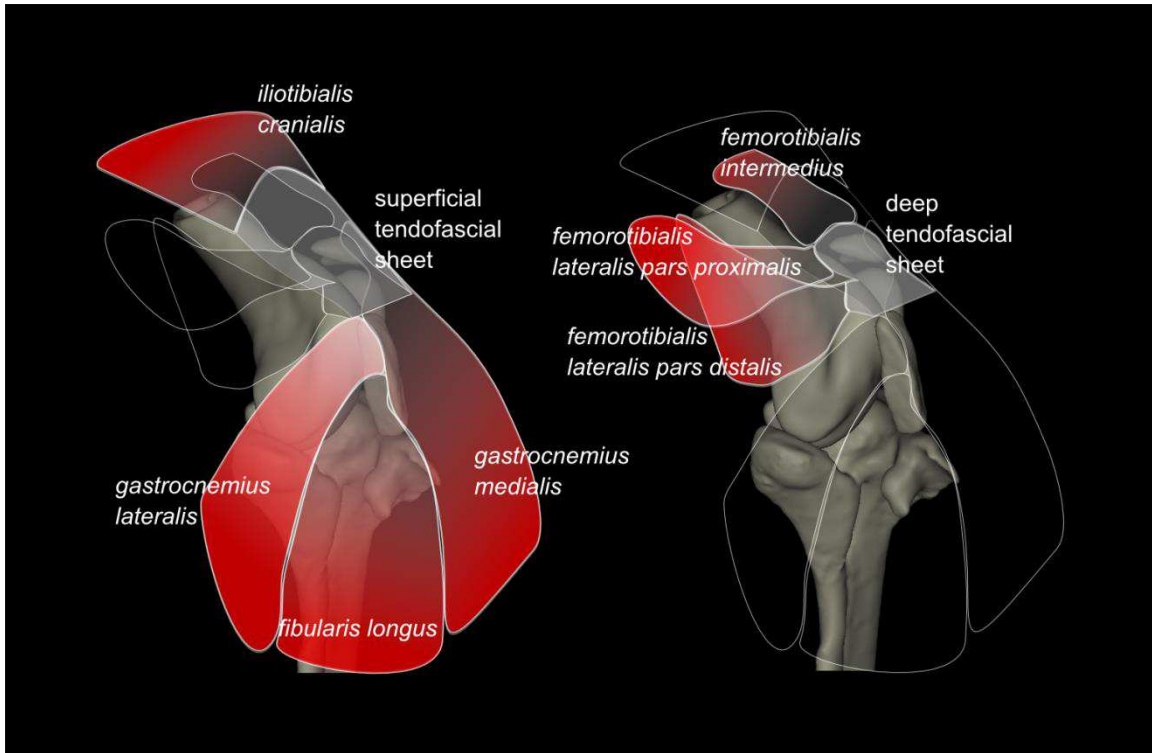
Table 1: The measured lengths of the distal patella and femur in dissected and museum specimens, as well as the ratio of the two. Specimen RVC2 in italics is the main individual in this study. *These specimen possess both femora and distal patellae; average lengths are shown. NHMUK specimen numbers pertain to osteological specimens held in The Natural History Museum, Tring, Hertfordshire, UK.



319
320
321 **Figure 2: Three-dimensional model of the ostrich knee, showing bones, ligaments, and**
322 **menisci.** A) Proximal view of ligaments, menisci, tibia, and fibula; B) Cranial view of femur, tibia,
323 fibula, proximal patella, distal patella, ligaments, and menisci.



324
325
326 **Figure 3: A) Proximal view of the proximal right tibia and fibula, showing distal cruciate ligament and**
327 **meniscal insertion sites B) craniate (speckled) and meniscal (solid) attachment sites on the distal**
328 **femur (left and right columns) and proximal tibia (central column). Attachment sites shown in Fuss**
329 **(1992; top row) compared with what we observed (bottom row). Figure modelled after Fuss (1992).**
330



331
332
333 **Figure 4: Representation of superficial (left) and deep (right) muscles that attach to the**
334 **tendofascial sheet containing the two patellae.**
335

336 **References**

337

338 Abourachid A. 1991. Myologie du membre pelvien du dindon domestique *Meleagris*
339 *gallopavo*. *Anatomia, Histologia, Embryologia* 20(1):75-94.

340

341 Alexander R, Maloiy GMO, Njau R, & Jayes AS. 1979. Mechanics of running of the ostrich
342 (*Struthio camelus*). *Journal of Zoology* 187(2):169-178.

343

344 Barnett, CH, & Lewis, OJ. 1958. The evolution of some traction epiphyses in birds and
345 mammals. *Journal of Anatomy* 92(4):593.

346

347 Benjamin M, & Ralphs JR. 1997. Tendons and ligaments-an overview. *Histology and*
348 *Histopathology* 12(4):1135-1144.

349

350 Bezuidenhout AJ. 1999. Anatomy. In: Deeming DC, ed. *The ostrich: biology, production and*
351 *health*. CABI Publishing 13-50.

352

353 Carter DR. 1987. Mechanical loading history and skeletal biology. *Journal of Biomechanics*
354 20(11):1095-1109.

355

356 Carter DR, Mikić B, & Padian K. 1998. Epigenetic mechanical factors in the evolution of long
357 bone epiphyses. *Zoological Journal of the Linnean Society* 123(2):163-178.

358

359 Cracraft J. 1971. The functional morphology of the hind limb of the domestic pigeon,
360 *Columba livia*. *Bulletin of the AMNH* 144:171-268.

361

362 De Vriese B. 1909. Recherches sur l'anatomie comparée de la rotule. *Bulletin de*
363 *L'Academie Royale de Medecine de Belgique*.

364

365 Fowler ME. 1991. Comparative clinical anatomy of ratites. *Journal of Zoo and Wildlife*
366 *Medicine* 22(2):204-227.

367

368 Fuss FK. 1989. Anatomy of the cruciate ligaments and their function in extension and flexion
369 of the human knee joint. *American Journal of Anatomy* 184(2):165-176.

370

371 Fuss FK. 1991. Anatomy and function of the cruciate ligaments of the domestic pig (*Sus*
372 *scrofa domestica*): a comparison with human cruciates. *Journal of Anatomy* 178:11.

373

374 Fuss FK. 1996. Tibiofibular junction of the South African ostrich (*Struthio camelus australis*).
375 *Journal of Morphology* 227(2):213-226.

376

377 Fuss FK, & Gasser CR. 1992. Cruciate ligaments of the avian knee: insight into a complex
378 system. *Journal of Morphology* 214(2):139-151.

379

380 Gangl D, Weissengruber GE, Egerbacher M, & Forstenpointner G. 2004. Anatomical
381 description of the muscles of the pelvic limb in the ostrich (*Struthio camelus*). *Anatomia,*
382 *Histologia, embryologia* 33(2):100-114.

383

384 Giori NJ., Beaupre GS, & Carter DR. 1993. Cellular shape and pressure may mediate
385 mechanical control of tissue composition in tendons. *Journal of Orthopaedic Research*
386 11(4):581-591.

387

388 Haines RW. 1942. The tetrapod knee joint. *Journal of Anatomy* 76(3):270-301.

389

- 390 Haughton S. 1864. Notes on animal mechanics: No. 3. On the muscular mechanism of the
391 leg of the ostrich. *Proceedings of the Royal Irish Academy* 9:50-61.
392
- 393 Hutchinson JR. 2002. The evolution of hindlimb tendons and muscles on the line to crown-
394 group birds. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative*
395 *Physiology* 133(4):1051-1086.
396
- 397 Hutchinson JR, Rankin JW, Rubenson J, Rosenbluth KH, Siston RA, Delp SL. (2014)
398 Musculoskeletal modelling of an ostrich (*Struthio camelus*) pelvic limb: Influence of limb
399 orientation on muscular capacity during locomotion. *PeerJ PrePrints* 2:e513v1
400 <http://dx.doi.org/10.7287/peerj.preprints.513v1>
401
- 402 Kim HT, Olson WM, & Hall BK. 2009. Effects of hind limb denervation on the development of
403 appendicular ossicles in the dwarf African clawed frog, *Hymenochirus boettgeri* (Anura:
404 Pipidae). *Acta Zoologica* 90(4):352-358.
405
- 406 Macalister A. 1864. On the anatomy of the ostrich (*Struthio camelus*). *Proceedings of the*
407 *Royal Irish Academy* 9:1-24.
408
- 409 Mikic B, Johnson, TL, Chhabra AB, Schalet BJ, Wong M, & Hunziker EB. 2000. Differential
410 effects of embryonic immobilization on the development of fibrocartilaginous skeletal
411 elements. *Journal of Rehabilitation Research and Development* 37(2):127-134.
412
- 413 Nowlan NC, Prendergast PJ, & Murphy P. 2008. Identification of mechanosensitive genes
414 during embryonic bone formation. *PLoS Computational Biology* 4(12):e1000250.
415
- 416 Osborne AC, Lamb KJ, Lewthwaite JC, Dowthwaite GP, & Pitsillides AA. 2002. Short-term
417 rigid and flaccid paralyzes diminish growth of embryonic chick limbs and abrogate joint cavity
418 formation but differentially preserve pre-cavitated joints. *Journal of Musculoskeletal and*
419 *Neuronal Interactions* 2(5):448-456.
420
- 421 Regnault S, Pitsillides AA, Hutchinson JR. 2014. Structure, ontogeny and evolution of the
422 patellar tendon in emus (*Dromaius novaehollandiae*) and other palaeognath birds. *PeerJ*
423 *PrePrints* 2:e404v1.
424
- 425 Rehder, U. 1983. Morphometrical studies on the symmetry of the human knee joint: femoral
426 condyles. *Journal of Biomechanics* 16(5);351-361.
427
- 428 Rewcastle, SC. 1983. Fundamental adaptations in the lacertilian hind limb: a partial analysis
429 of the sprawling limb posture and gait. *Copeia* 476-487.
430
- 431 Roddy KA, Kelly GM, Van Es MH, Murphy P, & Prendergast PJ. 2011. Dynamic patterns of
432 mechanical stimulation co-localise with growth and cell proliferation during morphogenesis in
433 the avian embryonic knee joint. *Journal of Biomechanics* 44(1):143-149.
434
- 435 Rubenson J, Lloyd DG, Besier TF, Heliams DB, & Fournier PA. 2007. Running in ostriches
436 (*Struthio camelus*): three-dimensional joint axes alignment and joint kinematics. *Journal of*
437 *Experimental Biology* 210(14):2548-2562.
438
- 439 Rubenson J, Lloyd DG, Heliams DB, Besier TF, & Fournier PA. 2010. Adaptations for
440 economical bipedal running: the effect of limb structure on three-dimensional joint
441 mechanics. *Journal of The Royal Society Interface* rsif20100466.
442
- 443 Sarin VK, & Carter DR. 2000. Mechanobiology and joint conformity regulate endochondral
444 ossification of sesamoids. *Journal of Orthopaedic Research* 18(5):706-712.

- 445
446 Sarin VK, Erickson GM, Giori NJ, Bergman AG, & Carter DR. 1999. Coincident development
447 of sesamoid bones and clues to their evolution. *The Anatomical Record* 257(5):174-180.
448
- 449 Scapinelli R, & Little K. 1970. Observations on the mechanically induced differentiation of
450 cartilage from fibrous connective tissue. *The Journal of Pathology* 101(2):85-91.
451
- 452 Shufeldt RW. 1883. Remarks upon the Osteology of *Phalacrocorax bicristatus*. *Science*
453 41:640-642.
454
- 455 Shufeldt RW. 1884. Concerning some forms assumed by the patella in birds. *Proceedings of*
456 *the United States National Museum* 7:324-331.
457
- 458 Smith NC, Wilson AM, Jespers KJ, & Payne RC. 2006. Muscle architecture and functional
459 anatomy of the pelvic limb of the ostrich (*Struthio camelus*). *Journal of Anatomy* 209(6):765-
460 779.
461
- 462 Stannius H. 1850. Nouveau manuel d'anatomie compare. Tome II: Animaux vertébrés. 286.
463
- 464 Vickaryous MK, & Olson WM. 2007. Sesamoids and ossicles in the appendicular skeleton.
465 *Fins into limbs: evolution, development, and transformation* 323-341.
466
- 467 Vogel KG, & Peters JA. 2005. Histochemistry defines a proteoglycan-rich layer in bovine
468 flexor tendon subjected to bending. *J Musculoskelet Neuronal Interact* 5(1):64-69.
469
- 470 Wagner M. 2004. Die osteologie der hinterextremität und des beckengürtels beim
471 afrikanischen strauss (*Struthio camelus linné* 1758). Doctor Medicinae Veterinariae
472 Dissertation, Veterinärmedizinische Universität Wien.
473
- 474 Walker ML. 1890. On the form of the quadrate bone in birds. In: Thompson DW, ed. *Studies*
475 *from the Museum of Zoology in University College, Dundee*
476
- 477 Zinoviev AV. 2006. Notes on the hind limb myology of the ostrich (*Struthio camelus*).
478 *Ornithologia* 33:53-62.