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MYOLOGY OF THE PECTORAL APPENDAGE IN KINGBIRDS (*TYRANNUS*) AND THEIR ALLIES

MARY C. McKITRICK

ABSTRACT.—The forelimb muscles of several species of the kingbird group are here described and illustrated, with the goal of discovering character states of use in delineating clades within the Tyrannidae. These muscles conform in all species to the oscine pattern as described by other authors, with the exception of a few features.

Special attention is given to M. latissimus dorsi caudalis, the only muscle that varies widely among, as well as within, the species examined. Absence of this muscle in the species of *Myiozetetes* could mean that this group is a clade. Variation in other tyrannids, however, indicates that closely related species may be losing M. latissimus dorsi caudalis independently.

The present study of wing muscles in the "kingbird assemblage" (Traylor 1977) was undertaken as part of a larger study, to determine whether the appendicular musculature of New World flycatchers (Tyrannidae) can provide information of use in constructing phylogenetic hypotheses for this group. Anatomical data from the work of Garrod (1876), Ames (1971), Midtgård (1982), and W. E. Lanyon (pers. comm.) have recently been used in a cladistic analysis of relationships within the Tyrannoidea (McKitrick 1985). Other anatomical data for this group are scarce and incomplete, and much additional information is needed from a variety of anatomical (and molecular) systems to clarify relationships within this group.

A few published studies of the forelimb muscles of oscines exist, e.g., Swinebroad (1954), Hudson and Lanzillotti (1955), George and Berger (1966), Borecky (1977), and Raikow (1977, 1978), but I have found virtually no such information for suboscines. I undertook to describe and illustrate the forelimb muscles of several species of the kingbird group, and compare them with what is known of these muscles in other passerine birds. My purpose was to determine polarities of character states, and thereby assess the potential of this anatomical system for phylogenetic analysis. Similar data for the hindlimb muscles are provided in McKitrick (in press). My working hypothesis was that the Tyrannidae is monophyletic (McKitrick 1985) and, further, that the kingbird group is also a clade (Lanyon 1984).

MATERIALS AND METHODS

I dissected fluid-preserved specimens of the following species: Tropical Kingbird (*Tyrannus melancholicus* USNM 504538 and 504539), Rusty-margined Flycatcher (*Myiozetetes cayanensis* USNM 504542), Piratic Flycatcher (*Legatus leucophaius* USNM 510867), and Variegated Flycatcher (*Empidonomus varius* FMNH 288494), all members of the kingbird group. One muscle, M. latissimus dorsi caudalis, was intraspecifically variable, and I examined this muscle in 39 other species of Tyrannidae to assess the extent of variation. Dissections were done under a stereomicroscope at 6×, 12× and 25×, with the use of iodine stain (Bock and Shear 1972) to enhance visibility of muscle fibers. Anatomical nomenclature is from Baumel et al. (1979), and abbreviations are, for the most part, from Zusi and Bentz (1984). Descriptions of muscles refer to *Tyrannus melancholicus,* and are the same in the other species unless otherwise stated. Comparisons with other passerine species are noted where differences occur.

Abbreviations for museums from which specimens were borrowed are as follows: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; FMNH, Field Museum of Natural History; KU, University of Kansas; LSU, Louisiana State University; USNM, National Museum of Natural History; YPM, Peabody Museum, Yale University. Collection data were reported in McKitrick (1984).

RESULTS AND COMPARISONS

M. rhomboideus superficialis (Fig. 1:RS) is a thin, flat, essentially parallel-fibered muscle, lying deep to M. latissimus dorsi pars cranialis and superficial to M. rhomboideus profundus. It arises by an aponeurosis from the neural spines of the last two cervical vertebrae and the neural spines of the first dorsal vertebrae. It passes craniolaterally to insert by a narrow aponeurosis on the dorsomedial surface of the cranial two-thirds of the scapula. The cranialmost fibers insert at the very cranial tip of the

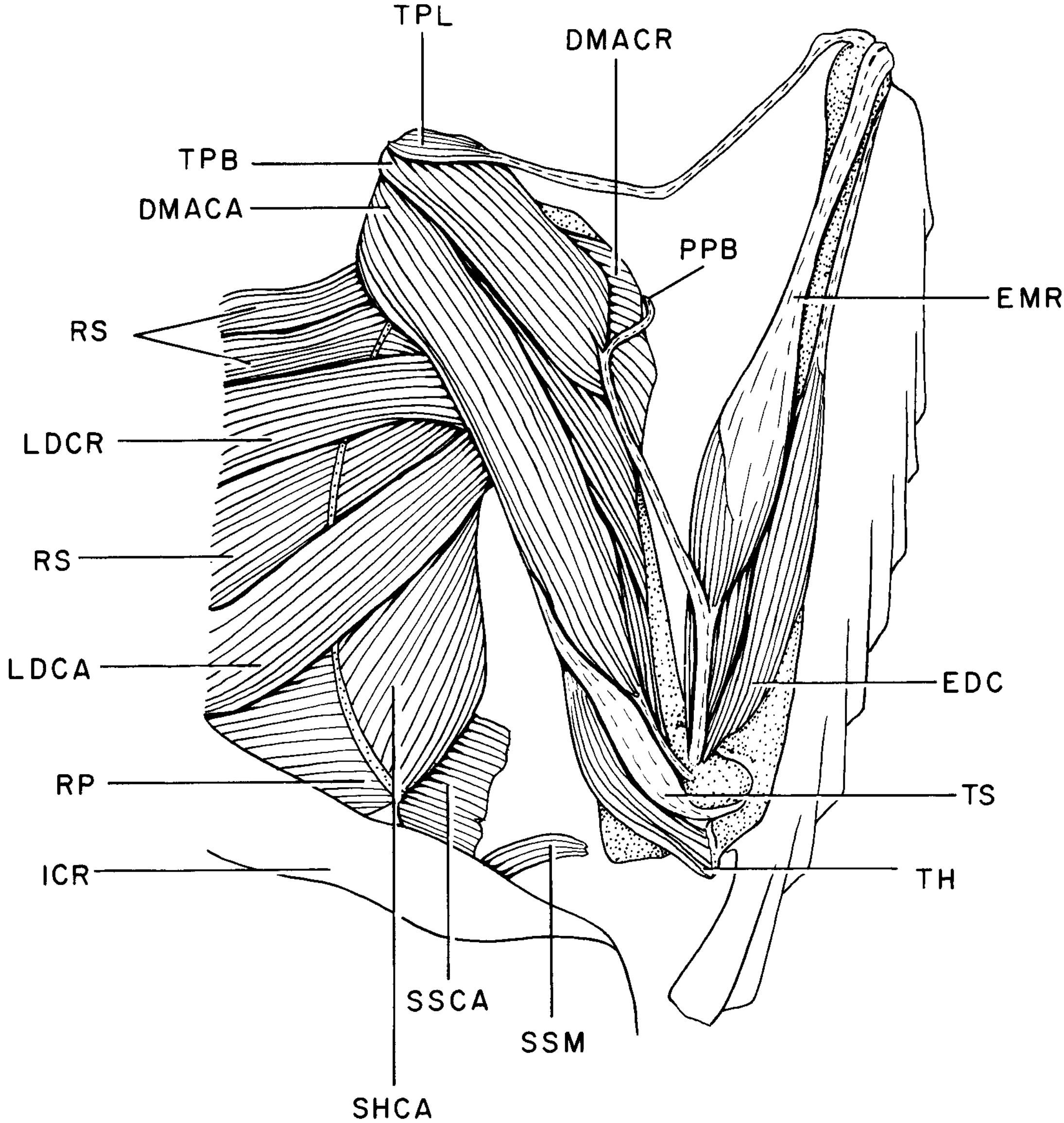

FIGURE 1. Superficial dorsal muscles of the forelimb (all figures illustrate *Tyrannus melancholicus*). Abbreviations for Figs. 1–11: ABA, M. abductor alulae; ADA, M. adductor alulae; ADM, M. abductor digiti majoris; B, M. brachialis; BB, M. biceps brachii; CCA, M. coracobrachialis caudalis; DMACA, M. deltoideus major caudalis; DMACR, M. deltoideus major cranialis; DMI, M. deltoideus minor; EC, M. ectepicondylo-ulnaris; EDC, M. extensor digitorum communis; ELA, M. extensor longus alulae; ELDM, M. extensor longus digiti majoris; EMR, M. extensor metacarpi radialis; EMU, M. extensor metacarpi ulnaris; ES, M. extensor secundariorum; FCU, M. flexor carpi ulnaris; FCU a, M. flexor carpi ulnaris, accessory belly; FDM, M. flexor digiti minoris; FDP, M. flexor digitorum profundus; FDS, M. flexor digitorum superficialis; HUP a, humero-ulnar pulley, pars accessoria; HUP ha, humero-ulnar pulley, pars humeralis accessoria; HUP u, humero-ulnar pulley pars ulnaris; ICR, M. iliotibialis cranialis; ID, M. interosseus dorsalis; IV, M. interosseus ventralis; LDCA, M. latissimus dorsi caudalis; LDCR, M. latissimus dorsi cranialis; P, M. pectoralis; PPB, M. pectoralis pars propatagialis brevis; PPL, M. pectoralis pars propatagialis longus; PRP, M. pronator profundus; PRS, M. pronator superficialis; RP, M. rhomboideus profundus; RS, M. rhomboideus superficialis; SBC d, M. subcoracoideus, dorsal head; SBC v, M. subcoracoideus, ventral head; SBS LA, M. subscapularis caput laterale; SBS M, M. subscapularis caput mediale; SC, M. sternocoracoideus; SHCA, M. scapulohumeralis caudalis; SHCR, M. scapulohumeralis cranialis; SP, M. serratus profundus; SP ca, M. serratus profundus, caudal head; SP cr, M. serratus profundus, cranial head; SSCA, M. serratus superficialis pars caudalis; SSCR, M. serratus superficialis pars cranialis; SSM, M. serratus superficialis pars metapatagialis; SU, M. supinator; SUP, M. supracoracoideus; TH, M. humerotriceps; TPB, M. tensor propatagialis pars brevis; TPL, M. tensor propatagialis pars longa; TS, scapulotriceps; UD, M. ulnometacarpalis dorsalis; UV, M. ulnometacarpalis ventralis.

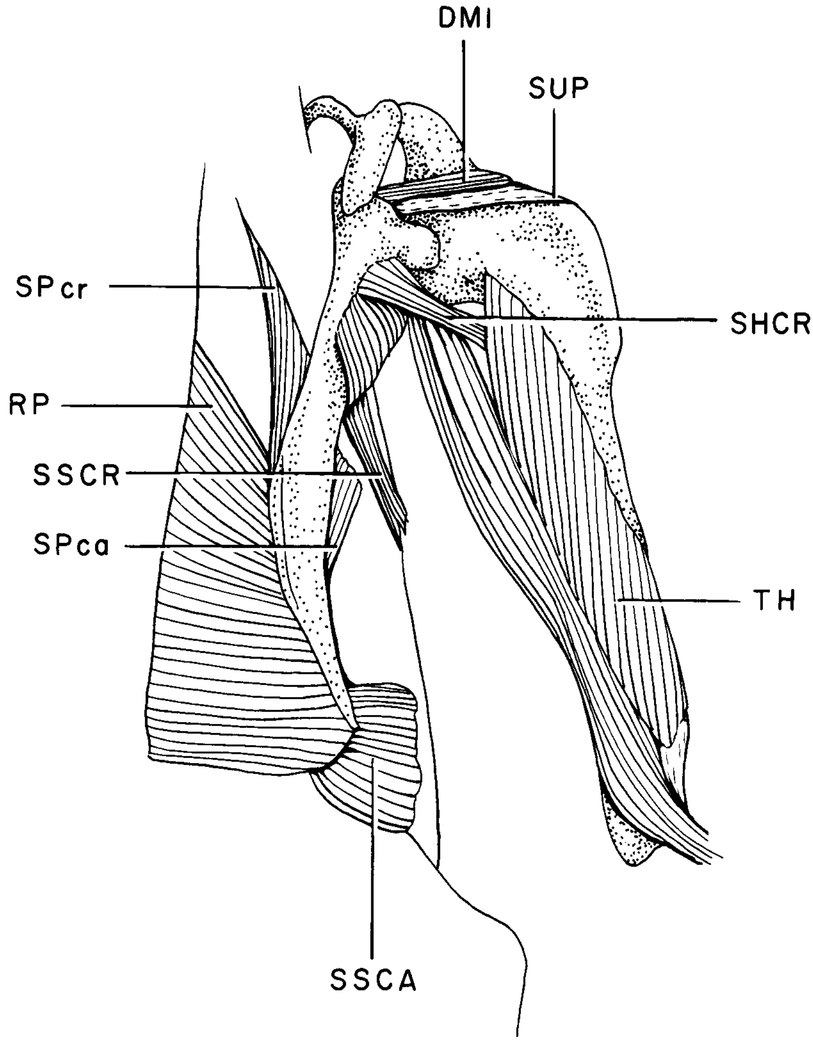

FIGURE 2. Second layer of dorsal muscles of the forelimb.

scapula and are slightly separated from the rest of the belly.

In *Myiozetetes* and *Legatus,* this muscle inserts on the cranial three-fourths of the scapula.

M. rhomboideus profundus (Figs. 1, 2:RP) is a thin, flat, triangular muscle, lying deep to M. rhomboideus superficialis. It arises by a narrow aponeurosis from the neural spines of the dorsal vertebrae, caudal to the proximal origin of M. rhomboideus superficialis; it inserts fleshily on the caudal two-thirds of the scapula.

In the other species that I examined, this muscle is as described above, except for the relative length of the insertion (see McKitrick 1984).

M. serratus superficialis (Figs. 1, 2:SS) consists of a caudal, a metapatagial, and a cranial part. Pars caudalis (SSCA) is a fan-shaped belly, arising by an aponeurosis from the true ribs. The caudal fibers insert fleshily on the apex of the scapula and the cranial fibers insert by a tendinous sheet on the ventromedial surface of the distal end of the scapula.

Pars metapatagialis (SSM) is a narrow, strap-shaped belly, arising fleshily on the lateral surface of the true ribs ventral to the distal end of the scapula and inserting under the patagial skin near the elbow.

Pars cranialis (SSCR) has lateral and medial heads of origin. The medial head arises on the cervical rib, from just distal to the uncinate process to nearly the distal end of the rib. The lateral head arises from the first true rib, from its uncinate process all the way to the articulation with the sternal rib. Both bellies are essentially strap-shaped, the lateral one being wider than the medial one. They are separated by a slight gap on the dorsal surface of the origin. The two bellies extend cranidorsally between the two heads of M. subscapularis, and insert together by a tendon on the ventral margin of the cranial end of the scapula.

Whereas in *Tyrannus melancholicus* the lat-

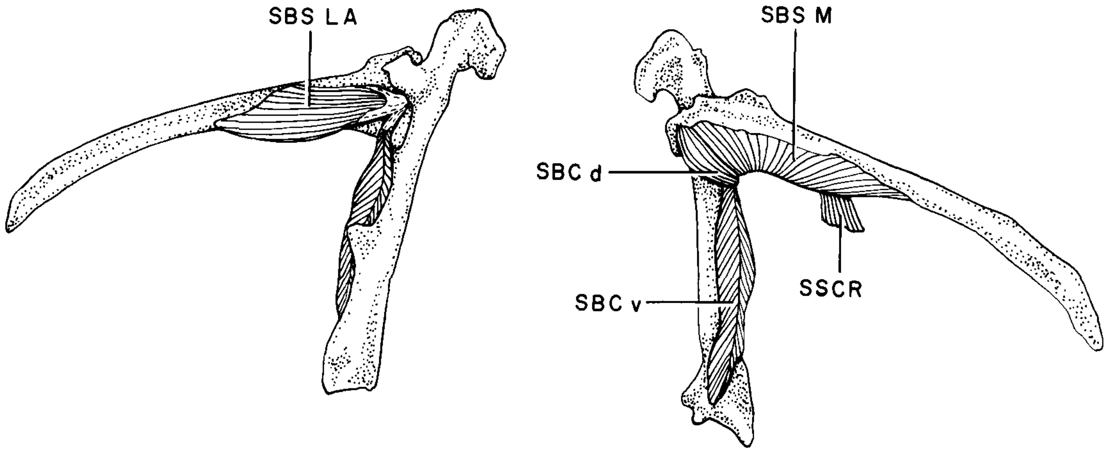

FIGURE 3. Left: muscles on the lateral surface of the scapula and coracoid. Right: muscles on the medial surface of the scapula and coracoid.

eral belly of pars cranialis completely overlies the medial belly, in *Myiozetetes* and *Legatus,* the two bellies are farther apart because the origin of the lateral belly is limited to the region of the uncinate process. In *Tyrannus,* the two bellies fuse at the insertion and insert by a single tendon, but, in *Myiozetetes* and *Legatus,* the two bellies remain separated. The insertion is, therefore, slightly broader in *Myiozetetes* and broader still in *Legatus.* In *Empidonomus,* the lateral belly is as in *Tyrannus,* extending to the articulation with the sternal rib. The bellies are nevertheless separated because the cervical rib protrudes slightly.

In *Empidonomus varius* the two bellies of pars cranialis are separated by a gap of about 2 mm at the origin, but on the ventral surface rather than the dorsal surface as in *Tyrannus* and *Myiozetetes.* The two bellies fuse two-thirds of the way distally to form a common belly, unlike *Tyrannus,* in which the two bellies do not fuse until their insertion.

M. serratus profundus (Fig. 2:SP) possesses three more-or-less strap-shaped heads, sometimes poorly defined. The caudal and middle ones arise from the dorsal surface of the true ribs, ventromedial to the scapula, and the cranial one arises from the cervical vertebrae, lateral to the scapula. All three insert on the medial surface of the scapula, cranial to the insertion of M. rhomboideus profundus.

M. scapulohumeralis cranialis (Fig. 2:SHCR) is an essentially parallel-fibered muscle, slightly wider at its origin than at its insertion. It arises fleshily on the dorsolateral surface of the proximal end of the scapula, and passes cranially between the ventral and dorsal heads of M. humerotriceps to insert fleshily on the cranial margin of the pneumatic fossa of the humerus.

M. scapulohumeralis caudalis (Fig. 1:SHCA) is a bipennate, fan-shaped muscle arising on the caudal two-thirds of the scapula. The superficial fibers arise fleshily on the dorsal surface and medial border of the scapular blade, while the deeper ones arise by an aponeurosis on the caudolateral margin of the blade. The muscle narrows considerably as it passes cranially; it inserts by a broad, dense tendon on the dorsal surface of the bicipital crest of the humerus, on the medial border of the pneumatic fossa.

M. subscapularis (Fig. 3:SBS) arises by two unipennate heads. The lateral head (SBS LA) arises fleshily on the dorsolateral, lateral, and ventrolateral surfaces of the proximal end of the scapular blade (not near the glenoid lip as in *Loxops* [Raikow 1978]). The medial head (SBS M) arises fleshily deep to this on the medial surface of the scapula, beginning near the acromion. The two heads fuse to insert by a short tendon on the ventral tuberculum of the humerus. The heads are separated by the insertion of M. serratus superficialis cranialis.

M. subcoracoideus (Fig. 3:SBC) arises by two heads. The ventral head (SBC v) is narrow and bipennate, arising fleshily on the ventral surface of the caudal half of the coracoid. The smaller, dorsal head (SBC d) arises on the ventromedial surface of the head of the scapula, just ventral to its articulation with the clavicle. The fibers of the two heads converge on a stout tendon, which is closely associated with the tendon of insertion of M. subscapularis, with which it passes over the ventral surface of the head of the coracoid to insert on the ventral tuberosity of the humerus.

M. coracobrachialis cranialis (CCR) is vestigial, being reduced to ligamentous tissue.

M. coracobrachialis cranialis is vestigial in the "corvid assemblage" (Borecky 1977). It is absent in most New World nine-primaried oscines, but well developed in *Vireo* and *Vireolanius* (Raikow 1978). It was present in *Fregilupus varius* (Sturnidae; Berger 1957). It is reported to be "weakly developed" in *Procnias nudicollis* (Cotingidae; George and Berger 1966: 315).

M. coracobrachialis caudalis (Fig. 8:CCA) is a bipennate muscle, lying lateral to M. supracoracoideus and arising fleshily on the lateral surface of the distal half of the coracoid. The fibers insert on the dorsal surface of an aponeurosis that arises on the ventral surface of the belly and gives rise to the tendon of insertion. The latter inserts on the Tuberculum ventrale of the humerus, dorsal to the insertion of M. subscapularis.

M. sternocoracoideus (Fig. 8:SC) is a short, broad, parallel-fibered muscle that arises fleshily from the distal ends of the sternal ribs and the sternocoracoidal process of the sternum. It inserts fleshily, and by an aponeurosis arising on its ventral surface, on the sternocoracoidal impression of the coracoid.

M. pectoralis (Fig. 7) comprises three parts. Pars thoracicus (P) is a large, fan-shaped muscle, arising fleshily from the sternal carina, from the caudolateral third of the sternal plate, the lateral trabecula of the sternum, the membrane overlying the sternal ribs, the lateral surface of the clavicle, and the coracoclavicular membrane. It inserts on the Crista pectoralis (deltoid crest) of the humerus by fleshy fibers and by a broad, dense, tendinous sheet arising on the dorsal surface of the belly.

Pars propatagialis longus (PPL) is a strap-shaped belly (large compared to its condition in drepanidids [Raikow 1977]—13 mm in *Tyrannus melancholicus* USNM 504538), arising fleshily on the ventral surface of pars thoracicus near the clavicle. A narrow tendon arises from its cranioventral surface and joins the tendon of M. tensor propatagialis longus at a right angle.

Pars propatagialis brevis (PPB) is a tiny, flat tendon, arising on the cranioventral surface of pars thoracicus near the Crista pectoralis of the humerus. The tendinous origin of pars propatagialis brevis is about four times the width of the tendon itself. Pars propatagialis brevis passes distally to form a common tendon with M. tensor propatagialis brevis, at the proximal end of the tendon of insertion of the latter (Fig. 1).

Pars propatagialis longis is aponeurotic or tendinous, rather than fleshy in the following: *Agelaius phoeniceus* and *Spizella arborea* (George and Berger 1966), *Paradisaea rubra* (Berger 1956), and the 19 species of Corvidae examined by Hudson and Lanzillotti (1955), and the "corvid assemblage" (Borecky 1977); it is fleshy (but minute) in *Dendroica kirtlandii* (Berger 1968), and fleshy in *Fregilupus varius* (Berger 1957).

M. supracoracoideus (Fig. 8:SUP) is a large, asymmetrically bipennate muscle, arising fleshily on the dorsal fourth of the entire length of the sternal carina, the craniomedial two-thirds of the sternal plate, and the dorsolateral surface of the coracoclavicular membrane. The muscle narrows to a stout tendon that passes through the triosseal canal to insert on the dorsal surface of the deltoid crest of the humerus. The dorsal fibers occupy about one-fourth of the surface of the belly.

M. latissimus dorsi (Fig. 1:LD) consists of a cranial and a caudal belly in *Tyrannus melancholicus.* Pars cranialis (LDCR) is a narrow, strap-shaped belly, lying superficial to M. rhomboideus superficialis. It arises by an aponeurosis from the neural spines of the last cervical and first dorsal vertebrae. It passes craniad between Mm. scapulotriceps and humerotriceps, and superficial to M. latissimus dorsi pars caudalis, to insert fleshily on the dorsal surface of the proximal end of the humeral shaft.

Pars caudalis (LDCA) is a strap-shaped belly, about equal in width to pars cranialis. It lies superficial to M. rhomboideus profundus and arises by an aponeurosis from the neural spines of the dorsal vertebrae. It passes craniad between Mm. scapulotriceps and humerotriceps, narrows to a tendon about 2 mm long, and inserts on the dorsal surface of the proximal end of the humeral shaft just cranial to the insertion of pars cranialis.

I examined M. latissimus dorsi for the presence of pars caudalis in an additional 22 species of kingbirds, as well as in 17 species of Tyrannidae outside the kingbird group. I found no instances of asymmetry in the presence or absence of pars caudalis in any of the specimens dissected, although Raikow (1978) did find asymmetry in M. latissimus dorsi in some nine-primaried oscines.

Pars caudalis is present in the following tyrannid species (sample size in parentheses where greater than one): *Pitangus lictor, Megarynchus pitangua* (2), *Conopias inornatus, C. parva, Empidonomus varius* (3), *E. aurantioatrocristatus, Tyrannus niveigularis, T. melancholicus* (7), *T. vociferans* (2), *T. verticalis* (14), *T. forficatus* (3), *T. savana* (3), *T. tyrannus* (3), *T. dominicensis, T. caudifasciatus, Pyrocephalus rubinus, Savornis phoebe, Agriornis livida, Fluvicola pica,* and *Hirundinea ferruginea.*

Pars caudalis is absent in the following tyrannid species: *Myiozetetes luteiventris, M. ca-*

yanensis (4), *M. similis* (15), *M. granadensis, Conopias trivirgata* (2), *Myiodynastes luteiventris* (4), *M. bairdii, Legatus leucophaius, Camptostoma obsoletum, Elaenia flavogaster, Mionectes oleagineus, Phaeomyias murina, Lophotriccus galeatus, Tolmomyias sulphurescens, Platyrinchus coronatus, Contopus virens, Empidonax virescens, Machetornis rixosus, Attila spadiceus, Myiarchus crinitus* (2).

Pars caudalis is variable in the following tyrannid species (+ denotes presence, − denotes absence): *Pitangus sulphuratus* (6 +, 1 −), *Myiodynastes maculatus* (3 +, 2 −).

Pars caudalis is present in *Paradisaea rubra* (Paradisaeidae; Berger 1956); *Sturnus vulgaris* and *Aplonis tabuensis* (Sturnidae; Berger 1957); 19 species in 14 genera of Corvidae (Hudson and Lanzillotti 1955); most of the "corvid assemblage" (Borecky 1977); *Apalis flavida, Orthotomus atrogularis* (Sylviinae), *Turdus migratorius, Catharus ustulatus* (Turdinae), *Dumetella carolinensis* (Mimidae), *Nectarinia sperata* (Nectarinidae), four genera of Vireonidae, *Peucedramus taeniatus* (incertae sedis), *Thraupis episcopus* (Thraupinae), and *Cacicus cela* (Icterinae; Raikow 1978); *Vidua* and all Ploceinae, Bubalornithinae, Lonchurae, and Poephilae examined by Bentz (1979). The muscle is absent in *Strepera graculina* (Cracticidae; Leach 1914, confirmed by Hudson and Lanzillotti 1955); *Fregilupus varius* (Sturnidae) and *Artamella* (Vangidae; Berger 1957); *Agelaius phoeniceus* (Icterinae; George and Berger 1966); *Dendroica kirtlandii* (Parulinae; Berger 1968); *Lamprotornis, Cinnyricinclus, Speculipastor, Neocichla* and *Saroglossa* (Sturnidae), *Dendrocitta* and *Pseudopodoces* (incertae sedis), and the Cracticidae (Borecky 1977); the majority of the New World nine-primaried oscines (Raikow 1978); numerous Estrildidae and three species of Passerinae (Bentz 1979).

M. latissimus dorsi caudalis is widespread in non-passerines (George and Berger 1966: 288–294).

M. tensor propatagialis (Figs. 1, 7) consists of two separate bellies. Pars longa (TPL) is a small, triangular belly that arises by a short tendon from the tip of the clavicle. It gives rise to a long tendon (tendo longa) which forms the cranial border of the patagium. The tendon is joined at its proximal end by the tendons of Mm. cucullaris capitis pars propatagialis and pectoralis pars propatagialis longus.

Tendo longa divides into two main branches. One branch splits into three parts, of which one inserts on the craniodistal surface of digit I, one at the base of the follicle for the remex on the dorsal surface of digit I, and one on the craniodorsal surface of the Processus extensorius of the carpometacarpus dorsal to M. abductor allulae and just distal to the insertion of M. extensor metacarpi radialis. The other main branch attaches broadly on the distal end of the radius, and on the joint capsule, inserting on the Os radiale.

Pars brevis (TPB) is a spindle-shaped belly, lying superficial to Mm. deltoideus major cranialis and deltoideus major caudalis from the dorsal surface of the upper arm. It arises by a short tendon on the dorsal surface of the apex of the clavicle, passes distally about halfway down the humerus, and gives rise to a tendon. This tendon is joined by the tendon of insertion of M. pectoralis pars propatagialis longus. It anchors on the proximal end of M. extensor metacarpi radialis about 6 mm distal to the humeral origin of the latter. The tendon then passes along the surface of M. extensor metacarpi radialis and inserts on the dorsal epicondyle of the humerus. It has its own, distinct insertion, separate from that of M. extensor metacarpi radialis, as do all other passerines studied (Raikow 1982).

There is a scapular tendon as described for drepanidids by Raikow (1977).

M. deltoideus major cranialis (Fig. 1: DMACR) is a large, fan-shaped muscle, situated cranial to M. deltoideus major caudalis. It arises fleshily on the Os humeroscapulare and surrounding ligaments. The muscle inserts by fleshy fibers on the caudal half of the dorsal surface of the Crista pectoralis, and by tendinous fibers on the proximal one-half of the humeral shaft (i.e., the entire insertion extends two-thirds the length of the humerus).

In *Legatus leucophaius* the entire belly extends less than half the length of the humerus, or about one-third of the length of the shaft. In the other species that I examined, this muscle is as described for *Tyrannus melancholicus.*

George and Berger (1966) reported that M. deltoideus major cranialis is composed of two parts in *Agelaius phoeniceus,* one arising from the Os humeroscapulare as in the tyrannids, the other from the scapula. This is also the case in corvids (Hudson and Lanzillotti 1955), *Fregilupus varius, Sturnus vulgaris, Aplonis tabuensis* and *Artamella viridis,* (Berger 1957); *Dendroica kirtlandii* (Berger 1968), and the "corvid assemblage" (Borecky 1977). The condition in *Procnias nudicollis* is apparently like that in tyrannids (George and Berger 1966), as is that in most passerines for which data exist (see Raikow 1978). In *Pityriasis gymnocephala* (Laniidae), Mm. deltoideus major cranialis and deltoideus major caudalis are fused for most of their length (Raikow et al. 1980).

M. deltoideus major caudalis (Fig. 1:DMACA) is a long, strap-shaped muscle that arises

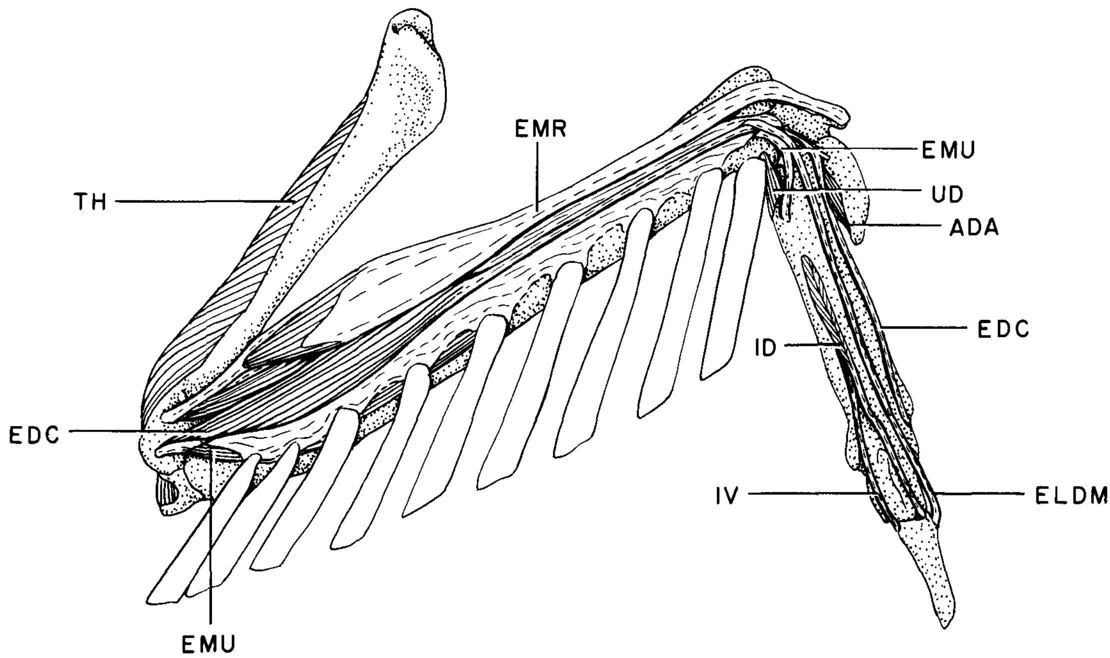

FIGURE 4. Third layer of dorsal muscles of the forelimb.

fleshily from the medial surface of the proximal end of the clavicle. It extends down the dorsal surface of the upper arm, superficial to M. scapulotriceps and caudal to M. deltoideus major cranialis. It becomes tendinous in its distal fourth, and the narrow tendon inserts on the dorsal surface of the distal end of the humerus, just proximal to the Processus supracondylaris dorsalis. A narrow scapular anchor arises from the deep portion of the medial margin and inserts on the dorsomedial surface of the scapula cranial to the insertion of M. latissimus dorsi.

I did not detect a scapular anchor in *Myiozetetes cayanensis.*

M. deltoideus minor (Fig. 8:DMI) is a small, strap-shaped muscle, lying deep to M. tensor propatagialis brevis on the dorsal surface of the shoulder. It arises fleshily from the lateral surface of the acromion of the scapula and inserts by semitendinous fibers on the head of the humerus, just cranial to the insertion of M. supracoracoideus.

In many passerines, M. deltoideus minor has only one, scapular head of origin. George and Berger (1966) noted an additional, coracoidal head in *Agelaius phoeniceus.* This additional head occurs in the Ptilonorhynchidae, *Paradisaea* (Paradisaeidae), and *Corcorax* (Grallinidae; Borecky 1977), as well as "universally" in the Carduelinae and Drepanididae; in most Emberizinae, *Icteria* and *Seiurus* (Parulinae) and *Rhodinocichla* (Thraupinae; Raikow 1978). Bentz (1979) reported a coracoidal head for 13 species of Estrildidae.

M. triceps brachii comprises Mm. scapulotriceps and humerotriceps. *M. scapulotriceps* (Fig. 1:TS) has one head of origin in *Tyrannus melancholicus,* arising by a short tendon from the dorsocaudal border of the Facies articularis humeralis of the scapula and on the surrounding ligaments. The strap-shaped belly proceeds distally to become tendinous in its distal fourth; the tendon contains a sesamoid between the humerus and ulna. Here, a short tendon (humeral anchor) branches off the main tendon and passes to the medial surface of the humeral shaft just proximal to the dorsal condyle. The main tendon inserts on the caudolateral surface of the Processus cotylaris dorsalis of the ulna.

M. scapulotriceps arises by two scapular heads in *Fregilupus varius* (Berger 1957), *Agelaius phoeniceus* (George and Berger 1966), *Dendroica kirtlandii* (Berger 1968) and nine species of Drepanididae (Raikow 1977). Only one head is present in corvids (Hudson and Lanzillottii 1955) and *Paradisaea rubra* (Berger 1956).

The humeral anchor apparently has not been reported for other passerines, although it is present in a number of non-passerines (Beddard 1898, George and Berger 1966).

M. humerotriceps (Figs. 1, 2, 4, 5, 8, 9:TH) consists of a ventral and a dorsal head, that arise fleshily from the ventral and dorsal bor-

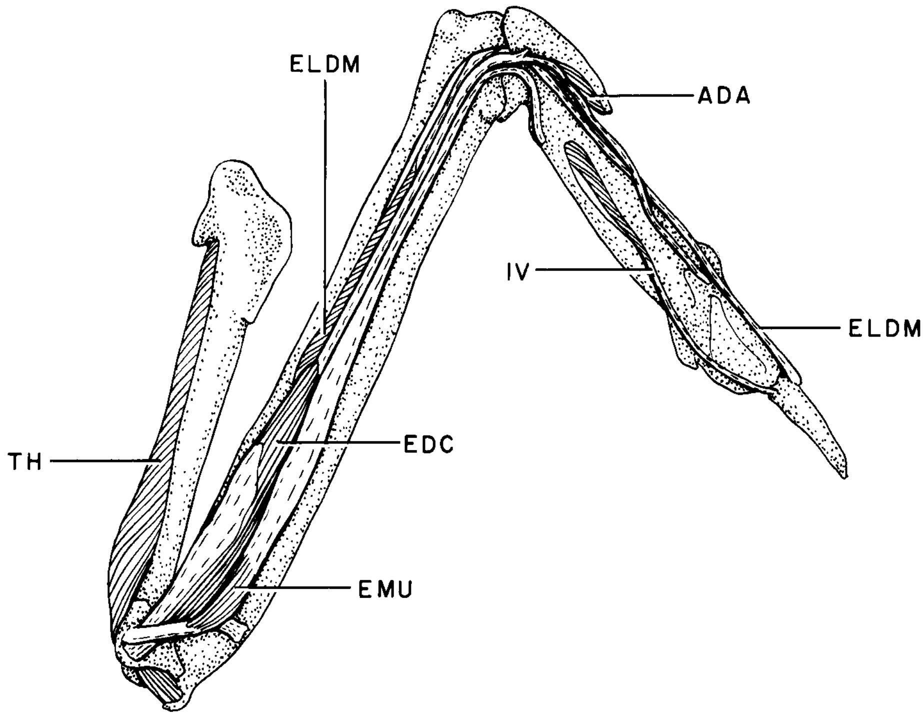

FIGURE 5. Fourth layer of dorsal muscles of the forelimb.

ders, respectively, of the pneumatic fossa of the humerus. The dorsal fibers of the ventral belly arise from within the pneumatic canal. The two fuse to form a single, bipennate belly about half-way down the humeral shaft, and insert by tendinous fibers on the olecranon of the ulna. Some fibers insert on the tendon of insertion of M. scapulotriceps, proximal to the sesamoid. The two heads are separated at the origin by the insertion on the humerus of M. scapulohumeralis cranialis.

M. biceps brachii (Fig. 8:BB) is a large, spindle-shaped muscle, arising by two heads. One, caput coracoideum, arises by a stout tendon on the ventromedial surface of the proximal end of the head of the coracoid and by elastic fibers from the humerocoracoidal ligament; the other, caput humerale, arises by a short tendon from the ventral border of the peneumatic fossa of the humerus. It inserts by three tendons: one on the proximocranial end of the radius (Tuberculum bicipitale of the radius), and two side by side on the Tuberculum bicipitale of the ulna.

The insertion of M. biceps brachii is by two tendons in most birds, one on the radius and a larger one on the ulna, rather than by three. Swinebroad (1954) reported only one tendon of insertion, on the ulna, in *Passer domesticus, Cardinalis cardinalis, Zonotrichia albicollis* and *Melospiza melodia*; however Bentz (1979), who also dissected *Passer domesticus,* made no reference to such a condition.

M. expansor secundariorum (Figs. 10, 11: ES) is a small, triangular muscle that arises fleshily from the ventral surface of the humeroulnar pulley. The belly passes superficial to all the ventral muscles of the forearm and fans out to insert at the base of the proximal three secondary remiges.

M. brachialis (Fig. 10:B) is a short, parallel-fibered, rectangular muscle, arising fleshily on the ventral surface of the Fossa M. brachialis of the distal end of the humerus, and passing across the joint to insert fleshily on the proximoventral surface of the ulna between the two heads of origin of M. flexor digitorum profundus.

M. pronator superficialis (Fig. 9:PRS) is a spindle-shaped muscle that arises by a tendon on the ventral surface of the distal end of the humerus, distal and ventral to the origin of M. brachialis. The tendon of origin passes deep within the belly, and the ventral fibers of the belly originate along it, about 3 mm distal to the origin of the dorsal fibers. The insertion is on the ventral surface of the shaft of the radius, by a tendinous sheet arising along the distal two-thirds of the length of the belly.

M. pronator profundus (Fig. 9:PRP) is a spindle-shaped muscle on the ventral surface of the forearm between Mm. extensor metacarpi radialis and flexor digitorum superficialis, deep to M. pronator superficialis. It arises by a tendon from the ventral epicondyle of the humerus between the origins of Mm. pronator

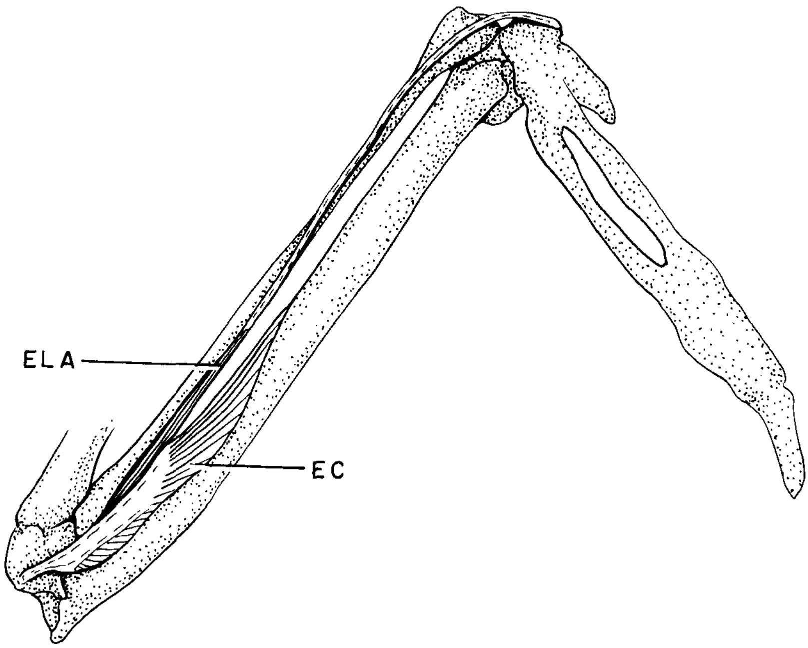

FIGURE 6. Deep dorsal muscles of the forelimb.

superficialis and flexor digitorum superficialis. It inserts by fleshy fibers, and, at its proximal and distal ends, by tendinous ones, on the medial surface of the radius, immediately deep to the insertion of M. pronator superficialis. The belly has the appearance of being bipennate, with two sets of fibers converging on an aponeurosis that covers part of the ventral surface of the belly.

On the right side of *Tyrannus melancholicus* CM 345, M. pronator superficialis was attached, at the distal end of its belly, to the distal end of the belly of M. pronator profundus. In addition, it had a long tendon of insertion that attached near the distal end of the forearm to the tendon of M. flexor digitorum profundus. The distal end of M. pronator profundus was also attached to this evidently extra tendon. This condition seems anomalous, as I did not observe anything like it on the left side or in other specimens.

In many passerines, M. pronator profundus originates from the humero-ulnar pulley as well as from the humerus. This is true of corvids (Hudson and Lanzillotti 1955), *Agelaius phoeniceus* (George and Berger 1966), *Dendroica kirtlandii* (Berger 1968), the "corvid assemblage" (Borecky 1977), most New World nine-primaried oscines (Raikow 1978), and 13 species of Estrildidae (Bentz 1979).

M. flexor carpi ulnaris (Fig. 9:FCU) is the most caudal muscle on the ventral surface of the forearm. It arises by a tendon from the cranioventral surface of the flexor process of the humerus. The tendon passes through the humero-ulnar pulley deep to M. expansor secundariorum and gives rise to a spindle-shaped belly. This belly extends half-way down the forearm, and inserts by a stout tendon on the Os ulnare. The humerocarpal band, which invests the belly of M. flexor carpi ulnaris and the tendon of insertion of Mm. flexor carpi ulnaris and flexor digitorum superficialis, sends tendinous branches to the base of the six outer secondaries (see description for M. flexor digitorum superficialis).

A smaller, accessory belly (FCU a) arises from the caudal surface of the proximal end of the main belly, and passes one-third of the way down the forearm, giving rise to a slender accessory tendon. This tendon is attached to the base of the six outer secondaries, not by simple, slender, tendinous bands as in *Loxops* (Raikow 1977), but broadly by a fibrous tissue, either muscular or elastic in composition.

The humero-ulnar pulley (trochlea humeroulnaris of Baumel et al. [1979]) (Fig. 11) arises by a narrow strap from the caudal surface of the ventral epicondyle of the humerus (pars humeralis accessoria). Two narrow straps arise on the flexor process of the humerus, one (not described by Bentz and Zusi 1982) passing deep to M. flexor carpi ulnaris and the other (pars humeralis), more delicate strap passing superficial to it. Both attach on pars humeralis near its junction with pars ulnaris. Pars ulnaris is a broad band that arises from the ventral surface of the proximal end of the ulna and attaches on the dorsal surface of the pulley.

A slender tendon, arising on the ulna prox-

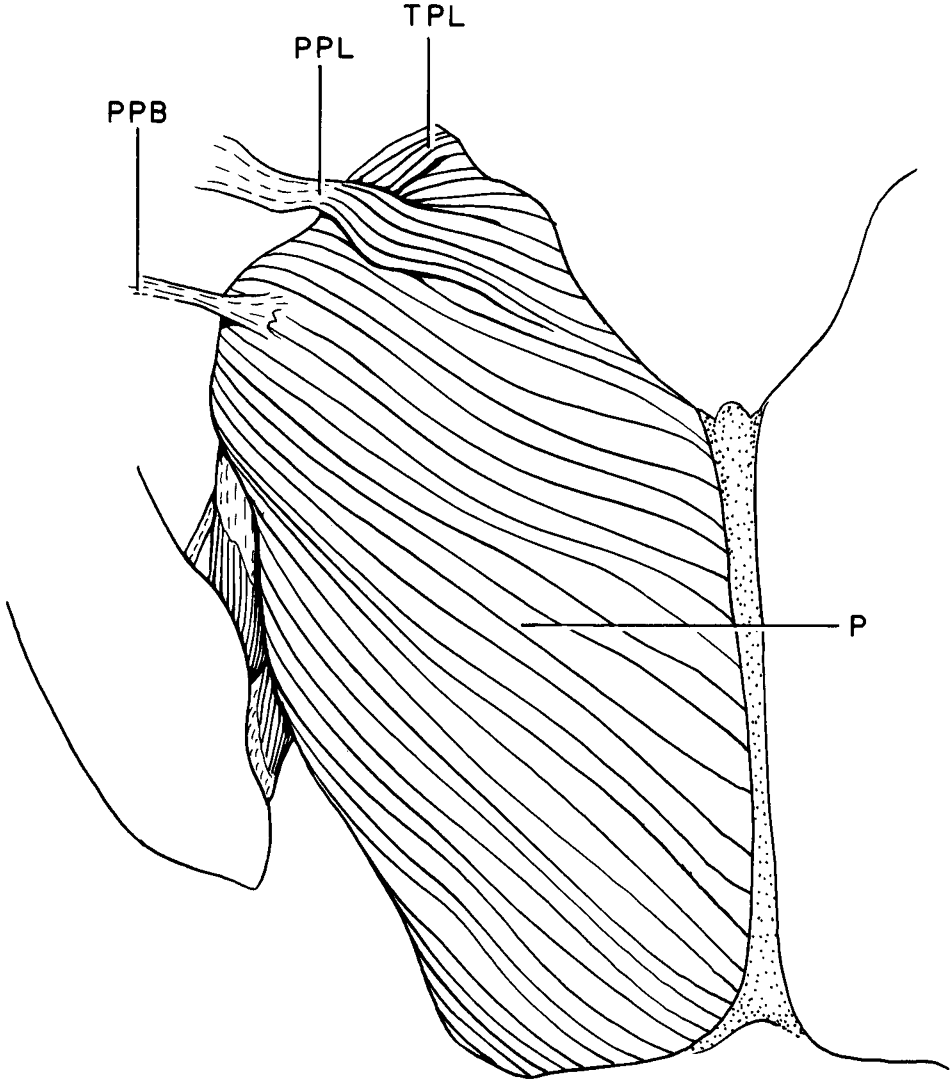

FIGURE 7. Superficial ventral muscles of the forelimb.

imal to the ulnar anchor of M. extensor metacarpi radialis, inserts on the deep surface of the humero-ulnar pulley (ligamentous sling of Bentz and Zusi [1982]).

M. flexor digitorum superficialis (Fig. 9:FDS) is a spindle-shaped muscle that arises by a stout tendon from the caudoventral surface of the flexor process of the humerus, distal to the origin of M. pronator profundus. It passes about one-third of the way down the forearm before giving rise to the tendon of insertion. This tendon is closely associated proximally with that of M. flexor carpi ulnaris via the humerocarpal band (described below). The tendon passes around the Os ulnare and across the manus to insert on the ventrodistal surface of the first phalanx of digit II.

The humerocarpal band arises on the medial epicondyle of the humerus as part of the origin of M. flexor digitorum superficialis. It partially envelops the belly and tendon of insertion of M. flexor digitorum superficialis and the main belly of M. flexor carpi ulnaris. With the tendons of those muscles, it passes across the Os ulnare, whence it sends tendinous branches to the base of the alula, to the bases of the first three primary remiges, to the distal end of the radius, and to ensheathe the tendon of insertion of Mm. flexor digitorum profundus and ulnometacarpalis ventralis at the point where these enter the manus.

This muscle is essentially the same in the other species that I examined, except that in *Legatus* and *Empidonomus,* the belly extends only about one-fourth of the way down the forearm.

M. flexor digitorum profundus (Fig. 9:FDP) is a spindle-shaped muscle along the ventral surface of the ulna caudal to M. pronator profundus and superficial to M. ulnometacarpalis

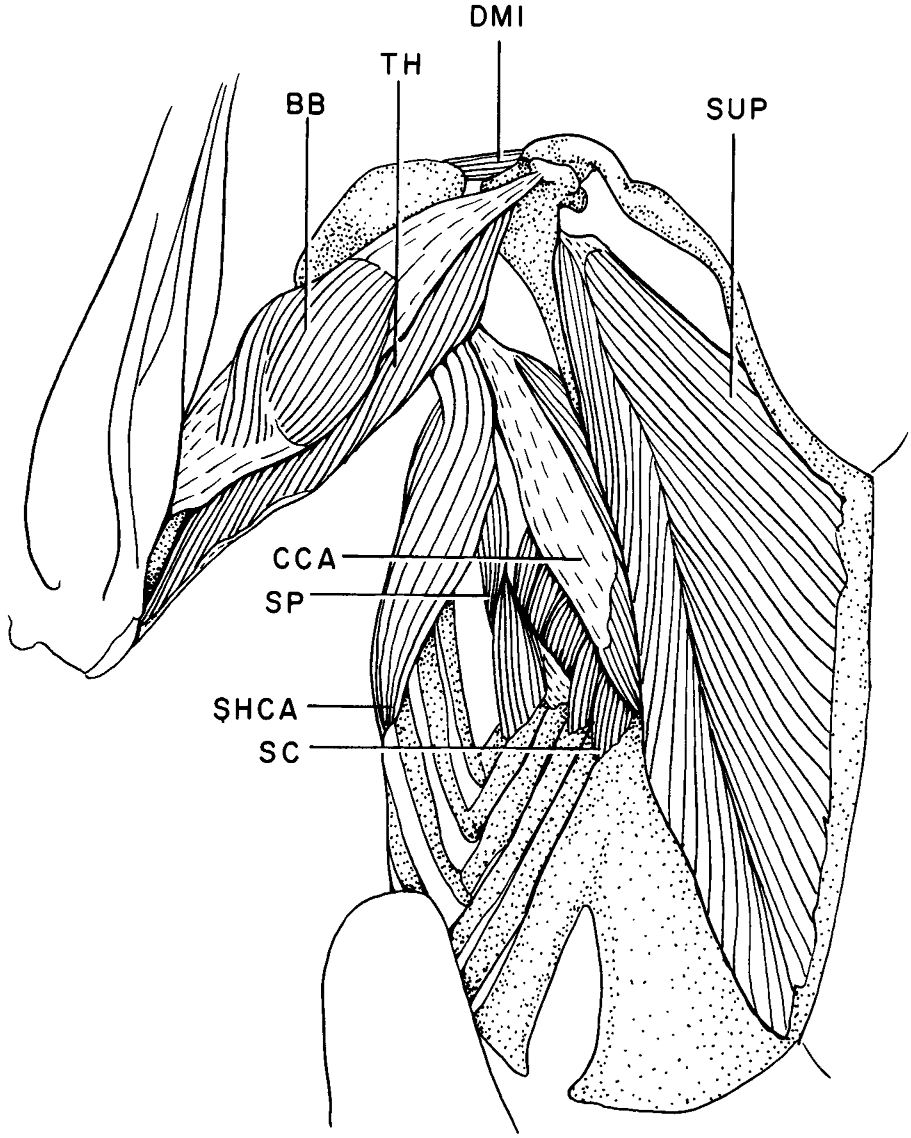

FIGURE 8. Second layer of ventral muscles of the forelimb.

ventralis. It arises fleshily by two heads from the proximoventral surface of the ulna, the dorsal head arising just distal to the ulnar insertion of M. biceps brachii. M. brachialis inserts between the two heads, and distal to this point, the two heads fuse. The single belly passes half-way down the forearm and gives rise to a tendon. The tendon passes around the Processus intermetacarpalis, deep to a ligament connecting the distal end of the radius and the Processes intermetacarpalis, then across the manus to insert on the proximal end of the second phalanx of digit II.

M. extensor metacarpi radialis (Fig. 9:EMR) is the most superficial muscle on the dorsal surface of the forearm. It is a large, bipennate muscle with four points of origin. The anconal belly arises by two distinct tendons on the Processus supracondylaris dorsalis, one (Tendon 1) from the dorsal surface and one (Tendon 2) from the caudal surface. The two tendons fuse a few millimeters distad to form a common belly. Pars intermedius arises by a tendon on the dorsocaudal surface of the Processus supracondylaris dorsalis, distal to the origin of Tendon 1 (see above), and by fleshy fibers in the intercondylar region between pars anconalis and pars palmaris (i.e., just ventral to the Processus supracondylaris dorsalis). Pars palmaris arises by fleshy and tendinous fibers in the intercondylar region just ventral to pars intermedius.

Pars intermedius fuses with pars palmaris about one-fourth of the way down the forearm,

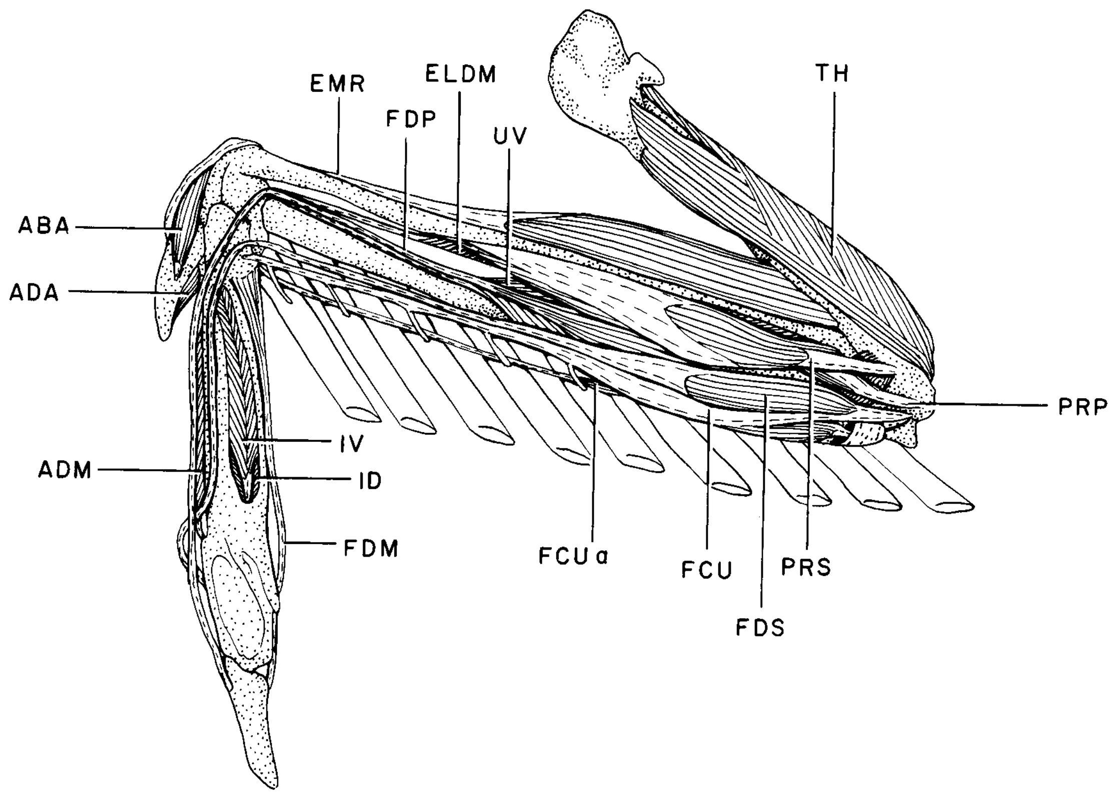

FIGURE 9. Third layer of ventral muscles of the forelimb.

but the point of attachment is narrow, and pars palmaris continues distad as a unipennate belly. Pars palmaris and anconalis fuse three-fourths of the way down the forearm and give rise to the common tendon of insertion. This tendon inserts on the Processus extensorius of the carpometacarpus.

This condition is similar to that in *Loxops virens* (although not noted as such by Raikow [1977]), with some exceptions. The intermediate head is considerably smaller in *Loxops* (pers. observ.). In *Loxops,* pars anconalis and pars palmaris are about equal in size at their origin, with pars intermedius barely visible in between. In *Tyrannus melancholicus* the fleshy origins of pars intermedius and of pars palmaris are about equally large and pars anconalis is relatively slender. Also, in that species, pars anconalis has no fleshy origin on the Processus supracondylaris dorsalis, only a dorsal tendinous one, while in *Loxops,* there are both a fleshy and a dorsal tendinous origin.

M. extensor digitorum communis (Figs. 4, 5:EDC) is a spindle-shaped muscle, caudal to M. extensor metacarpi radialis on the dorsal surface of the forearm. It arises by a tendon from the dorsal epicondyle of the humerus and the belly extends nearly half-way down the forearm before giving rise to the tendon of insertion. This tendon passes around the ulna and into the manus, bifurcating at digit I. The smaller branch inserts on the caudodorsal surface of the base of digit I; the main branch continues distad within the Sulcus tendineus of the carpometacarpus, passes over the distal end of the carpometacarpus with a sesamoid, and inserts on the dorsal surface of phalanx 1 of digit II.

The aponeurosis antebrachialis dorsalis arises on the dorsal epicondyle of the humerus, in common with M. extensor digitorum communis. It attaches along the distal two-thirds of the shaft of the radius, and ensheathes the bellies of Mm. extensor digitorum communis and extensor metacarpi ulnaris. The aponeurosis attaches to the bases of the follicles for the first eight secondary remiges, and then to the dorsal surface of the distal end of the radius.

M. extensor metacarpi ulnaris (Figs. 4, 5: EMU) is a bipennate muscle that arises by a tendon from the dorsal surface of the distal end of the humerus just cranial to the dorsal epicondyle, and by a broader tendon (the ulnar anchor) from the craniodorsal surface of the proximal end of the ulnar shaft. Arising just proximal to the ulnar anchor is a slender tendon that passes down to insert on the deep surface of the humero-ulnar pulley, the "ligamentous sling" of Bentz and Zusi (1982). It

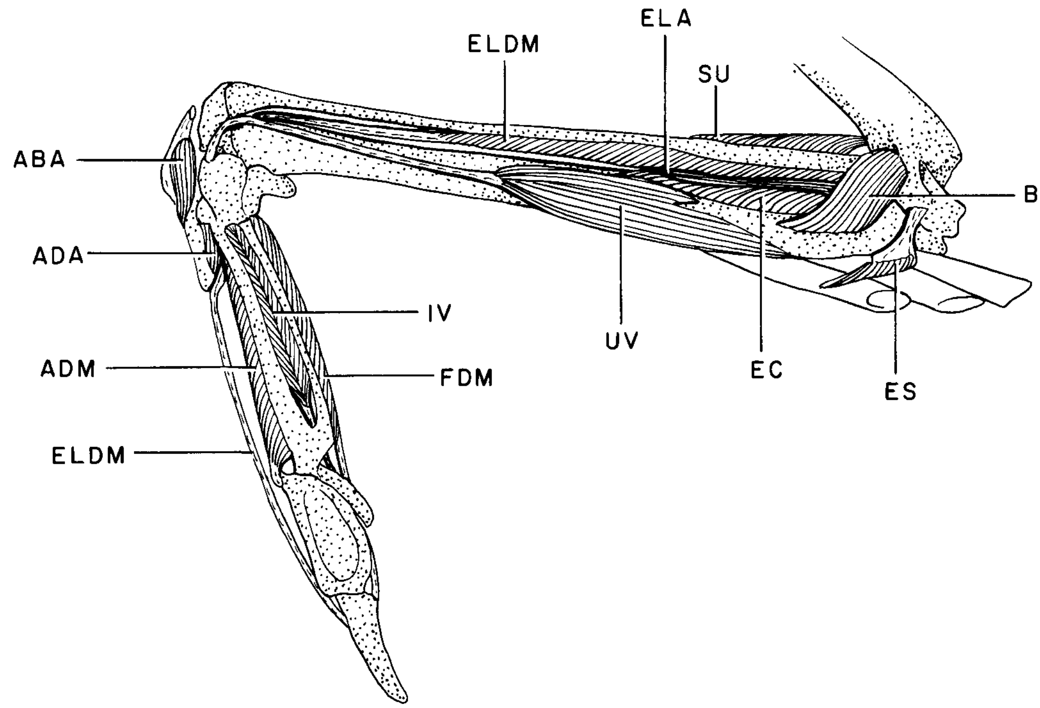

FIGURE 10. Deep layer of ventral muscles of the forelimb.

does not contain a sesamoid in these tyrannids, as it does in hummingbirds.

The single belly narrows to a tendon about two-thirds of the way down the shaft, and passes around the Tuberculum ventrale to insert on the carpometacarpus at the base of the minor metacarpal.

M. extensor longus alulae (Figs. 6, 10:ELA) is a tiny muscle, arising fleshily on the dorsolateral surface of the ulna medial to M. extensor longus digiti majoris. Half-way down the forearm, it gives rise to a hair-like tendon that passes distally along the ulna deep to the tendon of insertion of M. extensor metacarpi radialis, and inserts lateral to that tendon on the Processus extensorius of the carpometacarpus.

The inserting tendon of this muscle fuses with that of M. extensor metacarpi radialis for a common insertion on the carpometacarpus in *Fregilupus varius* and *Sturnus vulgaris* (Berger 1957) and *Agelaius phoeniceus* (George and Berger 1966). In other passerines reported in the literature, the two tendons are separate but closely associated, as in the tyrannids.

M. extensor longus digiti majoris (Figs. 4, 5, 9, 10:ELDM) is a narrow, bipennate muscle that arises fleshily on the caudodorsal surface of the proximal two-thirds of the shaft of the radius. It narrows to a tendon about three-fourths of the way down the shaft. The tendon passes around the distal end of the ulna into the manus to insert on the craniodorsal border of the base of phalanx 2, digit II.

M. supinator (Fig. 10:SU) is a narrow, fan-shaped muscle, arising by a slender tendon from the dorsal epicondyle of the humerus. It passes about one-fourth of the way down the radius and inserts fleshily on the craniodorsal surface of that bone.

M. ectepicondylo-ulnaris (Figs. 6, 10:EC) is a fan-shaped muscle that arises by a tendon from the craniodorsal surface of the dorsal condyle of the humerus. It passes across the elbow joint, giving rise to a long, narrow belly that extends about half-way down the cranioventral surface of the ulna and inserts fleshily on that bone.

M. ulnometacarpalis dorsalis (Fig. 4:UD) is a small, fan-shaped muscle, arising by a narrow tendon on the ligament ensheathing the distodorsal end of the ulna. It inserts fleshily on the proximocaudal surface of the minor metacarpal.

The muscle is absent in *Spizella arborea* (George and Berger 1966) and *Dendroica kirtlandii* (Berger 1968). George and Berger (1966) reported it to be present as a ligament in *Agelaius phoeniceus,* but Berger later (1969) claimed it to be absent in *Agelaius.* He may have been referring to a functional rather than an actual absence. He did not mention the muscle for *Paradisaea rubra* (Berger 1956) or *Fregilupus varius* (Berger 1957); in other lit-

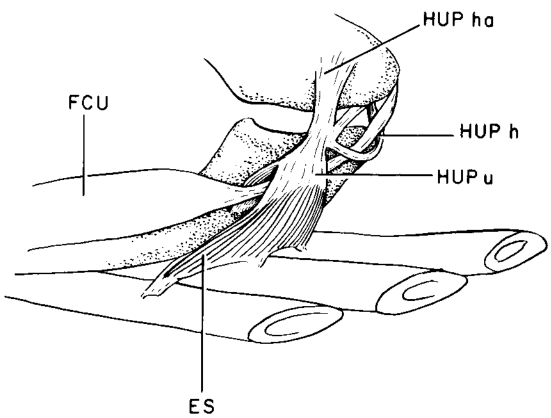

FIGURE 11. M. expansor secundariorum and humero-ulnar pulley.

erature on passerines, the muscle is reported as present, but always small.

M. ulnometacarpalis ventralis (Figs. 9, 10: UV) is an elongate, fan-shaped muscle along the ventral surface of the ulna deep to M. flexor digitorum profundus. It arises fleshily on the cranioventral surface of the proximal end of the ulna, and on the caudoventral surface of the ulna about one-third of the way down the shaft. This "double" origin gives the muscle the appearance of having two heads. The common belly extends to two-thirds of the way down the ulnar shaft, and its tendon of insertion arises as an aponeurosis on the ventral surface of the belly. The tendon passes over the ventral condyle of the ulna and with a sesamoid over the Os radiale. It inserts near the base of the Processus extensorius of the carpometacarpus.

M. ulnometacarpalis ventralis has a proximal and a ventral head of origin in *Dendroica kirtlandii* (Berger 1968), which is presumably an exaggeration of the condition described above.

M. interosseus dorsalis (Figs. 4, 9:ID) is a tiny, bipennate muscle, arising fleshily on the proximal margin of the interosseal space of the carpometacarpus and the surface of the alular and minor metacarpal. It is about one-third of the length of the adjacent M. interosseus ventralis. It narrows to a fine tendon that inserts on the dorsoproximal surface of the second phalanx of digit II.

M. interosseus ventralis (Figs. 4, 5, 9, 10:IV) is a tiny, bipennate muscle that arises fleshily on the proximal margin of the interosseal space and the margins of the alular, major, and minor metacarpals. It narrows to a fine tendon that passes over the dorsal surface of phalanx 1 of digit II, and inserts half-way down the caudodorsal margin of the second phalanx of digit II (it has the anchor of unknown composition, as described for *Loxops* by Raikow 1977).

M. abductor alulae (Figs. 9, 10:ABA) is a small, spindle-shaped muscle, arising fleshily on the ventral surface of the distal end of the inserting tendon of M. extensor metacarpi radialis. It passes ventral to the Processus extensorius of the carpometacarpus, giving rise to a fine tendon that inserts on the caudoventral surface of digit I.

M. adductor alulae (Figs. 4, 5, 9, 10:ADA) is a narrow, spindle-shaped muscle that arises fleshily at the base of the Processus extensorius of the carpometacarpus. It inserts fleshily on the caudal surface of digit I and on the inserting tendon of M. extensor digitorum communis.

M. abductor digiti majoris (Figs. 9, 10:ADM) is a tiny, fan-shaped muscle, arising fleshily on the cranioventral surface of the alular metacarpal. It extends the length of the cranial surface of the carpometacarpus, and inserts by a fine tendon on the base of the first phalanx of digit II.

M. abductor digiti majoris was reported to be "vestigial or absent in many passerine birds" (George and Berger 1966). It is absent in *Agelaius phoeniceus* (ibid), *Passer domesticus, Cardinalis cardinalis, Zonotrichia albicollis* and *Melospiza melodia* (Swinebroad 1954), and *Dendroica kirtlandii* (Berger 1968). It is "small and inconspicuous" in corvids (Hudson and Lanzillotti 1955), and rudimentary in *Paradisaea rubra* (Berger 1956). Borecky (1977) found the muscle in the "corvid assemblage," and Raikow (1977, 1978) found it in many oscines. Its presence may have been overlooked in some species because it is difficult to see without staining.

M. flexor digiti minoris (Figs. 9, 10:FDM) is a long, narrow, bipennate muscle that arises fleshily on the caudal surface of the minor metacarpal, and by a tendon on the distal end of the ulna. It extends the length of the carpometacarpus and inserts by a fine tendon on the caudal surface of digit III.

In *Agelaius phoeniceus,* this muscle has a tiny, deep head as well (George and Berger 1966).

DISCUSSION

My investigation confirms, for the group that I studied, that the suboscine forelimb musculature conforms to the passeriform pattern reported by other authors for the oscines. Differences among species in the forelimb muscles appear to occur primarily in M. latissimus dorsi caudalis. My survey of this muscle in passerines and nonpasserines suggests that its presence is the primitive condition in birds, and that it has been lost numerous times, especially within the Passeriformes. It has been lost repeatedly within the Tyrannidae as well. In the kingbird group, most species possess pars caudalis, but all members of *Myiozetetes* that I examined invariably lacked the muscle (15 specimens of *similis,* four *cayanensis,* one *granadensis,* one *luteiventris*), as did *Legatus leucophaius* (one specimen dissected), *Conopias trivirgata* (two dissected), and *Myiodynastes luteiventris* (four dissected). Of seven *Pitangus sulphuratus,* one specimen lacked it, as did two out of five specimens of *Myiodynastes maculatus.* Many tyrannids outside of the kingbird group lack the muscle. The species of *Myiozetetes* may indeed constitute a clade; however, it would be unsatisfying to cluster them with the other species that lack M. latissimus dorsi caudalis. This muscle is clearly prone to frequent, and probably independent, loss and, therefore, an unreliable basis for phylogenetic hypotheses. The individual variation in the occurrence of M. latissimus dorsi caudalis may represent a polymorphism in species undergoing loss of the muscle, an idea that I have explored elsewhere (McKitrick 1984).

Several features of the forelimb musculature of the kingbird group differ from those in other birds; these are the occurrence of a humeral anchor in M. scapulotriceps, three (rather than two) tendons of insertion of M. biceps brachii, and the condition of the humero-ulnar pulley and of M. extensor metacarpi radialis. The humeral anchor occurs in non-passerines and may be primitive for tyrannids, but the other features are probably derived at some level. Furthermore, the occurrence of a ligamentous sling between the ulnar shaft and the humero-ulnar pulley is apparently limited in its distribution, having been reported so far only in suboscines, Apodidae, and Trochilidae (Bentz and Zusi 1982). Future studies of tyrannids and other suboscines should pay particular attention to these character states to determine their utility for delineating clades within the suboscines. As I found virtually no variation in most of the forelimb muscles among the species that I examined, however, these muscles appear to be of little use for clarifying relationships within the kingbird assemblage.

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Department of Biological Sciences, University of Pittsburgh, Pittsburgh, Pennsylvania 15260. Present address: Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024. Received 22 October 1984. Final acceptance 27 March 1985.

The Condor 87:417

RECENT PUBLICATIONS

International registry of poultry genetic stocks/A directory of specialized lines and strains, mutations, breeds and varieties of chickens, Japanese quail and turkeys.—Ralph G. Somes, Jr. [1985] Bulletin 469, Storrs Agricultural Experiment Station, The University of Connecticut, Storrs. 96 p. Paper cover. $3.00. Source: Storrs Agricultural Experiment Station, Storrs, CT. This is the fifth edition of a reference for poultry fanciers and researchers who use poultry in their work. It is organized like its predecessor (noted in Condor 84:202), but has again been enlarged so as to include stocks from more suppliers. Incidentally, the registry demonstrates the major roles played by domesticated birds in studies of avian genetics.

Bobwhite thesaurus.—Thomas G. Scott. 1985. International Quail Foundation. 306 p. $29.95. Source: I.Q.F., P.O. Box 550, 206 Buncombe St., Edgefield, SC 29824. This is an indexed bibliography of *Colinus virginianus,* including more than 3,000 publications that were issued before 1983. The index is unusually thorough for works of this kind, as it comprises over 100 principal subject-categories and up to three levels of subordinate categories. Even the page references for each specific piece of information are given. The book is nicely made and has a color frontispiece by wildlife painter Bob Carey. It will be a useful tool for quail biologists and managers.

The Puffin.—M. P. Harris. 1984. T&AD Poyser, Carlton, England. 224 p. $32.50. Thirty years after Lockley's *Puffins,* here is a new book about *Fratercula arctica,* one of the most generally familiar and widely appealing of seabirds. It offers comprehensive treatment of the species' distribution, behavior, breeding and feeding biology, natural and man-caused threats to survival, and population dynamics. Material has been drawn from the author's own studies and those of other ornithologists at several island colonies in the north Atlantic and western Arctic waters. Commendably, the book manages to report a great deal of accurate and detailed information, yet in a readable, non-technical style. Various additional data are given in 20 tables at the back. The volume is well illustrated with maps, diagrams, monochrome photographs, and drawings by Keith Brockie. List of references, index. Harris is correct in saying that his book complements rather than supersedes Lockley's. Read the new book for up-to-date facts and analysis, and the old one for a vivid, admittedly personal, account of life in a puffin colony.

Ecogeographical variation in size and proportions of Song Sparrows (*Melospiza melodia*).—John W. Aldrich. 1984. Ornithological Monographs No. 35, American Ornithologists' Union, Washington, D.C. 134 p. Paper cover. $10.50 ($8.50 to AOU members). Source: Frank R. Moore, Department of Biology, University of Southern Mississippi, Southern Station Box 5018, Hattiesburg, MS 39406; all orders must be prepaid and include a $0.50 handling charge. In this monograph, Aldrich examines patterns of morphological variation in a species with a wide breeding range in order to learn their probable adaptive significance. Measurements and proportions of the wing, bill, tarsus, tail, and middle toe are correlated with certain ecological categories (Life Areas and Ecoregions) of North America. Multitudes of data are reported and analyzed. The patterns are, for the most part, clear and irrefutable, but the adaptive reasons behind them, while plausible, remain to be established. Aldrich concludes that "the ecological forces selecting adaptive genetic differences have a greater effect on morphological change or microevolution than do geographical separation or isolation." His rich findings should stimulate further research into the ways by which environmental factors influence the evolution of avian taxa. Maps, graphs, list of references, appendices.