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Notes on Pelvic and Hindlimb Myology and Syndesmology of *Emeus crassus* and *Dinornis robustus* (Aves: Dinornithiformes)

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Abstract — *Dinornis robustus* and *Emeus crassus* represent two variants of moa locomotor adaptations, *Dinornis* being more cursorial. Their overall hindlimb anatomy resembles that, inferred for primitive birds. While the hindlimb anatomy and syndesmology of moa resemble that of Tinamiformes and geographically close Apterygiformes and Casuariiformes, the development of *m. iliofemoralis externus* is peculiar to Dinornithiformes and far surpasses the bulk recorded for this muscle in other birds. In addition, moa appear to have a unique insertion of *m. iliofemoralis internus*, although additional observation of mummies would be desirable. On the anterior surface of the femoral shaft, this muscle inserts just distally to the neck where it must have changed its regular function of a weak outward rotator of femur. The attachment of *m. iliofemoralis* on the posterior surface of femur is unusually long and comparable to the structure observed only in Dinornithiformes and *Apteryx*. Terminal tendons of the long digital flexors to the second toe were, at least in *D. robustus*, separated from those to the other foretoes. This feature might indicate that the second toe played a major role in scratching and digging, an activity reported as one of the ways moa obtained their food. Caudal migration of the center of gravity, proposed for moa in comparison to other birds and for *Dinornis* in relation to other moa, does not have anatomical support.

Key words: Dinornithiformes, hind limbs, morphology, syndesmology, locomotion

Introduction

Since the first account (POLACK 1838) and the group's formal description in the following year (OWEN 1839), moa have been the subject of meticulous scientific study (for an overview, see WORTHY & HOLDAWAY 2002). As representatives of the order Dinornithiformes, moa represent the most striking example of insular ratite vicariance (WORTHY *et al.* 2005). Despite long standing problems in moa classification due to their high level of morphological variability and unprecedented levels of sexual dimorphism, the latest morphometric and genetic studies support the major division of Dinornithiformes among three families, Emeidae, Dinornithidae and Meg-

alapterygidae (BUNCE *et al.* 2009). Bones of the pelvic girdle and its appendages are among the best preserved and their morphology and proportions have traditionally played a major role in the group's taxonomy. In fact, OWEN (1879) based his initial classification solely on the basis of the hindlimb bones but he was not always correct. In his earliest paper, OWEN (1839) describes morphological features related to the muscular insertions (ridges and reticulate surface) on a fragment of femur, concluding, (p. 170) "... the Struthious bird indicated by the present fragment to have been heavier and more sluggish than the Ostrich; its femur, and probably its whole leg, was shorter and thicker". Many of his later works (collected in OWEN 1879), which support

the conclusion of sluggishness in the dinornithiforms, contain comments on certain ligamentous and muscular structures of moa hind limbs. “Strongly marked and indented ... muscular impressions” on the hindlimb bones of moa were also early noticed by COLENSO (1843). But it was not until 1869, when the description of anatomical features of hind limbs, other than bones, was provided. OWEN (1869) described mummified tendons, sesamoids and integumentary solepads of the inner toe of the right foot of *Dinornis robustus* OWEN, 1846, discovered in Manuherikia Valley (South Island). Later, COUGHTREY (1874a, b) described some muscles, tendons, ligaments and integuments of the mummified legs of *Emeus crassus* OWEN, 1846 (femur and tibia), found in Earnsclough Cave near Alexandra and *D. robustus*, found in the lowlands of the Knobby Range on the South Island. Another mummified foot of *Dinornis* (= *Megalapteryx*) *didinus* OWEN, 1883 was described by OWEN (1883b). Besides describing the integument and feathers still attached, OWEN made an important suggestion of how the feet of *Megalapteryx* might have once been used. He wrote (p. 260) “From the osseous structure of the foot, especially the strength and curvature of the unguis phalanges of the digits ii, iii, iv, it was inferred that the hind limbs of the Moas might have been put to the work of uprooting the ferns which, from the unusual proportion of nutritious matter their roots contain, are peculiar to New Zealand, and still afford the material of a favourite bread of the Maoris”.

CRACRAFT (1974, 1976a, b, c) used certain morphological characters and the dependence between the size and shape of hindlimb bones to calculate the groups diversity and position within ratites. He suggested that the unusual degree of diversity in the hindlimb bones was related the prolonged growth period in moas, attaining maximum weight only after their long bones reached maximal length. He also noted that members of the genus *Dinornis* might have been more cursorial, than other moas.

ALEXANDER (1983a, b, 1985) tried to determine the meaning of the unusual proportions of moa hind limbs using allometrical equations developed for flying birds. Dinornithidae fell well into the allometric continuum of flying birds,

while members of Emeidae did not. He suggested that this situation in moas was the product of a caudal migration of the center of mass coincident with the reduction of the wings. To keep the feet within the projected center of mass, the moa must have shortened its tarsometatarsus. In contrast, the narrow posterior part of the trunk in living ratites retains the center of the mass in the old position. The structure of *Apteryx* argues against such a hypothesis by having short tarsometatarsi along with a strongly narrowed posterior part of the pelvic girdle. ALEXANDER concluded that although moa were able to run, the absence of terrestrial predators led to the development of the robust graviportal limbs with unusually high optimum factors of safety.

KOOYMAN (1985), in his PhD dissertation on moas and archaeological evidence for moa hunting, provided functional interpretations of osteological hindlimb landmarks, used in the classification of moa. This not only allowed refinement of the existing classification but also led the author to the uncovering of some trends in moa locomotor diversification. *Megalapteryx* was found to be less agile, while members of genus *Dinornis* were the most cursorial and differed from their relatives by the position of their center of gravity. Feet of *Anomalopteryx* might have been better adapted to digging and scratching (KOOYMAN 1991).

Two other moa mummies with hind limbs (*Megalapteryx didinus* and *Anomalopteryx didiformis* OWEN, 1844) were found in 1980s (FORREST 1987; WORTHY 1989), but details of their anatomy have remained undescribed. The same can be said for specimens found in 1884 in the Hector Range (*Pachyornis elephantopus* OWEN, 1856) and in 1894 in the Old Man Range (*Megalapteryx didinus*) (BULLER 1888; ANDERSON 1989).

Here I offer the first detailed restoration of pelvic and hindlimb myology and syndesmology for two species of moa, belonging to two distinct families. I establish the basis for further comparative studies that link functional interpretations and morphological characters in an effort to understand the peculiarities of moa locomotor adaptations.

Material and Methods

I used pelvic and hindlimb bones of two species of moa from the collection of Museum für Naturkunde, Humboldt Universität zu Berlin (MB). An almost complete, mounted skeleton of adult Eastern Moa *Emeus crassus* (MB. Av. 1571) that included a sternum and part of the skull was shipped to Germany by Julius von HAAST sometime before 1850. His handwritten labels, referring to *Dinornis casuarinus*, are still preserved but, unfortunately, more detailed records describing the site, where this specimen was found, are missing in Germany and in New Zealand. The “Exchange Book” of Canterbury Museum at Christchurch begins only in 1856. Femora, tibiotarsi and tarsometatarsi of the skeleton are perfectly preserved (only pieces of both cristae cnemiales craniales are slightly abraded, apparently during transportation). Distal halves of both fibulae are missing. Cranial edges of alae preacetabulares and postacetabular portions of both ilia, both ischia and pubes are broken off. Several phalanges are missing, including the third of the third toe and the unguis of the fourth on the right foot; the unguis of the second toe and second, third and fourth (unguis) of the fourth (*Emeus* had normally only four phalanges in the outer toe) on the left foot. The hallux and related metatarsal elements are missing on both limbs.

A skeleton of an adult female of South Island Giant Moa *Dinornis robustus* (MB. Av. 1570, labeled as *Dinornis novaezealandiae*), once mounted, was originally found in Glenmark Swamp near Canterbury. The specimen preserves both alae preacetabulares ilii of the pelvis, both acetabula and the postacetabular part of the right ilium along with right ischium and pubis. As in the skeleton of *Emeus crassus*, the cranial portions of both preacetabular portions of iliac bones are broken off. Cavities in the right femur still contain portions of swampy soil. Surfaces of the femoral head, trochanteric ridge and both condyles are abraded exposing the spongy inner structure. Both tibiotarsi are preserved, showing similar abrasion of protruding surfaces (cristae cnemiales, condyles, caudal edges of proximal articular surfaces). Both fibulae are preserved with only the most distal and thinnest portions missing. The right tarsometatarsus is in particularly good con-

dition, showing only slight traces of abrasion in the hypotarsal and trochlear areas. The foretoes are well preserved; only the unguis phalanx of the right fourth toe is missing and substituted by artificial one. The hallux or hind toe and its metatarsal elements are missing.

Because many of the mounted skeletons from the 19th century are composites, often including material from different taxa, I made sure, that each bone belonged to *E. crassus* or *D. robustus* (WORTHY & HOLDAWAY 2002; WORTHY, pers. comm.), although not always to the same individuals.

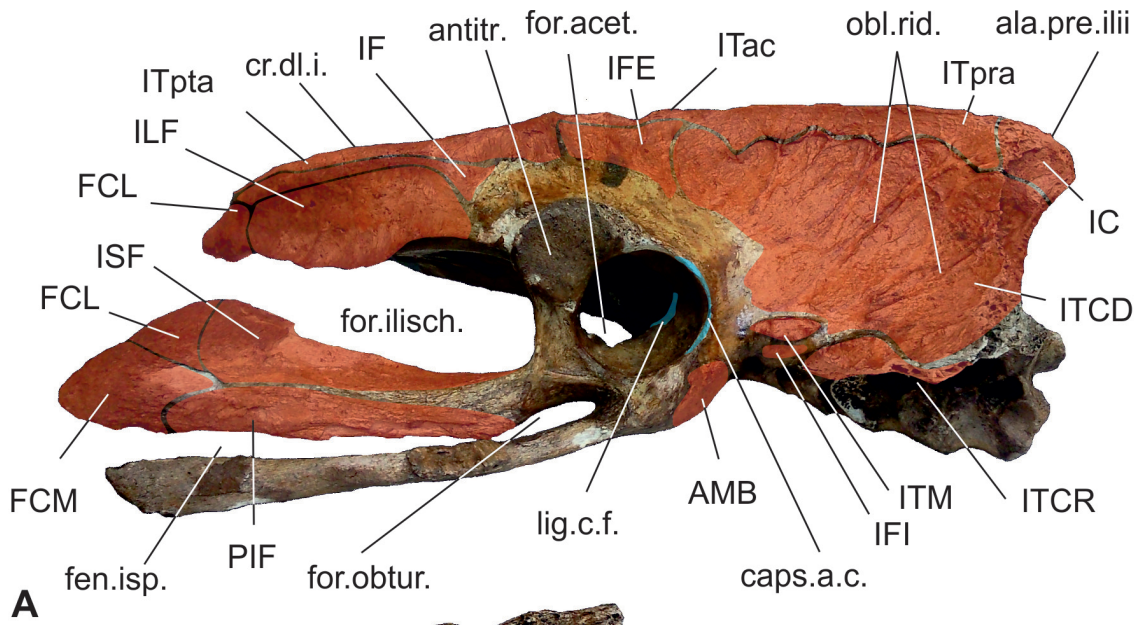
In the reconstruction, I depended on the extensive comparative data on pelvic and hindlimb osteology, myology and syndesmology for Class Aves in ZINOVIEV (2010). I also followed certain rules of reconstruction, which had been successfully applied in the earlier reconstruction of the hind limbs of *Hesperornis regalis* MARSH, 1872 (ZINOVIEV 2011). Although members of Casuariiformes are considered the closest living relatives of moa (JOHNSTON 2011), I was extremely cautious in direct extrapolation of morphological characters from extant paleognaths (*Dromaius*, *Casuaris*, *Apteryx*) onto dinornithid material. Besides being graviportal and often attaining great dimensions, moa retained the primitively broad pelvis (CRACRAFT 1974) with pedomorphically unfused ilia, ischia and pubes. In this way they may have differed from more specialized runners such as *Dromaius* or *Casuaris* and even *Apteryx*. Beautiful lithographs from OWEN’s papers were also quite instructive for interpreting absent or damaged osteal parts in the material.

Anatomical names follow *Nomina Anatomica Avium* II (BAUMEL *et al.* 1993) with some changes and additions made by ZINOVIEV (2010).

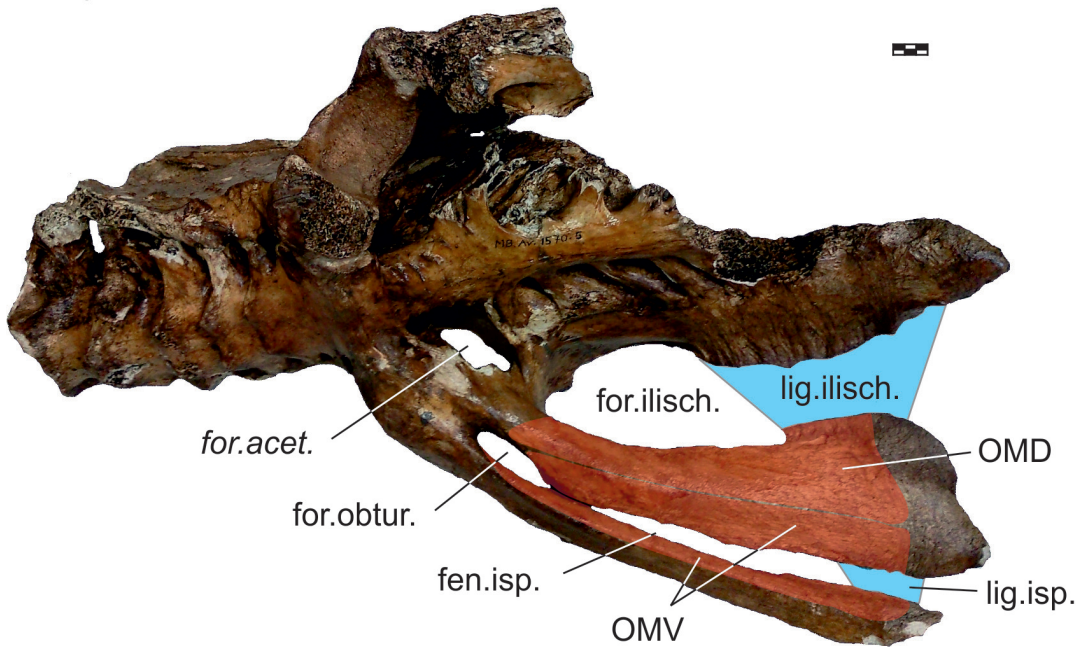
Myology and syndesmology

Hip joint

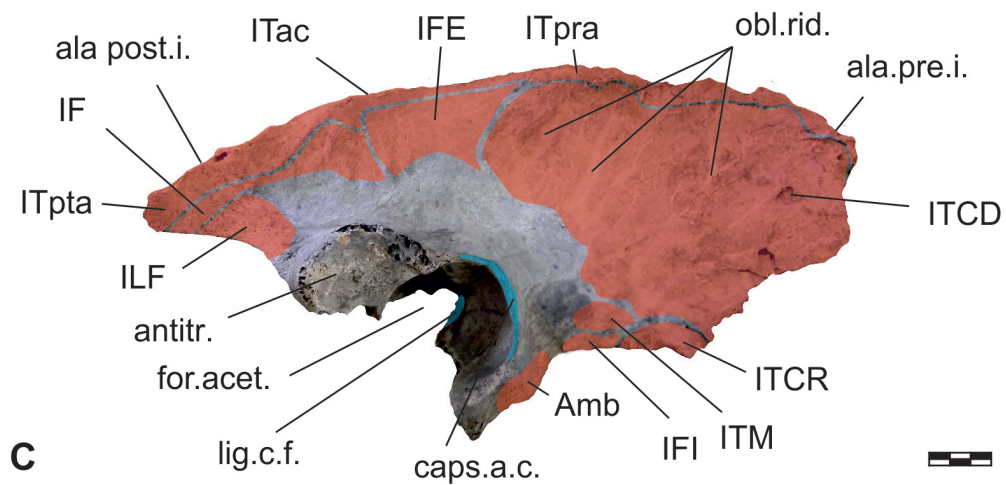
The hip joint belongs to the so called congruent joints in which the articular surfaces of both counterparts match each other closely (Figs 1, 2). The femoral head fits snugly in the acetabulum, where it is held in place by the well-developed ligamentum capitis femoris. In moa, the origin of



A



B



C

this stout ligament is marked on the cranial rim of the acetabular foramen by a concavity with osseal papillae which gradually fades towards the ventral rim of the opening, blending there clearly with the membrana acetabuli. The insertion of the ligament is in a fovea lig. capitis near the top of the femoral head. In our specimen of *E. crassus* the insertion of lig. capitis femoris was slightly moved proximally from the apex capitis, thus making it protrude and giving to entire head the conical appearance. In contrast, the femoral head of *D. robustus* was perfectly round with a more typical, centered fovea lig. capitis. The functional significance of this variation is obscure and, perhaps, non-existent, since in some specimens of *E. crassus* the femoral head is reported to be as rounded as in *Dinornis* (KOOYMAN 1991). Lig. capitis femoris and the articular cartilage that retained their flexibility were recorded for a specimen of a femoral head from *Dinornis* (ALLIS 1864).

The hip joint in birds is not limited to the acetabular region. It extends onto adjacent trochanteric surface of the femur, which rests on the antitrochanter of the ilium. This trochanter-antitrochanter complex produces the habitual, somewhat horizontal position of femur. The proposed position of the femur contrasts with some earlier reconstructions but is consistent with the structure of all extant birds with the exception of penguins and some specialized foot-propelled divers. A proposed difference for the position of the center of gravity that distinguishes the Dinornithidae and other moas from other birds (ALEXANDER 1983a; KOOYMAN 1985, 1991) is thus not supported by the position of the femur. The

femur is not close to vertical (ALEXANDER 1983a).

The origin of capsula articularis coxae is well-defined on the cranial and dorsal surfaces of the elevated acetabular rim. There is an area of tendinous attachment on the cranial surface of the proximal femoral shaft distal to the femoral head and medial to the crista trochanteris. This area is round and slightly excavated in *Dinornis* and longitudinally extended and deeply excavated in *E. crassus*. Although the area appears to be the place of insertion for the lig. iliofemoralis (ZINOVIEV 2010), the absence of an equally strong origin of this ligament on the ilium suggests an alternate explanation; it is possible that m. iliofemoralis internus (OWEN 1858) or m. femorotibialis internus (KOOYMAN 1991) have inserted here.

Pelvic muscles

For the description of pelvic muscles (Figs 1, 2, 4) I used the sequence reconstructed for *Hesperornis* (ZINOVIEV 2011). The deepest muscles, which control the movements in the hip joint, usually leave the clearest traces on the bones. This is especially true for the group mm. ilirotrochanterici, which resist supination (outward rotation) of the femur caused by the action of the femoral retractors (ZINOVIEV & DZERZHINSKY 2000). These muscles traditionally extend across the entire surface of ala preacetabularis ilii, leaving definite traces of their fleshy and tendinous origins.

Mm. ilirotrochanterici — In both species studied here, there are pronounced traces of muscular and tendinous origin of mm. ilirotrochanterici on

◀ **FIGURE 1.** Pelves of moa, showing attachments of muscles and ligaments: **A, B**, *Dinornis robustus* (MG. Av. 1570), lateral and ventrolateral views; **C**, *Emeus crassus* (MB. Av. 1571), lateral view. Origins and insertions of muscles are filled with red and those of ligaments with blue. Muscular attachments of pubis are not shown due to the complete erosion of its surface.

Abbreviations: ala post. i., ala postacetabularis ilii; ala pre. i., ala preacetabularis ilii; AMB, m. ambiens; antitr., antitrochanter; caps. a. c., capsula articularis coxae; cr.dl.i., crista dorsolateralis ilii; FCL, m. flexor cruris lateralis; FCM, m. flexor cruris medialis; fen. isp., fenestra ischiopubica; for. acet., foramen acetabuli; for. ilisch., foramen ilioischadicum; for. obtur., foramen obturatum; IC, m. ilirotibialis cranialis; IF, m. iliofibularis; IFE, m. iliofemoralis externus; IFI, m. iliofemoralis internus; ILF, m. iliofemoralis; ISF, m. ischiofemoralis; ITac, m. ilirotibialis lateralis pars acetabularis; ITCD, m. ilirotrochantericus caudalis; ITCR, m. ilirotrochantericus cranialis; ITM, m. ilirotrochantericus medius; ITpra, m. ilirotibialis lateralis pars preacetabularis; ITpta, m. ilirotibialis lateralis pars postacetabularis; lig. c. f., lig. capitis femoris; lig. ilisch., lig. ilioischadicum; lig. isp., lig. ischiopubicum; obl. rid., oblique ridges; OMD, m. obturatorius medialis pars dorsalis; OMV, m. obturatorius medialis pars ventralis; PIF, mm. puboischiofemorales.

ala preacetabularis ilii (Figs 1A, C; 2A, B, D, E). Unfortunately, both specimens lack the fragile cranial edges and, consequently, I am unable to reconstruct the cranialmost parts of the muscle group. However, the preserved surface of ala preacetabularis ilii shows the beginning of the most powerful of the ilioprochanterici – m. ilioprochantericus caudalis. Its origin covers almost the entire surface of ala preacetabularis ilii extending from its cranial part approximately to the line passing vertically through the middle of the acetabular opening. The structure of this muscle must have been as complex, as it is in the large living ratites (SUDILOVSKAYA 1931; ZINOVIEV, 2006). The short muscular fibers of m. ilioprochantericus caudalis started from the preacetabular portion of the ilium but also originated from a number of aponeuroses. Origins of these aponeuroses on ala preacetabularis ilii are marked by prominent oblique ridges. Muscle fibers ended on a number of intramuscular aponeuroses, contributing to a large aponeurosis on the lateral surface of the muscle. This aponeurosis gave rise to a stout terminal tendon, which inserted into the crescent-like rugosity on the cranio-lateral surface of the greater trochanter, proximal to the insertion of m. ilioprochantericus medius. The area cranial to this insertion is smooth and variable in different species of moa (KOOYMAN 1991) and was covered by a sheet of cartilage that facilitated sliding of the terminal tendon of m. ilioprochantericus caudalis over the crista trochanteris (ZINOVIEV 2010). The large and powerful belly of m. ilioprochantericus caudalis covered the smaller bellies of mm. ilioprochanterici cranialis et medius. The fleshy origin of m. ilioprochantericus medius is marked on the lateral surface of ala preacetabularis ilii by an oval rugose area between the beginning of m. ilioprochantericus caudalis and m. ilioprochantericus cranialis. In many birds this muscle fuses with the more powerful m. ilioprochantericus cranialis (ZINOVIEV 2010). The presence of a separate medial ilioprochanteric muscle in moas is also marked by its well-defined place of insertion on the rugose area between the insertions of m. ilioprochantericus caudalis and m. ilioprochantericus cranialis. The insertion of m. ilioprochantericus cranialis on the cranio-lateral surface of the femoral shaft is also marked by rugosity. A shallow saddle-shaped

area marks the passage of the terminal tendon of this muscle over the distal part of crista trochanteris. The origin of m. ilioprochantericus cranialis, like that of m. ilioprochantericus caudalis, is a combination of muscular and tendinous attachments. The area of origin is from the ventral rim of ala preacetabularis ilii and the adjacent area of its lateral surface just below the origins of other ilioprochanterici. Remains of terminal tendons of mm. ilioprochanterici caudalis et cranialis were reported by COUGHTREY (1874a).

Comparison — As in other large cursorial birds, mm. ilioprochanterici of moa are well developed with a complex structure and bear the closest topological resemblance to those of *Dromaius* and *Apteryx* of Ratitae (MCGOWAN 1979; PATAK & BALDWIN 1998). However, the position of mm. ilioprochanterici in moa is typical of most of birds and can be considered primitive (ZINOVIEV 2010). Mm. ilioprochanterici of other ratites, such as *Rhea* and *Struthio*, show features of specialization (GANGL *et al.* 2004; ZINOVIEV 2006; PICASSO 2010).

M. iliofemoralis internus — The presence of a minute m. iliofemoralis internus (Figs 1A, C; 2A, C, E) is marked by a rugosity on the lateral surface of ala preacetabularis ilii just caudal to the origin of m. ilioprochantericus cranialis and cranial to that of m. ambiens. This muscle is weak and parallel-fibered in birds, other than *Struthio*, and inserts on the ventromedial surface of femoral shaft often leaving no trace of its insertion. In *E. crassus*, a slight tuberosity in the corresponding area is likely the point of insertion for this muscle. However, an oval tuberosity (deeply excavated in *E. crassus*) on the cranio-medial surface of the femoral shaft, just distal to the *caput femoris*, could also be a candidate for the point of insertion (OWEN 1858). COUGHTREY (1874a) found several fibers still attached to this area and followed OWEN in attributing them to m. iliofemoralis internus. Such an unusual insertion for the internal iliofemoral muscle poses a problem of interpretation. Although generally weak and sometimes absent in birds, this muscle in its regular position turns the femur outwards, thus regulating movements in hip joint (ZINOVIEV 2007). In the position, proposed by OWEN (1858), it would be an extremely ineffective inward rota-

tor of the femur, compared to the much more powerful mm. ilioprochanterici.

Comparison — *M. iliofemoralis internus* is quite uniformly weak in the majority of birds. Among ratites it is generally weaker in Casuariiformes but strongly developed with shift in the point of origin in *Struthio*. None of the recent or extinct birds show a comparable shift of the insertion of this muscle (ZINOVIEV 2010, 2011).

M. iliofemoralis externus — The origin and insertion of a strong m. iliofemoralis externus (Figs 1A, C; 2D) are well marked in moa. Like m. ilioprochantericus caudalis it had fleshy and tendinous origin (multipinnate) on ala preacetabularis ilii just caudal to the origin of the aforementioned muscle. The extent of the caudal expansion of this muscle is limited by the beginning of crista dorsolateralis ilii. The insertion of this muscle on the femoral trochanter is among the most prominent. An extensive, slightly oblique scar is situated between insertion of mm. ilioprochanterici and that of m. ischiofemoralis. On its way to the insertion, a strong and broad tendon of m. iliofemoralis externus must have crossed underlying terminal tendons of m. ilioprochantericus caudalis and m. obturatorius medialis. The remains of this tendon are described by COUGHTREY (1874a).

Comparison — *M. iliofemoralis externus* is generally a weakly developed femoral abductor in birds, as more powerful protractors and retractors of the femur also abduct it (ZINOVIEV & DZERZHINSKY 2000). However, in cursorial and, especially, large cursorial birds, it is better developed (ZINOVIEV 2007, 2010). Among ratites this muscle is stronger in *Apteryx* (OWEN, 1849a) and *Dromaius*, the latter having multipinnate m. iliofemoralis externus (PATTERSON, 1983).

M. ambiens — In *D. robustus* m. ambiens (Fig. 1A, C) arose from a rugose area at the junction of the ilium and the pubis (the pectineal process in moa is not prominent). The rugose area is more expansive on the ilium. The course of the muscle is obscure, since it does not insert on a bone in birds; its terminal tendon fuses with aponeurosis communis fibularis upon crossing the knee joint.

Comparison — Generally vestigial, m. ambiens disappears in a number of perching birds. In

cursorial birds it is better developed and associated with locomotion in groups with single limb supported phases (ZINOVIEV 2007). Ratites show considerable variation in the morphology of this muscle. In *Struthio*, it originates from the center of ala preacetabularis ilii, whereas in others it originates from the pectineal process. It is reportedly absent in Casuariiformes (GARROD 1873; GADOW 1880; BEDDARD 1898). However, a slip that originates from proc. pectineus and fuses with the tendon of m. femorotibialis medius could be the remnant of m. ambiens. It shows tendencies for similar fusion in Rheiformes (GADOW & SELENKA 1891).

*M. obturatorius medialis*¹ — *M. obturatorius medialis* is the only muscle in modern birds which originates on the visceral surface of the pelvis (Figs 1B; 2B, D). Traces of its origin in *D. robustus* suggest that it must have had two bellies. The dorsal belly originated aponeurotically from the medial surface of the postacetabular ilium, immediately adjacent to foramen ilioischadicum as well as from the dorsal half of the ischium facing the foramen. The main bulk of muscular fiber of the dorsal portion undoubtedly arose from membr. ilioischadica itself. The ventral belly originated from membr. ischiopubica and adjacent surfaces of the ischium and pubis that are tilted towards it. It is difficult to reconstruct the expansion of the bellies caudally, since they have not left definite traces. However, they must have expanded to some extent along the strengthened caudal portions of membr. ilioischadica and membr. ischiopubica (ligg. ilioischadicum et ischiopubicum). The terminal tendon passed through foramen obturatum, which was separated from fenestra ischiopubica by the tendinous bridge. It inserted on the lateral surface of the proximal femur just caudal to the insertion of m. ilioprochantericus caudalis. The passage of the terminal tendon along the femur is marked by smooth area that was undoubtedly covered by the thin layer of cartilage. Remains of the terminal tendon are reported by COUGHTREY (1874a).

1 *M. obturatorius lateralis*, which is always present in birds (ZINOVIEV 2010), sheathes the terminal tendon of m. obturatorius medialis and must have been present in moa. However, it leaves such faint traces on bones, that its precise reconstruction is not possible.

Comparison — *M. obturatorius medialis* is quite uniform in birds, sometimes having two heads of origin. It is quite variable in Ratitae; *Struthio* is the only bird, in which part of the muscle starts from lateral surfaces of lamina ischiopubica and adjacent areas of ischium and pubis (ZINOVIEV 2007). Casuariiformes and Rheiformes also have two heads of this muscle (GADOW 1880; GADOW & SELENKA 1891; PATTERSON 1983; PICASSO 2010).

M. ischiofemoralis — The deepest muscle of the acetabular pelvis is *m. ischiofemoralis* (Figs 1A; 2B, D, F). Origins of muscles of the postacetabular pelvis are difficult to reconstruct because they leave only faint traces on the bones. This is also the case for *m. ischiofemoralis*, the large part of which originates from the lateral surface of membr. ilioischiadica. This membrane was undoubtedly present in moa (see the description of the previous muscle) as indicated by the sharp rims of the ilium and ischium that project towards each other. Only the ventral border of *m. ischiofemoralis* is detectable on the ischial bone of *D. robustus*. The muscle's belly started from the dorsal half of the ischium, near the level of the caudal half of foramen obturatum, and extended about two-thirds along that bone. To what extent it expanded over membr. ilioischiadica or perhaps originated on the adjacent area of the postacetabular ilium, as in many modern birds, remains unclear. A strong tendon of this muscle inserted on the lateral side of the femoral shaft on a tuberosity just caudal and distal to the insertion of *m. iliofemoralis externus*. This area is quite pronounced in *E. crassus* but much fainter in *D. robustus*.

Comparison — *M. ischiofemoralis* is quite morphologically conservative in birds and moas are not an exception.

M. iliofemoralis* and *m. caudofemoralis — The presence of a well-developed *m. iliofemoralis* (Figs 1A, C; 2 B, F) is defined by attachment to a ridge, which extends along the caudal border of the femoral shaft from the insertion of *m. ischiofemoralis* to the proximal point of insertion of pars accessoria *m. flexor cruris lateralis*. This ridge in *E. crassus* runs very close to that of the medially situated *mm. puboischiofemorales*,

whereas *D. robustus* shows a greater distance between the two ridges. The pelvic origin of *m. iliofemoralis* should have started somewhere on the ilium between crista iliaca dorsolateralis and membr. ilioischiadica. In life, part of it might also have started on the membrane. There are no definite traces of the presence of *m. caudofemoralis* in either species of moa examined in this study.

Comparison — Although proceeding from the position of the adjacent muscular bellies, the shape of the belly of *m. iliofemoralis* in *D. robustus* must have been similar to that of the majority of birds, its extended insertion on the femoral shaft is a rare feature, which was earlier recorded only for *Apteryx australis* (MCGOWAN 1979). The postacetabular portion of the pelvis in *E. crassus* was not available for the study. As for *m. caudofemoralis*, it might have been altogether absent in moa. The presence of this muscle is usually related to the development of the tail, which it bends sideways. It is absent in Rheiformes and *Dromaius*, vestigial in *Casuarius* (GARROD 1873; GADOW 1880; PYCRAFT 1900; PATTERSON 1983; PICASSO 2010), but present in *Apteryx* and *Struthio* (GADOW 1880; OWEN 1849a; MCGOWAN, 1979).

Mm. puboischiofemorales — These major femoral retractors, *mm. puboischiofemorales* (Figs 1A; 2B, F), are always present in birds and consist of two parts, one superficial or lateral and another deeper or medial. The beginning of the lateral portion is partially detectable on the pelvis of *D. robustus*. It started from the ventral half of the ischium, leaving free only its caudal fifth. The deeper part must have originated ventrally from the same bone and also from the part of membr. ischiopubica. The insertions of the muscles are on the ridge, running along the caudal surface of the femoral shaft medial to the ridge marking the insertion of *m. iliofemoralis*. The ridge starts from the level of insertion of *m. ischiofemoralis* and terminates at the distal level of the insertion of pars accessoria *m. flexor cruris lateralis*.

Comparison — As major femoral retractors, *mm. puboischiofemorales* are quite uniform in birds, and the moa does not show any deviations from the general plan.

Mm. flexores crures lateralis et medialis — Both flexors of the knee joint and inward rotators of

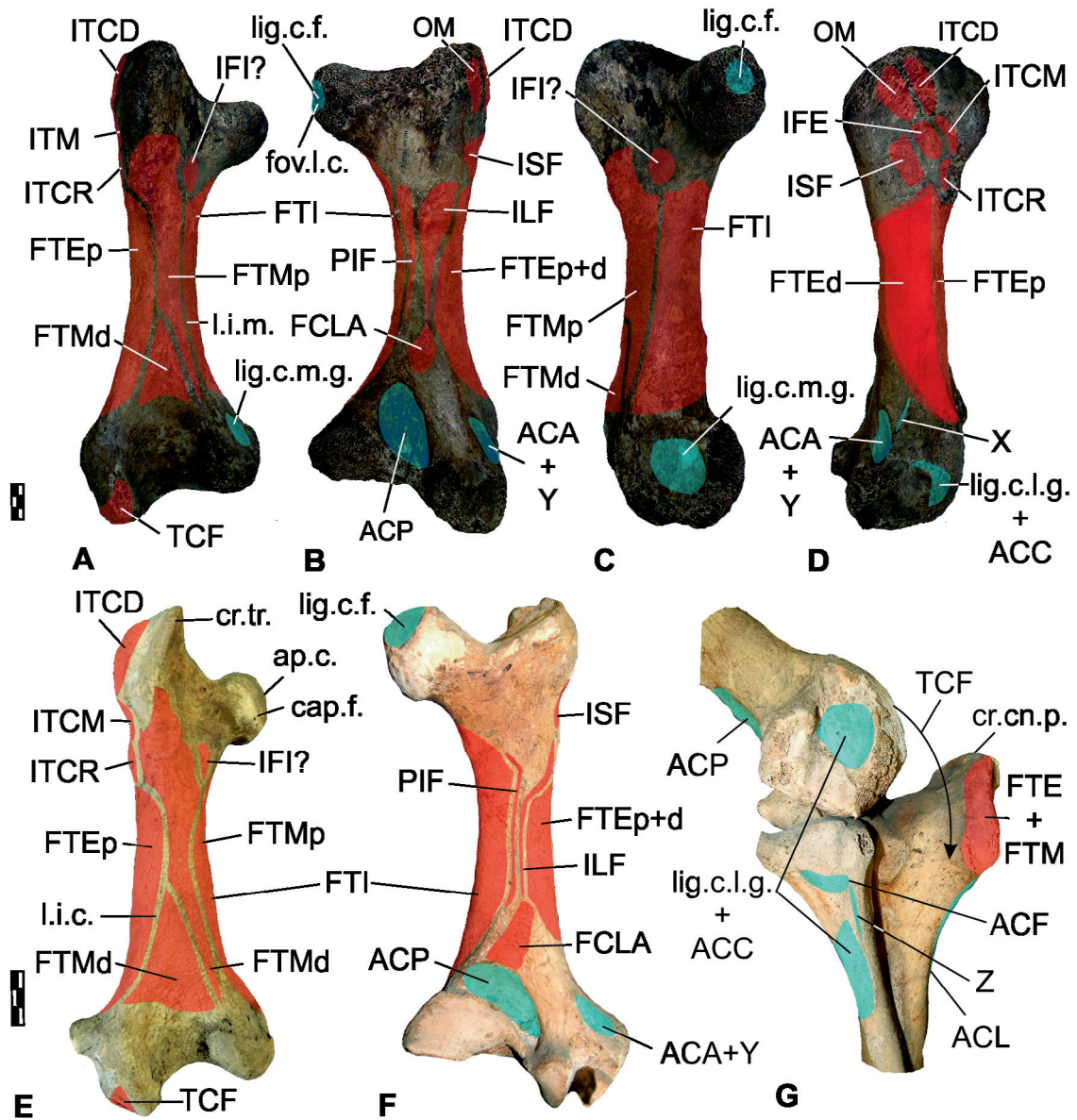


FIGURE 2. Right femora of: **A-D**, *Dinornis robustus* (MG. Av. 1570) cranial, caudal, medial and lateral aspects; **E-F**, *Emeus crassus* (MB. Av. 1571), cranial and caudal aspects, **G**, right knee joint of the same *Emeus* specimen, showing attachments of some muscles and ligaments.

Abbreviations: ACA, apon. communis ansae; ACC, apon. communis collateralis; ACF, apon. communis fibularis; ACP, apon. communis poplitea; ap. c., apex capitis; cap. f., caput femoris; cr. cn. p., crista cnemialis patellaris; cr. tr., crista trochanteris; FCLA, m. flexor cruris lateralis pars accessoria; fov. l. c., fovea lig. capitatis; FTE, m. femorotibialis externus; FTEd, m. femorotibialis externus pars distalis; FTEp, m. femorotibialis externus pars proximalis; FTEp+d, m. femorotibialis externus partes proximalis et distalis; FTI, m. femorotibialis internus; FTM, m. femorotibialis medius; FTMd, m. femorotibialis medius pars distalis; FTMp, m. femorotibialis medius pars proximalis; IFI, m. iliofemoralis internus; ILF, m. iliofemoralis; ISF, m. ischiofemoralis; ITCD, m. iliotrochantericus caudalis; ITCR, m. iliotrochantericus cranialis; ITM, m. iliotrochantericus medius; lig. c. f., lig. capitatis femoris; lig. c. l. g., lig. collaterale laterale genus; lig. c. m. g., lig. collaterale mediale genus; l. i. c., linea intermuscularis cranialis; l. i. m., linea intermuscularis medialis; OM, m. obturatorius medialis; PIF, mm. puboischiofemorales; TCF, m. tibialis cranialis caput femorale; X, pars proximalis ansae m. iliofibularis; Y pars lateralis ansae m. iliofibularis.

the shank, mm. flexores crures lateralis et medialis, were present in moa (Figs 1A, B; 2B, F). The origin of the lateral one is detectable on the ischium caudal to the origin of m. ischiofemorialis. It might have also originated from the caudal part of the postacetabular ilium and strong ligament, which united ilium and ischium (see above). But these traces are not detectable. The medial muscle started from the apical part of the ischium, ventral to the origin of lateral part and caudal to that of mm. puboischiofemorales. Both bellies ran towards the tibiotarsus to insert on its medial surface at the pronounced, slightly oblique rugosity cranial to the insertion of lig. collaterale mediale genus. Before providing the terminal tendon for the common tibiotarsal insertion, the lateral part gave a rise to an accessory belly whose fleshy part attached to the triangular area proximal to aponeurosis commuis poplitea.

Comparison — Both muscles are well developed in cursorial birds, including ratites. Their origin may migrate onto several tail vertebrae (Rheiformes, Apterygiformes), which is impossible to prove for moa. However, it is almost certain, that the lateral muscle had a tendinous connection with the intermediate head of m. gastrocnemius, which is characteristic for all the Ratitae and a majority of basal birds.

M. iliofibularis — Moa exhibit a muscular organization seen in other birds in which m. iliofibularis originates along almost the entire length of postacetabular ilium, just above the origins of m. ischiofemorialis and m. iliofemorialis and below the postacetabular portion of m. iliotibialis lateralis (Figs 1A, C; 4C, D). It gradually tapered distally and a tendon of insertion passed through the tendinous loop (as described in the section on the knee joint, below) to insert on tuberositas m. iliofibularis on the lateral side of the fibula, just distal to the insertion of lig. collaterale laterale genus. The tendinous evidence for this insertion in *D. robustus* is reported by COUGHTREY (1874a).

Comparison — This muscle is quite uniformly developed through the entirety of Class Aves, regardless of variation in locomotor habits (ZINOVIEV 2010).

Mm. iliotibiales lateralis et cranialis — The most superficial muscles of the thigh, mm. iliotibiales

lateralis et cranialis were extremely well developed in moa. Although the most cranial part of ala preacetabularis ilii is missing in our material, the caudal surface of the origin of m. iliotibialis cranialis is fortunately preserved (Fig. 1A, C). It shows a thick combination of fleshy and tendinous origins but not the aponeurotic type seen in many birds. The preacetabular portion of m. ilioprochantericus lateralis shows a similar origin that extended up to the beginning of m. iliofemorialis externus. The acetabular portion of the muscle had a much thinner origin, providing adequate space for the origin of m. iliofemorialis externus. The beginning of the postacetabular portion was equally thick and extended to a point slightly behind the caudal edge of the antitrochanter. From that point, a much thinner line of origin for the postacetabular portion ran caudally along the rest of crista iliaca dorsolateralis. Both muscles contributed to the formation of the patellar tendon, which inserted on crista cnemialis lateralis and crista cnemialis patellaris. Part of the tendinous insertion of these muscles is reported by COUGHTREY (1874a).

Comparison — Well developed mm. iliotibiales are characteristic for cursorial birds and are especially strong in ratites (ZINOVIEV 2011).

Femoral muscles

The femoral muscle complex of birds (Fig. 2) consists of three major parts, which envelope almost the entire femoral shaft. The primary function of these muscles is to extend of the knee joint. The lateral and medial portions of this complex can also supinate and pronate the crus (ZINOVIEV 2010). These muscles are especially well developed in cursorial birds.

M. femorotibialis externus — Both proximal and distal parts of m. femorotibialis externus were present in *D. robustus* and *E. crassus* (Fig. 2A, B, D-G). They were better defined in the latter species with greater femoral relief. Pars proximalis originated from an area, bordered cranially by crista trochanteris; proximally, by the insertion of m. ilioprochantericus caudalis; proximovertrally, by the insertion of m. iliofemorialis externus and m. ischiofemorialis; and ventrally, by the extended insertion ridge for m. iliofemorialis (see above).

On the cranial surface of the femoral shaft the expansion of pars distalis is restricted by linea intermuscularis cranialis, whose lateral branch goes to the condylus lateralis. Pars distalis was covered by the proximal portion and partially had the same ventral and proximal borders. Its cranial expansion on the lateral side of the femoral shaft was limited by a faint ridge, which starts at the point between the insertions of m. iliofemoralis externus and m. ischiofemoralis and runs along the lateral surface of the femoral shaft to a point slightly beyond the proximal level of the insertion of pars accessoria m. flexorius cruris lateralis. Both, proximal and distal parts contributed to the lateral part of patellar tendon that inserted on the external edge of crista cnemialis lateralis.

Comparison — The development of m. femorotibialis externus in moa is typical for cursorial birds. In ratites the proximal part of the muscle completely covers the distal one, which extends proximally along the femoral shaft (ZINOVIEV 2010).

M. femorotibialis medius — M. femorotibialis medius had the fleshy origin along the entire cranial surface of the femoral shaft (Fig. 2A, C, E, G). It was also divided into proximal and distal parts. The proximal part had a tendinous origin from the tuberosity on the distal portion of crista trochanteris and a fleshy origin from the area between linea intermuscularis cranialis (with a branch to condylus medialis) and linea intermuscularis medialis, dividing the belly of m. femorotibialis medius from that of m. femorotibialis internus. The extent of proximal migration of the m. femorotibialis medius belly between crista trochanteris and caput femoris is not clear. A terminal tendon from the proximal part contributed to the formation of the patellar tendon. The distal part of m. femorotibialis medius had a fleshy origin in a well-defined area between branches of linea intermuscularis cranialis. It was completely covered by the proximal part of mm. femorotibiales lateralis et medius. Muscle fibers of the distal part, most likely, inserted directly to the proximal border of the patella, as in the majority of birds. Some muscular fibers of m. femorotibialis medius were described by COUGHTREY (1874a).

Comparison — As for the previous muscle, the development of m. femorotibialis medius in

moa is typical for cursorial birds. Ratites show progressive enlargement of the distal part of the muscle, which reaches its maximal development in *Struthio* (ZINOVIEV 2010).

M. femorotibialis internus — The origin of m. femorotibialis internus was confined to the medial and caudomedial surfaces of the femoral shaft (Fig. 2A, C, E, F). Its body was restricted caudally by the ridge of insertion for mm. puboischiofemorales and cranially by linea intermuscularis medialis. The extent to which m. femorotibialis internus expanded proximally is not clear. However, there is an excavated area near the proximal reaches of the muscle that strongly suggests a tendinous origin. Such a structure is unique for Dinornithiformes. If it does not reflect the insertion of m. iliofemoralis internus, the strengthened tendinous part of the other (superficial) head of m. femorotibialis internus might have been solely responsible for this feature. In this suggestion I agree with the interpretation of KOOYMAN (1991).

Comparison — M. femorotibialis internus generally consists of two bellies (ZINOVIEV 2010). Ratites show many deviations from the general type by having up to two or three bellies (Struthioniformes, Rheiformes, Casuariiformes). The unusual rugose pit near the beginning of m. iliofemoralis internus belly might represent a deviation strictly confined to Dinornithiformes.

Knee joint

Due to the migration cranially of the center of gravity in birds, the knee joint has become the major pivot, around which the hind limb moves (Figs 2, 3, 4). Despite the majority of locomotor adaptations, avian knee joint is morphologically conservative, showing striking similarity among the various ecological groups (ZINOVIEV 2010) and does not differ from the general type, even in highly specialized birds (ZINOVIEV 2011). Therefore, it seems very likely that the moa, residing well within Neornithes, had a knee joint similar to that of other modern birds. All evidence suggests that this is, in fact, so.

In addition to the relatively feeble joint capsule, the knee of moa was stabilized by a robust set of collateral ligaments. Lig. collaterale laterale genus originated in a deeply excavated

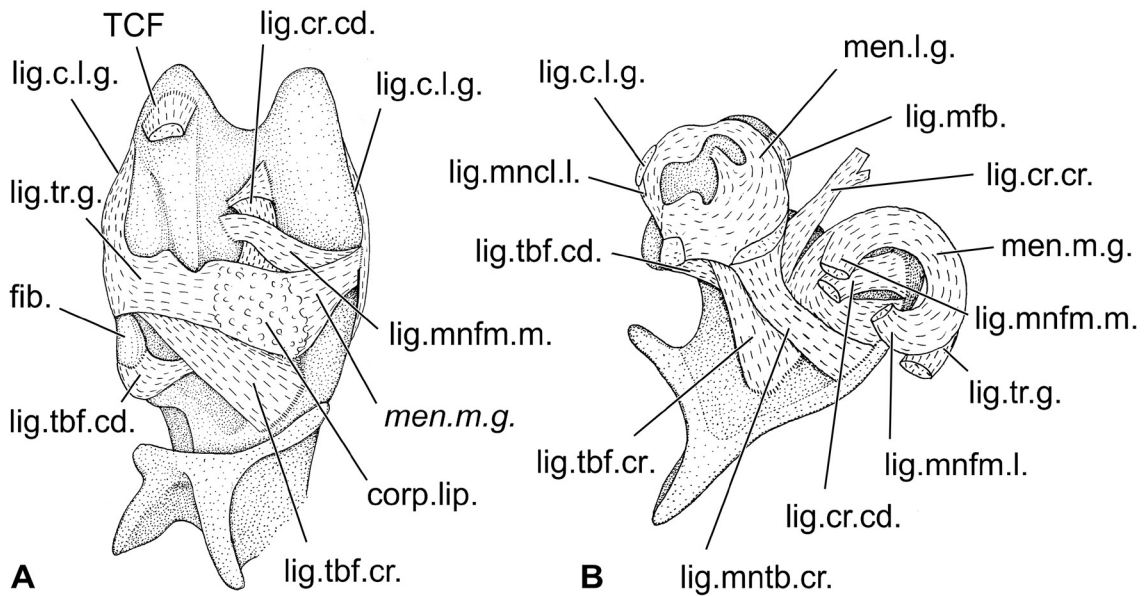


FIGURE 3. Right knee joint of *Dromaius novaehollandiae* (Museum of Natural History of the University of Kansas, without no.) **A**, overflexed, cranial view; **B**, distal articular surface. From ZINOVIEV (2010) with changes. Abbreviations: corp. lip., corpus liposum; fib., fibula; lig. c. l. g., lig. collaterale laterale genus; lig. cr. cd., lig. cruciatum caudale; lig. cr. cr., lig. cruciatum craniale; lig. mfb., lig. meniscofibulare; lig. mncl. l., lig. menisco-collaterale laterale; lig. mnfm. l., lig. meniscofemorale laterale; lig. mnfm. m., lig. meniscofemorale mediale; lig. mntb. cr., lig. meniscotibiale craniale; lig. tbf. cr., lig. tibiofibulare craniale; lig. tbf. cd., lig. tibiofibulare caudale; lig. tr. g., lig. transversum genus; men. l. g., meniscus lateralis genus; men. m. g., meniscus medialis genus; TCF, m. tibialis cranialis caput femorale.

fossa on the lateral surface of corresponding femoral condyle. Its passage to the place of insertion is marked by a groove on the lateral femoral condyle and a smoothed area on the lateral surface of the fibula. The lateral collateral ligament of the knee was inserted on the lateral surface of the fibular shaft just proximal to the insertion of m. iliofibularis. Lig. collaterale mediale genus started from a less deeply excavated fossa on the medial side of the corresponding femoral condyle. Its passage across the knee joint is marked by a slight depression in condylus femoris medialis. The ligament inserted on the medial surface of the tibiotarsal shaft slightly distal to the insertion of its lateral counterpart. The place of insertion of this ligament was covered by the common tibiotarsal attachment of mm. flexores crures lateralis et medialis. The articular surfaces have been damaged in the mounted skeleton of *E. crassus* and in the previously mounted specimen of *D. robustus* and did not allow us to prepare clear illustrations. However, the position of ligg. cruciata and other ligaments, which held both menisci in place, and ligaments holding the head

of fibula against tibiotarsus, closely resembled those of *Dromaius* (Fig. 3).

Muscles of the crus

As noted in an earlier publication (ZINOVIEV 2011), the reconstruction of the crural muscles is difficult due to the limited space available for their origin on the distal femur and proximal crus (Figs 1, 4–6). This shortage of space and the necessity to retain mobility in the knee joint has resulted in crowding of the origins for crural muscles near the knee. They often share an origin on common aponeuroses rather than originating separately from the bones (ZINOVIEV 2003a). However, the aponeuroses leave clear traces on the bones and thus can be reconstructed with the high degree of confidence (ZINOVIEV 2011). Those attached to cnemial crests might have been relatively smaller than in the majority of other birds (a feature, already noted by earlier authors: OWEN 1849c) and closely approached proportions seen in *Apteryx* (see Discussion). The following description includes the reconstruction of the

ligamentous loop (ansa m. iliofibularis), which is intimately associated with aponeuroses originales (Figs 2, 4).

Aponeuroses originales communes musculorum cruris

Aponeurosis communis ansae (Fig. 2B, F) — originates in all known birds on the lateral femoral epicondyle and is associated with the lateral branch of ansa m. iliofibularis. It was enormously developed in moa. Both of the species studied here and others show a deep elongated or circular fossa at the same location on the lateral femoral epicondyle. The feature was correctly interpreted by KOOYMAN (1991), who associated the fossa with the lateral branch of the loop (Fig. 2D) and with the beginning of the lateral part of m. gastrocnemius. Aponeurosis communis collateralis (Fig. 2D, G) is intimately associated with the beginning of lig. collaterale laterale genus and is detectable in moa. It started from a site near the origin of the mentioned collateral ligament and expanded cranioproximally along the lateral surface of the femoral condyle. The cranial branch of ansa m. iliofibularis (Figs 2G, 4C) left a longitudinal rugosity on the lateral side of the fibular shaft between the fibular head and the beginning of lig. collaterale laterale genus. Aponeurosis communis poplitea (Fig. 2B, F, G) started from the entire popliteal area, in front and slightly mediad to the insertion of accessory part of m. flexor cruris lateralis. The presence of aponeurosis communis fibularis (Figs 2G, 4C) is marked by rugosity on the lateral surface of the fibular head just above the insertion of the cranial branch of the ligamentous loop². Whether it was associated with the terminal tendon of m. ambiens, as in the majority of birds possessing this muscle, or not, is unclear. There are no traces of m. ambiens crossing the knee joint; no such traces have been reported for the preserved patella (OWEN 1883a). The beginning of aponeurosis communis lateralis (Figs 2G, 4A–C) is traceable along the distal portion of crista cnemialis lateralis. In contrast, the beginning of aponeurosis communis dorsalis (Fig. 4A, B) is quite continuous, starting

2 Lig. collaterale laterale genus and aponeurosis communis are often fused at the insertion on fibula, so their division on Fig. 2G is very approximate.

on the cranial cnemial crest and extending down the tibiotarsus well to the beginning of sulcus extensorius. The last, proximal, branch of ansa m. iliofibularis started from the slight depression on the lateral surface of the femoral shaft cranioproximally from the place of beginning of aponeurosis communis ansae (Fig. 2D).

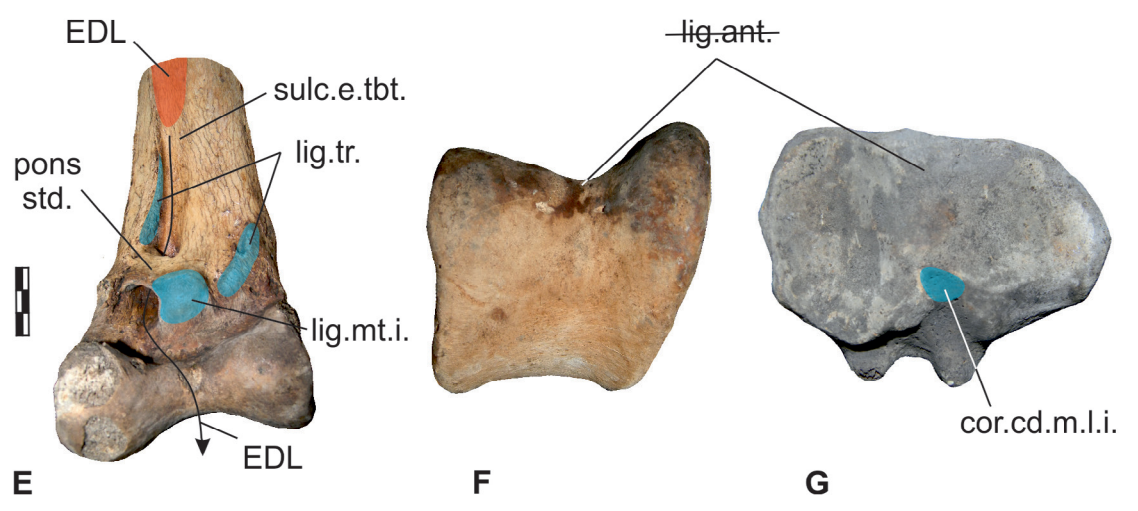
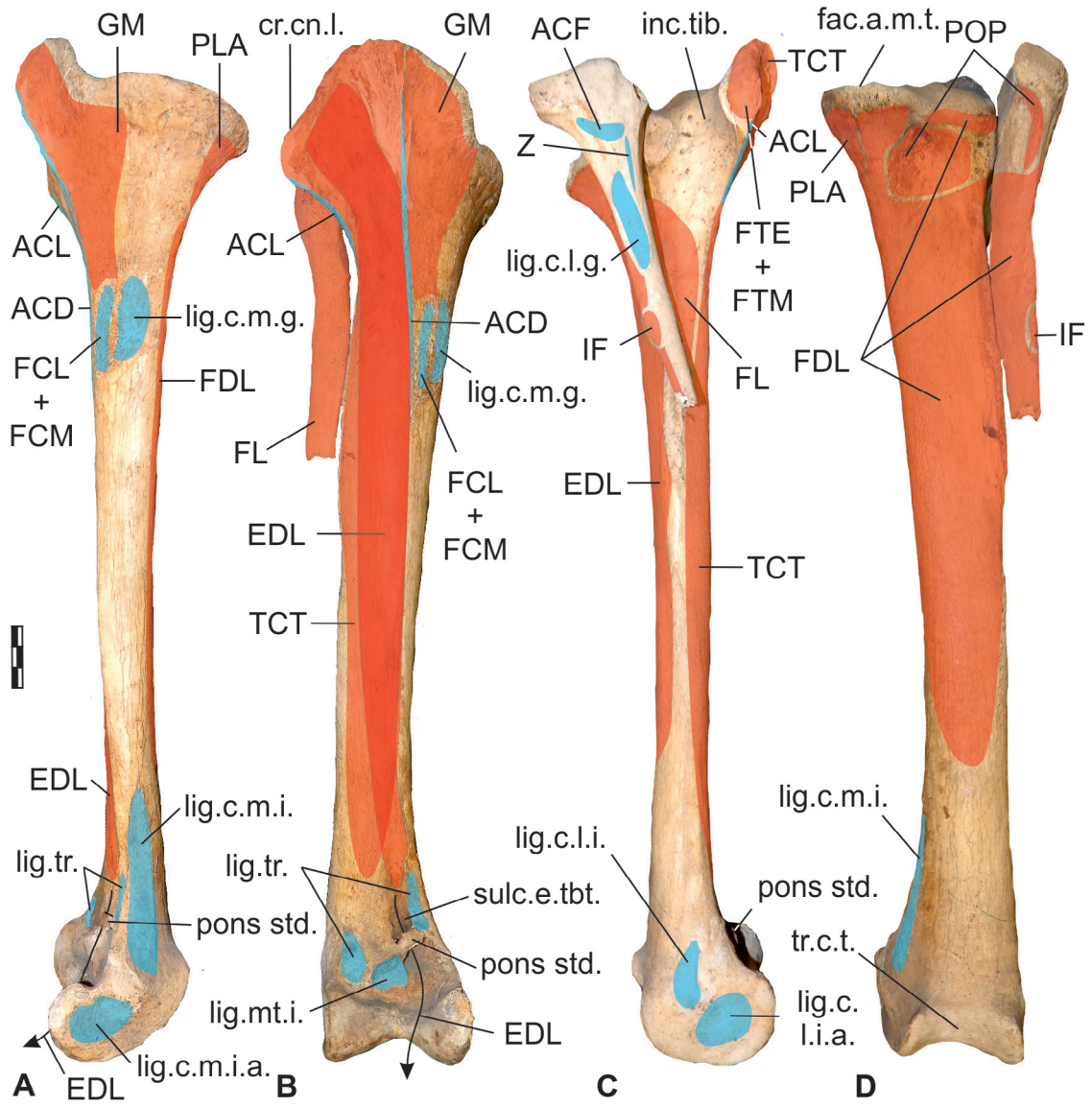
M. popliteus — The inward rotator of the crus, m. popliteus (Fig. 4D), is essential in assisting cursorial birds to place the foot accurately under the body's centre of mass (ZINOVIEV 2011). It was well developed in moa and started from a slightly elevated area on the ventral surface of the fibular shaft just distal to the fibular head. The muscle inserted on a rugose area of the ventral tibiotarsus just below facies articularis medialis tibiotarsi.

Comparison — *M. popliteus*, when present, is quite uniform in birds. It is well developed in ratites. *Apteryx* might be an exception by having a vestigial m. popliteus. It was reported for *Apteryx australis* by OWEN (1849a), but has not been mentioned by the later authors (BEDDARD 1899; MCGOWAN 1979; VANDEN BERGE 1982).

M. plantaris — The beginning of m. plantaris is clearly marked in *E. crassus* by the relatively small unevenness on the ventromedial surface of tibiotarsus just below facies articularis medialis (Fig. 4A, D). This part of the tibiotarsus in the specimen of *D. robustus* has unfortunately been eroded. Undoubtedly small in *E. crassus*, it was partially covered near its origin by lig. collaterale mediale genus. The insertion must have been typical to the proximomedial edge of the tibial cartilage. The terminal tendon of this muscle is so feeble in ratites, that it might have not been preserved in the mummy of *D. robustus*, inspected by COUGHTREY (1874b).

Comparison — This muscle is small, vestigial or sometimes absent in Ratitae (ZINOVIEV, 2010).

M. extensor digitorum longus — The common extensor of foretoes had a fleshy origin in moas, arising from the area between cnemial crests (Figs 4A, B, C; 5A; 6A, C, D, E, G, H). Due to the restriction of this area in Dinornithiformes and relatively small size of the cnemial crests, the bulk of the muscle must have been distributed distally along the cranial shaft of the tibiotarsus



with some of the muscular fibers starting on the lateral surface of aponeurosis communis dorsalis. Other fibers might have started on the cranial surface of fibular shaft, as in Rheiformes (HAUGHTON 1868; GADOW & SELENKA 1891). As discussed above, most of the muscles originating along the tibiotarsal shaft do not leave well-defined traces on the bone. Moa are not an exception. Keeping in mind the graviportal nature of New Zealand's feathered giants, I can assume that the belly of this muscle ended near the beginning of sulcus extensorius tibiotarsi, in which only the terminal tendon of the muscle entered. The oval terminal tendon of *m. extensor digitorum longus* passed under ligamentum transversum together with the terminal tendon of *m. tibialis cranialis*. The transverse ligament, the presence of which is marked by two corresponding tuberosities, was slightly elevated medially, as in other birds. After emerging from beneath lig. transversum, the terminal tendon of the long extensor of the foretoes passed through canalis extensorius below the ossified pons supratendineus and crossed the intertarsal joint in incisura intercondylaris. The terminal tendon then followed a path medial to the insertion of *m. tibialis cranialis* and was held in place by retinaculum extensorium tarsometatarsi, which medial insertion lies immediately cranial of the insertion of lig. collaterale mediale intertarsale. After emerging from under the retinaculum, the terminal tendon attained a central position on the dorsal surface of the tarsometatarsus. There are no traces of its passage along the anterior surface of the tarsometatarsus and only the most proximal portion is preserved on the mummy of *D. robustus*

studied by COUGHTREY (1874b). However, the terminal tendon must have widened before trifurcating near the distal end of tarsometatarsus to send three branches to the foretoes. The pattern of further branching is too complex and variable among birds to be reconstructed with confidence in moa (ZINOVIEV 2010). The only thing I can be sure of that all three branches inserted to the extensorial tuberosities of the corresponding ungual phalanges.

Comparison — The muscle is quite uniform in birds (ZINOVIEV 2010). In Casuariiformes and Apterygiformes the branch to the third toe bifurcates. However, that can not be proved for Dinornithiformes. In the majority of Ratitae and some other birds the terminal tendon of *m. extensor digitorum longus* perforates that of *m. tibialis cranialis*. The absence of this feature in Dinornithiformes makes them similar to Tinamiformes and Apterygiformes.

M. tibialis cranialis — *M. tibialis cranialis* is a dorsal flexor of the intertarsal joint and consists of two heads (Figs 2A, E, G; 3A; 4B, C; 5A, E). The femoral head had its tendinous origin in fovea tendineus *m. tibialis cranialis* on the anterior surface of the lateral condyle of the femur. It passed then through incisura tibialis and merged with the belly of the tibiotarsal head. The tibiotarsal head overlaid *m. extensor digitorum longus*, originating from facing surfaces of the cnemial crests and of aponeuroses communes lateralis et dorsalis, as well as from the cranial surface of the tibiotarsal shaft. The breadth of the muscle's belly can be traced along the bone to the origin

◀ **FIGURE 4.** Right tibiotarsus and proximal half of fibula of *Emeus crassus* (MB. Av. 1571), **A–D**, medial, cranial, lateral and caudal aspects; left tibiotarsus of *Dinornis robustus*, **E**, distal fourth, cranial aspect; proximal and distal articular surfaces of right intertarsal joint of *E. crassus*, showing attachments of some muscles and ligaments, **F, G**. *Fig.—ant.* illustrates the absence of any traces of lig. intercondylare. Abbreviations: ACD, apon. communis dorsalis; ACF, apon. communis fibularis; ACL, apon. communis lateralis; cor. cd. m. l. i., cornu caudale menisci lateralis intertarsi; cr. cn. l., crista cnemialis lateralis; FCL, *m. flexor cruris lateralis*; FCM, *m. flexor cruris medialis*; EDL, *m. extensor digitorum longus*; fac. a. m. t., facies articularis medialis tibiotarsi; FDL, *m. flexor digitorum longus*; FL, *m. fibularis longus*; FTE, *m. femorotibialis externus*; FTM, *m. femorotibialis medius*; GM, *m. gastrocnemius medialis*; IF, *m. iliofibularis*; inc. tib., incisura tibialis; lig. c. l. g., lig. collaterale laterale genus; lig. c. l. i., lig. collaterale laterale intertarsi; lig. c. l. i. a., lig. collaterale laterale intertarsi accessorium; lig. c. m. g., lig. collaterale mediale genus; lig. c. m. i., lig. collaterale mediale intertarsi; lig. c. m. i. a., lig. collaterale mediale intertarsi accessorium; lig. mt. i., lig. meniscotibiale intertarsi; lig. tr., lig. transversum; PLA, *m. plantaris*; pons std., pons supratendineus; POP, *m. popliteus*; sulc. e. tbt., sulcus extensorius tibiotarsi; TCT, *m. tibialis cranialis caput tibiotarsale*; tr. c. t., trochlea cartilaginis tibialis; Z, pars distalis anae *m. iliofibularis*.

of sulcus extensorius tibiotarsi, as in the previous case. The terminal tendon passed superficially to the terminal tendon m. extensor digitorum longus, under lig. transversum tibiotarsi and then, over pons supratendineus. It crossed the intertarsal joint in sulcus intercondylaris tibiotarsi and inserted in the deeply excavated fossa on the cranial surface of the proximal tarsometatarsus. It was not penetrated by the terminal tendon of the long flexor of the foretoes (see above). No such penetration was found by COUGHTREY (1874b) on the mummy of *D. robustus*, which preserved only “a tuft of the insertion” of the terminal tendon of m. tibialis cranialis.

Comparison — The muscle is quite uniform in birds and better developed in those, for which the flexion of intertarsal joint is of particular importance (cursorial, raptorial, foot-propelled swimming etc.). As it was mentioned above, the tendon of m. extensor digitorum longus penetrates the terminal tendon of the muscle in some birds. This is characteristic for ratites, except for the Tinamidae and *Apteryx*.

M. flexor digitorum longus — The deepest of avian digital flexors, m. flexor digitorum longus originated on the posterior surfaces of tibiotarsus and fibula (Figs 4C, D; 5B, C, D, F, G, H). Both surfaces of the bone are rough, suggesting the fleshy origin for the muscle. The exact extent of the muscle’s belly is impossible to reconstruct as it has not left definite traces of its borders. Nor is their evidence to suggest a third origin of the muscle from the ventral surface of the lateral femoral condyle. The terminal tendon of the muscle crossed the intertarsal joint in the tibial cartilage, the presence of which in moa is marked by a well-developed trochlea cartilaginea tibialis. The tibial cartilage is clearly illustrated on the drawing from COUGHTREY (1874b). In *D. robustus* the lateral portion of it contained a sesamoid bone. The surface, incorporating similar bone is also seen in *E. crassus*. The terminal tendon travelled along the plantar surface of the tarsometatarsus in a channel deeper than other flexorial tendons. After branching at the base of the toes and going over sesamoid cartilages, reported by Coughtrey only for the second and third toes, the terminal tendon of m. flexor digitorum longus serviced three foretoes with the

main slips inserted on tubercula flexorii of the unguis phalanges. Variably arranged additional slips attached to the proximal phalanges. Unfortunately, the description, given by COUGHTREY (1874b), is not sufficiently clear to understand the exact arrangement of the branching.

Comparison — The belly of the muscle is quite uniform in birds, the size of it and expansion on the femur are being slightly variable. The pattern of terminal tendon branching is much more variable, being a subject of individual variation (RAIKOW 1978).

M. flexor hallucis longus — All the Dinornithiformes possessed a hallux, which was, however, much reduced and elevated. It must have been supplied by m. flexor hallucis longus. This muscle is always present in birds even in those that lack a hind toe. The tendinous bridge, vinculum tendineum flexorum, which runs obliquely from the terminal tendon of m. flexor hallucis longus to that of m. flexor digitorum longus, allows the former to assist in the flexion of the foretoes. Upon the disappearance of the hallux and the corresponding tendon of m. flexor hallucis longus, m. flexor hallucis longus becomes an accessory flexor of the foretoes. Being superficial to m. flexor digitorum longus, it has more space to expand. These novel duties explain why m. flexor hallucis longus is not only preserved in birds that lack a hallux, but is sometimes enlarged. Its exact development in moa is impossible to reconstruct, since this muscle is rarely in contact with bone, typically originating from some common aponeuroses (e.g. aponeuroses communes fibularis et poplitea) and from superficial aponeurosis of the deeper belly of the long flexor of the foretoes. As in living ratites, which retained a vestigial hallux (some of Tinamiformes and Apterygiformes), m. flexor hallucis longus of moa should have made a main contribution through the aforementioned tendinous bridge to the terminal tendon of m. flexor digitorum longus, sending a much weaker tendon to the hallux. This is a Type II of the deep plantar tendon configuration (RAIKOW 1985; ZINOVIEV 2008).

Comparison — Other members of the Ratiatae have quite uniform muscle, which might have two tibial heads (Tinamiformes: PICASSO 2010) or additional femoral head (Apterygiformes: BEDD-

ARD, 1899). In *Struthio*, it sends a branch to each of the two remaining foretoes.

Mm. flexores perforantes et perforati digitorum 2 et 3 and mm. flexores perforati digitorum 2, 3 et 4 — A cluster of muscles, mm. flexores perforantes et perforati digitorum 2 et 3 and mm. flexores perforati digitorum 2, 3 et 4, provide flexion for individual digital phalanges (Fig. 6B-D, F-H, J-L). As for the previous muscle, the reconstruction of their bellies is impossible for moa, as they mostly start from the common aponeuroses. However, all of them were present in moa. Their passage along the plantar surface of tarsometatarsus in *D. robustus* and some patterns of insertion on the toes are described by COUGHTREY (1874b). Tendons of flexors to the second toe passed through the separate aponeurotic sheath and possessed an individual cartilaginous semi-sesamoid. M. flexor perforatus digiti 2 inserted to the base of the first phalanx, being penetrated by m. flexor perforans et perforatus digiti 2 and by the corresponding branch of m. flexor digitorum longus. The details of their insertion remain unknown due to the absence of the rest of the toe in the mummified foot. However, two rugosities on the plantar surface of the second phalanx of the second toe in both species of moa indicate that m. flexor perforans et perforatus digiti 2 inserted there, being penetrated by the branch of long digital flexor. Tendons of flexors for toes three and four were held by a common aponeurotic sheath. The description, given by COUGHTREY (1874b), does not provide the necessary information to interpret details of branching and insertion of the muscles. However, the osseal material shows, that m. flexor perforatus digiti 3 inserted to the base of the first phalanx of the corresponding toe, being penetrated by other tendons. The same is true for m. flexor perforans et perforatus digiti 3, which penetrated the tendon inserted at the base of the second phalanx. Two pronounced rugose surfaces on the base of the first phalanx of the fourth toe show the insertion of the proximal branches of m. flexor perforatus digiti 4. The insertion of distal branches is variable in avian taxa and can not be reconstructed with confidence.

Comparison — The insertions of mm. flexores perforates et perforate digiti 2 et 3 and mm.

perforati digiti 2 et 3 of moa are typical to the majority of birds including the Ratitae (except for *Struthio* which lacks the second toe). The branching pattern of the terminal tendon of m. flexor perforatus digiti 4 is variable in birds. The direct comparison will be possible only after further studies of mummified feet in moa.

M. fibularis longus — Extensor (along with m. gastrocnemius) of intertarsal joint, m. fibularis longus is better developed in cursorial species. The beginning of this muscle in moa is detectable by the uneven surface on the cranial surface of the fibula (Figs 4B, C; 5F, G). Its points of origin from crista cnemialis lateralis and the fibula itself are difficult to define, as they coincide with the origins of several other muscles. Although the mummy of *D. robustus* did not preserve the insertion of the m. fibularis longus to the proximalateral edge of tibial cartilage, it must have been the point of insertion for the well developed m. fibularis longus as it is in all other cursorial birds (ZINOVIEV 2010). Besides the main insertion, the long fibular muscle has a second tendinous branch leading to the terminal tendon of m. flexor perforatus digiti 3. This muscle, in turn, has a connection to the terminal tendon of m. flexor perforans et perforatus digiti 3 by vinculum tendinum flexorum. This tendinous bridge transmits the power of the large m. fibularis longus to the base of the second phalanx of the third toe, thus preventing overextension during a propulsive push. This vinculum is excellently developed in cursorial birds and would be expected in moa, along with a corresponding branch of m. fibularis longus. In fact, this branch did leave a trace on the lateral surface of the tarsometatarsus as noted, but not interpreted, by OWEN (1874). The trace is a smooth, oblique depression that starts near the level of insertion of m. tibialis cranialis and ends at the middle of the tarsometatarsal shaft. Its passage is fairly clear in *D. robustus* (Fig. 5F, G) but extremely faint in *E. crassus*.

Comparison — The reconstructed details of m. fibularis longus morphology in moa correspond to those of other cursorial birds, including members of the Ratitae.

M. fibularis brevis — The presence and degree of development of an inward rotator of the tar-

sometatarsus, m. fibularis brevis, is correlated with the degree of rotational freedom in intertarsal joint (ZINOVIEV 2000, 2011). In moa, strong collateral ligaments, poorly developed menisci, and the absence of lig. anticum indicate highly restricted rotational movement in the intertarsal joint (see below), to the point where I might expect the absence of m. fibularis brevis. In fact, I can detect neither traces of a retinaculum to hold the terminal tendon of this muscle near the distal end of the tibiotarsus (medial to the ligamentum transversum tibiotarsi) nor an insertion on the medial side of the proximal end of the tarsometatarsus. COUGHTREY (1874b) did not report the terminal tendon of this muscle on an otherwise well-preserved lateral aspect of the proximal tarsometatarsus of *D. robustus* and, consequently, the tuberosity, found by KOOYMAN (1991) on the lateral aspect of pons supratendineus, cannot be associated with a retinaculum m. fibularis brevis.

Comparison — In ratites, m. fibularis brevis is either altogether lost (Struthioniformes, Rheiformes, Casuariiformes) or extremely vestigial (Tinamiformes, Apterygiformes).

Mm. gastrocnemii — Powerful extensors of intertarsal joint, mm. gastrocnemii are well-developed in cursorial birds (Figs 4A, B, 5B–D, F–H). Being the most superficial muscles of the shank, they originate from common aponeuroses shared with deeper muscles (except for the medial part, which originates from the medial surface of cranial cnemial crest and adjacent area of the shank of the tibiotarsus). Thus, their exact morphology can not be reconstructed from skeletal material. Well-developed origins of aponeuroses communes popliteus et collateralis show correspondingly well developed lateral and intermedial parts of m. gastrocnemius. The medial surface of crista cnemialis cranialis is large enough to harbor the origin of powerful medial part of the muscle. All three parts contributed to a common tendon of insertion, which ran superficially to the tibial cartilage, on the plantar surface of the tarsometatarsus, to form the tendinous sheath over the terminal tendons of the long digital flexors. This sheath was found by COUGHTREY (1874b) in mummified foot of *D. robustus*. The insertion of it is marked by two wide rugosities running on both sides of the tar-

sometatarsus, from its proximal end almost to the base of the second and fourth trochleae. This feature is more pronounced in *D. robustus* and much fainter in *E. crassus*. The lateral side of the tendinous sheath is penetrated by the cranial branch of the terminal tendon of m. fibularis longus. The medial side of the sheath passes laterally to the insertion of the first metatarsal element.

Comparison — The composition, degree of development, and the insertion of mm. gastrocnemii in moa are typical for cursorial birds, including ratites.

Intertarsal joint

Avian intertarsal joint chiefly provides flexion-extension movements, being held in place by the capsule of the joint and by a number of ligaments (Figs 4, 5). Traces of strong collateral ligaments are well defined in moa. There were two lateral collateral ligaments. Lig. collaterale laterale intertarsi originated from a tuberosity on the level of the lateral attachment for lig. transversum tibiotarsi. It then crossed the intertarsal joint and attached to the tuberosity on the lateral side of the proximal tarsometatarsus but extended no further than the insertion of m. tibialis cranialis. Lig. collaterale laterale intertarsi accessorium originated from depressio epicondylaris lateralis and inserted on the previously mentioned tuberosity, in front of lig. collaterale laterale intertarsi. There were also two ligaments on the medial side of the intertarsal joint. Lig. collaterale mediale, which was far longer its lateral counterpart. It originated from a deeply imprinted tuberosity that starts on the same level as the beginning of the distinct sulcus extensorius tibiotarsi. Lig. collaterale mediale inserted on the tuberosity on the medial side of the proximal tarsometatarsus, extending slightly behind the level of the medial attachment of retinaculum extensorium tarsometatarsi. Lig. collaterale mediale intertarsi accessorium was much shorter and originated in the depressio epicondylaris medialis. It inserted on the lateral surface of the proximal tarsometatarsus in front of, and much proximally to the previous tendon. As the medial articular surface of tarsometatarsus is more congruent with the corresponding condyle of the tarsometatarsus, it was covered by only by a thin layer of articular cartilage, which

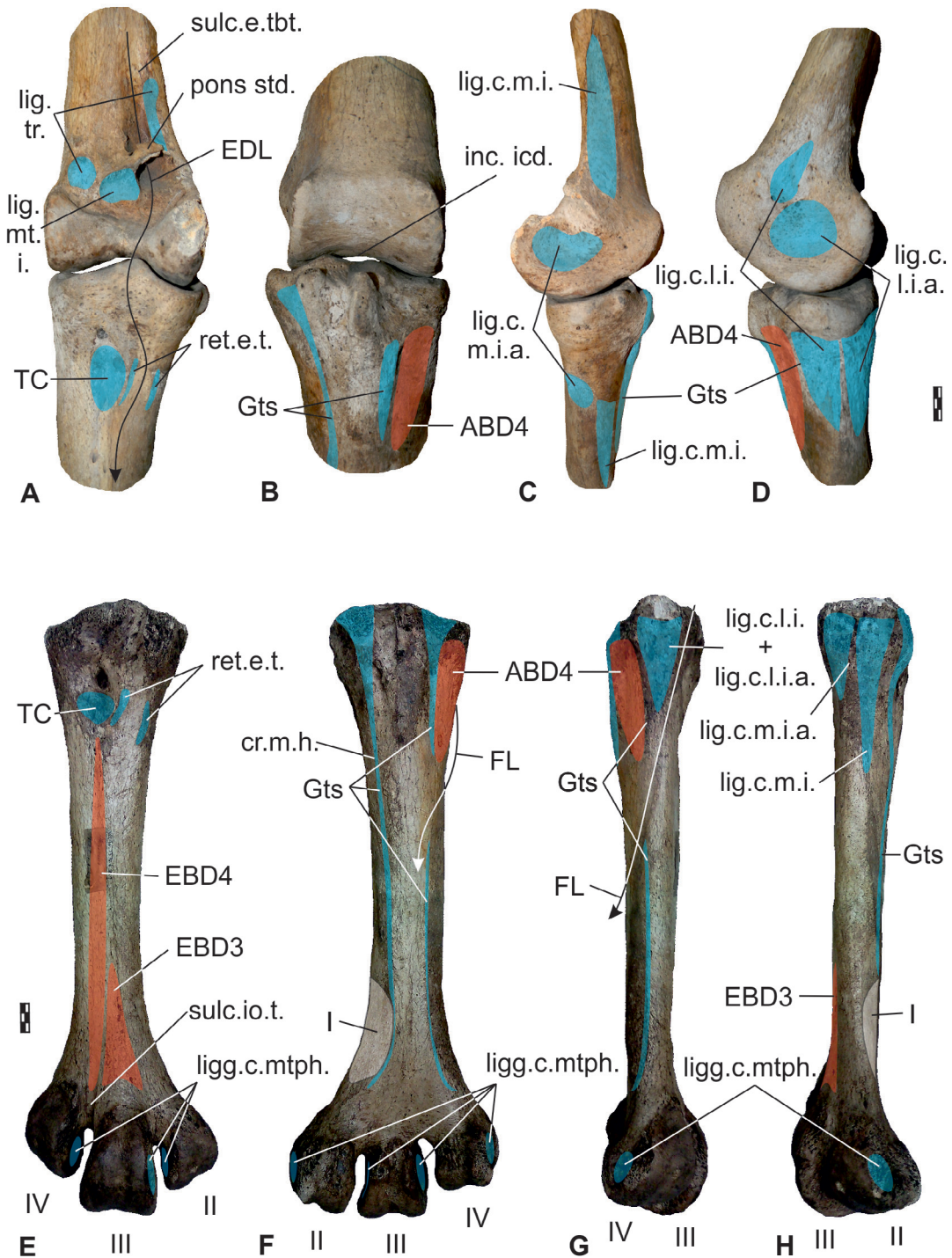


FIGURE 5. Right intertarsal joint of *Emeus crassus* (MB. Av. 1571), **A–D**, cranial, caudal, medial and lateral aspects; right tarsometatarsus of *Dinornis robustus* (MG. Av. 1570) **E–H**, dorsal, plantar, lateral and medial aspects, showing attachments of some muscles and ligaments. I–IV, metatarsal elements (I is missing).

Abbreviations: ABD4, m. abductor digiti 4; cr. m. h., crista medialis hypotarsi; EBD3, m. extensor brevis digiti 3; EBD4, m. extensor brevis digiti 4; EDL, m. extensor digitorum longus; FL, m. fibularis longus; Gts, m. gastrocnemius tendinous sheath; inc. icd., incisura intercondylaris; lig. c. l. i., lig. collaterale laterale intertarsi; lig. c. l. i. a., lig. collaterale laterale intertarsi accessorium; lig. c. m. i., lig. collaterale mediale intertarsi; lig. c. m. i. a., lig. collaterale mediale intertarsi accessorium; lig. tr., lig. transversum; ligg. c. mtph., ligamentai collateralia metatarsophalangealia; pons std., pons supratendineus; ret. e. t., retinaculum extensorium tarsometatarsi; sulc. e. tbt., sulcus extensorius tibiotarsi; sulc. io. t., sulcus interosseus tendineus; TC, m. tibialis cranialis.

formed a marginal rim and corresponds to the observations by COUGHTREY (1874b). The lateral articular surface of the tarsometatarsus and its corresponding condyle showed less congruency. It was achieved by the presence of meniscus lateralis intertarsi, whose cornu caudale attached in the fossa on the caudal margin of area intercotylaris tarsometatarsi (Fig. 4G). The presence of meniscus lateralis intertarsi is also reported by COUGHTREY (1874b). The cranial insertion of the lateral meniscus (its cornu craniale) was through lig. meniscotibiale intertarsi on the prominent tubercle, lateral to the distal opening of pons supratendineus tibiotarsi. There were no traces of lig. intercondylare (Fig. 4F, G), which is therefore presumed to be absent in moa. A large sesamoid bone is reportedly attached to the caudal rim of the lateral tarsometatarsal cotyla (COUGHTREY 1874b). It was connected to the lateral meniscus by lig. meniscoseseamoideum intertarsi, indirectly reported by the same author. The tibial cartilage, mentioned above, is also associated with the intertarsal joint.

Muscles of the foot

The foot possesses a group of intrinsic muscles (Figs 5, 6) associated with individual toes. These muscles in birds are usually small owing to the well developed extrinsic (starting proximally to tarsometatarsus) synergists (ZINOVIEV 2011). Unfortunately, intrinsic muscles rarely leave prominent traces on the tarsometatarsus and thus many of them cannot be reconstructed in detail. *M. extensor hallucis longus*, *m. adductor digiti 2*, *m. extensor digitorum brevis lateralis* (ZINOVIEV 2003b) and *m. lumbricalis* were almost certainly present in moa, but did not leave traces on the bones of the material available for examination. Radiological studies of mummified moa feet might greatly improve our understanding of the

muscles and ligaments of the foot of *Dinornithiformes*. Here I describe three muscles, which either left traces on bones or have been described by other authors.


M. abductor digiti 2 — *M. abductor digiti 2* is the only intrinsic muscle of the foot, reported by COUGHTREY (1874b) from his examination of a mummified specimen of *D. robustus*. He failed to identify it but described its characteristic tendinous insertion. The extent of which the muscle's belly expanded over the craniomedial surface of the tarsometatarsus remains unclear (Fig. 6A, C).

Comparison — The muscle is present and moderately developed in all members of the Ratitae, excluding *Struthio* (ZINOVIEV 2010).

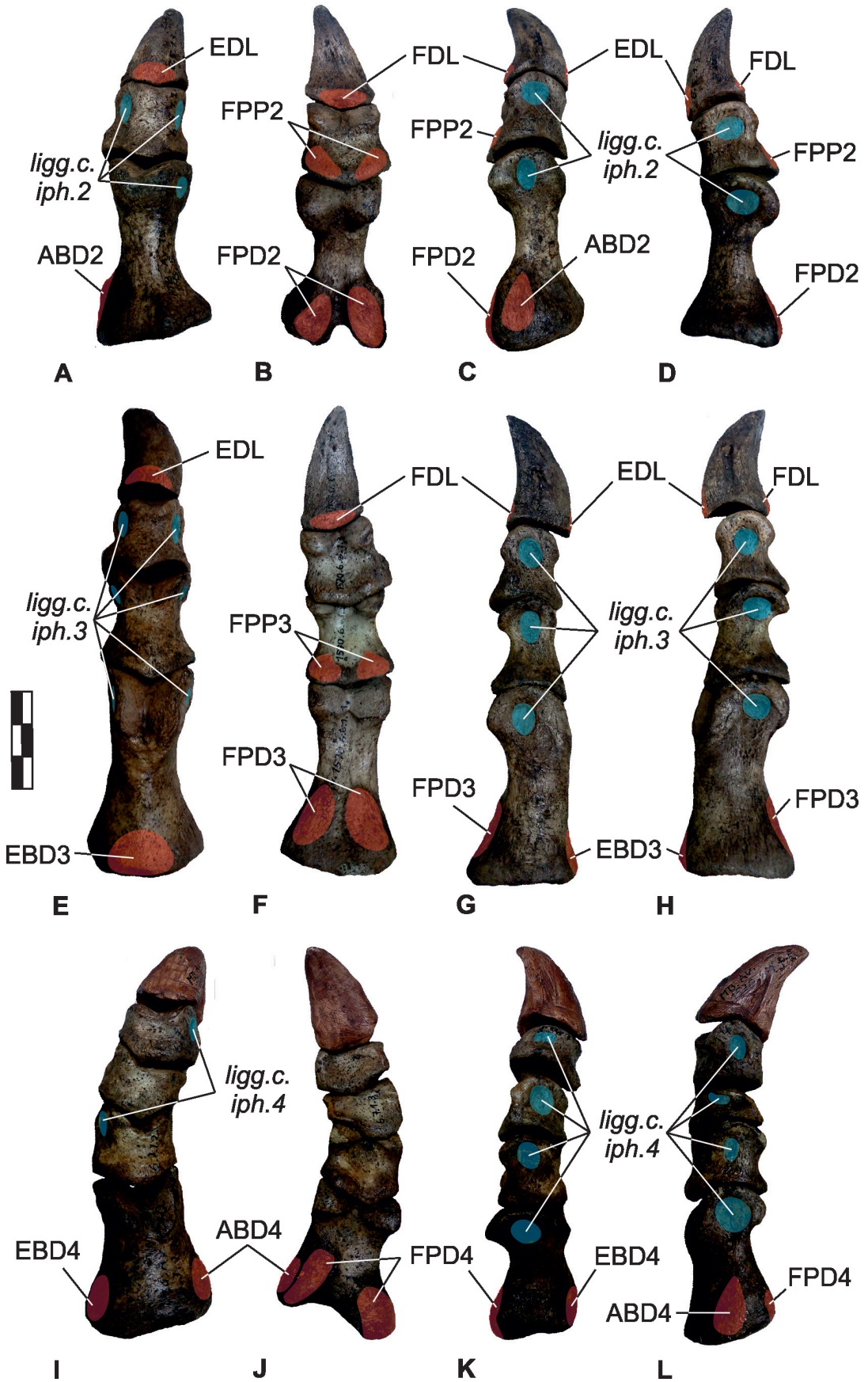
M. abductor digiti 4 — The belly of *m. abductor digiti 4* originated from a depressed and slightly rugose area just distal to the proximal end of the tarsometatarsus and lateral to crista lateralis hypotarsi (KOOYMAN 1991) (Figs 5B, D, F, G; 6I, J, L). The muscular belly rapidly tapered towards the terminal tendon, which ran along the lateral side of an aponeurotic sheath formed by the terminal tendon of *mm. gastrocnemii*. The insertion of *m. abductor digiti 4* on the lateral surface of the proximal end of the basal phalanx of the toe is not well-marked. The area of fleshy origin is most clear in *D. robustus* and much fainter in *E. crassus*.

Comparison — The proximal displacement of the muscle's belly is quite typical for Ratitae and many other long-legged birds (ZINOVIEV 2010). There is often a small proximal head, but its presence in moa cannot be proved.

M. extensor brevis digiti 4 — The size of lateral intermetatarsal sulcus shows the shape and development of *m. extensor brevis digiti 4* (Figs 5E, 6I, K). It was long and thin in *D. robustus*, starting from the distal level of tuberositas *m.*

FIGURE 6. Right foretoes of *Dinornis robustus* (MG. Av. 1570): **A–D**, second; **E–H**, third; **I–L**, fourth, dorsal, plantar, medial and lateral aspects, showing attachments of some muscles and ligaments. Attachments are not shown on the ungual phalanx of the fourth toe, since it is artificial. 

Abbreviations: ABD2, *m. abductor digiti 2*; ABD4, *m. abductor digiti 4*; EBD3, *m. extensor brevis digiti 3*; EBD4, *m. extensor brevis digiti 4*; EDL, *m. extensor digitorum longus*; FDL, *m. flexor digitorum longus*; FPD2, *m. flexor perforatus digiti 2*; FPD3, *m. perforatus digiti 3*; FPD4, *m. flexor perforatus digiti 4*; FPP2, *m. flexor perforans et perforatus digiti 2*; FPP3, *m. flexor perforans et perforatus digiti 3*; ligg. c. iph. 2, ligamenta collateralia interphalangealia digiti 2; ligg. c. iph. 3, ligamenta collateralia interphalangealia digiti 3; ligg. c. iph. 4, ligamenta collateralia interphalangealia digiti 4.



tibialis cranialis. Its shape is not clear in *E. crassus* due to the absence of definite impressions on the bone. The terminal tendon of *m. extensor brevis digiti 4* passed through sulcus interosseus tendineus between the third and fourth trochleae to insert on the dorsomedial side of the base of the first phalanx of the fourth toe.

Comparison — The length of the belly of *m. extensor brevis digiti 4* was variable among moa (KOOYMAN 1991). In the majority of birds, the terminal tendon passes through canalis interosseus tendineus, but that structure is absent in moa and, reportedly in Struthioniformes and Apterygiformes. It is also absent in juvenile *Dromaius*, but present in the adult (PATTERSON 1983).

M. extensor brevis digiti 3 — *M. extensor brevis digiti 3* is a short extensor of the third toe that had a fleshy origin from the distal half of the dorsal surface of the tarsometatarsus (Figs 5E, H; 6E, G, H). The belly lay on the elevated surface of the third metatarsal. The terminal tendon must have inserted on the dorsal surface of the base of the first phalanx of the third toe.

Comparison — The muscle is quite uniform in birds. In the majority of Ratitae its belly is restricted to the distal half of the tarsometatarsus.

Metatarsophalangeal and interphalangeal joints

Ligg. collateralia metatarsophalangealia as well as lig. collateralia interphalangeales of all the foretoes were well-developed and started in fossae on the lateral sides of the trochleae or on the sides of distal ends of phalanges, other than unguis (Figs 5, 6). They inserted laterally and medially to the bases of the corresponding distal phalanges. COUGHTREY (1874b) found them all except lig. collaterale metatarsophalangeale mediale digiti 2. Nevertheless this ligament was present in moa and possessed a prominent fossa at its origin (Fig. 5E). COUGHTREY also reported the presence of grooved cartilagine subarticulares metatarsophalangeales digitorum 2, 3 et 4 as well as cartilagine subarticulares interphalangeales digitorum secundi, tertii et quarti. He also observed vaginae fibrosae sheathing separately flexorial tendons to the third and fourth toes, and those to the second toe.

Discussion

D. robustus and *E. crassus* represent two branches of locomotory adaptation in moas. *Dinornis* is more agile whereas *Emeus* is less (ALEXANDER 1983a, b; KOOYMAN 1985, 1991). Nevertheless, the number and the position of their hindlimb muscles are almost identical. The locomotory specializations appear to depend on the relative development of particular muscles associated with the length of the leg elements. The overall anatomy of the hind limbs in these species resembles that, inferred for other primitive birds (HUDSON 1937; ZINOVIEV 2010). In particular, the hindlimb anatomy and syndesmology of moa resemble that of the Tinamiformes, whose ancestors are now accepted as being close to ancestral palaeognaths. They are also similar to geographically close Apterygiformes and Casuariiformes. Other member of Ratitae, such as Rheiformes and especially Struthioniformes show significant differences related to their own distinct locomotor adaptations.

There are, however, certain traits in hindlimb morphology that characterize the Dinornithiformes. First of all, the enormous development of *m. iliofemoralis externus* far surpasses the bulk of this muscle in other birds. It is truly unfortunate that information on this muscle in *Aepyornis* is missing. Generally reduced in most birds, this muscle abducts the femur, preventing passive adduction of this bone during the single support stance phase of locomotor cycle. As in other massive ratites with wide pelvis, moa must have exerted the maximal power of femoral abductors (*m. iliofemoralis externus*, *m. iliotibialis lateralis pars acetabularis*) to keep the body balanced. *M. iliotibialis* in moa was also very powerful.

A caudal shift in the center of gravity, proposed for moa in comparison to other birds (ALEXANDER 1983a) and especially for *Dinornis* in relation to other moa (KOOYMAN 1985, 1991), does not have anatomical support. Proceeding from the position of antitrochanter, the femur of the moa was carried in the same position as in other cursorial birds. Thus their center of gravity must have been aligned with the knee joints.

The proposed insertion of *m. iliofemoralis internus* is unusual and may represent another unique characteristic for moa. *M. iliofemoralis*

internus appears to have inserted just distally to the femoral neck on the cranial surface of femoral shaft. Such a position implies a change in function from that of a weak, outward rotator of the femur. The significance of such a shift is unclear and needs to be reexamined in additional mummified remains. Of other pelvic muscles *m. iliofemoralis* had an unusually long attachment on the posterior surface of the femoral shaft. Outside of *Dinornithiformes* such a feature is seen only in *Apteryx* (MCGOWAN 1979).

Femoral and tibiotarsal muscles are well-developed, which is expected in cursorial birds. Traces of their origin on the femur are more pronounced in *E. crassus*, which, however, may not be related to the degree of femoral muscle development. Muscles of the shank in moa were long-bellied, as in *Apteryx*. In cursorial birds, there is strong selection to lighten the distal components of the limb but there is no such pressure on graviportal species. Thus cnemial crests of moa were relatively small, since the bulk of the shank muscles were more evenly distributed along the length of tibiotarsus. Most of the shank muscles, including powerful *m. gastrocnemii*, originated on the common aponeuroses whose configuration appears to have been similar to that in the majority of birds. Movements in the intertarsal joint, which lacked *lig. anticum* and its stabilizer, *m. fibularis brevis*, were restricted to flexion and extension, as in many specialized cursorial birds, including members of the *Ratitae*. The relative length of the tarsometatarsus is greater in *Dinornis*, which corresponds to its greater agility. Although the majority of the intrinsic muscles must have been preserved in moa, their relative development is difficult to assess due to the faintness of traces that they left on the tarsometatarsus. Abductors of the second and fourth toes and extensors of the third and fourth toes were slender and long, corresponding to the length of the tarsometatarsus. Terminal tendons of the long digital flexors to the second toe were, at least in *D. robustus*, separated from those to the other foretoes. This feature might indicate, that the second toe might have played a major role in the scratching and digging reported as a foraging activity of moa attempting to obtain fern rhizomes (OWEN 1849b, 1883b; KIRK 1875; WHITE 1925; BURROWS *et al.* 1981).

Conclusions

The muscular anatomy of hind limbs in moa was modified according to their weight and their degree of graviportal locomotion. The retention of the wide pelvis makes their pelvic muscles look less modified than comparable muscles in their narrow hipped relatives in the *Apterygiiformes*, *Casuariiformes*, and *Struthioniformes*. Resembling in the overall hindlimb anatomy geographically close species of *Apteryx* and *Dromaius*, moas were probably adapted to scratching and digging.

Hopefully, in the future, I will be able to test these anatomical hypotheses on more abundant material.

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