MYOLOGY OF THE LEG IN SWALLOWS

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While studying the functional morphology of swallows, I noted that the gross myology of their legs differed in a number of features from the pattern usually described for passerines. A review of the literature revealed that, although there are no myological studies devoted exclusively or even primarily to the swallows, various authors have mentioned one or another oddity in hirundinid leg musculature. Some of these, such as the much reduced M. iliotibialis, are noted in recent review literature (e.g. George and Berger, 1966); some, perhaps because the references are obscure, have been overlooked or, perhaps pending confirmation, ignored; others are undescribed. In view of this and inasmuch as I had on hand a considerable collection of assorted swallows, including the rare and taxonomically suspect *Pseudochelidon,* it seemed appropriate to undertake an examination of leg myology in the family Hirundinidae as a whole.

The names of muscles described herein are those of George and Berger (1966); the taxonomy is that of Peters (1960), except *Psalidoprocne holomelaena* is referred to *P. pristoptera* (*cf.* S.A.O.S. List Committee, 1963). Specimens whose legs I have dissected entirely or in part include:

Subfamily Pseudochelidoninae (African River Martin):
Pseudochelidon eurystomina (2 entire, 2 carcasses with thighs intact);
Subfamily Hirundininae (typical swallows):
Tachycineta bicolor (4), *T. albilinea* (4), *T. thalassina* (4), *Progne subis* (10), *Notiochelidon cyanoleuca* (1 carcass complete to midpoint of crus), *Stelgidopteryx ruficollis* (14), *Riparia paludicola* (1), *R. riparia* (18), *Phedina borbonica* (1), *Ptyonoprogne obsoleta* (2), *Hirundo rustica* (10), *H. angolensis* (1), *Cecropsis striolata* (1), *Petrochelidon pyrrhonota* (17), *Psalidoprocne pristoptera* (1).

If the muscle in question deviates from the pattern usually found in passerines, I have so commented in the description of that muscle. Differences between typical swallows, *Pseudochelidon,* and other passerines are summarized in Table 1.

M. sartorius.—In the Hirundininae this most anterior muscle of the leg arises directly or by a very short aponeurosis from the crests of the neural spines of the last three dorsal vertebrae and from the anterior margin of the ilium as far ventrad as the margin of M. iliotibialis. There is no connection to the median ridge of the synsacrum nor to aponeuroses of other muscles. The thin straplike belly of parallel fibers passes down the leading edge of the thigh to insert by fleshy fibers on the anteromedial surface of the head of the tibiotarsus just proximal to the origin of M. gastrocnemius pars anterior.

In *Pseudochelidon,* M. sartorius is structurally as in the Hirundininae, but it differs slightly in origin and insertion. In this species, the vertebral origin is from the last two dorsal vertebrae. The insertion is more anterior and proximal than in typical swallows, being in the usual passerine position along the proximomedial edge of the inner cnemial crest and the anteromedial edge of the articular surface of the tibiotarsus rather than the medial face.

M. sartorius varies greatly within the passerine assemblage. In those species in which there is a single head (two heads have been described for some species), the origin of this muscle has been described as involving one or two dorsal vertebrae and, frequently, the median ridge of the synsacrum. Thus, the condition here described for *Pseudochelidon* represents an anterior placement within the previously noted range of variation. In typical swallows the origin has spread anteriad to include the posterior half of an additional dorsal vertebra. Also, the insertion appears to have migrated slightly mediad of the position generally found in passerines.

M. iliotibialis.—This is a fairly small, triangular muscle covering the anterolateral surface of the thigh. It arises via an extensive aponeurosis, which is shared posteriorly with M. biceps femoris, from the anterior iliac crest and, posteriorly, from the dorsal surface of the ilium. There is a small, fleshy connection to the anterior iliac process. The small belly is more extensive anteriorly. Distally fibers shade into an aponeurosis that converges anteriorly to join with and become a part of the patellar ligament.

Hudson (1937) noted that the postacetabular portion of M. iliotibialis is absent in *Stelgidopteryx ruficollis* and *Petrochelidon albifrons.* It is absent in all swallows, including *Pseudochelidon,* that I have dissected. The muscle has been reported as entire in all other passerines studied to date except the Tyrannidae. I have found it entire in *Artamus.*

Mm. femorotibialis externus et medius.—It is possible to treat each of these muscles separately, but in passerines they are so intimately connected that they are virtually inseparable and they are therefore treated here as a single structural unit. This is not to imply that the complex serves a single biologic role.

The externus arises by a very short aponeurosis and/or fleshy fibers from a point between the trochanter and the inserting tendon of M. iliotrochantericus anterior. In *Pseudochelidon* fibers extend onto the trochanter. The anterior edge of the muscle covers the insertion of M. iliotrochantericus anterior. Fibers from the posterolateral margin of the femur continue to contribute to the belly for most of its length. The belly passes along the lateral and posterolateral femoral shaft to give rise to a heavy aponeurosis that in turn becomes a major portion of the patellar ligament. It has no distinct distal head.

The medius originates via tendinous fibers from the anterior edge of the trochanter and by fleshy fibers along most of the anterior margin of the femur. It is a rather heavy muscle, somewhat triangular in cross-section. For two-thirds of its length in typical swallows, from about the level of origin of the externus to just below the point of the divergence of the externus and internus, deep fibers arise from a common raphe. Thus although the muscle is parallel fibered when viewed from its lateral surface, a medial view gives the appearance of a bipinnate muscle with the convergence directed away from the insertion. In *Pseudochelidon* the raphe is shorter, and convergence is not so dramatic. While aponeuroses from the muscle undoubtedly contribute to the patellar ligament, the prime insertion is by fibers directly onto the patella.

The Mm. iliotrochantericus anterior and iliotrochantericus medius pass over the tapering head of M. femorotibialis medius to insert between it and M. femorotibialis externus. Just distal to this point the Mm. femorotibiali fuse along their lateral margins for most of their length, diverging slightly as they approach their insertions.

M. femorotibialis internus.—The structure of this muscle shows considerable variation within the passerine assemblage. In the Hirundininae it exhibits dual origins and insertions and probably should be considered two-headed, but the fibers mingle to such an extent within the main belly that it is virtually impossible to distinguish them. Nor is it at all evident that fibers from either origin contribute exclusively to the formation of either insertion.

The proximal origin is immediately distal to the insertion of M. iliacus in typical swallows and extends to the level of that insertion in *Pseudochelidon.* In typical swallows the spindle-like belly then passes down the medial surface of the femur to blend with the distal head. Medial fibers from both heads contribute to a tendon that lies along the midline of both bellies and inserts on the medial surface of the tibial head between the insertion of M. sartorius and the origin of M. gastrocnemius pars interna.

The broad, triangular, deep distal head is formed from fibers arising from the femoral shaft in its distal third. Fibers not contributing to the above mentioned tendon, and probably some fibers from the proximal head, insert beneath and slightly posteriad to the tendinous insertion.

In *Pseudochelidon* the two heads are more distinct proximally and fuse distally. The proximal head gives rise to a short tendon to which portions of the distal head gradually contribute. The final insertion is common to both heads.

Passerines appear to be divided along no clear systematic lines into those in which M. femorotibialis internus is distinctly two-headed and those in which the heads are more or less fused. With some degree of variation at the subfamilial level, the swallows exhibit the latter condition.

M. iliotrochantericus posterior.—This large muscle arises by fleshy fibers from the anterior iliac crest and the entire iliac fossa. Fibers converge on a broad, heavy tendon that inserts on the lateral head of the femur dorsad to the trochanter.

M. iliotrochantericus anterior.—This muscle originates by a short aponeurosis from the anterior iliac process and fleshily from the anterior third to half of the ventral margin of the iliac fossa. For much of its length the dorsal margin lies under the ventral margin of M. iliotrochantericus posterior. The insertion is via a short tendon, and sometimes fleshy fibers, to the midlateral line of the femur slightly distal to the trochanter. The belly passes over M. femorotibialis medius, and the tendon attaches just beyond and beneath the anterior margin of M. femorotibialis externus. The inserting tendon varies somewhat in width, e.g. from 0.5 to 1.5 mm in four Cliff Swallows.

M. iliotrochantericus medius.—This small, delicate muscle arises just posterior to the origin of M. iliotrochantericus anterior. It inserts proximally and somewhat anteriorly to M. iliotrochantericus anterior.

M. biceps femoris.—The biceps in swallows arises by fleshy fibers from the posterior iliac crest as far posteriad as M. semitendinosus and shares an aponeurosis with M. iliotibialis. The aponeurosis is fused to the dorsal surface of the ilium from the dorsal margin of M. iliotrochantericus anteriorly to the origin of M. levator coccygis posteriorly. Fibers of the biceps cover the head of the femur, thus extending forward of the acetabulum. The belly tapers to a long tendon that passes through the biceps loop and inserts about midway down the fibula. The sling is composed of a tendon extending from the femur proximal to the origin of M. gastrocnemius pars externa and looping back to share the insertion of that muscle. From approximately the center of the loop a third arm extends to just below the head of the fibula.

Mm. semitendinosus et accessorius semitendinosi.—M. semitendinosus lies lateral to Mm. ischiofemoralis and piriformis pars caudofemoralis and the dorsal half of M. semimembranosus. It arises by fleshy fibers from the posterior half of the posterior iliac crest and by aponeurotic connections, the limits of which are indistinct in the Hirundininae, to the fascial sheet separating the dorsal and ventral tail muscles. The belly tapers anteroventrally to a complex insertion. A short tendon fuses to the posterior margin of M. gastrocnemius pars media, while a delicate but strong aponeurosis passes medial to the gastrocnemius and unites with the medial surface and tendon of M. semimembranosus. The separation of the two insertions is distinct. The tendon to the gastrocnemius arises from lateral and inferior (morphologically posterior) fibers, while the aponeurosis to the semimembranosus arises from the more medial and superior (anterior) fibers.

Accessorius: Except for rare cases the accessory is absent in all members of the Hirundinidae investigated.

The Mm. semitendinosus and accessorius semitendinosi are respectively the "X" and "Y" of leg-muscle formulae. George and Berger (1966) state that both muscles are present in all Passeriformes except *Dicrurus,* in which the accessory is absent, but Lowe (1938) noted that *Pseudochelidon, Hirundo,* and *Riparia* were "AX," in contrast to the "AXY" pattern of *Artamus.* My dissections have failed to reveal a definite accessory muscle in all but one individual. In one Barn Swallow (*Hirundo rustica erythrogaster*), a small raphe was present in the usual position behind the knee. From this a few delicate fibers extended forward to insert on the posterior margin of the femur just proximal to the external condyle.

A dual involvement of M. semitendinosus with both M. gastrocnemius pars media and M. semimembranosus appears to be usual for passerines (cf. Hudson, 1937; Stallcup, 1954; George and Berger, 1966). Thus, the insertion described above is essentially one of the variations found in passerines.

M. piriformis pars caudofemoralis.—The pars caudofemoralis is the only portion of the piriformis complex present in passerines. It does not differ in structure or placement in swallows from the pattern described for other passerines. It arises by a rather long tendon from the base of the pygostyle. The belly passes forward deep to M. semitendinosus and lateral to Mm. semimembranosus and ischiofemoralis to insert by a tendon about midway down the posterolateral surface of the femoral shaft.

M. ischiofemoralis.—This large, leaf-shaped muscle arises by fleshy fibers from most of the ischium and the caudal quarter of the ventral surface of the posterior iliac crest. In the most caudal portion of the muscle some fibers may arise from the ilium. Attachment to the membrane of the ischiopubic fenestra in *Pseudochelidon* is by a short aponeurosis. The belly converges to form a short, wide tendon that inserts on the lateral surface of the femur slightly proximal to the insertion of M. iliotrochantericus anterior.

M. semimembranosus.—This muscle arises by fleshy fibers from the ventrolateral surface of the caudal portion of the ischium. The line of origin is parallel and slightly dorsal to the border of the ischiopubic fenestra. The belly passes forward between the pars externa and pars media of M. gastrocnemius to insert by a broad, flat tendon (± 2 mm) on the medial surface of the tibiotarsus. At approximately the point of origin of the inserting tendon, M. semimembranosus receives on its medial surface a short aponeurotic connection from M. semitendinosus. There is extensive fascial connection with both M. gastrocnemius pars media and M. adductor longus et brevis.

M. adductor longus et brevis.—In passerines this muscle is usually separated into two parts, an anterior and lateral belly, the pars anterior, and a more medial posterior belly, the pars posterior. In swallows the two portions are very closely associated. Separation, when possible at all, is effected only with considerable difficulty and, I fear, no little imagination. For this reason I judge it better to treat the muscle as a unit.

The anterior portion of the origin is by fleshy fibers from the ischium just below the obturator foramen, thence it continues onto the dorsal border of the ischiopubic foramen where it becomes aponeurotic. The fleshy insertion is onto the posterior margin of the femoral shaft in its distal two-thirds. Near the most distal portion of its insertion the adductor is intimately associated with the medial surface of M. gastrocnemius pars media.

M. obturator externus.—The external obturator has been reported as comprised of single or dual heads (a dorsal and a ventral) in various passerines. In swallows the muscle is quite small and difficult to dissect, but appears to be a single mass originating from the anterior, ventral, and posterior margins of the obturator foramen. It is thus essentially ventral. The fibers pass forward and laterad to insert on the posterolateral surface of the trochanter beneath the tendon of M. obturator internus.

M. obturator internus.—This oblanceolate muscle arises on the medial surfaces of the pubis, ischiopubic membrane, and ventral ischium. Its structure is basically bipinnate, with the central tendon forming in the caudal two-thirds. The strong inserting tendon passes through the obturator foramen and becomes intimately associated with the more lateral fibers of M. obturator externus. Insertion is onto the posterior trochanteric ridge.

M. iliacus.—This very small muscle arises by fleshy fibers from the ilium ventral to the origin of M. iliotrochantericus medius. It passes posteriad and laterad to a fleshy insertion just below the head of the femur on its medial surface.

M. gastrocnemius.—This muscle is comprised of three separate heads, the pars externa, media, and interna. Each head gives rise to a broad, flat, heavy tendon. These converge across the medial surface of the crus and fuse to form the Achilles tendon.

Pars externa: This is the most lateral portion, less than a third of it being visible from the medial surface. It originates via a short tendon from the posterolateral shaft of the femur just proximal to the lateral condyle. The origin is intimately involved with tendons of the biceps loop. In the Hirundininae the distal tendon of the biceps loop fuses with the tendon of the pars externa. The proximal tendon inserts separately just above this common insertion. In *Pseudochelidon* both tendons of the biceps loop and the tendon of pars externa are fused. The rather bulky belly of the pars externa extends about a third of the way down the posterior margin of the crus. The tendon of insertion passes distad and slightly anteriad.

Pars media: This smallest of the three heads lies deep to the inserting tendon of M. semimembranosus. It arises by fleshy (tendinous in *Pseudochelidon*) fibers from the posterior margin of the femur proximal to the internal condyle. The origin is extensively involved with the insertion of M. adductor longus et brevis. M. semitendinosus inserts about halfway down the belly of pars media on its posterior margin. There is extensive fascial involvement with both of these muscles and with M. semimembranosus.

Pars interna: This is the largest of the three heads, covering most of the anteromedial surface of the crus in its proximal two-thirds. The head arises by fleshy fibers from the anterodorsal edge and entire medial surface of the cnemial crest and the head of the tibiotarsus as far as the shaft, with a few fibers coming from the most proximal portion of the shaft. The anterior margin of the belly wraps around the leading edge of the crus onto the lateral surface to cover the anterior margin of M. peroneus longus. In *Pseudochelidon* a few fibers may arise from the lateral edge of the inner cnemial crest. About halfway down its length the belly tapers sharply posteriad.

The fusion of tendons of these three heads forms the Tendo Achillis. This runs distad around the posterior margin of the tibial cartilage to a primary insertion on the posterior surface of the hypotarsus. It then continues distad to a final insertion on the posterolateral surface of the tarsometatarsus near its external condyle. For the length of its passage down the tarsometatarsus the tendon is closely associated with the overlying skin. Together they form a sheath for the deeper tendons of the toe muscles.

M. peroneus longus.—The mode of origin of this muscle is variable within the Hirundinidae. It may arise completely by fleshy fibers, a combination of fleshy and tendinous fibers or both of these combined with aponeuroses. The variation appears to be related more to size than to species specific differences, partially tendinous and/or aponeurotic origins being more frequent in the larger species. The origin is constant, being along the anterior edges of the cnemial crest, rotular crest, and lateral outer cnemial crest. In *Pseudochelidon* the origin from the outer cnemial crest is distinctly aponeurotic and associated with the origin of M. tibialis anterior. This is less so in the Hirundininae. In species for which the origin is primarily aponeurotic, e.g. *Progne subis,* the aponeurosis tends to pass proximal to the head of the tibiotarsus and to become involved with the patellar membranes.

In members of the Hirundininae the belly is more or less divided longitudinally by central thinning into anterior and posterior heads joined in the midline of the belly by an aponeurosis and a variable amount of fibers. Although the division is always evident, especially distally near the tendon, its extent is variable both among and within species. When the division is particularly strong, origin of the posterior head from the outer cnemial crest is via a short tendon. Fibers of the posterior head extend down the crus to its distal quarter, where they give rise to the tendon of insertion. Fibers of the anterior head produce an aponeurosis about halfway down the crus. This converges onto the anterior margin of the posterior head and the tendon.

In *Pseudochelidon* a division into two heads is not especially evident. There is a slight distal indentation, and the anterior portion of the belly is short and gives rise to an aponeurosis as in the Hirundininae. Its fibers appear to slant somewhat more toward the midline of the belly than do those of the posterior portion. The main portion of the belly is quite robust and shows no hint of central thinning.

No tendency to central thinning of the belly seems to have been noted or figured in the literature, but it occurs in numerous other passerines, e.g. *Parus, Passer,* and *Hesperiphona.* George and Berger (1966) note that the development of M. peroneus longus varies greatly and is probably of little taxonomic value.

In all swallows the inserting tendon attaches to the posterolateral corner of the tibial cartilage.

Mitchell (1913) noted that the peroneus longus of *Hirundo rustica* differs from the usual "almost tiresome" passerine pattern in two respects. First there is little deep (to the shafts of the fibula and tibiotarsus) or fascial (to neighboring muscles) attachment. I am inclined to say that there is no deep attachment, but there does appear to be some very light fascial, and perhaps fibrilar, involvement between the

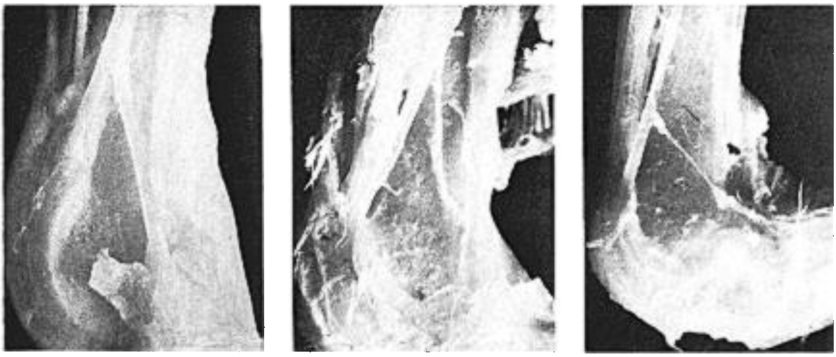

Figure 1. Bifurcation of the tendon of M. peroneus longus in *Passer domesticus* (left), *Pseudochelidon eurystomina* (center), and *Hirundo angolensis* (right). Considerable connective tissue has been cleared away in the two hirundinids to reveal the minute long branch; only the epidermis has been removed from the sparrow. The muscles of *Pseudochelidon* have been torn by a compound fracture. Shaft diameter just proximal to the condyle is about 2 mm in all specimens; muscles in *Passer* increase the apparent diameter to about 3.5 mm.

posterior margin of M. peroneus longus and the anterior edge of M. flexor perforans et perforator digiti III.

In passerines the inserting tendon of M. peroneus longus bifurcates just proximal to the intertarsal joint. The short branch passes to the tibial cartilage, while a longer, often more delicate branch crosses the joint superficial to the insertion of M. peroneus brevis and inserts onto the tendon of insertion of M. flexor perforatus digiti III. Mitchell stated that the long branch was absent in *Hirundo*. Such was my initial impression, but the long branch is present (Figure 1) although highly reduced. It is hairlike, lies adjacent to the bone, and is rendered almost invisible by the surrounding connective tissue. So delicate is it that any teasing of the short tendon, or any but the most gentle removal of the tissues in which it is embedded will sever it. The condition of the long branch is identical in typical swallows and in *Pseudochelidon*.

M. peroneus brevis.—This muscle arises by fleshy fibers from the lateral aspect of the distal half of the fibula and distally by fleshy fibers from the shaft of the tibiotarsus. Just proximal to the external condyle the fibers produce a tendon that passes through a ligamentous loop on the anterolateral aspect of the tibiotarsus and continues to insert almost immediately on the lateral surface of the proximal end of the tarsometatarsus.

M. tibialis anterior.—Most of this muscle is covered by M. peroneus longus. It is comprised of two heads that fuse before giving rise to a common tendon of insertion. The femoral (deep) head arises by a short tendon from the apex of the anterior crest of the external condyle of the femur. The tendon and the most proximal fibers pass along the posterior surface of the outer cnemial crest to emerge on the lateral aspect of the tibiotarsus. The tibial head arises by fleshy fibers from the inner portion of the outer cnemial crest, rotular crest, and lateral surface of the inner cnemial crest along a line just distal to the origin of M. peroneus longus. The two bellies fuse about halfway down the anterior margin of the crus and continue in common to the distal quarter of the femur. The tendon of insertion passes through the ligamentum transversum and inserts near the proximal end of the tibiometatarsus on its anterior surface.

M. extensor digitorum longus.—The medium-sized bipinnate belly of this muscle arises deep to the origin of M. tibialis anterior from the lateral surface of the inner cnemial crest, medial surface of the outer cnemial crest, and anterior surface of the tibial shaft. In *Pseudochelidon* those fibers arising from the tibial shaft form a rather distinct flat bundle. Whether they should be considered a separate head is perhaps a matter of taste. Fibers extend well into the distal quarter of the tibiotarsus. The tendon of insertion passes through the ligamentum transversum deep to the tendon of M. tibialis anterior, thence through an osseous tunnel in the distal end of the tibiotarsus and another in the proximal end of the tarsometatarsus. It emerges to pass down the anterior surface of the tarsometatarsus, near the distal end of which it trifurcates, sending small tendons down the dorsal surfaces of digits II and IV and a heavy tendon to digit III. The former two send small slips to the bases of all phalanges beyond the proximal one and come to their major insertions on the terminal phalanges. The heavy central tendon passes down the dorsal surface of digit III, bifurcating at the base of the second phalanx, but otherwise inserting as for the other two digits.

M. flexor perforans et perforatus digiti III.—This large bipinnate muscle, one of the outstanding features of the lateral aspect of the hirundinid leg, is of complex origin. Anteriorly fibers arise from the lateral edge and posterior surface of the outer cnemial crest, from the patellar ligament, and from the head and shaft of the fibula. Posteriorly an origin via tendon from the posterior edge of the external condyle of the femur is shared with M. flexor perforans et perforatus digiti II.

The tendon passes through a canal in the posterior surface of the tibial cartilage, then through a medial bony tunnel in the hypotarsus. It extends down the posterior surface of the tibiometatarsus to the base of digit III, where it broadens markedly and perforates the tendon of M. flexor perforatus digiti III. It then passes down the ventral surface of the third digit and is itself perforated by the tendon of M. flexor digitorum longus at the midpoint of the second phalanx and before it inserts on either side of the ventral base of the third phalanx.

M. flexor perforans et perforatus digiti II.—This, the smallest of the major toe muscles, lies posterior to M. flexor perforans et perforatus digiti III and deep to M. gastrocnemius pars externa. It originates by tendon or tendinous fibers from the posterior surface of the external condyle of the femur immediately distal to the origin of M. gastrocnemius pars externa. The site of origin is shared with M. flexor perforatus digiti II and M. flexor hallucis longus. The belly produces a delicate flat tendon that tapers to a fine thread-like tendon. The tendon passes through the tibial cartilage deep to that of M. flexor perforans et perforatus digiti III, thence through a medial tunnel in the hypotarsus and down the posterior surface of the tarsometatarsus. At the base of digit II, the tendon plunges deep through a pulley. It then widens and, about midway down the proximal phalanx, splits to permit passage of the tendon of M. flexor digitorum longus. It then inserts on the base of the second phalanx.

M. flexor perforatus digiti IV.—This muscle arises via an aponeurosis in common with M. flexor perforatus digiti III. The aponeurosis originates from the intercondylar region of the femur together with the most medial of the inserting fibers of M. flexor hallucis longus. In addition to the shared aponeurosis, the bellies of Mm. flexor digiti III and flexor perforatus digiti IV have extensive fascial and fibrilar connections in their proximal portions. The tendon of insertion passes through the tibial cartilage and then through an open canal on the lateral surface of the hypotarsus. Near the base of digit IV the tendon broadens to ensheath the tendon of M. flexor digitorum longus. As it extends along the plantar surface of digit IV, it sends a stout branch to the plantar joint pad between the proximal two phalanges, then splits to permit passage of the tendon of M. flexor digitorum longus, and inserts on the plantar joint pad between the second and third phalanges.

M. flexor perforatus digiti III.—The origin of this deep, rather large muscle is in common with that of M. flexor perforatus digiti IV in the manner described above. The tendons of these two muscles share a common course, with that of M. flexor perforatus digiti III being the deeper, to their divergence at the distal end of the tarsometatarsus. There the tendon of M. flexor digiti III thickens and is perforated near the midpoint of the proximal phalanx by the tendons of Mm. flexor perforans et perforatus digiti III and flexor digitorum longus. It then inserts on either side of the plantar joint pad between the first and second phalanges.

M. flexor perforatus digiti II.—This muscle shares its tendon of origin and the major portion of its belly with the lateral head of M. flexor hallucis longus. The point of origin is the lateral condyle of the femur distal to the fleshy origin of M. flexor hallucis longus. The belly of M. flexor perforatus digiti II extends slightly beyond the midpoint of the crus but is independent of the M. flexor hallucis longus in only its distal third. Proximal to the point of divergence the two muscles share a common raphe along their anterior (deep) margins. The tendon of insertion passes through a posterolateral canal in the tibial cartilage and a medial tunnel of the hypotarsus, then inserts on the lateromedial corner of the base of the proximal phalanx of digit II without being perforated.

M. plantaris.—In *Pseudochelidon* this is a very small muscle about 3.5 × 0.9 mm. It originates by fleshy fibers from the posteromedial head of the tibiotarsus and gives rise to a long, delicate tendon that inserts on the proximomedial corner of the tibial cartilage. It is absent in the Hirundininae. M. plantaris is the "F" of leg muscle formulae. I am unaware of any other report of its absence in Passeriformes. Therefore its absence in all species of typical swallows that I have examined must be considered a signal deviation from the passerine norm.

M. flexor hallucis longus.—This is a rather large muscle of complex origin. One head arises via a tendon from the external condyle of the femur in common with M. flexor perforatus digiti II. A second, deep origin is by fleshy fibers from the intercondylar region distal to the insertion of M. adductor longus et brevis. The common aponeurosis of Mm. flexor perforatus digiti III and flexor perforatus digiti IV is appressed to the medial face of this origin. The two heads of M. flexor hallucis longus are separated by the tendon of M. biceps femoris. The fused bellies pass down most of the length of the crus before giving rise to a stout tendon. This passes through the tibial cartilage and medial tunnel of the hypotarsus. At the distal end of the tarsometatarsus, the tendon plunges deep between the hallux and digit II and enters a thick sheath that encloses it for the remainder of its passage down the plantar surface of the hallux to its insertion on the terminal phalanx.

M. flexor digitorum longus.—This large, essentially bipinnate muscle originates from the femur, fibula, and tibiotarsus. The femoral origin is by fleshy fibers from the posterior surface of the external condyle distal to the origin of M. flexor hallucis longus and spreads to the intercondylar region. Laterally fleshy fibers arise from the shaft of the fibula immediately distal to the insertion of M. biceps femoris. Distal to the fibula the anterior margin of the belly continues to receive fibers from the posterolateral aspect of the shaft of the tibiotarsus. Fleshy fibers arise also from the posteromedial aspect of the tibiotarsus along the entire course of the belly down the shaft. The muscle is bipinnate for all but its proximal quarter.

The heavy tendon of insertion becomes independent of the belly near the distal end of the tibiotarsus and passes through the tibial cartilage deeper than any other tendon. It then passes through a deep medial tunnel in the hypotarsus. At the distal end of the tarsometatarsus the tendon divides into three stout branches that pass down the plantar surfaces of digits II, III, and IV. Each branch sends a stout viniculum to the plantar joint pad between the two most distal phalanges in its respective digit, then inserts on the base of the ultimate phalanx. The branch to digit II passes through a pulley near the base of the digit and perforates the tendon of M. flexor perforans et perforatus II near the distal end of the proximal phalanx. The tendon to digit III, together with the tendon of M. flexor perforans et perforatus III, perforates the tendon of M. flexor perforatus digiti III near the base of the proximal phalanx, then perforates the tendon of M. perforans et perforatus III at the base of the second phalanx. The branch to digit IV perforates the tendon of M. flexor perforatus digiti IV near the distal end of the proximal phalanx.

M. flexor hallucis brevis.—This is a very small, bipinnate muscle originating from the anteromedial corner of the hypotarsus. The tendon of insertion passes down the posterior aspect of the tarsometatarsus and around the base of the proximal phalanx of the hallux to insert on the same pad that ensheaths the tendon of M. flexor hallucis longus.

M. extensor hallucis longus.—This muscle is so delicate in swallows that I was unable to determine fiber directions. It arises from the anteromedial corner of the tarsometatarsus and possibly a portion of the shaft. The hairlike tendon passes down the dorsal surface of the hallux to the midpoint of the proximal phalanx where it inserts on a broad ligament that continues to the distal end of the ungual phalanx.

DISCUSSION

Variation in pattern of leg myology in swallows is negligible below the level of subfamily. A few deviations of significance occur at the individual level, e.g. the one Barn Swallow with a vestigial M. accessorius semitendinosi. Other than these, variation is confined to minor differences in the extent of tendinous and/or aponeurotic involvement in the origins of some muscles and in the widths of inserting tendons. In general the larger the species, the more likely the origin to be partially or wholly aponeurotic or tendinous. A number of variations occur at the subfamilial level, the most outstanding of which are the presence of M. plantaris, the lack of a longitudinal division of the belly of M. peroneus longus, and the more posterior origin and anterior insertion of M. sartorius in *Pseudochelidon.* In respect to all of these the River Martin more closely resembles the usual passerine pattern than do the typical swallows.

Considering leg myology in the Hirundinidae as a whole, we find that deviations from the passerine pattern are in the direction of reduction in size, number, and complexity. Such might be expected in a group whose foraging is almost completely aerial, but this interpretation must be approached with caution. Certainly those swallows that utilize their legs for

TABLE 1

MAJOR DIFFERENCES BETWEEN HIRUNDINID AND TYPICAL PASSERIFORM LEG MUSCLE PATTERNS

Bold face designates differences considered critical. Note that *Pseudochelidon* conforms to the hirundinid pattern in three of four of these.

Muscle	Hirundininae	Pseudochelidoninae	Passeriformes
Sartorius			
a. origin	involves 3 dorsal vertebrae	involves 2 dorsal vertebrae	involves 1 or 2 dorsal vertebrae
b. insertion	medial	anteromedial	anteromedial
Iliotibialis	postacetabular portion **absent**	postacetabular portion **absent**	postacetabular portion present
Femorotibialis internus	both origin and insertion dual	dual origin, single insertion	variable
Accessorius semitendinosi	**absent**	**absent**	present (except *Dicrurus*)
Adductor longus et brevis	heads united	heads united	heads separate
Peroneus longus			
a. belly	longitudinally divided by an aponeurosis	not divided	variable
b. tendon	long branch **vestigial**	long branch **vestigial**	long branch strong
Plantaris	**absent**	present	present

digging burrows have need for strong pelvic musculature. Moreover in my opinion the locomotory usage of the leg by swallows has been grossly underestimated. I have spent many evenings watching large, mixed flocks of swallows gathering on sand bars or sand piles. If a bird wished to move any great distance, it flew, but there was much scurrying around, the birds sometimes "running" for distances of several meters. No collector who has tried to catch a wounded swallow, nor any bander who has tried to retrieve a nestling swallow that has jumped from the nest will quibble about its ability to run.

The taxonomic position of *Pseudochelidon* continues to be questioned despite the work of Lowe (1938). Mayr and Amadon (1951) assert that *Pseudochelidon* "is very doubtfully a member of the swallow family" and Schouteden (1955: 483) accords it separate familial rank. Schouteden's reasons for removing the River Martin from the swallows are not clear. Mayr and Amadon based their decision on dissections of syringes of several specimens of *Pseudochelidon*. They found that this species possessed half bronchial rings and a bronchidesmus, while typical swallows supposedly possess complete bronchial rings and no bronchidesmus. These authors did not dissect any member of the Hirundininae. Peter Ames tells me (pers. comm.) that a bronchidesmus is variably present in typical swallows and that he does not consider the condition of the bronchial rings to be of special significance.

With regard to leg muscle formulae, *Pseudochelidon* (ACEFX) falls midway between typical swallows (ACEX) and most other passerines (ACEFXY). The absence of M. plantaris in typical swallows is of unknown functional significance and is likely to remain so pending a far clearer understanding of their ecologies than now exists. Its presence in *Pseudochelidon* is probably best considered as representing a primitive condition.

Systematic speculations based solely upon the presence or absence of a single muscle in two specimens are hardly appropriate. When dealing with muscles, one must consider the overall patterns as much as possible. The absence of M. accessorius semitendinosi, of a postacetabular portion of M. iliotibialis, the reduction of the long branch to the tendon of M. peroneus longus, and the unified belly of M. adductor longus et brevis constitute a pattern found only in swallows and clearly link *Pseudochelidon* to them (Table 1). Additional support for this interpretation can be found in the neck musculature. I have previously reported (Gaunt, 1965) that Mm. cucullaris and rectus lateralis form a single complex in typical swallows. In the River Martin these two muscles are easily separated, but are in very close and intimate relation. In this character, too, *Pseudochelidon* appears to represent a primitive stage between typical swallows and other passerines. All of these results support the conclusions of Lowe, and I judge it best to treat *Pseudochelidon* as an early offshoot from a primitive hirundinid stock. As such, its inclusion within the Hirundinidae as a separate subfamily is clearly justified. According it separate familial rank only obscures its probable phylogenetic relationships.

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SUMMARY

The gross myology of the leg in the Hirundininae differs from the pattern generally described for Passeriformes in a number of respects, both

major and minor. The most important differences are the absence of 1) the postacetabular portion of M. iliotibialis, 2) M. accessorius semitendinosi, 3) M. plantaris, and the extreme reduction of the long branch of the inserting tendon of M. peroneus longus. *Pseudochelidon* conforms to the hirundinid pattern in all respects except that it does have an M. plantaris. The River Martin therefore appears to represent an early offshoot from the primitive hirundinid stock. As such its inclusion within the family Hirundinidae as a separate subfamily, Pseudochelidoninae, is clearly justified.

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