MUSCLES OF THE AVIAN HIP AND THIGH

BY A. BRAZIER HOWELL

AN increase of interest in the myology of birds is apparent. The more recent papers on the subject, however, concern themselves with a comparison of the muscles of different avian groups, and pay but slight attention to homologies. There have been few contributions toward an understanding of the latter, and most authors refer to Gadow's work of forty-six years ago (in Bronn's 'Klassen und Ordnungen des Tier-Reichs,' 1891). Exceptional in this respect have been two papers of Romer, one (Jour. Morph., 43: 347–385, 1927) on the development of the muscle groups of the pelvic limb of the chick, and another (Bull. Amer. Mus. Nat. Hist., 48: 533–552, 1923) that considers the muscles of birds rather incidentally with those of (chiefly) *Alligator*. Hudson's paper ('Studies on the muscles of the pelvic appendage in birds,' Amer. Midland Nat., 18: 1–108, 1937) is a notable contribution to our knowledge of interordinal variations of the muscles of the pelvic limb in birds, but unfortunately for the morphological myologist, he failed to consider the innervations, and hence his paper is of little use from this aspect.

Recently I have completed a study of the muscles of hip and thigh of all vertebrate classes, and the results of this, as bearing on mammalian homologies, are contained in a paper now in press, 'Morphogenesis of the architecture of hip and thigh.' This contains only minor references to the conditions in birds, however, for Aves are usually considered, whether rightly or wrongly, as being too specialized to have much bearing on the morphogenesis of other vertebrate classes. Accordingly it appears advisable to offer a separate paper dealing with birds. As the topographical myology of birds is well known, descriptions are reduced to the minimum compatible with a clear presentation. *Gallus gallus* was chosen as the subject for discussion, since it is a type relatively unspecialized and is easily procurable. It is deemed unnecessary to repeat the discussions offered in my paper referred to above; hence the two papers should be used together. A few pertinent points regarding the osteology are mentioned for a better understanding of the discussions.

The posture of birds varies considerably. In some, as penguins, loons, grebes, the position of the trunk, when on land, is largely vertical, in order to bring the center of gravity above the acetabula, and may be likened to that of man. In other sorts the body is inclined at an angle when at rest or while walking, but in many terrestrial types (as *Gallus*) the body is carried with its long axis almost parallel to the ground, a position assumed by no bipedal mammal nor extinct bipedal reptile without a heavy tail for a counterbalance. This is made possible by a relative decrease in the preacetabular and an increase in postacetabular weight. These different positions of the body have various effects upon the pelvic architecture and its controlling musculature. Of influence also is another factor of moment. As in man, the only exclusively bipedal mammal, so in birds, when travelling on land, the pelvic limbs are the sole support of the body, and supply exclusively the propulsive force. Because of the shift in the center of gravity and the fact that the abdomen is interposed between the thighs, the latter are less approximated than is usual in mammals.

As is to be expected, birds in general have a modified, or even an accentuated, reptilian type of pelvis, with an ilium extending for a relatively great distance both caudal and cranial to the level of the acetabulum, and fused solidly to the sacral vertebrae. The bar-like ischium is directed largely caudally and parallel to the ventral border of the ilium, while the pubis, also bar-like, is more variable in position, but is directed caudoventrally. Whether or not these bones are largely fused with their neighbors, there is always a vacuity between ilium and ischium for the passage of peroneal and tibial nerve branches, and between ischium and pubis for the passage of the obturator nerve and muscle.

In many, if not all, birds, including *Gallus*, the roots of the 'lumbar' plexus emerge from the sacral vertebrae, thus indicating that in this class the pelvis has experienced a secondary forward movement, doubtless induced by bipedal habits and the consequent shift in the center of gravity.

All striated muscles are arranged in pairs of groups,—prime movers and their antagonists,—although in the course of specialization of movements the distinctiveness of individual units of these two groups may become obscured. Similarly, nerves to muscles are arranged in corresponding dorsal and ventral branches, to primitive extensor and flexor muscle groups, respectively. Experience has abundantly shown that the innervation of a muscle is the most reliable criterion of its identity; but nerves are subject to evolutionary changes and not only must other factors, as topography in regard to other muscles and nerve trunks, be considered, but the evidence offered by the nerves themselves may be so obscured as to mislead even the most careful anatomist. On the whole, homologies that do not consider the innervations are valueless; if correct they chance to be so on the basis of incomplete evidence.

Because in tetrapods, including birds, the ilium has thrust dorsalward between the lumbar and sacral plexus, there are four main nerve groups and four corresponding muscle groups to the pelvic limb, one pair prozonal and the other metazonal, each pair comprising one dorsal and one ventral element. The femoral (dorsal) and obturator (ventral) are prozonal, but the latter has been secondarily encompassed by the pubis, as in other vertebrates, so that it now passes through the 'obturator foramen,' between pubis and ischium, and thus has become mesozonal. The peroneal (dorsal) and tibial (ventral) nerves are metazonal, passing between ilium and ischium. Even the highest, shortest branches to the deep hip musculature belong to one or another of these four nerve groups.

There is much evidence in comparative anatomy that in the basic tetrapod condition the dorsal nerve components (femoral and peroneal) innervated a single extensor muscle sheet in the thigh, with corresponding ventral nerve elements (obturator and tibial). This arrangement of single muscle sheets, in layers, dually innervated, still occurs in various degrees in lower tetrapods, and the general topography still suggests it in birds. It is noteworthy, however, that in Aves there is survival of original duality of innervation of but one primitive muscle complex, while there has been established but one new fusion of two unrelated muscle units (biceps and femorocrural), and this incompletely. Thus the primitive condition in mammals, in which there appears to have been segregation of all muscle units into singly innervated slips, is approached.

In spite of the extreme specialization of birds there are only a few muscles of hip and thigh (such as femorocruralis, obturator, insertion of ambiens) that have become markedly altered, and even these, for the most part, present no great difficulty. The remainder, with few exceptions, are readily homologized with the muscles of tetrapods when all pertinent factors are considered. Within the class, however, there is considerable variability in muscle pattern.

Unfortunately the names of the muscles of the vertebrates below mammals are in a state of great confusion; the chief reason is that many of them are compounds of mammalian units. The terms used herewith are those based on the group (extensor or flexor), origin and insertion, or else the homologous mammalian names where there is little or no doubt of the equivalence. Following the name of each muscle I have placed in parenthesis the comparable terms used by Gadow and Hudson, when these differ from mine.

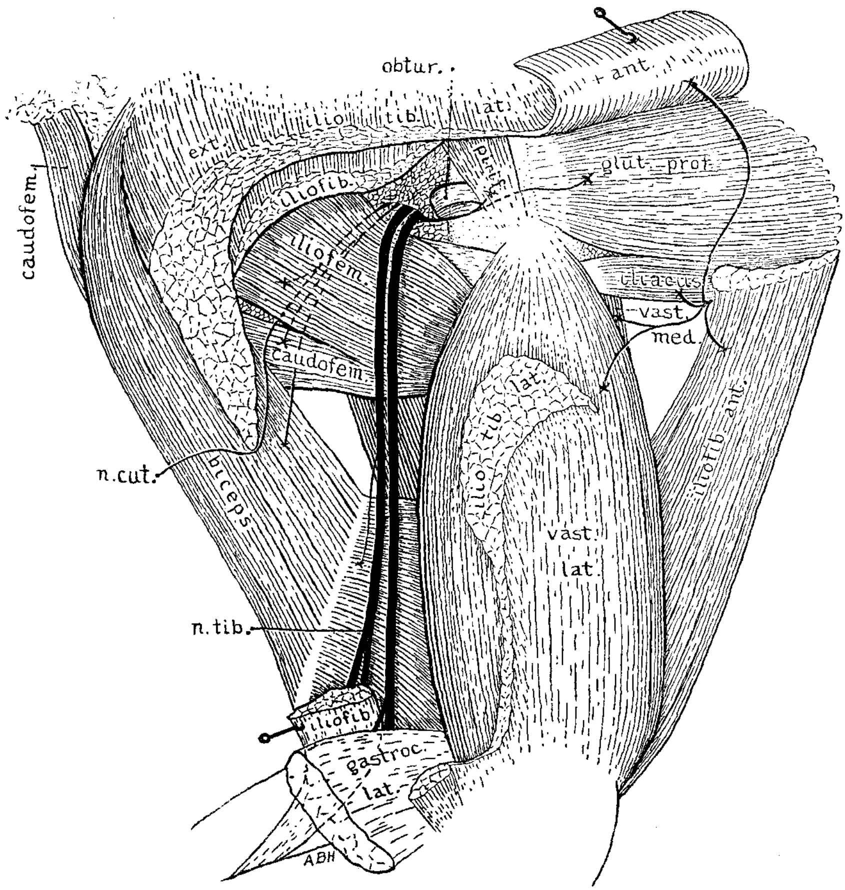
DORSAL (EXTENSOR) DIVISION

Coxocrural extensors consist of a superficial dual sheet (iliotibialis); an anterior derivative of this; an ambiens; and an extensor iliofibularis.

M. extensor iliotibialis lateralis has origin from the dorsal fascia. The insertion of the cranial part has retreated in *Gallus* and now ends on fascia. The caudal part inserts only slightly on the tibia and mostly upon the surface of the vastus lateralis. Femoral and peroneal nn.

M. extensor iliotibialis anterior (i. internus Gadow) is an anterior derivative of the last, from the dorsal margin of the anterior ilium, inserting medial to the knee. Femoral n.

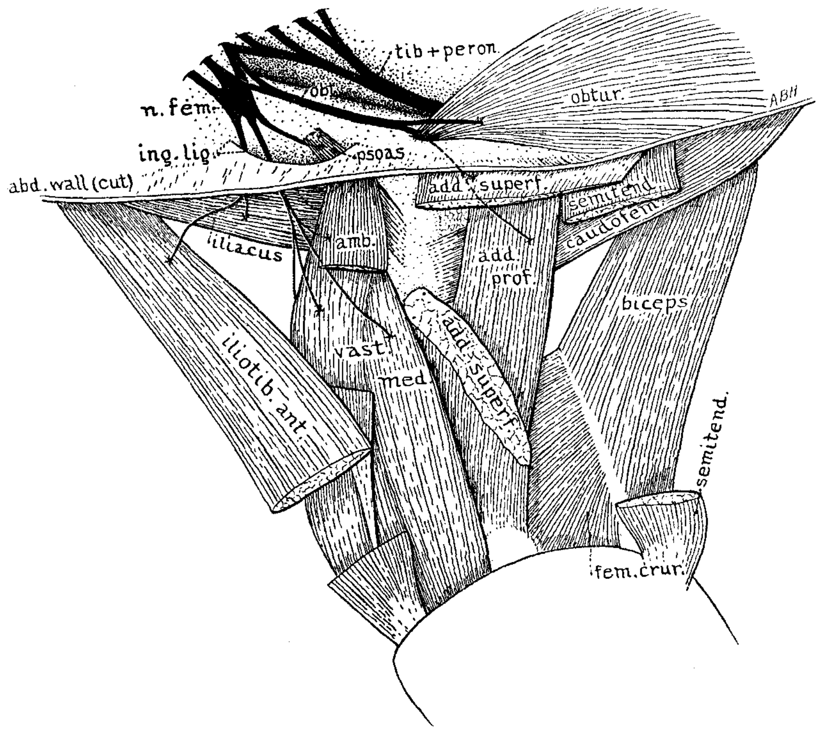
M. ambiens arises from the spine of the pubis, develops a slender tendon that passes deep to the iliotibialis anterior, then lateralward deep to the patellar tendon, and is inserted in the complicated manner characteristic of birds. It is undeveloped in many genera. Femoral n.



TEXT-FIG. 1.—Lateral view of right hip and thigh of *Gallus*, with some of the muscles cut to show deeper details.

M. extensor iliofibularis (biceps femoris Hudson).—Origin is from the dorsal border of the entire caudal half of the ilium, deep to iliotibialis lateralis. Insertion is on a marked process of the fibular shaft medial to the lateral gastrocnemius, by a long tendon passing through the usual (in birds) tendinous sling. It is very uniform in birds, and it is interesting that in this class it passes medial to the lateral gastrocnemius, but lateral to that muscle in mammals. In other words, in one class this head has developed and extended lateral to the iliofibularis, as well as to the peroneal nerve, while in the other class (and in Reptilia) it passes medial to both. Peroneal n.

As in reptiles, the more cranial part of the lateral iliotibialis (peroneal n.) is a gluteus superficialis, and is homologous with the mammalian gluteus longus (femorococcygeus) and gluteus maximus. The more cranial part



TEXT-FIG. 2.—Medial view of right hip and thigh of *Gallus*, with abdominal wall cut close to pelvis to show lumbosacral plexus and origins of neighboring muscles.

(femoral n.) and the anterior iliotibial division together are equivalent to the sartorius element. Whether both are represented by the mammalian sartorius or which one, is impossible to say. The evidence indicates that the anterior iliotibial has split off from the lateral sheet; hence in birds there is no long extensor unit that could represent a part of the vastus lateralis that migrated over the hip joint to become a two-joint extensor, and accordingly in this class the rectus femoris is undeveloped.

It is characteristic of the ambiens that it arises medial to the iliacus and accordingly is associated with the vastus medialis, from which it is believed to have been derived by proximal migration of its origin, as the rectus femoris of tetrapods was formed from the vastus lateralis. The element is present in reptiles (*Iguana*) and absent in mammals. Why birds developed such a tortuous insertion of this muscle is unknown.

The extensor iliofibularis appears to constitute a layer that has split from the deep surface of the caudal (peroneal n.) part of the lateral iliotibialis. It is about as far removed from relationship with biceps femoris as could well be, but is the avian representative of the tenuissimus of mammals.

Femorocrural extensor (femoritibialis Gadow, Hudson) comprises a *vastus lateralis,* and a *vastus medialis* that occurs in two divisions. Evidently developed from a single mass, origins of the two parts have separated and migrated proximally, the lateralis to the base of the greater trochanter and the latter to the medial neck of the femur between iliacus and psoas. There is no part of the vasti in this situation in mammals, and accordingly this part, and its derivative, the ambiens, are undeveloped in that class.

Coxofemoral extensors occur in prozonal (femoral n.) and metazonal (peroneal n.) parts. The former comprises iliacus and psoas elements, and the latter the other gluteal units mentioned.

M. iliacus (iliotrochantericus anterior Gadow, Hudson).—The term iliacus is permissible for this muscle as there appears to be no doubt of its homology. In *Gallus* it arises ventrolateral to the gluteus profundus from the more lateral part of the gluteal fossa of the ilium, and inserts distal to the greater trochanter, between the origins of the two vasti. Femoral n.

M. psoas (iliofemoralis internus Gadow, iliacus Hudson) is a very small muscle arising from the ventral surface of the pelvis. It emerges with the femoral nerve from the abdominal cavity beneath the "inguineal ligament" and inserts upon the "lesser trochanter" just caudal to the origin of the vastus medialis. Femoral n.

The avian "iliotrochanterici" (gluteus profundus, iliacus, psoas) of Gadow are variable in the number and arrangement of the slips. The gluteus and iliacus can be identified on the basis of innervation, while the psoas has a diagnostic origin.

It is noteworthy that in *Gallus,* and apparently generally in birds, the insertions of iliacus and psoas are separated by the origin of the vastus medialis, which undoubtedly has secondarily migrated proximally to this position, rather than caudal (or medial) to both, as in *Iguana.* This need occasion no surprise, however. The bellies of the muscles are widely separated, doubtless because of the exigencies of avian specialization. Both are innervated by the femoral nerve, and the anterior unit, arising from a situation comparable to that in many mammals, clearly is to be identified as an iliacus, while the posterior one must be comparable to the unit termed psoas major, at least, in mammals.

M. gluteus profundus (iliotrochantericus posterior Gadow, Hudson).—This is a single mass, from the gluteal fossa of the ilium, inserting upon the cranial border of the greater trochanter. Deep (anterior) gluteal branches of peroneal n.

M. piriformis (iliofemoralis externus Gadow, gluteus medius et minimus Hudson) is absent in many birds. In *Gallus* it is a narrow, partly tendinous slip from the margin of the ilium dorsal to the acetabulum, inserting upon the dorsal part of the greater trochanter. Branch of the nerve to the gluteus profundus.

Gluteus profundus and piriformis comprise the same element that gives rise in mammals to gluteus medius and minimus, piriformis, and tensor fasciae latae, the units innervated by the superior gluteal nerve. In *Gallus* these two glutei are undivided, tensor fasciae latae is not developed, and piriformis occupies its mammalian position. The last muscle may not be in birds the precise equivalent of that in mammals, but it simulates it closely enough to receive the same name, being a slip obviously separated from the posterior border of the deep gluteal matrix.

VENTRAL (FLEXOR) DIVISION

M. caudofemoralis (caudiliofemoralis Gadow, piriformis Hudson).—This muscle has a caudal origin and passes between the two crural flexors to insert upon the femur. It is a representative of the element of the same name in reptiles, and hence is not basically a member of the ventral division of the limb, but has become so, receiving its innervation by a crural flexor branch of the tibial n. Its homologue in mammals is the presemimembranosus, at times fused with adductor magnus. It has nothing whatever to do with the piriformis, a muscle of the dorsal division. It shows great variability in birds.

In amphibians, reptiles, and mammals, a superficial two-joint sheet, dually innervated, split from the medial part of the flexor musculature, giving rise to a puboischiotibial layer in amphibians and reptiles, and to gracilis and one of the crural flexors (probably semimembranosus) in mammals. In birds it seems that this sheet did not become differentiated, and hence did not develop a two-joint character. Accordingly birds lack a gracilis and apparently one of the crural flexors that occur in mammals. Instead they have an adductor mass, occurring in two layers, and two crural flexors, neither of which inserts upon the lateral crus as does the mammalian biceps femoris.

Coxocrural flexors, in birds, consist of but two units, as follows:

Flexor cruris medialis (ischioflexorius Gadow, semimembranosus Hudson) arises from the ischiopubis (partly between the two) lateral to the origin of the adductor profundus. Insertion is upon the tibia. It is always present in birds. Crural flexor branches of tibial n.

M. flexor cruris lateralis (caudilioflexorius Gadow, semitendinosus Hudson) arises from the caudal process of the ilium, passes lateral to the caudofemoralis, and inserts chiefly upon a raphe common to this and the femorocruralis, but partly upon the fascia of the medial gastrocnemius. Absent in some birds. Crural flexor branches of tibial n.

As the most medial sheet of the ventral musculature is undeveloped in birds, it is logical to infer, but is not certain, that the most medial,—semimembranosus,—is the crural flexor that is lacking in Aves. The flexor cruris medialis should then be equivalent to semitendinosus and the lateralis to biceps femoris of mammals. The basis of the latter interpretation is not only topography in general, but the fact that it connects by a raphe with the femorocruralis, which will be further discussed under the last-named muscle. Both of these crural flexors represent the caudal (tibial n.) part of the adductor mass and have split therefrom at some stage of their phylogeny. The fact that the more lateral is lateral to the caudofemoralis and that the latter muscle is also lateral to the adductor mass, probably means merely that this crural flexor had already become differentiated at the time that the caudofemoralis migrated to a femoral insertion via a fascial plane.

Coxofemoral flexors comprise two layers of adductors (pubo-ischiofemoralis Gadow), obturator, and two layers of short tibial flexors.

M. adductor superficialis (pubo-ischiofemoralis (part) Gadow, adductor longus Hudson) arises from the pubis (?) and inserts upon most of the femur. Obturator n. No tibial innervation was detected, but if it receive this additional innervation (as in *Iguana*) it would not be unexpected, this then indicating that crural flexor fibers had remained fused with it.

M. adductor profundus, deep to the last (pubo-ischiofemoralis (part) Gadow, adductor brevis Hudson), arises from the ischiopubis (perhaps only one element, but I could not be certain) and inserts upon most of the femur. The two adductors, occasionally fused, seem largely uniform in birds. Obturator n.

M. obturator (part with tendinous insertion, obturator internus Hudson; part with fleshy insertion, obturator externus Hudson) arises from within the pelvis over a broad area, passes through the obturator foramen, and inserts by a large round tendon, accompanied by a few muscle fibers, upon the caudal aspect of the greater trochanter, passing around the caudal aspect of the bone. It is uniformly present in Aves. Obturator n. to the fleshy belly.

The adductor superficialis, superficial to the terminal part of the obturator nerve, is the homologue of the pectineus and adductor longus of mammals. The deep adductor is the equivalent of the mammalian adductores brevis et magnus. In origin the obturator is somewhat suggestive of the mammalian obturator internus, for which it has uniformly been mistaken.

That the latter interpretation is incorrect, however, is attested by the facts that it receives twigs of n. obturatorius within the pelvis, passes *through* the obturator foramen rather than dorsal to the border of the ischium, and it is segregated from any muscle with tibial innervation. Insertion has shifted only to a slight and unimportant degree as compared with that of the mammalian obturator externus, and beyond question it is the equivalent of that muscle. The stimulus for a longer muscle, has been the same, resulting in the extension of origin to within the pelvis of the externus in birds and the internus in mammals, but the obturator internus is an extension of a part of the gemellus mass and this does not occur in any vertebrate class but Mammalia.

The short tibial flexors of the hip comprise a superficial *flexor iliofemoralis* and directly deep to it a thicker *flexor ischiofemoralis* of equal extent, the names of which indicate the origin. Both insert upon the caudal aspect of the greater trochanter, the former fleshily and the latter by a broad tendon. Both are innervated by twigs accompanying the crural flexor nerves, from the tibial, but the nerves to the crural flexors pass between the two. Hence the iliofemoralis is superficial (lateral) to these nerves. There is no mammalian muscle with the same characteristic. It seems to be a peculiar and unique development in birds,—a thin sheet of muscle that has extended along a fascial plane. It *could* have developed from either the caudofemoralis or the ischiofemoralis (there appears no other source from which it could come), but why, in either case, it should pass lateral to the nerves is difficult to understand. I have no convictions in this regard based on my own work, but Romer's (1927) embryological evidence seems to place it with the caudofemoralis, and I follow this allocation tentatively.

The ischiofemoralis element represents the tibial flexors of the hip in mammals,—quadratus femoris and the gemellus mass (with its undifferentiated obturator internus).

Femorocrural flexors consist of but one unit,—*m. femorocruralis* (accessorii m. obturator Gadow, accessorius semitendinosi Hudson). It appears to be extremely variable in birds and often appears to be unrepresented, but in *Gallus* it passes from the distal half of the shaft of the femur to the raphe that it shares with the more lateral crural flexor, while its more distal fibers continue to the fascia of the medial gastrocnemius, in fact almost merging with that muscle. Tibial n. Gadow gave the innervation as a fine twig of n. obturatorius. I sought such innervation without success on six limbs of *Gallus*. The innervation is by the most filamentous of twigs of n. tibialis, diverging from the main nerve in the middle of the thigh. They were almost too fine to determine grossly, and verification was secured by faradic stimulation of the nerves on two live fowls under anaesthetic.

Homologies of muscles of hip and thigh in Iguana, Mammalia, and Gallus

(F) indicates innervation by the femoral nerve; (O) by the obturator (both prozonal); (P) by the peroneal; and (T) by the tibial nerve (both metazonal).

	Iguana	*Mammalia*	*Gallus*
Caudofem.	caudofemoralis (2)	caudofemoralis	caudofemoralis —(iliofemoralis?)
Coxocrural extensors	undeveloped	(F) rectus femoris	undeveloped
	(F) pubotib.anter. (F) pubotib.med.c.prof.	undeveloped	(F) ambiens
	(F) pubotib.med.c.superf.	(sart.accessor.?)	(F) sartorius
	(F-P) iliotibialis	(F) sartorius (P) gluteus longus (P) gluteus maximus	(F+P) iliotibialis
	(P) iliofibularis	(P) tenuissimus	(P) iliofibularis
Femorocrural extensors	(F) vastus lateralis	(F) vasti	(F) vastus lateralis
	(F) vastus medialis	(F) undeveloped	(F) vastus medialis
	(P) none	(P) none	(P) none
Coxofemoral extensors	(F) pubo-ischiofem.	(F) iliacus (F) psoas	(F) iliacus (F) psoas
	(P) iliofemoralis	(P) gluteus medius (P) gluteus minimus	(P) gluteus prof.
		(P) piriformis	(P) piriformis
		(P) tensor fasciae fem.	undeveloped
Coxocrural flexors	(O+T) pubo-ischiotib. (T) flex.cruris	(O) gracilis	undeveloped
		(T) semimembranosus	undeveloped?
		(T) prox.pt.biceps fem.c.long.	(T) flex.cruris lat.?
		(T) semitendinosus	(T) flex.cruris med.?
Coxofemoral flexors	(O+T) adduc.fem.	(F.sic) pectineus (O) adductor longus	(O) adduc.superf.
	(O+T) pubo-ischiofem.	(O) adductor magnus (O) adductor brevis (O) obtur.extern.	(O) adduc. prof.
	(T) ischiotroch.	(T) gemelli (T) obtur.intern. (T) quadratus fem.	(T) ischiofem.
Femorocrural flexors	unrecognizable	(T) dist.pt.biceps fem.c.long.	(T) femorocruris

In the interpretation of this muscle there appear to be but two possibilities: either it is a proximal migration of the medial gastrocnemius, which its conformation seems to suggest, or it represents the femorofibularis of Caudata. The point at which its nerve diverges from n. tibialis, and the fact that in life it is seen to be a "white" muscle, while the gastrocnemius is "red," renders the second hypothesis the more attractive. The difference in insertion in Caudata and *Gallus* is a matter of small importance, for there is abundant evidence that the insertions of the crural flexors at least can shift about over the fascia of the posterior crus to any situation best suited to particular function. Similarly, it is tentatively believed that the same element now forms the distal part of the mammalian biceps, and so it is logical to term as biceps the crural flexor with which it is functionally fused in birds.

It should again be stressed that no claim is made that all the above homologies have been established. Cases of individual muscles have been argued according to the evidence that is available to me, and the homologies that seem most reasonable have been chosen for inclusion in the table, some of them only tentatively. It is hardly possible that every one of them will stand the test of time.

Department of Anatomy
Johns Hopkins University
Baltimore, Maryland