Notes on the Pelvic Musculature of *Emeus crassus* and *Dinornis robustus* (Aves: Dinornithiformes)¹

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Abstract—*Dinornis robustus* and *Emeus crassus* display two variants of moa locomotor adaptations, *Emeus* being less cursorial. The number and topography of their pelvic muscles are similar and resemble that of Tinamiformes and geographically close Apterygiformes and Casuariiformes. Nevertheless, a number of features are probably peculiar to Dinornithiformes. The strong iliotibiales and iliofemoralis externus muscles, which prevent passive adduction of the femur, far surpass the bulk recorded for these muscles in other birds. The iliofemoralis internus muscle has a unique insertion to the cranial surface of the femur distal to the femoral head, although further inspection of mummified remains is required to prove this. The less modified pelvic muscles of moa in comparison with that of Apterygiformes, Casuariiformes, Rheiformes, and Struthioniformes are related to the retention in Dinornithiformes of the wide pelvis.

Keywords: hind limb, musculature, Dinornithiformes

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INTRODUCTION

Since the first report (Polack, 1838) and subsequent formal description of the group (Owen, 1839), moas have been the subject of detailed scientific studies (for review, see Worthy and Holdaway, 2002). Despite the long standing problem in moa classification due to their high level of morphological variability and sexual dimorphism, the latest morphometric and genetic studies support the division of Dinornithiformes into three families: Emeidae, Dinornithidae, and Megalapterygidae (Bunce et al., 2009). Bones of the pelvic girdle and hind limbs are usually best preserved; hence, their morphology and proportions traditionally play the major role in their taxonomy. In fact, Owen’s first classifications were based on the morphology of hind limb bones alone. In his earliest paper on the subject, Owen (1839, p. 170) described morphological features related to the muscular insertions in a femur fragment shipped from New Zealand, concluding that “… the Struthious bird indicated by the present fragment to have been heavier and more sluggish than the Ostrich; its femur, and probably its whole leg, was shorter and thicker.” Many of his later works (collected in Owen, 1879) contain comments on certain ligamentous and muscular structures of moa hind limbs. Strongly marked muscular impression on the hind limb bones of moa were also noticed by Colenso (1843). But it was not until 1869, when the first description of soft tissues of hind limbs was provided. Owen (1869) described mummified tendons, sesamoids, and integumentary sole-pads of the second toe of the right foot of *D. robustus*. Later, Coughtrey (1874a, 1874b) described some mummified muscles and ligaments of *D. robustus* and *E. crassus*. Eleven years later, Owen (1885) described a mummified foot of *Dinornis (=Megalapteryx) didinus*. Kooyman (1985) in his PhD Thesis devoted to moa and moa hunting provided interpretation of marks on moa hind limb bones, which had been widely used in classification of Dinornithiformes, as left by certain muscles and ligaments. Despite discoveries of several additional mummified legs of moa (Forrest, 1987; Anderson, 1989; Worthy, 1989) as well as the presence of two other mummies found at the end of 19th century (Buller, 1888), a detailed reconstruction of hind limb myology and syndesmology of moa has never been undertaken. The present study fills the gap, being a part of more extensive reconstruction provided elsewhere.

MATERIALS AND METHODS

The material includes pelvic and hind limb bones of two species of moa from the collection of the Museum of Natural History of the Humboldt University in Berlin. A skeleton of the Eastern moa *E. crassus* Owen, 1846 (specimen MB. Av. 1571) was shipped by Julius von Haast to Germany some time before 1850. The second skeleton belongs to the Giant moa *D. robustus* Owen, 1846 (specimen MG. Av. 1570) from South Island, found in Glenmark Swamp and shipped to Germany soon after its discovery on January 4, 1857.

¹ The article was translated by the author.
The reconstruction is based on the extensive comparative literature and original data on osteology, myology, and syndesmology of avian hind limbs (Zinoviev, 2010). We also followed certain rules of reconstruction, which were successfully applied in the previous study of Hesperornis regalis (Zinoviev, 2011). Although members of the order Casuariiformes are considered the closest living relatives of moa (Johnston, 2011), we were extremely cautious in extrapolation of morphological characters of emu and cassowary, or even kiwi, to dinornithids. Besides being graviportal and heavy, moa retained wide pelvis with unfused ilia, ischia, and pubes. In this respect they differ from specialized cursorial ratites with narrow pelves. Beautiful lithographs from Owen’s papers helped us to use osteological characters, absent in the material.

Anatomical names follow the latest version of Nomina Anatomica Avium II (Baumel et al., 1993), with some changes made by Zinoviev (2010).

This paper is illustrated by drawings showing only the origins of pelvic muscles (except for m. iliofemoralis internus). Drawings illustrating their insertions will be provided in the upcoming paper.

**PELVIC MUSCULATURE**

In the reconstruction of moa pelvic muscles, I followed the same sequence as in the case of Hesperornis (Zinoviev, 2011). The deepest muscles, which control movements in the hip joint, leave better traces on the bones (Fig. 1). This is especially true for mm. iliotrochanterici, which resist supination of the femur caused by the femoral retractors (Zinoviev, Dzerzhinsky, 2000). These muscles expand over almost the entire lateral surface of the ala preacetabularis ili, leaving pronounced traces of both muscular and tendinous origins.

**Iliotrochanterici muscles.** Both species show pronounced traces of muscular and tendinous origins of these muscles on the ala preacetabularis ili. Unfortunately, both specimens lack cranial edges of the alae and, hence, it is impossible to reconstruct the cranial-most parts of the muscle group. However, it is possible to reconstruct in detail the origin of the iliotrochantericus caudalis muscle, the most powerful of the iliotrochanterici. Its origin covers almost the entire lateral surface of the ala preacetabularis ili, extending from its cranial part to the vertical passing through the middle of the acetabulum. The structure of this muscle must have been complex, as in living ratites (Sudilovskaya, 1931; Zinoviev, 2006). The short muscular fibers of the m. iliotrochantericus caudalis originated from the preacetabular portion of the ilium but also originated from a number of aponeuroses. The origins of these aponeuroses on the ala preacetabularis ili are marked by prominent oblique ridges (Fig. 1a). Muscle fibers inserted on a number of intramuscular aponeuroses, contributing to a large aponeurosis on the lateral surface of the muscle. This aponeurosis gave rise to a stout terminal tendon, which inserted to a crescentic rugosity of the greater trochanter, just proximal to the insertion of the m. iliotrochantericus medius. The area cranial to this insertion is smooth and must have been covered by a thin layer of cartilage for better sliding of the terminal tendon of the iliotrochantericus cranialis muscle (Zinoviev, 2010). A large and powerful belly of the iliotrochantericus caudalis muscle covered smaller bellies of the iliotrochanterici cranialis et medius muscles. A fleshy origin of the iliotrochantericus medius is marked on the lateral surface of the ala preacetabularis ili by an elevated rugose area between the beginnings of the iliotrochantericus caudalis and iliotrochantericus cranialis muscles. In many birds, this muscle is fused with the more powerful iliotrochantericus cranialis muscle. The presence of a separate medial iliotrochantericus muscle in moa is also marked by its well-defined place of insertion on a rugose area between the insertions of the iliotrochanterici caudalis et cranialis muscles. The beginning of the m. iliotrochantericus cranialis, like that of the m. iliotrochantericus caudalis, is also a combination of muscular and tendinous attachments. Its area of origin is from the ventral rim of the ala preacetabularis ili and its lateral surface. Remains of the terminal tendon of the m. iliotrochantericus cranialis were described by Coughtrey (1874a).

Large, with a complex structure, mm. iliotrochanterici resemble that of Dromaius and Apteryx (McGowan, 1979; Patak and Baldwin, 1998). The iliotrochantericus muscles of other ratites, such as Rhea and Struthio, show features of specialization (Gangl et al., 2004; Zinoviev, 2006; Picasso, 2010).

**Iliofemoralis internus muscle.** The presence of this minute muscle is marked in moa by the rugose lateral surface of the ala preacetabularis ili just caudal to the origin of the m. iliotrochantericus cranialis and cranial to that of the m. ambiens. Insertion of the muscle in the cranial surface of the femoral shaft near the femoral head is unusual for birds (Fig. 2). Coughtrey (1874a) observed several fibers still attached to this area, following Owen (1862) in attributing them to the m. iliofemoralis internus.

The m. iliofemoralis internus is rather uniform in birds. Among ratites, it is generally weaker in Casuariiformes and well-developed with the shifted origin in Struthio. None of extant or extinct birds show a comparable shift of the insertion of this muscle, suggested by Owen and Coughtrey.

**Iliofemoralis externus muscle.** The origin and insertion of this muscle in moa are well marked. Like m. iliotrochantericus caudalis, the external iliofemoral muscle had a fleshy and tendinous origin (multipinnate) on the ala preacetabularis ili just caudal to the origin of the aforementioned muscle. The caudal expansion of the muscle is limited to the beginning of the crista dorsolateralis ili. The muscle inserted on a prominent, slightly oblique scar between insertions of the mm. iliotrochanterici and m. ischiofemoralis.