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A critical re-evaluation of the hindlimb myology of moa (Aves: Dinornithiformes)

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ABSTRACT

The extinct moa of New Zealand were an enigmatic group of flightless birds, some attaining gigantic size. To better understand the biomechanical consequences of their large size and unique anatomy on stance and locomotion, a critical re-evaluation of the evidence for muscular attachment in the hindlimb of moa was undertaken. Three focal taxa, *Dinornis robustus*, *Emeus crassus* and *Pachyornis elephantopus*, were studied in detail, although other moa species were also addressed. More than one thousand individual bones from a diverse array of localities across the South Island of New Zealand were examined, and interpretations were made within the context of extant palaeognath birds. The interpretations and reconstructions produced largely concur with those of previous workers in many respects. The reconstructed myology of these moa species is also quite comparable to that in extant palaeognaths, although some important differences are hypothesised to exist. The most significant of these is that it moa are posited to have had a very well-developed iliotrochantericus caudalis in comparison to extant palaeognaths. Digital computer reconstruction of this muscle in an adult female *D. robustus* supports this hypothesis. The great development of the iliotrochantericus caudalis in moa may be related to their large size, or reflect a different locomotor behaviour compared to extant palaeognath species. Finally, a number of myology-related features have been identified that may prove useful in the taxonomic identification of isolated or poorly preserved bones. ❒ *Moa; hindlimb; myology; extinct; fossil; palaeognath; Dinornis robustus; Emeus crassus; Pachyornis elephantopus*.

The extinct moa (Aves: Palaeognathae: Dinornithiformes) of New Zealand are an intriguing group of flightless birds that included some of the largest birds to have ever existed. It has been estimated that some moa species may have weighed 250 kg or more (Alexander 1983a; Anderson 1989; Worthy & Holdaway 2002; Murray & Vickers-Rich 2004; Brassey *et al.* 2013). In addition to their large body size, moa possessed a suite of anatomical features that may have influenced their stance and gait in comparison to extant birds. Moa completely lacked any wings (unique among Aves), had an acarinate sternum and their pelves were very broad caudal to the acetabulum (except in the smaller species, *Megalapteryx didinus* and *Anomalopteryx didiformis*). The whole-body centre of mass in moa may consequently have been more caudally located in comparison to extant birds, which in turn would influence how the limbs were positioned when standing and during locomotion (Alexander 1983a). The femoral trochanter in moa is exceptionally developed among palaeognaths, raised well above the level of the femoral head. This makes the facies for articulation with the antitrochanter markedly concave, and in turn the antitrochanteric facies on the pelvis is markedly convex. In addition, non-*Dinornis* moa possess a well-defined, ball-shaped femoral head that is separate from the remainder of the femur by a distinct neck (Worthy & Holdaway 2002). Among large palaeognaths, such a feature is only seen elsewhere in *Casuarius* and *Emuarius* (Boles 1992).

A further interesting aspect of moa anatomy concerns the proportions of their main hindlimb bones. Moa have the most extreme limb segment proportions of any flightless, terrestrial bird (extinct or extant), in possessing a long tibiotarsus and short tarsometatarsus (Gatesy & Middleton 1997). Moreover, in non-*Dinornis* species the tarsometatarsus is shorter than the femur, often significantly so (Worthy & Holdaway 2002). The limb bones of several moa species also appear to be exceptionally robust compared to other birds. This is not simply due to these birds' large absolute size, however, for several comparative studies have shown that moa hindlimb bones are in fact more robust than would be expected for their body size (Alexander 1983a,b; Doube *et al.* 2012; Brassey *et al.* 2013).

Questions concerning how the aforementioned anatomical features may have influenced moa stance and gait, and why such features may have evolved, can be addressed through comparative biomechanical analysis of the hindlimbs of moa and extant bird species. Fundamental to such analysis is having a thorough understanding of the musculoskeletal anatomy of the hindlimbs in these animals (Hutchinson *et al.* 2005; Maidment & Barrett 2011; Bates & Schachner 2012; Dilkes *et al.* 2012; Maidment *et al.* 2014). Two previous attempts have been made at reconstructing parts of the hindlimb myology in moa. Kooyman (1985, 1991) restricted his analysis of all moa species to the femur, tibiotarsus and tarsometatarsus. Without considering the pelvis, fibula and phalanges, his interpretations may have been significantly influenced, and in any case cannot be related to these particular bones. Additionally, Kooyman drew his inferences largely from comparison with the hindlimb myology of only kiwi (*Apteryx* spp.), which could have further influenced his interpretations. More recently, Zinoviev (2013) produced a complete myological reconstruction for two species of moa, the dinornithid *Dinornis robustus* and the emeid *Emeus crassus*.

Whilst Zinoviev's (2013) work was thorough, he only had very limited fossil material (one specimen per species) upon which to base his reconstructions. This prevented him from assessing variability in surface morphology both within and across species, which can be considerable in moa (Worthy 1988; Kooyman 1991; Worthy & Holdaway 2002). Furthermore, it is clear from several of the photographs figured by Zinoviev that most of the bones studied by him were incomplete or were of sub-ideal preservation. The generality of his interpretations therefore remain uncertain.

To build and improve upon this research, a critical re-evaluation of the osteological evidence of muscle attachment in the hindlimb of moa was undertaken here. In addition to the two species addressed by Zinoviev (2013), a further species, *Pachyornis elephantopus*, was also investigated in detail, although the bones of most species of moa were examined throughout the course of this study. Besides producing a more soundly supported set of myological reconstructions, it was also sought to identify myology-related features which tend to be found only in certain species. These features may in the future help distinguish between species, and hence prove useful in identifying the taxonomic affinity of isolated, incomplete or poorly preserved bones. They may also help to better understand potential differences in locomotor behaviour between different moa species.

MATERIALS AND METHODS

The taxonomy for moa outlined by Worthy & Scofield (2012) is followed here. This study was based upon the very extensive collection of moa bones in the Canterbury Museum, Christchurch, New Zealand, as well as the much smaller collection in the Queensland Museum, Brisbane, Australia. A list of the exemplar specimens studied is given in Appendix 1 (available online http://www.qm.qld.gov.au/About+Us/Publications/Memoirs+of+the+Queensland+Museum/MQM+Vol+59); specimens with the prefix CM are from the Canterbury Museum collections and specimens with the prefix QMF are from the Queensland Museum collections. The specimens examined derive from many localities throughout the South Island of New Zealand, including the large swamp deposits of Pyramid Valley (Waikari), Glenmark, Cheviot, Kapua (Waimate) and Enfield (Oamaru). Hence, the observations and interpretations detailed herein are not biased by one or two select populations. Only bones from skeletally mature adults was examined (cf. Turvey & Holdaway 2005), as muscle scarring is usually only minimally developed in immature individuals. Furthermore, only specimens whose taxonomic identity was certain were studied. In many cases, such as the Pyramid Valley and Cheviot swamp specimens, this was known because the bones derived from articulated or associated specimens. In concert with the large number of bones studied, this scrutinization allows for the nature of intraspecific variation in a given anatomical feature to be properly assessed and interpreted.

Myological Reconstructions. Interpretation of osteological evidence for muscle attachment, and subsequent reconstruction of myology in the hindlimbs of moa, follows the approach of the 'extant phylogenetic bracket' (EPB; Witmer 1995; Carrano & Hutchinson 2002; Maidment & Barrett 2011). Here, soft tissues in the extinct taxon are reconstructed on the basis of inferred homology within a phylogenetic framework comprising extant species. A phylogenetic approach facilitates the identification of homologous osteological correlates of soft tissue attachment in the extant taxa that phylogenetically 'bracket' the extinct taxon. These homologous osteological correlates may then be identified as present or absent in the extinct taxon. By considering multiple extant outgroup taxa, such an approach also allows ancestral (symplesiomorphic) and derived (apomorphic) character states to be identified for a particular soft tissue attachment. This helps avoid false comparisons with derived extant taxa, and in turn the most phylogenetically parsimonious inferences can be made in the extinct taxon. Additionally, by focusing on extant 'bracket' taxa, this avoids potentially misleading comparisons to more distantly related taxa, such as neognaths in the case of the present study. By framing musculoskeletal hypotheses for extinct taxa within a phylogenetic context, this therefore allows for the degree of uncertainty present in a given reconstruction to be more easily qualified.

The EPB approach minimally requires the bracketing of the extinct taxon of interest between the two most closely related extant taxa (Bryant & Russell 1993; Witmer 1995). In the case of moa, however, strict application of the EPB approach is problematic, since it is uncertain as to exactly what taxa constitute their EPB. Most recent studies of palaeognath phylogeny that have utilised molecular (genetic) data strongly suggest that tinamous are the sister taxon to moa (Phillips *et al.* 2010; Haddrath and Baker, 2012; Smith *et al.* 2013; Mitchell *et al.* 2014). However, it remains unresolved as to what constitutes the next most closely related taxon, despite a multitude of molecular and morphological phylogenetic studies. Thus, in recent years the EPB of moa has been hypothesised to be: *Apteryx* and all other 'ratites' (Livezy & Zusi 2007; Bourdon *et al.* 2009; Worthy & Scofield 2012); tinamous and 'ratites' (Baker & Pereira 2009); tinamous and *Apteryx* + casuariids (Phillips *et al.* 2010; Mitchell *et al.* 2014); *Rhea* and *Apteryx* + casuariids (Johnston 2011); tinamous and non-ostrich 'ratites' (Haddrath & Baker 2012); tinamous and *Rhea* + *Pterocnemia* (Smith *et al.* 2013). In light of this lack of consensus, the EPB approach is employed here in a somewhat loose fashion: assuming a tinamou-moa sister relationship, any extant palaeognath group could be the next most closely related taxon. Moreover, as moa have never been hypothesised to be the most basal of the 'modern' palaeognaths, their EPB has always comprised extant palaeognath species (i.e., no neognath groups). Hence, in this study the myological reconstructions were

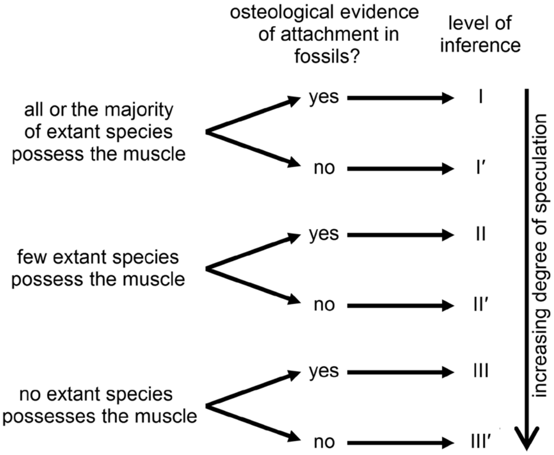

FIG. 1. Defining the level of speculation inherent in a soft tissue reconstruction, according to the scheme of Witmer (1995). This is based on the degree of support the reconstruction receives from extant taxa that phylogenetically bracket the extinct taxon of interest (indirect evidence), as well as osteological evidence in the fossils themselves (direct evidence). A level I inference is less speculative (better supported) than a level I′ inference, which is less speculative than a level II inference, and so on.

framed within the context of the anatomy of extant palaeognaths only.

In lieu of undertaking first-hand dissections, a comparative basis of hindlimb myology in extant palaeognaths was drawn from the literature thus: *Dromaius* (Patak & Baldwin 1998; Lamas *et al.* 2014), *Casuarius* (Gadow 1880; Pycraft 1900), *Struthio* (Gangl *et al.* 2004; Smith *et al.* 2006; Zinoviev 2006; Schaller *et al.* 2009; Hutchinson *et al.* 2015); *Rhea* (Gadow 1880; Pycraft 1900; Picasso 2010); *Apteryx* (Owen 1879; McGowan 1979; Kooyman 1991); tinamous (Hudson *et al.* 1972). A comparative basis of hindlimb osteology in extant palaeognaths was developed through examination of neontological skeletal material in the collections of the Queensland Museum, Canterbury Museum and Museum Victoria, Melbourne, Australia.

By considering all extant palaeognaths as forming a loosely defined EPB of moa, without a strict phylogenetic framework in place, this may lead to ambiguity in character polarity, and hence how a muscle is interpreted to have appeared in moa, if it in fact did exist. Given that different taxa can display different topologies or characteristics for a particular muscle or muscle group, this uncertainty could lead to the reconstructed musculature of a given moa species becoming somewhat 'generalised'.

This problem is countered to some extent by the great prevalence of direct osteological evidence for muscle attachment on the fossil limb bones of moa, as described below. In many cases this can eliminate the problem of uncertainty in the presence or absence of a muscle, or its nature of origin or insertion. This issue is further addressed by use of Witmer's (1995) 'levels of inference' (Fig. 1; see also Carrano & Hutchinson 2002). These gauge the level of speculation inherent in the reconstruction of a particular muscle, based on the amount of support it has from osteological data (direct evidence) and comparative data (indirect evidence). Thus, it helps define the confidence that can be placed in the reconstructions. More importantly, they provide a means by which to objectively compare alternative interpretations, hence allowing the most parsimonious one to be identified. This study follows Carrano & Hutchinson (2002) in minimally requiring a level II inference in order to reconstruct a muscle; a reconstruction of level II′ or lower is deemed too speculative. It should be noted that reconstructions of the main ligaments of the hindlimb (collateral ligaments) are presented here with limited discussion or justification. The reason for this is that in almost every case the situation in extant palaeognaths is unambiguous and consistent, and moreover, there are clear scars on the fossil moa bones which are readily interpretable as such (i.e., level I inferences throughout).

Every bone of the hindlimb of *D. robustus* is illustrated here, to show the pattern of surface morphology and muscle scarring in the moa hindlimb skeleton. Features of the bones of the other species that were studied are illustrated only where they differ significantly from that exemplified by *D. robustus*. Each illustration is a composite, based upon many specimens so as to depict the 'typical' appearance of each

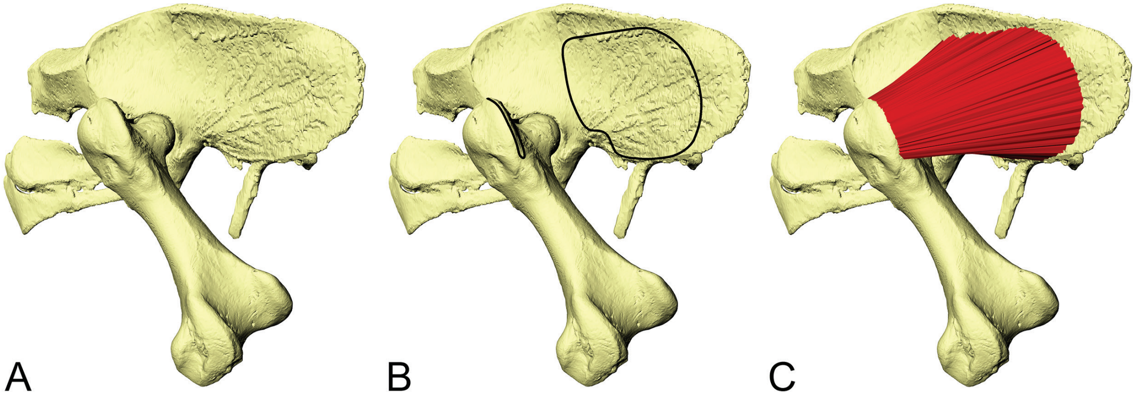

FIG. 2. Estimating the size of the iliotrochantericus caudalis in *D. robustus* using a digital computer model. A, the digital model of the pelvis and femur in articulation (only the right side is shown for clarity); B, the boundaries of the area of origin and insertion of the muscle on the bones are identified; C, computer-aided design software is used to render a solid geometric representation of the muscle. From this the volume, and in turn mass, of the muscle is estimated.

bone. In some illustrations several of the scars are enhanced, to show their appearance more clearly. All illustrations are of bones from the right side of the body.

Digital Muscle Modelling. Throughout the course of myological reconstruction, a point of biomechanical interest became apparent, in regards to the size of the iliotrochantericus caudalis in moa. The reconstructions produced here (detailed below) posit that this muscle originated from much of the preacetabular iliac blade. As the ilium of moa (especially *Dinornis*) is distinctive among large palaeognaths, in that the preacetabular ilium is dorsoventrally deep and is considerably longer than the postacetabular ilium (Worthy & Holdaway 2002), this suggests that the iliotrochantericus caudalis may have been enlarged in moa compared to extant palaeognaths.

This hypothesis was investigated by developing a digital computer model of the pelvis and femur in a large female individual of *D. robustus*, CM Av8422, and using it to estimate the volume of the iliotrochantericus caudalis (Fig. 2; cf. Persons & Currie 2011a, b; Hutchinson *et al.* 2011; Persons & Currie 2012). The geometry of the bones was obtained, as part of another study, through X-ray computed tomographic scanning (Siemens Somatom Definition Flash, 140 kV peak voltage, 307 mAs exposure for pelvis, 166 mAs exposure for femur, 1000 ms exposure time, slice thickness 0.4 mm, 0.96 mm pixel resolution for pelvis, 0.50 mm pixel resolution for femur) and digital segmentation and rendering of the resulting scans (Mimics 17.0, Materialize NV, Belgium). The models of the pelvis and femur were then virtually articulated in the computer-aided design software Rhinoceros 4.0 (McNeel, USA) (Fig. 2A). The articulation followed current consensus regarding the habitual position of the moa femur (Worthy & Holdaway 2002; Zinoviev 2013), namely that the bone was oriented subhorizontally with the trochanter in close apposition to the antitrochanter. Subsequently, the boundary of the area of origin on the pelvis was mapped out according to the reconstructions (Fig. 2B). The insertion on the femur was taken to be the cranial aspect of the appropriate portion of the trochanter (described below), in order to keep the model as simple and assumption-free as possible. Using the 'loft' option in Rhinoceros, these boundaries were used to produce a prismatic object that forms a first approximation of the bulk of the iliotrochantericus caudalis (Fig 2C). The volume of this object was then calculated in Rhinoceros. It is important to note that as the muscle would likely have been rounded to some degree in life, rather than purely straight-sided, the geometric model developed here

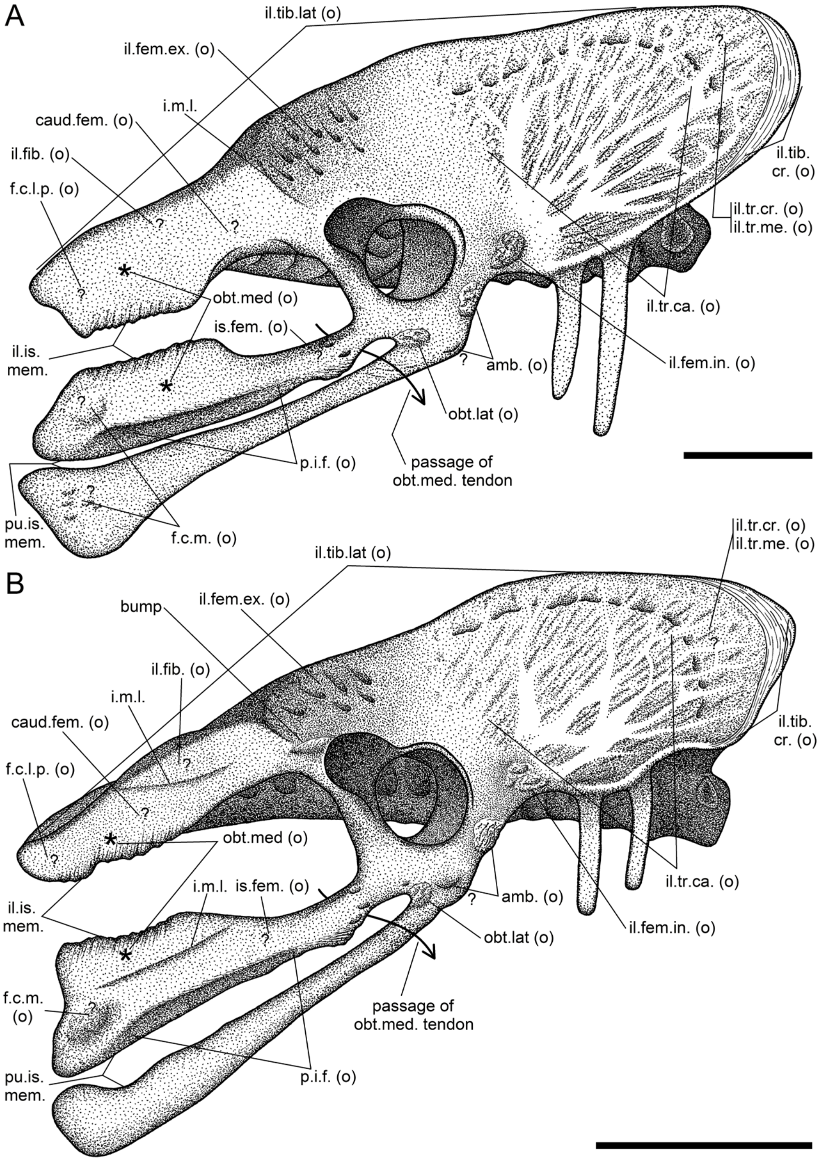

FIG. 3. Osteological evidence of muscle attachment on the pelvis of moa, with corresponding myological interpretations. A, *D. robustus*; B, *E. crassus*. The asterisk indicates that the origin of the obturatorius medialis is inferred to have been situated on the medial aspect of the bones or membrane to which it attached. In this figure and those that follow, question marks indicate uncertainty as to the exact location or extent of a given muscle attachment. Scale bars = 100 mm. Abbreviations: *amb.*, ambiens; *caud.fem.*, caudofemoralis; *f.c.l.p.*, flexor cruris lateralis pars pelvica; *f.c.m.*, flexor cruris medialis; *il.fem.ex.*, iliofemoralis externus; *il.fem.in.*, iliofemoralis internus; *il.fib.*, iliofibularis; *il.is.mem.*, ilioischiadic membrane; *il.tib.cr.*, iliotibialis cranialis; *il.tib.lat.*, iliotibialis lateralis; *il.tr.ca.*, iliotrochantericus caudalis; *il.tr.cr.*, iliotrochantericus cranialis; *il.tr.me.*, iliotrochantericus medius; *i.m.l.*, intermuscular line; *is.fem.*, ischiofemoralis; *(o)*, muscle origin; *obt.lat.*, obturatorius lateralis; *obt.med.*, obturatorius medialis; *p.i.f.*, puboischiofemoralis; *pu.is.mem.*, pubischiadic membrane.

is almost certainly an underestimate of the muscle's true bulk.

RESULTS

For each muscle, a synopsis of the comparative anatomical context in extant palaeognaths is provided, and the osteological evidence observed in moa is detailed. The interpretations and myological reconstructions are also presented and discussed here, for the sake of fluency and clarity. In addition to the osteological illustrations provided (Figs 3–13), a restoration of the muscles as they may have appeared in life is presented (Fig. 14). This restoration is tentative and is not designed to illustrate the relative size of the muscles, nor the extent (or nature) of their attachments, but rather is intended to help place many of the muscles in the context of the whole limb. All references to the anatomy of extant palaeognaths are drawn from the abovementioned literature sources, unless noted otherwise. The more general terms of hip, knee and ankle are used instead of the more formal junctura coxae, junctura genus and junctura tarsi, respectively.

Ilioischiadic membrane
(Fig. 3; il.is.mem.)

General comments. The ilioischiadic membrane is present in all extant palaeognaths, spanning much of the space between the ilium and ischium.

Observations. The presence of the membrane in moa is indicated by well-defined, and often fimbriate, ridges on the ventrolateral surface of the postacetabular ilium and the dorsal surface of the ischium. These ridges are usually most pronounced caudally, although they are present for most of the length of their respective elements, a condition also observed in extant palaeognaths.

Remarks. Reconstruction of this soft tissue is a level I inference.

Puboischiadic membrane
(Fig. 3; pu.is.mem.)

General comments. The puboischaidic membrane is present in all extant palaeognaths, spanning between the ischium and pubis.

Observations. As with the ilioischiadic membrane, its presence in all moa species is given by marked ridges on the ventral aspect of the ischium and dorsal aspect of the pubis for most of their length.

Remarks. Reconstruction of this soft tissue is a level I inference. In some species, such as *P. elephantopus* and *Dinornis* spp., very little of the puboischiadic membrane would have actually existed in life, for the pubis and ischium are typically in close proximity along their entire length.

Iliotibialis (Figs 3, 6, 7; il.tib.)

General comments. In extant palaeognaths, this muscle is divided into three parts, the iliotibialis cranialis (il.tib.cr), lateralis pars preacetabularis and lateralis pars postacetabularis (il.tib.lat.); the lateralis pars postacetabularis is itself further divided into two parts in *Struthio* (Gangl *et al.* 2004). They take origin from the dorsal iliac crest (cranial to the acetabulum) and the dorsolateral iliac crest (caudal to the acetabulum), and insert on the patellar tendon and surrounding connective tissue. This in turn inserts on one or both of the cnemial crests of the tibiotarsus, and perhaps also the proximomedial tibiotarsus (iliotibialis cranialis in *Dromaius* and *Struthio*).

Observations. Both the dorsal and dorsolateral iliac crests of *D. robustus*, *P. elephantopus* and *E. crassus* are pronounced, and are indeed slightly proud of the surrounding bone surface. The fine, striated scarring on these crests indicates the attachment of the iliotibiales in these species. In *D. robustus*, the dorsolateral iliac crest may also bear several ill-defined tubercles. In all three species, the scarring of the dorsal iliac crest extends around the cranial margin of the preacetabular iliac blade, where it widens to cover a significant area behind the cranial margin of the bone, indicating that the iliotibialis cranialis also extended onto the cranial edge, as in *Apteryx* and *Rhea*. The striations here are more or less parallel with the margins of the bone. There is no evidence from the osteology as to the exact delimitations of the attachment of each part of the iliotibialis to the ilium, and it is possible that they originated via a shared aponeurosis. The presence of both cnemial crests on the moa tibiotarsus attests to the presence of strong, tendinous insertions of the iliotibiales and patellar tendon, and indeed the margins of the crests are often slightly recessed into the surrounding bone as a result of this attachment.

Remarks. Moa appear not to have had an osseous patella, unlike some extant palaeognath species; the presumed 'patella' noted by Owen (1883) in a specimen of *A. didiformis* is more likely to have been a misinterpreted tarsal sesamoid (Regnault *et al.* 2014). Regardless of this fact, reconstructing the iliotibiales cranialis et lateralis in *D. robustus*, *P. elephantopus* and *E. crassus* is a level I inference, although inferring the presence of separate partes preacetabularis and postacetabularis has only level I′ support, since osteological evidence is lacking.

Iliofemoralis externus

(Figs 3–5; il.fem.ex.)

General comments. This muscle is present in all extant palaeognaths, originating from the ilium dorsal to the acetabulum and just ventral to the dorsal iliac crest. It inserts on the lateral aspect of the femoral trochanter along with the iliotrochantericus heads, obturatorius heads and the ischiofemoralis. Whilst different variations in the exact spatial pattern of insertion occur in extant palaeognaths, a common basic topology exists, which is evident throughout all neornithine birds (Hutchinson 2001). The cranialmost insertions on the trochanter are those of the iliotrochanterici, proceeding proximal to distal in the order of caudalis, medius, cranialis; sometimes the medius and cranialis heads are fused to a variable degree, as in *Struthio, Dromaius, Apteryx* and at least some tinamous (*Tinamus* and *Crypturellus*). The obturatorius medialis et lateralis insert on the proximocaudal aspect of the trochanter, with the insertion of the medialis proximal to that of the lateralis; sometimes the two share a common insertion. The ischiofemoralis inserts distal to the insertion (or insertions) of the obturatorius, and the iliofemoralis externus inserts somewhere in the middle of the aforementioned insertions.

Observations. The pelves of *D. robustus*, *P. elephantopus* and *E. crassus* exhibit a broad area of marked surface rugosity (with individual rugae directed toward the acetabulum) in the area corresponding to the origin of this muscle in extant palaeognaths. This is interpreted as marking the origin of the iliofemoralis externus in moa. In several specimens of *D. robustus* and *P. elephantopus* examined, a faint striated ridge, directed toward the acetabulum, forms the posterior boundary of this area. This ridge is interpreted to be an intermuscular line bounding the posterior extent of the origin of the iliofemoralis externus in these species. The pattern of surface scarring on the femoral trochanter of moa is evidently no exception to the general neornithine pattern noted above, and a clear, rugose scar of insertion of the iliofemoralis externus is evident in the middle of the trochanter in *D. robustus*, *P. elephantopus* and *E. crassus*. Its fibrous texture, directed proximally to cranioproximally, is suggestive of the presence of abundant Sharpey's fibres (Carrano & Hutchinson 2002).

On the pelvis of *E. crassus*, as well as *Euryapteryx curtus*, there is a subcircular bump, ventral to the inferred origin of the iliofemoralis externus and dorsocaudal to the antitrochanter (bump, Fig. 3B). It ranges in size from quite small (< 5 mm diameter) to large (>20 mm in greatest dimension); in one specimen of *E. crassus* examined (CM Av8331), the bump is present on the left side of the pelvis but not the right. The surface texture of the bump varies from being rough (with tubercles, pits and striations) to completely smooth; typically the larger bumps are smoother. What soft tissue attachment this bump was for is uncertain, but its position on the pelvis suggests that it could be associated with the iliofemoralis externus,

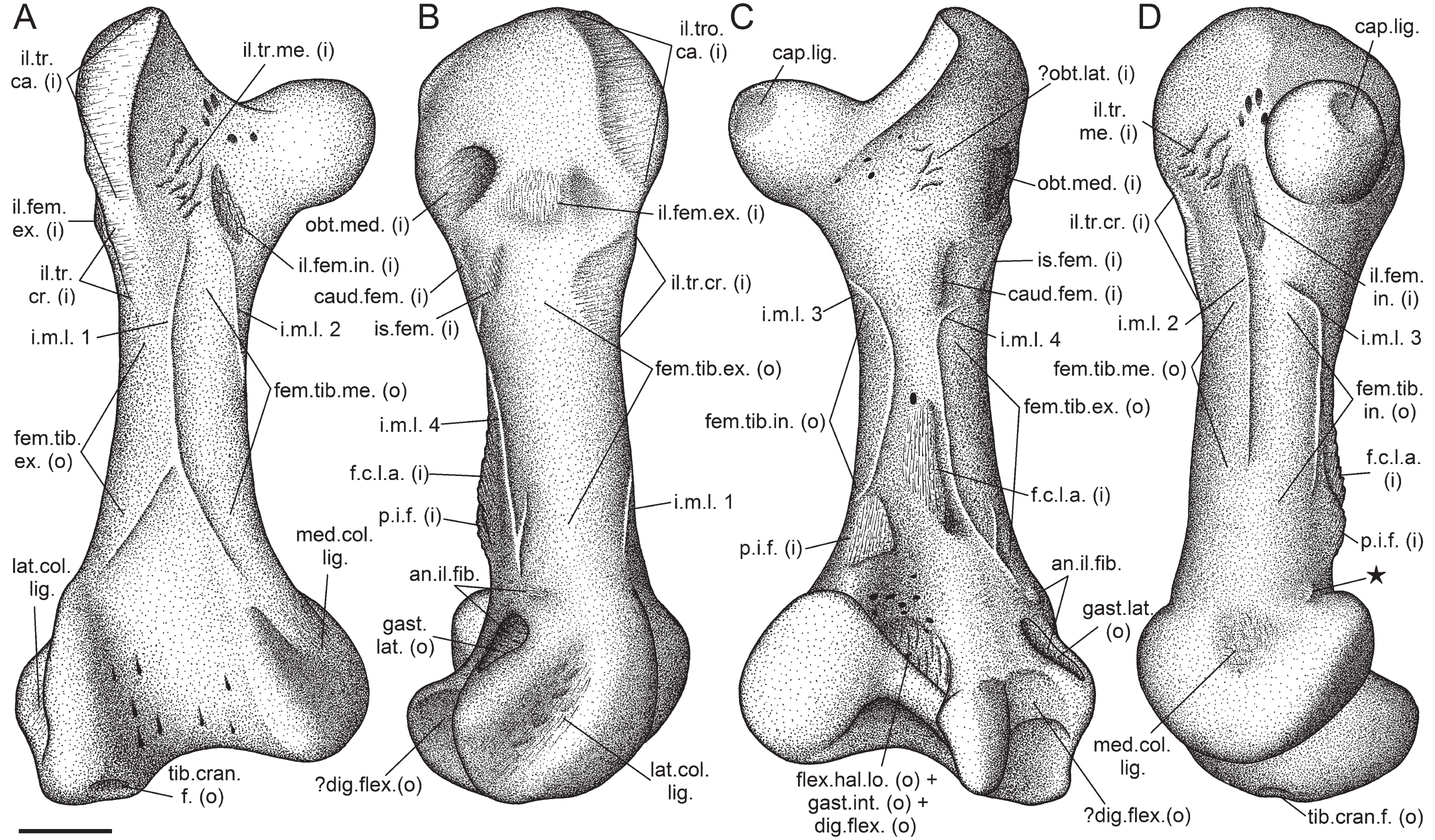

FIG. 4. Osteological evidence of muscle attachment on the femur of *D. robustus*, with corresponding myological interpretations. A, cranial view; B, lateral view; C, caudal view; D, medial view. The star indicates the small scar which may be for a fourth head of the gastrocnemius, or alternatively the flexor perforatus digiti III. Scale bar = 50 mm. Abbreviations: *an.il.fib.*, ansa iliofibularis; *cap.lig.*, capital ligament; *caud. fem.*, caudofemoralis; *dig.flex.*, digital flexors; *f.c.l.a.*, flexor cruris lateralis pars accessoria; *fem.tib.ex.*, femorotibialis externus; *fem.tib.in.*, femorotibialis internus; *fem.tib.me.*, femorotibialis medius; *flex.hal.lo.*, flexor hallucis longus; *gast.int.*, gastrocnemius intermedia; *gast. lat.*, gastrocnemius lateralis; *(i)*, muscle insertion; *il.fem.ex.*, iliofemoralis externus; *il.fem.in.*, iliofemoralis internus; *il.tr.ca.*, iliotrochantericus caudalis; *il.tr.cr.*, iliotrochantericus cranialis; *il.tr.me.*, iliotrochantericus medius; *i.m.l. 1–4*, intermuscular lines 1–4; *is.fem.*, ischiofemoralis; *lat.col.lig.*, lateral collateral ligament; *med.col.lig.*, medial collateral ligament; *(o)*, muscle origin; *obt.lat.*, obturatorius lateralis; *obt.med.*, obturatorius medialis; *p.i.f.*, puboischiofemoralis; *tib.cran.f.*, tibialis cranialis caput femorale.

iliofibularis or caudofemoralis pars pelvica (see below), or perhaps even a ligament spanning the hip joint. What does appear certain, however, is that this feature is only present in *E. crassus* and *E. curtus*.

Remarks. Reconstruction of the iliofemoralis externus in moa is a level I inference.

Iliofemoralis internus

(Figs 3–5; il.fem.in.)

General comments. Among extant palaeognaths the iliofemoralis internus typically originates from the caudoventral rim of the preacetabular ilium, cranial to the preacetabular tubercle. In *Struthio*, however, it originates from between the origins of the iliotrochanterici cranialis et medialis (Gangl *et al.* 2004; Zinoviev 2006), while in *Rhea* it does so from the cranial aspect of the acetabulum (Picasso, 2010). The insertion of this muscle is on the medial to craniomedial surface of the femur, distal to the base of the femoral neck.

Observations. In *D. robustus*, *P. elephantopus* and *E. crassus* there exists a discrete elevation of variable rugosity on the caudolateral rim of the preacetabular ilium, immediately cranial to the pubic peduncle of the ilium; this corresponds to the origin of the iliofemoralis externus in most extant palaeognaths, and is interpreted as such. Its development varies within and between species, ranging from being constricted in size with highly pronounced scarring, through to being a broad, oval-shaped region of less pronounced rugosity. In some instances (particularly in *E. crassus*) it may form one or two heavily striated flanges of bone which project laterally to ventrolaterally. Regardless of its morphology, in all cases this scar is clearly distinct from that of the ambiens (see below), the two being of different character and being separated by smooth bone. The craniomedial surface of the proximal femur of moa always possesses a region of complex rugosity, although its appearance and extent varies. This feature is recognised as homologous to the insertion scar of the iliofemoralis internus in extant palaeognaths. In *E. crassus* this region is strongly recessed into the bone surface, forming a deeply excavated pit (Worthy & Holdaway 2002).

Remarks. In addition to the iliofemoralis internus, Zinoviev (2013) posited that the iliotrochantericus medius also originated from the caudolateral rim of the preacetabular ilium, on the basis of finding two rugosities on the surface of his specimens. As noted above, however, the appearance of the scar of the iliofemoralis internus is variable in moa, and the large sample of specimens studied here illustrates that this variation is expressed along a continuum, from a single discrete scar to two apparently distinct rugosities. Furthermore, among extant palaeognaths the iliotrochantericus medius is only closely associated with the iliofemoralis internus in *Struthio*, owing to a more dorsal location of the latter muscle's origin (Gangl *et al.* 2004; Zinoviev 2006), and even then the two muscles never actually fuse. Elsewhere among extant palaeognaths, the iliotrochantericus medius originates from a more cranial position on the preacetabular ilium. These observations suggest that the scarring in moa is for a single muscle, albeit one that may vary in internal architecture (e.g., the presence and number of internal fibrous planes). The most parsimonious interpretation is that the scar marks the origin of the iliofemoralis internus (a level I inference).

As regards the insertion of the iliofemoralis internus, Worthy & Holdaway (2002), Worthy & Scofield (2012) and Zinoviev (2013) considered the possibility that the pronounced scar on the femur was for the insertion of the iliofemoral ligament, rather than a muscle. This is not supported by osteological evidence (as noted above), and moreover, a mummified femur of *E. crassus*, described by Hutton & Coughtrey (1875b) and figured by Rawlence *et al.* (2012b), shows that muscle fibres and not a ligament inserted here. The most parsimonious interpretation therefore is that the scar indicates the insertion of the iliofemoralis internus in all moa (also a level I inference).

Iliotrochanterici

(Figs 3–5)

General comments. The iliotrochanterici cranialis (il.tr.cr.), medius (il.tr.me.) et caudalis (il.tr.ca.) occur in all extant palaeognaths, with the caudalis being the largest of the three. The

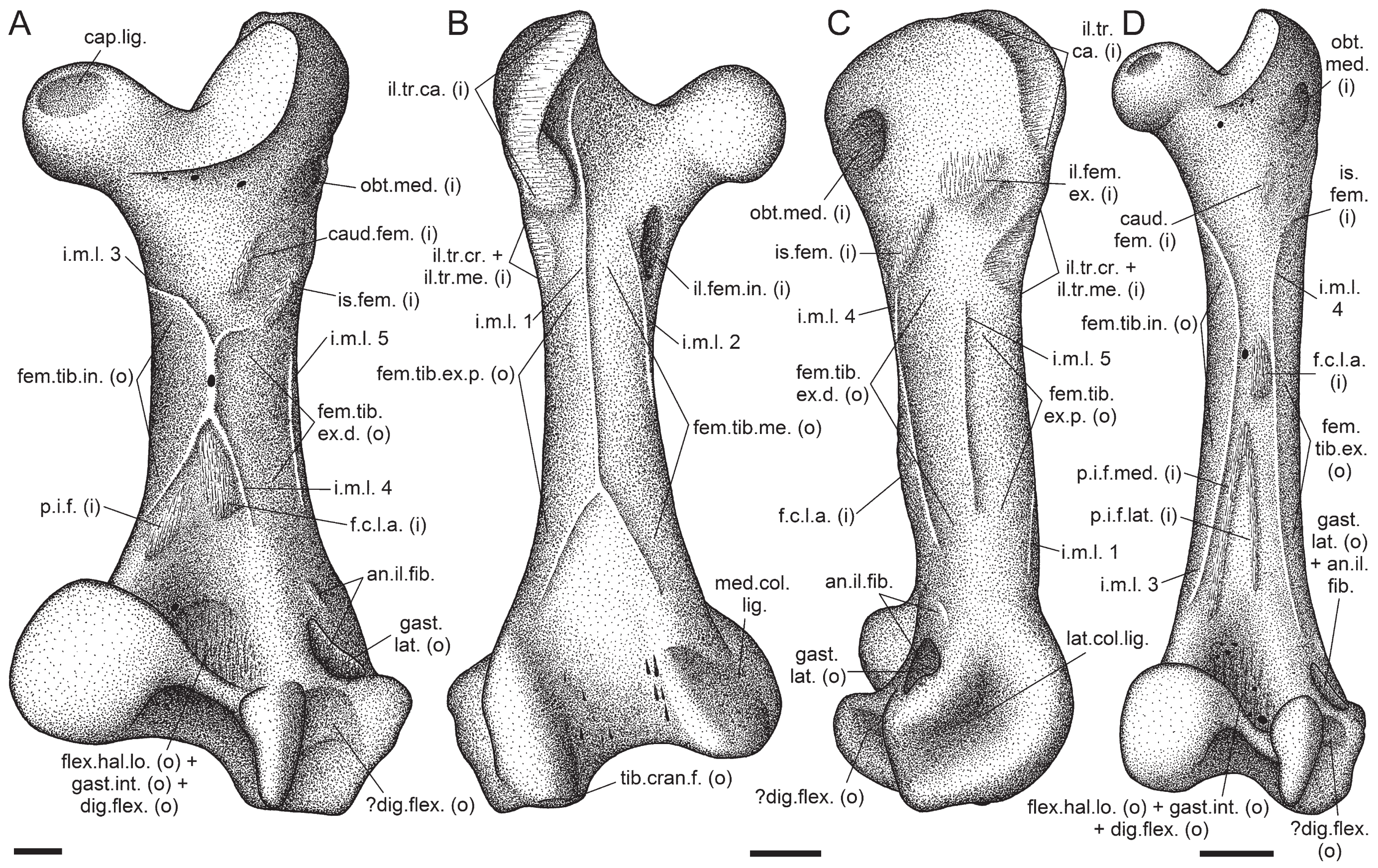

FIG. 5. Osteological evidence of muscle attachment on the femora of non-*Dinornis* moa, with corresponding myological interpretations. A, *P. elephantopus*, caudal view; B, *E. crassus*, cranial view; C, *E. crassus*, lateral view; D, *M. didinus*, caudal view. Scale bars = 20 mm. Abbreviations: *an.il.fib.*, ansa iliofibularis; *cap.lig.*, capital ligament; *caud.fem.*, caudofemoralis; *dig.flex.*, digital flexors; *f.c.l.a.*, flexor cruris lateralis pars accessoria; *fem.tib.ex.d.*, femorotibialis externus pars distalis; *fem.tib.ex.p.*, femorotibialis externus pars proximalis; *fem.tib.in.*, femorotibialis internus; *fem.tib.me.*, femorotibialis medius; *flex.hal.lo.*, flexor hallucis longus; *gast.int.*, gastrocnemius intermedia; *gast.lat.*, gastrocnemius lateralis; *(i)*, muscle insertion; *il.fem.ex.*, iliofemoralis externus; *il.fem.in.*, iliofemoralis internus; *il.tr.ca.*, iliotrochantericus caudalis; *il.tr.cr.*, iliotrochantericus cranialis; *il.tr.me.*, iliotrochantericus medius; *i.m.l. 1–5*, intermuscular lines 1–5; *is.fem.*, ischiofemoralis; *lat.col.lig.*, lateral collateral ligament; *med.col.lig.*, medial collateral ligament; *(o)*, muscle origin; *obt.med.*, obturatorius medialis; *p.i.f.*, puboischiofemoralis; *p.i.f.lat.*, puboischiofemoralis lateralis; *p.i.f.med.*, puboischiofemoralis medialis; *tib.cran.f.*, tibialis cranialis caput femorale.

muscles' origination typically occupies almost the entire preacetabular iliac blade, and their insertion on the femoral trochanter follows a fairly consistent pattern (see above).

Observations. In *D. robustus*, *P. elephantopus* and *E. crassus*, the three muscles' origin from the preacetabular ilium is indicated by an uneven surface texture with extensive and strong, often striated, ridges and elongate tubercles, directed toward the acetabulum. (These scars should not be confused with the numerous anastomosing, smooth-surfaced blood vessel channels that etch the iliac surface.) Toward the dorsal and cranial margins of the preacetabular ilium is a long line of tuberosities and short ridges, which runs from the dorsal part of the preacetabular ilium and around the cranial margin, and often loops back along the cranioventral margin. Each tubercle or ridge is striated, with the striations directed toward the acetabulum. The degree of development of these tuberosities and ridges is variable in all species studied: in some specimens they are well developed and unite to form a single, well-defined ridge, whereas in others they consist of several low tubercles that are broadly aligned. This line of scarring is interpreted as an intermuscular line separating the origins of at least two of the iliotrochanterici, with the origin of the iliotrochantericus caudalis likely being situated caudal to the line. The exact location of origins of the iliotrochanterici cranialis et medius is not able to be determined. The distinctive scarring of the iliotrochanterici does not extend onto the sacral ribs fused with the ilium in any species, suggesting that the muscles' origins did not either.

The existence of the iliotrochanterici in *D. robustus, P. elephantopus* and *E. crassus* is also evidenced by their well-marked scars of insertion on the femoral trochanter, which although variable in appearance, is consistent with that observed in extant palaeognaths (level I inference). The topography of the femoral trochanter in all moa is dominated cranially by a very long and deep furrow which parallels the cranial margin of the bone; this gives the cranial part of the trochanteric ridge a medial inflection in proximal view. At its caudal end, the furrow is strongly scarred, with striations and ridges pointing cranially to cranioproximally; here the furrow can also become so deeply recessed that it forms a long pocket. In *E. crassus* the scarring in the distal part of this region extends onto the cranial aspect of the trochanter. The entire region of scarring corresponds to the insertion of the iliotrochantericus caudalis in extant palaeognaths, and is interpreted as such here for *D. robustus, P. elephantopus* and *E. crassus*. Distal to this scar is a broad region of coarse striations, which are again cranially to cranioproximally directed; the striations are most strongly developed around the margins of this area. This scarring, which extends onto the cranial aspect of the trochanter in *P. elephantopus*, is distinct from the aforementioned scarring located proximal to it, and often they are separated by smooth bone. In extant palaeognaths this region of scarring corresponds to the insertion of both the iliotrochantericus cranialis and medius. In lieu of any further discrete scarring in this region of the femur in *P. elephantopus* and *E. crassus*, it is hypothesised that both iliotrochanterici cranialis et medius inserted here in these species, sharing a common insertion.

In *D. robustus* the situation is different. Here, the craniomedial aspect of the femoral trochanter is scarred with well-developed tubercles and ridges (Fig. 4A). (This area of the bone is relatively smooth in *P. elephantopus* and *E. crassus*; any uneven texture is related to the presence of pneumatic diverticula.) They often bear fine striations (presumably Sharpey's fibres), which are directed transverse to their long axes, roughly toward the femoral head. That the striations are pointing in this direction, and not distally, argues against them being associated with the femorotibialis muscles (see below), where they would be expected to point distally. Indeed, in a number of specimens the medial extent of the scarring is bounded by an intermuscular line of the femorotibialis medius (see below). It is posited here that these scars are for the insertion of the iliotrochantericus medius. In two specimens (CM Av 8469, 13461), these scars are united into a single, massive tubercle some 20 mm across, pointing toward the femoral head.

Thus, the iliotrochantericus cranialis in *D. robustus* is posited to have inserted separately in the usual position on the lateral aspect of the trochanter. The medial aspect of the trochanter in *D. robustus* also shows a variable level of pneumatization, with pockets, furrows and large foramina dotting the surface (indicating the presence of diverticula), but these are easily distinguished from the hypothesised insertion of the iliotrochantericus medius because they produce no positive surface relief, and the bone surface itself is smooth, as opposed to the coarse and fibrous scarring of the muscle insertion.

Remarks. Although evidence for each separate iliotrochantericus head is not always present on the bones of a given moa species, inferring the presence of all three heads in moa is supported by the fact that they exist in all extant palaeognaths (a level I′ inference). Both the origin and insertion of the iliotrochantericus caudalis is evidenced by well-developed and unambiguous osteological indicators of its attachment to the pelvis and femur, respectively. Hence, the proposed reconstruction of this head is well supported (level I inference).

The origins of the iliotrochantericus cranialis et medius are proposed here to have likely originated more or less cranial to the origin of the iliotrochantericus caudalis. This arrangement differs markedly from that hypothesised by Zinoviev (2013), who reconstructed both heads as originating ventral to the origin for the iliotrochantericus caudalis. His specimens were both incomplete, however, lacking the cranial part of the preacetabular iliac blade. Consequently, he may not have been able to observe the long line of tuberosities and ridges that are consistently present, which are interpreted here as an intermuscular line. This may in turn have influenced his interpretations. Moreover, the iliotrochantericus cranialis at least is typically wholly or partially cranial to the main bulk of the iliotrochantericus caudalis in extant palaeognaths. Considering both osteological and comparative evidence together, the proposed arrangement receives level II support, whereas Zinoviev's reconstruction only has level II′ support.

The iliotrochantericus cranialis et medius on the femur of *P. elephantopus* and *E. crassus* are both posited to have shared a single common insertion, based on the osteological evidence. A common insertion of the iliotrochanterici cranialis et medius is a feature seen in several extant palaeognaths (*Dromaius*, *Struthio*, *Apteryx*, *Tinamus* and *Crypturellus*), such that the interpretation for *P. elephantopus* and *E. crassus* is a level II inference. The reconstructed position of the insertion for the iliotrochantericus medius in *D. robustus*, on the medial aspect of the femoral trochanter and separate to that of the iliotrochantericus cranialis, is distinct from that observed in all extant palaeognaths. Nonetheless, its proximodistal position on the femur is comparable to that observed in extant palaeognaths and inferred in other moa species. Furthermore, hypothesizing that the scars on the medial aspect of the trochanter are for a different muscle would be more speculative, as all other muscles in the general region of the bone can be accounted for with other surface scars (detailed above and below).

Femorotibialis (Figs 4–7; fem.tib.)

General comments. This comprises a minimum of four parts in extant palaeognaths, namely, externus pars proximalis (fem.tib.ex.p.), externus pars distalis (fem.tib.ex.d.), medius (fem.tib.me.) and internus (fem.tib.in.). (Note that Hudson *et al.* (1972) termed the femorotibialis externus pars proximalis of tinamous the 'lateral head of the femorotibialis medius', and also termed the femorotibialis medius the 'medial head of the femorotibialis medius'.) Except in *Apteryx*, the pars internus is further subdivided in the various species of palaeognaths, although the homology of these parts between species is uncertain, especially of the 'pars pectineus' of *Struthio* (Zinoviev 2006; Hutchinson *et al.* 2015). The origins of the various heads of the femorotibialis effectively enclose the whole shaft of the femur in extant palaeognaths, and they typically insert on the cranial cnemial crest of the tibiotarsus, either directly or via the patellar tendon and surrounding connective tissue. The femorotibialis externus pars distalis,

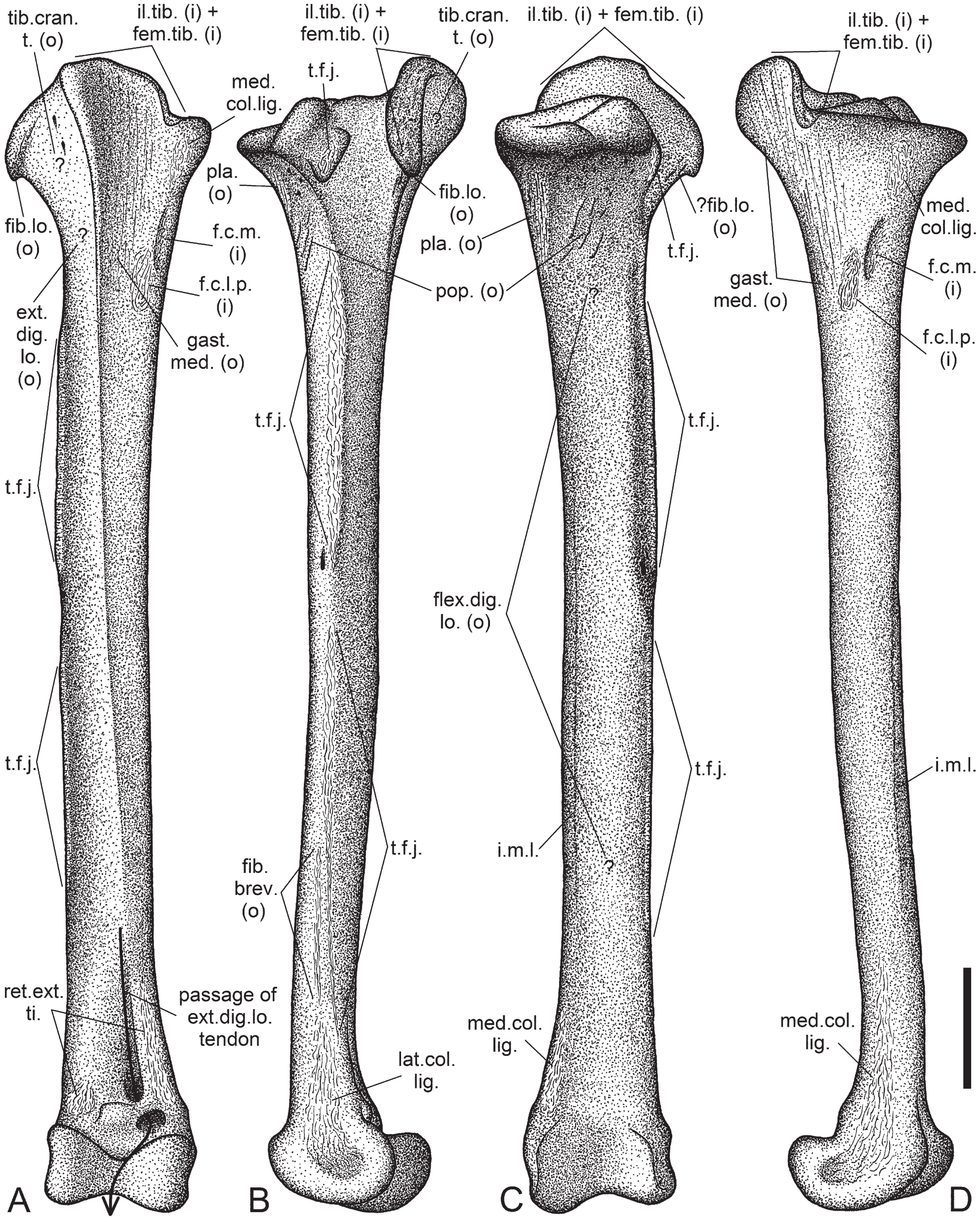

FIG. 6. Osteological evidence of muscle attachment on the tibiotarsus of *D. robustus*, with corresponding myological interpretations. A, cranial view; B, lateral view; C, caudal view; D, medial view. Scale bar = 100 mm. Abbreviations: *ext.dig.lo.*, extensor digitorum longus; *f.c.l.p.*, flexor cruris lateralis pars pelvica; *f.c.m.*, flexor cruris medialis; *fem.tib.*, femorotibialis; *fib.br.*, fibularis brevis; *fib.lo.*, fibularis longus; *flex.dig. lo.*, flexor digitorum longus; *gast.med.*, gastrocnemius medialis; *(i)*, muscle insertion; *il.tib.*, iliotibialis; *i.m.l.*, intermuscular line; *lat.col.lig.*, lateral collateral ligament; *med.col.lig.*, medial collateral ligament; *(o)*, muscle origin; *pla.*, plantaris; *pop.*, popliteus; *ret.ext.ti.*, retinaculum extensorium tibiotarsi; *t.f.j.*, ligament of the tibiofibular junction; *tib.cran.t.*, tibialis cranialis caput tibiale.

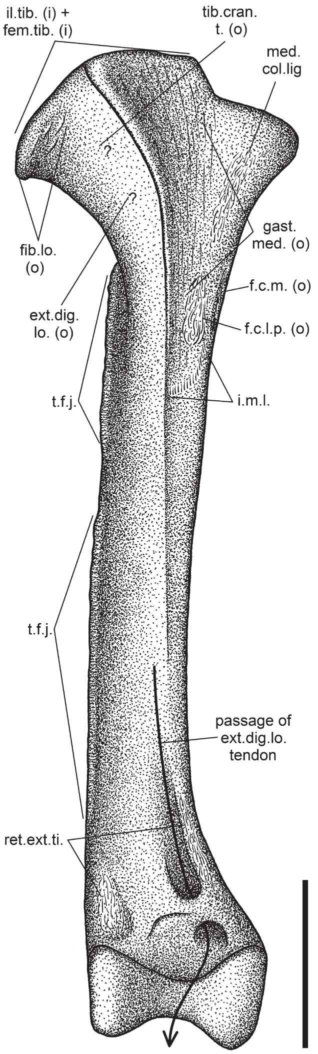

FIG. 7. Osteological evidence of muscle attachment on the cranial tibiotarsus of *P. elephantopus*. Note in particular the coarse intermuscular line bounding the distal extent of the origin of the gastrocnemius medialis. Scale bar = 100 mm. Abbreviations: *ext.dig. lo.*, extensor digitorum longus; *f.c.l.p.*, flexor cruris lateralis pars pelvica; *f.c.m.*, flexor cruris medialis; *fem.tib.*, femorotibialis; *fib.lo.*, fibularis longus; *gast. med.*, gastrocnemius medialis; *(i)*, muscle insertion; *il.tib.*, iliotibialis; *i.m.l.*, intermuscular line; *med.col.lig.*, medial collateral ligament; *(o)*, muscle origin; *ret.ext. ti.*, retinaculum extensorium tibiotarsi; *t.f.j.*, ligament of the tibiofibular junction; *tib.cran.t.*, tibialis cranialis caput tibiale.

however, inserts on the lateral aspect of the lateral cnemial crest.

Observations. The femur of *D. robustus*, *P. elephantopus* and *E. crassus* possesses several well-defined, longitudinal ridges along the shaft, which occupy the same general position as the femorotibialis intermuscular lines on the femora of extant large palaeognaths, and they are therefore interpreted as such. These ridges usually bear fine striations along their length, which are always directed distally. The longest ridge (intermuscular line 1) runs from the craniomedial aspect of the trochanter down the cranial aspect of the shaft; it bifurcates halfway to three-fifths of the way down, sending a branch each to the proximal extent of the lateral and medial condyles. This ridge is homologous with the linea intermuscularis cranialis of extant birds (cf. Baumel *et al.* 1993). In moa its proximal extent along the craniomedial trochanter is variable, sometimes reaching up to the level of the proximal aspect of the femoral head. A second, fainter ridge (intermuscular line 2) runs proximodistally along the craniomedial shaft, distal to the insertion scar of the iliofemoralis internus. Intermuscular line 2 sometimes extends proximal to the insertion scar of the iliofemoralis internus (in *E. crassus* it can run either lateral or medial to the iliofemoralis internus scar). In some specimens it is so proximally extensive that it joins up with intermuscular line 1 on the craniomedial aspect of the femoral trochanter. This feature is particularly prevalent in *E. crassus* and *Euryapteryx curtus*, where intermuscular line 1 also has a considerable proximal extent (cf. Fig. 5B).

Two ridges are present on the caudal surface of the femur, which run along the bone's caudomedial aspect (intermuscular line 3) and caudolateral aspect (intermuscular line 4). In *D. robustus* these ridges are always well separated, whereas in *E. crassus*, they can be quite close to each other, although the fine striations on the apices of the ridges remain separate. In *P. elephantopus* the ridges are very close to one another, and in the great majority of cases they actually unite along the middle of the caudal shaft to form a single intermuscular line which runs adjacent to – or indeed straight across –

the central nutrient foramen (Fig. 5A). Thus, in *P. elephantopus*, the entire femoral shaft (at the level of the midpoint in the bone) is enveloped by the femorotibiales. It is proposed here that both intermuscular lines 3 and 4 (or the union thereof) are homologous with the single linea intermuscularis caudalis of extant birds (cf. Baumel *et al.* 1993); moa seem to be exceptional here in that these lines are largely separate in most species. In *Apteryx* spp. the caudal aspect of the femur possess two faint longitudinal ridges on its caudal aspect, but one is not a femorotibialis intermuscular line, rather it marks the (extended) attachment of the caudofemoralis pars caudalis (McGowan 1979).

In all moa, the proximal end of intermuscular line 3 curves medially and heads towards the insertion scar of the iliofemoralis internus. Intermuscular line 4 typically runs all the way from the ventral edge of the insertion scar of the ischiofemoralis (see below), down past the pronounced caudal tuberosities and nearly to the ectocondylar fossa. In *D. robustus* a small accessory line of similar scarring (with striations directed distally) is occasionally present, branching off the distal part of intermuscular line 4. A fifth ridge (intermuscular line 5) is present in most specimens examined, although it is only rarely present on the femora of *D. robustus*. It is situated between intermuscular lines 1 and 4 on the bone's lateral aspect, typically in line with the scar of insertion of the iliofemoralis externus, and runs proximodistally. This ridge is homologous with the linea intermuscularis lateralis of extant birds (cf. Hutchinson 2001).

As in extant palaeognaths, the abovementioned intermuscular lines would have delimited, to a large extent, the areas of origin of the femorotibialis heads. The femorotibialis externus would have originated from much of the lateral surface of the shaft, between intermuscular lines 1 and 4. Furthermore, the presence of intermuscular line 5 in most specimens supports reconstructing the division of this muscle into partes proximalis and distalis; as in extant palaeognaths, the pars proximalis would presumably have originated cranial to the pars distalis. It is uncertain as to whether the division of the femorotibialis externus was a consistent feature in *D. robustus*. The femorotibialis medius would have originated along the cranial aspect of the shaft between intermuscular lines 1 and 2; the great proximal extent of line 1 in *E. crassus* and *Euryapteryx curtus* indicates that the muscle took origin from the medial aspect of the trochanter, as in *Apteryx* (McGowan 1979; Kooyman 1991). The femorotibialis internus would have originated from much of the medial aspect of the shaft between intermuscular lines 2 and 3.

The proximal and lateral margins of both cnemial crests in moa show evidence of soft tissue attachment, with distinct areas of a roughened, fibrous texture, slightly recessed into the surrounding bone surface. Although the femorotibiales presumably inserted on these parts, as in extant palaeognaths, it is not possible to differentiate the insertions of the femorotibialis from those of the iliotibiales.

Remarks. Identification of the femorotibialis intermuscular lines on the moa femur, and the largely conservative nature of the femorotibialis in extant palaeognaths, means that reconstruction of the femorotibialis externus pars proximalis, externus pars distalis, medius and internus in moa are all strongly supported (level I inferences). However, a lack of osteological evidence precludes determining whether the femorotibialis internus was further subdivided or not.

The interpretations presented here differ slightly from those offered by Zinoviev (2013) in two respects. Firstly, Zinoviev reconstructed the proximal part of the femorotibialis medius as originating from the distocranial aspect of the trochanter, but this is not supported by the osteological evidence. Specifically, intermuscular lines 1 and 2 indicate that if the muscle's origin did indeed reach as far proximally as the trochanter, it would have been restricted to the medial aspect of the trochanter only. The second difference in interpretations relates to the subdivision of the femorotibialis medius. Zinoviev suggested that a second part of the femorotibialis medius existed, the 'pars distalis', which took origin from the distal femur between the two branches of intermuscular line 1. No evidence for this attachment was observed in any of the specimens examined in this study; the surface of the bone here is either smooth, or any unevenness present appears to be fluting caused by blood vessel channels. Furthermore, only in *Struthio* does such a second part exist. Thus, without osteological evidence, it is less parsimonious to reconstruct a 'pars distalis' in moa (a level II′ inference) than to refrain from doing so (a level I′ inference).

Ambiens (Fig. 3; amb.)

General comments. Except in *Struthio*, where it originates from the ventrolateral margin of the preacetabular ilium (Gangl *et al.* 2004; Zinoviev 2006; but see Hutchinson *et al.* 2015), the ambiens originates from the preacetabular tubercle (or 'pectineal process') in extant palaeognaths. The ambiens runs down to the knee, where it becomes a tendon that perforates the aponeurosis surrounding the knee medially. Two exceptions to this are tinamous, where the perforation occurs on the lateral side (Hudson *et al.* 1972), and *Apteryx*, where it the tendon actually perforates the patella (McGowan, 1979). Distal to the knee, the tendon inserts on the origin (or origins) of the flexor perforatus digiti II, the flexor perforatus digiti III, or both. In casuariids, the tendon terminates at the knee (Gadow, 1880; Patak & Baldwin 1998; Lamas *et al.* 2014).

Observations. Moa lack a preacetabular tubercle, but a low, broad area of pronounced rugosity is present in the same region of the pelvis, on the craniolateral aspect of the acetabular rim; this is taken to mark the origin of the ambiens (level I inference). In one specimen of *D. robustus* (CM Av9049) and two specimens of *P. elephantopus* (CM Av8383, 8387), this scar is slightly recessed into the surrounding bone surface. In *D. robustus*, *P. elephantopus* and *E. crassus*, there is also occasionally a poorly developed area of roughened bone, sometimes with a small tubercle or flange, located ventral to this broad area of rugosity on the craniolateral 'corner' of the proximal pubis. This may mark the origin of a second head of the ambiens, as evidenced by the fact that the tubercle or flange points ventrolaterally, towards the in-life position of the knee. The ambiens of moa would have presumably run at least as far as the knee, but whether it terminated or continued toward the distal limb, and in what manner, cannot be determined.

Remarks. Reconstructing the site of origination for this muscle in moa is well supported (a level I inference), as is the hypothesis that it ran toward the knee (a level I′ inference). How it may have terminated, and where in the limb it may have done so, remains uncertain, as there is no osteological evidence in the moa fossils, and the situation in extant palaeognaths is variable; any reconstruction would have level II′ support at best.

Iliofibularis (Figs 3–5, 8; il.fib.)

General comments. In all extant palaeognaths, the iliofibularis takes origin from most of the length of the postacetabular ilium, immediately ventral to the origin of the iliotibialis lateralis pars postacetabularis on the dorsolateral iliac crest. It inserts via a thick tendon on a pronounced tubercle on the posterolateral shaft of the fibula. (*Struthio* possesses a small second insertion, the 'crus caudale' of Gangl *et al.* (2004), which separates from the main muscle mass distally and inserts on the caudal fascia of the gastrocnemii). Before it inserts on the fibula, the tendon of this muscle always runs through a ligamentous loop, the ansa iliofibularis (an.il.fib.). The nature of bony attachment of the ansa is poorly documented in extant palaeognaths. It may also be variable, as Owen (1879) described attachments to the lateral femur and tibia in *Apteryx*, yet McGowan (1979) and Kooyman (1991) found two attachments to the femur only. In *Rhea*, Gadow (1880) described one attachment of the ansa to the distal lateral femur, and another apparently to the lateral collateral ligament of the knee. In *Struthio* there are two attachments to the distal femur, which are very close together (J.R. Hutchinson, pers. comm. 7.2.13).

Observations. Although visible surface scarring is lacking in the vast majority of specimens examined, the iliofibularis is inferred to have occupied the same relative position on the ilium in *D. robustus*, *P. elephantopus* and *E.*

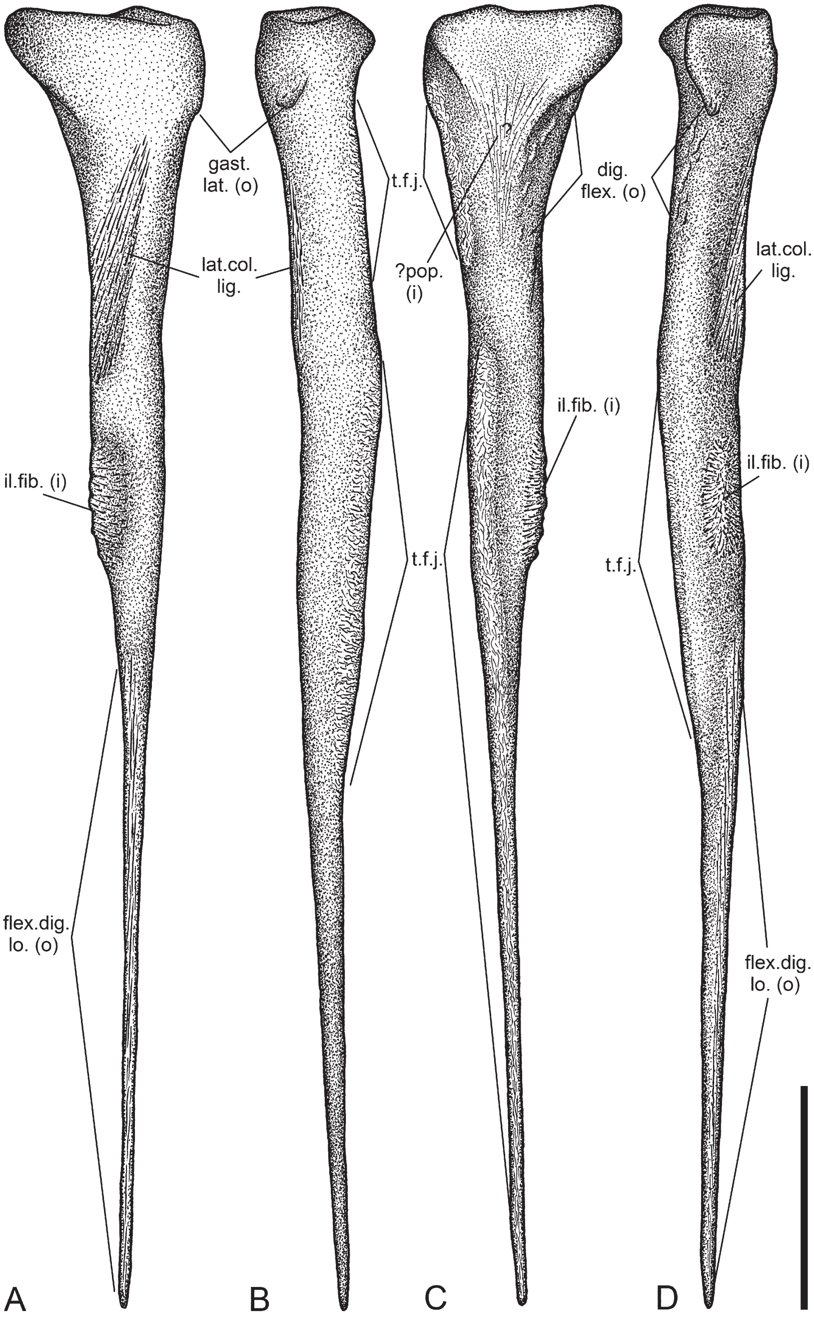

FIG. 8. Osteological evidence of muscle attachment on the fibula of *D. robustus*, with corresponding myological interpretations. A, lateral view; B, cranial view; C, medial view; D, caudal view. Scale bar = 100 mm. Abbreviations: *dig.flex.*, digital flexors; *flex.dig.lo.*, flexor digitorum longus; *gast.lat.*, gastrocnemius lateralis; *(i)*, muscle insertion; *il.fib.*, iliofibularis; *lat.col.lig.*, lateral collateral ligament; *(o)*, muscle origin; *pop.*, popliteus; *t.f.j.*, ligament of the tibiofibular junction.

crassus as in extant palaeognaths. In a few *P. elephantopus* and *E. crassus* specimens examined, there existed a broad, roughened ridge with longitudinal striations, positioned a little ventral to the dorsolateral iliac crest. This ridge may be some form of intermuscular line demarcating the boundary between the origin of the iliofibularis and another muscle. The insertion of the iliofibularis in moa is unambiguous, for the fibula possesses a very distinct tubercle on its posterolateral aspect. It is large and broad, although its degree of development is variable; in some specimens of *P. elephantopus*, the scar of insertion is slightly recessed into the surrounding bone. The tubercle is always well separated, and distinct, from the large area of strong scarring proximally; this area would have been for the attachment of the lateral collateral ligament, as indicated by the coarse striations and fine tubercles directed proximally.

There are two candidate attachment sites for the ansa on the femur of moa, the ectocondylar fossa (as also suggested by Worthy & Scofield 2012), and a small scar cranioproximal to this (Figs 4B, C, 5A, C, D). Both are recognisable in *Apteryx* as the attachments for the ansa (McGowan 1979; Kooyman 1991).

Remarks. The reconstruction of this muscle in moa in the typical palaeognath condition is supported, both proximally (a level I′ inference) and distally (a level I inference). The nature of its associated ansa is somewhat uncertain, however. Two attachments for the ansa are reconstructed here, but Zinoviev (2013) suggested that a third attachment existed, to the proximolateral fibula. This is the condition present in most neognaths (Baumel *et al.* 1993). No discrete scar on the proximolateral fibula, separate from that of the lateral collateral ligament of the knee, was discernable in any of the material examined in this study, nor is any appropriate scar evident on the lateral tibiotarsus. Hence, it is deemed too speculative to reconstruct a third attachment for the ansa in moa, especially in light of the lack of knowledge of this feature in most extant palaeognaths.

Flexor cruris lateralis
(Figs 3–7)

General comments. In extant palaeognaths, the flexor cruris lateralis comprises two parts, the partes pelvica (f.c.l.p.) and accessoria (f.c.l.a). The pars pelvica originates from the caudal end of the postacetabular ilium, caudal to the origin of the iliotibialis, although in various taxa it may also take origin from the first few unfused caudal vertebrae (*Casuarius*, *Rhea*, tinamous), the caudal end of the ischium (*Struthio* and *Rhea*, related to the fusion of the caudal ilium and ischium in these taxa), or ilioischiadic membrane (*Struthio*). The pars pelvica gives off the pars accessoria distally, which inserts on the caudal aspect of the femoral shaft; see the description of the puboischiofemoralis below for a treatment of this muscle's insertion in moa. The pars pelvica itself becomes tendinous distally and inserts on the proximomedial surface of the tibiotarsus, adjacent to that of the flexor cruris medialis (the two may share a common insertion, as in *Struthio* and sometimes *Rhea*).

Observations. Although no osteological evidence has been observed in *D. robustus*, *P. elephantopus* or *E. crassus*, this muscle likely originated from the caudal end of the postacetabular ilium or the region thereabouts. On the proximomedial tibiotarsus of *D. robustus*, *P. elephantopus* and *E. crassus*, there are three diffuse areas of roughened, sometimes rugose, bone. One of these is more proximal to the other two, and the three areas are not always completely separate from each other. The proximal area is suggested to be the scar of the lateral collateral ligament of the knee, and the distal two are the insertion scars of the flexores cruris medialis et lateralis pars pelvica. In *Dromaius*, the flexor cruris lateralis pars pelvica inserts cranial to the flexor cruris medialis (Lamas *et al.* 2014), and without any evidence to the contrary this was probably also the case in moa. In *E. crassus*, *Euryapteryx curtus* and *A. didiformis*, the flexor cruris lateralis pars pelvica may have been associated with the head of the gastrocnemius medialis (see below), as the scar of insertion of the former muscle is often more cranially situated, where it almost contacts the procnemial ridge and thereby would have been very close to the latter's origin. Moreover, the scar of the flexor cruris lateralis pars pelvica is often sometimes closely associated with the striations of the gastrocnemius medialis origin (see below).

Remarks. Reconstructing this muscle in the manner typical among palaeognaths is well-supported, being a level I′ inference proximally and level I inference distally. Zinoviev (2013) suggested that the more cranial of the two distal scars on the proximomedial tibiotarsus of moa was for the insertion of both the flexor cruris lateralis pars pelvica and the flexor cruris medialis (implying a common insertion), and that the more caudal scar was for the insertion of the medial collateral ligament of the knee; he did not mention the proximal scar. It is more likely that the more proximal scar was for the insertion of the collateral ligament, rather than either of the distal ones; this is because the distal scars are always a fair distance from the proximal end of the bone compared to other birds, including ostriches (Chadwick *et al.* 2014).

Flexor cruris medialis

(Figs 3, 6, 7; f.c.l.m.)

General comments. In extant palaeognaths, this muscle usually takes origin from the lateral aspect of the caudal end of the pubis, or the caudal end of the pubis and ischium and the lateral aspect of the intervening puboischaidic membrane; in *Struthio* it may also originate from the ilioischiadic membrane (Gangl *et al.* 2004). *Rhea* is distinct different from all other extant palaeognaths in that the muscle takes origin from the cranioventral ischium, just caudal to the acetabulum (Picasso 2010). As noted above, the muscle invariably inserts on the proximomedial tibiotarsus, adjacent to (or with) that of the flexor cruris lateralis pars pelvica.

Observations. The muscle very likely existed in *D. robustus*, *P. elephantopus* and *E. crassus*. On the distal ischium or pubis of these species, there is usually some form of low, broad tubercle with a rougher surface texture than the surrounding bone, sometimes associated with a localised thickening of the bone. This is likely associated with the origin of the flexor cruris medialis, although the muscle may have also originated from the puboischiadic or ilioischiadic membranes. As described above, a scar exists on the proximomedial tibiotarsus in all moa that is interpreted as that for the insertion of the flexor cruris medialis. The scar for the collateral ligament may be confluent with the scar of the flexor cruris medialis, although they can be easily distinguished: the scar of the muscle is recessed, often deeply, into the bone surface, whilst that of the ligament is not.

Remarks. Reconstructing both the origin and insertion of this muscle in moa is a level I inference.

Obturatorius medialis

(Figs 3–5; obt.med.)

General comments. Always present in palaeognaths, this muscle has a variable origin, which can include the medial surface of the ischium (the most common manifestation), the medial surfaces of the puboischiadic membrane and pubis, and, less frequently, the medial surface of the ilioischiadic membrane and even the ventral postacetabular ilium. *Struthio* is unusual in that this muscle originates from the lateral aspect of the puboischiadic membrane (Gangl *et al.* 2004; Zinoviev 2006). In the casuariids and *Rhea* it comprises two separate parts (Gadow 1880; Patak & Baldwin 1998; Picasso 2010; Lamas *et al.* 2014). In marked contrast to this variation, the muscle's manner of insertion in extant species is highly consistent: it sends a tendon through the obturator foramen (formed between the closely aligned proximal pubis and ischium; Fig. 3), to insert on the proximocaudal aspect of the femoral trochanter.

Observations. All moa likely possessed an obturatorius medialis, although it is not certain as to where it originated; presumably, it would have originated from the medial surface of whatever element or membrane it attached to. As described above, a suitable insertion for this muscle is present on the proximal femur of *D. robustus*, *P. elephantopus* and *E. crassus*, as indicated by a large, roughened depression rimmed with coarse-textured bone. In all three species the scar is often so well developed that it is recessed into the surrounding bone surface at its cranial end, forming a pocket. In *D. robustus*, there is sometimes a secondary pocket within the main pocket, which may mark the insertion of the obturatorius lateralis (see below).

Remarks. This muscle's reconstruction in moa is well supported both at its origin (level I′ inference) and insertion (level I inference). Zinoviev (2013) posited that the obturatorius medialis in *D. robustus* was bipartite, comprising dorsal and ventral bellies. He cited osteological evidence in support of this – "[t]races of its origin in *D. robustus* suggest that it must have had two bellies" (p. 259; see also his fig. 1B) – yet he did not describe the evidence itself. A bipartite obturatorius medialis does exist in some extant palaeognaths, and this is typically associated with a faint longitudinal ridge along at least part of the ventromedial aspect of the ischium, probably marking the junction of the aponeuroses of the two bellies with the bone. However, no ridge or any other feature, was observed on the medial surface of the ischium in any moa specimen examined in this study. Reconstructing a bipartite obturatorius medialis in moa is therefore not well supported (level II′ inference), and is avoided here.

Obturatorius lateralis

(Figs 3, 4; obt.lat.)

General comments. This muscle is always present in extant palaeognaths, typically originating from the margin of the obturator foramen, just caudal to the acetabulum. The point of insertion of the obturatorius lateralis on the proximocaudal femur is closely associated with that of the obturatorius medialis in extant palaeognaths, although they are usually distinct.

Observations. The scarring surrounding the obturator foramen on the pelvis of *D. robustus*, *P. elephantopus* and *E. crassus* is exceptionally variable, in terms of the number, position and degree of development of tubercles and ridges. One feature which does appear to be consistent in each species is the presence of a prominent and coarse tuberosity immediately cranial to the obturator foramen, which is interpreted as marking the origin (or part thereof) of the obturatorius lateralis. Other scars in the vicinity may also mark the origin of this muscle, but they may also be where the ischiofemoralis originated from (see below). There is often a small, rugose area on the proximocaudal surface of the femur of *D. robustus*, *P. elephantopus* and *E. crassus*, caudal to the insertion scar of the obturatorius medialis, which could be the insertion scar of the obturatorius lateralis, although this was not present in every specimen examined. In *D. robustus*, an accessory pocket inside the main scar of the obturatorius medialis may indicate that the two muscles were more closely associated in that species.

Remarks. Reconstructing the general areas of origin and insertion of this muscle is well supported (level I inferences), although the exact position of each are difficult to identify. Moreover, these positions may vary somewhat both within and between species.

Ischiofemoralis

(Figs 3–5; is.fem.)

General comments. In extant palaeognaths this muscle originates from the dorsolateral aspect of the ischium and the adjacent ilioischiadic membrane, although there are minor differences between species. For example, its area of origin includes most of the ischium in *Apteryx* and tinamous, but only the cranial third of the ischium in *Struthio*, and only the caudal part of the ischium in *Dromaius* (where it is often fused with the caudofemoralis pars pelvica; but see Lamas *et al.* 2014). As described above, the ischiofemoralis inserts on the caudolateral aspect of the femoral trochanter in extant palaeognaths, just distal to the insertion of the obturatorius.

Observations. Unambiguous osteological evidence of this muscle's origin is wanting in *D. robustus* and *P. elephantopus*. The muscle presumably took origin from part of the dorsolateral ischium, and in the proximal part of the bone there are usually a number of tubercles or ridges, but these may be associated with the origin of the obturatorius lateralis. In *E. crassus*, there is sometimes a faint, but distinct, ridge on the lateral surface of the distal ischium, trending roughly parallel with the bone (Fig. 3B). This may be an intermuscular line demarcating part of the origin of the muscle in this species. The femora of all moa exhibit a strongly developed scar in the region corresponding to the insertion of the ischiofemoralis in extant palaeognaths, distal to the insertion scar of the obturatorius medialis. This scar typically consists of an elongate oval-shaped to linear region of raised bone with pronounced roughness. In *D. robustus*, the scar is sometimes developed into a roughened depression with a pronounced and rugose distal rim. In *E. crassus*, it may be partly confluent with the scar of insertion of the iliofemoralis externus, but they can always be distinguished by the different orientation of the fibres or striations in each scar (directed proximally to cranioproximally in the iliofemoralis externus scar, directed proximocaudally to caudally in the ischiofemoralis scar).

Remarks. Reconstructing the ischiofemoralis in moa is well supported both for its origin (level I′ inference) and its insertion (a level I inference), although the exact size and position of its origin in *D. robustus* and *P. elephantopus* is uncertain.

Caudofemoralis

(Figs 3–5; caud.fem.)

General comments. This muscle consists of two parts in extant palaeognaths, the pars caudalis and the pars pelvica. The pars caudalis is absent in *Dromaius* and *Rhea*, but in other palaeognaths it originates from the lateral aspect of several unfused caudal vertebrae (which vertebrae are involved varies from species to species). The pars pelvica has a more varied origin, which can include the ventrolateral postacetabular ilium, ventral to the origin of the iliofibularis, ilioischiadic membrane, dorsocaudal pubis and the synsacral caudal vertebrae. In *Dromaius*, the pars pelvica is often fused with the ischiofemoralis (but see Lamas *et al.* 2014), the combined muscle originating from the caudal ilium, ischium and ilioischiadic membrane. The two parts of the caudofemoralis (when both are present) both insert on the proximal caudolateral surface of the femoral shaft, near the insertion of the ischiofemoralis; their insertions are often fused into a single attachment. *Apteryx* is distinctive in that the insertion continues distally for a considerable distance along the caudal aspect of the femur (McGowan 1979).

Observations. The unfused caudal vertebrae of *D. robustus*, *P. elephantopus* and *E. crassus* possess a slightly fluted or uneven surface on their ventral and ventrolateral aspects, but this varies both within and between individuals of the same species, as well as between species. Other caudal muscles were likely also present in this region of the tail, and since there is no discrete scarring which may be recognised as the attachment of the cadudofemoralis pars caudalis, it is uncertain as to whether these taxa possessed this muscle or not. Moa almost certainly possessed a pars pelvica, but the great variability in its origin in extant palaeognaths, and lack of visible surface scarring on the pelvis, precludes an identification of its exact area of origin.

On the proximal caudal surface of the femur of *D. robustus*, *P. elephantopus* and *E. crassus* is an area of relatively faint scarring, located caudal to (and distinct from) the large insertion scar of the ischiofemoralis on the caudolateral aspect of the femoral trochanter. This scarring corresponds to similarly positioned scarring for the caudofemoralis in extant palaeognaths, and is interpreted as such for moa. The scarring in *P. elephantopus* is usually more medially situated away from the scar of the ischiofemoralis, lying proximal to the bend in intermuscular line 3; the two scars are well separated by smooth bone. The scar's exact size, shape and positioning vary modestly in *E. crassus*, and in roughly half of the specimens examined the scar is confluent with that of the ischiofemoralis. In *Euryapteryx curtus*, the scar is almost always confluent with that of the ischiofemoralis; sometimes only a single large area of scarring is present in this part of the femur. In *D. robustus*, *P. elephantopus* and *E. curtus*, a small but rugose region of scarring is occasionally found proximal to scar of insertion of the caudofemoralis, caudal to the scar of the obturatorius insertion. This may be for the caudofemoralis (perhaps the pars caudalis, if it existed) or instead may be for the obturatorius (perhaps the smaller lateralis head).

Remarks. It is currently too ambiguous to reconstruct the caudofemoralis pars caudalis in moa (it would be a level II′ inference), but reconstructing the pars pelvica is more supported (level I′ inference for origin, level I inference for insertion). No scarring on the proximal caudal femur of any kind was mentioned by Zinoviev (2013), and consequently the caudofemoralis pars pelvica (his 'iliofemoralis') was reconstructed as inserting elsewhere, on intermuscular line 4. This has been argued above to instead reflect the attachment of the femorotibialis externus, or part thereof. That intermuscular line 4 (as with the other intermuscular lines) typically bears fine striations that point distally further refutes Zinoviev's interpretation, for the striations would be expected to point proximally if the caudofemoralis inserted there. Moreover, the scar inferred here as marking the insertion of the caudofemoralis is clearly separated from intermuscular line 4 by smooth bone, indicating that the insertion of the caudofemoralis did not extend onto the ridge. Zinoviev did concur with the current study in considering that the caudofemoralis pars caudalis (his 'caudofemoralis') was possibly absent in moa.

Puboischiofemoralis
(Figs 3–5, p.i.f.)

General comments. In all extant palaeognaths, this muscle comprises two parts, lateralis (p.i.f.lat.) and medialis (p.i.f.med.), which are closely associated. They typically originate from the ventral ischium and adjacent puboischiadic membrane, and in *Struthio* and tinamous the origin extends onto the dorsal pubis (Hudson *et al.* 1972; Gangl *et al.* 2004). The insertion of the puboishiofemorales on the caudal femur is somewhat variable in extant taxa, with the insertion being extensive in some, such as along almost the entire length of the femur in *Apteryx* (McGowan 1979) and *Rhea* (Picasso 2010), and relatively restricted in others. In all cases its insertion is medial to that of the flexor cruris lateralis pars accessoria. Furthermore, the two parts of the puboischiofemoralis tend to have a more or less single, common insertion.

Observations. The caudal ischium of *D. robustus*, *P. elephantopus* and *E. crassus* typically bears a long ridge of coarse, longitudinally striated bone on its ventral half, which can extend as far cranially so as to become confluent with the scarring on the obturator flange. This ridge is often well developed, forming an overhang above the ventralmost part of the ischium, especially in larger individuals. In small individuals the ridge may be entirely absent. The ridge and associated scarring is interpreted to be the dorsal border of the origin of the puboischiofemoralis in all three species. The muscle in moa would presumably have comprised both lateralis and medialis parts, as in extant palaeognaths.

In *D. robustus*, there are always two prominent and large tuberosities on the caudal femoral shaft, that are well separated from each other by smooth bone; the smaller, medial one is more distally located than the larger, lateral one. This feature is diagnostic for *Dinornis* (Worthy 1988; Worthy & Holdaway 2002; Worthy & Scofield 2012). Both tuberosities are also present in *M. didinus* and emeid moa, although in emeids they are associated with each other to a variable degree: their appearance ranges from two distinct points of elevation, the fibrous textures of which are separate, through to a single discernable tuberosity. The presence of two tuberosities – which are separated by smooth bone in *D. robustus* and *M. didinus* – suggests that two muscles inserted on this part of the moa femur, rather than one. Given that the medial of the two caudal tuberosities is separated from intermuscular line 3 by smooth bone, and likewise the lateral caudal tuberosity is separated from intermuscular line 4 by smooth bone, it is suggested that the medial caudal tuberosity is for the insertion of the puboischiofemoralis, and the lateral caudal tuberosity is for the insertion of the flexor cruris lateralis pars accessoria. This interpretation implies that in emeid moa the puboischiofemorales and flexor cruris lateralis pars accessoria are closely associated distally, to a varying degree.

The condition in *M. didinus* is unusual (Fig. 5D). The scars of insertion of the flexor cruris lateralis pars accessoria and puboischiofemoralis on the femur are clearly distinct and well-separated from each other (as in *Dinornis* spp.), with the scar of the flexor cruris lateralis pars accessoria situated just proximal to the shaft's midpoint. More importantly, the scar of the puboischiofemoralis consists of two parts, both long and linear, which are nearly fully separated for their entire length; the lateral part of the scar is typically less developed than the medial part. These are both clearly separate from intermuscular line 3 that runs adjacent to the medial scar. This arrangement indicates that in *M. didinus* the puboischiofemoralis comprised well-separated lateralis and medialis parts; in this respect, *M. didinus* is unusual among palaeognaths, where the two parts of the puboischiofemoralis are usually closely associated with each other.

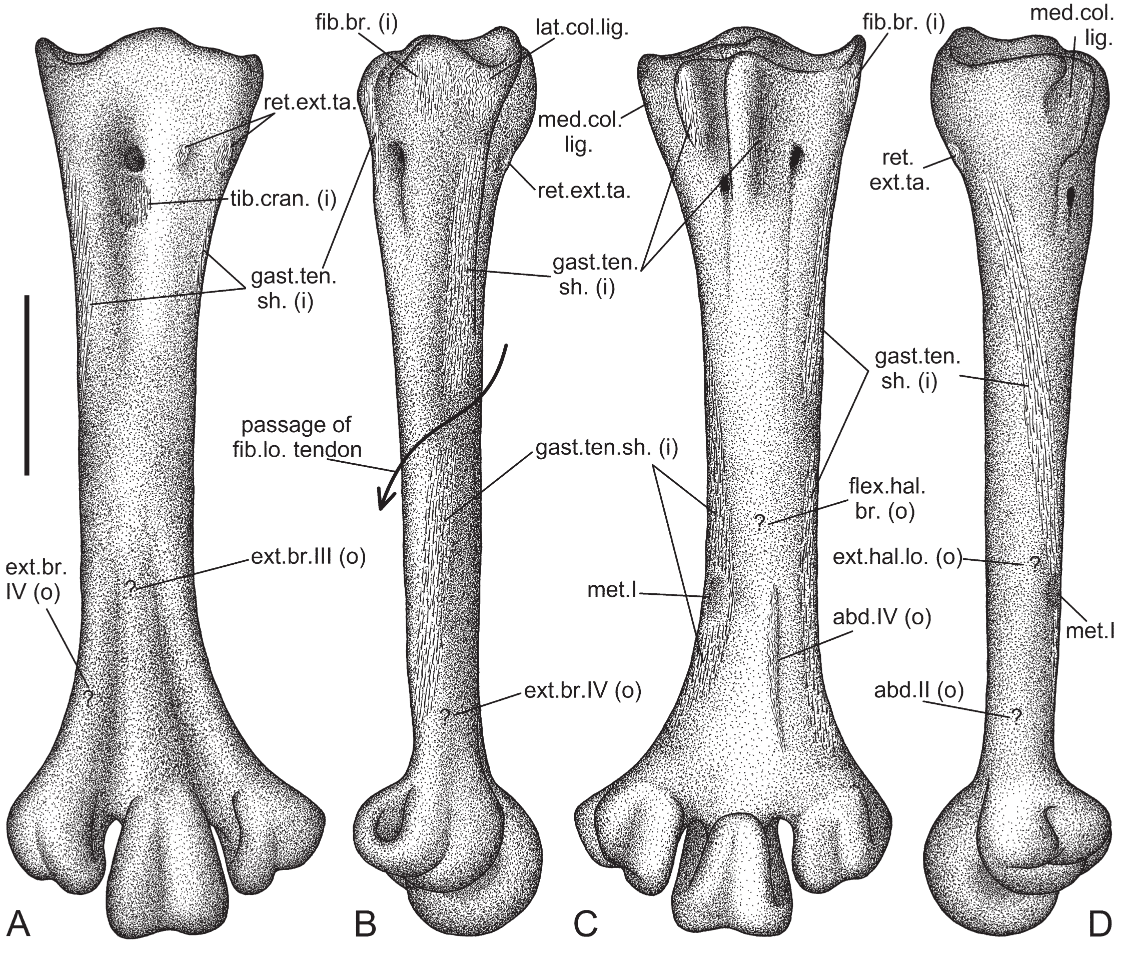

FIG. 9. Osteological evidence of muscle attachment on the tarsometatarsus of *D. robustus*, with corresponding myological interpretations. A, cranial view; B, lateral view; C, caudal view; D, medial view. Scale bar = 100 mm. Abbreviations: *abd.II*, abductor digiti II; *abd.IV*, abductor digiti IV; *ext.br.III*, extensor brevis digiti III; *ext.br.IV*, extensor brevis digiti IV; *ext.hal.lo.*, extensor hallucis longus; *fib.br.*, fibularis brevis; *fib.lo.*, fibularis longus; *flex.hal.br.*, flexor hallucis brevis; *gast.ten.sh.*, tendinous sheath of gastrocnemii; *(i)*, muscle insertion; *lat.col.lig.*, lateral collateral ligament; *med.col.lig.*, medial collateral ligament; *met.I*, attachment scar of metatarsal I; *(o)*, muscle origin; *ret.ext.ta.*, retinaculum extensorium tarsometatarsi; *tib.cran.*, tibialis cranialis.

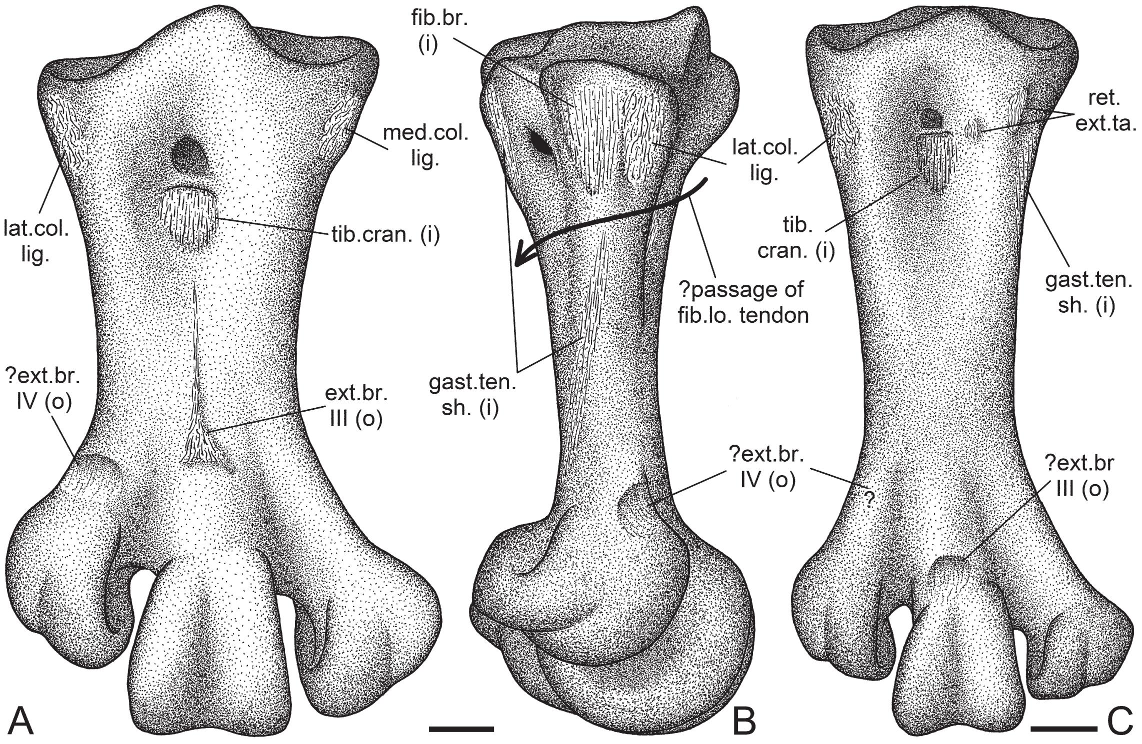

FIG. 10. Osteological evidence of muscle attachment on the tarsometatarsi of non-*Dinornis* moa, with corresponding myological interpretations. A, *P. elephantopus*, cranial view; B, *P. elephantopus*, lateral view; C, *E. crassus*, cranial view. Scale bars = 20 mm. Abbreviations: *ext.br.III*, extensor brevis digiti III; *ext.br.IV*, extensor brevis digiti IV; *fib.br.*, fibularis brevis; *fib.lo.*, fibularis longus; *gast.ten.sh.*, tendinous sheath of gastrocnemii; *(i)*, muscle insertion; *lat.col.lig.*, lateral collateral ligament; *med.col.lig.*, medial collateral ligament; *(o)*, muscle origin; *ret.ext.ta.*, retinaculum extensorium tarsometatarsi; *tib.cran.*, tibialis cranialis.

Remarks. Reconstruction of this muscle in *D. robustus*, *P. elephantopus* and *E. crassus* is well supported by osteology and comparative anatomy (level I inferences for both origin and insertion). That the medial caudal tuberosity of moa is for the insertion of the puboischiofemorales was also reached independently by Kooyman (1991) in his study. Zinoviev (2013) did not mention either the medial or lateral caudal tuberosities, and his reconstructions for both *D. robustus* and *E. crassus* show that the area where both tuberosities are situated was occupied only by the insertion of the flexor cruris lateralis pars accessoria. Additionally, the puboischiofemorales would have inserted on the ridge on the caudomedial aspect of the shaft (which has been identified as intermuscular line 3 here). This reconstruction is rejected on the grounds that all longitudinal ridges on the femur of all moa can be homologized with the femorotibialis intermuscular lines of extant palaeognaths, and hence they reflect the origins of the femorotibialis, not the insertions of other muscles. Furthermore, the presence of two distinct tuberosities argues strongly against a single muscle insertion on this area of the femur.

Gastrocnemius
(Figs 4–10)

General comments. The gastrocnemius is ubiquitously the largest muscle of the crus in extant palaeognaths, comprising three heads, lateralis (gast.lat.), intermedia (gast.int.) and medialis (gast.med.); in *Dromaius* and *Rhea*, the intermedia is further divided into partes medialis and caudalis (Patak & Baldwin 1998; Picasso 2010). The gastrocnemius lateralis takes origin from the lateral aspect of the lateral condyle of the femur, in common with (or immediately adjacent to) the distal attachment of the ansa iliofibularis. In some extant palaeognaths, the gastrocnemius lateralis also takes origin from the lateral aspect of the patellar tendon of the knee (*Dromaius*, *Struthio*) or from the cranial or lateral aspects of the fibular head (*Dromaius*, *Rhea*). The gastrocnemius intermedia originates from the distocaudal shaft of the femur, either from (via an aponeurosis) or just proximal to the popliteal fossa. The medial head of the gastrocnemius always originates from the medial aspect of the cranial cnemial crest of the tibiotarsus in extant palaeognaths, although this origin can also extend onto the patellar tendon and the proximal shaft of the tibiotarsus. In some tinamou genera, such as *Tinamus* and *Crypturellus*, the origin of this head is very extensive, including the entire cranial (and even craniolateral) aspect of the patellar tendon.

The three heads of the gastrocnemius give off tendons which unite proximal to the ankle; the common tendon goes around the caudal aspect of the ankle (being the most superficial one that does so in extant palaeognaths) and inserts on the caudal surface of the tarsometatarsus. It usually inserts on just the proximal part of the bone (including in some cases the hypotarsal ridge or ridges), although in tinamous this insertion extends for most of the bone's length. In all cases, the tendon forms a broad sheath (the tendo calcaneus, gast.ten.sh.) which covers the tendons of the digital flexors. In doing so, it inherently attaches to the tarsometatarsus only along its lateral and medial edges.

Observations. The ectocondylar fossa of the femur of moa is the appropriate site for the distal insertion of the ansa iliofibularis, and its exceptional size and degree of scarring in moa indicates that the gastrocnemius lateralis originated from here as well. In some specimens, the fibres or striations are so well developed that they come straight out of the bone surface, directed roughly caudally. A pronounced tuberosity is present on the craniolateral corner of the head of the fibula of *D. robustus*, *P. elephantopus* and *E. crassus*, which can be plausibly interpreted as a second origin of the gastrocnemius lateralis. The tuberosity bears many fine striations and tubercles (<1 mm diameter), which are directed distally.

On the distocaudal femur of moa is a pronounced tuberosity (medial caudal tuberosity), but this is interpreted as the attachment of the puboischiofemoralis (see above), rather than one of the heads of the gastrocnemius. Evidence supporting this interpretation is seen in the fine striations on the tuberosity, which probably reflect Sharpey's fibres (Carrano & Hutchinson 2002), and which are directed proximally. This would be expected if the puboischiofemoralis inserted here, whereas if the gastrocnemius intermedia inserted here, the striations would be expected to point distally. Given the lack of other visible scars in this region of the femur, the gastrocnemius intermedia probably originated from the popliteal fossa (or some part thereof), the surface of which is very heavily scarred in all moa, with pockets, striations and tubercles.

Reconstructing the origin of the gastrocnemius medialis in *D. robustus, P. elephantopus* and *E. crassus* as on the medial surface of the cranial cnemial crest is supported by osteological evidence, as much of this part of the tibiotarsus is covered with fine, longitudinally oriented striations. These scars almost merge onto the distinct and more rugose (and unstriated) scar of insertion of the flexor cruris lateralis, suggesting a close association between the two muscles (see above). In *P. elephantopus* and *E. crassus*, there is often a curved line of scarring located about two-fifths of the way down the shaft of the tibiotarsus, where the scars consist of fine striations oriented longitudinally, transverse to the line (Fig. 7); this is interpreted as an intermuscular line delimiting the distal extent of the origin of the gastrocnemius medialis. Furthermore, in *E. crassus* the insertion of the flexor cruris lateralis encroaches upon the procnemial ridge, such that near its origin the gastrocnemius medials would have been divided nearly into two.

There is usually a small scar of pronounced surface rugosity located proximomedial to the proximal end of the medial condyle of the femur on its caudomedial aspect (Fig.4D); it is absent in *M. didinus*, although this may be related to the relatively small size of the femora examined. Its appearance is somewhat variable with regards to size, degree of development and exact position. What soft tissue attached here is ambiguous. In *Dromaius* and *Rhea*, there exists a small, fourth head to the gastrocnemius which takes origin from this general area of the femur (Patak & Baldwin 1998; Picasso 2010). Additionally in *Dromaius*, the flexor perforatus digiti III also takes origin from the same general area, but more from the medial aspect of the medial condyle, not proximal to it (Patak & Baldwin 1998). Hence, the attachment responsible for the scar could plausibly be that of a fourth head of the gastrocnemius or the flexor perforatus digiti III; both hypotheses are equally speculative.

Concerning the insertion of the gastrocnemius, direct evidence of the nature and extent of the insertion in *D. robustus* is given by way of a remarkable partial mummified foot, described by Hutton & Coughtrey (1875a). The tendinous sheath of the muscle in this specimen had an insertion most similar to that seen in tinamous, where it extended for most of the length of the caudal aspect of the tarsometatarsus. This produces two tracts of striated texture on the bone, which start proximally on the lateral and medial aspects and progress caudolaterally and caudomedially going towards the distal end (level I inference). In *D. robustus* the lateral tract is interrupted by smooth bone about midway down the shaft, marking the point where the tendon of the fibularis longus would have likely passed (Fig. 9B; see also below). A similar pattern of scarring is also present on the tarsometatarsus of *P. elephantopus* and *E. crassus*, although there is no break in the lateral tract, suggesting that the passage of the fibularis longus tendon was very proximally situated, possibly passing between the gastrocnemius tendinous sheath and the lateral collateral ligament of the ankle (Fig. 10B). There is also evidence for insertion of the gastrocnemius on some part of the hypotarsal ridges in *D. robustus*, *P. elephantopus* and *E. crassus*, in the form of similar striations.

Remarks. Reconstruction of the origin of each head of the gastrocnemius is supported by both osteology and comparative anatomy (level I inferences). Inferring the presence of a second head to the gastrocnemius lateralis, originating from the cranial aspect of the fibular head, is less supported (level II inference). Reconstructing the insertion of the common tendinous sheath on the tarsometatarsus is also supported (level I inference). Zinoviev (2013) did not mention the presence of any tuberosity or scarring on the cranial aspect of the fibular head in the material he studied, and consequently no fibular origin of the gastrocnemius lateralis was reconstructed. Likewise, no mention was made of the small rugosity located proximomedial to the proximal end of the medial condyle of the femur, although this feature is variable in its degree of development.

Popliteus

(Figs 6, 8; pop.)

General comments. The popliteus is present in all extant palaeognaths (except *Apteryx*: McGowan 1979) as a small muscle, running from the proximocaudal tibiotarsus, lateral to the origin of the plantaris, to the proximal fibula (either the head or just distal to it).

Observations. In all large extant palaeognaths the origin of this muscle is associated with obliquely oriented, subparallel ridges on the proximocaudal tibiotarsus, which are often strongly developed, and are directed towards the in-life position of the head of the fibula. A similar condition is observed on the proximocaudal tibiotarsus of moa, and these are therefore interpreted as marking the origin of this muscle. The insertion of this muscle on the proximal caudal or medial fibula is not readily identifiable from scarring on the bones. There are usually one or more small tubercles on the proximocaudal fibula where the shaft starts to expand into the head; in small specimens they can be reduced to a small area of relatively faint scarring, in the form of a 'mottled' texture. This may mark the insertion of the popliteus, as suggested by Zinovev (2013). However, the fine striations on the tubercles are directed distally (rather than medially), which suggests that the tubercles were more likely for the attachment of one or more digital flexors (see below).

Remarks. Reconstruction of this muscle is well supported (level I inference for origin, level I′ inference for insertion).

Plantaris
(Fig. 6; pla.)

General comments. The plantaris occurs in all extant palaeognaths. Its origin is largely fleshy, and is somewhat variable in size and position. It originates from the caudal or caudomedial aspect of the proximal tibiotarsus, near the insertions of the flexores cruris lateralis et medialis and the medial collateral ligament of the knee. The muscle usually inserts, via a long tendon, on the proximal tibial cartilage surrounding the ankle joint, but in some species its tendon also merges with that of the gastrocnemii.

Observations. On the proximocaudal tibiotarsus of *D. robustus*, *P. elephantopus* and *E. crassus* is a faintly depressed area, roughly oval-shaped (sometimes elongate) and with fine longitudinal striations; in *P. elephantopus* these striations may also be accompanied by a 'mottled' texture. This depression is interpreted here as marking the origin of the plantaris in moa. It is distinct from the strong ridges of the popliteus located immediately lateral to it, the two regions sometimes separated by a raised 'wall' of bone. In *P. elephantopus* the medial edge of the depression is often bounded by a pronounced ridge with longitudinal striations; a similar ridge is less frequently present on the lateral edge of the depression. The plantaris of moa may have originated from the medial collateral ligament of the knee, as occurs in *Apteryx* (where it originates from both the ligament and the caudal tibiotarsus), but this is not supported by osteological evidence. Currently it is not possible to recognise the presumably soft-tissue insertion of the plantaris in moa, although examination of mummified specimens may yield otherwise.

Remarks. Whilst osteological evidence on the proximocaudal tibiotarsus supports the reconstruction of a plantaris in *D. robustus*, *P. elephantopus* and *E. crassus* (level I inference), the nature of its distal insertion remains uncertain (level I′ inference). Kooyman (1991) suggested that the plantaris of moa originated from the proximocaudal tibiotarsus on an area with strong subparallel ridges oriented obliquely to the bone's long axis. His interpretation was based on *Apteryx*, however, in which the popliteus is absent; as noted above, in other extant palaeognaths, it is the popliteus which takes origin from these coarse, linear rugosities.

Tibialis cranialis
(Figs 4–7, 9, 10; tib.cran.)

General comments. In all extant palaeognaths this muscle has two heads, the caput femorale (tib.cran.f.), which originates from a small fovea on the distal end of the lateral condyle of the femur, and the caput tibiale (tib.cran.t.), which usually originates from much of the broad sulcus between the cranial and lateral cnemial crests of the tibiotarsus. In some extant palaeognaths the caput tibiale may also extend its origin onto the lateral aspect of the patellar tendon (*Apteryx*: McGowan 1979), or even the fibular head (*Rhea*: Picasso 2010). The manner of insertion of this muscle is highly conserved among extant palaeognaths: the two heads fuse and the tendon of insertion passes under a retinaculum on the distal tibiotarsus (retinaculum extensorium tibiotarsi) before inserting on the proximocranial tarsometatarsus. Its insertion leaves a characteristically distinct region of strong scarring.

Observations. Both of the osteological correlates for the origins of the tibialis cranialis are present in moa, and are comparable to that seen in extant palaeognaths, although in *E. crassus* the attachment of the caput femorale on the femur is sometimes a low, broad tubercle rather than a fovea. The insertion of this muscle in moa is in the same position of the tarsometatarsus as in extant palaeognaths, and is indicated by a subcircular region of very coarse texture; it is often well excavated to the point that the area is recessed into the surrounding bone. The scars of attachment of the retinaculum extensorium tibiotarsi to the distal cranial tibiotarsus are also present and are clearly identifiable as such, corresponding to those present on the surface of the tibiotarsus of extant palaeognaths.

Remarks. The reconstruction of this muscle in moa is supported by both osteological and comparative data (level I inferences both proximally and distally).

Extensor digitorum longus

(Figs 6, 7, 9–12; ext.dig.lo.)

General comments. This muscle is present in all palaeognaths, typically originating from the distal lateral and cranial cnemial crests of the tibiotarsus, as well as the sulcus in between. Lying deep to the tibialis cranialis caput tibiale, its origin is just distal to that of the former muscle. The muscle gives off a tendon distally which passes under the retinaculum extensorium tibiotarsi and the pons supratendinous (which may or may not be ossified: Worthy & Scofield 2012), before crossing the ankle joint. It then passes under another retinaculum, the retinaculum extensorium tarsometatarsi, after which it trifurcates, sending a branch each to digits II, III and IV (except in *Struthio*, where digit II is absent: Gangl *et al.* 2004). The manner of insertion of each branch onto the phalanges of its respective toe is variable among extant palaeognaths; a commonality, however, is that they insert on the extensor processes of the unguals of each digit.

Observations. The distal extent of the origin of the extensor digitorum longus, down the cranial surface of the tibiotarsus, is variable among extant palaeognaths and cannot be determined precisely for *D. robustus*, *P. elephantopus* and *E. crassus*. However, it probably continued down along much of the shaft in these species, given the extent of the procnemial ridge, to which the muscle would have likely had an aponeurotic attachment (the procnemial ridge taking on the form of an intermuscular line distally). The presence of the retinaculum extensorium tarsometatarsi on the tarsometatarsus of *D. robustus* and *E. crassus* is indicated by two small tuberosities located proximomedially to the scar of insertion of the tibialis cranialis. In large *D. robustus* individuals (e.g., CM Av8422, 8473, 8488), these tubercles are sometimes drawn out into proximodistally elongate patches of scarring. No such tuberosities or scars were observed on the cranial tarsometatarsus in any *P. elephantopus* material examined. The extensor processes of the unguals in all moa species are well developed, particularly the larger species, and they bear fine, proximodistally oriented striations, ridges or tubercles, which presumably indicate the insertion of the extensor digitorum longus.

Remarks. Reconstruction of the extensor digitorum longus in moa is well supported (level I′ inference proximally, level I at ankle and toes), the only uncertainty lying in the extent of the muscle's origin, and whether the muscle inserted on non-ungual phalanges.

Fibularis longus

(Figs 6, 7, 9, 10; fib.lo.)

General comments. This muscle, the most superficial of the cranial crus, typically originates in extant palaeognaths from one or both cnemial crests of the tibiotarsus and also the craniolateral aspect of the patellar tendon; in tinamous it also takes origin from a considerable area on the lateral surface of the fibula (Hudson *et al.* 1972). The muscle sends a tendon distally which typically bifurcates, inserting on the tibial cartilage of the ankle joint, and also on the tendon of the flexor perforates digiti III at the level of the proximal tarsometatarsus, on its caudal aspect.

Observations. The fibularis longus is probably responsible for coarse ridges and tubercles on the apex of the lateral cnemial crest in *D. robustus*, *P. elephantopus* and *E. crassus*, which are often swollen into a pronounced, craniodistally directed tuberosity. There is also occasionally a very faint fluted texture adjacent to the tuberosity on the lateral cnemial crest, on the caudolateral aspect of the ectocnemial ridge (Fig. 6C), which may have been for attachment of the fibularis longus. Where else the muscle may have originated from cannot be

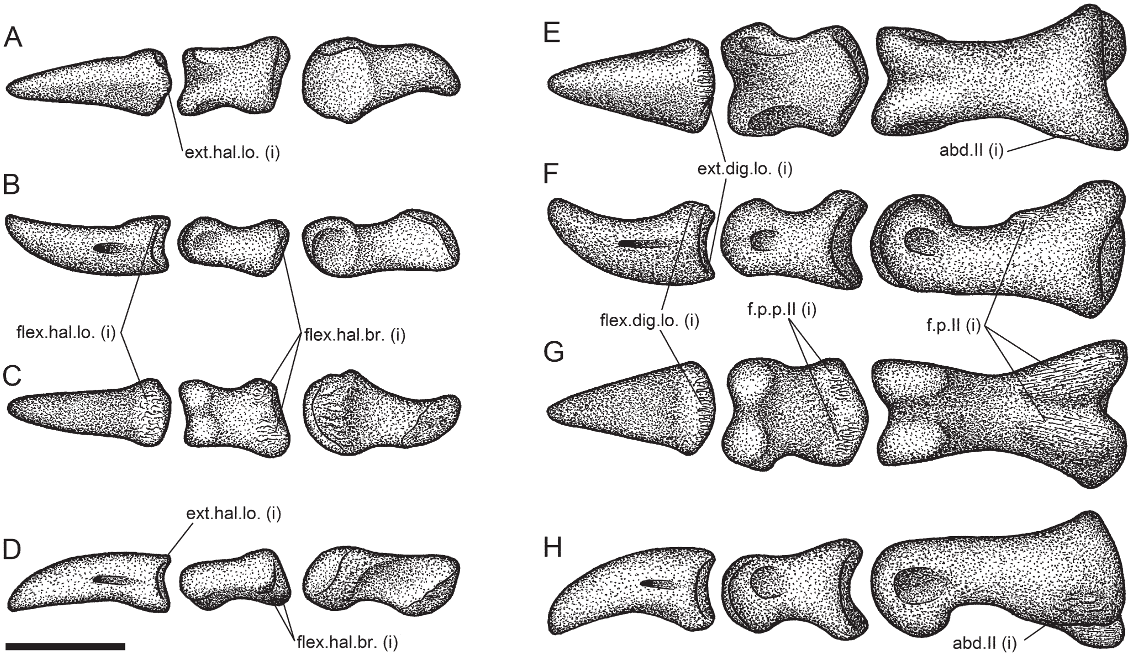

FIG. 11. Osteological evidence of muscle attachment on digits I and II of *D. robustus*, with corresponding myological interpretations. A–D, digit I; E–H, digit II; A and E are dorsal views, B and F are lateral views, C and G are plantar views, D and H are medial views. Scale bar = 50 mm. Abbreviations: *abd.II*, abductor digiti II; *ext.dig.lo.*, extensor digitorum longus; *ext.hal.lo.*, extensor hallucis longus; *flex.dig.lo.*, flexor digitorum longus; *flex.hal.br.*, flexor hallucis brevis; *flex.hal.lo.*, flexor hallucis longus; *f.p.II*, flexor perforatus digiti II; *f.p.p.II*, flexor perforans et perforatus digiti II; *(i)*, muscle insertion.

determined with certainty, since other muscles attach to the cnemial crests too (iliotibialis, femorotibialis), and no attachment to the fibula is evident, either. Although there is no direct osteological evidence of the muscle's insertion in *D. robustus, P. elephantopus* and *E. crassus*, the typical pattern may be reconstructed for these species, since it is quite consistent among extant taxa. In *D. robustus*, the lateral scar of the gastrocnemius insertion on the tarsometatarsus is interrupted by a span of smooth bone about halfway along the bone's length. This corresponds to the point, noted by Hutton & Coughtrey (1875a), where the tendon of the fibularis longus passes from the cranial side to the caudal side of the tarsometatarsus, underneath the tendinous sheath of the gastrocnemius, to insert on the tendon of the flexor perforatus digiti III. As discussed above, in *P. elephantopus* and E. crassus the likely passage of the tendon around to the caudal tarsometatarsus was very proximally situated, so much so that the tendon may have passed between the tendinous sheath and the lateral collateral ligament of the ankle.

Remarks. Reconstructing this muscle as having the typical palaeognath condition is well supported (level I inference proximally, level I′ inference distally). The postulated origin of this muscle in moa, from the apex of the lateral cnemial crest, was also suggested by Kooyman (1991), although he also suggested that it may have also served as the origin for the flexores perforantes et perforatus digitorum II et III (see below for a treatment of these muscles).

Zinoviev (2013) suggested that the origin of the fibularis longus in *D. robustus* and *E. crassus* also included the cranial surface of the fibula and the proximolateral surface of the tibiotarsus, immediately cranial to the fibular crest and distal to the lateral cnemial crest. The only osteological evidence Zinoviev (2013) cited in support of this interpretation was an "uneven surface on the cranial surface of the fibula" (p. 269). Aside from the tubercle on the fibular head (which is here proposed as the origin of a second head of the gastrocnemius lateralis), no evidence of muscular attachment was observed in the material studied here. Additionally, this topology is not present in any extant palaeognath; only in tinamous does the muscle gain origin from the fibula (Hudson *et al.* 1972), and here it is from the lateral, not cranial, surface of the bone. Zinoviev's interpretation of an extended origin for the fibularis longus is hence not well supported (a level II' inference).

Fibularis brevis
(Figs 6, 9, 10; fib.br.)

General comments. This muscle only occurs in some extant palaeognaths, and in these species it varies in both degree of development and area of origination. In *Struthio* it is reduced to a tendinous vestige that originates from a small area on the lateral tibiotarsus just distal to the end of the fibular spine (Schaller *et al.* 2009), whereas in *Apteryx* it is very well developed, originating from much of the lateral surface of the fibular shaft (distal to the insertion of the iliofibularis) and the proximal caudolateral surface of the tibiotarsus (McGowan 1979). The insertion of the fibularis brevis in extant palaeognaths, where present, is typically on the proximal caudolateral surface of the tarsometatarsus, except in *Apteryx*, where the tendon of insertion fuses with that of the flexor digitorum longus (McGowan 1979).

Observations. On the distal lateral tibiotarsus of *D. robustus*, *P. elephantopus* and *E. crassus* is a well-defined linear area of fibrous scarring, proximal to the scar of attachment of the lateral collateral ligament of the ankle. In large *D. robustus* specimens this scarring can become elevated into a course ridge. This scarring does not reflect the attachment of the fibula, and is not a proximal extension of the origin of the collateral ligament, because the scarring

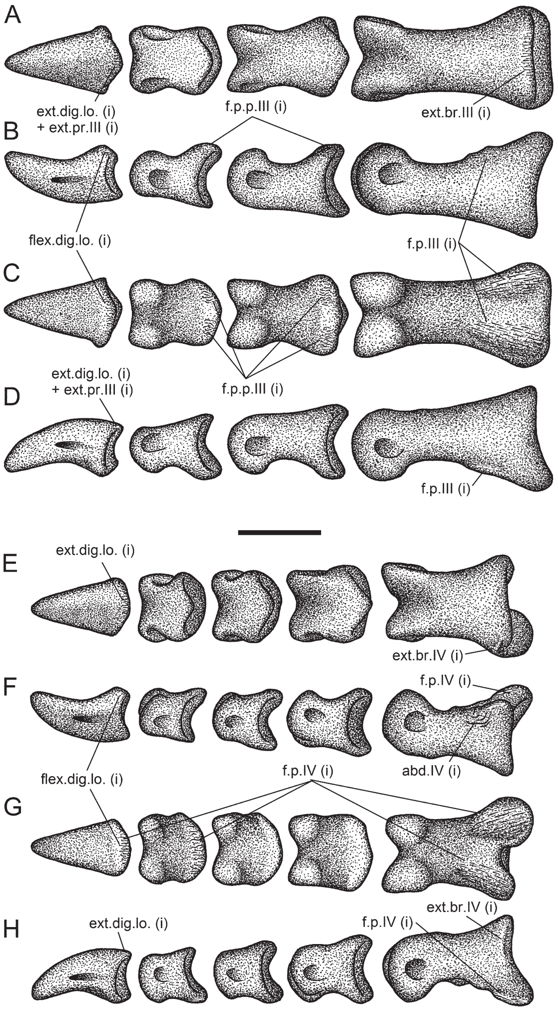

FIG. 12. Osteological evidence of muscle attachment on digits III and IV of *D. robustus*, with corresponding myological interpretations. A–D, digit III; E–H, digit IV; A and E are dorsal views, B and F are lateral views, C and G are plantar views, D and H are medial views. Scale bar = 50 mm. Abbreviations: *abd.IV*, abductor digiti IV; *ext.br.III*, extensor brevis digiti III; *ext.br.IV*, extensor brevis digiti IV; *ext.dig.lo.*, extensor digitorum longus; *ext.pr.III*, extensor proprius digiti III; *flex.dig.lo.*, flexor digitorum longus; *f.p.III*, flexor perforatus digiti III; *f.p.IV*, flexor perforatus digiti IV; *f.p.p.III*, flexor perforans et perforatus digiti III; *(i)*, muscle insertion.

is separated from the fibular crest scarring and the collateral ligament scar by smooth bone. It is therefore inferred that this scar marks the origin of the fibularis brevis. In several specimens, such as CM Av8381 (*P. elephantopus*), the scarring of the fibular crest is unbroken and continues cranial to the scar for the fibularis brevis, indicating that the muscle originated caudal to the fibular spine. In *D. robustus*, *P. elephantopus* and *E. crassus* the proximolateral tarsometatarsus bears two distinct – although often not fully separated – areas of coarse scarring, which are interpreted as the insertions of the lateral collateral ligament (the cranial one) and the fibularis brevis (the caudal one). The cranial scar is a diffuse area of rough, somewhat mottled scarring, and the caudal one is occasionally recessed in *D. robustus* and *P. elephantopus* to form a rough fovea.

Remarks. Reconstructing the origin and insertion of the fibularis brevis is a level II inference, receiving support from osteology and comparative anatomy. Zinoviev (2013) suggested that this muscle was absent in moa, for he did not find evidence of a retinaculum on the distal lateral tibiotarsus that would have held the tendon of the muscle in place, or evidence of its insertion on the tarsometatarsus. The supposedly 'required' retinaculum may well have been present, but simply could have been part of the large lateral collateral ligament, leaving no trace of its own on the bones. Furthermore, plausible osteological correlates of both the origin and insertion of the fibularis brevis have been identified in the material examined here.

Flexores perforantes et perforatus digitorum II et III, flexores perforatus digitorum II, III et IV

(Figs 4, 5, 8, 11, 12)

General comments. These digital flexor muscles are invariably present in all extant palaeognaths (except *Struthio*, where those associated with digit II are absent: Gangl *et al.* 2004). They exhibit extreme interspecific variability in their origins, which include the origin of the gastrocnemius lateralis on the distal femur (*Dromaius*), proximal fibula (*Dromaius*, *Rhea*, tinamous), medial aspect of the medial condyle of the femur (*Dromaius*), cranial cnemial crest (*Struthio*, tinamous), popliteal fossa (*Struthio*, *Rhea*, *Apteryx*, tinamous; usually via an aponeurosis from which other digital flexors can also originate), ansa iliofibularis (*Casuarius*, *Struthio*, *Rhea*), origin of the gastrocnemius intermedia (tinamous) and the patellar tendon or its surrounding aponeuroses (casuariids). Furthermore, in some taxa particular muscles have multiple heads of origin rather than just one, and some muscles may take origin from the heads of others (e.g., casuariids, *Struthio*).

All of these digital flexors in extant palaeognaths give off tendons which run distally to pass around the caudal aspect of the ankle, before typically running through the sulcus associated with the hypotarsal ridge (or ridges) on the proximal caudal tarsometatarsus. Some of the tendons pass through the tibial cartilage on their way and some pass superficial to it (deep to the tendo calcaneus), but there is no consistent pattern in the extant species as to what a given muscle does. There is, however, some consistency in the manner of insertion of these muscles' tendons onto the phalanges:

- The flexor perforans et perforatus digiti II (f.p.p.II) inserts on the proximoplantar aspect of II-2; in tinamous this insertion extends proximally to include the distoplantar aspect of II-1 (Hudson *et al.* 1972).
- The flexor perforans et perforatus digiti III (f.p.p.III) inserts on III-2, typically on the proximoplantar aspect, but in *Struthio* and the tinamous it inserts on the distoplantar aspect, in which the insertion extends to the proximoplantar aspect of III-3 (Hudson *et al.* 1972; Gangl *et al.* 2004).
- The flexor perforatus digiti II (f.p.II), when present, invariably inserts on the proximoplantar aspect of II-1 in extant palaeognaths.
- The flexor perforatus digiti III (f.p.III) either inserts on the proximoplantar aspect of III-1 (casuariids, *Rhea* and *Apteryx*) or alternatively on the distoplantar aspect of III-1, in which it extends to the proximoplantar aspect of III-2 (*Struthio* and tinamous).

- The flexor perforatus digiti IV (f.p.IV) always inserts on IV-1 in extant palaeognaths, although it may also have further insertions on IV-2 (*Dromaius*, tinamous), IV-3 (tinamous), IV-4 (tinamous), and the first and second interphalangeal joints (*Struthio*).

Observations. The great variability in the nature of these muscles' origins in extant palaeognaths renders it extremely difficult to reconstruct the origins of any of them in moa with great clarity. Their ubiquitous presence among extant species, however, does imply that they were all present in moa. The popliteal fossa of the moa femur, as noted above, is heavily scarred and probably served as the origin (likely via an aponeurosis) for at least some of the digital flexors. There is usually a small scar located proximomedial to the proximal end of the medial condyle of the femur, which may be for the flexor perforatus digiti III, or alternatively for a fourth head to the gastrocnemius (see above). Additionally, on the femur, there also exists a distinct region immediately distal to the ectocondylar fossa between the proximal extents of the lateral and fibular condyles, which may have also served as the origin for one or more of these muscles, although it often does not show any surface scarring *per se*. Alternatively, it may have functioned as a receptacle for the fibular head during strong flexure of the knee. On the caudal aspect of the proximal fibula of *D. robustus*, *P. elephantopus* and *E. crassus*, below the expansion of the head, there are usually several small tubercles and ridges of varying shape and size. In specimens where the tuberosities are very well developed, distinct striations or fibres are evident; these are directed distally. In *P. elephantopus* (and occasionally in *E. crassus*) most of these scars sometimes unite to form a large C-shaped ridge of striated bone; this feature was observed in every *P. elephantopus* specimen examined from Cheviot Swamp, but it is less prevalent in other sampled populations. This may indicate the origin of one or more of the digital flexors, or the flexor digitorum longus, or both.

Two well-developed hypotarsal ridges are present on the proximal caudal tarsometatarsus in all moa species, such that at least some of the tendons of the digital flexors probably ran through the sulcus formed between them, on their way to the digits. As regards the insertions of the individual muscles, the following interpretations are presented:

- In *D. robustus*, *P. elephantopus* and *E. crassus* there are two subtle tubercles on the proximoplantar aspect of II-2, which may be confluent with each other in some instances. These probably mark the insertion of the flexor perforans et perforatus digiti II.
- In *D. robustus* there are faint raised rugositites on both the proximoplantar and distoplantar aspects of III-2 (the distoplantar ones are less frequently present), indicating the insertion of the flexor perforans et perforatus digiti III. The proximoplantar aspect of III-3 also bears faint rugosities, suggesting that the muscle had a 'dual insertion' on both phalanges, as in *Struthio* and the tinamous. A similar condition exists in *P. elephantopus* and *E. crassus*, although no scarring on the distoplantar aspect of III-2 was observed.
- Phalanx II-1 of *D. robustus*, *P. elephantopus* and *E. crassus* possesses two very large and well-developed rugosities on its proximoplantar aspect, signifying the attachment of the flexor perforatus digiti II.
- The proximoplantar aspect of III-1 in *D. robustus*, *P. elephantopus* and *E. crassus* possesses two large, heavily scarred rugosities, which likely mark the insertion of the flexor perforatus digiti III. Similar scars are present on the proximoplantar aspects of III-2 and III-3; these could have been for both the flexor perforans et perforatus and the flexor perforatus, or just the flexor perforans et perforatus (see above).
- In *D. robustus* there are two strong scars on the proximoplantar aspect of IV-1, and a more diffuse region of fainter scarring on the proximoplantar aspect of IV-4, as well as the flexor tubercle of the ungual. These probably all mark the attachment of the

tendon of the flexor perforatus digiti IV. In one specimen (CM Av8422), there was also distinct scarring on the proximoplantar aspect of IV-2, suggesting a further insertion to this phalanx. In *P. elephantopus* and *E. crassus*, scarring of a similar character to that observed in *D. robustus* is present on the proximoplantar aspects of phalanges IV-1 to IV-4 (IV-4 being the ungual in *E. crassus*, which only has four phalanges in digit IV), although that on IV-3 is typically less substantial.

Remarks. Whilst the exact origins of each muscle in *D. robustus*, *P. elephantopus* and *E. crassus* are uncertain, reconstructing them is nevertheless well supported by comparative data (level I′ inference). The presence of clear scars on the phalanges also supports this; distally, each muscle can be reconstructed with considerable confidence (level I inferences). The observations of mummified foot specimens of *D. robustus* and *P. elephantopus*, made by Hutton & Coughtrey (1875a) and Buller (1888), respectively, further support the inferences made here. One small difference, however, is that Hutton & Coughtrey (1875a) did not find an attachment of the flexor perforans et perforatus digiti III to III-2 in their specimen. This may reflect individual anatomical variation with respect to this muscle. In the phalanges of smaller *E. crassus* individuals (e.g., CM Av8344), some of the scars on the phalanges are less well developed, and in some instances are even absent.

Flexor digitorum longus

(Figs 6, 11, 12; flex.dig.lo.)

General comments. The deepest of the caudal muscles of the crus, the flexor digitorum longus is present in all extant palaeognaths. It originates from the caudal aspects of the tibiotarsus and fibula, except in *Apteryx*, where it comes from the popliteal fossa (McGowan 1979). Gadow (1880) described a second small head to the muscle in *Rhea*, as originating from the distocaudal femur. The extent of origin of the muscle from the tibiotarsus is variable, being restricted to the proximal end in *Rhea* (Picasso 2010), but extending across two-thirds of the caudal surface of the bone in *Struthio* (Gangl *et al.* 2004). In all extant palaeognaths, the flexor digitorum longus gives off a tendon which passes around the caudal margin of the ankle, through the tibial cartilage, before trifurcating on the caudal aspect of the tarsometatarsus, sending a branch each to digits II, III and IV (except *Struthio*, where digit II is absent; Gangl *et al.* 2004). The tendons typically insert on the flexor tubercles of the unguals of each digit, although in tinamous they also give off slips to various other phalanges as well (Hudson *et al.* 1972).

Observations. On the caudomedial aspect of the tibiotarsus in *D. robustus* and *P. elephantopus*, and rarely in *E. crassus*, about two-thirds to three-quarters of the way towards the distal end, there is sometimes a faint, longitudinal ridge. This ridge may be extensive proximally, and is interpreted as an intermuscular line demarcating the medial extent of the origin of the flexor digitorum longus; it thus indicates that the muscle had an extensive origin. An origin from the caudal fibula in moa seems probable, and in *D. robustus*, *P. elephantopus* and *E. crassus*, there is often some form of linear scarring (striations, or more rarely, ridges and elongate, distally directed tubercles) running down the caudal or caudolateral surface of the shaft. This scarring starts at about the level of the iliofibularis insertion scar and progresses distally, and probably marks an additional attachment of the flexor digitorum longus. Although the fibularis brevis may also take origin from this region of the fibula in *Apteryx* (McGowan 1979) and most tinamous (Hudson *et al.* 1972), there is, as noted above, a distinct region of scarring distal to the fibular crest on the tibiotarsus which seems the more probable origin of that muscle in moa. The flexor digitorum longus may have also taken origin from the small tubercles and ridges on the caudal aspect of the proximal fibula, but these may have alternatively been for other digital flexor muscles (see above). The unguals of digits II, III and IV of all moa all have strongly scarred flexor tubercles (which tend to be better developed in larger individuals), attesting to the muscle's insertions.

Remarks. Reconstruction of this muscle is well supported (level I inferences both proximally and distally), although the extent of its origin is not entirely certain.

Flexor hallucis longus

(Figs 4, 5, 11; flex.hal.lo.)

General comments. This muscle originates from the distocaudal femur in extant palaeognaths, typically from the popliteal fossa, although in *Dromaius* and *Rhea* it also takes origin, via a second head, from an area proximal to the lateral femoral condyle on the caudal surface of the femur (Patak & Baldwin 1998; Picasso 2010). In extant palaeognaths lacking digit I, the tendon of insertion of this muscle fuses with that of the flexor digitorum longus prior to the latter muscle splitting to the toes, about halfway down the tarsometatarsus. In tinamous that have retained digit I, the tendon of the flexor hallucis longus inserts on the flexor tubercle of the ungual (Hudson *et al.* 1972). *Apteryx* is unusual in that the muscle (termed the 'ligament to hallux' by McGowan 1979) is vestigial and entirely tendinous, originating from the tendon of the flexor digitorum longus and inserting on the ungual.

Observations. No distinct area of scarring is present on the distocaudal femur of *D. robustus*, *P. elephantopus* and *E. crassus* that would be in the appropriate position for this muscle's origin. It seems likely that the flexor hallucis longus originated from the popliteal fossa, probably along with other muscles as noted above. The ungual of digit I in *D. robustus*, *P. elephantopus* and *E. crassus* has a modestly developed flexor tubercle with fine scarring, suggesting the insertion of this muscle here.

Remarks. As only tinamous and *Apteryx* have retained digit I among extant palaeognaths, comparisons between moa and extant outgroups are limited. Consequently, any inference concerning the muscles of digit I in moa can only receive limited support. Reconstructing the origin of the flexor hallucis longus in moa as done here is a level I′ inference, whilst the reconstructed insertion is a level II inference. The muscle may have been vestigial and displayed an *Apteryx*-like condition, but this is a more speculative suggestion (level II′ inference).

Flexor hallucis brevis

(Figs 9, 11; flex.hal.br.)

General comments. In extant palaeognaths, this muscle is only present in tinamous, where it originates from the middle of the caudal surface of the tarsometatarsus and inserts on the base of I-1 (Hudson *et al.* 1972).

Observations. There is no osteological evidence of this muscle's origin in *D. robustus*, *P. elephantopus* or *E. crassus*, distinct from the scarring of the gastrocnemius (but see below). However, the proximoplantar aspect of I-1 presents two faint flexor tubercles, which may be interpreted as the insertion of this muscle.

Remarks. Reconstruction of this muscle in *D. robustus*, *P. elephantopus* and *E. crassus* is tentative (level II inference).

Extensor hallucis longus

(Figs 9, 11; ext.hal.lo.)

General comments. Among extant palaeognaths this muscle is only present in *Apteryx* and those species of tinamou with a hallux (Hudson *et al.* 1972; McGowan 1979). It typically originates from about the medial aspect of the tarsometatarsus, just proximal to the attachment of metatarsal I, and inserts on the dorsolateral aspect of I-1 (*Apteryx*) or the ungual (tinamous).

Observations. No distinct osteological evidence exists as to its origin on the tarsometatarsus in *D. robustus*, *P. elephantopus* or *E. crassus*, but the ungual of the hallux normally possesses an extensor process with fine (< 1 mm diameter) tubercles, supporting its reconstruction in these species. In small individuals the extensor process of the ungual can be poorly developed or even absent. In *D. robustus* there is occasionally a small, elongate, proximodistally trending tubercle on the caudomedial aspect of the proximal tarsometatarsus. This may be for the origin of the extensor hallucis longus in this species, but this would be unusual being so proximally situated.

Remarks. Reconstructing this muscle in *D. robustus*, *P. elephantopus* or *E. crassus* is a level II inference.

Extensor proprius digiti III

(Fig. 12; ext.pr.III)

General comments. This muscle typically originates from some part of the soft tissues of the ankle joint in extant palaeognaths, either the joint capsule or the lateral meniscus, except in *Dromaius*, where it originates from the proximocranial tarsometatarsus, just distal to the insertion of the tibialis cranialis (Patak & Baldwin 1998). In all extant palaeognaths this muscle inserts on the extensor process of III-4 (ungual), along with a branch of the extensor digitorum longus.

Observations. No evidence of the *Dromaius*-type origin from the proximocranial tarsometatarsus was observed, so although its exact origin is uncertain, it is nevertheless reasonable to reconstruct this muscle in *D. robustus*, *P. elephantopus* and *E. crassus*. An extensor process is present on III-4 in moa, suggesting that the extensor proprius digiti III may have inserted here.

Remarks. No unequivocal osteological evidence exists to support the reconstruction of this muscle in moa, yet its wide distribution among extant palaeognaths suggests that it was present (level I′ inference). As regards the insertion, whilst the extensor process of III-4 may have only received the tendon of the extensor digitorum longus, it is more parsimonious to reconstruct the extensor proprius digiti III as inserting here as well (level I inference), than to be inserting elsewhere (level II′ inference).

Extensor brevis digiti III

(Figs 9, 10, 12; ext.br.III).

General comments. The extensor brevis digiti III is present in all extant palaeognaths, but its origin on the cranial aspect of the tarsometatarsus is fleshy and variable in location and extent. It typically inserts on the proximodorsal aspect of III-1.

Observations. No discernable scarring exists on the cranial surface of the tarsometatarsus of *D. robustus*. In contrast, on the cranial surface of the tarsometatarsus of *P. elephantopus*, about two-thirds of the way towards the distal end, is a gently elevated rugosity. This may extend proximally to form a long, proximodistally oriented ridge (as seen in the type specimen illustrated by Owen 1858, pl. 44). This scar was likely for the origin of the extensor brevis digiti III (a level I inference). In many specimens of *E. crassus*, there is a small depression (approximately 10 mm in diameter) on the cranial aspect of the distal tarsometatarsus, just proximal to the trochlea for digit III. It has a rough surface texture, and is usually rimmed by rough bone as well, although in specimens from Kapua the depression is mostly smooth. This depression may mark the origin of the extensor brevis digiti III in this species, or alternatively it may simply be present to facilitate hyperextension of the tarsometatarsophalangeal joint. The middle of the proximodorsal aspect of III-1 in *D. robustus*, *P. elephantopus* and *E. crassus* bears a small patch of fine, subparallel ridges that are oriented proximodistally, suggesting the insertion of the extensor brevis digiti III here.

Remarks. Reconstructing the origin and insertion of this muscle is well-supported in *P. elephantopus* (level I inference), slightly less so for *D. robustus* and *E. crassus* (level I′ inference proximally, level I inference distally). The rugosity and ridge on the cranial surface of the tarsometatarsus of *P. elephantopus* may have alternatively (or additionally) been for the origin of the extensor proprius digiti III, similar to that seen in *Dromaius*, but this is more speculative (a level II inference) than what is reconstructed here.

Extensor brevis digiti IV

(Figs 9, 10, 12; ext.br.IV)

General comments. Present in all extant palaeognaths except *Dromaius* (Patak & Baldwin 1998), this muscle is very much like the extensor brevis digiti III in that it has a fleshy and variable origin on the cranial tarsometatarsus, lateral to the origin of the latter muscle. The extensor brevis digiti IV typically inserts on the medial or dorsomedial aspect of the proximal end of IV-1.

Observations. Significant scarring can be present on the craniolateral aspect of the proximal third of the tarsometatarsus of *D. robustus*, *P. elephantopus* and *E. crassus*, but as it covers one diffuse area, it likely is for the insertions of the gastrocnemius and lateral collateral ligament of the ankle too. In contrast, in about two thirds of *P. elephantopus* specimens examined, and most *M. didinus* specimens, there is a small oval patch of slightly roughened bone, immediately proximal to the trochlea for digit IV. This patch is gently recessed somewhat, and often bears a roughened rim. This may mark the origin of the extensor brevis digiti IV in these two species, or (as with the depression proximal to the middle trochlea in *E. crassus*) it may be present to facilitate tarsometatarsophalangeal hyperextension. The proximal end of IV-1 in *D. robustus*, *P. elephantopus* and *E. crassus* often bears a small, elongate area of marked roughness, suggesting the insertion of the extensor brevis digiti IV in these species.

Remarks. Zinoviev (2013) suggested that the origin of the extensor brevis digiti IV in *D. robustus* occupied much of the lateral half of the cranial aspect of the tarsometatarsus, but no scars have been observed that supports this interpretation. Nevertheless, inferring the presence of this muscle in *D. robustus*, *P. elephantopus* and *E. crassus* is well supported (level I′ inference or higher for origin, level I inference for insertion).

Abductor digiti II

(Figs 9, 11; abd.II)

General comments. Present in all palaeognaths except *Struthio* (where digit II is absent; Gangl *et al.* 2004), this muscle originates from the distomedial aspect of the tarsometatarsus, although in tinamous the origin can encroach onto the craniomedial aspect (Hudson *et al.* 1972). It typically inserts on the proximomedial aspect of II-1.

Observations. The distomedial tarsometatarsus of *D. robustus*, *P. elephantopus* and *E. crassus* is smooth, with no osteological evidence of muscle attachment. However, phalanx II-1 in all three species bears a broad area of rough scarring proximomedially, either as a shallow depression or a low tuberosity; this is presumably for the insertion of the abductor digiti II. The scarring in *E. crassus* is somewhat continuous with that found on the plantar surface.

Remarks. The muscle's reconstruction is supported both proximally (level I′ inference) and distally (level I inference). Of the mummified foot of *D. robustus* discussed above, Hutton & Coughtrey (1875a p. 273) described a small tendon running to the first phalanx of digit II, "ending in the outer side of the base of this bone." They probably used the word 'outer' to mean 'medial' in this instance, for the outer aspect of digit II in life would be the medial aspect of the pes. If this is correct, then Hutton & Coughtrey (1875a) were referring to an abductor digiti II, and since no other tendon running to the base of II-1 was described by these authors (except the flexor perforatus digiti II, noted above), this would imply the absence of the adductor digiti II (see below). On the other hand, if Hutton & Coughtrey (1875a) used the word 'outer' to mean 'lateral', then the tendon they so described would be that of the adductor digiti II, which in turn would imply that the abductor digiti II was absent in their specimen. The first possibility is considered more likely here, since there is a distinct scar for reception of a tendon on the fossil specimens examined.

Abductor digiti IV

(Figs 9, 12; abd.IV)

General comments. This muscle occurs in all extant palaeognaths. It originates from the caudolateral aspect of the tarsometatarsus, although its extent is rather variable between species. It characteristically inserts on the proximolateral aspect of IV-1.

Observations. In *D. robustus*, *P. elephantopus* and *E. crassus* there is a coarse, longitudinally elongate scar or ridge on the distocaudal shaft of the tarsometatarsus, positioned on the lateral half of the bone, which may mark the origin of the abductor digiti IV. The proximolateral aspect of IV-1 in all three species bears a broad area of surface rugosity, suggesting the insertion of the muscle here (level I inference). This scarred area is usually confluent with the more prominent scars on the proximoplantar aspect of the bone, for insertion of the flexor perforatus digiti IV.

Remarks. Reconstructing the abductor digiti IV in the three species is a level I inference for both origin and insertion. In contrast to the reconstruction proposed here, Kooyman (1991) and Zinoviev (2013) suggested that the abductor digiti IV originated from the lateral aspect of the proximal end of the tarsometatarsus, adjacent to the insertion of the lateral collateral ligament of the ankle. This interpretation is not supported by the osteological evidence observed here. Fine striations in the scarring in this region of the bone all point proximally (reflecting the insertion of the collateral ligament and the fibularis brevis; see above); if the abductor digiti IV attached here then a portion of them would be expected to point distally. Kooyman (1991) also suggested that the longitudinal ridge on the distocaudal tarsometatarsus was associated with the lumbricalis (see below), rather than the abductor digiti IV. However, in all extant palaeognaths the lumbricalis originates from the dorsal (deep) surface of the tendon of the flexor digitorum longus; having no direct interaction with the tarsometatarsus itself, the lumbricalis would not be expected to leave any osteological correlates on that bone. The scarring may alternatively indicate the origin of the flexor hallucis brevis, or alternatively marks the origin of both muscles, acting as an intermuscular line. Whilst the situation is unclear, it seems more likely that the scarred area in question is for the abductor digiti IV only, since it is located on the lateral half of the caudal surface of the tarsometatarsus, and is always rougher on its lateral side.

Adductor digiti II

General comments. This muscle is absent in *Struthio* (owing to the loss of digit II: Gangl *et al.* 2004), and is also absent in *Apteryx* (McGowan 1979). In other extant palaeognaths it originates from the distocaudal tarsometatarsus. The insertion of this muscle in digit II is varied, ranging from II-1 in tinamous to II-3 in *Dromaius*; typically, it inserts on the lateral aspect of the phalanx.

Observations. In *D. robustus*, *P. elephantopus* and *E. crassus* the distocaudal tarsometatarsus lacks any osteological evidence of muscle attachment, separate from that interpreted as the scar of the abductor digiti IV. Additionally, no scar of attachment is evident on the lateral aspect of any phalanx examined.

Remarks. It is too speculative to reconstruct this muscle in moa (level II′ inferences proximally and distally). Additionally, Hutton & Coughtrey (1875a) appear not to have found this muscle in their mummified specimen of *D. robustus* (see above).

Adductor digiti IV

General comments. This muscle has only been reported in *Dromaius* where it originates from the distal craniolateral tarsometatarsus and inserts on the medial aspect of IV-1 (Patak & Baldwin 1998).

Observations. No osteological evidence of either origin or insertion was observed in any of the *D. robustus*, *P. elephantopus* or *E. crassus* material examined.

Remarks. Reconstructing the adductor digiti IV in moa is too speculative (level II′ inference).

Lumbricalis

General comments. The lumbricalis is present in all extant palaeognaths, taking origin from the dorsal (deep) surface of the tendon of the flexor digitorum longus just before it trifurcates (or bifurcates in the case of *Struthio*). Its insertion is somewhat varied, but it is typically the trochleae or surrounding soft tissues of metatarsi III and IV (and II in *Apteryx*: McGowan 1979); in *Casuarius* and *Rhea*, it inserts on III-1 instead (Gadow 1880).

Observations. No direct, osteological evidence of this muscle was observed on the bones of *D. robustus*, *P. elephantopus* and *E. crassus*.

Remarks. Despite the lack of osteological evidence, the ubiquity of this muscle in extant palaeognaths implies that the lumbricalis was also present in moa (level I′ inference).

Soft tissues surrounding the tarsal sesamoid (Fig. 13)

General comments. Moa are distinct among 'modern' palaeognaths in possessing a sizeable tarsal sesamoid, located in the lateral half of the ankle joint, between the tibiotarsus and the tarsometatarsus. The sesamoid is, very roughly, a triangular prism in shape with three faces.

Observations. The two faces that articulate with the tibiotarsus (cranioproximal face) and tarsometatarsus (craniodistal face) are smooth and devoid of any texture. The third, caudal face presents a fibrous, roughened texture suggestive of a broad attachment of collagenous soft tissue. Whilst no discrete regions of scarring are observable, a consistent pattern is present in that there are strong 'fibres' directed proximally at the proximal margin, and there are also strong 'fibres' directed medially at the bone's medial margin.

Remarks. Hutton and Coughtrey (1875a) observed in their mummified *D. robustus* pes that the sesamoid was connected to the proximal tarsometatarsus (and possibly also the tibiotarsus) by a number of ligaments. Hence, it seems possible that the sesamoid was an ossified complement to the tibial cartilage: no muscles *per se* appear to have inserted on it or originated from it, but their tendons may have crossed over it (caudally) as they ran to the pes. This can potentially be investigated further through examination of other mummified specimens.

Size of the iliotrochantericus caudalis. The volume of the iliotrochantericus caudalis in the geometric model of *D. robustus* was determined to be 2275.02 cm^3. Assuming a bulk density for striated muscle of 1.06 g/cm^3 (Hutchinson *et al.* 2015), this equates to a mass of 2.412 kg.

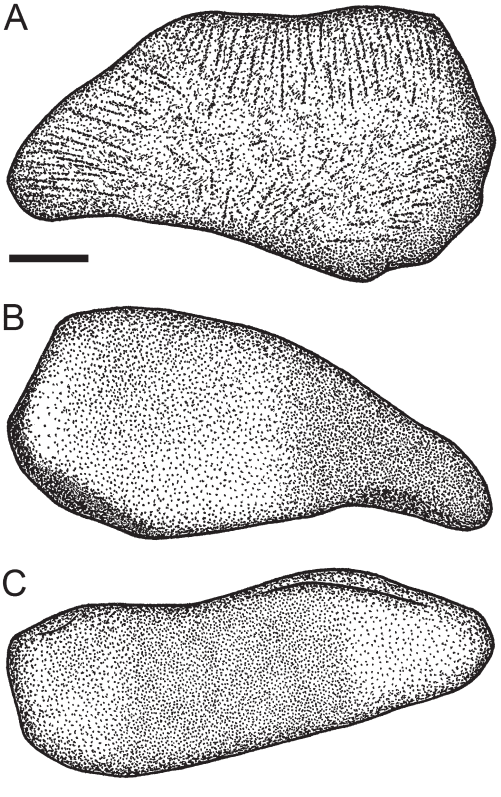

FIG. 13. Osteological evidence of soft tissue attachment on the tarsal sesamoid of *D. robustus*. A, outer (caudal) face; B, cranioproximal face; C, craniodistal face. In A and B, proximal is to top of page; in C, cranial is to top of page. Scale bar = 10 mm.

DISCUSSION

Comparison to the work of Zinoviev (2013)

The reconstructions of Zinoviev and those produced here are largely in agreement as regards the presence or absence of certain muscles, and the general location of their origins and insertions. Nonetheless, there are a number of important differences between the two sets of reconstructions, pertaining to the exact location of a given muscle's origin or insertion. These include the site of origin of the iliotrochanterici medius et cranialis, the extent of origin and manner of subdivision of the femorotibialis medius, the manner of subdivision of the obturatorius medialis, the insertions of the flexores cruris lateralis pars pelvica, lateralis pars accessoria et medialis, the insertions of the flexor cruris lateralis pars accessoria, caudofemoralis and puboischiofemoralis, insertion of the popliteus, the extent of origin of the fibularis longus and the site of origin of the abductor digiti IV. Additionally, Zinoviev did not reconstruct two muscles in the distal limb, the fibularis brevis and flexor hallucis brevis, which have been reconstructed here.

Many of the differences between the interpretations of Zinoviev (2013) and those made here likely stem from the limited material Zinoviev had at his disposal. It is clear from this study that, just as with whole-bone osteology (Worthy 1988; Kooyman 1991; Worthy & Holdaway 2002; Worthy & Scofield 2012), muscle scarring in the hindlimb of moa shows a high degree of intraspecific and interspecific variation. Hence, it is important to study abundant and well-preserved material when making myological inferences in this group of birds. The differences in interpretations probably also result from differences in the approach used. Zinoviev drew his inferences through comparison to the anatomy of all extant birds, whereas the phylogenetic scope of this study was restricted solely to palaeognaths. Additionally, the inferences made in this study were framed in the context of homology (Bryant & Seymour 1993; Witmer 1995), in order to identify the most phylogenetically parsimonious myological reconstructions.

This study also differs from that of Zinoviev (2013) in that it refrains from interpreting the exact boundaries of attachment for most muscles, whereas Zinoviev explicitly reconstructed the areas of muscle origins and insertions for all muscles. Some of the boundaries illustrated by Zinoviev were rather complex in geometry, yet osteological evidence was not described in support of his reconstructions. That the fleshy origin of many muscles in extant palaeognaths varies both between and within species (cf. Owen 1879; McGowan 1979; Kooyman 1991; Patak & Baldwin 1998; Gangl *et al.* 2004; Smith *et al.* 2006; Zinoviev 2006; Lamas *et al.* 2014; Hutchinson *et al.* 2015) cautions against making such explicitly detailed reconstructions without supporting osteological evidence. This point is all the more pertinent given the high level of variation in the nature of muscle scarring in moa as described in this study.

In some parts of the moa skeleton, such as the preacetabular iliac blade and the femoral shaft, there exist well-defined intermuscular lines that delineate much of the area of attachment of one or more muscles. In the majority of cases, however, there is simply not enough (if any) osteological evidence to permit an accurate reconstruction of the shape of a muscle's attachment in its entirety (cf. McGowan 1979; Bryant & Seymour 1990). For instance, the postacetabular ilium and the distal ischium and pubis of *D. robustus* is interpreted here to have been the site of origin (or part thereof) of at least six muscles (Fig. 3). Yet for only one of these muscles can a boundary be consistently identified (puboischiofemoralis, delineated dorsally by a pronounced, striated ridge), and even then its entire area of origin remains uncertain. Hence, it remains ambiguous as to exactly where these muscles would have attached to the bones. Without explicitly detailing how much evidence a given reconstruction is based upon, this can limit the reliability of the reconstructions as a whole. Identifying the areas of uncertainty in a reconstruction is also important in that it can point out aspects for future research. One such line of enquiry is the examination of mummified moa remains (see Rawlence *et al.* 2012b).

The utility of muscle scarring in taxonomic identification.

Despite variability in the nature of muscle scars, a number of patterns were found in the presence or nature of muscle scarring that may be used to distinguish between moa species.

The femora of *P. elephantopus* and South Island populations of *Euryapteryx curtus* are very similar in appearance, to the extent that isolated bones can be exceedingly difficult to assign to one or the other species, owing to population-dependent variation in bone robusticity. Features that have been used to aid identification previously (e.g., Worthy 1988; Worthy & Holdaway 2002), such as the relative location of the popliteal and ectocondylar fossae and the caudal extent of

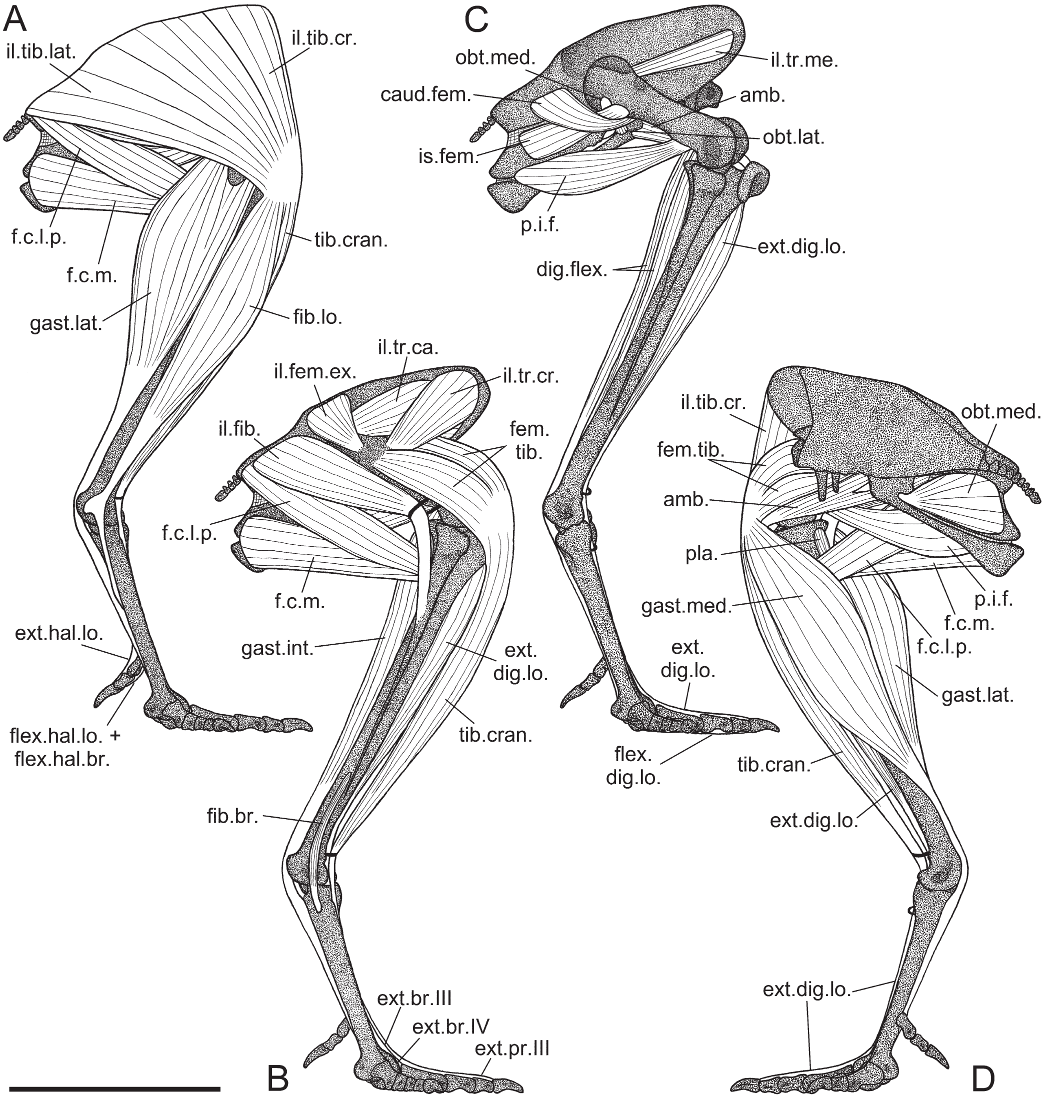

FIG. 14. Tentative restoration of how the hindlimb musculature of *D. robustus* may have appeared in life. **A**, lateral view showing superficial musculature; **B**, lateral view showing deeper muscles with outer muscles removed; **C**, lateral view showing deepest muscles; **D**, medial view showing superficial musculature. Scale bar = 500 mm. Abbreviations: *amb.*, ambiens; *caud.fem.*, caudofemoralis; *dig.flex.*, digital flexors; *ext.br.III*, extensor brevis digiti III; *ext.br.IV*, extensor brevis digiti IV; *ext.dig.lo.*, extensor digitorum longus; *ext. hal.lo.*, extensor hallucis longus; *ext.pr.III*, extensor proprius digiti III; *f.c.l.p.*, flexor cruris lateralis pars pelvica; *f.c.m.*, flexor cruris medialis; *fem.tib.*, femorotibialis; *fib.br.*, fibularis brevis; *fib.lo.*, fibularis longus; *flex.dig.lo.*, flexor digitorum longus; *flex.hal.br.*, flexor hallucis brevis; *flex.hal.lo.*, flexor hallucis longus; *gast. int.*, gastrocnemius intermedia; *gast.lat.*, gastrocnemius lateralis; *gast.med.*, gastrocnemius medialis; *il.fem. ex.*, iliofemoralis externus; *il.fib.*, iliofibularis; *il.tib.cr.*, iliotibialis cranialis; *il.tib.lat.*, iliotibialis lateralis; *il.tr. ca.*, iliotrochantericus caudalis; *il.tr.cr.*, iliotrochantericus cranialis; *il.tr.me.*, iliotrochantericus medius; *is.fem.*, ischiofemoralis; *obt.lat.*, obturatorius lateralis; *obt.med.*, obturatorius medialis; *p.i.f.*, puboischiofemoralis; *pla.*, plantaris; *tib.cran.*, tibialis cranialis.

the trochanteric ridge, have been found to be variable in these species (T.H. Worthy, pers. comm., 7.1.14; pers. obs.). Additionally, it was considered that *P. elephantopus* femora could be distinguished from those of *E. curtus* on the basis of the cross-sectional shape of the shaft at the mid-point of the bone (Worthy 1988, 1989; Worthy & Holdaway 2002), with the craniocaudal depth typically being markedly greater than the mediolateral width in *P. elephantopus*. This criterion is usually successful, and the distinction is clearly apparent when the femora of both species are compared side-by-side. With isolated specimens, however, it is difficult to apply this criterion with certainty.

Two myology-related features may help resolve this problem. The first is that, in *P. elephantopus*, intermuscular lines 3 and 4 are always in very close proximity, and are almost always fused to form a single intermuscular line on the middle of the caudal surface of the bone (Fig. 5A). These intermuscular lines were observed to be distinctly separate in all *E. curtus* femora examined. Hence, whilst the presence of a single intermuscular line on the middle of the caudal femur is indicative of *P. elephantopus*, the presence of two intermuscular lines is ambiguous, because a very small fraction of *P. elephantopus* femora examined showed two separate, although closely spaced, lines. The second myology-related feature is the relative disposition of the scars of insertion of the ischiofemoralis and caudofemoralis pars pelvica. In *P. elephantopus* the two scars are always well-separated by smooth bone, whereas in *E. curtus* the two are usually confluent (normally at their distal ends), sometimes so much so that only a single large area of scarring is present.

Paralleling the situation with the femur, the tarsometatarsus of *P. elephantopus* and South Island populations of *E. curtus* can also be difficult to distinguish in isolation. This is again due to variation within and between populations, even in those features previously proposed as taxonomically useful, such as the morphology of the middle trochlea (Worthy 1988; Worthy & Holdaway 2002; T.H. Worthy pers. comm. 7.1.14). Two myology-related features were observed which may be of use. The two small tuberosities for attachment of the retinaculum extensorium tarsometatarsi are absent in *P. elephantopus* (Fig. 10A), whereas they were present in approximately half of the *E. curtus* specimens examined. (In some individuals of *E. curtus*, the tuberosities were present on one tarsometatarsus but not on that from the other foot.) Thus, whilst the absence of the tuberosities is an ambiguous result, their presence indicates that the tarsometatarsus is of *E. curtus*. The other feature is a roughened depression proximal to the trochlea for digit IV on the cranial aspect of the bone, which is present in approximately two-thirds of the *P. elephantopus* specimens examined (Fig. 10A,B), but which is absent in *E. curtus*. The presence of this feature, which may or may not be associated with the extensor brevis digiti IV (see above), is therefore indicative of *P. elephantopus*, but its absence is an ambiguous result.

The femur of *M. didinus* is usually easily distinguished from that of other moa species by virtue of its slenderness and small size, although the femur of large individuals are difficult to distinguish from that of *A. didiformis*, especially if the distal end is poorly preserved (Worthy & Holdaway 2002). Uniquely among moa, however, is the nature of the two caudal tuberosities in *M. didinus* (Fig. 5D). The lateral caudal tuberosity (insertion for the flexor cruris lateralis pars accessoria) is positioned in the proximal half of the bone, whereas in all other species it is located in the distal half. Additionally, the medial caudal tuberosity in *M. didinus* (insertion for the puboischiofemoralis) is bipartite, whereas in all other species it is singular. The clear separation of the lateral and medial caudal tuberosities in *M. didinus* is also seen in *Dinornis* spp. Considering the current consensus of moa interrelationships (Bunce *et al.* 2009; Worthy & Scofield 2012), this indicates that an association between the puboischiofemoralis and the flexor cruris lateralis pars accessoria is apomorphic for emeids.

Moa and the reconstruction of musculature in extinct vertebrates

Moa have been shown to display a considerable degree of variability in the manifestation of muscle attachment. Despite this, the basic topology and location of muscle scarring in moa is relatively consistent across species, and is generally comparable with extant palaeognaths. Coupled with overall conservatism in palaeognath hindlimb myology, this has made the task of myological reconstruction in moa relatively straightforward for most muscles. Also aiding the process is that moa are a group of animals for which there are abundant fossil remains, and in which muscle scarring is well pronounced on the bones studied. This is due to several factors, the most important being the exceptional preservation of many of the specimens examined. These specimens are very recent, in some instances less than 1,000 years old, and have undergone little taphonomic degradation (e.g., Allentoft *et al.* 2012, 2014; Rawlence *et al.* 2012a). Furthermore, in some swamp localities, such as Pyramid Valley, Kapua and Cheviot, differential staining of the bones has highlighted muscle attachment scars. An additional factor is that the muscles of larger animals tend to leave larger, more distinct scars of attachment on the bones.

The prevalence of muscle scarring in moa, and the relatively straightforward process of myological reconstruction in this group, prompts reflection on the sentiments of McGowan (1979), who raised concerns over the ability of palaeontologists to accurately reconstruct the myology of extinct species. Using moa as an example, he was only able to recognise osteological correlates of a small proportion of hindlimb muscles in a skeleton of *E. crassus*, and thus claimed that it would be impossible to accurately reconstruct the hindlimb musculature in moa.

McGowan based his work only on the musculo-skeletal anatomy of *Apteryx mantelli*, however, and attempted to extrapolate his findings directly from this small bird to a much larger species. The osteological correlates of muscle attachment in *Apteryx* spp. are small and usually poorly developed, or are absent entirely (McGowan 1979; pers. obs.). Consequently, McGowan was able to recognise fewer osteological correlates common to both *Apteryx* and *E. crassus*. Being a much larger bird, however, there are a multitude of other attachment scars on the bones of *E. crassus* that are not evident in *Apteryx*, which would have further hampered McGowan's comparison. Indeed, of the 48 muscles (or muscle parts) that have been reconstructed here in *D. robustus*, *P. elephantopus* and *E. crassus*, the proportion that are consistently recognisable by osteological correlates is 44%, 50% and 46 % (respectively) for muscle origins and 88%, 83% and 83% (respectively) for muscle insertions. Considering origins or insertions together, the proportion of muscles which can be consistently recognised by osteological correlates is 96%, 94% and 94% (respectively). That is, almost every muscle in the hindlimb of these three species can be recognised by an osteological correlate of attachment somewhere on the skeleton. This means that the origins and insertions of a considerable number of these muscles, particularly those of the proximal limb, may be confidently inferred for moa. Considering the great prevalence of scars of muscle attachment in moa, the preservation of the fossil bones, their recent extinction and the overall conservatism in extant palaeognath hindlimb myology, moa may be seen as an exception to the general difficulty facing palaeontologists who attempt to reconstruct musculature in extinct vertebrates (Bryant & Seymour 1990).

McGowan's inability to reconstruct the hindlimb myology of *E. crassus* more fully also highlights the importance of making comparisons to multiple extant relatives, as done here. In the years following McGowan's (1979) work, the advent of the EPB approach (Bryant & Russell 1993; Witmer 1995) has helped facilitate defensible inferences of musculature (and other soft tissues), even when direct osteological evidence is absent. For those few muscles that lacked any osteological evidence, they were still able to be hypothesised as present and so reconstructed here in *D. robustus*, *P. elephantopus* and *E. crassus* through this approach. Moreover, where osteological evidence of an origin or insertion is wanting, the EPB can guide the reconstruction of the approximate region from which the origin or insertion would have most likely been. As with all extinct vertebrates, however, little, if anything, may be inferred about muscle size, gross geometry, internal architecture (parallel-fibred *versus* pennate) or histochemistry (Bryant & Seymour 1990).

Biomechanical considerations

The myological reconstructions produced for the three moa species studied will help facilitate comparative biomechanical analysis of locomotor behaviour in moa. Throughout the course of the current study, two points of interest concerning the biomechanics of the moa hindlimb have arisen. These are briefly discussed here.

Relative size of the iliotrochantericus caudalis. The iliotrochantericus caudalis is active during the stance (support) phase of walking and running in extant birds (Gatesy 1994, 1999), and is hypothesised to be the main muscle responsible for maintaining stability of the hip joint during stance. Specifically, its contraction effects medial (inward) long-axis rotation of the femur, which, because of the subhorizontal orientation of the femur in birds, helps to resist adduction of the limb as a whole under the weight of the body (Hutchinson & Gatesy 2000). The muscle is hence one of the most important antigravity muscles in the avian hindlimb. Digital computer modelling of the iliotrochantericus caudalis in an adult female *D. robustus* has estimated that the muscle in this individual had a mass of 2.412 kg. As explained above, this estimate should be viewed as an absolute minimum.

The *D. robustus* individual utilised here (CM Av 8422) is very similar in size to that studied by Brassey *et al.* (2013), who estimated its mass as 196 kg (with a 95% confidence interval of 155–245 kg). Assuming these values here, the modelled iliotrochantericus caudalis thus occupies a minimum of 0.984–1.56% of total body mass. This is a very large proportion. For comparison, in a 65.3 kg ostrich, Hutchinson *et al.* (2015) measured the mass of the iliotrochantericus caudalis as 0.311 kg, or approximately 0.476% of body mass; and in a 42 kg emu, Lamas *et al.* (2014) measured the mass of the muscle as 0.336 kg, or approximately 0.8 % of body mass. Therefore, the iliotrochantericus caudalis in *D. robustus* is disproportionately large compared to both the emu and ostrich, by a factor of at least 1.2 for the emu and 2.1 for the ostrich. This supports the hypothesis that, in having an enlarged preacetabular iliac blade, at least some species of moa had a relatively enlarged iliotrochantericus caudalis in comparison to other palaeognaths. Being a primary antigravity muscle, the large size of the iliotrochantericus caudalis in moa undoubtedly reflects the larger size of moa compared to ostriches and emus. Its disproportionately greater size may be an allometric effect, since the force-generating capacity of muscle scales with negative allometry: all other factors being equal, force scales proportional to cross-sectional area, and thus length^2, whereas mass scales proportional to volume, and thus length^3 (Vogel 2003). Indeed, Lamas *et al.* (2014) found that the mass of the iliotrochantericus caudalis scaled with positive allometry across an ontogentic sample of emus. The great size of the iliotrochantericus caudalis in moa may alternatively, or additionally, reflect a difference in the locomotor behaviour of moa compared to ostriches and emus, and thus opens up further avenues for future biomechanical investigation.

Function of the tarsal sesamoid. As discussed above, no muscle appears to have originated or inserted on this bone in moa, but the tendons of one or more digital flexors may have passed over it as they ran around the caudal aspect of the ankle joint. If this interpretation is correct, then the tarsal sesamoid of moa may have possibly functioned in an analogous fashion to the proximal sesamoid bone of the horse metacarpus, which acts to increase the moment arm of the digital flexors as they cross the metacarpophalangeal joint (Thomason 1985). Interestingly, biomechanical modelling by Hutchinson (2004a, b) suggested that the ankle joint is the 'weakest link' in the hindlimb of a biped, in terms of the ability of extensor (antigravity) muscles to support the limb during stance and prevent it from collapsing. The presence of a tarsal sesamoid in moa may have therefore been advantageous in these large birds, by increasing the mechanical efficacy of distal limb muscles in preventing limb collapse during locomotion. An alternative, or perhaps even complementary, function that the tarsal sesamoid may have conferred is providing a measure of stability to the ankle joint.

CONCLUSIONS

Utilising a large sample of fossil specimens from many localities throughout the South Island of New Zealand, the hindlimb myology of three moa species, *D. robustus*, *P. elephantopus* and *E. crassus*, has been reconstructed in detail. The reconstructions presented here are well supported by both osteological correlates of muscle attachment on the fossil bones themselves, as well as through comparison with extant, phylogenetically close birds (palaeognaths). Nevertheless, the high level of variation in moa osteology and muscle scarring morphology suggests that it would be worthwhile testing these reconstructions on hitherto unsampled populations from other sites around the South Island. It would also be worthwhile studying the mummified remains of moa to better understand their hindlimb musculoskeletal anatomy, through the non-destructive approaches of magnetic resonance imaging and X-ray computed tomography.

Several features pertaining to the attachments of muscles have been identified that may be of use in the taxonomic identification of isolated, incomplete or poorly preserved moa limb bones.

Moa are rather unique among extinct vertebrates in that the reconstruction of much of their hindlimb musculature has proven to be a relatively straightforward process. It remains to be seen as to whether this holds true for other parts of the moa body, such as the neck and head.

The myological reconstructions produced here provide a solid anatomical basis upon which comparative biomechanical investigation of moa locomotor behaviour can be undertaken. This can help shed light on the posture and gait of moa, as well as the reason or reasons underlying the unique skeletal proportions of the moa hindlimb. Additional features have also been identified which would be worthy of biomechanical investigation, such as the significance of a large preacetabular iliac blade, and the role of the tarsal sesamoid.

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