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MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 85

The Myology of the Pectoral Appendage of Three Genera of American Cuckoos

BY

ANDREW J. BERGER

ANN ARBOR
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Corrigenda to The Myology of the Pectoral Appendage of Three Genera of American Cuckoos, by Andrew J. Berger

Miscellaneous Publications, Museum of Zoology, University of Michigan, No. 85, 1954.

p. 13. *M. dorsalis scapulae*, 3rd sentence. To read:

The fleshy fibers continue almost to the insertion, which is by a strong tendon on the proximal end of the anconal surface of the bicipital crest of the humerus.

p. 27. Osteology. 3rd sentence. To read:

Length of the manus (carpometacarpus plus digit II) is progressively shorter from *Coccyzus* to *Geococcyx;* a 12.9 per cent decrease from *Coccyzus* to *Crotophaga;* a 17.6 per cent decrease from *Coccyzus* to *Geococcyx.*

p. 28. 3rd sentence. To read:

We seem to be dealing with the loss of a "tendency to flight as a means of locomotion," rather than with a "progressive loss of flight ability."

p. 30. TABLE II. Second muscle from bottom, to read:

Extensor pollicis longus.

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ILLUSTRATIONS

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THE MYOLOGY OF THE PECTORAL APPENDAGE OF THREE GENERA OF AMERICAN CUCKOOS*

THE complete myology of the wing has been described for only one cuckoo, *Coua caerulea* (Berger, 1953). Fürbringer (1888) presented brief descriptions of certain wing muscles of *Phaenicophaeus, Zanclostomus*, and *Cuculus*. Marshall (1907) described the shoulder-girdle musculature of *Geococcyx californianus*, but her paper contains several errors and misconceptions.

The three genera reported in this paper were selected for study largely because of the marked differences in their locomotor habits. The Roadrunner (*Geococcyx californianus*) is a terrestrial bird with a running speed of 10 to 15 miles per hour (Hunt, 1920: 186-87; Sheldon, 1922: 180; Cottam and others, 1942: 131); it flies very little, using the wings chiefly as an aid in leaping and for volplaning. The Black-billed Cuckoo (*Coccyzus erythropthalmus*) is almost entirely arboreal and has a swift, graceful flight. The Groove-billed Ani (*Crotophaga sulcirostris*) is intermediate in habits, is as much at home on the ground as in trees, and uses its wings in short flights and long glides (Skutch, in Bent, 1940: 33). The two species of *Coccyzus* studied are migratory, as well as arboreal, birds. *Crotophaga* and *Geococcyx* are nonmigratory.

I dissected both wings of ten specimens of the Black-billed Cuckoo and four specimens each of the Roadrunner and the Groove-billed Ani. Generic names alone are given in the following descriptions, but unless otherwise specified, references are to the species just named. Five specimens of *Coccyzus americanus* exhibited the same myology as *C. erythropthalmus*, except for minor mensural differences.

The terminology of muscles follows Fisher (1946); that for bones follows Howard (1929). All dissection was done with the aid of a binocular microscope, x10 magnification.

No accurate method has been devised for correlating the size of muscles with their efficiency of action in different animals. Even when one overlooks the inaccuracies inherent in volumetric or total-length measurements, he still must recognize the fact that a knowledge of the gross morphology of a muscle does not necessarily explain the relative functioning of that muscle in birds of different locomotor habits. Muscles work in groups, not as isolated units. It is known, however, that a muscle can contract by one-third to one-half the total length of its individual fleshy fibers. Certain total-length measurements may, therefore, be useful in explaining differences in locomotor habits. Consequently, I have given exact measurements of certain muscles. Variation in length does occur, but I have been impressed by the small amount of variation found in the

*Accepted for publication November 5, 1953.

specimens I dissected. For measurements of bones in computing ratios I have used the average measurements given in my paper on the pelvic appendage of the same three genera (Berger, 1952).

DESCRIPTIONS OF MUSCLES

M. pectoralis superficialis (Fig. 1)

In all three genera (*Geococcyx, Crotophaga,* and *Coccyzus*) this is a large single muscle which covers Mm. supracoracoideus, coracobrachialis posterior, sternocoracoideus, the proximal part of biceps brachii, and most of coracobrachialis anterior. It is not divided into a superficial and a deep part (Fisher, 1946: 577). The muscle inserts on the ventral surface of the entire deltoid crest ("pectoral crest," Shufeldt, 1890: 70). The insertion is mostly fleshy, but is completely surrounded by a dense tendinous envelope. A very small fleshy fasciculus ("M. pectoralis pars propatagialis" of Gadow) splits off from the superficial surface of the belly. This fasciculus soon becomes tendinous and attaches to the distal end of the common belly of Mm. tensores patagii longus et brevis and to the tendon of M. tensor patagii longus. Gadow's "pars abdominalis M. pectoralis" ("M. dermo-humeralis" of Shufeldt, 1890: 13) is wanting.

In *Geococcyx* M. pectoralis superficialis ("pectoralis major," Shufeldt, 1886: 472; 1890: 69) arises from all but the anterobasal part of the carina, from a V-shaped area on the posterolateral aspect of the body of the sternum, from the internal lateral and external lateral xiphoid processes and the interxiphoidal membranes, and from the anterolateral and posterior surfaces of the furculum for almost its entire length (i.e., about 27 mm.). The belly extends dorsolaterad to the upper margin of the sternal ribs.

In *Crotophaga* this bulky muscle arises from all of the posterior 5 mm. of the carina, but from only the ventral third of the rest of the carina; from the posterolateral surface of the body of the sternum; from the xiphoid process (single) and membrane; from the sternocostal membrane, extending dorsad above the xiphoid process for a distance of 5 mm.; from the lateral and posterior surfaces of the furculum to within 3 mm. of the head; and from the coracoclavicular membrane adjacent to the furculum.

In *Coccyzus* this muscle arises from all of the posterior 4 mm. and from the ventral half of the rest of the carina; from the posterolateral aspect of the body of the sternum; from the two xiphoid processes; from the interxiphoidal membranes; from the sternocostal membrane, extending dorsad above the lateral margin of the sternum for a distance of 4 mm.; from the lateral and posterior aspects of the furculum to within 4 mm. of the head; and from an area about 3 mm. wide on the coracoclavicular membrane adjacent to the furculum.

M. supracoracoideus (Fig. 2)

In *Geococcyx* this muscle ("pectoralis secundus," Shufeldt, 1886: 472) arises from the anteromedial half of the body of the sternum and base of the carina; from the sternal half (14 mm.) of the coracoid on its anterior and anteromedial surfaces; from the lower two-thirds of the coracoclavicular membrane, extending from the coracoid to the clavicle; and from the posterior face of the sternal end of the clavicle (about 10 mm.). The tendon forms on the deep, coracoidal aspect, but the belly remains fleshy as it passes anterodorsolaterad through the triosseal canal. The short, stout tendon inserts on the anterior edge of the humerus at the junction of articular head and deltoid crest. The tendon is covered superficially by M. coracobrachialis anterior. Laterally the belly is in contact with M. coracobrachialis posterior, and superficially both muscles are covered completely by M. pectoralis superficialis.

In *Crotophaga* this muscle arises from the anteromedial three-fourths of the body of the sternum, from the basal two-thirds of the anterior half of the carina, from the medial and posterior surfaces of the coracoid in its basal 12 mm., and from the basal 12 mm. of the coracoclavicular membrane. Superiorly, a fleshy component, arising from the coracoid, overlaps the tendon in its course through the triosseal canal and extends nearly to the insertion. Insertion is the same as in *Geococcyx*. The tendon, however, is not covered by M. coracobrachialis anterior, and its area of insertion is anterior to that of M. deltoideus minor.

In *Coccyzus* M. supracoracoideus arises from a triangular area on the anteromedial surface of the body of the sternum and extends caudad to within 4.5 mm. of the caudal end of that bone, from a triangular area on the base of the carina, from the basal 9 mm. of the anteromedial aspect of the coracoid, and from the basal 14 mm. of the coracoclavicular membrane, but it does not arise from the furculum. Forming on the lateral margin of the belly, the tendon passes through the triosseal canal and inserts as in *Crotophaga*. Fleshy fibers from the medial part of the belly surround the tendon and extend with it to the insertion. The tendon is not covered by the belly of M. coracobrachialis anterior.

M. coracobrachialis posterior (Fig. 2)

This muscle ("pectoralis tertius," Shufeldt, 1886: 472) arises from the sternocoracoidal process of the coracoid, from the lateral and posterior surfaces of approximately the basal half of the coracoid, and from the inner surface of the coracoclavicular membrane (except in *Coccyzus*) adjacent to the coracoid. It inserts by a short, stout tendon on the internal tuberosity of the humerus. This insertion is in a pit on the apex of the tuberosity in *Geococcyx* and *Crotophaga* and on the capital groove surface of the tuberosity in *Coccyzus*.

M. latissimus dorsi (Fig. 3)

This is the most superficial muscle complex on the dorsum and is, in reality, two muscles plus a dermal component. Near the junction of the distal and middle thirds of the bellies pars posticus swings deep to pars anticus, and the two parts enter the arm musculature between Mm. scapulotriceps and humerotriceps. The general structure is similar in the three genera, but there are differences in extent of origin and in the relationships of the tendons of insertion.

In *Geococcyx* the anterior, sheetlike part (pars anticus) arises from a mid-line aponeurotic raphe attached to the neural spines of the last three cervical and the first two dorsal vertebrae, but from the anterior tip only of dorsal vertebra No. 2. The posterior, much heavier, part (pars posticus) arises from the neural spines of dorsal vertebrae Nos. 2 and 3.

Pars anticus inserts by a broad (7 mm. wide), flat tendon on the shaft of the humerus, beginning about 10 mm. inferior to the junction of articular head and deltoid crest and anterior to the area of origin of the internal head of M. humerotriceps. Pars posticus inserts by a strong, round tendon on the anconal surface of the humerus about 10 mm. distal to the proximal end of that bone and immediately distal to the area of insertion of M. proscapulohumeralis and between the uppermost fibers of origin of the two heads of M. humerotriceps. Thus, the areas of insertion of pars anticus and pars posticus are separated by the area of origin of the internal head of M. humerotriceps.

A small dermal component arises from the surface of pars posticus in the region of the spine of dorsal vertebra No. 2. The small, straplike belly (1.5 mm. wide) passes forward, upward, and outward to insert into the skin adjacent to the insertion of the dermal component of M. serratus posterior at the posterior margin of the humeral feather tract.

In *Crotophaga* pars posticus is less bulky than in *Geococcyx,* and the anterior margin is more closely applied to the posterior margin of pars anticus. Pars anticus arises by a mid-line raphe from the neural spines of the last two cervical and the first dorsal vertebrae. Pars posticus arises by an aponeurosis from the spines of the first three dorsal vertebrae.

Pars anticus inserts by a short, thin aponeurosis (4 mm. wide) on a ridge at the base of the deltoid crest, beginning about 3 mm. inferior to the junction of articular head and deltoid crest. About 12 mm. caudal to the area of insertion pars posticus swings deep to the belly of pars anticus. A thin, bandlike aponeurosis, about 1.5 mm. wide and 5 mm. long, continues the course of the posterior belly and inserts immediately posterior to the proximal part of the tendon of pars anticus; both tendons insert on the same ridge, and both areas of insertion begin 3 mm. inferior to the junction of humeral head and deltoid crest. Since the tendon of pars posticus inserts anterior to the internal head of M. humerotriceps, not posterior to it as in *Geococcyx,* the tendon of pars posticus has no close relationship to the insertion of M. proscapulohumeralis. A small dermal component has the same relationships as in *Geococcyx.*

In *Coccyzus* pars anticus is less developed than in the other genera. It arises by an aponeurosis from the neural spines of the last cervical vertebra (No. 14 in one specimen; No. 13 in all others dissected) and the first dorsal vertebra. Pars posticus arises from the spines of dorsal vertebrae Nos. 2 and 3. Pars anticus inserts on the humerus, primarily by a thin fleshy band (3 mm. wide), beginning 6 mm. inferior to the junction of articular head and deltoid crest. Pars posticus inserts by a strong, flat tendon (4 mm. long and 1 mm. wide), proximal to, and continuous with, the tendon of insertion of pars anticus. The dermal component has the same relationships as in *Geococcyx.*

M. rhomboideus superficialis (Figs. 3, 4)

Shufeldt (1890: 82) called this muscle the trapezius. Howell (1937: 365), however, stated: "Birds have no spinal accessory nerve"; therefore, none of the superficial back muscles can be considered homologous to the mammalian M. trapezius. On the other hand, Ariëns Kappers, Huber, and Crosby (1936, 1: 619) commented: "The mammalian spinal accessory nerve probably is represented in avian and reptilian forms by the fibers of von Lenhossék." Further research will be necessary to determine whether the muscles innervated by these fibers are homologous with the trapezius and sternocleidomastoid complex of mammals.

In each genus the fibers of this muscle run forward and outward to insert fleshy on the dorsomedial surface of the scapula in its cranial four-fifths, beginning on the acromion process: 34 mm. in *Geococcyx,* 24 mm. in *Crotophaga,* 19 mm. in *Coccyzus.* The posterior part of the muscle is covered by M. latissimus dorsi pars anticus, but the anterior part lies immediately deep to skin and to the superficial fascia.

In *Geococcyx* this muscle arises primarily by an aponeurosis from the neural spines of the last four cervical vertebrae (Nos. 11-14) and the first dorsal vertebra. The anterior one-fifth of the origin is fleshy. The muscle is about 24 mm. wide at its origin and is 10 mm. long.

In *Crotophaga* it also arises primarily by an aponeurosis from the neural spines of the last four cervical vertebrae (Nos. 11-14) and the first dorsal vertebra. A few fibers insert on the posteromedial surface of the furcular head inferior to the area of origin of M. tensor patagii brevis. The muscle is 17 mm. wide at its origin and 5 mm. in length.

In *Coccyzus* this muscle arises from the neural spines of the last three cervical vertebrae (Nos. 11-13 normally; 12-14 in one specimen) and the first two dorsal vertebrae. A few fibers insert on the head of the furculum as in *Crotophaga.* The belly is 18 mm. wide at its origin and 5 mm. in length.

M. rhomboideus profundus (Fig. 4)

Whereas the fibers of M. rhomboideus superficialis pass forward and outward, those of the profundus pass backward and outward to insert fleshy on the dorsomedial edge of the caudal part of the scapula. The muscle is overlapped in its anterior half by the fibers of M. rhomboideus superficialis. Anteriorly, the insertion overlaps the most posterior fibers of insertion of M. serratus profundus.

In *Geococcyx* and *Crotophaga* M. rhomboideus profundus arises fleshy from the neural spines of the last three cervical and the first two dorsal vertebrae. In *Coccyzus* it arises from the neural spines of the last two cervical vertebrae (Nos. 12-13 normally; Nos. 13-14 in one specimen) and the first two dorsal vertebrae. It inserts on slightly less than the posterior half of the scapula in *Geococcyx,* on the posterior half in *Crotophaga,* and on somewhat more than the posterior half in *Coccyzus.*

M. coracobrachialis anterior (Fig. 2)

This muscle shows a progressive reduction in development from *Geococcyx* to *Coccyzus*.

In *Geococcyx* this large bulky muscle ("coracohumeralis," Shufeldt, 1890: 86) is situated primarily on the ventral surface of the scapulohumeral joint, but its belly extends around to the anconal surface of the humeral head and lies in contact with M. deltoideus minor; the two bellies completely cover the tendon of insertion of M. supracoracoideus. The belly is about 11 mm. long and 7 mm. in maximum width at its insertion on the ventral surface of the humerus immediately distal to the head and between the areas of insertion of Mm. pectoralis superficialis and supracoracoideus. M. coracobrachialis anterior arises semitendinous from the anterolateral aspect of the head of the coracoid dorsal to the origin of M. biceps brachii, but posteriorly the belly is overlapped by the long tendon of origin of the latter muscle.

In *Crotophaga* this muscle is less developed than in *Geococcyx* in that the belly does not cover the anterior edge of the humerus and, consequently, does not cover the tendon of M. supracoracoideus. The muscle is 9 mm. long and about 5 mm. wide at its insertion just distal to the humeral head. It arises by mixed tendinous and fleshy fibers from the head of the coracoid.

In *Coccyzus* this muscle is about 5 mm. long and 4 mm. wide at its insertion, but it is a much thinner muscle, absolutely and relatively, than in the other genera. It is similar to *Crotophaga* in areas of origin and insertion.

M. tensor patagii brevis (Figs. 1, 3)

Shufeldt (1886: 470-71 and Pl. 43) described and illustrated this muscle in *Geococcyx californianus*. In this genus M. tensor patagii brevis is a strap-shaped muscle which arises fleshy from the superomedial surface of the furculum. The belly is about 24 mm. long and 5 mm. in maximum width and is, except near the distal end, completely fused with M. tensor patagii longus; it lies superficial to M. deltoideus minor. The tendon of M. tensor patagii brevis passes distad parallel to the humerus. Its main attachment is by a strong band, 1 mm. wide, on the belly of M. extensor metacarpi radialis, about 10 mm. distal to the humeral origin of that muscle. A small tendon arising at right angles to the main attachment runs proximad to the lateral supracondylar ridge where it attaches superficial to the tendon of origin of M. extensor metacarpi radialis. The remainder of the tendon of the brevis fans out posteriorly over the other muscles of the anconal surface of the forearm and fuses with the antibrachial fascia.

In *Crotophaga* the belly of M. tensor patagii brevis is about 16 mm. long and 5 mm. wide. Its origin is semitendinous from the medial aspect of the furcular head. Six millimeters distal to the lateral supracondylar ridge the main tendon of the brevis fuses at right angles with a very dense, flat band which attaches to the lateral supracondylar ridge. Distal to the point of fusion this band fans out and gives origin on both its surfaces to fleshy fasciculi of M. extensor metacarpi radialis. Thus, the relationship of the brevis tendon to M. extensor metacarpi radialis is different from that in *Geococcyx*. A thinner, more superficial part of the brevis tendon complex fuses with the antibrachial fascia.

In *Coccyzus* the fleshy belly of this muscle is 13 mm. long and 5 mm. wide. It arises as in *Crotophaga*. As it passes over the proximal end of the belly of M. extensor metacarpi radialis, part of the tendon fuses with that muscle about 5 mm. from its origin, but the main tendon runs proximad, to insert on the ectepicondylar process of the humerus superficial to the tendon of origin of M. extensor metacarpi radialis. Thus, the insertion is similar to that in *Crotophaga*, but the tendon is partly fused with the superficial fascial envelope of M. extensor metacarpi radialis. A dense fascial sheet is given off from the posterior margin of the main tendon and fuses with the antibrachial fascia; a secondary attachment is made to the tendinous origin of M. extensor digitorum communis. As in the other genera, a strong tendinous band arising from M. pectoralis superficialis inserts on the distal end of the belly of M. tensor patagii brevis.

M. tensor patagii longus (Figs. 1, 3)

In *Geococcyx* a short fibrous band (about 8 mm. long) enters the anterior edge of the propatagium at the distal end of the common belly of Mm. tensores patagii longus et brevis. From this fibrous part a thin round tendon forms and runs in the leading margin of this fold. Upon reaching the distal end of the radius the tendon fans out and becomes continuous with the deep fascia covering the anconal and palmar surfaces of the wrist and hand, including especially the bases of the alula feathers and the proximal primaries. There is a minor attachment to the posteropalmar tip of the extensor process of metacarpal I. A small tendinous slip from M. pectoralis superficialis fuses with the fibrous part of M. tensor patagii longus.

In *Crotophaga* the bellies of the two tensors of the patagium also are completely fused except at the distal end, where two short muscular tongues form. From one of these short muscle tongues a fibrous tendon (about 1.5 mm. wide) runs distad in the propatagium. The insertion is like that in *Geococcyx*.

In *Coccyzus* at the distal end of the common belly a short tongue of muscle gives rise to a relatively wide (1 mm.) fibroelastic band, which runs distad in the anterior patagial fold for a distance of 14 mm. and then tapers to a fine tendon. The insertion is like that in *Geococcyx*.

M. deltoideus major (Figs. 1, 3, 4)

The major deltoid muscle exhibits a uniformity of development among the three genera. It arises by two heads, but has a single insertion which is tendinous only in its most distal area.

In *Geococcyx* the larger part of this bulky muscle arises fleshy and tendinous from the lateral surface of the acromion process of the scapula over a distance of about 6 mm. The area of origin lies immediately cephalad to the origin of M. scapulotriceps and inferior to the origin of M. deltoideus minor. The smaller muscular head arises from the os humeroscapulare, a small sesamoid found in the anconal part of the capsule of the scapulohumeral joint. The two heads fuse almost immediately and insert by fleshy fibers on the anconal surface of the deltoid crest and on the shaft of the humerus for a total distance of 26 mm. The total length of the fleshy belly is about 35 mm.

In *Crotophaga* the separation of the two heads proximally is somewhat more distinct than in *Geococcyx* or *Coua caerulea*. The origin of the two heads is similar, however, to their origin in those genera. Fibers from the short head insert primarily on the deltoid crest, whereas the fused belly inserts on the humeral shaft for a distance of 14 mm. distal to the crest, making a total distance of insertion of 17 mm. The over-all length of the belly is 25 mm.

In *Coccyzus* the larger head arises fleshy from the lateral surface of the acromion process for a distance of about 3 mm. and, by a tough tendinous band, from the anteroinferior edge of the acromion process. The smaller head arises from the os humeroscapulare. The belly inserts primarily by fleshy fibers on the deltoid crest and on the humeral shaft for a total distance of 15 mm. The over-all length of the belly is 22 mm.

M. deltoideus minor (Fig. 4)

In *Geococcyx* this muscle ("scapulohumeralis," Shufeldt, 1890: 86) is a short, straplike muscle, 10 mm. long, lying between Mm. deltoideus major and coracobrachialis anterior. It is covered superficially by M. tensor patagii brevis, and it covers the tendon of M. supracoracoideus. It arises fleshy from the lateral surface of the acromion process. It inserts into a small depression at the junction of the humeral head and the deltoid crest, where it lies adjacent to the tendon of insertion of M. supracoracoideus.

In *Crotophaga* this straplike muscle is 8 mm. long. It arises from the lateral surface of the tip of the acromion process and passes outward to insert as in *Geococcyx*.

This muscle is absent in *Coccyzus erythropthalmus* and in *C. americanus*.

M. proscapulohumeralis (Figs. 3, 4)

This short, straplike muscle ("supraspinatus," Shufeldt, 1890: 88) arises on the lateral surface of the scapula immediately caudal to the glenoid fossa, between the area of origin of M. scapulotriceps and the external head of M. subscapularis, and ventral to the area of insertion of M. rhomboideus superficialis. The muscle is fleshy throughout. The belly crosses superficial to the tail of M. subscapularis.

In *Geococcyx* M. proscapulohumeralis arises fleshy from a small area (7 mm. wide); in *Crotophaga* and *Coccyzus* the area of origin is about 2 mm. wide. The belly is about 9 mm. long in *Geococcyx* and about 7 mm. in *Crotophaga* and *Coccyzus*. It inserts entirely by fleshy fibers in the pneumatic fossa, beginning immediately distal to the pneumatic foramen and, in *Geococcyx*, extending to the insertion of M. latissimus dorsi pars posticus. It is in contact posteriorly with the external head of M. humerotriceps and anteriorly with the internal head of that muscle.

M. subscapularis

This bulky muscle arises by two fleshy heads which are separated by the tendon of insertion of the anterior fasciculus of M. serratus posterior. The superficial, or external, head arises from the lateral surface of the scapula, beginning immediately caudal to the origin of M. proscapulohumeralis, but with a few fibers arising dorsal to that origin. The deep or internal head arises primarily from the medial surface of the scapula, beginning on the acromion process (except in *Geococcyx*). The two heads fuse and insert by a short, stout tendon on the proximal surface near the base of the internal humeral tuberosity ("ulnar tuberosity," Shufeldt, 1890: 102). The insertion does not extend into the capital groove as in the Cathartidae (Fisher, 1946: 584).

In *Geococcyx, Crotophaga,* and *Coccyzus* the external head arises fleshy from an area 9, 5, and 6 mm. long, respectively. In *Geococcyx* the internal head arises for a distance of 19 mm., beginning 6 mm. caudal to the acromion tip. The internal head arises from an area 15 and 11 mm. long, respectively, in *Crotophaga* and *Coccyzus.*

M. dorsalis scapulae (Figs. 3, 4)

This well-developed muscle is similar in form and structure in the three genera. It arises by fleshy fibers from most of the lateral and ventral surfaces of the posterior part of the scapula. The fleshy fibers continue almost to their insertion by a strong tendon on the proximal end of the anconal surface of the bicipital crest of the humerus. Anteriorly, the belly overlaps the posterior margin of the external head of M. subscapularis. The posteriormost part of the belly is visible before M. latissimus dorsi pars posticus is reflected.

In *Geococcyx* this muscle ("teres et infraspinatus," Shufeldt, 1890: 90) arises fleshy and semitendinous from slightly less than the posterior half (20 mm.) of the blade of the scapula. Some proximal fibers of origin of the external head of M. humerotriceps arise on either side of the tendon of insertion.

In *Crotophaga* the muscle arises from slightly more than the posterior half (16 mm.) of the scapula and in *Coccyzus* it arises from slightly less than the posterior two-thirds (15 mm.) of the scapula. The fibers of origin of the external head of M. humerotriceps do not surround the tendon of insertion as they do in *Geococcyx.*

M. sternocoracoideus (Fig. 2)

This muscle ("subclavius" of Shufeldt, 1890: 94) is similar in all respects in the three genera. It arises by fleshy fibers from the entire lateral surface of the sternocoracoidal process of the sternum, and it inserts on the sternocoracoidal impression on the posterior surface of the base of the coracoid.

M. subcoracoideus (Fig. 2)

This muscle ("coracobrachialis," Shufeldt, 1890: 95) arises by two separate heads: one coracoidal and the other furcular. The two heads fuse and insert by a common tendon on the anconal surface of the internal tuberosity of the humerus immediately proximal to the humeral attachment of M. biceps. Although this muscle exhibits considerable variation in different groups of birds, a furcular origin is apparently uncommon (Gadow and Selenka, 1891: 238).

In *Geococcyx* the coracoidal head consists of a short (7 mm. long), flat band of fleshy fibers which arises from the posterior face of the coracoid and from the coracoclavicular membrane about 16 mm. inferior to the head of the coracoid. The larger, furcular, head arises fleshy from an area 8 mm. long on the medial surface of the head of the furculum, beginning inferior to the level of origin of M. tensor patagii brevis.

In *Crotophaga* the coracoidal head is 8 mm. in length. It arises entirely from the inner surface of the coracoclavicular membrane adjacent to the coracoid. The furcular head arises for a distance of 5 mm.

In *Coccyzus* the coracoidal head is triangular in shape, 3 mm. wide at its base and 8 mm. in length. It arises entirely from the coracoclavicular membrane, beginning immediately above the insertion of M. sternocoracoideus. The furcular head arises for a distance of 4 mm.; as in *Crotophaga,* this origin is continuous with the anterior fibers of M. subscapularis.

M. serratus posterior

M. serratus posterior ("serratus magnus anticus," Shufeldt, 1890: 92) forms a single layer in these cuckoos, not two layers as in the Cathartidae (Fisher, 1946: 586) and some other birds. A dermal component is present.

In *Geococcyx* this muscle arises by three separate and roughly rectangular slips. The first slip arises partly tendinous for a distance of 7 mm. from the anterolateral surface of the last cervicodorsal rib, inferior to the uncinate process. The second and third slips arise from the first and second true ribs, on the lateral surfaces of the uncinate processes and of the ribs inferior to them, for a total distance of 9 mm. The two anterior slips converge and give rise to a flat aponeurotic sheet which inserts on the ventral margin of the posterior three-fourths of the scapula. Anteriorly, this sheet passes between the two heads of origin of M. subscapularis. The most posterior slip inserts fleshy on the apex of the scapula for a distance of about 5 mm.

The dermal component arises from the first true rib inferior to the uncinate process. Its straplike belly passes upward and forward to attach to the skin at the posterior margin of the humeral feather tract, immediately posterior to the area of insertion of the dermal component of M. latissimus dorsi.

In *Crotophaga* the anterior, rectangular, fleshy fasciculus arises from the last cervicodorsal rib, inferior to the uncinate. It inserts by a thin, but dense, aponeurosis (4 mm. wide and 2 mm. long) on the ventrolateral edge of the scapula, after having passed between the two heads of M. subscapularis. The bulk of the fleshy belly arises from the uncinate processes of the first three dorsal ribs. The fasciculi fuse and insert by fleshy fibers on the apex of the scapula, but anteriorly give way to a thin aponeurosis which inserts on the ventral edge of the scapula. The dermal component arises fleshy from the third dorsal rib, inferior to the uncinate, and inserts as in *Geococcyx*.

The origin, structure, and insertion of M. serratus posterior in *Coccyzus* are similar to those in *Crotophaga*.

M. serratus anterior

In *Geococcyx* this muscle ("serratus parvus anticus," Shufeldt, 1890: 104) arises from the transverse process of cervical vertebra No. 12 and from the last cervicodorsal rib at about the mid-point of the rib. Fibers of both parts pass caudolaterad to insert fleshy for a distance of 12 mm. on the dorsomedial surface of the scapula near the apex, deep to the insertion of M. rhomboideus profundus and caudal to the insertion of M. serratus profundus.

In *Crotophaga* this muscle arises by two broad fasciculi, one from the last cervicodorsal rib, dorsal to the uncinate, and one from the penultimate cervicodorsal rib near the rib angle. Insertion is fleshy on the apex of the scapula for a distance of 6 mm., beginning immediately caudal to the insertion of M. serratus profundus.

In *Coccyzus*, too, the muscle arises by two broad slips (3 mm. and 4 mm. wide), one from the last cervicodorsal rib, dorsal to the uncinate, and one from the first true rib, also dorsal to the uncinate. The fibers of this muscle and those of M. serratus profundus form a continuous insertion on the medial aspect of the scapula, beginning about 10 mm. caudal to the acromion process and extending to the apex.

M. serratus profundus

This is "M. levator scapulae" of Shufeldt (1890: 98), but Howell (1937: 368) stated: "No bird, so far as I am aware, possesses a true levator scapulae arising from the more cranial of the cervical vertebrae. . . ."

In each of the three genera M. serratus profundus arises mostly by fleshy fibers from the transverse processes of certain of the posterior cervical vertebrae. The fibers pass caudolaterad to insert fleshy on the medial surface of the scapula, beginning somewhat anterior to the middle of that bone and extending caudad to the area of insertion of M. serratus anterior. The area of insertion lies ventral to the insertion of M. rhomboideus profundus.

In *Geococcyx* and *Crotophaga* M. serratus profundus arises by several fleshy fasciculi from cervical vertebrae Nos. 10, 11, and 12. The area of insertion begins 15 mm. and 11 mm., respectively, caudal to the acromion tip and extends caudad for 14 mm. and 12 mm.

In *Coccyzus* this muscle arises by two fasciculi from the transverse processes of cervical vertebrae Nos. 10 and 11. The insertional area begins 10 mm. caudal to the acromion tip and extends caudad for a distance of 3.5 mm.

M. biceps brachii (Figs. 1, 2)

Origin and insertion of this muscle are similar in the three genera. The origin is by an L-shaped tendinous sheet which takes attachment to the lateral surface of the head of the coracoid and to the proximal end of the bicipital crest near the base of the internal tuberosity of the humerus. The coracoidal part of the tendon is much stronger than the humeral part. The biceps slip to the tendon of M. tensor patagii longus is wanting in each of the three genera.

The length of the fleshy belly in *Geococcyx* is 30 mm. A short distance (about 5 mm.) proximal to the head of the radius the stout tendon bifurcates. The two tendons insert on the bicipital tubercles of the radius and ulna, 1 mm. and 3 mm., respectively, from the proximal articular surfaces of those bones.

In *Crotophaga* the belly is 22 mm. in length. The tendon bifurcates at a point 4 mm. superior to the head of the radius. The two tendons insert 1 mm. from the proximal articular surfaces of the radius and ulna.

The fleshy belly is 20 mm. long in *Coccyzus*. The coracoidal head is much stronger than in the other genera; the humeral origin from the base of the internal tuberosity is a thin fascial sheet. The tendon bifurcates about 6 mm. superior to the radial head. The two tendons insert as in *Crotophaga*.

M. triceps (Figs. 1, 2, 3)

There are minor differences in relationships, but for the most part this muscle exhibits the same relative development and structure in the three genera. M. triceps has two major parts, a scapulotriceps and a humerotriceps. The scapulotriceps (or scapular head) arises tendinous and also by a flat muscular band from the lateral surface of the scapula, on the posterior margin of the glenoid lip. The two heads of the humerotriceps arise from nearly the entire posterior extent of the humeral shaft. The internal and external heads of the humerotriceps are separable only at their proximal origins, where they form a V-shaped pattern, one head situated on either side of M. proscapulohumeralis. Fusion of the two heads begins at the distal end of the area of insertion of M. proscapulohumeralis.

The external head arises from the anconal surface of the bicipital crest, from the lateral crest of the pneumatic fossa, and from nearly the entire humeral shaft distal to these crests. In *Geococcyx* some fibers of the external head arise on either side of the insertional area of M. dorsalis scapulae; this is not true in *Crotophaga* and *Coccyzus*. In *Geococcyx* the origin of the internal head begins immediately proximal to the insertion of M. latissimus dorsi pars posticus and the lowermost inserting fibers of M. proscapulohumeralis. In *Crotophaga* and *Coccyzus*, on the other hand, since the origin begins at the distal end of the capital groove, it is more proximal than in *Geococcyx*. In the first two genera both pars anticus and pars posticus of M. latissimus dorsi insert anterior to the origin of the internal head of M. humerotriceps.

A tendon forms on the posterior margin of the external head and inserts on the olecranon process. A strong tendon also forms on the anterior edge of the scapular head and inserts on the proximal end of the ulna, anterior to the olecranon process. Fleshy fibers of the internal head insert on both tendons. There is a continuous insertion, tendinous and fleshy, on the entire proximal end of the ulna, since fleshy fibers insert on the ulna between the points of insertion of the two tendons.

M. expansor secundariorum (Fig. 1)

I have found several references stating that this muscle is present in the cuckoos (Garrod, 1876: 193-94, 199; Forbes, 1880: 471; Beddard, 1898a: 45, 1898b: 276, 1901: 205), but I have yet to discover a description of it for any member of the family Cuculidae. Forbes (1880: 471), commenting on the "peculiar" nature of this muscle in the Cuculidae, said that "its terminal tendon is *not* T-shaped, the sternal moiety being undeveloped." Recently, I stated that the structure of M. expansor secundariorum in the cuckoos is apparently unlike that previously described for other avian groups (Berger, 1953: 59). Since then I have found the same general structure in a Pygmy Falcon (*Polihierax semitorquatus*) as in the cuckoos. It will be surprising, indeed, if future workers do not find a similar condition in other birds. Fürbringer (1902: 571-77) discussed variation in this muscle, but made no reference to a humeral attachment. In the cuckoos the fleshy parts of M. expansor secundariorum lie at the bend of the elbow posterior to M. flexor carpi ulnaris.

Shufeldt (1886: 472) said that this muscle is absent in *Geococcyx californianus*, but this is not true. The larger belly, with an over-all length of 10 mm., arises by a strong tendon from the entepicondyle of the humerus, where the tendon attaches distal to the origin of M. pronator brevis and superficial to the other tendons arising there. From this point of origin, three tendons radiate: one superficial, one deep, and a small, proximal tendon. The bulk of the fleshy belly arises from the first two tendons and inserts on the bases of secondaries 6 through 10 (outermost counted as first); from the more proximal tendon a smaller belly arises and inserts on the bases of the distal tertials.

The smaller part of the muscle arises by a broad aponeurosis attached to the dorsomedial edge of the scapula. This aponeurosis covers the medial surface of M. subscapularis. It also is so intricately fused with the axillary fascia that possible extensions of this tendon could not be traced in preserved material. In the upper arm the aponeurosis tapers to a fine but discrete tendon which runs distad, mesial in position to the tails of Mm. dorsalis scapulae and latissimus dorsi. A short distance above the elbow the fine tendon (.5 mm. wide) passes through the internal tricipital groove and gives way to a small, triangular, fleshy belly 6 mm. in length and 3 mm. wide at its base, where it inserts on the bases of the distal tertials and the tenth secondary.

In *Crotophaga* there is a single belly from which two short muscle tongues extend proximad to the tendons of origin. The distal tendon arises from the entepicondyle of the humerus. The proximal tendon arises, as in *Geococcyx*, from the dorsomedial edge of the scapula as a broad aponeurosis which gives way in the axilla to a much stronger and more discrete tendon than in *Geococcyx*. Distally, this tendon passes through the internal tricipital groove and gives way to fleshy fibers about 5 mm. in over-all length. Insertion of the fleshy fibers is on the two innermost secondaries.

In *Coccyzus* also there are two tendons of origin. The proximal tendon arises as in the other genera. Its relations in the axilla are the same as in *Crotophaga*, but the tendon is stronger and more discrete. It passes through the internal tricipital groove and gives way to a triangular fleshy belly which fuses with the second belly. The latter arises by a strong flat tendon from the entepicondyle of the humerus. The total length of the fleshy fibers is about 6 mm. Insertion is by fleshy fibers on the bases of secondaries 7, 8, and 9.

M. brachialis (Fig. 1)

M. brachialis arises from the brachial impression on the distal end of the humerus. It inserts on the brachial impression of the ulna, beginning about 2 mm. distal to the proximal articular surface and extending distad 4, 5, and 6 mm., respectively, in *Coccyzus*, *Crotophaga*, and *Geococcyx*. The area of insertion on the ulna lies between the areas of origin of Mm. flexor digitorum profundus and extensor pollicis longus. M. brachialis is fleshy throughout.

M. extensor metacarpi radialis (Figs. 1, 3)

This is a powerful muscle with a single belly extending nearly the entire length of the forearm in each of the three genera. M. tensor patagii brevis sends a strong fascial band into the belly of M. extensor metacarpi radialis 10 mm., 6 mm., and 5 mm., respectively, in *Geococcyx*, *Crotophaga*, and *Coccyzus*, from the humeral origin of the latter muscle.

In each genus this muscle arises by fleshy fibers, surrounded by a dense tendinous envelope, from the ectepicondylar process of the humerus. A very stout, flat tendon forms near the distal end of the radius and passes through the tendinal groove on the radius and the radiale (scapholunar). It inserts on the extensor process of metacarpal I, superficial to the insertion of M. extensor pollicis longus. Just proximal to the area of insertion fleshy fibers of M. abductor pollicis take origin from the tendon. The fleshy belly is 32 mm. long in *Geococcyx*, 21 mm. in *Crotophaga*, 17 mm. in *Coccyzus*.

M. extensor digitorum communis (Fig. 3)

In *Geococcyx* this muscle arises by a tendon from the lateral supracondylar ridge of the humerus (i.e., immediately distal to the ectepicondylar prominence or eminence), deep to the tendon of origin of M. flexor metacarpi radialis. The tendon forms on the deep aspect of the belly, which is about 25 mm. in length. The tendon passes around the lateral surface of the external ulnar condyle in a fibrous canal which lies superficial to, and separate from, the fibro-osseous canal for the tendon of M. flexor metacarpi radialis. Opposite the base of the pollex the tendon bifurcates. One tendon inserts on the base of the pollex. The other tendon runs along the bases of the primaries in a groove on metacarpal II; near the distal end of that bone it passes deep to the tendon of M. extensor indicis longus and then passes through a fibro-osseous canal. Insertion is on the posteroanconal corner of the proximal phalanx of digit II.

In *Crotophaga* and *Coccyzus* the belly is, respectively, 18 mm. and 16 mm. in length. In these genera this extensor's tendon to the pollex crosses superficial to M. flexor metacarpi brevis, a relationship not found in *Geococcyx,* which lacks this flexor.

M. supinator brevis (Figs. 2, 4)

This is a long, thin muscle closely applied to the anterior surface of the radius. It arises tendinous from the lateral supracondylar ridge between the origins of M. anconeus and Mm. extensor digitorum communis and flexor metacarpi radialis. In *Geococcyx* and *Crotophaga* the fleshy belly is 20 mm. long; in *Coccyzus,* 15 mm. long. Insertion is fleshy, beginning in *Geococcyx* and *Coccyzus* 3 mm., in *Crotophaga* 2 mm. distal to the proximal articular surface of the radius and extending distad for about 16 mm. in *Geococcyx,* 17 mm. in *Crotophaga,* 13 mm. in *Coccyzus.*

M. flexor metacarpi radialis (Fig. 3)

This muscle arises by a Y-shaped tendinous band, the major attachment of which is on the lateral supracondylar ridge proximal to the origin of M. anconeus. The distal accessory attachment of this sheet is to the ulna, near it proximal end, and it also fuses with the fascia enveloping the bases of the secondaries.

In *Geococcyx* the distal attachment is primarily to the bases of the six proximal secondaries. The fleshy belly is 27 mm. long, and fleshy fibers form 9 mm. distal to the origin of the tendon. Accessory fleshy slips arise from the expanded tendon sheet and from the bases of the proximal secondaries. At the distal end of the ulna the belly gives way to a stout, round tendon which passes around the external ulnar condyle in a fibrous canal, then continues distad deep to the tendons of Mm. extensor digitorum communis and extensor indicis longus. The tendon inserts on the flexor tuberosity of metacarpal II, which is just proximal to the intermetacarpal space.

In *Crotophaga* the Y-shaped nature of the tendon is much less developed than in *Geococcyx* or *Coua caerulea,* but a band 4 mm. wide (not shown in the figure) is given off the main tendon and passes backward to fuse with the fascia surrounding the bases of the proximal secondaries. The fleshy belly is 17 mm. long. Fleshy fibers form 7 mm. distal to the origin of the tendon. A small tendon forms distally and has the same course and relationships as in *Geococcyx.* A few fibers of M. interosseus dorsalis arise from the tendon near its area of insertion.

In *Coccyzus* the main tendon immediately fans out into a broad sheet which attaches primarily to the bases of the proximal three secondaries. The small, spindle-shaped belly is 15 mm. long. Fleshy fibers form 8 mm. distal to the origin of the tendon. Insertion is like that in the other genera.

M. pronator brevis (Fig. 1)

M. pronator brevis has the most proximal origin of the muscles that arise on the posterodistal surface of the humerus. It arises by a broad, flat, semitendinous band proximal to the origin of M. pronator longus. Fleshy fibers form almost immediately, cross M. brachialis, and extend at least three-fourths of the distance down the radius. Insertion is fleshy on the anteromedial aspect of the radius, beginning about 5 mm. from the proximal articular surface and extending to within 3 mm. of the distal end of that bone in *Crotophaga* and to within 7 mm. in *Geococcyx* and *Coccyzus*. The fleshy belly is 34 mm., 24 mm., and 19 mm. long, respectively, in *Geococcyx, Crotophaga,* and *Coccyzus*.

M. pronator longus (Fig. 1)

This muscle arises tendinously from the entepicondylar eminence immediately adjacent to the tendon of origin of M. flexor digitorum sublimus, under cover of the humeral tendon of M. expansor secundariorum, and about 1.5 mm. distal to the origin of M. pronator brevis. Fleshy fibers arise from the deep surface of the tendon at its origin. The origin lies posterodistal to the humeral attachment of the anterior articular ligament (Howard, 1929: 318). The semitendinous part of the insertion is close to the origin of M. extensor indicis longus.

Insertion is fleshy and semitendinous on the ulnar and ventral surfaces of the radius; it begins about 4 mm. in *Coccyzus* and 10 mm. in *Crotophaga* and *Geococcyx* from the proximal end of that bone and extends distad 13 mm., 15 mm., and 21 mm., respectively, in the same series. The fleshy belly is 39 mm. long in *Geococcyx,* 27 mm. in *Crotophaga,* and 19 mm. in *Coccyzus*. This muscle is much shorter in *Coccyzus* than in the other genera, extending distad little farther than M. pronator brevis.

M. extensor pollicis longus (Figs. 2, 3, 4)

The long extensor of the pollex takes origin from both radius and ulna, the ulnar head being the larger. Proximally, the belly fills most of the interval between radius and ulna and lies in contact with the interosseous membrane. The tendon forms near the distal end of the ulna and passes through a fibrous-covered tendinal groove on the radius and radiale to insert on the extensor process of metacarpal I. In *Coccyzus* fleshy fibers of the extensor pollicis brevis muscle arise from the distal 2 mm. of the tendon.

The total length of the fleshy belly is 18 mm. in *Coccyzus,* 21 mm. in *Crotophaga,* and 32 mm. in *Geococcyx*. The origin of the ulnar head begins just distal to the proximal articular surface in *Crotophaga* and *Coccyzus,* distal to the insertion of the biceps tendon in *Geococcyx;* the area of origin is 11 mm. long in *Crotophaga* and *Coccyzus,* 15 mm. in *Geococcyx*. The radial head arises over an area 11 mm. long in *Crotophaga,* 14 mm. in *Geococcyx,* and 16 mm. in *Coccyzus;* the origin begins 5 to 7 mm. distal to the head of the radius.

M. anconeus (Figs. 3, 4)

This muscle arises from the distal end of the lateral supracondylar ridge distal to the origin of M. flexor metacarpi radialis. Fleshy fibers form almost at once. In *Geococcyx, Crotophaga,* and *Coccyzus* the belly is, respectively, 20 mm., 20 mm., and 15 mm. in length. It inserts by fleshy fibers on the anterior surface of the ulna, beginning about 3 mm. from the proximal articular surface in each of the genera and extending distad 17 mm., 18 mm., and 14 mm., respectively, in *Geococcyx, Crotophaga,* and *Coccyzus.*

M. extensor indicis longus (Figs. 2, 4)

This is a small muscle which arises from the radius and inserts into the base of phalanx 2, digit II.

The belly is 11 mm. long in *Coccyzus,* 13 mm. in *Crotophaga,* and 19 mm. in *Geococcyx.* The muscle arises primarily by fleshy fibers from approximately the middle third of the radius. In *Coccyzus, Crotophaga,* and *Geococcyx* the origin begins 8 mm., 10 mm., and 15 mm., respectively, from the head of the radius; in the same series the origin extends distad 10 mm., 11 mm., and 12 mm.

In *Crotophaga* and *Coccyzus* the strong, flat tendon forms near the distal end of the ulna; passes distad in the interval between ulna and radiale; receives, opposite the base of the pollex, the tendinous insertion of M. flexor metacarpi brevis; passes, about the middle of the carpometacarpus, superficial to the tendon of M. extensor digitorum communis; and runs along the anterior edge of digit II to insert into the base of phalanx 2; a fascial band may continue to the apex of that phalanx.

In *Geococcyx* the tendon inserts into the anteroproximal corner of phalanx 2, digit II, forming with the tendon of M. interosseus dorsalis a common insertion, from which a fascia extends to the distal end of the phalanx. M. flexor metacarpi brevis is absent in *Geococcyx,* but other relationships are like those in the other genera.

M. flexor digitorum sublimus (Fig. 1)

In all three genera this muscle arises by a tendon from the entepicondylar process of the humerus distal to the origin of M. pronator longus. The tendon fans out into a thin, aponeurotic sheet (5 to 8 mm. wide), which covers the posterior flat surface of the belly. Dorsally, this aponeurosis attaches to the bases of the secondaries; distally, it attaches to the base of the ulnare; in *Coccyzus* a palmar tendon also passes around the anterior surface of the ulnare, fuses with the deep fascia of the manus, and inserts on the base of the pollex.

The fleshy belly is 24 mm. long in *Geococcyx,* 16 mm. in *Crotophaga,* and 21 mm. in *Coccyzus.* Fleshy fibers begin 12 mm., 7 mm., and 4 mm., respectively, from the humeral origin of the tendon in *Geococcyx, Crotophaga,* and *Coccyzus.*

The main tendon of insertion forms at the level of the ulnare; swings around a groove on the anterior surface of the ulnare; continues distad, grooving the belly of M. abductor indicis; and passes deep to the tendon of M. flexor digitorum profundus. The main insertion is on the anteropalmar corner of the proximal phalanx of digit II, but a superficial fibrous slip runs distad some distance along the anterior edge of that phalanx.

Shufeldt (1890: 142), speaking of the Raven (*Corvus corax sinuatus*), stated that the tendons of Mm. flexor digitorum sublimus and flexor digitorum profundus fuse. This is not true in the cuckoos thus far investigated.

M. flexor digitorum profundus (Figs. 1, 2)

This muscle lies deep to M. flexor digitorum sublimus and superficial to M. flexor carpi ulnaris brevis. Proximally, its area of origin lies posterior to the area of insertion of M. brachialis. The total length of the fleshy belly is 32 mm. in *Geococcyx,* 23 mm. in *Crotophaga,* and 20 mm. in *Coccyzus*. The muscle arises by fleshy fibers from the ulna (and also from the volar humeroulnar ligament in *Crotophaga*), beginning just distal to the proximal articular surface. The area of origin extends distad 22 mm. in *Geococcyx,* 14 mm. in *Crotophaga,* and 12 mm. in *Coccyzus*.

The tendon forms on the superficial aspect of the muscle and swings around the anterior surface of the pisiform process, after which it grooves the surface of M. abductor indicis in its course distad. Near the distal end of the carpometacarpus the tendon passes superficial to the tendon of M. flexor digitorum sublimus and then runs in a fibrous-covered groove along the anteromedial edge of phalanx 1, digit II. Insertion is primarily on the base of the distal phalanx of digit II, but a flat tendon extends to the distal end of that phalanx.

M. flexor carpi ulnaris (Fig. 1)

This is the largest muscle of the forearm. Its heavy fusiform belly extends the entire length of the ulna and inserts on the proximal surface of the ulnare. It arises by a stout tendon (4 mm. long in *Geococcyx,* 3 mm. in the other genera) from the distal end of the entepicondyle of the humerus. At its origin the tendon is surrounded by a strong fibrous loop (the humeroulnar pulley of Shufeldt, 1890: 142), which attaches to the inner aspect of the entepicondyle and to the posterior face of the ulna just distal to the proximal articular surface. In *Crotophaga* some of the posterior fleshy fibers arise from this pulley. Dorsally, the muscle fascia is adherent to the fascia surrounding the bases of the secondaries, and fan-shaped fleshy fibers insert on the bases of several of the central secondaries.

M. flexor carpi ulnaris brevis (Figs. 1, 2)

In *Geococcyx* this is a short muscle whose belly is 11 mm. long. It arises from the distal fourth of the ventral and radial aspects of the ulna, beginning 10 mm. from the distal end of that bone and, as in the other genera, immediately distal to the area of origin of M. flexor digitorum profundus. The strong, flat tendon passes through a groove on the radiale, under cover of the tendons of Mm. extensor metacarpi radialis and extensor pollicis longus, to the anconal surface, where it inserts on the proximal edge of the carpometacarpus adjacent to the origin of M. extensor pollicis brevis. A few fibers of the latter muscle take origin from the tendon at its insertion.

In *Crotophaga* the belly is 10 mm. long. It arises fleshy over an area of 6 mm. on the ventral aspect of the ulna, beginning 10 mm. from the distal end of the bone. None of the fibers of M. extensor pollicis brevis arises from the tendon in *Crotophaga* or *Coccyzus*.

In *Coccyzus* M. flexor carpi ulnaris brevis has a more entensive origin, relatively, than in the other genera. It arises fleshy from the ventral, posterior, and radial surfaces of the ulna over an area 9 mm. long, beginning 11 mm. from the distal end of the ulna. The over-all length of the belly is 10 mm.

M. abductor pollicis (Fig. 1)

In *Geococcyx* this muscle ("extensor proprius pollicis," Shufeldt, 1890: 147) consists of two heads, both of which arise from the tendon of M. extensor metacarpi radialis. The superficial head arises fleshy and inserts by fleshy fibers near the base of the pollex, but also sends a strong tendon distad to the tip of the pollex. The deeper head arises under cover of the superficial head by a strong, flat tendon; its large fleshy belly overlaps the insertion of the superficial head and inserts on nearly the entire palmar aspect of the pollex.

In *Crotophaga* this muscle has the same general structure as in *Geococcyx*, but both heads are less developed. The deep head arises by a thin, rather than strong, tendon, and its much smaller fleshy belly does not overlap the insertion of the superficial head. Furthermore, it inserts on less than the basal half of the pollex, though a tendinous sheet continues to the tip of that digit.

In *Coccyzus* M. abductor pollicis appears to arise by a single head from the tendon of M. extensor metacarpi radialis. It inserts, both by fleshy and semitendinous fibers, on only the base of the pollex.

M. adductor pollicis (Fig. 2)

In *Geococcyx* this small muscle arises semitendinous from a small area (2 mm.) on the palmar surface of metacarpal II between the pisiform and extensor processes. It inserts by fleshy fibers on the posterior surface of the basal half of the pollex.

In *Crotophaga* it arises fleshy from an area about 1 mm. in diameter on the anterior surface of metacarpal II, opposite the base of the pollex. It inserts by fleshy fibers over a distance of 3 mm. on the posterior surface of the pollex, beginning distal to the insertion of M. extensor digitorum communis.

In *Coccyzus* it arises fleshy from an area about 1 mm. in diameter on metacarpal II, distal to the pisiform process and anterior to the area of origin of M. abductor indicis. It inserts fleshy on the posterior surface of the middle third of the pollex.

Mm. flexor digiti III and *flexor brevis digiti III* (Figs. 1, 2, 3)

In these cuckoos separation of the flexor mass to digit III into two muscles is difficult, if not impossible. Some specimens, however, exhibit a thin fasciculus of fleshy fibers arising from a long, narrow line on metacarpal III. This fasciculus corresponds to M. flexor digiti III of other birds and inserts on the tip of the posterior spine of digit III. The bulk of the muscle mass (M. flexor brevis digiti III) arises from the distal surface of metacarpal III and inserts on the entire posterior surface of the posterior spine and the body of digit III, proximal to the spine. The muscle completely fills the interval between the distal end of metacarpal III and digit III proximal to the spine. In *Coccyzus* the insertion on the tip of the posterior spine is tendinous, and fleshy fibers not only insert as in *Geococcyx* and *Crotophaga*, but also pass distad in a groove on the posterior surface of digit III to insert on the tip of that digit. The origin of most of the belly can be separated only with great difficulty from the distal fibers of insertion of M. flexor metacarpi posterior.

M. interosseus dorsalis (Fig. 3)

This muscle lies in the intermetacarpal space and arises by fleshy fibers from metacarpals II and III. From a mid-line raphe a strong cordlike tendon forms near the distal end of the carpometacarpus, passes distad on the anterior edge of the proximal phalanx of digit II, and inserts on the base of the distal phalanx of that digit. The tendon inserts adjacent to (in *Crotophaga* and *Coccyzus*), or in common with (in *Geococcyx*), the tendon of M. extensor indicis longus.

In *Geococcyx, Crotophaga,* and *Coccyzus* this muscle arises over areas of 5 mm., 7 mm., and 6 mm., respectively, on metacarpal II and 10 mm., 9 mm., and 6 mm. on metacarpal III.

M. interosseus palmaris (Fig. 4)

Similar in structure to the last-described muscle, M. interosseus palmaris arises fleshy from the facing surfaces of metacarpals II and III. The tendon forms as a mid-line raphe, crosses the metacarpophalangeal joint, passes distad on the posteroanconal surface of the proximal phalanx of digit II, and inserts on the distal phalanx of that digit. The tendon inserts just beyond mid-length on the anconal surface of phalanx 2 in *Geococcyx*, on the posterior surface of the distal half of the phalanx in *Crotophaga*, and near the tip of the phalanx in *Coccyzus*.

In *Geococcyx, Crotophaga,* and *Coccyzus* M. interosseus palmaris arises for distances of 6 mm., 8 mm., and 7 mm., respectively, on metacarpal II and 8 mm., 7 mm., and 8 mm. on metacarpal III.

M. extensor pollicis brevis (Fig. 3)

In *Geococcyx* this muscle arises from the base of the carpometacarpus adjacent to the insertion of M. flexor carpi ulnaris brevis, with some fibers arising from its tendon. There also is a long, but small, fasciculus which arises from the anconal radiale-carpometacarpal ligament and from the radiale; this fasciculus fuses with the main head near its origin.

The second major head arises fleshy from the distal surface of the extensor process of metacarpal I. The two heads fuse and insert, by fleshy and tendinous fibers, on the anteroanconal surface of the pollex.

In *Crotophaga* this muscle is similar to that in *Geococcyx,* though the long fasciculus is wanting. The larger head arises from the anteroanconal surface of the base of the carpometacarpus, distal to the area of insertion of M. flexor carpi ulnaris brevis. The second head (relatively smaller than in *Geococcyx*) arises from the distal surface of the extensor process. The two heads fuse near the insertion, which is semitendinous, on the anteroanconal edge of the base of the pollex. On the anterior surface the belly lies adjacent to that of M. abductor pollicis.

In *Coccyzus* M. extensor pollicis brevis is a roughly triangle-shaped muscle 3 mm. long with a maximum width of 3 mm. The origin, unlike that in the other two genera, is continuous from the distal face of the extensor process, from the tendon of M. extensor pollicis longus, and from the base of the carpometacarpus. It inserts as in *Crotophaga.*

M. abductor indicis (Fig. 1)

This is a well-developed muscle arising from the proximal end of the carpometacarpus and inserting into the proximo-anteropalmar edge of the proximal phalanx of digit II, adjacent to the insertion of M. flexor digitorum sublimus. It arises from the palmar and distal surfaces of the pisiform process and from metacarpal II for a distance of 11 mm. in *Geococcyx* and *Crotophaga* and 10 mm. in *Coccyzus.*

M. flexor pollicis (Fig. 1)

This muscle is weakly developed in the cuckoos under consideration. It arises by fleshy fibers from the base of the carpometacarpus and inserts semitendinous on the posteropalmar corner of the base of the pollex. The tendon of M. flexor digitorum profundus, in its course around the pisiform process, passes between Mm. flexor pollicis and abductor indicis.

In *Geococcyx* M. flexor pollicis has an over-all length of 5 mm. It arises from the carpal trochlea. The insertion and part of the belly are covered by M. abductor pollicis.

In *Crotophaga* the muscle is 3 mm. long and less than .5 mm. in diameter. It arises from the carpal trochlea and from the anterior surface of the base of the pisiform process. The latter origin is shared with M. abductor indicis.

In *Coccyzus* the muscle is 2 mm. in length. It arises primarily from the anterior and distal surfaces of the pisiform process.

M. flexor metacarpi posterior (Figs. 1, 3)

In each of the three genera this is a well-developed muscle arising by a strong tendon from a pit about 2 mm. from the distal end of the ulna. Fleshy fibers cross the wrist joint and insert on the posterior surface of metacarpal III. Distally, these fibers appear to fuse with fleshy fibers of origin of Mm. flexor digiti III and flexor brevis digiti III.

In *Geococcyx* this muscle inserts fleshy on metacarpal III for a distance of 8 mm. Fleshy fibers also insert on the bases of primaries 2 through 5 (innermost primary counted as first).

In *Crotophaga* and *Coccyzus* the insertion by fleshy fibers on metacarpal III covers a distance of 9 mm., and a large bundle of fleshy fibers inserts on the bases of primaries 2 through 7. On the posteropalmar surface of the carpometacarpus a semitendinous insertion forms an arch over the long, thin, fleshy fasciculus of M. flexor digiti III in *Crotophaga*.

M. flexor metacarpi brevis (Fig. 4)

This muscle is absent in *Geococcyx californianus* as it is in *Coua caerulea*.

In *Crotophaga* the total length of this muscle and tendon is 6 mm. It arises by a short tendon from the posterodistal edge of the radiale. The fusiform belly inserts partly fleshy and partly by a tendon on the anterior surface of the tendon of M. extensor indicis longus.

In *Coccyzus erythropthalmus* the belly of this muscle is triangular in shape, 2 mm. wide at its origin and 4 mm. in length. It arises fleshy on the carpal trochlea and on metacarpal I, distal to the extensor process. It inserts by a thin tendon on the tendon of M. extensor indicis longus about 6 mm. distal to the base of the carpometacarpus. The muscle is similar in development and relationships in *C. americanus*.

DISCUSSION

Too little is known about the anatomy of the family Cuculidae to permit comment on the ancestral type and, consequently, on the lines of evolution within the family, although the occurrence of the zygodactyl foot suggests an arboreal rather than a terrestrial ancestral form. I found it necessary to use one genus as a standard with which the other genera might be compared. Because this study began with American genera, I selected the genus *Coccyzus* as a standard. Nevertheless, I do not mean to imply that the anis represent a phylogenetic stage in the evolution of a terrestrial genus such as *Geococcyx*.

An analysis of the wing myology is beset with many more problems than a study of the leg myology. Some of the anatomical features which must form the basis for an analysis of flight pattern are: myology, limb proportions, wing area, shape of wing, shape and size of tail, and body weight. Not only is there little aerodynamic knowledge on bird flight, but there is little information on the pectoral musculature with which data can be compared. So far as I know, Fisher's paper (1946) on the Cathartidae is the only one which attempts to correlate muscular and osteological differences with flight patterns. Consequently, I have made considerable use of his paper and have made certain comparisons between his findings and mine, although recognizing that such comparisons between birds so widely separated in relationship and in habits have doubtful value. The fact that certain ratios are nearly the same in the vultures and the cuckoos emphasizes the need for caution in comparing unrelated forms. It also reveals that similarity in relative proportion of bones and muscles does not necessarily imply similarity in function. Phylogenetic characters of the pectoral musculature may be obscured because of the modification of the forelimb for flight. One obvious point may deserve emphasis. Whereas Fisher's investigation dealt with birds having relatively similar flight patterns, this study concerns three genera with different locomotor habits.

Osteology

The data obtained in my previous study (Berger, 1952: 524) reveal a 1.3 per cent increase in the ratio for humeral length to length of the dorsal region in *Geococcyx* over that ratio in *Coccyzus;* a 6.1 per cent decrease from *Coccyzus* to *Crotophaga*. With respect to the ulna, *Crotophaga* exhibits a greater decrease (17.1 per cent) from *Coccyzus* than does *Geococcyx* (10.0 per cent). Length of the manus (carpometacarpus plus digit II) exhibits a progressive decrease from *Coccyzus* to *Geococcyx;* a 12.9 per cent decrease from *Coccyzus* to *Crotophaga;* a 17.6 per cent decrease from *Crotophaga* to *Geococcyx*. I am unable to explain the greater decrease in ulnar length in *Crotophaga*. In his study of the wing skeleton in falconiform birds, Engels (1941: 68) came to the conclusion that "the intramembral proportions of the wing skeleton are not an infallible index to flight habit, except perhaps where they indicate an extreme pattern."

Because of the size differential in the three genera, it is necessary to know the length and area of the wing relative to the size of the bird in each genus. I computed several ratios involving the total length of the bony wing. I followed Fisher (1946: 553) in adding interacetabular width to length of the dorsal region in order to "give a two-dimensional aspect to body size." I also used a ratio involving wing length and a combined measurement of the dorsal region and the width of the pelvis at the posterior iliac crest. This was done because of the striking expansion of this region in *Geococcyx*. Although this feature is correlated with terrestrial locomotion in that genus, the measurement does give a truer index of body size than interacetabular width does. In a further attempt to compensate for the size discrepancy among the three genera, I computed the ratio between total wing length and the cube root of the body weight (see Amadon, 1943: 167-75). Table I presents ratios involving the total wing length.

The advisability of including in this table the three ratios on the right is obvious when one notes that if compared with length of the dorsal region, the bony wing in *Crotophaga* is the shortest of the three genera, but if compared with dorsal region plus interacetabular width, it is the longest. A better indicator of relative wing length to body size is obtained by adopting the measurement which includes the greatest width of the pelvis. The latter ratios indicate that *Coccyzus* has the longest wing, *Geococcyx* the shortest. The use of these linear measurements, however, considers body size indirectly. Thus, computation of ratios between total length of the bony wing and both body weight and cube root of body weight in the three genera does reveal that in spite of the absolute greater length of wing in *Geococcyx*, relatively, it is shorter than in the other genera.

TABLE I

RATIOS INVOLVING THE BONY WING
(In Percentage)

	Wing Length: Length of Dorsal Region[1]	Wing Length: Dorsal Region + Interacetabular Width	Wing Length: Dorsal Region + Pelvic Width[2]	Wing Length: Body Weight	Wing Length: Cube Root of Body Weight[3]
Coccyzus	433	254	234	170	100
Crotophaga	380	260	220	119	96.5
Geococcyx	395	248	167	57	88.9

[1] Length of dorsal region is the distance from the anterior articular surface of the centrum of the last cervical to the posterior articular surface of the centrum of the last dorsal vertebra.

[2] Greatest width of pelvis at the posterior iliac crest.

[3] The actual ratios were mutiplied by a factor which increased the largest ratio to 100.

As Engels correctly stated (1941: 62), differences in the patterns of proportion in the wing skeleton in these three cuckoos accompany functional differences, but do not explain the functional differences in flight pattern. On the basis of skeletal differences I agree with Engels (1941: 62) that this is a "reduction or regressive evolutionary phenomenon." There is a loss of the "tendency to flight as a means of locomotion," rather than a "progressive loss of flight ability." These two factors must be considered together, but it is interesting to note that the only evidence of degeneration (if, indeed, it be such) in the wing myology of *Geococcyx* is the absence of M. flexor metacarpi brevis.

Myology

An analysis of intramembral limb proportions in the three genera is successful in accounting for differences in flight pattern only when body weight is considered. In discussing the wing musculature also it is necessary to attempt to distinguish between differences correlated with type and degree of flight and those correlated with relative and absolute greater body weight.

There is a progressive increase in relative length of the fleshy belly of M. supracoracoideus from *Geococcyx* to *Coccyzus*. This increased length in the latter genus is correlated with sustained flapping flight. M. pectoralis superficialis appears to exhibit the same relative development in the three genera. Without the volumes of individual muscles it is not possible to analyze further the development of the pectoralis superficialis.

M. subscapularis exhibits a similar relative development in the three genera, but it has a more posterior origin in *Geococcyx* and therefore should be more effective in drawing the humerus posteriorly. M. dorsalis scapulae, however, has a greater area of origin in *Coccyzus;* this increased origin is presumed to be necessary because of the greater relative length of wing in that genus.

M. coracobrachialis anterior shows a progressive reduction in relative size from *Geococcyx* to *Coccyzus,* though the origin and insertion are similar in the three genera. In the Cathartidae, Fisher (1946: 583) found that this "muscle is almost twice as large relatively in *Gymnogyps* and *Vultur* as in *Cathartes*, *Sarcoramphus* and *Coragyps*. The greater size... is significant as an adaptation for better soaring." The greater development in *Geococcyx* seems to be correlated with gliding flight.

The ratio of length of power arm (the distance from the proximal end of the humerus to the most distal point of insertion of the muscle on that bone) to humeral length of the insertion of M. latissimus dorsi is as follows: *Geococcyx,* 37.6 per cent; *Crotophaga,* 20.8; *Coccyzus,* 32.2. The ratio of power arm to total wing length likewise indicates that this muscle can effect a more powerful, but slower, posterior movement of the humerus in *Geococcyx* than in the other genera: in *Geococcyx* the power arm is 14.1 per cent of the total wing length; in *Crotophaga* it is 7.5; and in *Coccyzus* it is 10.8. If it is assumed with Fisher (1946: 581) that this muscle "is useful in holding the humerus in a partly flexed condition as in flex-gliding," the conclusion must be reached that the intermediate ratio of *Coccyzus* reflects the relatively greater wing length in that genus; so far as I know, *Coccyzus* never glides. It must also be concluded that the low ratio of power arm to total wing length in *Crotophaga* is a reflection of the light body weight (as compared with *Geococcyx*), as well as of flight pattern. By the same token, the greater ratio in *Geococcyx* is a reflection of its body weight. Ratios between power arm (in centimeters) and body weight (in grams) substantiate this assertion.

Furthermore, the belly of pars posticus of M. latissimus dorsi exhibits its best development in *Geococcyx,* though it has a more extensive origin in *Crotophaga;* it shows its poorest development in *Coccyzus*. The wide separation of the tendons of insertion of the two parts of the latissimus dorsi in *Geococcyx* implies greater ability to control tilting actions of the humerus and thus of the rest of the wing. In view of the flight pattern in *Geococcyx,* however, it seems more reasonable to assume that it results in greater stability in maintaining a partly flexed wing if, of course, the two parts of the muscle contract simultaneously.

For M. deltoideus major the ratio of belly length (approximately the same as power arm in this case) to humeral length in *Geococcyx, Crotophaga,* and *Coccyzus* is 77.6, 74.6, and 78.8 per cent, respectively; in the same series, the ratio of belly length to total wing length is 29.0, 26.8, and 26.5 per cent, i.e., nearly the same. Ratios computed between the power arm and the body weight show that the power arm is, respectively, 1.7, 3.2, and 4.5 per cent of the body weight in *Geococcyx, Crotophaga,* and *Coccyzus*.

In an attempt to correlate myology with locomotor habits, I computed various ratios involving the total length of forearm muscles and other measurements. Certain of these ratios are given in Table II.

Unless circumstances indicate otherwise, one may assume that a greater relative length of fleshy belly implies a greater range in distance or extent of contraction. Why any wing muscle, therefore, should appear to be better developed in *Crotophaga* than in the other genera is obscure,

TABLE II

RATIOS INVOLVING CERTAIN FOREARM MUSCLES
(In Percentage)

	Belly Length: Ulnar Length	Belly Length: Ulna + Manus	Power Arm: Total Wing Length	Belly Length: Total Wing Length
Supinator brevis				
Geococcyx	51.9	26.4	15.7	...
Crotophaga	70.4	33.5	20.4	...
Coccyzus	55.9	27.3	19.3	...
Anconeus				
Geococcyx	51.9	26.4	16.5	...
Crotophaga	70.4	33.5	22.5	...
Coccyzus	55.9	27.3	20.5	...
Pronator brevis				
Geococcyx	88.3	45.0	23.5	...
Crotophaga	84.5	40.2	24.6	...
Coccyzus	70.8	34.6	21.3	...
Pronator longus				
Geococcyx	101.2	51.6	25.7	...
Crotophaga	95.0	45.2	26.8	...
Coccyzus	70.8	34.6	20.5	...
Flexor carpi ulnaris brevis				
Geococcyx	28.5	14.5	...	9.1
Crotophaga	35.2	16.7	...	10.7
Coccyzus	37.3	18.2	...	12.1
Flexor digitorum sublimus				
Geococcyx	62.3	31.7	...	19.9
Crotophaga	56.3	26.8	...	17.1
Coccyzus	78.3	38.2	...	25.3
Flexor digitorum profundus				
Geococcyx	83.1	42.3	...	26.5
Crotophaga	80.9	38.5	...	24.6
Coccyzus	74.6	36.4	...	24.1
Flexor metacarpi radialis				
Geococcyx	70.1	35.7	...	22.3
Crotophaga	59.8	28.4	...	18.2
Coccyzus	55.9	27.3	...	18.1
Extensor digitorum communis				
Geococcyx	64.9	33.1	...	20.7
Crotophaga	63.3	30.1	...	19.3
Coccyzus	59.7	29.1	...	19.3
Extensor policis longus				
Geococcyx	83.1	42.3	...	26.5
Crotophaga	73.9	35.1	...	22.5
Coccyzus	67.1	32.7	...	21.7
Extensor indicis longus				
Geococcyx	49.3	25.1	...	15.7
Crotophaga	45.7	21.7	...	13.9
Coccyzus	41.0	20.0	...	13.2

but one notes in *Crotophaga* a much greater ratio between belly length and ulnar length of Mm. supinator brevis and anconeus. This increased ratio, however, is a function of the greater reduction in ulnar length in *Crotophaga* as compared with that in *Coccyzus*. Ratios between belly length and a combined measurement of ulna and manus or between power arm and total wing length are probably more indicative of the efficiency of these muscles. One recognizes, of course, that increased efficiency may be interpreted in terms of either power or speed of action. The ratios of power arm to total wing length for the first four muscles in the table indicate the greatest relative efficiency for power in *Crotophaga*, but the magnitude of difference between *Crotophaga* and the other genera is reduced considerably from the ratios of belly length to ulnar length. These four muscles (supinator brevis, anconeus, pronator brevis, and pronator longus) aid in flexion of the forearm. In addition, the first two also aid in elevating the anterior edge of the wing or the forearm, whereas the latter two muscles depress the anterior edge of the forearm. Here, again, with linear measurements differences in ratios among the three genera are so small that little importance can be ascribed to them. Introduction of body weight into the analysis shows that each of these muscles is much better developed in *Coccyzus*, which is what one would expect in a bird using flapping flight.

TABLE III

RATIOS OF POWER ARM (CM.) TO BODY WEIGHT (GMS.)
(In Percentage)

	Geococcyx	*Crotophaga*	*Coccyzus*
Supinator brevis	9.0	24.3	32.6
Anconeus	9.4	26.9	34.6
Pronator brevis	13.3	29.5	36.1
Pronator longus	14.6	32.0	34.6

Fisher analyzed all muscles of the pectoral appendage with reference to the soaring and flapping flight patterns of the Cathartidae. He remarked (1946: 619): "Because the muscles flexing the forearm are longer and have longer power arms in *Coragyps* than in *Cathartes*, it must be concluded that *Coragyps* is better adapted for this particular movement.... The ability to flex the forearm is correlated with the ability to flap the wings." The ratio of belly length to humeral length of M. biceps is 66.5, 65.6, and 71.6 per cent, respectively, in *Geococcyx*, *Crotophaga*, and *Coccyzus*; and in the same series, the ratio of belly length to total wing length is 24.8, 23.6, and 24.1 per cent, i.e., practically the same. In addition, the points of insertion of the biceps tendon on the ulna should result in greater power in *Geococcyx*. The power arm with respect to ulna is 7.7, 3.5, and 3.7 per cent, respectively, in *Geococcyx*, *Crotophaga*, and *Coccyzus*. The insertion of M. tensor patagii brevis on M. extensor metacarpi radialis also forms a greater power arm in *Geococcyx* than in the other genera; the point of insertion in *Geococcyx, Crotophaga,* and *Coccyzus* is, respectively, 25.9, 21.1, and 18.6 per cent of the distance from the proximal to the distal end of the ulna. If, however, figures are adopted for *Coccyzus* as a standard (power arm = 18.6 per cent; length of the ulna plus manus = 54.9 mm.), theoretical values can be computed for the power arm in *Crotophaga* and *Geococcyx*. These theoretical values are found to be very close, indeed, to the actual ratios given above: *Crotophaga,* 20.2 and 21.1; *Geococcyx,* 25.3 and 25.9. This seems to indicate an equality in effectiveness of the power arm among the three genera in so far as linear measurements are concerned. If, however, body weight is again introduced into the ratio, the length of the fleshy belly of the biceps is 14.2, 28.2, and 40.8 per cent of the body weight, respectively, in *Geococcyx, Crotophaga,* and *Coccyzus*. Ratios involving the cube root of body weight also indicate the best development of this muscle in *Coccyzus*.

M. flexor carpi ulnaris brevis exhibits its best development in *Coccyzus*. After analyzing the development of this muscle in the vultures, Fisher (1946: 599) concluded that "no correlation with type of flight is possible." A correlation with degree and type of flight, however, is indicated in the cuckoos under consideration. The apparent small differences in ratios of belly length to total wing length among the three genera take on significant proportions when correlated with body weight. The development of the flexor carpi ulnaris brevis muscle in this instance appears to be correlated with sustained flapping flight.

In a discussion of M. flexor digitorum profundus Fisher (1946: 598) stated: "In the development of this muscle, as in many muscles affecting the distal parts of the wing, one finds a correlation with the type of flight. The master soaring types, the condors, possess larger muscles to provide for better control of the broad tip of the wing." There is little difference among the three genera of cuckoos in ratio of belly length to total wing length of the flexor digitorum profundus. On the other hand, *Coccyzus* shows an advantage in the development of M. flexor digitorum sublimus. Fisher found it "likely" that this muscle in cathartids "is represented in part by the wide tendon of the anterior part of M. flexor carpi ulnaris" (1946: 597), and he suggested (p. 621) that this tendon "may act as an automatic extensor of the hand when the forearm is extended." The flexor digitorum sublimus muscle is a separate and well-developed fleshy muscle in the cuckoos, and its development seems to be correlated with flapping flight.

The remaining forearm muscles (the last four in Table II) exhibit a remarkable uniformity in ratio of belly length to both total wing length and length of the ulna plus manus in *Coccyzus* and *Crotophaga*. In each instance, also, the ratios are slightly larger in *Geococcyx* than in the former two genera. The differences are small, however, and the relationship between length of belly and body weight shows that each muscle is better developed in *Coccyzus*.

Wing Area

Thus far only intramembral proportions and linear measurements of the bony wing have been considered. These data have a bearing on type of flight, but not necessarily on the shape and area of the wings.

I found no published information on the wing areas of *Geococcyx, Crotophaga,* or *Coccyzus erythropthalmus,* nor has it been possible to obtain such data for *Crotophaga.* Dr. George M. Sutton sent me the weights and tracings of wing areas of two Roadrunners collected in Oklahoma (during the first week of December, 1952). I obtained similar information on two Black-billed Cuckoos collected at Ann Arbor, Michigan (in May, 1953).

The average weight of the two Roadrunners is 526 grams; of the two Black-billed Cuckoos, 53.2 grams. The average wing area of the Roadrunners is 642 square centimeters; that of the Black-billed Cuckoos, 204 square centimeters. The ratio of wing area per gram of body weight is 1.22 and 3.83, respectively, in the Roadrunner and the Black-billed Cuckoo. Thus, these specimens indicate that though the Roadrunner is 9.8 times as heavy as the Black-billed Cuckoo it has a wing area only 3.1 times as large.

Conclusions

The development of certain muscles (e.g., supracoracoideus, coracobrachialis anterior, flexor carpi ulnaris brevis, and flexor digitorum sublimus) seems to be correlated with mode of flight. Because total wing myology is so uniform, however, analysis of that alone does not enable one to explain the differences in flight pattern in the three genera. It is necessary to compare the length and relative development of the muscles with body weight in order to give a possible explanation. One must conclude that although an increase in development of certain muscles in *Geococcyx,* in comparison with the other genera, may be an adaptation for its mode of flight, basically the increase may be simply a reflection of the greater amount of work required of its muscles in order to maintain flight in a heavy bird with a small, short wing.

Acknowledgments

I wish to express my appreciation to the following: Dr. George M. Sutton, Department of Zoological Science, University of Oklahoma, for sending tracings of wing areas of the Roadrunner; Dr. Harvey I. Fisher, Department of Zoology, University of Illinois, and Dr. Robert W. Storer and Dr. Josselyn Van Tyne, Museum of Zoology, University of Michigan, for reading the manuscript and offering many suggestions.

SUMMARY

This paper describes the myology of the pectoral appendage in three genera of American cuckoos: *Geococcyx, Crotophaga,* and *Coccyzus.*

The following wing muscles are wanting in each of the three genera: proscapulohumeralis brevis, abductor indicis brevis, abductor digiti II, and the biceps slip to the tendon of M. tensor patagii longus. M. deltoideus minor is wanting in *Coccyzus* and M. flexor metacarpi brevis in *Geococcyx.*

A single belly represents Mm. tensor patagii longus et brevis. M. deltoideus major arises by two heads, but has a single insertion. M. expansor secundariorum is present in each of the genera and exhibits minor differences in development. Gadow's "pars propatagialis musculi cucullaris" ("M. dermo-tensor patagii" of Shufeldt) does not insert on the tendon of M. tensor patagii longus. M. pectoralis superficialis is not divided into a superficial and a deep layer. M. abductor pollicis takes origin from the tendon of insertion of M. extensor metacarpi radialis. M. flexor metacarpi radialis arises by a Y-shaped tendinous band. M. subcoracoideus arises by two heads: one from the furculum, the other from the coracoid and/or the coracoclavicular membrane.

In *Coccyzus*, but not in the other genera, some fleshy fibers of M. extensor pollicis brevis arise from the tendon of insertion of M. extensor pollicis longus. In *Geococcyx* a few fibers of M. extensor pollicis brevis take origin from the tendon of M. flexor carpi ulnaris brevis. In *Crotophaga* and *Coccyzus* the tendon of M. flexor metacarpi brevis inserts on the tendon of M. extensor indicis longus. In *Geococcyx* the areas of insertion of pars anticus and pars posticus of M. latissimus dorsi are separated by the area of origin of the internal head of M. humerotriceps, whereas in *Crotophaga* and *Coccyzus* both pars anticus and pars posticus insert anterior to the origin of that muscle.

Differences in flight pattern in the three genera may best be explained in terms of a progressive reduction in relative wing area and a progressive increase in body size from *Coccyzus* to *Geococcyx*.

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Crotophaga sulcirostris

Fig. 1. Superficial muscles of the palmer surface of the right wing and pectoral region.

Fig. 2. Palmar view, showing a second layer of muscles.

Fig. 3. Superficial muscles of the anconal surface of the right shoulder and wing.

Fig. 4. Anconal view, showing a second layer of muscles.

ABBREVIATIONS USED IN FIGURES

Abd. in. — Abductor indicis
Abd. p. — Abductor pollicis
Add. p. — Adductor pollicis
An. — Anconeus
Bic. — Biceps brachii
Cb. ant. — Coracobrachialis anterior
Cb. post. — Coracobrachialis posterior
D. — Deltoideus major
D. min. — Deltoideus minor
Dor. scap. — Dorsalis scapulae
Exp. — Expansor secundariorum
Ext. dig. — Extensor digitorum communis
Ext. in. l. — Extensor indicis longus
Ext. meta. — Extensor metacarpi radialis
Ext. p. brev. — Extensor pollicis brevis
Ext. p. long. — Extensor pollicis longus
F. c. u. — Flexor carpi ulnaris
F. c. u. brev. — Flexor carpi ulnaris brevis
Flex. d. III — Flexor digiti III and Flexor brevis digiti III
Flex. dig. pro. — Flexor digitorum profundus
Flex. dig. sub. — Flexor digitorum sublimus
Flex. meta. — Flexor metacarpi radialis
Flex. meta. brev. — Flexor metacarpi brevis
Flex. meta. post. — Flexor metacarpi posterior
Flex. p. — Flexor pollicis
Inter. dor. — Interosseus dorsalis
Inter. palm. — Interosseus palmaris
Lat. dor. P. ant. — Latissimus dorsi pars anterior
Lat. dor. P. post. — Latissimus dorsi pars posterior
Pect. — Pectoralis superficialis
Pro. — Proscapulohumeralis
Pro. brev. — Pronator brevis
Pro. long. — Pronator longus
R. pro. — Rhomboideus profundus
R. sup. — Rhomboideus superficialis
Stern. — Sternocoracoideus
Sub. — Subcoracoideus
Sup. brev. — Supinator brevis
Supra. — Supracoracoideus
T. — Triceps
T. p. — Belly of tensores patagii brevis et longus
T. p. b. — Tendon of tensor patagii brevis
T. p. l. — Tendon of tensor patagii longus

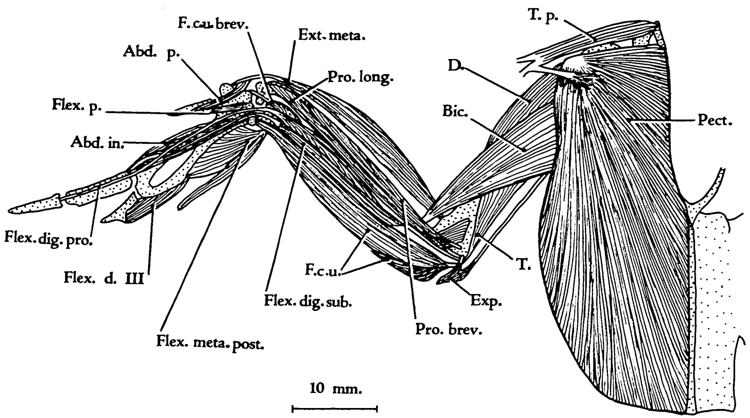

Fig. 1

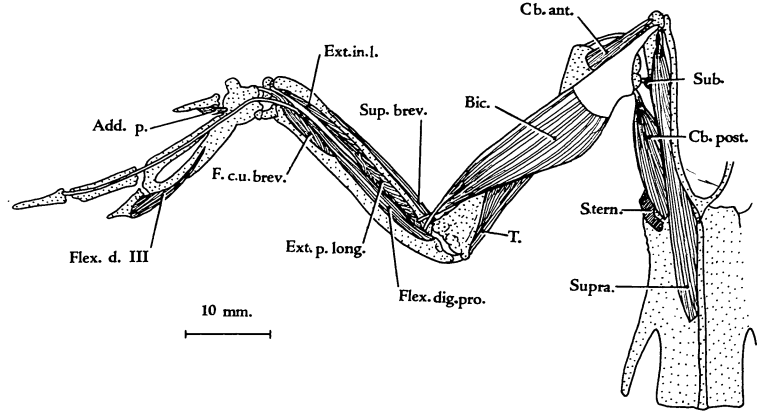

Fig. 2

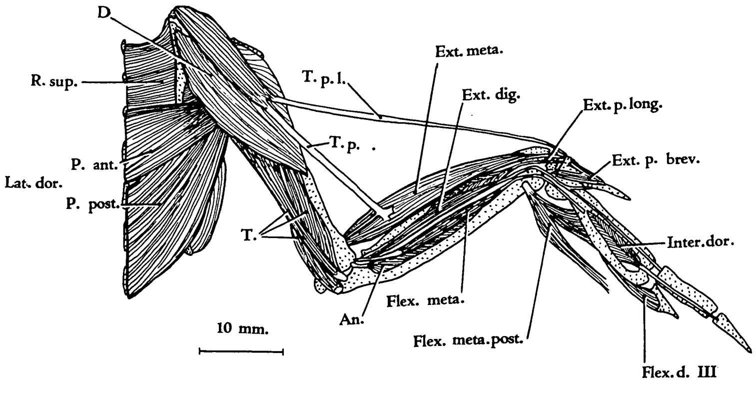

Fig. 3

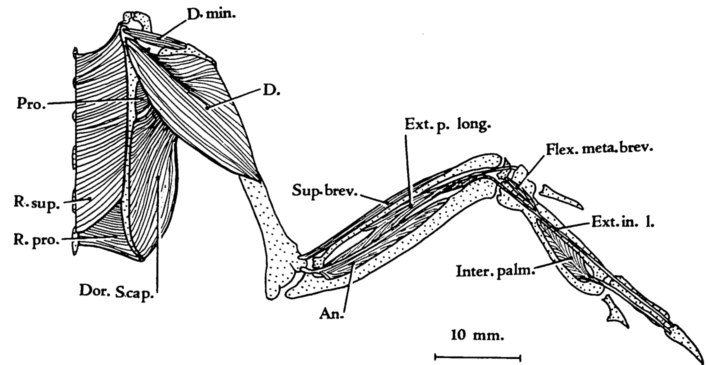

Fig. 4

Corrigenda to The Myology of the Pectoral Appendage of Three Genera of American Cuckoos, by Andrew J. Berger

Miscellaneous Publications, Museum of Zoology, University of Michigan, No. 85, 1954.

p. 13. *M. dorsalis scapulae*, 3rd sentence. To read:

The fleshy fibers continue almost to the insertion, which is by a strong tendon on the proximal end of the anconal surface of the bicipital crest of the humerus.

p. 27. Osteology. 3rd sentence. To read:

Length of the manus (carpometacarpus plus digit II) is progressively shorter from *Coccyzus* to *Geococcyx:* a 12.9 per cent decrease from *Coccyzus* to *Crotophaga;* a 17.6 per cent decrease from *Coccyzus* to *Geococcyx.*

p. 28. 3rd sentence. To read:

We seem to be dealing with the loss of a "tendency to flight as a means of locomotion," rather than with a "progressive loss of flight ability."

p. 30. TABLE II. Second muscle from bottom, to read:

Extensor pollicis longus.

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No. 64. Goniobasis livescens of Michigan. By Calvin Goodrich. (1945) Pp. 36, 1 plate, 1 figure, 1 map $0.35

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