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TRENDS IN THE EVOLUTION OF HINDLIMB MUSCULATURE IN AERIAL-FORAGING BIRDS

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ABSTRACT.—Previous studies of hindlimb muscles suggest that reduction and individual variation in M. flexor cruris lateralis may be causally related to ecological habits such as aerial-foraging behavior. Examination of the muscle in a number of behaviorally convergent birds suggests that such variation is phylogenetically very restricted. Comparison with a published phylogeny of hindlimb muscle characters indicates that behavior and morphology have not coevolved in the case of M. flexor cruris lateralis. Examination of other hindlimb muscles suggests that individual variation is not likely to interfere with attempts to reconstruct phylogeny using such data. *Received 3 October 1991, accepted 12 March 1992.*

IN AN EARLIER study (McKitrick 1985, 1986), I dissected large series of numerous species of tyrant flycatchers (Tyrannidae) and found considerable individual variation in several muscles of the hindlimb. In particular, M. flexor cruris lateralis showed a trend toward size reduction and, in some cases, loss of the accessory portion (pars accessoria) of the muscle (see McKitrick 1986:fig. 1). The function of the pelvic part of the muscle (pars pelvica) is to flex the shank (tibiotarsus), while pars accessoria extends the thigh (femur; Raikow 1985). The significance of individual variation in size of this muscle is unknown, but three hypotheses have been proposed (McKitrick 1986). (1) Adaptive-variation hypothesis: individuals with different morphologies forage in different ways, thereby dividing the resource spectrum and avoiding intraspecific competition. (2) Transformation hypothesis: the variation is transient and represents a temporary stage in the process of reduction and eventual loss of the accessory portion of M. flexor cruris lateralis. (3) Random-variation hypothesis: the morphology of the muscle is more or less irrelevant to aerially foraging birds, and the muscle may vary at random. Further work suggested that the variation is heritable (McKitrick 1990a, b), indicating that it is not entirely due to nongenetic developmental phenomena. However, marked left–right asymmetry in muscle size (McKitrick 1990b) hints that size is not under strong selective control, and preservation of variation by natural selection (hypothesis 1) is probably not occurring.

A few other hindlimb muscles showed qualitative individual variation of a lesser magnitude. M. iliotibialis lateralis varied in whether a strap-shaped remnant of pars postacetabularis was present. M. flexor hallucis longus varied in the presence and number (0–2) of intermediate heads. A quantitative variant of M. flexor digitorum longus also was striking: in some specimens the femoral head was very large, while in others it was tiny (McKitrick 1985).

I undertook this study for three reasons. The first was to determine the influence of phylogeny and ecology on individual variation in M. flexor cruris lateralis. Few studies of individual variation in avian limb musculature have been reported, but Berman et al. (1990) and Raikow et al. (1990) suggested that variation of the extent found by McKitrick (1986) may be uncommon in birds (i.e. the variation may be peculiar to tyrant flycatchers and, thus, simply a phylogenetic phenomenon).

Alternatively, the variation may be related to ecology. For example, a robust thigh extensor may be unnecessary in an aerial-foraging bird and may be lost over the course of evolutionary time, or at least released from constraint. In this case, "rules" for the evolution of the hindlimb musculature would apply to all species, regardless of phylogeny, and variation may conform to one of the hypotheses suggested by McKitrick (1986).

Finally, the variation could be related to both phylogeny and ecology (i.e. the variation is related to habit, but for some reason has only occurred in New World flycatchers). If this is the case, then the hypotheses set forward by McKitrick (1986) would apply only to tyrant flycatchers. To try to address these problems, I dissected representatives of a number of groups of birds whose aerial-foraging behavior is probably of independent origin, so as to determine whether similar patterns of individual variation will occur in species that have kingbirdlike aerial-foraging behavior.

A second component of this research addresses the question of the relationship between the origin of aerial-foraging behavior and the reduction of M. flexor cruris lateralis (FCL) among species. A preliminary survey within the Tyrannidae (McKitrick 1985, 1986) showed that the tyrannids with the most aerial foraging-habits (e.g. *Tyrannus, Sayornis, Contopus, Hirundinea*) have the most reduced FCL, whereas those with the most terrestrial habits (e.g. *Machetornis*) have the most robust FCL. From these observations, I hypothesized that the association between aerial-foraging behavior and muscle reduction is a causal one. If this hypothesis is correct, the association will be found in all birds showing the same behavior as these tyrant flycatchers. To test this prediction, I map the occurrence of kingbirdlike foraging behavior onto a phylogeny of birds based on hindlimb-muscle morphology (McKitrick 1991) in order to examine the relationship between the evolution of aerial-foraging behavior and the evolution of FCL within a historical context. Finally, I wished to examine variation in all the other hindlimb muscles and attempt to evaluate the conclusions of Raikow et al. (1990) that intraspecific variation in avian hindlimb musculature usually will not interfere with phylogenetic analysis.

METHODS

Species were chosen for study on the basis of their aerial feeding habits. Species were sought that typically forage for flying insects in a kingbirdlike manner: scanning the area from a stationary perch, sallying forth to capture the insect on the wing, and then perching again to consume the prey. Such species include bee-eaters (Meropidae; Fry 1972, pers. observ.), rollers (Coraciidae; Clancey 1964, Frith 1979), jacamars (Galbulidae; Fry 1970, Wetmore 1968), woodswallows (Artamidae; Frith 1979), and drongos (Dicruridae; Clancey 1964, Frith 1979, Keast 1972). I also selected three highly aerial species that forage for extended periods without perching between captures: a nighthawk (Caprimulgidae), a swift (Apodidae), and a swallow (Hirundinidae). This selection well represents the diversity in aerial-foraging behavior among birds.

Individuals of the following species were dissected (number of specimens indicated in parentheses): Caprimulgidae, *Chordeiles minor* (4); Apodidae, *Chaetura pelagica* (8); Meropidae, *Merops albicollis* (5), *M. viridis* (5, FCL only), *M. apiaster* (5, FCL only); Coraciidae, *Eurystomus orientalis* (2); Galbulidae, *Galbula ruficauda* (2); Artamidae, *Artamus leucorhynchus* (2); Dicruridae, *Dicrurus hottentottus* (2); Hirundinidae, *Hirundo rustica* (7, only FCL examined in 3 of these). The muscicapid *Terpsiphone mutata* (8) was used as a behavioral "outgroup" or control; this is an insectivorous species that is not highly aerial in its habits. The observations of *Passer domesticus* by Berman et al. (1990) and of *Hylocichla mustelina* and *Cardinalis cardinalis* by Raikow et al. (1990) serve as additional controls.

Methods of dissection are as described in McKitrick (1985). Specimens are referred to by their museum catalogue numbers with no preceding acronym; a list of the specimens dissected and the institutions from which they were borrowed is given in the Appendix. Dissections were unilateral due to restrictions by some lending institutions. Muscles were compared with those of *Tyrannus melancholicus* (McKitrick 1985). I noted where the muscles differed from the arrangement in that species; otherwise, the description was limited to "As in *T. melancholicus*" (for data tabulation on this species, see McKitrick 1991). Where no intraspecific variation is noted, all specimens of a given species had the same morphology.

For the phylogenetic analysis, transitions in FCL were examined using the results of McKitrick's (1991) phylogenetic analysis of hindlimb musculature. The latter analysis yielded 6,000 trees; a 75% majority-rule consensus tree revealed that of 80 groupings in that tree, 65 occurred in all 6,000 trees. The remaining 15 were present in 79% or more of all trees. In other words, the 6,000 trees were very similar in general pattern; one of these (tree 1) was selected for examination of the general pattern of evolutionary transitions in FCL.

RESULTS

Muscle descriptions are included below. The muscle is listed and then variants are detailed.

M. ILIOTIBIALIS CRANIALIS (ICR)

Merops albicollis, Eurystomus orientalis, Chordeiles minor, Galbula ruficauda, Dicrurus hottentottus, Artamus leucorhynchus, and *Terpsiphone mutata.*—All specimens as in *T. melancholicus.*

Chaetura pelagica.—As in *T. melancholicus,* but origin relatively broad (about 5 mm); passes over distal portion of M. scapulohumeralis caudalis. Insertion by semitendinous fibers on head of tibiotarsus. Gap of 1-3 mm occurs along lateral edge of M. iliotrochantericus caudalis between ICR and IL.

Hirundo rustica.—As in *T. melancholicus,* but varies in width at origin. Width is 5.87 mm in 2487, 6.34 mm in 2642, 7.11 mm in 3501, and 4.89 in 226,783.

M. ILIOTIBIALIS LATERALIS (IL)

Merops albicollis, Eurystomus orientalis, Chaetura pelagica, and *Hirundo rustica.*—As in *T. melancholicus;* only pars preacetabularis present.

Chordeiles minor.—Pars postacetabularis well developed, extending entire length of dorsolateral iliac crest. Pars acetabularis present, pars preacetabularis aponeurotic.

Galbula ruficauda.—Entire muscle absent.

Dicrurus hottentottus.—Pars preacetabularis and a very narrow postacetabularis present.

Artamus leucorhynchus.—Pars acetabularis and preacetabularis present; pars postacetabularis very slight.

Terpsiphone mutata.—All three parts present in most specimens. Pars postacetabularis absent in 345928.

M. ILIOFIBULARIS (IF)

Merops albicollis, Eurystomus orientalis, Chordeiles minor, Galbula ruficauda, Dicrurus hottentottus, Artamus leucorhynchus, Terpsiphone mutata, and *Hirundo rustica.*—As in *T. melancholicus.*

Chaetura pelagica.—As in *T. melancholicus.* A tendinous "string" runs from distal one-fourth of IF's lateral surface, down to GL and along latter's surface to its origin. Beddard (1898) found such a string in *Struthio,* Anatidae, some Rallidae, and some Alcidae.

M. ILIOFEMORALIS EXTERNUS (IFE)

Merops albicollis, Eurystomus orientalis, Chaetura pelagica, Galbula ruficauda, Artamus leucorhynchus, Hirundo rustica, and *Terpsiphone mutata.*—Absent.

Chordeiles minor.—Present in 506049, in which it is 2.04 mm wide distally and 2.5 mm long. Fibers oriented in different direction from ITCA. In other three specimens, it is difficult to determine whether muscle is actually present and independent, or fused with ITCA.

Dicrurus hottentottus.—Absent in 1971.3.5, but present in 1940.12.8.348 and as described by Raikow et al. (1979) for bowerbirds.

M. ILIOTROCHANTERICUS CAUDALIS (ITCA),
M. ILIOTROCHANTERICUS CRANIALIS (ITCR),
M. ILIOFEMORALIS INTERNUS (IFI),
M. FEMOROTIBIALIS MEDIUS (FTM),
M. FEMOROTIBIALIS INTERNUS (FTI),
M. CAUDOFEMORALIS (CF),
M. ISCHIOFEMORALIS (ISF)

All specimens as in *T. melancholicus.*

M. ILIOTROCHANTERICUS MEDIUS (ITM)

Chaetura pelagica.—Absent.

All other specimens as in *T. melancholicus.*

M. FEMOROTIBIALIS EXTERNUS (FTE)

Merops albicollis, Eurystomus orientalis, Artamus leucorhynchus, Chordeiles minor, Galbula ruficauda and *Terpsiphone mutata.*—As in *T. melancholicus.*

Chaetura pelagica.—Lacks pars distalis.

Dicrurus hottentottus.—In 1940.12.8.348 pars distalis, if present, not separable from pars proximalis.

Hirundo rustica.—Pars distalis not discernible in 226,783.

M. FLEXOR CRURIS LATERALIS (FCL)

Merops albicollis.—121,166 (Fig. 1c), only pars pelvica (FCLP) present. For 121,170, a small pars accessoria (FCLA) present in addition to FCLP (Fig. 1a). Muscle in this specimen most closely resembles variant 6a of McKitrick (1986:fig. 1), except insertion of FCLA is limited to intercondylar region of the femur; no fibers insert on lateral surface of the femoral shaft. In 121,171 (Fig. 1b) and 121,174, tendon G of FCLA present but lacking fibers. In 121,179, muscle as in 121,170 except FCLA smaller, barely separable from GI; tendons G and M are back to back.

Merops viridis.—Tendon G of FCLA present but lacking fibers in 61293, 61313, and 61324. Tendon G and FCLA both absent in 61297. A few distal fibers remain of FCLA (as in some *M. albicollis, M. apiaster,* and *Hirundo rustica,* see below) in 61310.

Merops apiaster.—Tendon G and small FCLA present in 538004, 540150 and 540153, as in some specimens of *M. albicollis* and one of *M. viridis.* Tendon G present but fibers absent in 539921 and 540148.

Eurystomus orientalis.—FCLA present. In 1925.11.1.85, FCLA robust, but insertion entirely intercondylar; no fibers insert on shaft of femur. In 1925.11.1.87, FCLA has a 3.47 mm insertion on femoral shaft. Origin of FCLA's fibers entirely from tendon G; none from surface of FCLP.

Chordeiles minor.—FCLA present and robust (Fig. 1d). Insertion on shaft of femur is 1.40 mm in 506049, and 0.84 mm in 506050. In 506055 insertion on femoral shaft limited to epicondyle and intercondylar region; in 506056, it is entirely intercondylar. Tendon G not exposed. FCLP has separate tendon from that of FCM, but the two insert in common.

Chaetura pelagica.—George and Berger (1966) reported that FCL is absent in swifts. More likely that FCLP failed to separate from FCM. Origin of combined muscle in these eight specimens extends over entire area where the two muscles originate in other birds (Fig. 1e1, 1e2). Very broad muscle with strong tendinous insertion on tibiotarsus. No FCLA. No sign of demarcation in large combined muscle in 039842, but in other seven specimens demarcation evident on medial surface, with caudal half of belly inserting about 4 mm farther distad onto tendon of insertion than cranial fibers.

Galbula ruficauda.—FCLA robust, but fibers do not extend all the way down tendon G to GI, such that a gap occurs on tendon G distally. Tendon M separated from tendon of FCM until level of PL, at which point the two tendons fuse and insert together on tibiotarsus.

Dicrurus hottentottus.—FCLP stout (4.66 mm in

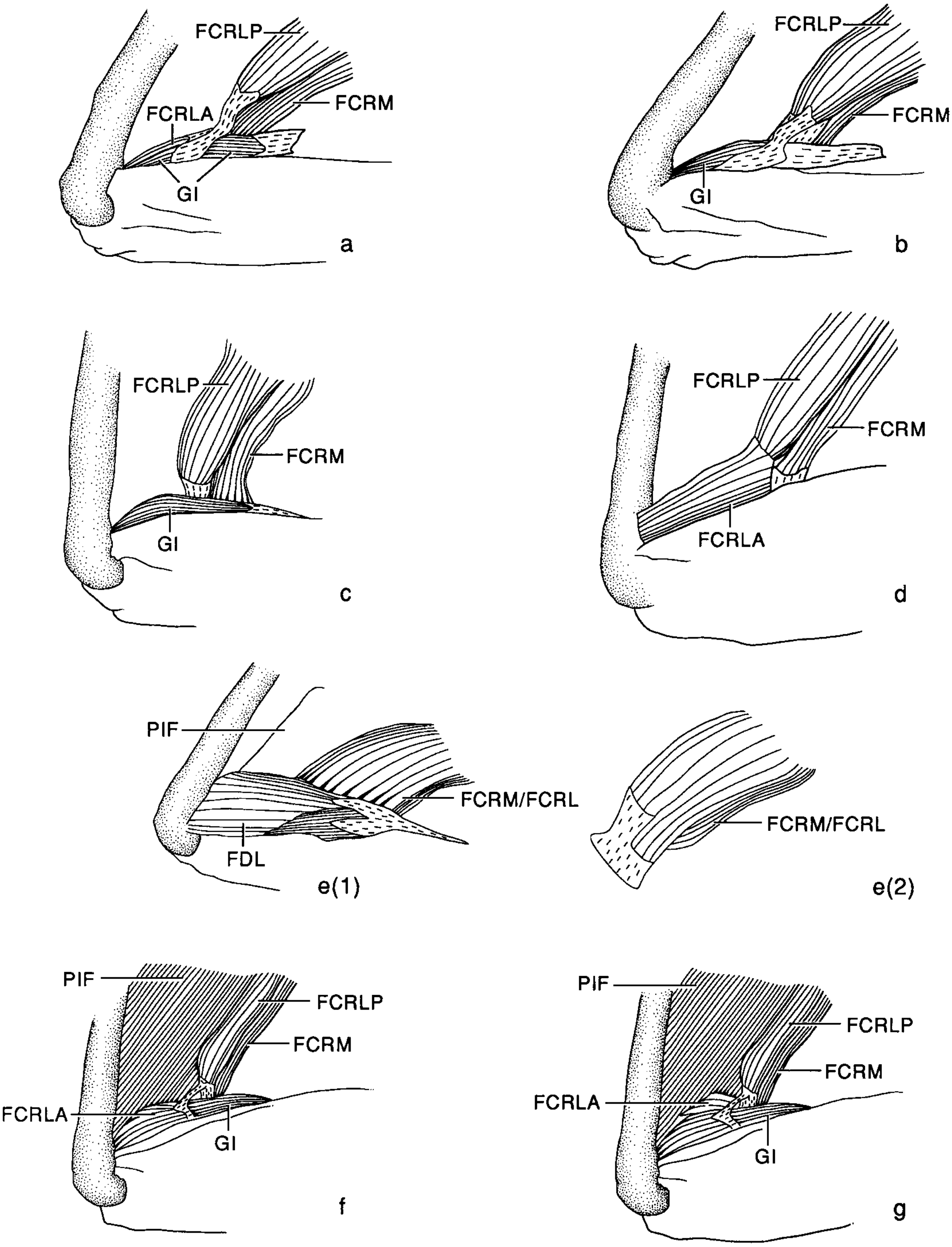


Fig. 1. Variation in M. flexor cruris lateralis in selected specimens: (a) *Merops albicollis,* RGMT 121170; (b) *Merops albicollis,* RGMT 121171; (c) *Merops albicollis,* RGMT 121166; (d) *Chordeiles minor,* USNM 506049; (e1) *Chaetura pelagica,* KU 039866 lateral view; (e2) with FDL removed; (f) *Hirundo rustica,* UMMZ 226914; (g) *Hirundo rustica,* UMMZ 226783.

A/1971.3.5; 3.6 mm in 1940.12.8.348), but FCLA absent.

Artamus leucorhynchus.—FCLA present; insertion on femoral shaft 0.43 mm in A/1969.15.420 (femur 18.76) and 0.40 mm in A/1969.15.421 (femur 18.3 mm). Tendon G not exposed. This morphology not exactly like any represented in McKitrick (1986: fig. 1); the raphe is as in fig. 1 (variant 2) but with narrow insertion.

Hirundo rustica.—Tendon G present in 2487, 2642, 3501, 225,913, 225,914, 226,243, and 226,783 with some fibers on lateral surface of GI that could be remainder of FCLA or part of GI (Fig. 1f). Insertion of FCLA entirely intercondylar. In 226,783 some fibers arise proximal to ambiguous ones and insert on surface of PIF (Fig. 1g). See descriptions for *Merops*, above.

Terpsiphone mutata.—FCLA present and large; slight gap between FCLA and GI occurs in 345895, but not in other seven specimens.

M. FLEXOR CRURIS MEDIALIS (FCM)

Chaetura pelagica.—See description of FCL. All other specimens as in *T. melancholicus.*

M. ILIOFEMORALIS (ILF)

Merops albicollis, Eurystomus orientalis, Chordeiles minor, Chaetura pelagica, Galbula ruficauda, Dicrurus hottentottus, Hirundo rustica, and *Terpsiphone mutata.*—Absent.

Artamus leucorhynchus.—Present in A.1969.15.420; absent in A.1969.15.421. Arises by tendinous fibers on dorsolateral iliac crest, caudal to ilioischiadic foramen. Strap-shaped belly narrows to slender tendon that inserts two-fifths of way down femoral shaft, just proximal to insertion of CF.

M. OBTURATORIUS LATERALIS (OL)

Merops albicollis.—Appears to have three heads of roughly equal size in 121,166, although two lower heads might be considered one. Dorsal (OLD) and intermediate heads divided by tendon of OM. Two heads present in 121,170, 121,171 and 121,174; dorsal head bisected by tendon of OM. Two heads present of equal size in 121,179: tendon of OM bisects OLD.

Eurystomus orientalis and *Galbula ruficauda.*—Pars dorsalis present and small (in terminology of Raikow 1978).

Chordeiles minor.—OLD present and small in 506049, small to medium in 506056, medium in 506050 and 506055.

Chaetura pelagica and *Hirundo rustica.*—OLD absent.

Dicrurus hottentottus.—OLD medium in 1971.3.5, medium to large in 1940.12.8.348.

Artamus leucorhynchus.—OLD medium.

Terpsiphone mutata.—345895 and 345910, OLD medium. In 345918, as 345895 except OLD is medium to large. In 345916, OLD small; OLD and OLV equal in length and OLD is one-half width of OLV. In 345921, OLD medium to large; OLD slightly longer than OLV, and the two are equal width. For 345924, 345928 and 345927, as in 345921 except OLD medium.

M. OBTURATORIUS MEDIALIS (OM)

Merops albicollis, Eurystomus orientalis, Chordeiles minor, Chaetura pelagica, Galbula ruficauda, Artamus leucorhynchus, Hirundo rustica, and *Terpsiphone mutata.*—As in *T. melancholicus.*

Dicrurus hottentottus.—As in *T. melancholicus,* but has two tendons of insertion that merge to insert as one.

M. PUBO-ISCHIO-FEMORALIS (PIF)

Merops albicollis and *Eurystomus orientalis.*—As in *Tyrannus melancholicus,* except divided into deep and superficial parts, not cranial and caudal parts.

Chordeiles minor.—Clearly divided into deep and superficial parts in all except 506055, in which no separation evident.

Chaetura pelagica.—One undivided muscle mass present.

Galbula ruficauda.—The two bellies of PIF fused distally on lateral surface of muscle in 1932.2.3.1, but not in 1932.2.3.2. On medial surface there is complete fusion.

Dicrurus hottentottus, Artamus leucorhynchus, Hirundo rustica, and *Terpsiphone mutata.*—As in *T. melancholicus.*

M. AMBIENS (AM)

Absent in all specimens.

M. GASTROCNEMIUS, PARS LATERALIS (GL)

All specimens as in *T. melancholicus.*

M. GASTROCNEMIUS, PARS INTERMEDIA (GI)

For all specimens except *Chaetura pelagica,* as in *T. melancholicus.*

Chaetura pelagica.—Muscle appears to have two heads of origin, but this may represent fusion of PL with GI. One head arises fleshy on proximal one-fourth of caudal surface of femoral shaft, and other arises on medial condyle of femur. Combined muscle passes half-way down tibiotarsus. PL arises on tibiotarsus, not femur, in birds; present case could represent shift in attachment of muscle mass.

M. GASTROCNEMIUS, PARS MEDIALIS (GM)

Merops albicollis.—Two heads of origin; medial one as in *T. melancholicus;* lateral one arises on head of tibiotarsus and passes lateral to insertion of FCL and FCM. Lateral head appears to "replace" PL; alternatively, it is PL and has fused with GM. The two heads fuse about one-third way down tibiotarsus. No patellar band.

Chaetura pelagica, Eurystomus orientalis, and *Galbula ruficauda.*—As in *T. melancholicus.* No deep head, and no patellar band.

Chordeiles minor and *Dicrurus hottentottus.*—Deep and superficial heads and patellar band present.

Artamus leucorhynchus and *Hirundo rustica.*—As in *T. melancholicus,* and divided into deep and superficial heads. No patellar band.

Terpsiphone mutata.—Divided into deep and superficial heads. A 0.60-mm patellar band present (see Raikow 1978:18). No patellar band in 345918.

M. PLANTARIS (PL)

Merops albicollis.—Maurer and Raikow (1981) reported this absent in bee-eaters, but see description under GM.

Eurystomus orientalis, Chordeiles minor, Galbula ruficauda, Dicrurus hottentottus, Artamus leucorhynchus, and *Terpsiphone mutata.*—As in *T. melancholicus.*

Chaetura pelagica.—Reportedly absent (George and Berger 1966), but see description of GI.

Hirundo rustica.—Absent.

M. FLEXOR PERFORANS ET PERFORATUS DIGITI II (FPPD2)

Merops albicollis.—Belly very small, arising by semitendinous fibers and a short tendon from proximocaudal surface of lateral femoral condyle. Bipinnate belly passes one-fourth tibiotarsus before giving rise to a slender tendon. Belly does not conceal FPPD3.

Eurystomus orientalis, Chaetura pelagica, Artamus leucorhynchus, and *Terpsiphone mutata.*—As in *T. melancholicus.*

Chordeiles minor.—Tendon splits and inserts on either side of base of phalanx 2, digit II.

Galbula ruficauda.—When tendon enters pes, it perforates tendon of FPD2 (contra Swierczewski and Raikow 1981) and bifurcates, thus allowing passage of FHL. Two branches insert on lateral and medial sides of base of phalanx 2, digit II.

Dicrurus hottentottus.—At level of first phalanx of digit II tendon is perforated, thus allowing passage of tendon of FDL.

Hirundo rustica.—As in *T. melancholicus,* but inserts on medial and lateral corners of base of phalanx 2, digit II.

M. FLEXOR PERFORANS ET PERFORATUS DIGITI III (FPPD3)

Merops albicollis.—Cranial fibers arise by tendon on lateral cnemial crest of tibiotarsus and from deep surface of patellar ligament; caudal fibers arise from deep surface of patellar ligament and lateral condyle of femur. Muscle is irregularly bipinnate. Belly passes half-way down tibiotarsus and gives rise to flat tendon. Tendon perforated by FDL, and two resulting branches insert on either side of phalanx 3 of digit III. There are no vincula other than one securing tendon to phalanx. In 121,179, insertion on distal end of lateral surface of phalanx 2, and at base of phalanx 3.

Eurystomus orientalis, Chaetura pelagica, Dicrurus hottentottus, Artamus leucorhynchus, Hirundo rustica, and *Terpsiphone mutata.*—As in *T. melancholicus.*

Chordeiles minor.—Inserts on either side of base of phalanx 3, digit III, except in 506049, which is missing third and ungual phalanx; tendon therefore stops at phalanx 2.

Galbula ruficauda.—Unipinnate but approaching a parallel-fibered condition. Single head arises from lateral cnemial crest of tibiotarsus and from patellar ligament by tendinous fibers. Tendon of insertion passes through lateral side of tibial cartilage and down plantar surface of tarsometatarsus. Perforates tendon of FPD3, and bifurcates, thus permitting passage of FDL; the two branches insert on lateral and medial sides of base of phalanx 3, digit III.

M. FLEXOR PERFORATUS DIGITI II (FPD2)

Merops albicollis.—Arises by aponeurotic sheet on medial surface of FPD3, emerging as belly about halfway down FPD3 and passing nearly length of tibiotarsus before becoming entirely tendinous. Tendon inserts on base of phalanx 1, digit II.

Eurystomus orientalis.—Arises fleshy from deep surface of tendon of origin of medial head of FPD3. Fibers arise nearly one-fourth way down tibiotarsus, and pass nearly length of that bone. Tendon of insertion ensheathes that of FPPD2 at distal end of tarsometatarsus.

Chordeiles minor.—Situated on caudal surface of shank, and arises tendinously from lateral condyle of femur and from intercondylar region.

Chaetura pelagica.—Absent.

Galbula ruficauda.—In 1932.2.3.1, very slender, arising by tendon from intercondylar region of femur. Branch of this tendon passes to deep surface of FPD3 and might be said to be a second origin of that muscle. In 1932.2.3.2, as above, except there is an unknown muscle arising in common with FPD2, from same tendon. That muscle is unipinnate, with fleshy belly arising one-third way down tibiotarsus and passing nearly length of that bone. Tendon passes through center of tibial cartilage and inserts onto tendon of insertion of FPD3 near proximal end of tarsometatarsus, as FL would do if present.

Dicrurus hottentottus, Artamus leucorhynchus, Hirundo rustica, and *Terpsiphone mutata.*—As in *T. melancholicus.*

M. FLEXOR PERFORATUS DIGITI III (FDP3)

Merops albicollis.—Arises by semitendinous and fleshy fibers from lateral condyle of femur in common with FPD4 and FPD2.

Eurystomus orientalis.—Has two heads of origin and lies deep to FPD4. Lateral head arises in common with that of distal head of FPD4. Medial head of FPD3 arises by its own tendon in intercondylar region of femur. Group of fleshy fibers arises from medial border of this tendon less than one-fourth way down tibiotarsus. The two heads join one-fourth way down that bone. In its proximal half, all fibers on lateral side of muscle are on deep surface of common tendon formed by fusion of the two heads. In distal half, fibers arise on superficial surface of muscle as well. Belly extends nearly length of tibiotarsus. Tendon bifurcates, thus allowing passage of tendon of FDL, and insertion is on lateral and medial sides of base of phalanx 2, digit III.

Chordeiles minor.—Large muscle arising in intercondylar region by fleshy and semitendinous fibers. There is also a tendinous connection with tendon of lateral head of FPD4, so muscle can be said to have two heads of origin. Belly extends nearly length of tibiotarsus.

Chaetura pelagica.—As in *Merops.*

Galbula ruficauda.—Arises in intercondylar region. A vinculum lies between FPD3 and FPPD3.

Dicrurus hottentottus.—As in *T. melancholicus.* FPD3 and FPD4 closely associated on their medial surface due to aponeurosis on that surface. Both muscles situated on medial surface of shank.

Artamus leucorhynchus.—As in *T. melancholicus.* A tendinous slip joins tendons of FPD3 and FPD4 about two-thirds way down tarsometatarsus.

Hirundo rustica and *Terpsiphone mutata.*—As in *T. melancholicus.*

M. FLEXOR PERFORATUS DIGITI IV (FPD4)

Merops albicollis.—FPD4, FPD3, FPD2, and FHL all closely associated. FPD4 arises by tendinous fibers from lateral condyle of femur. Unipinnate belly extends two-thirds tibiotarsus; tendon arises from aponeurosis on surface of distal third of belly. Slender tendinous branch attaches tendons of FPD4 and FPD3. Tendon of insertion attaches at base of 2nd and 4th phalanges, digit IV.

Eurystomus orientalis.—Arises by two heads: a small, distal head by slender tendon from lateral condyle of femur; and a larger, proximal head by flat tendon from intercondylar region of femur. Belly of distal head arises nearly one-fourth way down tibiotarsus. The two heads join nearly immediately one-fourth way down that bone to form common belly that extends about three-fifths that bone. Insertion on lateral side of base of phalanx 2 and either side of phalanx 3, and at base of ungual phalanx, digit IV.

Chordeiles minor.—After removal of FPPD2 and FPPD3, this is most superficial muscle remaining on lateral surface of shank. Arises by two heads: tiny lateral head arising by tendon on lateral condyle, and larger medial head arising in intercondylar region. Lateral belly fuses with medial belly after about 2 mm. Tendon of insertion splits to allow passage of FDL, sending a medial branch to insert at base of phalanx 2 and phalanx 3, and a lateral branch that inserts on same phalanges. In 506050, only first phalanx of digit IV present; muscle inserts by tendinous fibers on joint capsule between tibiotarsus and tarsometatarsus. Tendon of FDL passes among these fibers.

Chaetura pelagica.—Laterally situated, one head of origin. Tendon of origin about 6 mm long.

Galbula ruficauda.—Single belly arises fleshy in intercondylar region of femur. Closely associated on medial surface with belly of FPD3, with which it arises. Tendon does not bifurcate to allow passage of FHL. Single insertion is broad on plantar surface of base of phalanx 2, digit IV.

Dicrurus hottentottus, Hirundo rustica, and *Terpsiphone mutata.*—As in *T. melancholicus,* but lack distal head.

Artamus leucorhynchus.—As in *T. melancholicus.*

M. FLEXOR HALLUCIS LONGUS (FHL)

Merops albicollis.—Single head of origin arises by semitendinous fibers in close association with FPD2, FPD3, and FPD4 in intercondylar region of femur. Belly passes about seven-eighths tibiotarsus before giving rise to tendon of insertion. Tendon fuses with that of FDL, and common tendon gives rise to three distal branches that insert on digits II–IV. A medial branch emerging proximal to others inserts on digit I.

Eurystomus orientalis.—Has two heads of origin: large lateral head arising fleshy from lateral condyle and lateral portion of intercondylar region of femur (it appears very much like the large femoral head of FDL that occurs in some tyrant flycatchers); and medial head from intercondylar region deep to lateral head. The two heads fuse less than one-fourth way down tibiotarsus. Tendon of insertion joins lateral side of that of FDL about one-third way down tarsometatarsus.

Chordeiles minor.—Arises by one head, an extensive, fleshy origin in intercondylar region and on lateral epicondyle of femur. Has no tendinous origin from lateral condyle. Belly extends two-fifths of tibiotarsus. Tendon fuses with that of FDL in proximal one-fourth of tarsometatarsus.

Chaetura pelagica.—Arises by two heads: lateral or fibular head from dorsal surface of head and shaft of fibula; medial or tibial head arises on second fifth of dorsal surface of tibiotarsus. The two heads fuse one-third way down tibiotarsus. Tendon of insertion fuses with that of FDL as described below.

Galbula ruficauda.—Arises by three heads: lateral head from head of fibula; intermediate one from lateral condyle of femur; and medial one from intercondylar region of femur. The three merge less than one-fourth way down tibiotarsus. Tendon inserts on ungual phalanx of digits I, II and IV.

Dicrurus hottentottus.—Enormous muscle, largest of hindlimb. Medial head arises by semitendinous fibers independently of FPD3 and FPD4. The three bellies fuse about two-fifths way down tibiotarsus to form common belly, which extends length of latter bone. Tendon of FHB does not appear to ensheathe that of FHL.

Artamus leucorhynchus.—As in *T. melancholicus,* except tendon of FHB does not appear to ensheathe that of FHL.

Hirundo rustica.—Three heads of origin: tiny lateral head arises by tendon in common with that of FPD2, and belly itself arises one-fourth way down tibiotarsus. Large medial head arises as in *T. melancholicus;* tiny intermediate head arises by slender tendon in common with medial head and passes medial to tendon of IF. Some specimens of *T. melancholicus* are similar.

Terpsiphone mutata.—Muscle most closely resembles figure 16b in McKitrick (1985), except lateral head is quite small, and intermediate head is three to four times size of lateral head. The three heads fuse about one-fourth way down tibiotarsus. Insertion as in *T. melancholicus.*

M. FLEXOR DIGITORUM LONGUS (FDL)

Merops albicollis.—Most deeply situated muscle on shank. Has fibular and tibial head of origin. Fibular head arises medial to tendon of IF. See description of insertion under FHL (above). Where tendon of FDL trifurcates is a small bundle of muscle fibers; may be M. lumbricalis.

Eurystomus orientalis.—Two heads of origin. Fibular and tibial heads as in *T. melancholicus.* Two heads fuse less than one-fourth way down tibiotarsus. Insertion includes elastic bands at: distal end of phalanx 1, digit I; distal end of phalanx 2, digit II; base of phalanx 3 and distal end of phalanx 3 in digit III; and base of phalanx 4 and distal end of phalanx 4, digit IV.

Chordeiles minor.—No femoral head. Muscle extends nearly the length of tibiotarsus and inserts on ungual phalanx (where present) of each digit. Elastic band occurs at each phalanx. In 506050, which lacks most of digit IV, FDL sends no branch to digit IV.

Chaetura pelagica.—Extremely large, arising on distal half of femoral shaft; belly extends two-fifths way down tibiotarsus and gives rise to stout tendon. Tendon of FHL fuses with it after they emerge from tibial cartilage. About three-fifths way down tarsometatarsus, a branch to hallux arises and inserts on base of its ungual phalanx. Immediately distal to origin of this branch, tendon of FDL trifurcates. Branches insert on base of ungual phalanx on each of the three digits.

Galbula ruficauda.—Arises fleshy on medial surface of fibula about one-eighth way down tibiotarsus, and from caudolateral and caudomedial surface of that bone one-fourth way down. Belly passes length of tibiotarsus. Insertion at base of ungual phalanx of digit III.

Dicrurus hottentottus.—As in *T. melancholicus.* Femoral head 2.54 mm deep in 1971.3.5, and 4.74 mm in 1940.12.8.348.

Artamus leucorhynchus.—As in *T. melancholicus,* except no femoral head in 1969.15.420.

Hirundo rustica.—Has small fibular head, moderately sized femoral head, and a tibial head. Insertion as in *T. melancholicus.*

Terpsiphone mutata.—as in *T. melancholicus.*

M. POPLITEUS (POP)

Merops albicollis, Chaetura pelagica, Dicrurus hottentottus, Artamus leucorhynchus, Hirundo rustica, and *Terpsiphone mutata.*—Absent.

Eurystomus orientalis, Chordeiles minor, and *Galbula ruficauda.*—Small, parallel-fibered muscle arising on medial surface of head of fibula; inserts on caudolateral surface of tibiotarsus.

M. FIBULARIS LONGUS (FL)

Merops albicollis and *Chaetura pelagica.*—Absent.

Eurystomus orientalis.—Arises on distal end of fibula. Belly occupies only third quarter of tibiotarsus. Insertion as in *T. melancholicus.*

Chordeiles minor.—As in *T. melancholicus.* Has two points of insertion, one on tibial cartilage and one on tendon of FPD3.

Galbula ruficauda.—Absent, but see description for FPD2.

Dicrurus hottentottus and *Hirundo rustica.*—As in *T. melancholicus,* except tendon of insertion does not bifurcate, but simply attaches on proximolateral corner of tibial cartilage.

Artamus leucorhynchus.—As in *T. melancholicus.*

Terpsiphone mutata.—Has aponeurotic attachment on medial surface to medial surface of TCR. Aponeurosis arises from patellar crest. Some fibers from lateral surface of FB attach to deep surface of FL. Tibial head of TCR attaches firmly to tendinous sheet it shares with FL, proximally. This sheet arises from caudal surface of lateral cnemial crest.

M. FIBULARIS BREVIS (FB)

Merops albicollis.—As in *T. melancholicus* but arises only on distal one-fourth fibula and not held in place by retinaculum.

Chordeiles minor.—Absent.

Chaetura pelagica, Dicrurus hottentottus, Artamus leucorhynchus, and *Terpsiphone mutata.*—As in *T. melancholicus.*

Galbula ruficauda.—Slender and bipinnate, arising by semitendinous fibers on distal half of fibula. Passes length of shank. Tendon arises as aponeurosis on distal half of muscle's surface. Inserts as in *T. melancholicus,* but no retinaculum.

Hirundo rustica.—As in *T. melancholicus,* but no retinaculum.

M. TIBIALIS CRANIALIS (TCR)

Merops albicollis.—As in *T. melancholicus,* except femoral head smaller than tibial head, no "smaller tendon" by which femoral head arises, and no bifurcation of tendon of insertion.

Eurystomus orientalis, Chordeiles minor, Chaetura pelagica, Galbula ruficauda, Artamus leucorhynchus, Dicrurus hottentottus, Hirundo rustica, and *Terpsiphone mutata.*—As in *T. melancholicus.*

M. EXTENSOR DIGITORUM LONGUS (EDL)

Merops albicollis.—Arises fleshy from lateral surface of cranial and cnemial crest, from Sulcus intercristalis, and cranial surface of proximal half of tibiotarsus. Belly extends three-fourths tibiotarsus. Tendon trifurcates two-thirds way down tarsometatarsus and inserts on ungual phalanx of digits II–IV. Branches go through fibrous canal on dorsal surface of each basal phalanx. Branch to digit III divides at distal end of phalanx 2, inserting at base of phalanx 3 on craniomedial surface.

Eurystomus orientalis.—Origin from inner (caudal) surface of cranial cnemial crest and from caudal surface of tibiotarsus. Belly bipinnate nearly length of that bone. Insertions as follows: digit II with main branch on base of ungual phalanx and short broad branch on base of phalanx 2; digit III with branch attaching broadly to base of phalanges 2 and 3, and distal to phalanx 3 it narrows and inserts on ungual phalanx; digit IV with branch attaching broadly at base of phalanges 2–4, narrows to insert on ungual phalanx.

Chordeiles minor.—Bipinnate to over three-fourths tibiotarsus. Insertion as follows: digit II with main branch on base of ungual phalanx, and short (medial) branch on base of phalanx 2; digit III with branch inserting broadly at base of phalanx 2, then continues to ungual phalanx (except in 506049, in which only two phalanges present for digit III); digit IV with one branch to base of ungual phalanx (except in 506050, in which branch passes to plantar surface of tarsometatarsus and attaches broadly at distal end, near base of digit IV).

Chaetura pelagica.—Origin as in *T. melancholicus.* Belly extends nearly length of tibiotarsus and is bipinnate entire length. Insertion simpler than in *T. melancholicus,* tendon trifurcates at distal end of tarsometatarsus, and each branch inserts on ungual phalanx of its respective digit.

Galbula ruficauda.—Arises fleshy from lateral surface of cranial cnemial crest, and medial and lateral surfaces of lateral cnemial crest. Extends seven-eighths tibiotarsus. Tendon of insertion sends branch to digits II, III and IV. Branch to digit II simply inserts on dorsal surface of ungual phalanx. Branch to digit III inserts broadly on dorsal surface of 3rd phalanx, then sends branch to dorsal surface of ungual phalanx. Branch to digit IV inserts simply on ungual phalanx.

Dicrurus hottentottus.—For most specimens as in *T. melancholicus.* In 1940.12.8.348 a retinaculum holds tendon in place at distal end of tarsometatarsus, and a retinaculum holds each of main branches in place at proximal end of each of the three digits. Branch to digit III splits into four branches. More medial of two inner branches inserts on dorsal surface of base of phalanx 2. Medial and lateral branches insert together on dorsal surface of base of ungual phalanx. More lateral of two inner branches inserts on dorsal surface of base of phalanx 3. Branch to digit IV inserts on base of ungual phalanx, but sends short branch to insert at base of phalanx 2, one to phalanx 3, and one to phalanx 4. In 1971.3.5, on digit II it is medial branch that goes to ungual phalanx and lateral one to base of digit. Branch to digit IV ends at base of phalanx 4 and no insertion on ungual phalanx, although an elastic band occurs between 4th and ungual phalanges.

Artamus leucorhynchus.—Insertion as follows: on digit II, a tiny branch inserts at base of phalanx 2, while main branch inserts at base of ungual phalanx; on digit III, main branch splits into three, with central branch inserting at base of phalanx 2, and lateral and medial branches inserting together at base of ungual phalanx. Branch to digit IV bifurcates at base of phalanx 3; medial branch goes to base of phalanx 4 and lateral branch inserts at base of ungual phalanx.

Hirundo rustica.—Origin as in *T. melancholicus.* Insertion as follows: in digit II, branch attaches broadly at base of phalanx 2 and inserts on ungual phalanx; in digit III, branch bifurcates, with medial branch attaching at base of phalanx 2, then sending another branch to ungual phalanx, and lateral branch bifurcates distal to phalanx 1, with one part attaching at base of phalanx 3, and the other at ungual phalanx; in digit IV, a branch attaches medially to base of phalanx 4, lateral branch to ungual phalanx.

Terpsiphone mutata.—As in *T. melancholicus,* except branch to digit II inserts on ungual phalanx, with lateral branch to phalanx 2. At digit III, tendon branches in distal two-thirds of phalanx 1. Medial branch then bifurcates, and lateral part inserts at base of phalanx 2, while medial part inserts at base of ungual phalanx. Lateral branch bifurcates at base of phalanx 2; medial part inserts at base of phalanx 3 and lateral part inserts at base of ungual phalanx.

M. FLEXOR HALLUCIS BREVIS (FHB)

Merops albicollis.—As in *T. melancholicus,* except with double tendon of insertion. Tendon perforated by FDL at base of hallux.

Eurystomus orientalis.—Robust, bipinnate muscle arising on medial surface of hypotarsus and hypotarsal ridge. Extends nearly length of tarsometatarsus. Broad tendon of insertion ensheathes hallucal branch of FDL, thereby forming two branches. These give rise to tendinal "saddle" that inserts on lateral and medial sides of base of phalanx 1 of hallux.

Chordeiles minor.—As in *T. melancholicus,* except tendon is double distally, and is not perforated by FHL.

Chaetura pelagica.—Arises fleshy on caudal surface of medial cotyla of tarsometatarsus, and from medial surface of hypotarsus. Bipinnate to half of tarsometatarsus, and unipinnate to nearly length of that bone. Inserts by flat tendon on base of phalanx 1 of hallux. Belly covered proximally by aponeurosis arising on medial condyle of tibiotarsus and inserting on medial surface of tarsometatarsal shaft and caudal edge of EHL.

Galbula ruficauda.—Small, arising on medial surface of hypotarsus and from medial surface of hypotarsal ridge. Insertion as in *T. melancholicus.*

Dicrurus hottentottus and *Artamus leucorhynchus.*—As in *T. melancholicus.*

Hirundo rustica.—As in *T. melancholicus,* but no notch evident.

Terpsiphone mutata.—As in *T. melancholicus.* Slight notch in 345895, 345910, 345921 and 345924 but notch absent from other four specimens.

M. EXTENSOR HALLUCIS LONGUS (EHL)

Merops albicollis.—Arises by one head extending length of tarsometatarsus; inserts at base of ungual phalanx of hallux.

Eurystomus orientalis.—As in *T. melancholicus,* but robust. No origin from Tuberositas M. tibialis cranialis.

Chordeiles minor.—As in *T. melancholicus,* but a pars distalis present as illustrated in Hoff (1966: fig. 7 and 11 [muscle not labeled as such]).

Chaetura pelagica.—As in *T. melancholicus,* but no origin from Tuberositas M. tibialis cranialis.

Galbula ruficauda.—Slender, arising by fleshy and semitendinous fibers on craniomedial surface of medial cotyla of tarsometatarsus. Belly passes length of that bone, along dorsal (outer) surface of hallux; inserts at base of ungual phalanx.

Dicrurus hottentottus, Artamus leucorhynchus and *Hirundo rustica.*—As in *T. melancholicus.*

Terpsiphone mutata.—As in *T. melancholicus,* but small bundle of fibers arises on phalanx 1 of hallux and inserts on distal end of tendon of insertion.

M. ABDUCTOR DIGITI II (ABD2)

Merops albicollis, Dicrurus hottentottus, Artamus leucorhynchus, Hirundo rustica, and *Terpsiphone mutata.*—Absent.

Eurystomus orientalis.—Slender, bipinnate muscle arising fleshy in distal half of dorsomedial surface of tarsometatarsus. Inserts by short tendon on the ventromedial corner of first phalanx of digit II.

Chordeiles minor.—Small, irregularly fan-shaped muscle arising at distal end of dorsomedial surface of tarsometatarsus. Insertion as in *Eurystomus.*

Chaetura pelagica.—As in *Chordeiles.*

Galbula ruficauda.—As in *Eurystomus.*

M. ADDUCTOR DIGITI II (ADD2)

Merops albicollis.—Weak muscle extending one-half length of tarsometatarsus, giving rise to slender tendon.

Eurystomus orientalis.—Flat, bipinnate muscle arising in Sulcus flexorius deep to tendon of FDL but not connected with it in any way. Fibers pass two-thirds length of tarsometatarsus. Robust tendon inserts at base of digit II on lateroplantar surface.

Chordeiles minor and *Chaetura pelagica.*—Arises on lateral cotyla of tarsometatarsus and on hypotarsus. Extends length of tarsometatarsus, and narrows to slender tendon that inserts on lateral surface of base of phalanx 1.

Galbula ruficauda.—Arises just distal to, and on, lateral and medial hypotarsal crests. Passes slightly more than half tarsometatarsus. Insertion as in *Chordeiles* and *Chaetura.*

Dicrurus hottentottus, Artamus leucorhynchus, Hirundo rustica, and *Terpsiphone mutata.*—Absent.

M. EXTENSOR PROPRIUS DIGITI III (EPD3)

Merops albicollis.—In 121,166, 121,171 and 121,174, bipinnate. Extends length of cranial surface of tarsometatarsus and inserts on cranial surface of base of phalanx 1. In 121,170 and 121,179, insertion double. Tendon splits and the two branches insert on either side of base of phalanx 1.

Eurystomus orientalis and *Galbula ruficauda.*—Arises fleshy just distal to Tuberositas M. tibialis cranialis on dorsal surface of tarsometatarsus. Some fibers also arise on tendon of TCR near latter's insertion. Fibers arise from tarsometatarsus for nearly length of that bone. Insertion on dorsal surface of base of phalanx 1.

Chordeiles minor.—As in *Eurystomus* and *Galbula,* but confined to distal half of tarsometatarsus.

Chaetura pelagica, Dicrurus hottentottus, Artamus leucorhynchus, Hirundo rustica, and *Terpsiphone mutata.*—Absent.

M. ABDUCTOR DIGITI IV (ABD4)

Merops albicollis.—Narrow, unipinnate, lying on lateral surface of tarsometatarsus; extends length of that bone.

Eurystomus orientalis and *Galbula ruficauda.*—Arises just distal to lateral cotyla of the tarsometatarsus in Sulcus flexorius. Belly extends length of tarsometatarsus; tendon passes through retinaculum before inserting on lateroplantar surface of phalanx 1.

Chordeiles minor.—Lies on caudolateral surface of tarsometatarsus. Arises lateral to Sulcus flexorius one-third way down tarsometatarsus, passes length of that bone, and narrows to tendon. Inserts on lateral surface of base of phalanx 1.

Chaetura pelagica.—As in *Chordeiles,* but arises one-third to two-fifths way down tarsometatarsus.

Dicrurus hottentottus.—Tiny, irregularly strap-shaped muscle arising fleshy on caudal surface of lateral trochlea of tarsometatarsus. Has broad, tendinous insertion on surface of ligament between tarsometatarsus and base of phalanx 1.

Artamus leucorhynchus.—Absent in 1969.15.420. In 1969.15.421 a few weak fibers found in this area, but no well-defined muscle.

Hirundo rustica.—Absent.

Terpsiphone mutata.—Absent, although in 345918 and 345924 there appear to be a few fibers that could be a vestigial ABD4.

M. EXTENSOR BREVIS DIGITI IV (EBD4)

Merops albicollis, Dicrurus hottentottus, Artamus leucorhynchus, Hirundo rustica, and *Terpsiphone mutata.*—Absent.

Eurystomus orientalis.—Slender, bipinnate muscle lying on dorsolateral surface of tarsometatarsus. Arises fleshy the length of tarsometatarsus next to mystery extensor of digit III (see below). Passes between toes and appears to insert on plantar surface of base of phalanx 1. Action would appear to be flexion rather than extension.

Chordeiles minor and *Chaetura pelagica.*—Arises in Sulcus extensorius on dorsal surface of tarsometatarsus. Passes length of that bone and narrows to tendon that passes through canal in distal end of bone. Tendon inserts on medial surface of base of phalanx 1.

Galbula ruficauda.—Largest of intrinsic muscles of pes, occupying entire dorsolateral surface of tarsometatarsus. Bipinnate and arises fleshy from nearly entire length of tarsometatarsal shaft. Tendon inserts at base of phalanx 1.

M. LUMBRICALIS (L)

Merops albicollis.—See description under FDL (above).

Eurystomus orientalis, Dicrurus hottentottus, Artamus leucorhynchus, Hirundo rustica, and *Terpsiphone mutata.*—Absent.

Chordeiles minor.—Present on deep surface of common tendon of FDL and FHL.

Chaetura pelagica.—A few fibers present on tendon of insertion of FDL.

Galbula ruficauda.—A few fibers present on distal end of tendon of FDL in 1932.2.3.2, but none in 1932.2.3.1.

UNIDENTIFIED MUSCLES

In *Eurystomus orientalis,* two extra intrinsic muscles occur in foot. One, to digit II, arises fleshy just distal to Tuberositas M. tibialis cranialis, next to EPD3. Inserts by a very slender tendon at base of phalanx 1, digit II on dorsolateral side. Present in 1925.11.1.85, but not 1925.11.1.87. The second, to digit III, is present in both specimens of *Eurystomus.* Narrow but well-defined, bipinnate muscle arising on dorsal surface of proximal end of tarsometatarsus. Passes length of that bone and inserts by short tendon at base of phalanx 1, digit III, on dorsolateral side.

In *Chordeiles minor,* a narrow, very distinct strap-shaped muscle arises fleshy near tendon of EHL at distal end of caudal surface of tarsometatarsus, proximal to metatarsal I. Inserts by semitendinous fibers on caudal surface of metatarsal I, with some fibers inserting at base of phalanx I, digit I. Muscle was not mentioned by Hoff (1966). Does not appear to be homologous with EHL pars accessorius described for *Colius* by Berman and Raikow (1982).

DISCUSSION

INDIVIDUAL VARIATION

Individual variation in the hindlimb musculature may be summarized as follows.

M. iliofemoralis externus.—This muscle was present in one specimen of *Dicrurus,* and absent in the other.

M. flexor cruris lateralis.—In *Merops albicollis,* four variants were found in five specimens: tendon G and pars accessoria (FCLA) absent (one specimen); tendon G present, FCLA absent (one specimen); tendon G and very small FCLA present (one specimen); tendon G and small FCLA present (two specimens). In *M. viridis,* three variants were found in five specimens: tendon G and FCLA absent (one specimen); tendon G present, FCLA absent (three specimens); tendon G and very small FCLA present (one specimen). In *M. apiaster,* two variations occurred: tendon G present, FCLA absent (two specimens); tendon G and small FCLA present (three specimens). In *Eurystomus orientalis,* two variants were found in two specimens. In both, a robust FCLA was present, but in one, FCLA inserted only in the intercondylar region, while in the other, the insertion was in the intercondylar region and on the femoral shaft. Berman et al. (1990) and Raikow et al. (1990) found FCL to be robust and lacking individual variation in the species they examined.

M. iliofemoralis.—This was present in one specimen of *Artamus leucorhynchus,* but absent in the other.

M. flexor digitorum longus.—In *Artamus leucorhynchus,* a moderate-sized femoral head was present in one specimen, but absent in the other. In *Dicrurus hottentottus,* a large femoral head was present in both specimens, but it was nearly twice as large in one specimen as in the other.

M. extensor proprius digiti III.—In *Merops albicollis,* two specimens had a double tendinous insertion, and three had a single insertion.

Variations in muscle length or size.—The following muscles varied in length within species (details available from author): GL, GM, PL, FPPD2, FPPD3, FPD2, FPD3, FPD4, EDL, FHB, ABD4. OLD varies in size in *Terpsiphone mutata.*

Anomalies.—In *Galbula ruficauda,* one specimen had an unknown muscle arising from the same tendon as FPD2 and inserting onto the tendon of insertion of FPD3 as does FL; the latter muscle is absent in *Galbula.* One specimen of *Eurystomus orientalis* had an extra intrinsic foot muscle to digit II; both specimens had an extra extensor for digit III.

BEHAVIORAL CORRELATES AND HISTORICAL ANALYSIS

Aerial foraging and intraspecific variation in FCL.—The qualitative intraspecific variation found in this study (i.e. the variation in presence or absence of muscle parts within species) is almost exclusively in FCL. This was also the most variable muscle in the tyrant flycatchers (McKitrick 1985, 1986). Most of the within-species variation in the muscle in this study, however, was limited to members of the genus *Merops.* Individual bee-eaters had: (1) no FCLA; (2) tendon G but no FCLA fibers; or (3) tendon G and a small FCLA.

Bee-eater species show fewer variations in FCL than some tyrannid flycatchers (McKitrick 1986: table 1). However, although the extremes of variation in bee-eaters do not match those found in tyrannids, they are greater than those found in any other nontyrannid, and the variation in *Merops* is no less remarkable than that within species of flycatchers.

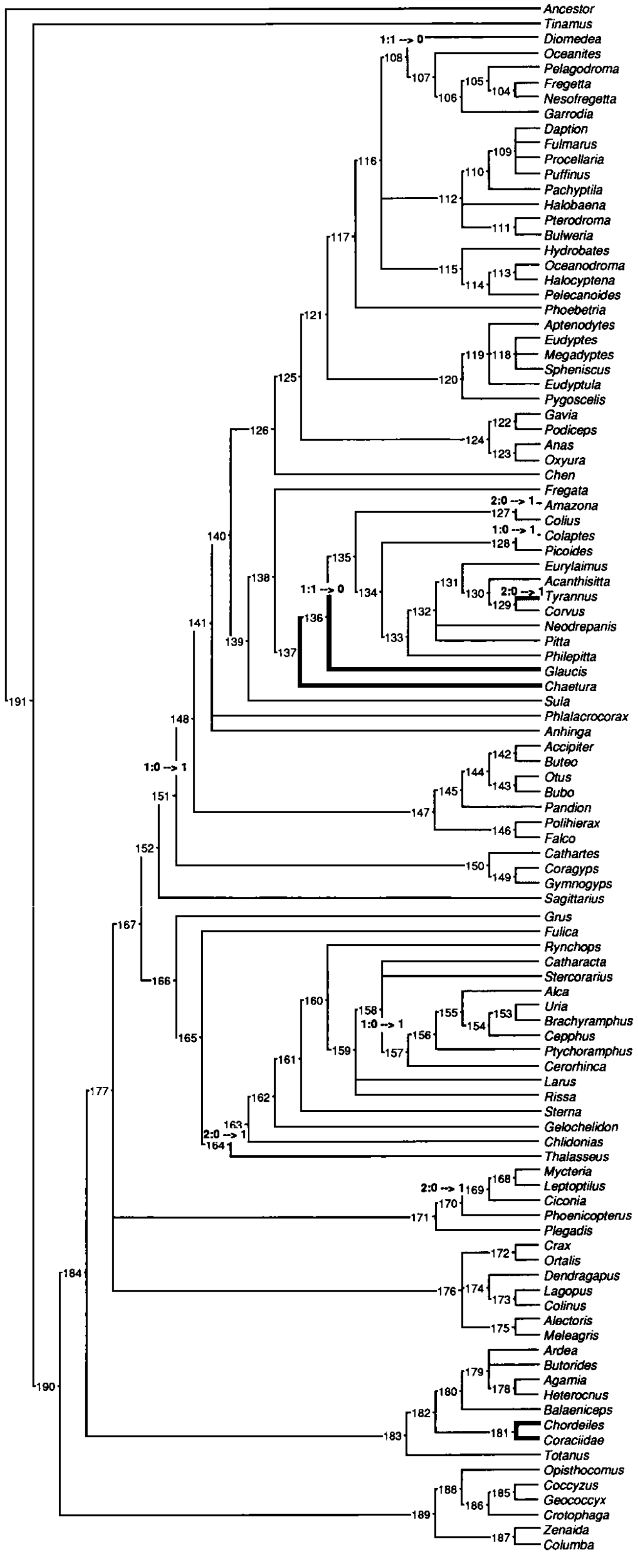
Aerial foraging and interspecific variation in FCL.—FCL consists of two parts in many birds, a pelvic and an accessory part. The accessory part is usually large and inserts extensively on the femoral shaft (George and Berger 1966, McKitrick 1991). Out of nine groups showing kingbirdlike aerial behavior, six showed a reduction in size of FCLA; the exceptions were the jacamar *Galbula,* the roller *Eurystomus* and the wood-swallow *Artamus.* The jacamar had a robust FCLA, while the roller and wood-swallow had a large FCLA that had no insertion on the femoral shaft except in one specimen. The control species *Terpsiphone* had a robust FCLA as did the species examined by Berman et al. (1990) and Raikow et al. (1990). The sample size of species is small, but only because the sample in nature also is small. Judging from the results of my study, the morphology of FCL is moderately correlated with the aerial foraging habit. Highly aerial birds such as swifts lack FCLA, and in swallows the FCLA is greatly reduced. FCL is entirely absent in hummingbirds (Zusi and Bentz 1984). Therefore, it appears that one can predict the morphology from behavior, and reduction has occurred independently in a variety of unrelated taxa. Some species exhibiting moderately aerial behavior (i.e. they catch prey on the wing but do not spend most of their time in the air), however, such as jacamars, rollers and wood-swallows, do not have reduced morphologies of FCL, whereas others such as bee-eaters and drongos do.

In Dendrocolaptidae, Raikow (pers. comm.) has found a trend toward reduction in FCLA, with a corresponding diversion of the fibers of FCLP to tendon M. Thus, some of the force of FCL is exerted on the tibiotarsus rather than the femur, which may be related to the birds' vertical climbing habits and the importance of flexing the hindlimb to prevent falling backwards. I have detected no such modifications in any of the birds with reduced FCLA examined here.

Historical analysis of interspecific variation in FCLA.—Stronger and more meaningful statements about the significance of reduction in FCLA may be made if one compares morphology and ecology within a phylogenetic context, as Donoghue (1989) has done for seed plants. McKitrick (1991) analyzed hindlimb-muscle variation, including that of FCLA, in 103 avian taxa, and some of the taxa examined in the present study were included in that analysis. Tree 1 from McKitrick (1991) is depicted in Figure

⟶

Fig. 2. Cladogram (from McKitrick 1991) showing occurrence of aerial foraging behavior (heavy black lines) and hypothesized transitions in M. flexor cruris lateralis. Character 1 is FCL pars accessoria (presence = 0, absence = 1). Character 2 is FCL pars accessoria (unreduced = 0, reduced = 1). The designation "1:1→0" indicates a transition from 1 to 0 in character 1.


Ancestor
Tinamus
1:1 --> 0
Diomedea
Oceanites
Pelagodroma
Fregetta
Nesofregetta
Garrodia
Daption
Fulmarus
Procellaria
Puffinus
Pachyptila
Halobaena
Pterodroma
Bulweria
Hydrobates
Oceanodroma
Halocyptena
Pelecanoides
Phoebetria
Aptenodytes
Eudyptes
Megadyptes
Spheniscus
Eudyptula
Pygoscelis
Gavia
Podiceps
Anas
Oxyura
Chen
Fregata
2:0 --> 1
Amazona
Colius
1:0 --> 1
Colaptes
Picoides
Eurylaimus
Acanthisitta
2:0 --> 1
Tyrannus
Corvus
Neodrepanis
Pitta
Philepitta
1:1 --> 0
Glaucis
Chaetura
Sula
Phlalacrocorax
Anhinga
1:0 --> 1
Accipiter
Buteo
Otus
Bubo
Pandion
Polihierax
Falco
Cathartes
Coragyps
Gymnogyps
Sagittarius
Grus
Fulica
Rynchops
Catharacta
Stercorarius
Alca
Uria
Brachyramphus
Cepphus
1:0 --> 1
Ptychoramphus
Cerorhinca
Larus
Rissa
Sterna
Gelochelidon
2:0 --> 1
Chlidonias
Thalasseus
Mycteria
Leptoptilus
2:0 --> 1
Ciconia
Phoenicopterus
Plegadis
Crax
Ortalis
Dendragapus
Lagopus
Colinus
Alectoris
Meleagris
Ardea
Butorides
Agamia
Heterocnus
Balaeniceps
Chordeiles
Coraciidae
Totanus
Opisthocomus
Coccyzus
Geococcyx
Crotophaga
Zenaida
Columba
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1:1 --> 0
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CHARACTER 1

node 151 0 ==> 1 node 148
node 108 1 ==> 0 node 107
node 136 1 ==> 0 node 135
node 128 0 ==> 1 *Picoides*
node 158 0 ==> 1 node 157

CHARACTER 2

node 127 0 ==> 1 *Amazona*
node 129 0 ==> 1 *Tyrannus*
node 164 0 ==> 1 node 163
node 170 0 ==> 1 node 169
node 182 0 ---> 1 node 181

Fig. 3. Transitions in M. flexor cruris lateralis (FCL) (ACCTRAN optimization) For: character 1, FCL pars accessoria (presence = 0, absence = 1); and character 2, FCL pars accessoria (unreduced = 0, reduced = 1). Arrows with double lines denote unambiguous transitions that are same for all optimization assumptions. Arrow with a single line (character 2 only) denotes transitions that vary with optimization assumptions.

2. The occurrence of aerial-foraging behavior (heavy black lines) is shown on the cladogram. These occurrences are hypothesized to be independent at each node; however, there is some ambiguity at nodes 137 and 136. It is equally parsimonious to suggest either one origin of aerial foraging at node 137 and loss at 135, or independent origins in *Glaucis* and *Chaetura*. This ambiguity makes little difference for the present analysis.

The hypothesized transitions obtained for this tree in two characters are shown on the cladogram (Fig. 2): (1) occurrence of FCLA (presence = 0, absence = 1); (2) reduction of FCLA (no reduction = 0, reduction = 1). Figure 3 summarizes these transitions and indicates which transitions are primitive and which derived with respect to the origin of aerial-foraging behavior.

Merops is not included in the cladogram, but Maurer and Raikow (1981) noted that, among the Coraciiformes, FCLA is absent only in Trogonidae and, possibly independently, in the Alcedinoidea, a group that includes Meropidae and the kingfisher group Alcedinidae. Kingfishers are essentially aerial piscivores, and Bent (1940) gave a report of Belted Kingfishers (*Ceryle alcyon*) also catching moths and butterflies on the wing. Although the feet are not used for prey capture (Johnston 1989), they are used in the excavation of nest burrows (White 1953). Bee-eaters also nest in burrows and use their feet to excavate them (Fry 1972). In this case, the members of a clade showing reduced or absent FCLA are ecologically similar; in other words, phylogeny, ecology (aerial behavior), and the transformation of FCLA are coincident.

Eurystomus is represented on the cladogram by Coraciidae at node 181. It shows a slight reduction in FCLA, but the reduction is not at all comparable to that found in some other aerially-foraging species examined in the present study. Coraciidae is clustered with *Chordeiles* (node 181), another aerial species that also does not show reduction in FCLA. Thus, the aerial habit is not coincident with significant muscle reduction.

Swifts (*Chaetura*) and hummingbirds (*Glaucis*) do not emerge together in the cladogram, contrary to traditional classifications. If this separation is valid, then aerial behavior may be independently derived in the two groups. However, as indicated in Figure 3, loss of FCLA is primitive for each of these groups, so these groups cannot be considered to provide evidence for the causal loss of FCLA with the evolution of aerial behavior: the muscle loss preceded the evolution of aerial behavior.

Galbula is not included in the cladogram, although its relatives among the woodpeckers are included. *Galbula* does not exhibit reduction of FCLA, although like *Merops* and kingfishers, it catches its prey on the wing and lives in burrows that it excavates with its feet (Skutch 1937). In this case, aerial-foraging behavior apparently is derived, but FCLA is primitive.

Unfortunately, few passerine species are represented in the cladogram. However, of the passerines whose hindlimb muscles have been studied, most show a robust FCLA (George and Berger 1966, Raikow 1976, 1978, 1980, 1987, Borecky 1977, McKitrick 1985). The aerial passerines examined in the present study (*Dicrurus, Hirundo, Artamus*) are probably sufficiently distantly related that the first two can be said to represent independent data points (see Felsenstein 1985) in support of the causal link between reduction of FCLA and aerial behavior. *Artamus*, however, does not exhibit reduction of the muscle.

The relationship between the evolution of aerial behavior and reduction of FCLA is summarized in Table 1. It shows that there are four independent cases where the evolution of the aerial habit and reduction of FCLA are coincident, and five cases where the two are not coincident. Most strikingly, the cladogram (Fig. 2) shows that reduction or loss of FCLA is primitive for many birds that are widely divergent in the manner in which they use their hindlimbs, such as penguins, loons, grebes, ducks, and many procellariiforms.

Several tests of significance of association of characters are currently available. One such test, devised by Maddison (1990), takes into account the entire tree topology to determine whether the dependent variable (reduction of FCLA) occurs with the independent variable (aerial-foraging behavior) significantly more often than would be expected by chance. Unfortunately, the taxa included in the present study are not all represented in McKitrick's (1991) phylogeny, and Maddison's test, therefore, is not applicable. At present, however, it is clear that, with four cases of derived association and five without, the aerial habit does not invariably lead to reduction of FCLA. Evidently, it is unimportant to an aerial-foraging bird whether the muscle is robust or reduced; once a bird evolves this habit, the muscle may be free to vary at random as suggested by McKitrick's (1986, 1990b) random-variation hypothesis. This is in contrast to the suggestion made by Regal (1977) that loss of useless structures is brought about by selection in response to the evolutionary need for developmental "noise suppression."

In making comparisons of this kind, there is always the danger that our analogies will be imperfect; that is, incomplete knowledge about the ecology and natural history of the organisms compared, or about the functional demands on the structures, prevents us from knowing the degree to which our comparisons are meaningful. For example, perhaps the requirements for digging burrows with the feet do not permit reduction of FCL in some species (although in *Merops* they clearly do); perhaps other unknown functional constraints are operating to balance the pressures on muscle morphology imposed by the aerial habit. The temptation is then strong to fall back upon the questionable concept of "phylogenetic constraint" to explain the messy details of the picture that emerges (McKitrick in press). In order to maximize our understanding of such problems, a research program integrating ecology, functional morphology, and phylogenetic systematics is needed (Wake 1991). In the meantime, however, it is clear that attempts to make comparisons across species are most meaningful when done within a phylogenetic context, so that the details of character transformations can be observed. Despite the hazards of generalizing across species that differ in many ways, this approach allows one more clearly to identify the problems in comparisons and, thereby, to inch towards the truth. The current truth appears to be that the origin of aerial-foraging behavior and reduction or loss of FCL are not causally related.

TABLE 1. Summary of data on link between evolution of aerial habit and reduction of FCRLA. In all cases, aerial foraging behavior is assumed to be derived.

	FCRLA[a]		
Taxon	Primitively robust	Primitively absent	Reduced (derived)
Galbula	+		
Merops, kingfishers			+
Eurystomus, *Chordeiles*	+		
Chaetura		+	
Glaucis		+	
Hirundo			+
Dicrurus			+
Artamus	+		
Tyrannus			+

[a] In three states, respectively, of FCRLA. Association of morphology and behavior: absent; present but not derived; present and derived.

ISSUE OF CIRCULARITY

The notion has been raised numerous times that characters whose evolution one wishes to study should not be included in any phylogeny that forms the framework for such research (e.g. Brooks and McClennan 1991). I cannot agree that there is any circularity in such a method. A phylogenetic analysis based on any character system is a hypothesis about the evolution of that system. It is almost incidental that the names of the organisms that own those characters are printed at the branch tips of the resulting cladograms. An alternative to using this type of analysis in the study of character evolution is to use a tree derived from a different group of data sets and then optimize the muscle characters (in this case) on a tree derived from other data. This practice will not itself lead to unambiguous hypotheses about character transformation, however; selecting among possible alternative transition patterns still involves a parsimony procedure. Presumably, all character sets are more or less equal in their potential to yield historical data; if they are not, only a phylogenetic analysis will reveal this. If one believes that the best phylogenetic hypotheses are those based on as much information as possible, then eliminating data from one's analyses would be counterproductive, especially when there are so few cases where multiple, large data sets are available for the same group of taxa.

INDIVIDUAL VARIATION AND PHYLOGENETIC ANALYSIS

Most of the individual variation in the hindlimb musculature of the specimens examined falls into the category of "minor variants" as described by Raikow et al. (1990). These include variations in size and shape that are noteworthy but are not useful for phylogenetic analysis. If such variants were interspecific rather than intraspecific, they would certainly be phylogenetically informative; only dissection of series can reveal this, but it is beginning to be evident that such within-species variation can be expected in specific muscles.

The presence or absence of entire muscles is noteworthy. Few muscles varied intraspecifically in whether or not they were present; these were Mm. iliofemoralis (ILF), iliofemoralis externus (IFE) and flexor cruris lateralis pars accessoria (FCLA). ILF was found in one specimen of the wood-swallow *Artamus;* it also was found on one side of a specimen of *Artamus* by Raikow et al. (1979). Further dissection would be needed to determine which condition is typical for the species.

IFE was present in one specimen of the drongo *Dicrurus.* This muscle is absent in most members of the Passeriformes, but Raikow et al. (1979) found IFE typically to be present in the passerine bowerbird assemblage (Ptilonorhynchidae, Callaeidae, Paradisaeidae). They also found the muscle occasionally to be present as an anomaly in some species of starlings (Sturnidae), a group thought by Borecky (1977) to be the sister group to the bowerbird assemblage. These groups are placed relatively close together in the *Peters' Check-list* (Mayr and Greenway 1962); Sibley et al. (1988) placed them all in the Parvorder Corvida, along with Dicruridae. Raikow et al. (1979) suggested that the genetic information for development of IFE is suppressed in most passerines, and that the tendency for its reactivation may have been present in the ancestors of the group that includes starlings and bowerbirds. The reactivation may then have become permanent in the latter group, but not the former. The same could apply to drongos; however, insufficient data are available on the distribution of IFE in this group to state with certainty that absence of IFE is typical of drongos.

FCL, as stated above, may vary within species in the presence or absence of pars accessoria, and dissection of series is necessary to determine if there is a species-typical condition. Ecology may have an influence on the morphology of this muscle, but the morphology is likely to have a strong phylogenetic component as well and, therefore, may be useful in constructing hypotheses of relationship.

I concur with Raikow et al. (1990) in their recommendations for the use of limb-muscle data in phylogenetic analysis. Bilateral or multiple dissections, if possible, will greatly reduce the likelihood of mischaracterization of the limb musculature for any given species. Berman et al. (1990) found "novelties" in four hindlimb muscles in House Sparrows (*Passer domesticus*) that were well represented in a large sample, suggesting that some "errors" would still be likely in studies relying on dissection of one or a few specimens. Dissection of series of one or a few reference species, therefore, is essential, but for the most part the muscles that will vary intraspecifically are predictable. Furthermore, the one muscle that is most likely to vary within species that typically exhibit aerial behavior, namely M. flexor cruris lateralis, is situated such that it can be easily examined in multiple specimens with a mimimum of damage to the specimens.

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APPENDIX. Specimens dissected.

Chordeiles minor, USNM 506049, 506050, 506055, 506056 (National Museum of Natural History). *Merops viridis,* DMNH 61293, 61297, 61310, 61313, 61324 (Delaware Museum of Natural History). *M. apiaster,* USNM 538004, 539921, 540150, 540153 (National Museum of Natural History). *M. albicollis* RG 121.66, 121.170, 121.171, 121.174, 121.179 (Musee Royal de l'Afrique Centrale). *Eurystomus orientalis,* BMNH 1925.11.1.85, 1925.11.1.87 (British Museum of Natural History). *Chaetura pelagica,* KU 039842, 039848, 039849, 039858, 039861, 039862, 039864, 039866 (Museum of Natural History, University of Kansas). *Galbula ruficauda,* BMNH 1932.2.3.1, 1932.2.3.2 (British Museum). *Dicrurus hottentottus,* BMNH 1940.12.8.345, A/1971.3.5 (British Museum of Natural History). *Artamus leucorhynchus,* BMNH A/1969.15.420, A/1969.15.421 (British Museum of Natural History). *Hirundo rustica,* CM 2487, 2642, 3501 (Carnegie Museum), UMMZ 225,913, 225,914, 226,243, 226,783 (University of Michigan Museum of Zoology). *Terpsiphone mutata,* FMNH 345895, 345916, 345918, 345921, 345924, 345928, 345927 (Field Museum of Natural History).