

## THE THIGH MUSCULATURE OF THREE SPECIES OF SCOLOPACIDAE

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This paper reports the results of a comparative study of the thigh musculature of three species of the family Scolopacidae, the snipes, woodcocks, and sandpipers. In 1874 Garrod first presented a formula for representing the presence or absence of certain muscles in the thighs of birds. Hudson (1937) has since modified the original formula, which now includes: A = M. piriformis, pars caudofemoralis; B = M. piriformis, pars iliofemoralis; C = M. iliotrochantericus medius; D = M. gluteus medius et minimus; X = M. semitendinosus; Y = Accessorius semitendinosi; Am = M. ambiens. "V" in the formula indicates a vinculum connecting the tendon of M. flexor perforatus digiti III with that of M. flexor perforans et perforatus digiti III.

The muscle formula of the family Scolopacidae, as represented by *Totanus melanoleucus* and *T. flavipes*, was reported to be ADXYAmV by Hudson (1937). Previously, Beddard (1898) had reported the abbreviated formula of AXY+ (D and V having been added to the formula by Hudson) for the scolopacids *Calidris* (= *Tringa*), *Gambetta* (= *Totanus flavipes*), *Gallinago* (= *Capella gallinago*), *Limosa*, *Machetes* (= *Philomachus*), *Scolopax rusticola*, *Strepsilas* (= *Arenaria interpres*), "*Totanus*," and *Tringa* (= *Calidris canutus*). When Witherby *et al.* (1940) and Verheyen (1958) listed *Limnodromus* as having the formula ABXY, it appeared that the muscle formula A(D)XY was not constant within the Scolopacidae. Verheyen (1958) also reported the formula of *Numenius* and *Aechmorrhynchus* as being ABXY, and Lowe (1931) found the same condition in *Bartramia*.

The purposes of my study were to check the muscle formula of *Limnodromus* and to ascertain the formula of *Tryngites*, which apparently has not been previously reported. A comparative study of the thigh musculature of *Limnodromus griseus*, *Capella gallinago*, and *Tryngites subruficollis* was then undertaken.

A total of eight alcoholic specimens from the collection at The University of Michigan Museum of Zoology were examined. These specimens included: three *Limnodromus griseus*, two *Tryngites subruficollis*, two *Capella gallinago* (one was a partial specimen), and one *Totanus flavipes*. The presence or absence of the formula muscles was noted, and the origins and insertions of most of the thigh muscles and the peroneal muscles of the three species studied were recorded. No innervations were examined during this study. The terminology of the musculature follows Berger (1960).

*Muscle formulae.* Upon examining three specimens of *Limnodromus griseus*, I found the muscle formula to be ACDXYAm. M. piriformis, pars iliofemoralis ("B") was not present in any of the scolopacids that I studied. The formula for *Tryngites* is also ACDXYAm as it is in *Capella gallinago* and *Totanus flavipes*. I did not investigate the condition of the vinculum, V in the muscle formula, because Berger (1960:307) stated that it could be found in all birds "except in some Ardeidae, *Upupa*, and the Passeriformes (except Eurylaimidae)."

*Peroneal muscles.* Mitchell (1913:1068) stated that "with a few, a very few, exceptions . . . there is a close conformity between the conditions of the peroneals and what appears to be the most securely founded systematic division." Berger (1960) felt that the condition of the M. peroneus longus and M. peroneus brevis might be helpful in determining closeness of relationship on the generic or subfamilial level.

Mitchell (1913) reported that in the scolopacids *Limosa*, *Gallinago*, and *Scolopax* the *M. peroneus longus* was a superficial muscle with a fascial origin from the tibiotarsus and with very little deep origin from the edge of the fibula; the *M. peroneus brevis* was reduced in size and arose from the proximal part of the fibula and adjacent tibiotarsus. I have observed the same condition in the peroneals of *Limnodromus*, *Tryngites*, and *Capella*. There were essentially no differences in the condition of the peroneals in the three species I examined. In each case, the *M. peroneus longus* was much more extensively developed than was the *M. peroneus brevis*.

*Comparative musculature of the thigh.* In studying the thigh muscles of *Limnodromus*, *Tryngites*, and *Capella*, I have compared the condition found in those birds with the generalized account of pelvic musculature given by Berger (1960). Reported here will be only those muscles whose condition seems to be distinctive.

*M. ilioprochantericus medius* ("C" of Hudson's revised muscle formula). In the three birds reported on in this paper, this muscle is separable from *M. ilioprochantericus anterior*, and I believe it is distinct enough to be included in the muscle formula. Hudson (1937) reported these muscles to be fused in *Totanus flavipes* and *T. melanoleucus*. I have checked *T. flavipes*, and the muscle appears to be separable from *M. ilioprochantericus anterior*. *M. ilioprochantericus medius* appears to have a distinct insertion on the anterior edge of the femoral shaft just dorsal to the insertion of *M. ilioprochantericus anterior*.

*M. femorotibialis externus*. This muscle has two bellies in the species I have studied. A lateral belly arises proximally from the lateral and posterior edges of the femur just distal to the insertion of the *M. ilioprochantericus anterior*; this belly covers the posterior belly. It contributes to the patellar ligament and inserts via a tendon to the proximal tibial crest. The posterior belly arises from the distal posterior half of the femoral shaft and inserts via a tendon on the lateral tip of the proximal tibial crest; it also contributes to the patellar ligament.

I could find no significant differences in the condition of this muscle in the three species studied here.

*M. femorotibialis medius*. This muscle arises from the proximal anterior edge of the femur. Along most of its length it is in close connection with the lateral belly of the above muscle. It, too, inserts on the proximal crest of the tibia and contributes to the patellar ligament.

The condition of this muscle is constant in the three species.

*M. femorotibialis internus*. This muscle has one tendon of insertion in the three species studied.

*M. piriformis, pars iliofemoralis* ("B" in Hudson's formula). This muscle is missing in all three species.

*M. piriformis, pars caudofemoralis* ("A" in Hudson's formula). This muscle is present in each of the three species, and it originates via a tendon from the fascia of the depressor muscles of the tail and from the ventral tip of the pygostyle. The insertion is fleshy and inserts one third of the way distally on the posterior edge of the femur in *Limnodromus* and *Tryngites*; in both of these species the muscle is about 6 mm wide in the middle of the belly. In *Capella* the *pars caudofemoralis* is reduced in size, being only about 2 mm at its greatest width, and it inserts on the femur one third of the way distally via a thin tendon. The origin of this muscle in *Capella* is also very weak (see figs. 1-3).

*M. semitendinosus + accessorius semitendinosi* ("X" and "Y" in Hudson's formula). The condition of this muscle is essentially the same as that described by

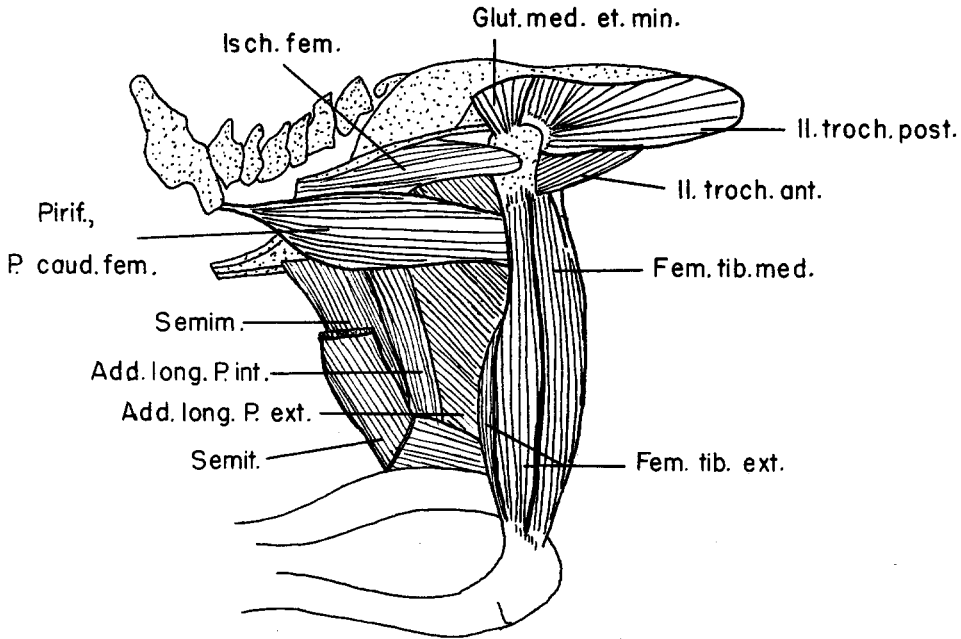


Figure 1. *Limnodromus griseus*. Lateral view of the right leg showing the third layer of muscles. The following abbreviations have been used in all figures: Add. long. P. ext.—M. adductor longus, pars externus; Add. long. P. int.—M. adductor longus, pars internus; Fem. tib. ext.—M. femorotibialis externus; Fem. tib. med.—M. femorotibialis medius; Glut. med. et min.—M. gluteus medius et minimus; Il. troch. ant.—M. iliotrochantericus anterior; Il. troch. post.—M. iliotrochantericus posterior; Isch. fem.—M. ischiofemoralis; Pirif. P. caud. fem.—M. piriformis, pars caudofemoralis; Semim.—M. semimebranosus; Semit.—M. semitendinosus + accessorius semitendinosi. In each of the figures the following muscles have been wholly or partly removed: M. biceps femoris, M. gastrocnemius, pars externus, M. iliotibialis, M. sartorius, and M. semitendinosus.

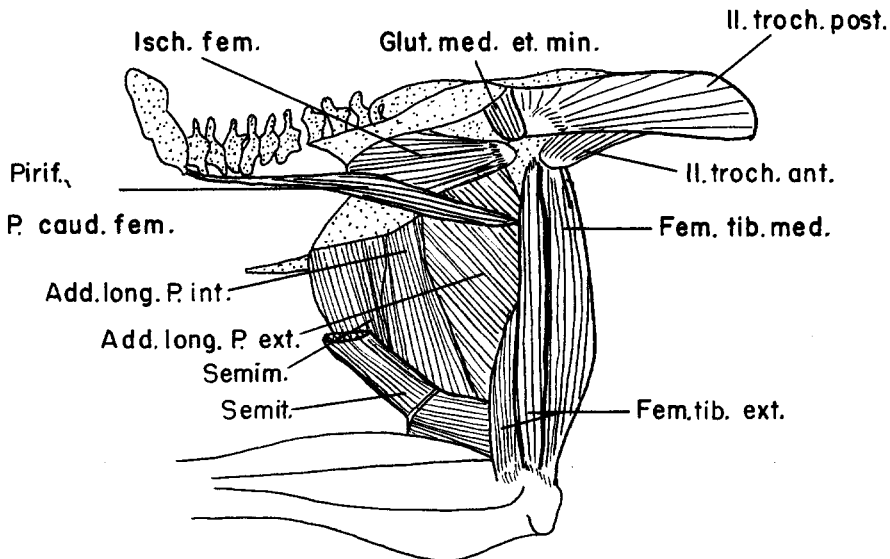


Figure 2. *Capella gallinago*. Lateral view of the right leg showing the third layer of muscles.

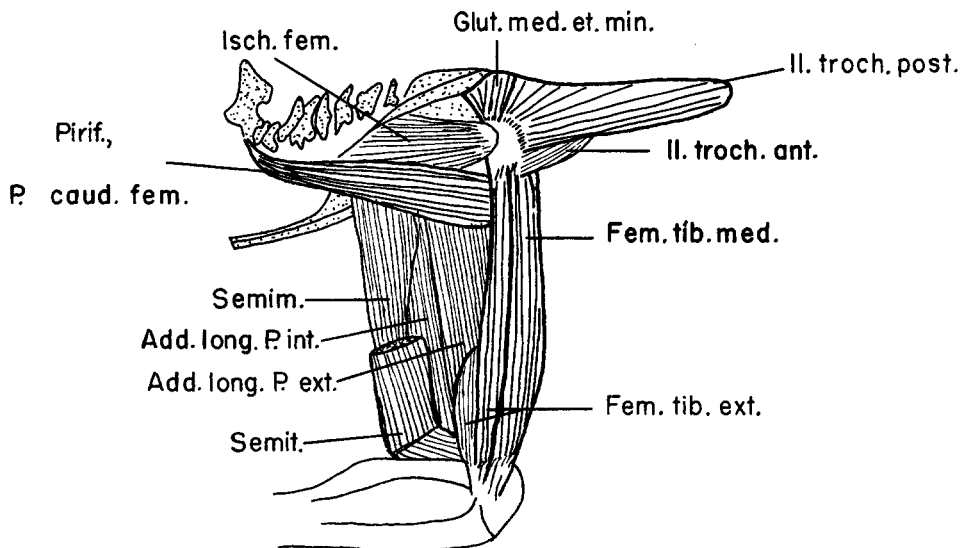


Figure 3. *Tryngites subruficollis*. Lateral view of the right leg showing the third layer of muscles.

Berger (1960). The raphe of the accessorius semitendinosi inserts on the fascia of *M. gastrocnemius, pars media*.

I found no significant differences in this muscle in the three species studied.

*M. adductor longus et brevis*. A pars externa and pars interna are present in all three species. The pars interna originates from the lateral surface of the pubis by a broad, thin tendon. In all three species the belly of pars interna is split by a triangular tendinous area.

From the above report of the thigh-muscle formulae, peroneal muscles, and comparative thigh musculature, it is seen that the three species, *Limnodromus griseus*, *Tryngites subruficollis*, and *Capella gallinago*, are quite similar in these respects. The muscles represented by the formula ACDXYAm are present in the three species, and the condition of the peroneals agrees with that reported for other scolopacids by Mitchell (1913).

The only significant difference found in the thigh musculature was the reduced condition of *M. piriformis, pars caudofemoralis* in *Capella gallinago*. Only two examples of this species were examined (one was a poorly preserved partial specimen), so that an anomalous condition cannot be discounted. Berger (1956) warns that morphological variation is the rule, not the exception.

If pars caudofemoralis is reduced in *Capella*, however, there might be interesting functional correlations involved. Hudson (1937) states that the action of this muscle upon contraction is to pull the femur backwards and the tail laterally and downwards. Berger (1952) adds that the pars caudofemoralis also elevates the anterior portion of the longitudinal axis with the head of the femur serving as a fulcrum.

In *Limnodromus* and *Tryngites*, in which the pars caudofemoralis is strongly developed, this muscle might be an effective flexor of the thigh. In *Capella*, where it is weakly developed, the pars caudofemoralis probably acts only on the tail. Fisher

(1946:666) stated that in *Cathartes* and *Coragyps* "the weak tendinous condition of the pars caudofemoralis and the absence of the pars iliofemoralis make the action of the muscle effective chiefly on the tail."

In comparing the behavior of the three species studied, it might be seen why the pars caudofemoralis is strong in *Limnodromus* and *Tryngites* and is reduced in *Capella*. Witherby *et al.* (1940) give brief accounts of the habits of these three species. Both *Limnodromus griseus* and *Tryngites subruficollis* display on the ground during their breeding seasons; *Limnodromus* also has an aerial display. *Tryngites* is quite terrestrial and runs from intruders in a zig-zag manner along the ground. Only ground displays were reported for *Tryngites*.

*Capella gallinago* has both a ground and an aerial display. In both types of courtship behavior, the tail is spread. During its aerial display *Capella* produces sound primarily by the vibration of its two outer tail feathers; slow quivering of the half-opened wings serves to modulate the rapid quivering of the tail feathers, so that a tremulous quality of sound is generated (Witherby *et al.*, 1940:199). When flushed, the bird resorts to immediate flight rather than a running escape.

From this brief account of the differences in behavior, it would seem that *Limnodromus* and especially *Tryngites* are quite "cursorial," whereas *Capella* is more aerial and uses its tail more while displaying. Perhaps these differences in behavior have some bearing on the functional development of *M. piriformis*, pars caudofemoralis. Perhaps *Capella* uses the muscle in lowering and moving the tail while displaying. In contrast, *Limnodromus* and *Tryngites* may use pars caudofemoralis principally as a flexor of the femur in walking and displaying on the ground.

In conclusion, it can be seen that in the small part of the total morphology studied these three species are quite similar. The muscle formula of *Limnodromus* and *Tryngites* is ACDXYAm. The condition of the peroneal muscles and other thigh muscles examined was very similar in all three species. In assigning relationships among birds, the myology (especially the muscle formula) is only a fraction of the evidence needed to complete the picture. It seems, however, that just as "heritage" or a common genetic background operates on external morphology in closely related species and genera, "heritage" should play a part in molding the myological features. In considering the total musculature, it would appear that the greater the degree of relatedness, the greater the number of similarities in musculature.

Only a small number of muscles have been examined in this study, so I feel that nothing can be said of the degree of relatedness among *Limnodromus*, *Capella*, and *Tryngites*. It would be very interesting to study a large number of examples of the Scolopacidae to ascertain the amount of myological variation that exists in this family and to see whether comparative myology can serve as a useful tool in assigning relationships among birds below the familial level.

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