

NOTES ON THE MYOLOGY OF THE PELVIC LIMB IN KIWI (*APTERYX*) AND IN OTHER BIRDS

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ABSTRACT.—Anatomical variants of the musculature of the pelvic limb in *Apteryx*, based on a review of the published literature, are considered from the aspect of (1) errors in descriptive myology, (2) probable misidentification or misrepresentation of muscles, and (3) variations in a given muscle set that have not been thoroughly examined in terms of a form-function complex. A more accurate interpretation of these relationships is suggested as a basis for further studies of the pelvic limb myology in birds. Received 2 March 1981, accepted 30 June 1981.

THE first account of the somatic musculature of any species of kiwi (*Apteryx australis*, *A. haastii*, *A. owenii*) was apparently based on a paper read by Richard Owen on 22 February 1842 and published as a "descriptive portion of this communication" in the *Proceedings of the Zoological Society of London* of the same year (pp. 22–41). The principal muscles described included the extensive, striated *Musculi subcutanei*, the trunk musculature, shoulder muscles, and the muscles of the pelvic limb. Later some of this descriptive material was incorporated into a longer paper with the addition of plates of illustrations (1849). The latter was essentially reprinted in Owen's "Memoirs" (1879).

In the 35 yr subsequent to these memoirs, there were at least five additional papers that considered the somatic musculature of *Apteryx* based, at least in part, upon independent dissections. These include, in chronological order, the well-known papers of Garrod on the thigh muscles (1873, see Fig. 6, *A. owenii*) and on the deep plantar tendons in birds [1875, see Fig. 2, *A. "mantelli"* (= *australis*)], the general anatomy and embryology paper of Parker (1891) as well as that of Beddard (1899), selected comments by Pycraft (1900), and finally the comprehensive study of Mitchell (1913) on the peroneal musculature in birds ("three examples" of *Apteryx*, p. 1043). The most recent paper on the subject is that of McGowan (1979) on the musculature of the pelvic limb in *A. australis* based on a dissection of two specimens.

In many of the preceding studies, the somatic musculature of kiwis is often described with reference to that of the "ratites" or "pa-

laeognathous" birds (see, e.g. Garrod and Mitchell). The pelvic musculature of the latter is described by Gadow (1880) and Pycraft (1900). More recently, Hudson et al. (1972) describe the appendicular musculature of tinamous, a group that some consider to be allied with ratites. (There is some indication that the latter investigators also dissected at least one specimen of *Apteryx*; see p. 248.)

Although McGowan completed his recent study in an attempt to resolve certain "shortcomings" in descriptive myology (what he later equates with "lapsi calami," p. 64), I propose to review and discuss at least three of his descriptions of morphological variation in the pelvic musculature of *A. australis* that seem to differ significantly from anatomical variants described in other specimens of *A. australis*, in other species of kiwi, and in at least some other avian groups. I will also show that certain components of the pelvic musculature are apparently not described by McGowan, or anyone else, in any specimens of the kiwi.

One of these anatomical variants, namely *M. iliotrochantericus medius*, is a constituent of the expanded Garrod muscle formula (symbol C; see Hudson 1937: 12). I suggest that this muscle is incompletely described in many avian groups and is, therefore, not sufficiently well-known in terms of morphological relationships to justify its use in terms of conclusions regarding phylogenetic affiliation. I will show that two other anatomical variants, in the peroneal musculature and in the deep digital flexor muscles, are most probably described both inaccurately and incompletely by Owen and McGowan and, in the latter study, are the

basis for erroneous statements regarding possible phylogenetic affinities among *Apteryx*, "ratites," and other birds. Finally, I will suggest that a restudy of at least one muscle set, M. caudo-iliofemoralis, may serve as a test of the evolution of functional modalities in a muscle complex and as a related test of recent theories of paleognath monophyly (Bock 1963, Cracraft 1974).

My review of these anatomical variants, from the aspect of descriptive morphology, is based on my interpretation of descriptive data and illustrations in all previously cited references regarding *Apteryx*, my own previous dissections of specimens exemplifying numerous avian groups (Hudson et al. 1966, 1969, with Hudson's unpublished notes on Falconiformes as well as Charadrii; Vanden Berge 1970, 1975, 1976), and my own participation in the substantial review of avian musculature incorporated in the first attempt to formulate a standardized nomenclature (see Myologia in "Nomina Anatomica Avium," Baumel et al. 1979).

Mm. ilioprochantericus caudalis (= "posterior"), cranialis (= "anterior"), medius. Synonymy: Owen (1842, 1849, 1879), glutaeus medius, minimus (cranialis and medius included); Beddard (1899), glutaeus secundus, tertius, quartus.

M. ilioprochantericus caudalis is apparently the largest of these three muscles in *Apteryx*, as in most other birds (but see George and Berger 1966: 390); the insertion on Trochanter femoris (Baumel 1979a) is subtended by a Bursa synovialis (Vanden Berge 1979) in *A. australis* (Owen 1842: 34) and most likely in other birds as well in view of the probable functional role of this muscle (Cracraft 1971).

According to McGowan (1979: 51), M. ilioprochantericus cranialis is absent in one of two specimens of *A. australis*; medius is presumably present in both. This variant seems to be rather unusual among birds generally. M. ilioprochantericus medius is more frequently described as "absent" in birds, if it is not independently developed with respect to M. ilioprochantericus cranialis, and, instead, is characterized by some continuity of the respective tendons of insertion if not the actual aponeurotic sheath of the contractile tissue itself. This is the basis upon which Beddard (1899: 395) described the variation of the two muscles in *A. australis* and *A. haastii*, and this is also the

basis upon which Hudson (1937: 12) suggested that the variants of medius be recognized by formula letter "C." Owen initially stated that "[medius] is peculiar to *Apteryx*, and the preceding portion [i.e. cranialis] is absent in most birds" (1842: 34), but later stated that "one of them (i.e. either cranialis or medius) is absent in most birds" (1879: 55). Intraspecific variation in relative development of certain muscles does occur among birds (see, e.g. Raikow 1975, Raikow et al. 1979) and may have occurred then in McGowan's two specimens of *A. australis*.

I suggest that the passage of a neurovascular bundle (N. coxalis cranialis, Breazile and Yasuda 1979) between the respective proximal attachments of the cranialis and medius muscles (see George and Berger 1966, Klemm 1969, Vanden Berge 1970) is a principal morphological criterion for assessing the anatomical status of both muscles in any avian specimen. In my experience, this criterion seems to be uniformly applicable among birds and is more "predictable" than suggested variations in continuity of the tendons of insertion in terms of "presence" or "absence" of either muscle. Until such time as this interrelationship of a neurovascular bundle to proximal attachments of the two muscles is more fully described, the addition of M. ilioprochantericus medius as a component of the Garrod leg-muscle formula will be of limited significance in terms of designating any degree of phylogenetic affinity among birds (see Table IX in George and Berger 1966).

One other component of the expanded Garrod leg-muscle formula, namely "V," the Vinculum tendinum flexorum, which binds the tendon of M. flexor perforans et perforatus digiti III to that of M. flexor perforatus digiti III as these two tendons traverse the foot, is of uncertain status in the kiwi: present, according to Beddard (1899: 398); absent, according to McGowan (1979: 62); no relationship described in any of Owen's three papers. Furthermore, M. flexor hallucis brevis and M. adductor digiti II are two muscles that *no one* describes in *any* specimen of kiwi, at least to my knowledge. Both muscles are described in some tinamous (Hudson et al. 1972); M. adductor digiti II is apparently present in *Rhea* and *Casuaris* but absent in *Struthio* (Gadow 1880).

Mm. fibularis (peroneus) longus and brevis. Syn-

onymy: longus is equivalent to "superficialis" and brevis to "profundus," as described by some investigators (see, e.g., Mitchell 1913).

According to McGowan (p. 72), the tendon of insertion of *M. peroneus longus* does *not* form a conjoined tendon with that of *M. flexor perforatus digiti III* in his specimens of *A. australis*, although this statement appears to contradict his description of both muscles (pp. 60–61 and pp. 64–65) as well as his illustrations (Figs. 17, 18, 22, and 23). McGowan also states that this anatomical variant represents a morphological distinction between ratites and carinates and that this distinction is supported by the original description in Gadow (1880).

The five principal morphological characteristics of *M. peroneus longus* in terms of a general avian pattern (as exemplified in *Chauna chavaria*, Anhimidae) include (1) a large, fleshy, superficial belly on the craniolateral aspect of the crus; (2) a deep attachment along the shaft of the fibula; (3) a tendinous connection (aponeurosis) to the *Cartilago tibialis* (see Baumel 1979a); (4) a tendon that traverses a bony sulcus on the lateral aspect of the proximal end of the tarsometatarsus; and (5) the formation of a conjoined tendon where the tendon of insertion unites with that of *M. flexor perforatus digiti III* on the plantar aspect of the foot. In the kiwi and in ratites, these five characteristics differ from *Chauna* only in "minor detail," according to Mitchell (1913). Gadow (1880: 45) describes the conjoined tendon in *Struthio*, *Rhea*, and *Casuaris* as follows: "Diese Sehne [*M. peroneus longus*]*—sich mit der Sehne des M. flexor perforatus digiti medii (M. flexor perforatus digiti III) verbindet und daher zur Zehenbeugung beiträgt.*" On the basis of these two references, the anatomical variant of *M. peroneus longus* in *Apteryx* is similar to that in other ratites and similar to that in at least some other avian groups, despite the statements to the contrary as given in McGowan.

Although both Owen (1849: 295–296, Plates 31, 32, and 35, tendon 7; 1879: 59–60, Plate II) and Beddard (1899: 397) describe a conjoined tendon, they either describe a most unusual *intraspecific* morphological variation in *Apteryx australis*, or they inadvertently introduce considerable confusion in use of the term "perforatus" and "perforans" in terms of the associated digital flexor muscle (see Myologia,

"*Nomina Anatomica Avium*," Annot. 121; see also Frewein 1967 and Greenlee et al. 1975 for a discussion of the digital flexor tendons and their tendon sheaths as described for *Gallus*). Confusion in the proper use of the descriptive terms seems to be most probable. For example, Owen's description of the conjoined tendon and his illustrations in the 1849 paper differ from those in the memoirs of 1879. In all of the above papers, however, the tendon of *M. peroneus longus* does become conjoined with a tendon of a digital flexor muscle, most probably that of *M. flexor perforatus digiti III*, in sharp contrast to McGowan's statement as previously cited.

In contrast to the morphological variation in *M. peroneus longus* in *Apteryx*, *M. peroneus brevis* is said to be very much reduced in terms of relative development (Mitchell 1913: 1043) and apparently absent in some specimens (Beddard 1899: 397). Owen, in fact, does not describe a "typical" *brevis* in any of his three papers.

McGowan describes a short peroneal muscle in his specimens of *A. australis*. In the next section, however, I will attempt to show that "peroneus brevis" as described by McGowan is a synonym for "peroneus medius" in Owen's papers (1849, 1879, but *not* 1842) and that, in both cases, the muscle so described has no morphological relationship to the peroneal musculature described in other birds. In fact, it is probably *not* a component of the peroneal musculature at all.

M. flexor hallucis longus. Synonymy: Owen (1842, 1849, 1879), *M. flexor perforans digitorum*, tendon 1; McGowan (1979), *M. flexor digitorum longus*.

M. flexor digitorum longus. Synonymy: Owen (1842), *M. flexor perforans digitorum*; Owen (1849 and 1879), "*Peroneus medius* Cuvier, *Accessorius flexoris digitorum* Vicq d' Azyr"; Beddard (1899), *M. flexor profundus*; McGowan (1979), *M. peroneus brevis*.

According to McGowan (p. 65), *M. flexor hallucis longus*, as a deep digital flexor of the hallux, is *not* present in either specimen of *A. australis* that he dissected, although he states that the muscle is represented by a specific tendon of "flexor digitorum longus" to the hallux. The anatomical relationships of this latter muscle as described in his specimens of *Apteryx* differ very little from those of *M. flexor hallucis longus* described in other specimens of kiwi

(Beddard 1899). Furthermore, the morphological relationship of the long (deep) flexor of the hallux to the deep flexor of the digits in *A. australis* is illustrated as a definitive example of Type II morphological variant in the original paper on this subject (Garrod 1875: 341, Fig. 2; see also Gadow and Selenka 1891).

If the muscle described by McGowan as "flexor digitorum longus" is, in fact, *M. flexor hallucis longus*, then either *M. flexor digitorum longus* is itself absent in the same specimens of kiwi, or the deep digital flexor muscle is likewise misidentified. The latter is almost certainly the case here, based on McGowan's description of the anatomical relationships of "peroneus brevis" with respect to its proximal attachments in the crus, the position of the tendon as it traverses the tibial cartilage, the formation of a conjoined tendon (with *M. flexor hallucis longus*) in the foot, and a trifurcation into a deep flexor tendon to each of the three toes. *M. peroneus brevis* has never been so described in any other birds (see Mitchell 1913, Hudson 1937, and numerous other investigators), and the above mentioned morphological characters are those most often associated with *M. flexor digitorum longus*.

As previously mentioned, Owen does not describe *M. peroneus brevis* in any of his three papers, nor any other muscle having the expected morphology described for other birds. Furthermore, the anatomical description of "flexor perforans digitorum" (1842: 40–41) is virtually identical to that of "Peroneus medius Cuvier, Accessorius flexoris digitorum Vicq d' Azyr" of the later papers (1849, 1879). In all three papers, Owen states that the tendon of insertion "receives a strong accessorial tendon from the muscle which bends the innermost toe, and finally divides into three strong perforating tendons" (emphasis mine). Gadow (1880: 51) gives an interesting footnote to what he describes as the "outer head of flexor profundus." In that footnote he quotes directly from Owen's paper of 1849 and clearly states that Owen's use of "Peroneus medius Cuvier, Accessorius flexoris digitorum Vicq d' Azyr" as a synonym for *M. flexor digitorum longus* in *Apteryx* was erroneous and that Cuvier, at least, was describing *M. peroneus longus*! I am not able to confirm this reference to the work of Cuvier, however.

In view of the apparent discrepancies between the morphological relationships of the

peroneal musculature and deep digital flexor muscles as described in *Apteryx* by Owen, Beddard, Mitchell, and McGowan, and the same relationships in ratites and other birds, McGowan's statement (p. 72) that "the fusion of the tendons of insertion of the *Mm. peroneus brevis* and *flexor digitorum longus* is not unique to *Apteryx* but is a condition which is shared with other ratites," is not substantiated.

The preceding review of the status of the peroneal musculature, and the deep digital flexor muscles, suggests that neither of these muscle sets is predictive of phylogenetic relationships between *Apteryx* and ratites, or between ratites (collectively) and other birds. They do not constitute a "distinction between ratites and carinates," as suggested by McGowan (1979: 71–72).

M. caudo-iliofemoralis: *M. caudofemoralis*, *M. iliofemoralis*. Synonymy: Owen (1842, 1849, 1879), *M. adductor brevis femoris*, *M. adductor longus*; Garrod (1873), Beddard (1899), femoro-caudal and accessory femoro-caudal (including also "superficial femoro-caudal"?); McGowan (1979), *M. piriformis*, pars caudofemoralis, pars iliofemoralis.

Both axial and pelvic components of this muscle complex are present in *Apteryx*. The axial component, *M. caudofemoralis*, is differentiated from the pelvic component even though it is "slender, straplike, of only moderate size" (McGowan 1979: 53). This muscle is also described as the "femoro-caudal" and is illustrated in *A. owenii* (Garrod 1873, Fig. 6). Beddard (1899), however, indicates that there is no clear separation between the two muscle components in other specimens of kiwi.

M. caudofemoralis is clearly differentiated in most tinamous (except *Eudromia*, Hudson et al. 1972), but much less so in ratites. The caudofemoralis is very weakly differentiated in *Struthio* (Gadow 1880) and *Casuarius* (Gadow 1880, Garrod 1873, Pycraft 1900) and absent in *Rhea* and *Dromaius* (Garrod 1873, Pycraft 1900). Other variants of this muscle in carinate birds are well known in the literature (George and Berger 1966, Table IX, symbol A).

Of particular interest, however, is the apparent hypertrophic development of the pelvic constituent, *M. iliofemoralis*, in *Apteryx* (*A. owenii*, Garrod 1873, Fig. 6; *A. australis*, McGowan 1979, Figs. 10 and 11) as well as in some ratites (*Casuarius*, Gadow 1880, Plate III, Fig.

1; Pycraft 1900, Fig. 6), and in tinamous (Hudson et al. 1972, Fig. 10). In all of these specimens, as illustrated, the proximal "fixed" attachment of *M. iliofemoralis* is "perforated" by peripheral branches of *Plexus sacralis* and accompanying vessels, principally *Arteria ischiadica* (Baumel 1979b; not "femoral vessels" as labelled in McGowan's Figs. 9–11), as this neurovascular bundle emerges through Foramen ilioischiadica to enter the postacetabular region of the thigh. The distal (functional) attachment of this muscle in these avian groups includes an extensive linear attachment on the shaft of the femur, apparently separate from (but contiguous with) the femoral aponeurosis of *M. caudofemoralis* (see, e.g. McGowan, pp. 52–53).

If the *M. caudo-iliofemoralis* complex in birds is derived from the coccygeofemorales muscle system in reptiles, as suggested by Romer (1927), then *M. caudofemoralis* may be assumed to be the "primitive" component and to be of common occurrence among birds. Also, the principal morphological and functional relationships of this axial component would be correlated with the musculature of the tail (see Fisher 1957, Owre 1967, Baumel 1971, Cracraft 1971), rather than the pelvic limb.

M. iliofemoralis would then represent a secondarily derived, appendicular component (see Romer 1927) whereby the muscle set gained a stationary attachment to the postacetabular ilium (and ischium, in some species). This new morphological relationship may have been a primary anatomical adaptation that permitted subsequent hypertrophic development of the appendicular component and directly contributed to the evolution of a new functional modality for the caudo-iliofemoralis muscle complex. I hope to test this hypothesis for a myological correlate of a "form-function complex" (see Bock 1974) in a new study of this muscle complex in a sample of specimens from selected avian groups.

CONCLUSIONS

As Homberger (1980) mentions in her review of the "Nomina Anatomica Avium," our knowledge of avian anatomy is still incomplete in the sense of not having been checked and rechecked by countless researchers, and, indeed, there is a very real danger that inaccurate

or incomplete anatomical descriptions may be accepted as authoritative, more so than in human or veterinary anatomy, for example. In the previous discussion of a series of anatomical variants of selected muscles, as exemplified in *Apteryx*, I have attempted to demonstrate some aspects of the "incomplete" status of avian anatomy based on (1) descriptive myology, (2) probable misidentification or misrepresentation of muscles, and (3) morphological variations in a muscle set that have not been thoroughly examined in terms of a form-function complex.

Studies of the musculature of the pelvic limb in birds should continue to be a source of information on anatomical variation in somatic muscle patterns among vertebrates if the proper anatomical questions are first proposed. Then the relative development of individual muscles and/or functional groups of muscles, muscle structure (pennation, fiber types, aponeuroses, innervation, etc.), and musculoskeletal parameters of form and function should all contribute to the informational value of anatomical studies and to the interpretation of anatomical variation at several levels of scientific inquiry (see Cracraft 1971, Helmi and Cracraft 1977, Raikow 1978, Zusi and Bentz 1978, for several different applications). Unfortunately, until very recently the nomenclature for avian anatomy, especially the musculature, has been a source of considerable confusion, but the standardization of the anatomical nomenclature should help to alleviate this problem.

What is the present status of our knowledge concerning the myology of the pelvic limb in *Apteryx* relative to that in ratites and carinates? Somehow, it seems ironic that a comment by T. J. Parker (1891: 103–104) on "deficiencies" in the original papers of Owen might still be applicable nearly 100 yr later: "It is a curious circumstance that whenever subsequent observers have had occasion to correct the original description of *Apteryx*, the result has been to show the bird to be less aberrant and more typically avian than it was considered to be by the distinguished anatomist [i.e. Owen] to whom we owe our first knowledge of its structure."

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I have attempted to verify the morphological relationships of the muscles described by any investigator cited, with one or more illustrations of the

same in that text or some other related publication. I wish to thank W. J. Bock, J. Cracraft, S. L. Olson, R. J. Raikow, and R. L. Zusi for their respective critiques of a much longer and more detailed draft of this manuscript.

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