THE HINDLIMB MUSCULATURE OF THE MOUSEBIRDS (COLIIFORMES)

SUSAN L. BERMAN[1] AND ROBERT J. RAIKOW

Department of Biological Sciences, University of Pittsburgh, Pittsburgh, Pennsylvania 15260 USA

ABSTRACT.—The hindlimbs of two species of mousebirds (*Colius striatus* and *C. leucocephalus*) were dissected in order to provide myological descriptions, to elucidate the mechanism of digit rotation and other characteristic locomotor habits, and possibly to yield clues to the systematic position of the order Coliiformes. Among the myological peculiarities, the unusually large M. iliofemoralis externus, the accessory belly of M. pubo-ischio-femoralis, and the extensive femoral insertion of M. flexor cruris lateralis and origin of M. flexor hallucis longus are features related to the hanging postures of the Coliiformes. Digit rotation is accomplished primarily by enlargement and slight changes in the insertions of four intrinsic foot muscles. Two small intrinsic foot muscles, not previously described in birds, also appear to be associated with digit rotation. In the species dissected, the extensor digitorum longus tendon sends a branch to the hallux as well as to the three forward digits. This condition has previously been described only in the Psittaciformes, and may possibly suggest a common ancestry for the two orders. *Received 16 March 1981, accepted 21 July 1981.*

THE Coliiformes is an order of birds inhabiting scrub and lightly wooded areas of sub-Saharan Africa. The single genus *Colius* includes six living species commonly called colies or mousebirds. They are differentiated primarily on the basis of plumage (Sclater 1903, Friedmann 1930, Chapin 1939, Mackworth-Praed and Grant 1962). Whereas the systematics within the order are not a problem, because of certain peculiarities in their habits and morphology the relationship of the Coliiformes to other avian orders has always been uncertain. At various times and for various anatomical and behavioral reasons, affinities to the Passeriformes, Piciformes, Psittaciformes, Coraciiformes, Apodiformes, and Caprimulgiformes have been suggested (Murie 1872, Garrod 1896, Pycraft 1907, Lowe 1948, Verheyen 1956). Ballman (1969: 192–195) studied fossil mousebirds from the Miocene of France. He briefly described several skeletal elements, and corrected errors of family allocation made by earlier workers.

The most conspicuous feature distinguishing the Coliiformes from other birds is their ability to rotate both the first and fourth hindlimb digits to either a cranial or caudal position. This gives them the option of being anisodactyl, zygodactyl, or pamprodactyl (Fig. 1). Our extensive observations of living mousebirds reveal no correlation between any digit configuration and any particular activity. Whatever position is most effective for the object being grasped is the one put to use. As indicated in Fig. 1, the same configuration is not necessarily most appropriate for both feet at the same time.

In addition to the peculiarities of their feet, mousebirds are capable of a variety of very odd movements and postures, which are accompanied by some unlikely contortions of the hind limb. They creep rapidly through dense vegetation in a rodent-like manner, with the longitudinal axis of the body parallel to the branch they are grasping. They are seldom seen perching in a conventional position. When resting, even for a moment, there is usually a tendency for the body to drop below the feet, so that the bird is hanging to some degree (Fig. 1).

Mousebirds use their hindlimbs extensively in feeding. Small food items are held in one foot in a parrot-like manner, while the bird hangs or supports itself by the other (Fig. 1). The foot has considerable manipulative ability when used in this way, the digit configuration being modified as the item is consumed and changes shape.

Finally, our observations of the use of the

[1] Present address: Department of Biology, College of the Holy Cross, Worcester, Massachusetts 01610 USA.

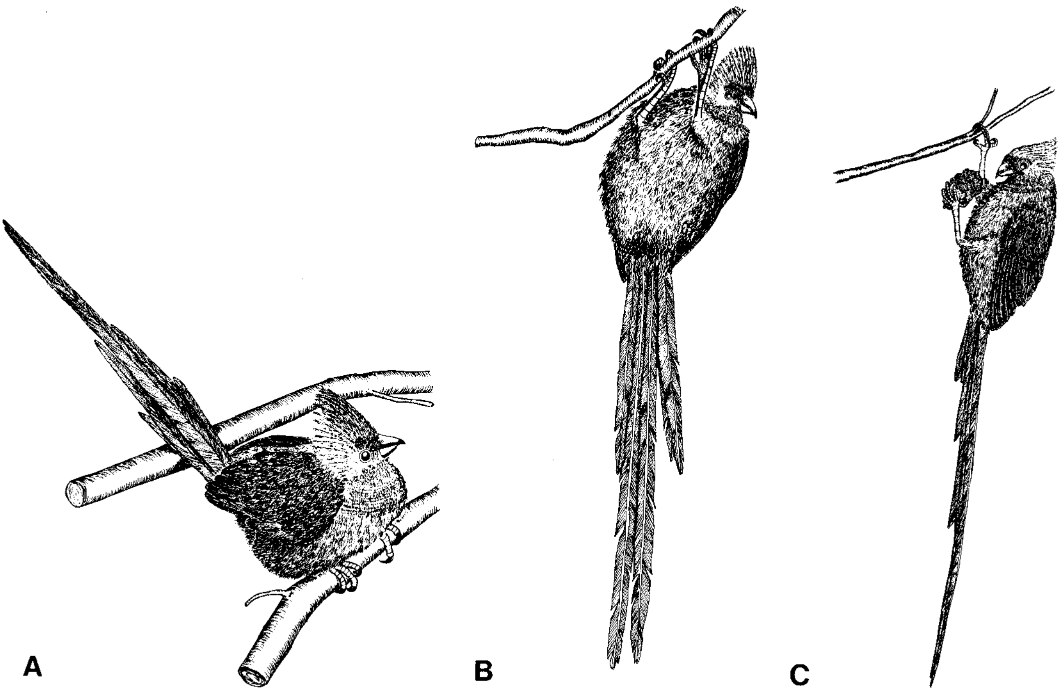


Fig. 1. A. *Colius striatus* "perching," with the right and left feet in anisodactyl and zygodactyl configurations, respectively. Note the tendency for the body to sink downward on the perch, and the use of the tail in bracing. B. *Colius striatus* in the typical hanging position. Note the pamprodactyl digit configuration. C. *Colius striatus* in a typical feeding posture. Note the use of the foot in holding food, and the use of only digits II and III in hanging. Drawn from photographs with the aid of a camera lucida.

hind limb during aggressive encounters are noteworthy. A common sequence was for one bird to approach another, raise its foot, and either use it in grasping the subordinate bird's head, or, if the latter began to move away, grasp its tail and pull the bird off its perch.

Despite the odd uses of the hind limb and the unique feet of mousebirds, there have been no comprehensive myological studies of this order. Previous anatomical studies deal only with those features considered relevant to the systematic position of the Coliiformes (Murie 1872, Garrod 1896, Pycraft 1907, Verheyen 1956). One recent work (Decoux 1975) describes the functional significance of the branching of the extensor digitorum longus tendon, but gives no further myological data.

The present study provides detailed descriptions of the hind limb muscles of two species of *Colius*. This is followed by a discussion of the myological peculiarities encountered and their possible bearing on the unusual locomotor habits and the systematic position of these birds.

Materials and Methods

One hind limb of each of 4 preserved specimens (3 *Colius striatus* and 1 *C. leucocephalus*) were dissected under a stereomicroscope, using magnifications of 6–25×. Iodine stain (Bock and Shear 1972) was used to elucidate fiber architecture and to demonstrate very small muscles more clearly. Drawings were made with a camera lucida. Anatomical nomenclature follows the Nomina Anatomia Avium (Baumel et al. 1979). Where it was necessary to determine muscle actions by manipulation, freshly frozen specimens of *C. striatus* were used. Observations of postures, locomotion, and digit rotation were made on individuals in a small colony of *C. striatus* kept in a cage measuring 1.5 m × 1.5 m × 1.8 m.

Description of Hindlimb Muscles

M. iliotibialis cranialis (Fig. 2A, B).—This muscle arises by fleshy fibers from the cranial 6 mm of the dorsal crest of the synsacrum. The caudal border of

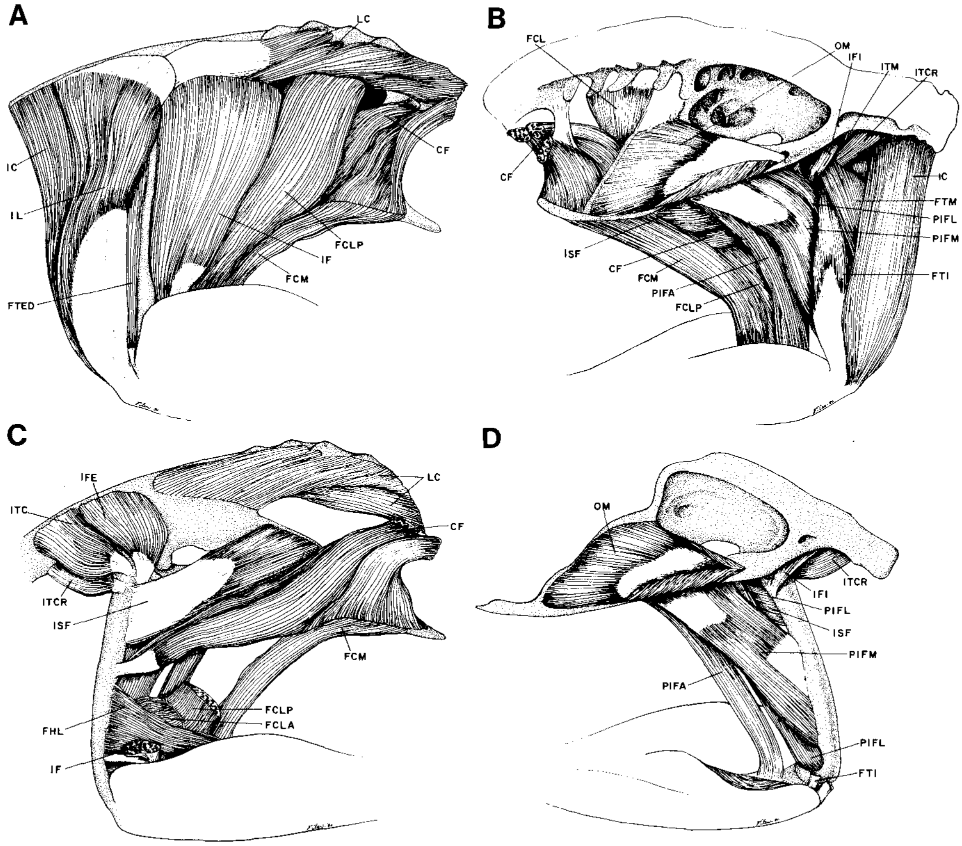


Fig. 2. The thigh of *Colius striatus.* A. Lateral view. Note the absence of the postacetabular part of M. iliotibialis cranialis. B. Medial view. Note the accessory belly of M. pubo-ischio-femoralis. C. Lateral view showing the deep muscles. The following muscles shown in Part A have been removed: M. iliotibialis cranialis, M. iliotibialis lateralis, M. femorotibialis externus, M. iliofibularis, and M. flexor cruris lateralis pars pelvica. Note the enlarged iliofemoralis externus. D. Medial view showing the deep muscles. The following muscles shown in Part B have been removed: M. iliotibialis cranialis, M. femorotibialis medius, M. femorotibialis internus, M. iliotrochantericus medius, M. caudiliofemoralis, M. flexor cruris medialis, and M. flexor cruris lateralis pars pelvica. Note the three bellies of M. pubo-ischio-femoralis. Abbreviations: CF, M. caudofemoralis; FCLA, M. flexor cruris lateralis pars accessoria; FCLP, M. flexor cruris lateralis pars pelvica; FCM, M. flexor cruris medialis; FHL, M. flexor hallucis longus; FTED, M. femorotibialis externus pars distalis; FTI, M. femorotibialis internus; FTM, M. femorotibialis medius; IC, M. iliotibialis cranialis; IF, M. iliofibularis; IFE, M. iliofemoralis externus; IFI, M. iliofemoralis internus; IL, M. iliotibialis lateralis; ISF, M. ischiofemoralis; ITC, M. iliotrochantericus caudalis; ITCR, M. iliotrochantericus cranialis; ITM, M. iliotrochantericus medius; LC, M. levator caudae; PIFA, M. pubo-ischio-femoralis pars accessoria; PIFL, M. pubo-ischio-femoralis pars lateralis; PIFM, M. pubo-ischio-femoralis pars medialis.

the origin lies deep to M. iliotibialis lateralis and superficial to M. iliotrochantericus cranialis. No deep head is present, nor is there any area of origin from the ilium, as in many birds. The strap-like belly extends down the cranial border of the thigh, passing to the medial surface. It inserts by fleshy fibers on the craniomedial surface of the patellar crest of the tibiotarsus, after passing superficial to the medial side of the patellar ligament.

M. iliotibialis lateralis (Fig. 2A).—Only a preacetabular portion is present. It arises by fleshy fibers from the dorsal crest of the synsacrum for about 2 mm caudal to the origin of M. iliotibialis cranialis, and by an aponeurosis from the dorsal crest of the synsacrum and from the dorsal iliac crest. The aponeurosis overlies M. iliofemoralis externus and the caudomedial part of M. iliotrochantericus caudalis. The sheet-like belly extends down the lateral surface of the thigh superficial to M. femorotibialis externus and, distally, to M. iliotibialis cranialis. It lies caudal to M. iliotibialis cranialis and cranial to M. iliofibularis. In the distal third of the thigh, M. iliotibialis lateralis gives rise to an aponeurosis that fuses with the lateral surface of M. femorotibialis externus and forms the superficial part of the patellar ligament.

M. iliotrochantericus caudalis (Fig. 2C).—This originates by fleshy fibers (partly aponeurotic in *C. leucocephalus*) from the dorsal crest of the synsacrum deep to the origins of Mm. iliotibialis cranialis and lateralis, and from the dorsal iliac fossa, dorsal to the origins of Mm. iliotrochantericus cranialis and medius, and cranial to the origin of M. iliofemoralis externus. The fan-shaped belly is bordered caudally by M. iliofemoralis externus. It extends caudolaterally to insert by a strong, flat tendon on the lateral surface of the femoral trochanter just cranial to that of M. iliofemoralis externus and distal to that of M. obturatorius medialis. This muscle is unusual in that its area of origin does not extend as far caudally as in most birds, owing to the unusually large size of the adjacent M. iliofemoralis externus (see below).

M. iliotrochantericus cranialis (Fig. 2B, C, D).—This muscle originates by fleshy fibers from the ventrolateral surface of the preacetabular ilium from the tip of the cranial iliac process caudally for about 4 mm. It lies deep to M. iliotrochantericus caudalis and cranial to M. iliotrochantericus medius. The narrowly fan-shaped belly tapers and fuses with that of M. iliotrochantericus medius a short distance proximal to their insertion. The common insertion is by a flat tendon onto the lateral surface of the femoral trochanter just distal to that of M. iliotrochantericus caudalis.

M. iliotrochantericus medius (Fig. 2B).—This arises by fleshy fibers from the ventrolateral border of the preacetabular ilium caudal to M. iliotrochantericus cranialis. The narrowly fan-shaped belly fuses with that of the latter muscle; their common insertion is described above.

M. iliofemoralis externus (Fig. 2C).—The origin is fleshy from the dorsal crest of the synsacrum caudal to M. iliotrochantericus caudalis, the dorsal iliac crest, and the caudomedial surface of the iliac fossa. The large, fan-shaped belly extends laterodistally and tapers to a flat tendon that inserts on the caudolateral surface of the femoral trochanter, superficial to the tendon of M. obturatorius medialis and caudal to that of M. iliotrochantericus caudalis. Distally M. iliofemoralis externus lies deep to the cranial border of M. iliofibularis. This muscle is unusually large in *Colius* compared to its condition in most birds.

A wide, flat ligament lies superficial to the insertion of this muscle. This ligament passes from the ilium at the dorsocranial corner of the ilioischiadic foramen to the femur, where it attaches between the insertions of Mm. iliofemoralis externus and iliotrochantericus caudalis. It does not appear to be named in Baumel et al. (1979).

M. femorotibialis externus (Fig. 2A).—This large, fusiform muscle covers the craniolateral surface of the thigh deep to M. iliotibialis lateralis. Both superficial (pars proximalis) and deep (pars distalis) heads are present. Pars proximalis arises semitendinously from the craniomedial surface of the femur just distal to the trochanter, and fleshy from the craniolateral surface of the proximal three-fourths of the femoral shaft. The semitendinous origin is shared with that of M. femorotibialis medius. The much smaller pars distalis arises fleshy from the middle third of the lateral femoral shaft and from the adjacent surface of the superficial head. It is somewhat fused with the superficial head throughout its length. Pars distalis is visible on the lateral surface of the thigh, caudal to the superficial head and cranial to M. iliofibularis. About halfway down the thigh a dense aponeurosis forms on the lateral surface of M. femorotibialis externus. Medially its fibers are closely associated with those of M. femorotibialis medius. Together these two muscles give rise to the patellar ligament, which inserts on the patellar crest of the tibiotarsus.

M. femorotibialis medius (Fig. 2B).—The origin is continuous with that of M. femorotibialis externus from the craniomedial surface of the femur just distal to the trochanter. The unipinnate belly extends down the craniomedial surface of the thigh, its deep fibers being closely associated with those of M. femorotibialis externus. Its fibers insert on an aponeurosis that arises from its medial surface. Toward the distal end of the femur the aponeurosis fuses with the caudomedial surface of M. femorotibialis externus, and contributes to the patellar ligament.

M. femorotibialis internus (Fig. 2B).—This arises from the medial shaft of the femur just distal to the insertion of M. iliofemoralis internus to the distal end of the medial femoral condyle. A few fibers arise from the surface of M. pubo-ischio-femoralis at its insertion on the femoral shaft. The belly extends down the medial surface of the thigh, caudal to that of M. femorotibialis medius, the medial surface of its distal half covered by a dense aponeurosis. It inserts by a short, strong tendon on the medial end of the patellar crest of the tibiotarsus, just medial to the insertion of the patellar ligament.

M. iliofibularis (Fig. 2A, C; Fig. 4C, D).—The origin is by fleshy fibers from the entire postacetabular wing of the ilium, and aponeurotically from the caudal end of the dorsal iliac crest; this aponeurosis is continuous with that of M. iliotibialis lateralis. The fan-shaped belly covers the lateral surface of the thigh caudal to M. iliotibialis lateralis and cranial to M. flexor cruris lateralis. It lies superficial to the caudal border of M. iliofemoralis externus, to Mm. ischiofemoralis and caudofemoralis, to the distal end of M. flexor cruris lateralis, and to the origin of M.

flexor hallucis longus. M. iliofibularis tapers to a strong, round tendon that passes through the biceps loop (ansa M. iliofibularis), entering the shank between Mm. gastrocnemius pars lateralis and flexor hallucis longus. It inserts on the iliofibular tubercle of the fibula.

The ansa M. iliofibularis consists of three arms—two femoral and one fibular. The proximal femoral arm is attached to the lateral femoral shaft about 4 mm from the distal end of the bone. It lies just lateral to the origin of M. flexor digitorum longus, and passes medial to the tendon of M. iliofibularis. The distal femoral arm passes lateral to the tendon of M. iliofibularis and attaches to the caudolateral surface of the femoral condyle about 2 mm distal to the proximal femoral arm. The fibular arm is attached to the cranial surface of the fibula just distal to its head. It is fused with the tendon of the fibular (distal) head of M. flexor perforatus digiti III, and with the distal head of M. flexor perforatus digiti IV, then passes lateral to the iliofibularis tendon and joins the two femoral arms as they form a sling around the tendon.

M. flexor cruris lateralis (Fig. 2A, B, C; Fig. 3; Fig. 4B).—Pars pelvica arises from an aponeurosis that extends between the transverse processes of the first three free caudal vertebrae and from the terminal process of the ilium. The large, parallel-fibered belly lies on the lateral surface of the thigh caudal to M. iliofibularis, cranial to M. flexor cruris medialis, and superficial to Mm. pubo-ischio-femoralis and caudofemoralis. About 10 mm caudal to the knee a ligamentous raphe separates pars pelvica from pars accessoria. An extension from the caudal end of the raphe runs distally to fuse with the aponeurosis on the medial surface of M. gastrocnemius pars intermedia. The main belly (pars pelvica) continues distally from the raphe and narrows to a thin, flat tendon that passes into the shank lateral to M. gastrocnemius pars medialis and medial to the accessory belly and pars media to insert by a tendon about 3 mm wide on the medial surface of the tibiotarsus about 4 mm from its proximal end. Pars accessoria inserts by fleshy fibers on the caudal surface of the femur for about 5 mm proximal to the condyles (Fig. 2C).

M. caudofemoralis (Fig. 2A, B, C).—M. iliofemoralis is lacking. M. caudofemoralis arises by an aponeurosis from the ventrolateral surface of the caudal end of the base of the pygostyle. The strap-like belly, about 4 mm wide, extends cranially to enter the thigh. It lies superficial to M. ischiofemoralis and deep to Mm. iliofibularis and flexor cruris lateralis. It tapers to a flat tendon about 2 mm wide that inserts on the caudal surface of the femur about halfway down the shaft.

M. ischiofemoralis (Fig. 2B, C, D).—This large muscle arises by two heads. The cranial head arises by fleshy fibers from the craniolateral surface of the wing of the ischium, and from the lateral surface of

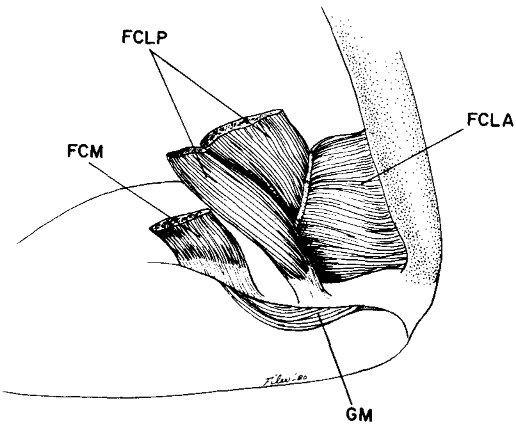


Fig. 3. Medial view of the distal thigh and proximal shank of *Colius striatus* showing the insertion of M. flexor cruris lateralis pars pelvica on the tibiotarsus. Its action as a flexor of the shank, as well as retractor of the femur, may be related to the hanging posture of mousebirds. Abbreviations are given with Fig. 2.

the ischial body. A few fibers arise from the caudal end of the dorsolateral crest of the ilium. The caudal head arises fleshy from the caudolateral edge of the ischium. The parallel-fibered belly is about 7 mm wide and extends cranially to insert by an aponeurosis on the posterolateral surface of the femoral shaft for about 6 mm distal to the trochanter.

M. flexor cruris medialis (Fig. 2A, B, C; Fig. 3).—This muscle arises by fleshy and short, tendinous fibers from the ventrolateral edge of the caudal end of the pubis for about 10 mm. The cranial edge of its origin lies deep to M. ischiofemoralis. The strap-like belly extends distally as the most caudal of the thigh muscles. Its cranial border lies deep to M. flexor cruris lateralis. It gives rise to a flat tendon, about 3 mm wide, that enters the shank between Mm. gastrocnemius intermedia and medialis. The tendon inserts on the tibiotarsus about 8 mm from its proximal end.

M. pubo-ischio-femoralis (Fig. 2B, D).—There are three bellies, all of which arise from a dense aponeurosis extending from the ventral edge of the body of the ischium to the adjacent surface of the pubis. The origin of the lateral belly (pars lateralis) extends for about 4 mm caudal to the obturator foramen. A smaller, caudal belly (pars accessoria) originates from the aponeurosis just caudal to the lateral head for about 3 mm. The medial belly (pars medialis) originates by an extension of the aponeurosis, immediately deep to both lateral and caudal heads. All three are parallel-fibered bellies. The lateral belly extends distally deep to Mm. ischiofemoralis and caudofemoralis, and inserts by fleshy fibers on the caudal surface of the femoral shaft, beginning about midway down its length and extending down to the medial surface of the medial condyle. The aponeurotic insertion on the condyle is medial to the origin of M. flexor cruris lateralis pars accessoria.

The medial belly extends immediately deep to the lateral belly and inserts medial to it on the caudal surface of the femoral shaft. Its insertion ends just proximal to the medial condyle. The proximal half of the insertion is aponeurotic, and the distal half is fleshy (entirely fleshy in *C. leucocephalus*).

The accessory belly remains on the same plane as the lateral belly, but extends distally to insert by a short, wide tendon onto the proximomedial corner of the tibiotarsus, deep to the insertion of M. gastrocnemius pars intermedia. This belly appears to have no known counterpart in other birds (see Discussion).

M. obturatorius lateralis (not shown).—Pars dorsalis is absent. Pars ventralis arises fleshy from the ventral and cranial margin of the lateral surface of the obturator foramen. It extends laterally to insert by fleshy fibers on the caudal surface of the proximal end of the femur, just distal to the trochanter. The insertion is distal to that of M. obturatorius medialis, proximocaudal to that of M. iliofemoralis internus, and medial to that of M. ischiofemoralis.

M. obturatorius medialis (Fig. 2B, D).—This well-developed, fan-shaped muscle occupies the entire medial surface of the postacetabular ilium and the ischiopubic fenestra. The main part arises fleshy from the medial surfaces of the ischiopubic membrane and wing of the ischium, and from the caudal and ventral borders of the ilioischiadic foramen. Its dorsalmost fibers are visible laterally through the ilioischiadic foramen. A fairly distinct ventral part (much more discrete in *C. leucocephalus*) arises by fleshy fibers from the ventral and medial borders of the pubis adjacent to the cranial half of the ischiopubic fenestra. Both parts converge cranially toward the obturator fenestra, and extend through the obturator foramen, their fibers inserting on a strong, flat tendon that arises from the aponeurosis. The tendon continues to receive fibers on its medial surface after it has passed through the obturator foramen. It extends laterally, passes deep to the tendon of M. iliofemoralis externus, and inserts on the lateral surface of the proximal end of the femur just proximal to that of M. iliotrochantericus caudalis.

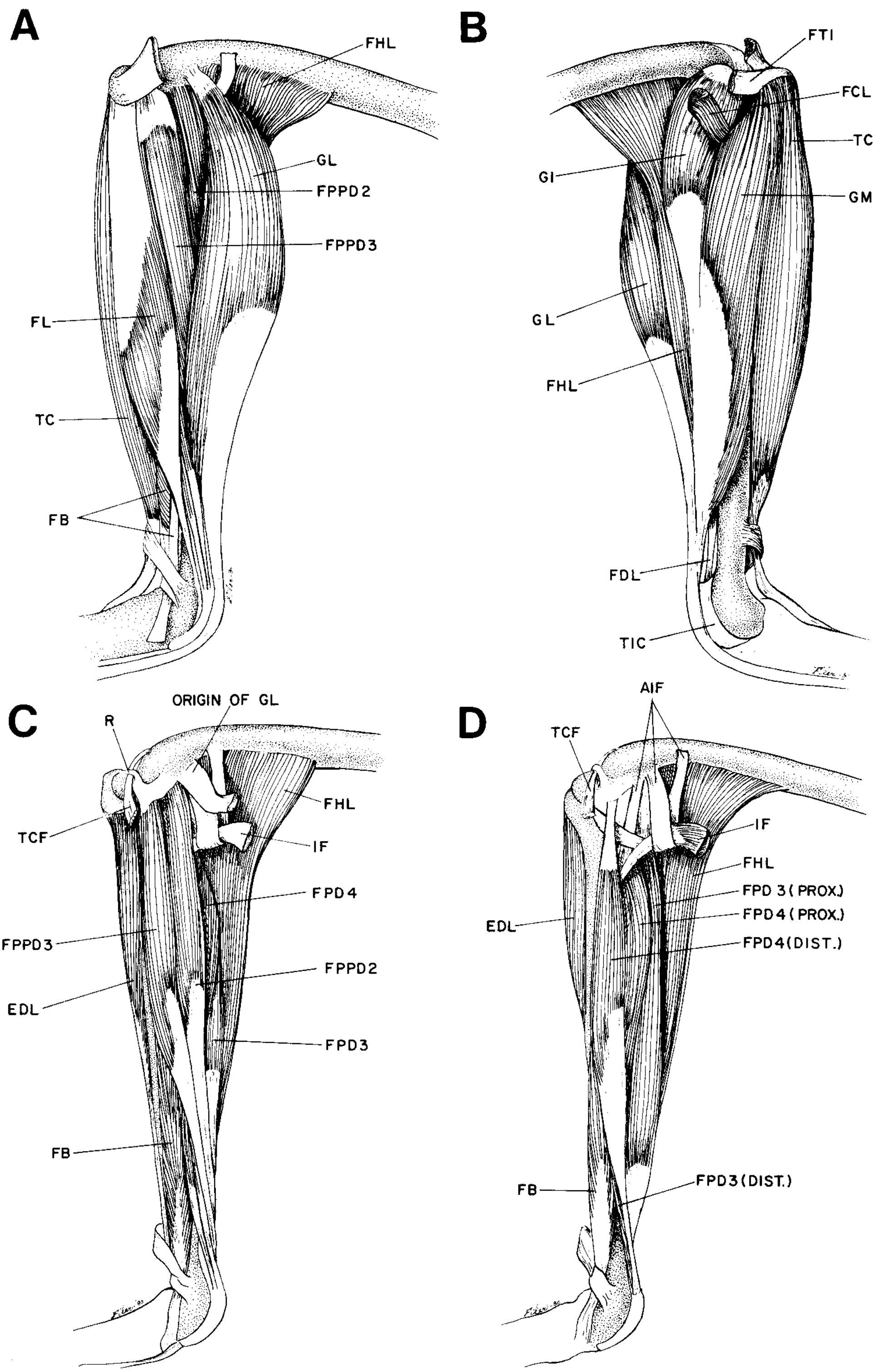
M. iliofemoralis internus (Fig. 2B, D).—M. iliofemoralis internus arises by fleshy fibers from a small area on the dorsal surface of the ilium between the iliosynsacral suture and the ventral edge of the ilium about 4 mm from the cranial border of this bone. It extends laterally as a band, less than 2 mm wide, to insert fleshy on the medial surface of the femur about 3 mm from its proximal end. The muscle lies deep to M. iliofemoralis externus. Caudally it is bordered by the insertion of M. ischiofemoralis.

M. gastrocnemius (Fig. 3; Fig. 4A, B, C).—There are three independent bellies. Pars lateralis is by far the largest of the bellies. It arises by a strong, flat tendon from the lateral epicondyle of the femur and the lateral surface of the distal arm of the biceps loop. Distally, the tendinous origin is continuous with an aponeurosis on the medial surface of the muscle. The fusiform belly extends down the caudolateral surface of the shank. It is bordered cranially by Mm. flexor perforans et perforatus digiti II and flexor perforans et perforatus digiti III. M. flexor hallucis longus is visible medially between pars lateralis and pars intermedia and medialis. Distally pars lateralis tapers to a very strong, broad tendon that fuses with those of pars intermedia and medialis about 5 mm from the distal end of the tibiotarsus to form the common tendon of insertion.

Pars intermedia arises by fleshy and tendinous fibers from the caudomedial surface of the median femoral condyle. The weakly developed fan-shaped belly passes distad for about 12 mm before tapering to form a flat tendon that fuses with an aponeurosis on the caudal surface of pars medialis. This tendon actually arises from the ligamentous raphe that sep-

→

Fig. 4. A. Lateral view of the shank of *Colius striatus.* Note the extensive origin of M. flexor hallucis longus from the femoral shaft and the absence of the long tendon of M. fibularis longus. B. Medial view of the shank. C. Lateral view of the shank showing the retinaculum for the tendon of M. tibialis cranialis caput femorale and ansa M. iliofibularis. The following muscles shown in Part A have been removed: M. tibialis cranialis and M. gastrocnemius pars lateralis. D. Lateral view of the shank showing the deep muscles and the three arms of ansa M. iliofibularis. The following muscles shown in Part C have been removed: M. flexor perforans et perforatus digiti II and M. flexor perforans et perforatus digiti III. Abbreviations: AIF, ansa M. iliofibularis; EDL, M. extensor digitorum longus; FB, M. fibularis brevis; FDL, M. flexor digitorum longus; FHL, M. flexor hallucis longus; FL, M. fibularis longus; FPD3, M. flexor perforatus digiti III; FPD4, M. flexor perforatus digiti IV; FPPD2, M. flexor perforans et perforatus digiti II; FPPD3, M. flexor perforans et perforatus digiti III; GI, M. gastrocnemius pars intermedius; GL, M. gastrocnemius pars lateralis; GM, M. gastrocnemius pars medialis; R, retinaculum; TC, M. tibialis cranialis; TCF, M. tibialis cranialis caput femorale; TIC, tibial cartilage.


A
FHL
GL
FPPD2
FPPD3
FL
TC
FB
B
FTI
FCL
TC
GI
GM
GL
FHL
FDL
TIC
C
ORIGIN OF GL
R
FHL
TCF
IF
FPD4
FPPD3
FPPD2
EDL
FPD3
FB
D
AIF
TCF
IF
FHL
FPD 3 (PROX.)
FPD4 (PROX.)
EDL
FPD4 (DIST.)
FB
FPD3 (DIST.)

arates pars pelvica from pars accessoria of M. flexor cruris lateralis. Pars accessoria and pars intermedia are closely associated at this point. Pars intermedia passes medial to M. flexor cruris medialis and lateral to M. flexor cruris lateralis.

Pars medialis arises by fleshy and tendinous fibers from the craniomedial corner of the patellar crest of the tibiotarsus, just distal to the insertion of M. femorotibialis internus, from the caudomedial surface of M. tibialis cranialis, and by a weak aponeurosis from the medial surface of the proximal two-thirds of the tibiotarsus. A few fasicles also arise from the surface of M. femorotibialis internus at its insertion. The unipennate belly is the most superficial muscle on the medial surface of the shank. The fibers give rise to a tendon on the muscle's caudal border. This tendon arises in part from an aponeurosis on the medial surface of the muscle, and in part from the tendon of pars intermedia. About 5 mm from the end of the tibiotarsus it joins the tendon of pars lateralis to form the common tendon of insertion.

The tendon of insertion of M. gastrocnemius passes over the tibial cartilage, attaching to its lateral and medial margins, thus forming a superficial compartment for the flexor tendons. It crosses the intertarsal joint and attaches to the lateral and medial margins of the hypotarsus, superficial to the flexor tendons. Distal to the hypotarsus it thins, but continues along the plantar surface of the tarsometatarsus, having attachments along the lateral and medial borders of this bone. About halfway down the length of the tarsometatarsus a few fibers of M. flexor hallucis brevis arise from the deep surface of the medial border of the tendon. Distally the medial margin of the gastrocnemius tendon thickens and runs deep to the lateral border of M. extensor hallucis longus. The lateral margin of the tendon of insertion in the distal third of the tarsometatarsus gives rise to a significant number of fibers of the adjacent M. abductor digiti IV. The tendon acts as a superficial aponeurosis covering lateral, medial, and plantar surfaces of the distal end of the tarsometatarsus.

M. tibialis cranialis (Fig. 4).—This is a large, fusiform muscle lying superficially on the cranial surface of the shank. It is bordered medially by M. gastrocnemius pars medialis and laterally by the aponeurosis of origin of M. fibularis longus. M. tibialis cranialis arises by two heads. The tibial head (caput tibiale) arises by fleshy fibers from the entire patellar crest of the tibiotarsus, just distal to the insertion of the patellar ligament. Its lateral margin is deep to the aponeurosis of origin of M. fibularis longus. The femoral head (caput femorale) arises by a ligament from the cranial surface of the lateral femoral condyle. As it passes across the craniolateral surface of the knee it is held in place by a retinaculum (Fig. 4C, D). Laterally and medially this retinaculum is reinforced by small sesamoid bones. It has a strong lateral attachment to the head of the fibula, and caudally it merges with the lateral semilunar cartilage. Two flat ligaments extend from the retinaculum medially, across the interior of the joint. One attaches to the medial semilunar cartilage, the other to the craniomedial corner of the tibiotarsus, just caudal to the patellar crest. After crossing the knee the femoral head extends down the craniolateral surface of the shank, deep to the tibial head. About 8 mm proximal to the end of the tibiotarsus the two heads fuse and taper to a very broad tendon. The tendon is held against the cranial surface of the bone, along with that of M. extensor digitorum longus, by a strong ligamentum transversum. As it crosses the intertarsal joint, the tendon turns slightly medially to insert on the tuberosity of M. tibialis cranialis, about 4 mm from the proximal end of the tarsometatarsus and just deep to the extensor digitorum longus tendon.

M. fibularis longus (Fig. 4A).—Commonly also called peroneus longus, this muscle overlies the lateral surface of M. tibialis cranialis. It is bordered caudally by M. flexor perforans et perforatus digiti III. M. fibularis longus arises by an aponeurosis from the lateral corner of the patellar crest and the lateral surface of the proximal third of M. tibialis cranialis. The cranial portion of the aponeurosis extends further distally than the caudal portion. The flat, parallel-fibered belly extends along the middle third of the shank, then tapers to a narrow tendon that inserts on the proximolateral corner of the tibial cartilage. In most birds a branch of the tendon passes to the plantar surface of the tarsus, where it joins the tendon of M. flexor perforatus digiti III. Such a branch is lacking in *Colius*.

M. extensor digitorum longus (Fig. 4C, D; Fig. 5; Fig. 8A).—This muscle lies deep to M. tibialis cranialis and is bordered medially by M. gastrocnemius pars medialis. It arises by fleshy fibers from the patellar crest and the cranial and lateral cnemial crests of the tibiotarsus, from the proximal third of the craniolateral and craniomedial borders of the tibiotarsus, and from a raphe separating it from M. gastrocnemius pars medialis. The bipennate belly extends down the cranial surface of the tibiotarsus and tapers to a flat tendon about 13 mm from the end of this bone. The tendon passes through the ligamentum transversum deep to that of M. tibialis cranialis, and then through a bony canal just proximal to the condyles. It then crosses the intertarsal joint, passes through another bony canal on the cranial surface of the proximomedial corner of the tarsometatarsus, and extends along the cranial surface of the tarsometatarsus. About 10 mm from the distal end of the bone it gives off a medial branch to the hallux, a very unusual condition among birds (see Discussion). After a short distance the main tendon bifurcates, sending a lateral branch to digit IV and a medial branch to the area between digits II and III. At the distal end of the tarsometatarsus this medial branch bifurcates, sending branches to digits II and III.

The branch to the hallux extends to the proximal end of metatarsal I, where it is held in place by a ligamentous band. Near the distal end of this element, a second ligamentous band holds the tendon in place. It crosses the metatarsal-phalangeal joint and passes through a third ligamentous band on the base of the first phalanx. The tendon inserts on a fibrous pad on the cranial surface of the distal end of the first phalanx. The fibrous pad arises as a tendon from the cranial surface of the first phalanx about 2 mm from its distal end, deep to the tendon of M. extensor digitorum longus. It inserts on the base of the second phalanx, after receiving the insertion of the latter muscle.

The branch to digit II crosses the second metatarsal-phalangeal joint and extends beneath a ligamentous band on the cranial surface of the base of the second digit. It is accompanied by a smaller tendon that arises from the branch to digit III. This smaller tendon extends along the cranial surface of the first phalanx, superficial to the main branch to digit II, and ends as an expansion over the first interphalangeal joint. The main branch to digit II perforates this expansion and emerges on the cranial surface of the second phalanx. It sends an attachment across the lateral surface of the first interphalangeal joint to insert on the joint pad on the plantar surface. The tendon continues along the cranial surface of digit II and inserts on a fibrous pad on the second interphalangeal joint, in the same manner as the tendon to the hallux.

The branch to digit III is formed by extensions from both lateral and medial divisions of the main tendon. It extends laterally, across the third metatarsal-phalangeal joint. In addition to the small tendon given off to digit II, arising from the medial extension is a narrow band extending to the ligamentous band that holds the tendons in place on the base of the second digit. About halfway along the cranial surface of the first phalanx the branch to digit III bifurcates into lateral and medial divisions. The two divisions extend along lateral and medial borders, respectively, of the cranial surface of the third digit. They expand over the surfaces of the first and second interphalangeal joints, forming attachments to the joint pads on the plantar surface as well as to each other. Toward the distal end of the third phalanx they turn toward the center of the cranial surface, and fuse. The tendon inserts on a fibrous pad at the third interphalangeal joint, in the same manner as the tendons to digits I and II.

There are actually two tendons of the EDL to digit IV. One arises as a continuation of the main tendon and crosses the metatarsal-phalangeal joint, extending onto the craniolateral surface of the first phalanx. The other, more superficial, accessory tendon arises from the union of two branches: a medial branch from the most proximal part of the branch to digit III, and a lateral branch from a broad extension of the main tendon onto the plantar surface of the distal end of the tarsometatarsus. The two branches unite on the cranial surface of the base of the first phalanx. As they do so, they form a sheath around the continuation of the main tendon. This accessory tendon extends along the craniomedial surface of the fourth digit, expanding and forming attachments at first, second, and third interphalangeal joints. Distal to the third interphalangeal joint, it becomes very narrow and turns onto the cranial surface of the fourth digit to insert on a fibrous pad at the fourth interphalangeal joint.

The continuation of the main tendon extends as a narrow band along the craniolateral surface of digit

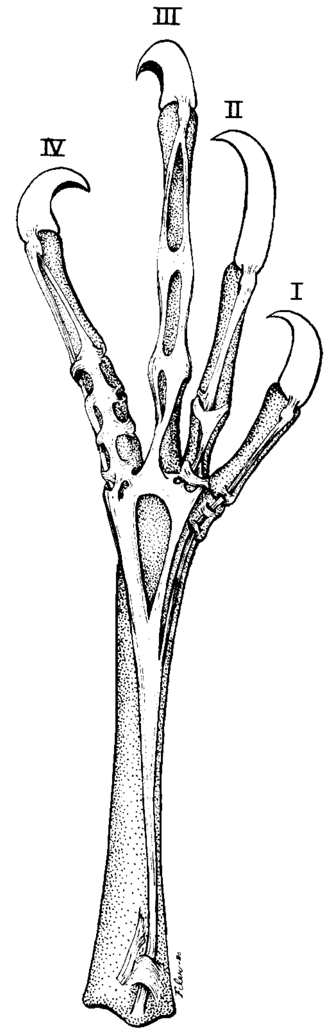


Fig. 5. Dorsal view of the left foot of *Colius striatus* showing the divisions of the tendon of M. extensor digitorum longus. Note the branch to the hallux, which has previously been described only in parrots.

IV, passing beneath ligamentous bands at each of the first three interphalangeal joints. Distal to the third joint it expands and turns onto the cranial surface of digit IV to insert on the fibrous pad at the fourth interphalangeal joint, just lateral to the insertion of the accessory tendon. The attachments of the fibrous pad are as those of digits I, II, and III.

M. fibularis brevis (Fig. 4A, C, D).—Often called peroneus brevis, this muscle arises by fleshy and tendinous fibers from the distal end of the fibula and from the craniolateral surface of the tibiotarsus from just distal to the insertion of M. iliofibularis to about 4 mm from the end of this bone. The roughly bipennate belly lies deep to M. tibialis cranialis. About 3 mm from the distal end of the tibiotarsus, M. fibularis brevis tapers to a flat tendon that passes through a retinaculum on the craniolateral surface of the tibiotarsus just proximal to the condyle. It crosses the intertarsal joint and turns onto the plantar surface of the tarsometatarsus to insert on the proximolateral corner of the hypotarsus.

M. flexor perforans et perforatus digiti III (Fig. 4A, C).—This is a superficial muscle on the lateral surface of the shank. It lies superficial to M. fibularis longus and cranial to Mm. flexor perforans et perforatus digiti II and gastrocnemius pars lateralis. It arises by two short tendons, one from the sesamoid bone of the retinaculum for the tendon of the femoral head of M. tibialis cranialis, the other from the caudolateral surface of the lateral femoral condyle. As the two tendons join they overlie the head of the fibula. The deep surface of the tendon provides the surface of origin for part of M. flexor perforatus digiti IV. The parallel-fibered belly of M. flexor perforans et perforatus digiti III extends down the shank superficial to M. flexor perforatus digiti IV. About halfway down the shank it tapers to a flat tendon that turns caudad and passes through a superficial compartment in the tibial cartilage, lateral to the tendon of M. flexor perforans et perforatus digiti II and medial to that of M. flexor perforatus digiti IV. It crosses the intertarsal joint superficial to the tendon of M. flexor perforatus digiti III and runs through a shallow groove in the hypotarsus. As the tendon extends down the plantar surface of the tarsometatarsus it turns to lie deep to that of M. flexor perforatus digiti III. About 2 mm from the distal end of metatarsal III it perforates the tendon of M. flexor perforatus digiti III. It crosses the metatarsal-phalangeal joint, extending onto the plantar surface of digit III. Just distal to the first interphalangeal joint the tendon is held in place by a ligamentous band as it is perforated by the tendon of M. flexor digitorum longus. The lateral and medial branches thus formed insert on lateral and medial surfaces, respectively, of a fibrous pad on the plantar surface of the second interphalangeal joint.

M. flexor perforans et perforatus digiti II (Fig. 4A, C).—This is a superficial muscle on the lateral surface of the shank, caudal to M. flexor perforans et perforatus digiti III. It arises from the superficial surface of the caudal limb of the latter muscle's tendon of origin, from the caudolateral surface of the lateral femoral condyle, just distal to the distal limb of the ansa M. iliofibularis, and from the superficial surface of the aponeurosis of origin of M. flexor perforatus digiti IV. The belly is parallel-fibered proximally, becoming bipennate distally. It extends one-third of the way down the shank before tapering to a flat tendon. At the distal end of the tibiotarsus the tendon turns caudally and passes through a superficial compartment in the tibial cartilage, lying medial to the tendon of M. flexor perforans et perforatus digiti III and superficial to that of M. flexor perforatus digiti II. As it crosses the intertarsal joint and passes through a fibrous canal in the hypotarsus, it lies lateral to the tendon of M. flexor perforatus digiti II and medial to that of M. flexor perforans et perforatus digiti III. It extends down the plantar surface of the tarsometatarsus, turning to lie superficial and then deep to the tendon of M. flexor perforatus digiti II. At the distal end of the tarsometatarsus it turns medially and crosses the metatarsal-phalangeal joint of the second digit. About halfway down the plantar surface of the first phalanx the tendon is perforated by that of M. flexor digitorum longus. Resulting lateral and medial branches extend distally to insert on caudolateral and caudomedial surfaces, respectively, of the fibrous pad on the plantar surface of the first interphalangeal joint. The medial branch is somewhat larger than the lateral. The tendon of M. flexor perforans et perforatus digiti II does not perforate that of M. flexor perforatus digiti II as it does in some other groups of birds.

M. flexor perforatus digiti IV (Fig. 4C, D).—There are two heads of origin. The proximal (femoral) head arises by a long, flat tendon shared with the proximal head of M. flexor perforatus digiti III, from the caudomedial surface of the lateral femoral condyle. It lies just distal and medial to the distal femoral arm of the ansa M. iliofibularis. The tendon extends deep to the fibular arm of the latter. The distal (fibular) head arises from an aponeurosis shared with the distal head of M. flexor perforatus digiti III. This aponeurosis originates from the lateral margin of the fibular head. It extends as a broad sheet superficial to the fibular arm of the ansa M. iliofibularis, to which it has attachments. The tendon of insertion of M. iliofibularis passes between the proximal and distal heads of M. flexor perforatus digiti IV about 6 mm from the proximal end of the fibula. The two parallel-fibered bellies extend distal, the proximal head lying caudal to the distal head. As a whole, the muscle lies superficial to the cranial part of M. flexor perforatus digiti III. About halfway down the shank (one-third in *C. leucocephalus*) the bellies fuse and taper to a flat tendon. The tendon passes through a superficial compartment in the tibial cartilage and crosses the intertarsal joint, lying lateral to that of M. flexor perforans et perforatus digiti III and superficial to that of M. flexor perforatus digiti III. Maintaining the same relationships to these tendons, the tendon runs through a shallow groove in the hypotarsus and extends along the plantar surface of the tarsometatarsus as the most lateral of the long flexor tendons. It passes through a ligamentous band at the distal end of the tarsometatarsus, adjacent to digit IV, and as it crosses the metatarsal-phalangeal joint it bifurcates. Both lateral and medial branches pass through a thick, ligamentous band on the plantar surface of the first interphalangeal joint, superficial to the tendon of M. flexor digitorum longus. The tendon of M. flexor digitorum longus passes between them as they emerge on the plantar surface of the second phalanx. The lateral branch inserts on the proximolateral corner of the second interphalangeal pad. The medial branch inserts on the medial corner of the base of the fourth phalanx.

M. flexor perforatus digiti III (Fig. 4C, D).—This lies deep to M. flexor perforatus digiti IV and superficial to Mm. flexor perforatus digiti II and flexor hallucis longus. The muscle has two bellies. The proximal belly originates in common with the proximal head of M. flexor perforatus digiti IV by a long, flat tendon from the intercondylar area, lateral to the origin of M. flexor hallucis longus and medial to the distal femoral arm of the ansa M. iliofibularis. The parallel-fibered belly develops about 5 mm distal to the origin. The smaller distal belly arises proximally by a long tendon (13 mm) in common with that of the distal head of M. flexor perforatus digiti IV. Distally it arises from an aponeurosis on the medial surface of the fibularis brevis. Its parallel-fibered belly becomes closely associated with that of the proximal belly about 9 mm from the distal end of the tibiotarsus. The two bellies fuse near the intertarsal joint. The tendon passes through the lateralmost compartment of the tibial cartilage, crosses the intertarsal joint, and extends over a shallow groove in the hypotarsus. It runs medial and then superficial to the tendon of M. flexor perforans et perforatus digiti III. As it crosses the metatarsal-phalangeal joint it is perforated by the tendons of Mm. flexor perforans et perforatus digiti III and flexor digitorum longus. The lateral and medial branches thus formed extend distad to insert on lateral and medial surfaces, respectively, of the first interphalangeal joint pad.

M. flexor perforatus digiti II (not shown).—This small muscle is visible on the lateral surface of the shank between the two heads of M. flexor perforatus digiti III. There are two heads of origin. The more proximal head arises by fleshy fibers from the caudal surface of the lateral femoral condyle, the caudolateral corner of the tibiotarsus, and the adjacent head of the fibula. The distal head arises by a 4 mm long, slender tendon from the deep surface of the fibular arm of ansa M. iliofibularis and from the tendon of

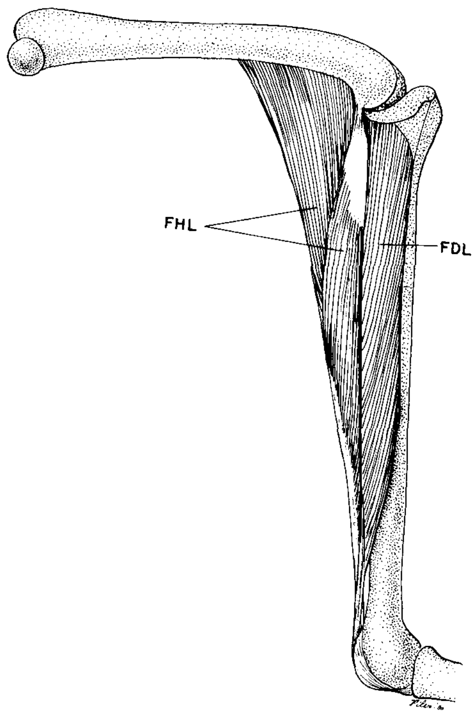


Fig. 6. Medial view of the shank of *Colius striatus* showing the two heads of M. flexor hallucis longus. Note the extensive origin of the proximal head from the femoral shaft. Abbreviations are as in Fig. 4.

origin of M. flexor perforatus digiti IV. The distal head lies superficial to the proximal head. About one-third of the way down the shank the two heads fuse and taper to a slender tendon that runs superficial to M. flexor digitorum longus and cranial to M. flexor hallucis longus. It passes through the tibial cartilage, crosses the intertarsal joint, and passes through a fibrous canal in the hypotarsus. As it extends along the plantar surface of the foot, it lies first medial to the tendon of M. flexor perforans et perforatus digiti II, then crosses it superficially to lie lateral to it. The tendon inserts on the caudolateral corner of the base of the proximal phalanx of digit II. It is not perforated by the tendons of Mm. flexor perforans et perforatus digiti II or flexor digitorum longus as in some birds.

M. flexor hallucis longus (Fig. 2C, Fig. 4, Fig. 6, Fig. 7).—This muscle lies on the caudal surface of the shank, superficial to M. flexor digitorum longus. The origin is by two heads. The proximal head arises by fleshy fibers from the caudal surface of the femur in the distal half of the shaft (an unusually extensive origin) in the intercondylar area. The distal head arises by a tendon from the intercondylar area. The two heads fuse about halfway down the shank, their fibers converging on a tendon that arises on the mus-

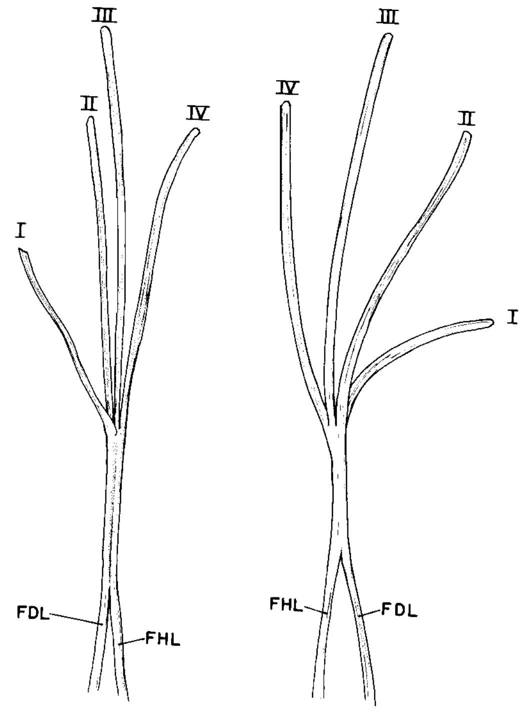


Fig. 7. Dorsal (left) and ventral (right) views of the flexor hallucis longus/flexor digitorum longus tendon in the right foot of *Colius striatus.* Although the tendons do fuse, making it type V in Gadow's classification, branches to digits II, III, and IV are in the same plane, separate from that of the branch to the hallux. Abbreviations are as in Fig. 4.

cle's craniolateral surface. The belly ends about 9 mm from the distal end of the tibiotarsus. The very large, flat tendon passes through a deep compartment in the tibial cartilage lateral to that of M. flexor digitorum longus. It crosses the intertarsal joint, passes through a deep, fibrous compartment in the hypotarsus, and emerges on the plantar surface of the foot as the deepest of the long flexor tendons. About one-third of the way down the tarsometatarsus the tendons of this muscle and M. flexor digitorum longus fuse. The distribution of the branches of the fused tendons is described below.

M. flexor digitorum longus (Fig. 4B, Fig. 6, Fig. 7).—This muscle lies deep to M. flexor hallucis longus and is the deepest muscle on the caudal surface of the shank. There are two heads of origin. The lateral head arises by fleshy fibers from the caudal surface of the fibula. The medial head arises by fleshy fibers from the caudal and medial surfaces of the tibiotarsus, and the flexor fossa to about halfway down the length of the bone. It runs lateral to the tendon of M. iliofibularis and Mm. flexor cruris medialis and gastrocnemius pars medialis. The two bellies fuse about one-third of the way down the shank. The common belly is bipennate, its fibers inserting on a tendon that develops on its caudal surface. About 6 mm from the distal end of the tibiotarsus the muscle tapers to a flat tendon that extends distally to run through the tibial cartilage. The tendon of this muscle is the most medial of the flexor tendons. It crosses the intertarsal joint and passes through a superficial fibrous compartment in the medial side of the hypotarsus. As it extends along the caudal surface of the foot, it lies medial and superficial to the tendon of M. flexor hallucis longus. About one-third of the way down the tarsometatarsus the tendons of Mm. flexor digitorum longus and flexor hallucis longus fuse. The common tendon then divides to send a branch to each of the four digits, making it Type V of Gadow's (1893–1896) classification. The distribution of the branch tendons is described below.

Flexor hallucis longus/flexor digitorum longus insertion.—The common tendon of these two muscles divides into four branches. The branch to digit I (the hallux) arises from the medioplantar surface of the tendon and runs superficial to the branch to digit II. The branches to digits II, III, and IV arise from about the same plane, slightly deep to the branch to digit I.

The branch to the hallux extends along a groove in the lateral surface of the first metatarsal, and is held in place by a retinaculum. The tendon lies superficial to that of M. flexor hallucis brevis. It crosses the medial surface of the metatarsal-phalangeal joint and passes down the plantar surface of the proximal phalanx. It is enclosed in a fibrous sheath in the proximal two-thirds of the bone. Distally the deep surface of the tendon gives rise to a vinculum that extends distally to insert on the interphalangeal joint pad. The tendon passes through a retinaculum and inserts on the plantar surface of the base of the terminal phalanx (flexor tubercle).

The branch to digit II arises from the main tendon deep to the branch to digit I and medial to the branches to III and IV. It extends through a cartilaginous canal to the distal end of the dorsal surface of the metatarsal II, and then crosses the metatarsal-phalangeal joint, lying in a groove formed by the two condyles on the proximal end of the first phalanx. The tendon perforates that of M. flexor perforans et perforatus digiti II before reaching the first interphalangeal joint. It passes through a fibrous sheath on the proximal two-thirds of the second phalanx. As it approaches the end of the second phalanx, the deep surface of the tendon gives rise to a vinculum that extends distally to insert on a fibrous pad on the dorsal surface of the second interphalangeal joint. The tendon inserts on the flexor tubercle at the base of the terminal phalanx.

The branch to digit III passes through a cartilaginous canal at the base of the third digit and crosses the metatarsal-phalangeal joint, extending onto the plantar surface of the proximal phalanx. The tendon perforates that of M. flexor perforatus digiti III about halfway down the phalanx. At the base of the second phalanx it perforates the tendon of M. flexor perforans et perforatus digiti III. The tendon of M. flexor digitorum longus is held in place at the interphalangeal joints by ligamentous bands. Toward the middle of the third phalanx a vinculum arises from the deep surface of the tendon. It extends distally to insert on the third interphalangeal joint pad. The main tendon inserts on the flexor tubercle at the base of the terminal phalanx.

The branch to digit IV passes through a cartilaginous canal at the base of digit IV onto the dorsal surface of digit IV. About halfway down the first phalanx it perforates the tendon of M. flexor perforatus digiti IV. It continues along the plantar surface of the digit, being held in place at each interphalangeal joint by ligamentous bands and by a fibrous sheath on the surface of digit IV. The tendon inserts on the flexor tubercle at the base of the terminal phalanx. A vinculum from its deep surface inserts on the distal interphalangeal joint pad as in the other digits.

M. flexor hallucis brevis (Fig. 8B).—This bipennate muscle lies on the plantar surface of the tarsometatarsus medial to the flexor digitorum longus/flexor hallucis longus tendon. It has an extensive origin from the medial hypotarsal crest, medial half of the flexor sulcus, and the medial plantar crest. About 6 mm from the distal end of the tarsometatarsus the belly gives way to a flat tendon that passes along a groove in the lateral surface of the first metatarsal. It is held in place at the base of this bone by a retinaculum, and inserts on the plantar surface of the base of the proximal phalanx of the hallux. Throughout its course this tendon remains entirely separate from that of M. flexor hallucis longus.

Mm. extensor hallucis longus and extensor hallucis longus accessorius (Fig. 8A).—Pars proximalis, the major and often only component of this muscle present in many birds, appears to have been lost in *Colius*, except that its tendon of insertion may be represented by the branch of the extensor digitorum longus tendon to the hallux (see Discussion). Pars distalis is a roughly unipennate muscle originating by fleshy fibers from the craniomedial surface of the distal three-fifths of the tarsometatarsus. Its fibers insert onto a flat tendon that extends onto the medial surface of the first metatarsal, where it is held in place by a ligamentous band. Distal to this the tendon crosses the metatarsal-phalangeal joint and inserts on the medial surface of the base of the proximal phalanx of the hallux, where it blends with the joint capsule.

A tiny muscle arises on the dorsolateral surface of metatarsal I and sends a tendon to insert on the ligamentous band connecting the bases of the proximal phalanges of digits I and II. The identity of this structure is uncertain as it does not appear to have been described previously. We have termed it an

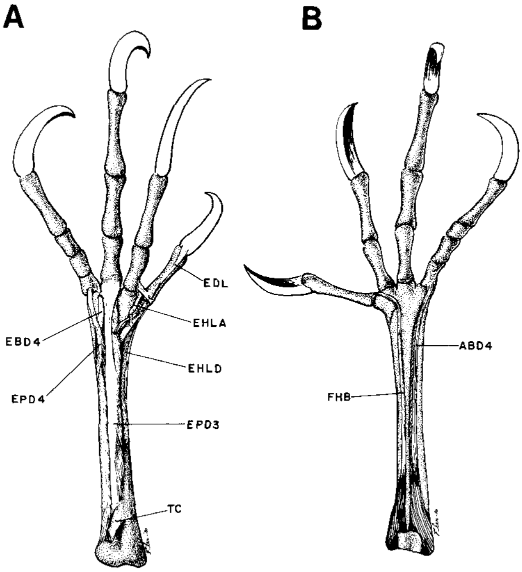


Fig. 8. A. Dorsal view of the left foot of *Colius striatus* showing two muscles not previously described in birds, Mm. extensor hallucis longus pars accessorius and extensor proprius digiti IV. Mm. extensor hallucis longus pars distalis and extensor brevis digiti IV are unusually large and have undergone changes in their insertions. These deviations from the typical avian condition are related to their functions. B. Plantar view of the left foot. Mm. flexor hallucis brevis and abductor digiti IV are well-developed and have undergone slight changes in insertion associated with their modified functions. Abbreviations: ABD4, M. abductor digiti IV; EBD4, M. extensor brevis digiti IV; EDL, M. extensor digitorum longus; EHLA, M. extensor hallucis longus accessorius; EHLD, M. extensor hallucis longus pars distalis; EPD3, M. extensor proprius digiti III; EPD4, M. extensor proprius digiti IV; FHB, M. flexor hallucis brevis; TC, M. tibialis cranialis.

accessory belly of M. extensor hallucis longus because of its position and because M. extensor hallucis longus is a rather variable muscle in birds (George and Berger 1966: 455).

M. extensor proprius digiti III (Fig. 8A).—This originates by fleshy fibers from the entire dorsal surface of the tarsometatarsus, medial to M. extensor brevis digiti IV and lateral to M. extensor hallucis longus pars distalis. The fibers insert onto a broad tendon that arises on almost the entire dorsal surface of the muscle. At the distal end of the tarsometatarsus the tendon inserts on the dorsal surface of the base of the proximal phalanx of digit III.

M. extensor brevis digiti IV (Fig. 8A).—This muscle arises by fleshy fibers from the craniolateral surface of the tarsometatarsus extending from the lateral cotyla to the trochlea for digit IV. A flat tendon arises along the dorsal surface of the muscle, passes beneath a bony bridge between the trochleae for digits III and IV, and inserts on the medial surface of the base of the proximal phalanx of digit IV.

M. extensor proprius digiti IV (Fig. 8A).—This small, bipennate muscle arises over the dorsal surface of the distal one-fourth of the belly of M. extensor brevis digiti IV, and inserts by a flat tendon onto the proximodorsal surface of the first phalanx of digit IV. This appears to be a previously undescribed muscle. Three muscles arising from the tarsometatarsus and inserting on digit IV are listed in the compilations of Hudson (1937), George and Berger (1966), and Baumel et al. (1979). Extensor brevis digiti IV and abductor digiti IV are present in *Colius*, while abductor digiti IV is located on the plantar surface of the tarsometatarsus in those few birds that possess it, and thus is probably not homologous with the present muscle. We have therefore provided the above new name for this muscle because its relation to the fourth digit is similar to that of M. extensor proprius digiti III to the third.

M. abductor digiti IV (Fig. 8B).—This lies on the plantar surface of the tarsometatarsus lateral to the deep flexor tendons. It originates by fleshy fibers from the lateral hypotarsal crest, the adjacent lateral surface of the tarsometatarsus, and from the lateral plantar crest to about 3 mm from the distal end of the element. The fibers insert on a flat tendon arising on the lateral surface of the muscle. The tendon crosses the lateral surface of the fourth metatarsal-phalangeal joint and inserts on the base of the proximal phalanx of digit IV.

M. lumbricalis.—This well-developed muscle arises by fleshy fibers from the caudal surfaces of the fused tendons of Mm. flexor digitorum longus and flexor hallucis longus in the central third of the tarsometatarsus. Distally it narrows to a short tendon that inserts on the proximal end of a joint pad on the medial surface of the trochlea of digit IV.

Discussion

Several notable features of the thigh and shank of *Colius* are very likely related to their propensity for hanging. In this position (Fig. 1), elevation of the body to an upright position requires retraction of the femur, flexion of the shank, and flexion of the tarsometatarsus. Muscles bringing about these actions must counteract the weight of the entire body. Handling captive *C. striatus* revealed it to be a surprisingly heavy bird for its size. Rowan (1967) records an average length of 326 mm, 204 mm of which is tail, and an average weight of 56.4 g. Wallace (cited by Murie 1872) was also impressed by the weight of these birds. Hence, it would be expected that the muscles bringing about these actions might be modified in some way.

The thigh.—M. iliofemoralis externus is usually small and often absent in birds (George and Berger 1966). Its very large size in *Colius* (Fig. 2C) is almost certainly related to its action as a retractor of the femur. Likewise, the extensive femoral insertion of M. flexor cruris lateralis (Fig. 3) is probably related to the need for powerful retraction of the femur.

The accessory belly of M. pubo-ischio-femoralis (Fig. 2B, D) has not been reported in any other group of birds. Whereas pars lateralis and medialis insert on the femur in a conventional manner, pars accessorius inserts on the tibiotarsus, thus functioning both in retraction of the femur and in flexion of the tibiotarsus. Because both actions are important in elevation of the body, it seems likely that the presence of this unique third belly is also related to the habit of hanging.

There are other peculiar features of the thigh for which the significance is uncertain. M. obturatorius medialis is much enlarged and consists of two bellies (Fig. 2B, D). Whereas the latter feature is not uncommon among birds, the enlargement of this muscle in *Colius* may be a compensation for the loosely articulated hip joint. The second head of origin for M. ischiofemoralis has not previously been reported among birds. But as the muscle as a whole is not noticeably enlarged, nor has it changed its areas of origin or insertion, the significance of this variation is obscure. Likewise, this study provides no explanation for the loss of M. iliofemoralis and the postacetabular portion of M. iliotibialis lateralis in *Colius*.

The shank.—At least two unusual features of the shank are probably related to hanging. The large size of the tibialis cranialis and the peculiar retinaculum just distal to its femoral origin (Fig. 4) may reflect this muscle's function as a flexor of the tarsometatarsus. The arthrology of the hindlimb was not included in this study, but observations on living birds and fresh specimens indicate a very loose articulation both at the hip and the knee. The retinaculum, with its complex attachments to the proximal end of the tarsometatarsus, may serve to stabilize the tendon when it is under considerable stress, as would be the case during body elevation.

The extensive origin of M. flexor hallucis

TABLE 1. Summary of muscular modifications associated with rotation of digits I and IV in *Colius*.

Digit	Action	Muscle	Modification
I	Cranial rotation	M. flexor hallucis brevis	Well-developed; insertion on lateral rather than plantar surface of digit
	Caudal rotation	M. extensor hallucis longus pars distalis	Well-developed; insertion on medial rather than dorsal surface of digit
IV	Cranial rotation	M. extensor brevis digiti IV	Well-developed
	Caudal rotation	M. abductor digiti IV	Well-developed; insertion more plantar than lateral

longus from the femoral shaft (Fig. 6) might also be correlated with hanging. Examination of this muscle on a fresh specimen revealed that in this position its action has some role in flexion of the shank. Alternatively, the enlargement of this muscle may simply reflect the importance of maintaining a strong grip under very diverse circumstances.

Pycraft (1907) contended that in the Coliiformes the tendon of M. flexor hallucis longus never fuses with that of M. flexor digitorum longus, but bifurcates, sending branches to digits I and II. This is incorrect, for although the distinction between the two tendons can be seen throughout their length, they are in fact fused. There is no doubt that the branch to the hallux is derived from that part of the tendon formed by the flexor hallucis longus tendon. When viewed dorsally (Fig. 7) the branch to digit II cannot be seen unless those to digits I and III are separated slightly, because it is deep to the branch to the hallux. Because it arises from the most medial part of the tendon, as does the branch to the hallux, from this view it could be interpreted as arising from the part of the tendon derived from M. flexor hallucis longus. The ventral view, however, clarifies the picture (Fig. 7). In spite of its medial origin, the branch to digit II arises in the same plane as those to digits III and IV. In this view it really looks as if the tendon of M. flexor digitorum longus trifurcates, and the branch to the hallux is the exceptional one, in that it arises from the dorsal surface of the common tendon.

One of the most distinctive features of the entire hind limb of *Colius* is the branch of the extensor digitorum longus tendon to the hallux (Fig. 5). This condition has been found in only one other order, the Psittaciformes, and could thus be taken as evidence that these two groups have shared a common ancestor. It must be borne in mind, however, that both parrots and mousebirds use their feet in a peculiar manner, thus providing an equally strong argument for convergence. Parrots are permanently zygodactyl, while mousebirds only occasionally hold their digits in this configuration. The ability to extend both caudally directed digits with the action of one muscle would seem to be an advantage. The normal arrangement, with branches only to digits II, III, and IV, is most efficient for the anisodactyl configuration. The hallux, the caudally directed digit, is often the only digit that acts in grasping during perching; hence its operation apart from the other three digits is necessary. In addition, both parrots and mousebirds have many more complex uses of their feet than perching. It is possible that the manipulative ability of the foot is enhanced by having extension of all four digits controlled by a single muscle. Mousebirds have lost pars proximalis of the extensor hallucis longus, and the entire muscle is absent in at least one parrot (*Melopsittacus undulatus*). In both cases it appears that the tendon of insertion of pars proximalis has been shifted to the extensor digitorum longus.

Although this character alone cannot demonstrate a common ancestry for the Coliiformes and Psittaciformes, it is more substantial evidence than any single feature previously offered in relating the Coliiformes to other groups. Thus, the possibility of this relationship should be kept in mind when considering other aspects of the anatomy of these two orders.

The foot.—Cranial and caudal rotation of digits I and IV is accomplished by several deviations from the basic avian plan (Table 1).

Considering first the hallux: The extensor hallucis longus consists of two parts in many birds, a pars proximalis and a pars distalis. Pars proximalis is typically the larger component, pars distalis being reduced or often absent (George and Berger 1966). In *Colius*, pars proximalis has been lost and pars distalis is well-developed. Furthermore, while pars distalis typically inserts on the dorsal surface of the base of the hallux, in *Colius* the insertion has moved to the medial surface of this digit. In this position its contraction brings about caudal rotation of the hallux.

The action of the very small extensor hallucis longus accessorius is difficult to demonstrate. As it is known only in Coliiformes, it seems likely that it is related to digit rotation. From its location it looks as if it might feebly augment cranial rotation.

M. flexor hallucis brevis is often small or absent in birds. When present, it normally inserts on the plantar surface of the base of the hallux (George and Berger 1966). This muscle is well-developed in mousebirds, and the insertion has shifted to the lateral surface of this digit, so that its contraction brings about cranial rotation of the hallux.

Caudal rotation of digit IV is less pronounced than that of the hallux. It can be actively rotated to only about 100°. Beyond this, its distal four phalanges can be rotated passively by contact against the substrate to about 160°.

M. extensor brevis digiti IV is typically small or absent in birds. When present, it inserts on the dorsal surface of the base of digit IV (George and Berger 1966). In *Colius*, this muscle is unusually large and its insertion has shifted medially. Its action in this position is not extension, but cranial rotation of digit IV. M. extensor proprius digiti IV, however, does insert on the dorsal surface of this digit. This muscle, not previously described in birds, may have replaced M. extensor brevis digiti IV as the short extensor of this digit.

The caudal rotator of digit IV is M. abductor digiti IV, and its action probably accounts for its enlargement in *Colius*. The insertion, normally on the lateral surface of the base of the digit (George and Berger 1966), has shifted to a slightly more plantar position in mousebirds, so that the action of this muscle goes beyond abduction to caudal rotation. This is not a very pronounced change, however, and it is likely that some modification of the fourth metatarsal-phalangeal joint is also involved in this action.

ACKNOWLEDGMENTS

We are grateful to Kenneth C. Parkes, Carnegie Museum of Natural History, for providing the preserved and frozen specimens for dissection, and to Norman Suhoski, Pittsburgh Aviary-Conservatory, for furnishing the live mousebirds. Thanks are also due to Jonathan Treasure for his technical assistance. Storrs L. Olson, Joel Cracraft, and an anonymous reviewer provided constructive criticisms of the manuscript. The figures were drawn by William R. Filer. This study was supported by N.S.F. grants DEB-7810715 and DEB-8010898 to R. J. Raikow. Studies of the frozen specimens and the colony of living birds were supported by the College of the Holy Cross.

LITERATURE CITED

BALLMAN, P. 1969. Les oiseaux Miocenes de la Grive-Saint-Alban (Isere). Geobios 2: 157–204.

BAUMEL, J. J., A. S. KING, A. M. LUCAS, J. E. BREAZILE, & H. E. EVANS (Eds). 1979. Nomina Anatomica Avium. London, Academic Press.

BOCK, W. J., & R. SHEAR. 1972. A staining method for gross dissection of vertebrate muscle. Anat. Anz. 130: 222–227.

CHAPIN, J. P. 1939. The birds of the Belgian Congo. Bull. Amer. Mus. Nat. Hist. 75: 469–479.

DECOUX, J. P. 1975. Le dispositif d'accrochage des griffes de *Colius striatus* (Coliiformes). Alauda 43: 271–278.

FRIEDMANN, H. 1930. Birds collected by the Childs Frick expedition to Ethiopia and Kenya colony. Part 1. Bull. U.S. Natl. Mus. 153: 321–337.

GADOW, H. 1893–1896. Muscular System. Pp. 602–620 *in* A. Newton (Ed.). A dictionary of birds, Part III. London, Adam and Charles Black.

GARROD, A. H. 1896. Notes on the anatomy of the colies (*Colius*). Proc. Zool. Soc. London 1896: 416–419.

GEORGE, J. C., & A. J. BERGER. 1966. Avian myology. New York, Academic Press.

HUDSON, G. E. 1937. Studies on the muscles of the pelvic appendage in birds. Amer. Midl. Natur. 18: 1–108.

LOWE, P. 1948. What are the Coraciiformes? Ibis 90: 572–582.

MACKWORTH-PRAED, C. W., & C. H. B. GRANT. 1962. Birds of the southern third of Africa, Vol. 1. London, Longmans, Green & Co., Ltd.

MURIE, J. 1872. On the genus *Colius*, its structure and systematic place. Ibis 1872: 263–280.

PYCRAFT, W. P. 1907. On the anatomy and systematic position of the colies. Ibis 1907: 229–253.

ROWAN, M. K. 1967. A study of the colies of southern Africa. Ostrich 38: 63–115.

SCLATER, W. L. 1903. The birds of South Africa, Vol. 3. London, R. H. Porter.

VERHEYEN, R. 1956. Note sur L'anatomie et la classification des Coliiformes. Inst. Roy. Sci. Natur. Belgique, Bull. 32(47): 1–7.

(*continued from p. 30*)

Altitudinal gradients in speciation of Andean forest birds; Susan Hannon, Female spacing behaviour in the Willow Ptarmigan and its relation to population regulation; Douglas B. Hay, Physiological and social ecology of roosting Pygmy Nuthatches (*Sitta pygmaea*); James L. Hayward, Reproductive strategies used by homosexual and heterosexual gulls; Linda Heald, Behavioral plasticity in a Tyrannid flycatcher: effects of environmental variability; Carlos M. Herrera, Ecology and evolution of avian frugivory in Spanish mediterránean habitats; Eve Sevier Hiatt, Annual cycle of plasma prolactin and follicle-stimulating hormone in a free-living population of the White-crowned Sparrow, *Zonotrichia leucophrys*; Wendy L. Hill, Effect of resource productivity on the intraspecific variation in reproductive behavior of the American Coot (*Fulica americana*); Anne E. Houde, Effects of nest site choice on the survival of Common Tern chicks; Peter Houde, Paleognathous birds from the Lower Eocene London clay; Karen E. Innes, Behavioral ecology of the White-throated Magpie Jay (*Calocitta formosa*) of Santa Rosa National Park, Costa Rica; Joel F. Jerabek, Territories of Vesper, Savannah, and Grasshopper Sparrows on reclaimed surface mines; Alan Charles Kemp, Systematic investigation of hornbills (Bucerotidae) and birds of prey (Falconiformes); E. N. Kurochkin, Avian fossils from the tertiary of the USSR and Mongolia; Barbara E. Kus, Raptor predation on wintering shorebirds; Stewart T. Levinson, Bird/fruit interactions in northern Florida; Charles S. Luthin, Comparative morphologies of 4 subspecies of the Buff-necked Ibis, *Theristieus caudatus*; Timothy D. Manolis, Reproductive interactions between Shiny Cowbirds and actual and potential hosts in Trinidad and Tobago; Leslie F. Marcus, Ecomorphological analysis of birds from Mediterranean habitats in Chile, California, and France; Kenneth D. Meyer, Sexual differences in the behavioral ecology of the Sharp-shinned Hawk (*Accipiter striatus*); Bruce Wayne Miller, Revision of the bird family Pittidae; Michael T. Murphy, Variability in insect abundance, foraging ecology, and nestling growth in the Eastern Kingbird; Erica Nol, Reproductive strategies in two species of oystercatcher; Christopher J. Norment, Avian communities of the alpine tundra/subalpine forest ecotone, Beartooth Mts., Wyoming; Gary L. Nuechterlein, Reproductive isolation of Western Grebe color phases in Mexico; Sally Olson, Habitat selection, breeding biology, and density of the Mountain Plover on the Charles M. Russell National Wildlife Refuge; Paula Peters, Vocal communication system of the Santa Cruz Island Scrub Jay; Ted N. Pettit, Incubation strategies of tropical seabirds on Christmas Island; Nina Pierpont, Foraging behavior of woodcreepers (Dendrocolaptidae) in Amazonian Peru; Melinda Pruett-Jones, Vocal copying in Macgregor's Bowerbird (*Amblyornis macgregoriae*); Stephen Glen Pruett-Jones, Ecology and evolution of social organization in *Parotia lawesii*, Lawes Six-wired Bird of Paradise; James Scott Quinn, Pairbond integrity, mate fidelity, and parental investment in Caspian Terns (*Sterna caspia*); Terry Edwin Quinney, Relationship between food abundance and breeding performance in the Tree Swallow (*Iridoprocne bicolor*); Susan St. Clair Raye, Bobwhite Quail (*Colinus virginianus*) vocalizations: ontogeny and function in sibling recognition; Mark F. Riegner, Foraging ecology of the Yellow-crowned Night Heron; Diane E. Riska, Breeding biology and communication behavior of the Brown Noddy, *Anous stolidus*, Dry Tortugas, Fla.; Scott K. Robinson, Ecology and social behavior of the Yellow-rumped Cacique in southeastern Peru; Stephen R. Sabo, Ecology and behavior of the Maui Parrotbill; Lilian J. Saul, Ecology and behavior of Red-headed and Red-bellied Woodpeckers in south-central Florida; William A. Searcy, Female choice of mates and male singing behavior in Song Sparrows; Erik Skadhauge, Activation of salt-gland function and regulation of coprodeal transport in the ostrich; Martin Luther Stephens, Parental behavior and ecology of the polyandrous Northern Jacana; Henry M. Stevenson, Birds of Florida; F. G. Stiles, Handbook of Costa Rican birds; Theresa A. Thompson, Social organization within eastern Wild Turkey flocks; Diana F. Tomback, Role of visual cues in seed cache retrieval by Clark's Nutcracker; Wayne Trivelpiece, Etho-ecology of the Magnificent Frigatebird (*Fregata magnificens*); Robert F. Tintle, Influence of male multiple nest building on female mate choice in Long-billed Marsh Wrens (*Telmatodytes palustris*); Alan Tye, Food supply, feeding behaviour, and territorial behaviour of the Wheatear (*Oenanthe oenanthe*) in Africa; Evelyn H. Weinstein, Nest site selection in Arctic Terns (*Sterna paradisaea*)

(*continued on p. 66*)