SOME ANATOMICAL CHARACTERS OF THE CUCULIDAE AND THE MUSOPHAGIDAE

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MOST authors have placed the African touracos ("plantain-eaters") and the cosmopolitan cuckoos in a single order, the Cuculiformes or Cuculi (e.g., Mayr and Amadon, 1951, Wetmore, 1951). Bannerman (1933), Moreau (1938, 1958), Lowe (1943), and Verheyen (1956*a*, 1956*b*), however, believed that the touracos deserve ordinal rank, the Musophagiformes. I agree with these authors but not for some of the reasons they cite.

I have been interested in the anatomy and relationships of these two groups of birds for over a decade, but it now seems unlikely that it will be feasible to continue this work. Consequently, I have decided to publish certain information which, although still very incomplete, may prove useful to other investigators. The complete appendicular myology of a touraco apparently has never been described. My plan, therefore, is to describe this musculature for *Tauraco leucotis donaldsoni* ("*Turacus donaldsoni*") and then to compare the myology, osteology, and pterylosis of this touraco with that of the cuckoos. Such a comparison can not be made properly without also analyzing differences in morphology within the family Cuculidae.

This paper is based on the dissection of one or more specimens of the following genera and species of cuckoos: *Carpococcyx radiceus, Centropus bengalensis, C. superciliosus, Ceuthmochares aereus, Chrysococcyx cupreus, Ch.* ("*Lampromorpha*") *klaas* and *caprius, Ch.* ("*Chalcites*") *basalis, Clamator jacobinus, Coccyzus americanus, C. erythropthalmus, Coua serriana, C. reynaudii, C. ruficeps, C. cristata, C. caerulea, Crotophaga sulcirostris, Cuculus canorus* and sp., *Dromococcyx pavoninus, Geococcyx californianus, Guira guira, Morococcyx erythropygus, Piaya cayana, Phaenicophaeus pyrrhocephalus, Saurothera merlini, Surniculus lugubris, Tapera naevia.* These 18 genera represent less than half of the 38 genera recognized by Peters (1940), although several of his genera have been suppressed by later workers (e.g., Mayr, 1944; Delacour and Mayr, 1945; Delacour, 1946; Berger, 1955*b*). Consequently, it must be borne in mind that conclusions and generalizations presented here may have to be altered when data become available on the remaining genera of cuckoos. As a matter of convenience for other workers, I have, by and large, used Peters' genera and species of cuckoos. I do this in part because I do not agree with those who propose that it is not necessary to examine the internal anatomy of a given species merely because an earlier genus has been suppressed and its contained species have been placed in some other genus. Evidence presented here certainly casts doubt on the wisdom of

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[1] I dedicate this paper to Erwin Stresemann on the occasion of his 70th birthday.

synonymizing some genera of cuckoos, as has been done on the basis of external characters alone.

Over the years I have received alcoholic specimens from several generous cooperators: Dean Amadon, Jacques Berlioz, Ernest P. Edwards, Herbert Friedmann, Mrs. Richard R. Graber, Theodore Miller, Renaud Paulian, Helmut Sick, George M. Sutton, P. B. Uzzell, and John G. Williams.

Some of the material from museums had been collected many years ago. In a few specimens, an incision through skin and muscle had been made from chin to vent. It is difficult (and sometimes impossible) to determine accurately the details of the ventral feather tracts in such birds. In two specimens, the articulations of the sternal ribs had been cut bilaterally and the viscera were held in place by strings tied around the body. When the strings were cut, the sternum fell out of the body! Shot damage to the specimen of *Dromococcyx* was so great that I could not study some important anatomical details. I made a plea several years ago (1955*a*) for better anatomical material. For the benefit of all students of pterylosis, myology, etc., I repeat that plea here. One often feels that it is better to have no representative of a species or genus than to have a specimen so mutilated by shot damage or by incisions that one can obtain only a portion of the information that one needs.

Anatomists sometimes are criticized for publishing information based on the dissection of only one or two specimens of a species. To be sure, the anatomist would be delighted to have a dozen or more specimens of each form that he is studying, but he is rarely so fortunate. In order to obtain the specimens that form the basis for this paper, I wrote well over a hundred letters to all parts of the world during a 12-year period. Perhaps this is the best example that I could cite to emphasize the continuing great need for well-preserved anatomical material.

WING MUSCLES OF *TAURACO LEUCOTIS DONALDSONI*

M. latissimus dorsi.—Pars anterior arises from the neural spines of the last two cervical and the first dorsal vertebrae. It inserts fleshily over an area 7 mm. long beginning 9 mm. from the proximal end of the head of the humerus. *Pars posterior* arises from the neural spines of the five dorsal vertebrae. It inserts by a flat tendon (2 mm. wide) immediately posterior to the proximal end of the insertion of pars anterior. *Pars metapatagialis*, the dermal component, is a very small band of fleshy fibers about 1 mm. in width. It arises from the superficial surface of pars posterior at the level of the spine of dorsal vertebra number 4; it inserts into the skin at the posterior margin of the humeral feather tract adjacent to the insertion of M. serratus metapatagialis.

M. rhomboideus superficialis arises by an aponeurosis from the neural spines of the last three cervical and the first two dorsal vertebrae. The fleshy fibers pass outward and forward to insert on the anterior 36 mm. of the scapula.

M. rhomboideus profundus arises by an aponeurosis from the neural spines of the last two cervical and the first two dorsal vertebrae. The muscle inserts on the posterior 28 mm. of the scapula.

M. cucullaris, pars propatagialis.—I did not find any tendon of this muscle inserting on the tendon of the tensor patagii longus.

M. serratus profundus has a typical origin from the posterior cervical vertebrae and from the cervicodorsal ribs. The several fasciculi pass backward to insert on the medial surface of the scapula.

M. serratus anterior arises by a superficial and a deep band of fibers. The larger and more superficial slip arises from the lateral surface of the first true rib, ventral to the uncinate process. The deeper slip arises from the ventral portion of the last cervicodorsal rib. The two slips fuse and give rise to a strong aponeurosis (6 mm. wide), which passes upward between the two heads of M. subscapularis to insert on the ventral edge of the scapula just caudal to the glenoid fossa.

M. serratus posterior arises by fleshy fasciculi primarily from the uncinate processes of true ribs numbers 1, 2, and 3. The complex is an extensive, but thin, sheet of fleshy fibers that inserts on the apex of the scapula (by fleshy fibers) and on the ventral edge of that bone (by an aponeurosis) as far craniad as the insertion of M. serratus anterior. *Pars metapatagialis,* the dermal component, has a typical origin. The belly, about twice as large as pars metapatagialis of M. latissimus dorsi, passes upward to insert into the skin at the posterior margin of the humeral feather tract.

M. proscapulohumeralis is a thin strap of fleshy fibers 4 mm. wide at its origin from the scapula immediately posterior to the glenoid lip and the origin of M. scapulotriceps. The belly is about 13 mm. in length. It has a typical insertion on the humerus between the two heads of origin of M. humerotriceps.

M. dorsalis scapulae arises from the lateral surface of the scapula in its posterior 33 mm. It inserts on the anconal surface of the bicipital crest of the humerus.

M. subscapularis has the usual two heads.—*Pars externa* arises for a distance of 8 mm. from the ventrolateral edge of the scapula, beginning a short distance caudal to the glenoid fossa. *Pars interna* arises from an area about 20 mm. long on the medial surface of the scapula. The two heads fuse and insert by a short stout tendon on the internal tuberosity of the humerus, adjacent to the insertion of M. subcoracoideus.

M. subcoracoideus arises by two heads, a clavicular head and a coracoidal head. The clavicular head is unusually well developed. It has an extensive origin from an area 17 mm. long on the medial surface of the superior end of the clavicle and from the acromion of the scapula. The coracoidal head arises from the basal 10 mm. of the posterior face of the coracoid and from the adjacent coracoclavicular membrane. The two heads fuse and insert in common on the internal tuberosity of the humerus.

M. coracobrachialis anterior is a well-developed muscle, although it does not cover the anterior surface of the head of the humerus. It arises from the head of the coracoid (and adjacent ligaments) immediately dorsal to the origin of M. biceps brachii. The belly (about 13 mm. long and 5 mm. in maximum width) passes outward, closely applied to the capsule of the shoulder joint, to insert on the proximal end of the humerus.

M. coracobrachialis posterior has a typical origin and insertion.

M. supracoracoideus has a typical origin from the sternum and the coracoclavicular membrane. A very large tendon of insertion is formed; the fleshy fibers continue through the triosseal canal (see p. 82) with the tendon and cover it almost to the point of insertion on the humerus.

M. sternocoracoideus has a typical origin and insertion.

M. pectoralis.—*Pars thoracicus* is very well developed; it has a typical origin and insertion. *Pars propatagialis longus et brevis* is a large fleshy fasciculus arising from the ventral surface of pars thoracicus. The fleshy bundle fuses with the distal end of the belly of M. tensor patagii longus, but it also gives rise to a flat bandlike tendon which appears to form the bulk of the tendon of M. tensor patagii brevis. The belly of the latter muscle appears to insert into the tendon formed from pars propatagialis. Near its formation, the tendon of pectoralis pars propatagialis has a tendinous anchor to the anterior edge of the deltoid crest of the humerus.

M. deltoideus major has a total length of belly (from the scapular origin) of about 44 mm.;the terminal tendinous insertion reaches to within 12 mm. of the distal end of the humerus. The longer head arises from the acromion of the scapula and by a strong aponeurosis from the ventral edge of that process, as in *Coua caerulea.* The much smaller anterior head arises from the very large os humeroscapulare; it inserts by fleshy fibers on the anconal surface of the deltoid crest.

M. deltoideus minor is, relatively, a fairly well-developed muscle in the touraco. It is a flat band of fleshy fibers 3 mm. wide and 14 mm. long. Unlike the origin in *Coua,* it arises from the acromion and from the coracoscapular and acromioclavicular ligaments. It has a typical insertion at the junction of the articular head and the deltoid crest of the humerus. The belly, which passes anterior to the os humeroscapulare and overlies the subjacent tendon of M. supracoracoideus, is visible anterior to M. deltoideus major after removal of Mm. tensores patagii longus et brevis.

Mm. tensores patagii longus et brevis are represented by a common belly which arises from the dorsal and medial surfaces of the apex of the clavicle and the tip of the acromion; posteriorly, the origin is shared with the posterior head of M. deltoideus major. The origin of this complex in *Tauraco leucotis* is like that found in the cuckoos and not like that illustrated for *Tauraco corythaix* by Lowe (1943). The insertion of the tensor patagii brevis seems to be similar in the two species, and I suspect that Lowe's separation of the tendon into two discrete slips in *corythaix* may have been an artifact. At any rate, in *leucotis* the tendon of the brevis is a single sheet (about 1.5 mm. wide) which inserts primarily into the belly of M. extensor metacarpi radialis, but an extension of this tendon-sheet proximally passes posteriorly over the forearm muscles to fuse with the antebrachial fascia, which is closely adherent to the bases of the proximal secondaries.

M. biceps brachii has a typical double origin from the coracoid and from the bicipital crest of the humerus. The belly, 37 mm. in length, extends to the distal end of the humerus. The tendon bifurcates to insert 2 mm. and 3 mm., respectively, from the proximal ends of radius and ulna. A biceps slip is not present.

M. triceps brachii exhibits about the same development as in the cuckoos. The scapulotriceps portion has a somewhat two-headed fleshy and tendinous origin: one head from the lateral surface of the scapula, dorsal to the glenoid fossa; the other head from the ventrolateral edge of the scapula just caudal to the glenoid lip. There is no humeral anchor. The humerotriceps can be divided into two heads only proximally, where the two heads arise on either side of the insertion of M. proscapulohumeralis. There is a typical insertion on the olecranon and the adjacent area on the proximal end of the ulna.

M. expansor secundariorum is similar in structure to that previously described for several cuckoos in that there is both a humeral and a scapular origin. The two tendons of origin give rise to fleshy fibers that insert on several of the proximal secondaries. The short tendon arises from the distal end of the humerus. The long tendon extends proximad through the metapatagial skin fold to the axilla where the tendon bifurcates. The dorsal branch attaches to the medial surface of the scapula, deep to the origin of M. subcoracoideus and at about the line of separation between this muscle and M. subscapularis (pars interna). The ventral branch attaches to the coracoid in relation to the origin of M. coracobrachialis posterior; this attachment I have not found in the cuckoos (see p. 77).

M. anconaeus coracoideus.—I did not find this muscle in the specimen I dissected.

M. brachialis is typical in origin and insertion.

M. pronator superficialis is a well-developed muscle (belly 35 mm. long) which extends to within 10 mm. of the distal end of the radius.

M. pronator profundus, with a belly 32 mm. long, extends distad almost as far as M. pronator superficialis. The origin of both muscles is typical.

M. flexor digitorum superficialis has a typical origin from the distal end of the humerus. The tendon of origin expands into a broad aponeurosis (the humerocarpal band) which extends the entire length of the ulna and fuses with the fascia around the bases of the secondaries; near the distal end of the ulna, the humerocarpal band gives rise to fleshy fibers (essentially a second belly for the muscle), which fuse with the main belly just before the tendon of insertion is formed. The main belly (30 mm. long) arises from the deep surface of the humerocarpal band, beginning 12 mm. from its humeral attachment. The muscle inserts on the base of the proximal phalanx of digit II.

M. flexor digitorum profundus arises by a single head from the ulna, posterior to the area of insertion of M. brachialis. The belly is about 33 mm. in length; it extends to the distal end of the ulna. The main tendon of insertion passes around the pisiform process of the carpometacarpus and then passes distad superficial to the tendon of the flexor digitorum superficialis to insert on an extensive area of the distal phalanx of digit II. A very unusual feature is the presence of a second tendon given off the main tendon opposite the base of the pollex; this tendon inserts on the palmar surface of the pollex.

M. flexor carpi ulnaris is a well-developed muscle, whose belly (37 mm. long) extends nearly the entire length of the forearm. The origin and insertion are typical, but fleshy fibers do not insert on the bases of the secondaries as they do in *Coua caerulea.*

M. extensor metacarpi radialis has a typical origin from the lateral epicondyle of the humerus. The belly is about 34 mm. long. The tendon of the tensor patagii brevis muscle inserts into the belly and its enveloping fascia about 10 mm. distal to the humerus. The tendon of M. extensor metacarpi radialis inserts on the extensor process of the carpometacarpus. M. abductor pollicis arises from the tendon a short distance before its insertion.

M. flexor metacarpi radialis arises by a tendon attached to the lateral epicondyle of the humerus. The belly is about 28 mm. long, and the fleshy fibers begin about 10 mm. from the humeral origin of the tendon. A fascial extension of the tendon of origin fuses with the fascia surrounding the bases of the proximal secondaries. The tendon inserts on metacarpal II, about 6 mm. from the proximal end of that bone at the proximal limit of the intermetacarpal space.

M. extensor digitorum communis arises by a tendon from the lateral epicondyle of the humerus. The fleshy fibers of the 33 mm.-long belly begin almost at the humeral origin of the tendon. Two tendons are formed near the base of the carpometacarpus. The shorter tendon inserts on the base of the pollex. The longer tendon runs in a groove on the dorsal surface of metacarpal II; near the distal end of that bone, the tendon turns abruptly around a bony tubercle to insert on the base of the proximal phalanx of digit II.

M. anconeus has a typical origin from the humerus. The belly (39 mm. long) extends nearly the entire length of the ulna.

M. supinator has a typical origin from the humerus. The belly is short (about 18 mm.), extending less than half the length of the radius, on which bone it inserts.

M. extensor indicis longus is a long (26 mm.), thin muscle arising from the radius only. Its tendon inserts on the base of the distal phalanx of digit II.

M. flexor metacarpi brevis is absent bilaterally.

M. flexor carpi ulnaris brevis is a short muscle, with a belly 13 mm. long, arising from the ventral surface of the distal third of the ulna. The tendon has a typical insertion on the dorsal surface of the base of the carpometacarpus.

M. extensor pollicis longus is a well-developed muscle with two heads of origin; the over-all length of the belly is 34 mm. The smaller head (24 mm. long) arises from the middle half of the radius. The larger head (30 mm. long) arises from the ulna, beginning at the level of insertion of M. biceps brachii. The tendon inserts on the extensor process of the carpometacarpus deep to the tendon of M. extensor metacarpi radialis.

M. extensor pollicis brevis is a triangular muscle with two heads of origin and with a total length of about 6 mm. The larger head arises from the base of the carpometacarpus. The smaller head arises from the base of the extensor process and from the tendon of insertion of M. extensor pollicis longus.

M. abductor pollicis, with a single belly 6 mm. long, has a typical origin from the tendon of insertion of M. extensor metacarpi radialis. It inserts by fleshy fibers on the pollex.

M. adductor pollicis arises fleshily from the anterior surface of the carpometacarpus near the base of the extensor process. It inserts by fleshy fibers on the posterior face of the pollex.

M. flexor pollicis is a very small band, less than 1 mm. in width, which arises from the carpometacarpus; it inserts on the base of the pollex, posterior and adjacent to the insertion of M. abductor pollicis.

M. abductor indicis is a well-developed muscle, arising from an extensive area on the base of the carpometacarpus, both anterior and posterior to the pisiform process, and from nearly the entire length of the anterior surface of metacarpal II. The muscle inserts by a stout tendon on the anterior surface of the proximal phalanx of digit II.

M. flexor metacarpi posterior has a typical origin by a strong flat tendon from the distal end of the ulna. The well-developed belly inserts on the posterior surface of about the proximal half of metacarpal III, and it also sends fleshy fasciculi into the bases of the proximal five or six primaries.

M. flexor digiti III arises along a narrow line from most of the palmar surface of metacarpal III, beginning at the proximal limit of the intermetacarpal space, and from the posterior surface of that same bone distal to the insertion of M. flexor metacarpi posterior. The muscle inserts by a tendon on the base of digit III and by fleshy fibers on the entire anconal surface of that digit.

Mm. interossei dorsalis et palmaris have typical origins from the facing surfaces of metacarpals II and III. M. interosseus dorsalis inserts by a tendon on the base of the distal phalanx of digit II. M. interosseus palmaris inserts by a tendon a little beyond mid-length of the distal phalanx of digit II.

"Leg" Muscles of *Tauraco leucotis donaldsoni*

M. sartorius arises from the anterodorsal end of the ilium only, i.e., it has no origin from the neural spine of the last dorsal vertebra. It inserts on the anteromedial corner of the head of the tibiotarsus.

M. iliotibialis is a very extensive muscle, covering all other muscles on the lateral aspect of the thigh except for parts of Mm. sartorius and semitendinosus. The central part of the complex is aponeurotic in its distal three-fifths. The muscle arises from the anterior iliac process and from the entire length of the anterior and posterior iliac crests. Most of the origin is by an aponeurosis (including that from the anterior iliac process), but the origin posteriorly is by fleshy fibers. Anteriorly, the origin is inseparably fused with the origin of M. sartorius. Distally, the tendon contributes to the formation of the patellar ligament, inserts on the tibiotarsus, and fuses with the deep fascia of the crus, particularly that covering M. peroneus longus.

M. iliotrochantericus posterior is well developed and has a considerable bulk of its fibers arising dorsal to the acetabulum. The muscle arises from the anterior iliac process and from all of the anterior iliac fossa. It inserts on the femur by a strong flat tendon, beginning 1 mm. distal to the trochanter.

M. iliotrochantericus anterior also is well developed. It arises from the posterior surface of the anterior iliac process and from the ventrolateral edge of the ilium. It inserts by a strong tendon (2 mm. wide) on the lateral surface of the femur, beginning 7 mm. distal to the proximal end of that bone.

M. iliotrochantericus medius is absent bilaterally.

M. gluteus medius et minimus is conspicuously developed, especially the long tendon of insertion, which passes superficial to the tendon of M. iliotrochantericus posterior to insert on the posterolateral edge of the femur about 7 mm. from the proximal end of that bone between the areas of insertion of Mm. iliotrochantericus anterior and ischiofemoralis. The fleshy belly is 5 mm. long; it arises from the most posterior part of the anterior iliac crest.

M. femorotibialis externus arises by fleshy and semitendinous bands (especially distally) from most of the lateral surface of the femur. The origin begins just distal to the level of insertion of M. iliotrochantericus anterior.

M. femorotibialis medius arises by tendinous and fleshy fibers from the trochanteric ridge and the femoral shaft distal to it. The belly is fused with that of M. femorotibialis externus. Both muscles contribute to the patellar ligament; their configuration is like that illustrated for *Coua caerulea* (Berger, 1953*a*: Fig. 6).

M. femorotibialis internus is a long thin muscle that arises from the medial surface of the femur, beginning 14 mm. inferior to the neck of that bone; the belly increases in size distally. It inserts by a single tendon on the anteromedial surface of the head of the tibiotarsus.

M. biceps femoris arises by two heads which fuse at about mid-thigh level. The anterior head is somewhat larger; it arises by an aponeurosis from the caudal portion of the anterior iliac crest and by fleshy fibers from the anterior 3 mm. of the posterior iliac crest. The more rounded posterior head arises by tendinous and fleshy fibers from a pronounced tubercle on the lateral surface of the ilium about 3 mm. ventral to the projecting posterior iliac crest. The muscle inserts by a stout, rounded tendon on the fibula about 16 mm. inferior to the head of that bone.

M. ischiofemoralis has a typical origin from the lateral surface of the ischium, dorsal to the origins of Mm. semimembranosus and adductor longus et brevis. It inserts by a strong tendinous band (2.5 mm. wide) beginning 5 mm. inferior to the trochanter and immediately posterior to the insertion of M. gluteus medius et minimus.

M. piriformis.—Both parts of this complex are well developed. *Pars caudofemoralis* arises from the base of the pygostyle by a wide (8 mm.) tendinous band and by fleshy fibers from the superficial surface of this band. The maximum width of the belly, inferior to the posterior iliac crest, is 10 mm. *Pars iliofemoralis* arises by fleshy fibers from the lateral surface of the ilium, ventral to the origin of Mm. semitendinosus and biceps femoris. The belly passes downward and forward, superficial to pars caudofemoralis, to insert on the posterolateral edge of the femur for a distance of 7 mm., beginning 10 mm. inferior to the trochanter. Pars caudofemoralis inserts by a tendon-sheet (4.5 mm. wide), beginning 12 mm. inferior to the trochanter and immediately medial to and in contact with the insertion of pars iliofemoralis.

Mm. semitendinosus and *accessorius semitendinosi.*—The bulky semitendinosus muscle arises from the ventral surface of the projecting posterior iliac crest in its posterior 8 mm.; there is no origin from the free caudal vertebrae. The raphe which separates this muscle from the accessory semitendinosus muscle behind the knee broadens into a 2 mm.-wide tendon, which inserts on the medial surface of the tibiotarsus 2 mm. posterior to the insertion of M. semimembranosus. The accessorius muscle inserts by fleshy fibers on the posterolateral edge of the femur in its distal 13 mm.

M. semimembranosus arises by an aponeurosis (shared in part with M. adductor longus et brevis, pars externa) attached to the lateral surface of the ischium a few millimeters dorsal to the ischiopubic fenestra. Most of the thin sheetlike belly of the semimembranosus muscle is concealed by the overlying semitendinosus muscle. M. semimembranosus inserts along a curved line (6 mm. long) on the anteromedial edge of the tibiotarsus, beginning 7 mm. inferior to the proximal end of that bone.

M. iliacus.—I found no evidence of this muscle in either leg.

M. ambiens is a thin strap of muscle, 30 mm. in length; it has a maximum width of 5 mm. near its origin from the pectineal process. It arises mostly by fleshy fibers. The tendon of insertion, like that in *Coua caerulea,* enters the patellar ligament and passes diagonally downward and laterad around the front of the knee. Below the knee the tendon fans out into an aponeurosis which gives origin to parts of Mm. flexores perforati digiti II, III, and IV.

M. obturator internus is a well-developed triangular-shaped muscle arising from the medial surface of the ischium and pubis; it also has a large portion arising in the renal depression, as in *Coua* and several other unrelated birds. The large tendon passes out of the obturator foramen and inserts on the lateral surface of the femur, proximal to the insertion of M. ischiofemoralis and beginning about 3 mm. inferior to the trochanter. The tendon of M. gluteus medius et minimus passes superficial to the tendons of insertion of Mm. obturator internus and externus.

M. obturator externus is a small band of fleshy fibers arising from the dorsal margin of the obturator foramen. A flat tendon forms and fuses with the proximal side of the tendon of M. obturator internus.

M. adductor longus et brevis is composed of two distinct parts. *Pars externa* arises by an aponeurosis (8.5 mm. wide) from the lateral surface of the ischium, beginning about 2 mm. caudal to the obturator foramen and 4 mm. dorsal to the ischiopubic fenestra. Pars externa inserts on the femur medial to M. piriformis and beginning at the inferior limit of the tendon of pars caudofemoralis and extending distad about 23 mm. *Pars interna* arises by a dense aponeurosis 10 mm. wide, beginning at the posterior margin of the obturator foramen and passing caudad along the dorsal margin of the ischiopubic fenestra. Fleshy fibers form at once in the anterior fifth, but posteriorly the aponeurosis extends distad about 15 mm. before fleshy fibers arise. Pars interna inserts on the femur mostly by an aponeurosis (by fleshy fibers superiorly), medial to the insertion of pars externa and extending for a distance of 33 mm.

M. tibialis anterior, as in other birds, has both a femoral and a tibial head. The femoral head arises by a stout tendon from the anterodistal end of the external femoral condyle. The tibial head arises in common with, but deep to, M. peroneus longus. The two heads fuse about a third the way down the crus. The over-all length of the belly is 60 mm., and it extends distad as far as the ligamentum transversum. A very large tendon of insertion is formed; it passes deep to the ligamentum transversum and inserts 7 mm. inferior to the proximal end of the tarsometatarsus. Just before the area of insertion, the tendon gives off a fascial band that fuses with the fascia covering the muscles of the anterior surface of the tarsometatarsus.

M. extensor digitorum longus arises by fleshy fibers from the proximal third of the anterior surface of the tibiotarsus and from the inner and outer cnemial crests of that bone. The belly extends for a distance of 60 mm., but the muscle is very small in its distal half. The tendon passes deep to the ligamentum transversum and then under a bony bridge on the anterior surface of the tibiotarsus. Continuing distad, the tendon is held in place by a strong ligament (and not by a bony bridge) on the proximal end of the tarsometatarsus. The tendon trifurcates in the distal third of the tarsometatarsus to supply digits II, III, and IV. The tendon complex to digit III (the largest digit) is unusually well developed; the small single tendon to digit II exhibits the poorest development. Attachments of the tendons are made to each of the phalanges of the respective digits.

M. peroneus longus arises by semitendinous bands, in common with the underlying muscles, from the outer and inner cnemial crests and the rotular crest of the head of the tibiotarsus. The belly is about 50 mm. long, and, although it covers all of the other muscles on the anterolateral surface of the proximal five-sevenths of the crus, it is a relatively thin sheet of muscle which does not extend around to the medial surface of the crus (as this muscle does in *Coua*). The tendon bifurcates near the distal end of the tibiotarsus. The shorter of the two tendons inserts on the tibial cartilage and associated ligaments. The longer tendon passes downward to insert on the tendon of M. flexor perforatus digiti III a short distance inferior to the proximal end of the tarsometatarsus.

M. peroneus brevis arises from the fibula and the tibiotarsus for a distance of about 45 mm., beginning at the level of insertion of M. biceps femoris. It inserts on the posterolateral corner of the proximal end of the tarsometatarsus at the base of the hypotarsus.

M. gastrocnemius has the typical three heads. *Pars externa* arises primarily by a flat aponeurotic band fused to the lateral surface of the distal arm of the biceps loop. *Pars media* arises from the posterior surface of the distal end of the femur, immediately distal to the area of insertion of M. accessorius. *Pars interna* arises from the entire medial surface of the inner cnemial crest of the tibiotarsus and from the fascia covering the anterior and medial aspects of the knee joint, where this head has an intimate relationship to the fleshy insertion of M. sartorius. None of pars interna covers the anterior or lateral portion of the crus, as it does in *Coua caerulea.* Pars media and pars interna are separated by the tendon of insertion of M. semimembranosus. There is also a strong fascial band extending from M. semitendinosus to both pars media and pars interna. The very strong common tendon of M. gastrocnemius inserts on the back of the hypotarsus and the posterior ridges of the tarsometatarsus throughout most of its length.

M. plantaris has a typical origin from the proximal end of the tibiotarsus. The belly is about 18 mm. in length. The small tendon of insertion expands distally and inserts on most of the proximal end of the tibial cartilage.

M. popliteus is a reasonably well-developed muscle, about 3 mm. wide and 6 mm. long. Both the origin and the insertion are semitendinous. It arises from the head of the fibula. The fleshy fibers pass downward and mesiad to the insertion on the tibiotarsus.

M. flexor perforatus digiti II is a small muscle with a belly 35 mm. long but only 3 mm. wide. It arises from the continuation of the ambiens tendon and from the deep surface of M. flexor perforatus digiti III. The tendon passes through the deep aspect of the lateral side of the tibial cartilage. The tendon of insertion is perforated by both of the deep flexor tendons to digit II (flexor digitorum longus and flexor perforans et perforatus digiti II) and then inserts on both sides of the proximal phalanx of digit II.

M. flexor perforatus digiti III arises from the femur (in common with Mm. flexor perforatus digiti IV and flexor hallucis longus) and from a broad aponeurosis which is a continuation of the ambiens tendon. The belly is 50 mm. in length. The long tendon of

M. peroneus longus inserts on the tendon about 8 mm. inferior to the proximal end of the tarsometatarsus. Near the distal end of the tarsometatarsus, the tendon is united by a vinculum ("V") with the tendon of M. flexor perforans et perforatus digiti III, which lies deep to the tendon of M. flexor perforatus digiti III. The vinculum arises from the deep surface of the latter tendon and then passes deep to the subjacent tendon of flexor perforans et perforatus digiti III, so that the vinculum fuses with the deep side of the latter tendon. The very large tendon of insertion of M. flexor perforatus digiti III is perforated by both of the deep flexor tendons to digit III and then inserts on both sides of the proximal phalanx and on the base of the second phalanx of digit III.

M. flexor perforatus digiti IV arises from the femur (in common with Mm. flexor perforatus digiti III and flexor hallucis longus) and from the ambiens tendon. The belly is 40 mm. in length. At the base of digit IV, the tendon of flexor perforatus digiti IV expands into a large mass, which ensheathes the tendon to that digit of M. flexor digitorum longus. The tendon then sends slips to attach to the proximal ends of phalanges 2, 3, and 4 of digit IV.

M. flexor perforans et perforatus digiti II appears to arise exclusively from the lateral femorofibular ligament (i.e., there is no direct origin from bone), immediately distal to the attachment of the distal arm of the biceps loop. The belly is 22 mm. long. The tendon inserts on both sides (the medial slip being the stronger) of the bones at the interphalangeal joint between phalanges 1 and 2 of digit II.

M. flexor perforans et perforatus digiti III arises by fleshy and tendinous fibers from the outer cnemial crest, the third arm of the biceps loop, and from adjacent ligaments on the anterolateral aspect of the knee, including the patellar ligament. The belly is about 40 mm. long. The tendon perforates the tendon of M. flexor perforatus digiti III and is itself perforated by the tendon of M. flexor digitorum longus. It inserts on both sides of the distal end of phalanx 2, digit III.

M. flexor digitorum longus arises by two distinct heads from the proximal end of the tibiotarsus, most of M. popliteus being visible between the two heads. The belly (55 mm. long) extends to within 15 mm. of the distal end of the tibiotarsus, so that this muscle is very well developed as compared with M. flexor hallucis longus. The tendon of M. flexor digitorum longus is the only one that passes through a bony canal in the hypotarsus. Inferior to that process, the tendon of the flexor hallucis longus passes diagonally downward and superficial to the tendon. The two tendons are connected by a small vinculum in the distal fourth of the tarsometatarsus. The tendon of the flexor digitorum longus muscle trifurcates. The primary insertion of each branch is on the ungual phalanx of digits II, III, and IV. Vinculae pass from the deep surface of the tendons to other phalanges of these digits.

M. flexor hallucis longus is, compared with the flexor digitorum longus, a weakly-developed muscle with an over-all belly-length of about 30 mm. It arises by two distinct but short heads from the distal end of the femur; both heads lie medial to the tendon of M. biceps femoris. The more lateral (anterior of Hudson, 1937:49) and fleshy head arises from the posterior face of the external condyle. The larger medial head arises by tendinous fibers from the intercondyloid area of the femur; this origin is shared with Mm. flexores perforati digiti III and IV. The tendon of insertion *does not* pass through a bony canal in the hypotarsus, but passes along the lateral surface of that process, where it is held in place by a fascial band. The tendon inserts on the ungual phalanx of the hallux.

M. flexor hallucis brevis is a bulky muscle whose belly (15 mm. long) is limited to the proximal third of the tarsometatarsus. The tendon expands to ensheath the tendon of M.

flexor hallucis longus and then inserts on both sides of the base of the proximal phalanx of the hallux.

M. extensor hallucis longus arises by two heads, one on each side of the tendon of insertion of M. tibialis anterior. The medial head is the larger of the two. The origin begins at the proximal end of the tarsometatarsus. The over-all length of the belly is 15 mm. The tendon is held in place by fibrous bands at the distal end of the tarsometatarsus. The single tendon inserts on the base of the ungual phalanx of the hallux.

M. extensor proprius digiti III is a long, thin and weakly-developed muscle, whose belly begins at the proximal end of the tarsometatarsus between M. extensor brevis digiti IV and the tendon of M. tibialis anterior. The tendon forms at the junction of the proximal and middle thirds of the tarsometatarsus. Fleshy fibers insert on this tendon to the level of the trochlea for digit III, so that the over-all length of the fleshy belly is 35 mm. The tendon expands to insert on most of the dorsal surface of the proximal phalanx of digit III.

M. extensor brevis digiti IV is another long, thin muscle, whose origin begins at the proximal end of the tarsometatarsus and extends distad about 32 mm. The tendon passes around the trochlea for digit IV and inserts on the medial side of the base of the proximal phalanx of that digit.

M. abductor digiti II is a fairly stout muscle, 10 mm. long, which arises from the distal end of the tarsometatarsus. It inserts by a tendon on the dorsomedial corner of the base of the proximal phalanx of digit II. The tendon is visible throughout its course.

M. lumbricalis is vestigial. A few fleshy fibers (about 7 mm. in length) arise from the deep side of the tendon of M. flexor digitorum longus near the distal end of the tarsometatarsus.

M. abductor digiti IV has a small belly 10 mm. long, which is limited to the proximal end of the tarsometatarsus. The long tendon is held in place by a ligament at the distal end of that bone. The tendon inserts on the ventrolateral corner of the base of the proximal phalanx.

Comparative Myology

My reasoning in the analysis that follows may be clearer if prefaced by some general remarks. If we assume with Hudson (1937:77) that the generalized condition is represented in those birds that possess the full complement of formulae and other muscles (as in the Galliformes), it follows that the absence of muscles represents a specialized condition. We assume also that, by and large, closely related birds will have lost the same muscles, and that either the hypertrophy or the loss of leg muscles must in general be correlated with locomotor habits or feeding habits (as in the birds of prey, with their very large flexor digitorum longus and flexor hallucis longus muscles). Further, we recognize that the age of a genus (and/or its geographical isolation and related factors) may be such that differences in locomotor pattern within the genus may not yet be accompanied by extensive myological changes. Finally, we assume that what we refer to as a "vestigial muscle" is a muscle that is in the process of being lost phylogenetically, that the degree of degeneration of such a muscle may vary among individual specimens of a genus or a species, and that one might expect some individual variation in the presence or absence of such a vestigial muscle.

Lowe (1943:512–514) made a considerable issue out of the alleged difference in development of M. iliotibialis between *Tauraco corythaix* and *Cuculus canorus.* I have been puzzled by the fact that I could not in any sense corroborate Lowe's description and illustration of M. iliotibialis in *Cuculus.* Actually, there is little resemblance between Lowe's figure of this muscle in *Cuculus* and what I found in the specimens available for dissection. Except for the fact that the central portion of this muscle is not aponeurotic from origin to insertion, M. iliotibialis in *Cuculus* is very similar to that muscle in *Chrysococcyx* ("*Lampromorpha*") *caprius* (Berger, 1955*b*: Fig. 71), and it is almost identical to the muscle in *Ch. cupreus* (Fig. 1).

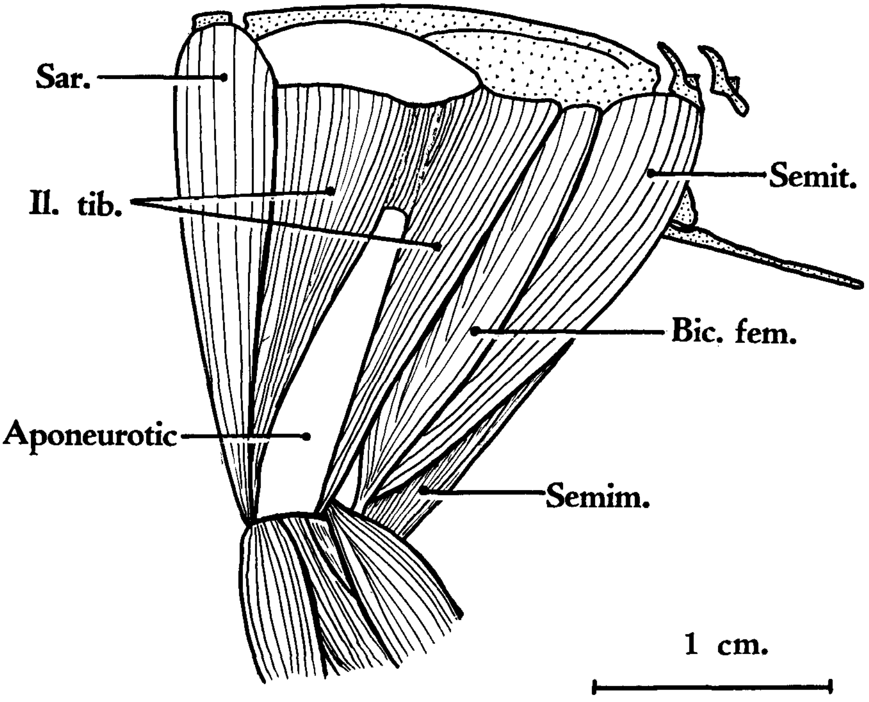

FIG. 1. Lateral view of thigh of *Chrysococcyx cupreus* to illustrate the relative weak development of M. iliotibialis. Bic. fem., biceps femoris; Il. tib., iliotibialis; Sar., sartorius; Semim., semimembranosus; Semit., semitendinosus.

In *Cuculus,* M. iliotibialis arises by fleshy fibers from the tip of the anterior iliac process and by an aponeurosis from the anterior iliac crest and the cephalic half of the posterior iliac crest. The caudal part of this aponeurosis overlies the origin of the anterior portion of M. biceps femoris (as in other cuculine genera), but the iliotibialis muscle has no direct attachment to the belly of the biceps muscle (as illustrated by Lowe). The posterior segment (the gluteus posterior of Gadow) of the iliotibialis muscle is poorly developed so that it does not conceal any part of Mm. semitendinosus or semimembranosus, and it conceals only a small proximal and anterior part of M. biceps femoris. The central portion of the iliotibialis muscle is aponeurotic in about its distal half, and few, if any, of the fleshy fibers of the relatively small anterior and posterior fleshy parts of the complex extend distad as far as the knee. Relative to other cuckoos, M. iliotibialis is poorly developed in *Cuculus* and in *Chrysococcyx.* In many cuckoos, however, the development of M. iliotibialis is equal to that found in *Tauraco.* Hence, this muscle does not offer any clues concerning the relationship between the touracos and the cuckoos. It might be well to add that, anatomically, *Cuculus* is perhaps the least "typical" genus of the family, and, therefore, that it is a poor genus to use as a basis for comparison with genera of other families. Although much information is needed on the habits of other parasitic cuckoos, it would appear that *Cuculus* is the most highly specialized genus in the family.

Hudson (1937:14) reported that among American genera of birds, M. iliacus is "present in all forms examined and is one of the most uniformly developed thigh muscles in birds." This muscle is present in some genera of cuckoos, absent in other (Old World) genera: *Carpococcyx, Centropus, Coua, Chrysococcyx,* and *Cuculus.* Moreover, I did not find this muscle in the specimen of *Tauraco leucotis* that I dissected.

M. iliacus is a small muscle at best (with a maximum width of about 1 mm. in most cuckoos examined), and it might easily be destroyed by shot or be torn away in dissecting. Except for *Carpococcyx,* however, I dissected two or more specimens of each of the other genera of cuckoos mentioned above and found no evidence of the muscle; it was absent in each of five species of *Coua.* Shot damage to both femora of the single specimen of *Dromococcyx* available for dissection made it impossible to determine whether or not M. iliacus is present in that genus. Because this muscle has been found in all other genera of American cuckoos examined, I assume tentatively that it is present in *Dromococcyx.* Relative to other muscles in the thigh, M. iliacus might well be considered vestigial or rudimentary (with a very weak action) in many birds. It is highly desirable for someone to conduct a study directed to determine whether or not the absence of this muscle within a genus or species is a matter of individual variation. Gadow and Selenka (1891:145) reported that M. iliacus was absent as an individual variation in *Bucorvus* and *Platycercus.*

Nevertheless, I have proposed (1959) that M. iliacus be included in leg-muscle formulae and that its presence be indicated by adding the letter "E" to such formulae. I would be among the first to agree that muscle formulae must be used with caution and that they often are misused. I think that this is especially the case when contemporary writers ignore data presented by Hudson and others and include only the symbols proposed many years ago by Garrod. Thus, if we use only Garrod's symbols, the muscle formula for *Tauraco leucotis* is ABXYAm; that for cuckoos is either ABXYAm or AXYAm. This is misleading because it does not tell the whole story; the myology of the hind limb is not that similar in the two groups of birds. This can be demonstrated by using Hudson's expanded muscle formula, with or without the addition of "E." The formula for *Tauraco* then becomes ABDXYAmV. For cuckoos the formulae are:

AXYAm—*Cuculus, Chrysococcyx*
AEXYAm—*Coccyzus, Piaya, Saurothera, Tapera, Clamator, Surniculus*
ABXYAm—*Coua, Carpococcyx, Centropus*
ABEXYAm—*Geococcyx, Morococcyx, Dromococcyx* (E?), *Crotophaga, Guira, Ceuthmochares, Phaenicophaeus*

It is my opinion that the presence of M. gluteus medius et minimus (D) and of the vinculum (V; between the tendons of Mm. flexor perforatus digiti III and flexor perforans et perforatus digiti III) in *Tauraco* and the absence of these structures in the cuckoos constitute a significant difference in their pelvic musculature. Another interesting difference is that in the cuckoos the two deep plantar tendons (the tendons of Mm. flexor digitorum longus and flexor hallucis longus) pass through separate bony canals in the hypotarsus, whereas in *Tauraco* there is a single bony canal that transmits only the tendon of M. flexor digitorum longus. M. flexor hallucis longus in *Tauraco* arises from the femur by two separate heads, both of which lie medial to the tendon of M. biceps femoris; in the cuckoos (but apparently not in *Centropus*) the muscle arises by a single head from the intercondyloid area of the femur.

Beddard (1898*a*:45) said that W. A. Forbes found the flexor hallucis longus muscle to be "totally absent" in *Centropus* (see also Verheyen, 1956*a*: 8), but I found it in both species examined. Beddard (1898*b*:276) further stated that the deep plantar tendons of *Centropus* are peculiar in that "no branch is sent to the hallux," and I found this to be true. M. flexor digitorum longus in *Centropus* is at least twice as bulky as M. flexor hallucis longus, although the latter muscle extends distad about half the length of the tibiotarsus. The tendons of both muscles pass through bony canals in the hypotarsus, below which the tendon of M. flexor hallucis longus fuses completely with the tendon of M. flexor digitorum longus. The resulting common tendon trifurcates to send branches to insert on digits II, III, and IV; *no branch is sent to the hallux.* There exists, however, a most unusual condition that I have not seen in any other genus. There is a very large automatic flexor of the hallux (Berger, 1953*a*:75). From its attachment to the trochlea and the fibrocartilaginous pulley for digit IV, the automatic flexor passes mesiad to the base of the hallux and then runs distad (held close to the bone by a vaginal sheath) to insert on the entire *plantar* surface of the base of the distal phalanx of the hallux. Consequently, the relationships of the automatic flexor to the phalanges in *Centropus* are identical to those of the flexor hallucis longus tendon when it is present as in the other cuckoos. The absence of the tendon of M. flexor hallucis longus to the hallux in *Centropus* is compensated for, in part, because M. extensor hallucis longus not only has a typical insertion on the dorsal surface of the distal phalanx but it also sends a strong slip to insert on the medial and plantar edge of the proximal phalanx of the hallux (for other examples of this double insertion, see Hudson, 1937:52).

The absence of pars iliofemoralis (B) of M. piriformis (=M. caudofemoralis) in some of the cuckoos raises interesting questions. The muscle is absent in the more arboreal members of the group; it is present in the more terrestrial members (but also in *Eudynamis*). In locomotor habits, *Guira* and *Crotophaga* are intermediate between the cursorial *Geococcyx* and the arboreal *Coccyzus.* Both *Guira* and *Crotophaga* possess the full cuculine complement of leg muscles, and they also share similar social nesting habits. In this instance, therefore, the similarity in development of leg muscles would seem to indicate closeness of relationship rather than locomotor pattern. I assume that the primitive cuckoos possessed both parts of the piriformis complex and that the loss of pars iliofemoralis in certain modern cuckoos is a secondary condition correlated with locomotor habits, in this instance with perching and arboreal habits (often also with parasitic breeding habits). One disadvantage of muscle formulae, however, is that they indicate nothing about the relative development of the muscles concerned. It is interesting to note, for example, that in *Ceuthmochares* (unlike any of the other genera possessing the muscle) pars iliofemoralis is vestigial; it is a minute band of fleshy fibers about 1 mm. in width. One might expect this muscle to be absent, either unilaterally or bilaterally, in some specimens of *Ceuthmochares.* As a possible similar example, I have pointed out elsewhere (1956:436) that pars caudofemoralis of the piriformis complex may be considered to be vestigial in the Sandhill Crane (*Grus canadensis tabida*), and Fisher and Goodman (1955:86) reported that pars caudofemoralis was absent in one of three specimens of the Whooping Crane (*G. americana*). In the cuckoos, pars caudofemoralis is relatively well developed in all species examined, although it is more strongly developed in the arboreal species. (For a discussion of the function of pars caudofemoralis, see Fisher, 1957.)

The relative development of Mm. peroneus longus and peroneus brevis in birds has been discussed by Mitchell and by Hudson (1937). Mitchell (1913: 1068) said: "I find it extremely difficult to associate the conditions of the peroneal muscles with differences in habit that point directly to functional adaptation," and that, with very few exceptions, "there is a close conformity between the condition of the peroneals and what appears to be the most securely founded systematic divisions. Birds seem to have this or that type of peroneal muscle, not because they are arboreal or terrestrial, swimmers or waders, scratchers, predatory or vegetarian, but because it is the type occurring in this or that systematic division."

One might agree in essence with such a generalization, but an analysis of these two muscles as found in the cuckoos may give one an insight into the difficulties involved as one attempts to determine which myological characters indicate closeness of relationship and which are a reflection of locomotor or other habits. These two factors are, of course, undoubtedly interrelated.

We may ignore for present purposes the fact that either of the peroneal muscles may be absent in a few non-cuculine genera. Among the cuckoos, then, we may say that M. peroneus longus exhibits its two extremes of development. At its highest degree of development, M. peroneus longus arises from the proximal end of the tibiotarsus, and its belly (or aponeurosis of origin) conceals all but the most distal parts of Mm. tibialis anterior and peroneus brevis (Berger, 1953*a*: Figs. 5, 8). This situation is found, in general, in terrestrial cuckoos (*Geococcyx, Morococcyx, Centropus, Carpococcyx, Coua, Crotophaga, Guira, Tapera,* and (?) *Dromococcyx*), but also in *Tauraco.* In a second group of primarily arboreal cuckoos, M. peroneus longus is a long, thin, and deeply situated muscle, concealing no part of M. tibialis anterior (Berger, 1952: Pl. II). This condition is found in *Coccyzus, Piaya, Saurothera, Ceuthmochares, Clamator, Chrysococcyx, Cuculus, Surniculus,* and *Phaenicophaeus.* With one exception (*Tapera*), the fully-developed peroneus longus muscle is found in those genera that possess both parts (AB) of M. piriformis. These genera either are essentially cursorial and terrestrial birds or they are well-defined genera whose distribution or breeding behavior appear to set them apart from the remaining cuckoos. Among the cuculine genera considered in this paper, we may conclude that the relative development of M. peroneus longus coincides reasonably well both with locomotor habits and with the two major subgroups of the family. The relative development of this muscle, however, is of no value in determining the relationship between the cuckoos and the touracos (as Lowe proposed, 1943:514).

The relative development of M. extensor proprius digiti III seems to be correlated with locomotor habits. In the more arboreal cuckoos (and in *Tauraco*) this muscle arises just distal (just proximal in *Tauraco*) to the insertion of M. tibialis anterior, and the belly extends to the distal end of the tarsometatarsus: *Coccyzus, Piaya, Saurothera, Crotophaga, Guira, Ceuthmochares, Surniculus, Clamator, Phaenicophaeus, Chrysococcyx, Cuculus.* In a second group, the entire muscle is limited to the distal half or less of the tarsometatarsus: *Geococcyx, Morococcyx, Dromococcyx, Tapera, Carpococcyx, Coua, Centropus.*

M. adductor digiti II is the smallest muscle of the pelvic limb in cuckoos. It seems proper to refer to it as a vestigial muscle in this group; it was, however, present (or absent) constantly in all specimens of the several genera examined. I did not find this muscle at all in *Cuculus, Chrysococcyx, Ceuthmochares, Surniculus, Phaenicophaeus, Centropus, Piaya,* or in *Tauraco.*

Certain tendon relationships in the foot appear to be correlated, in part, with zygodactylism, but there are curious exceptions. For example, the tendon of M. flexor perforatus digiti IV does not ensheathe the tendon of M. flexor digitorum longus in 16 of the genera studied, but it does ensheathe the longus tendon in *Dromococcyx* and in *Phaenicophaeus,* as well as in the semizygodactylous (see Moreau, 1938:666) *Tauraco. Phaenicophaeus* presents an intermediate condition in that about 95 per cent of the tendon inserts on the lateral side of the basal phalanx of digit IV, whereas the remainder of the tendon inserts on the medial side of the same phalanx. The tendon of M. flexor hallucis brevis forms a complete sheath around the tendon of M. flexor hallucis longus in all of the cuculine genera (as well as in *Tauraco* and many other birds) except *Centropus,* in which genus the flexor hallucis longus muscle does not insert on the hallux (see p. 73).

Another curious difference is found in the structure of M. femorotibialis internus in *Cuculus* and *Coua,* two distantly related cuckoos. In these two genera alone, M. femorotibialis internus has two independent heads, each of which inserts by its own tendon on the head of the tibiotarsus. The muscle is single in the other genera, including *Tauraco.*

Turning our attention now to the muscles of the wing, we find that Mm. tensores patagii longus et brevis in cuckoos (as in *Tauraco*) tend to be represented by a single muscle mass that gives rise to two tendons distally. There is a single fleshy origin from the dorsomedial surface of the furculum, also from the adjacent acromion of the scapula in some genera. In *Chrysococcyx* two bellies are discrete distally but the complex does not differ significantly from that in other cuckoos. The primary insertion of M. tensor patagii brevis in all cuculine genera (despite Lowe's statement and illustration) is on the tendinous surface of M. extensor metacarpi radialis, and part of the brevis tendon fans out posteriorly over the forearm muscles to fuse with the antebrachial fascia; the pattern is the same in *Tauraco* (see page 63, and Garrod, 1881, Pl. 22). There are secondary attachments of the brevis tendon-complex as follows: (1) to the lateral supracondylar ridge of the humerus—

Geococcyx; (2) to the lateral epicondyle (ectepicondylar process) of the humerus, superficial or proximal to the origin of M. extensor metacarpi radialis—*Coccyzus*; (3) to the tendon of origin of M. extensor digitorum communis—*Coccyzus, Morococcyx, Dromococcyx, Tapera, Chrysococcyx.* One must conclude that these secondary attachments are not important taxonomically.

M. expansor secundariorum has both a humeral and a scapular tendon of origin in all of the cuckoos. At the elbow there may be two independent bellies (as in *Coua, Geococcyx, Guira,* etc.) or a single muscle mass with two fleshy tongues directed proximally (as in *Crotophaga, Dromococcyx, Surniculus, Phaenicophaeus*) to the two primary (humeral and scapular) tendons of origin. This muscle is similar in *Tauraco,* but the axillary tendon bifurcates, the two resulting branches attaching respectively on the scapula and on the coracoid, i.e., the pattern of attachment is "ciconine" rather than "cuculine" (Garrod, Beddard). It seems likely that this is a significant difference between *Tauraco* and the cuckoos.

M. flexor metacarpi brevis is a small muscle, arising from the base of the carpometacarpus or from the os radiale and associated ligaments, and inserting on the tendon of insertion of M. extensor indicis longus. M. flexor metacarpi brevis is absent in *Coua, Carpococcyx, Geococcyx,* and *Morococcyx* (as well as in *Tauraco*) ; it is present in all other cuckoos examined. It should be noted that this muscle is present in all parasitic cuckoos and in all of those that lack pars iliofemoralis of the piriformis muscle. It is present also in *Crotophaga, Guira,* and in *Ceuthmochares* (in which genus pars iliofemoralis is vestigial) ; it is present but very much reduced in size in *Phaenicophaeus.*

Only in *Geococcyx, Morococcyx,* and *Coua* is M. coracobrachialis anterior a very large muscle, extending upward around the anterior edge of the humerus and to the dorsal surface of that bone. In the other genera, M. coracobrachialis anterior is a small muscle on the ventral surface of the humerus where it is closely applied to the capsule of the shoulder joint.

M. pectoralis propatagialis longus et brevis may be entirely tendinous (*Morococcyx, Dromococcyx, Tapera, Guira, Ceuthmochares, Centropus, Cuculus, Piaya*), or it may arise from M. pectoralis as a fleshy bundle (*Geococcyx, Crotophaga, Coccyzus, Saurothera, Coua, Carpococcyx, Clamator, Chrysococcyx, Surniculus, Phaenicophaeus*).

M. deltoideus minor apparently is absent only in *Coccyzus* and *Centropus.*

Three patterns in the relative development of Mm. pronator superficialis and pronator profundus are seen in the cuckoos: (1) the two muscles are about equal in length and both are relatively short—*Coccyzus, Dromococcyx, Chrysococcyx, Surniculus*; (2) they are about the same length and they extend nearly to the distal end of the radius—*Morococcyx, Guira, Centropus, Ceuth-*

mochares, Phaenicophaeus; (3) the profundus is longer than the superficialis —*Coua, Geococcyx, Crotophaga, Tapera, Piaya, Saurothera, Carpococcyx, Clamator, Cuculus.*

Cuculus and *Chrysococcyx* appear to differ from all other genera in that they possess an accessory flexor muscle of the pollex, which arises from the tendon of insertion of M. tensor patagii longus (Berger, 1955*b*: Fig. 70). In these two genera and in *Surniculus* and *Phaenicophaeus*, M. flexor digitorum profundus arises on both sides of the insertion of M. brachialis, rather than only posterior to it as in the other cuckoos.

The relative development of M. flexor carpi ulnaris brevis appears to be correlated with locomotor habits. The muscle is very short in *Geococcyx, Morococcyx, Dromococcyx, Tapera, Crotophaga, Coua, Carpococcyx, Centropus, Phaenicophaeus,* and *Ceuthmochares.* It is relatively long in *Coccyzus, Piaya, Saurothera, Guira, Clamator, Cuculus, Chrysococcyx,* and *Surniculus.*

Throughout the discussion above, I have used qualifying terms (e.g., primarily, in general, more arboreal) when referring to cuckoos as being arboreal or terrestrial. A review of the general habits and the myology of the couas may be instructive in this regard. The genus *Coua* contains a well-defined group of cuckoos that is restricted to Madagascar. Several years ago I (1953*a*: 53–54) quoted from a letter that Dr. A. L. Rand had written to me about this genus. He wrote, in part: "The three arboreal species *caerulea, cristata,* and *verreauxi* are geographical replacements. The terrestrial rain-forest species, *reynaudii* and *serriana,* have different food, one insects, one fallen fruit. In the dry forests and brush are four species, one rather wide-spread (*ruficeps*), but the other three are more restricted. *C. coquereli* and *cursor* are geographical representatives, and the much larger *C. gigas* co-exists with *C. coquereli* but overlaps the range of *C. cursor.*

"The group is, to my mind, a terrestrial type. The terrestrial species are at home, agile and graceful on the ground, swift of foot, and may prefer to escape danger on foot rather than by flying or seeking concealment. The arboreal species, and this includes *C. caerulea,* have carried over as much of this as possible into their arboreal life.

"The various modifications in range, habitat, and habits seem to be the result of an intra-group pressure and competition with little competition, in island isolation, from other groups. They have modified these without modification in structure. Thus, to use *C. caerulea* as an example of an arboreal cuckoo is a mistake. It is a terrestrial type that has taken to living in trees! Hence, its resemblance in leg proportions to *Geococcyx* is what I would expect."

Dr. Reynaud Paulian wrote (letter, January 16, 1956) that "*Coua ruficeps* walks along branches, just as the African *Musophaga* do, moving one leg after the other in alternating movements. Only when excited will it run by a series of sharp jumps on the ground. The *Coua* walks along the ground if not afraid, but it will take to the jumping run if at all disturbed."

In view of these statements made by two men who have observed the couas in the field, it is interesting to report that I found only one difference (not correlated to size difference) in the myology of five species of *Coua*, and there is a possibility of individual variation in this feature. In *C. serriana* and *C. reynaudii*, M. extensor pollicis brevis arises by two separate heads: one from the tendon of insertion of M. extensor pollicis longus; the other, from the base of the carpometacarpus adjacent to the insertion of the tendon of M. flexor carpi ulnaris brevis. M. extensor pollicis brevis has a single head in *caerulea*, *cristata*, and *ruficeps*. The remaining wing muscles and the leg muscles exhibit an identical pattern of development in the five species. We can, indeed, agree with Dr. Rand that the couas have modified their habits without extensive modification in myology. This suggests that myological data can be used with some degree of confidence for determining closeness of relationship, providing, of course, that other factors are taken into consideration. One does not find, however, a similar uniformity in the relative lengths of the bones of the appendages within the genus *Coua*. Milne-Edwards and Grandidier (1879: 170) commented on differences in development of the leg in various species of this genus. The following is a free translation of a portion of their comments: One does not perceive any relation between the habits of the birds and the dimensions of the tarsus; thus, the tarsi are long in *Coua caerulea*, which is arboreal, and in *C. gigas* and *C. ruficeps*, which are terrestrial; they are, on the contrary, short in *C. reynaudii* and in *C. cursor*, whose habits are very different, the first being a climber, and the second a runner. The chief difference in the leg muscles of the couas is in the increased length of the tendons in the long-legged forms.

Another example of difference in habit without elaborate modification in myology may be provided by the genera *Geococcyx* and *Morococcyx*. These two presumably closely related genera exhibit essentially an identical pattern in the myology of both limbs. The well-known Roadrunner (*Geococcyx*) is a terrestrial bird that has a running speed estimated at 10 to 15 mph. *Morococcyx* also is a "Ground-Cuckoo," but little seems to be known about its life history or habits. However, Dr. Ernest P. Edwards wrote (letter, January 23, 1953) that *Morococcyx* "*walks* along branches somewhat as a dove would walk along them." Perhaps *Morococcyx*, also, is a ground-cuckoo that has taken to living in trees.

A number of other cuckoos are intermediate in locomotor habits. For example, Delacour (1947:120) characterized the species of *Phaenicophaeus* (in which genus he included all the species of nine of Peters' genera) as being poor fliers, living among vines and bushes.

The correct interpretation of differences in myology within the family Cuculidae is complicated because some genera are parasitic and others are not. If one attempts to use myological formulae as well as breeding behavior in determining relationships among cuckoos, one is confronted with some puzzling situations, even if one excludes "E" from the muscle formulae. Among New World cuckoos, for example, *Tapera* is known to be parasitic, and the meager information available indicates that *Dromococcyx*, also, is parasitic (Giai, 1949; Neunteufel, 1951). *Tapera*, like all of the Old World parasitic cuckoos except *Eudynamis* and *Scythrops*, lacks pars iliofemoralis of the piriformis muscle, whereas *Dromococcyx*, *Eudynamis*, and *Scythrops* are, apparently, the only parasitic cuckoos that have what is traditionally considered the full cuculine muscle formula of ABXYAm. Hence, it would appear that one must discount either myological data or breeding behavior in deciding the relationships among the cuckoos. It must be emphasized, however, that we are handicapped seriously because so little is known about the life histories of the Neotropical (as well as many other) cuckoos.

Friedmann (1933) suggested that the parasitic habit is "of great antiquity" in the cuckoos and that *Tapera* developed its parasitism independently of the Old World cuckoos. I would suggest that the parasitic habit did not develop independently in *Tapera* and *Dromococcyx* but that "the ancestral Cuculine stock that reached the Americas brought with it a tendency towards parasitism (if not an actually developed parasitic habit) which has fructified in *Tapera*" (Friedmann, 1933:533) and in *Dromococcyx*. There are parasitic cuckoos in both hemispheres that possess the two basic types of cuculine muscle formulae: (1) AXYAm: Old World—*Cuculus*, *Chrysococcyx*, *Clamator*, *Surniculus*, etc.; New World—*Tapera*. (2) ABXYAm: Old World—*Eudynamis*, *Scythrops*; New World—*Dromococcyx*. Thus, if we are to place any value on morphological characters, we must assume either that parasitism has developed independently as many as four times in this one family (which seems highly unlikely) or that the parasitic habit (or tendency for it) developed in the primitive cuckoos (all ABXYAm) while still in the Old World ancestral home of the family.

COMPARATIVE OSTEOLOGY

Moreau recently called attention to the considerable difference of opinion expressed by the several classifications of the touracos that have been proposed during the past 34 years. I am in no sense prepared to comment on the classification of the touracos, but I can add some pertinent remarks on the osteology of the group. Several years ago, I examined the skeletons of 14 touracos, representing four of Moreau's (1958:75) five genera and eight of his

18 species: *Corythaeola cristata*; *Crinifer piscator*; *Corythaixoides concolor* and *personata*; *Tauraco corythaix* (including *persa* and *persa buffoni*), *macrorhynchus*, and *leucotis donaldsoni.*

Verheyen (1956*a*, 1956*b*) analyzed the skeletons of touracos and cuckoos in some detail, and from this and other information taken from the literature proposed systems of classification for both the touracos and the cuckoos. With regard to the touracos, Moreau (1958:77) commented: "I understand from Verheyen (*in litt.*) that his sub-families are not based on osteological characters except for the Corytheolinae (which have 20 pre-synsacrals and five dorso-sacra, compared with nineteen and four respectively in all the other Musophagidae). The separation of *Corytheola* in this way might perhaps be justifiable, but the allocation of the remaining Musophagidae into three subfamilies can hardly be accepted."

The separation of *Corythaeola* from the other musophagids on the basis of the number of cervical or presynsacral vertebrae is not justifiable. I studied two skeletons of *Corythaeola cristata*: one had 14 cervical and 5 dorsal vertebrae, or 19 presynsacral vertebrae as in the other musophagids; the other specimen had 15 cervical and 5 dorsal vertebrae, or 20 presynsacrals, as in the single specimen examined by Verheyen. This is surely another example of individual variation in the number of cervical vertebrae within a species; in my opinion, it has no taxonomic significance. I had for study only one specimen of *Corythaixoides* (= *Gymnoschizorhis*) *personata*, but it, too, had 20 presynsacral vertebrae. Each of two specimens of *Tauraco corythaix persa* (see Moreau, 1958) had 14 cervical vertebrae, but one had 5 dorsal vertebrae, the other only 4. Hence, one specimen had the typical musophagid number of 19 presynsacral vertebrae, whereas the other had only 18. Despite these few examples of individual variation, it seems likely that the typical number of presynsacral vertebrae in the musophagids is 19: 14 cervical and 5 dorsal vertebrae.

Among the specimens studied by Verheyen, the number of free caudal vertebrae varied from 6 to 8; among my specimens, from 5 to 7.

The number of ribs that articulate directly with the sternum varies, among the several genera and within a species, from 3 to 5, with 4 being the usual number. In one specimen of *Corythaixoides concolor*, five ribs articulated with the sternum on the right side, but only four did so on the left.

If we now turn our attention to the Cuculidae, we find that the typical number of presynsacral vertebrae in most genera is 18: 14 cervical and 4 dorsal vertebrae. However, I found that each of 30 specimens of the genus *Coccyzus* had only 13 cervical and 4 dorsal vertebrae, or a total of 17 presynsacral vertebrae; one additional specimen had 14 cervical and 4 dorsal vertebrae. According to Shufeldt, *Clamator glandarius* has only 13 cervical vertebrae; Verheyen (1956*a*:17) indicated that he examined four specimens of *C. levaillantii* and found 13 cervical vertebrae in this species; I found 13 cervical vertebrae in my single specimen of *C. jacobinus.* Apparently there are no reliable published data to indicate that any other cuculine genus has 13 cervical vertebrae. Fürbringer (1888:779), for example, is in error when he lists 13 cervical vertebrae for *Crotophaga,* except, of course, as a matter of individual variation; the genus typically has 14 cervical vertebrae. However, I found only 13 cervical and 4 dorsal vertebrae in single specimens of *Piaya* and *Saurothera.* One specimen of *Guira* had 14 cervical and 4 dorsal vertebrae, whereas a second specimen had 13 cervical and 5 dorsal vertebrae, certainly an abnormal number for cuckoos. The number of cervical and dorsal vertebrae within a genus appears to be relatively constant in the cuckoos (Berger, 1956:437), and it seems likely that the usual pattern in *Guira* is 14 cervical and 4 dorsal vertebrae. The osteology of only one genus (*Coccyzus*) can be considered to have been studied in sufficient numbers to justify much confidence in numerical data, however, so that much additional information is needed on the osteology of the cuckoos before the full significance of the data can be appreciated. Nevertheless, it is interesting to note that, apparently, *Coccyzus, Piaya, Saurothera,* and *Clamator,* each have 13 cervical vertebrae, and each genus has the same muscle formula of AEXYAm.

In my single specimen of *Carpococcyx* (United States National Museum No. 223,970), there were 15 cervical and only 3 dorsal vertebrae. There was, however, a well-developed thoracic rib (which, by definition, articulates dorsally with the synsacrum and not with a dorsal vertebra), and this rib had a direct articulation with the sternum, so that 4 ribs (3 true ribs and 1 thoracic rib) articulated with the sternum bilaterally. This represents a very unusual condition, at least among cuckoos. I suspect that it is an anomaly in this one specimen, and that *Carpococcyx,* like most other cuckoos, typically has 14 cervical and 4 dorsal vertebrae.

We may summarize some of the pertinent differences in the osteology of the two groups of birds. Touracos typically have 19 presynsacral vertebrae; most cuckoos have 18 presynsacral vertebrae, but a few have only 17. Touracos have a notched atlas; cuckoos, a perforated atlas. Touracos have a single bony canal in the hypotarsus; cuckoos have two bony canals. The sternum is double-notched in the touracos; the sternum is either single-notched or double-notched in cuckoos, sometimes (in older individuals?) it is merely fenestrate. In the touracos (all?) the clavicles are not fused ventrally to form a furcula, but the inferior ends are united by a ligament; a furcula is present in the cuckoos. As pointed out by Pycraft (1903:279) and Verheyen (1956*a*), the two dorsal processes of the coracoid are fused to form a bony canal in the touracos; the two processes do not fuse in the cuckoos. In the touracos, the tendon of M. supracoracoideus passes through the canal in the coracoid and then through the foramen triosseum, which is bounded only by coracoid and scapula. Lowe (1943) described and illustrated differences in the structure of the ectethmoid plate and the lacrimal bone between *Tauraco* and *Cuculus*. Some cuckoos (e.g., *Centropus*) are somewhat intermediate between *Cuculus* and *Tauraco* in the development of these characters, but the over-all pattern probably is distinctive for the two families (Fig. 2).

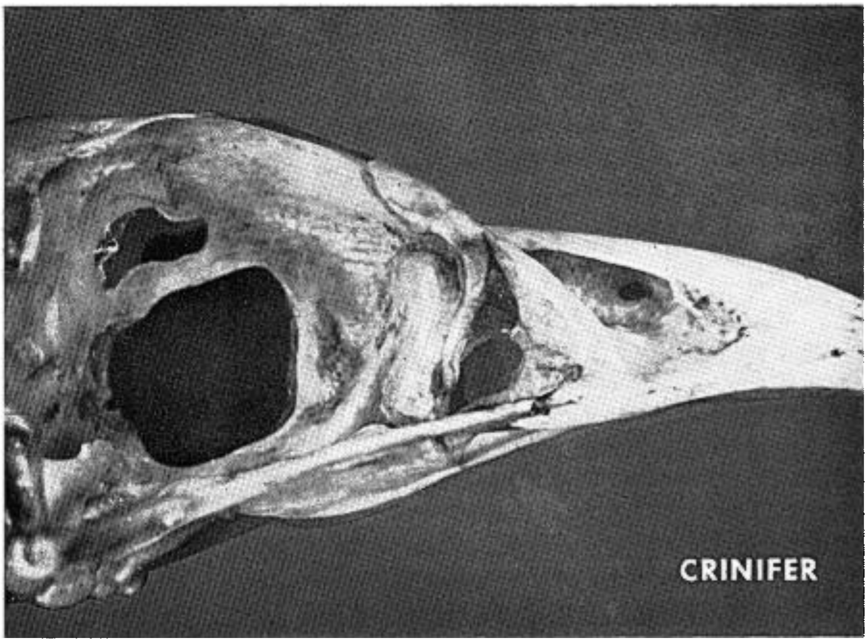

FIG. 2. Lateral view of part of skull of *Crinifer piscator* to emphasize the lacrimal bone.

COMPARATIVE PTERYLOSIS

Forbes (1885:212) remarked that the pterylosis of the Musophagidae "is peculiar, and gives no aid in determining their affinities." Nitzsch (1867: Pl. 6) illustrated the dorsal and ventral feather tracts of *Tauraco erythrolophus* ("*Musophaga paulina*"), and Lowe (1943) illustrated these tracts for *Musophaga violacea.* I found the feather tracts of *Tauraco leucotis donaldsoni* to be essentially the same as those shown in Lowe's figures.

Beddard (1885 and later) placed considerable emphasis on the value of the ventral feather tracts in determining relationships among the cuckoos, but the entire matter is in need of a thorough re-investigation. I have pointed out elsewhere (1953*a*, 1955*b*) that two of Beddard's assumptions were wrong. It has been demonstrated, however, that there are several patterns of feather tracts among the Cuculidae. In one group (*Cuculus, Cacomantis, Surniculus, Ceuthmochares, Clamator, Piaya, Coccyzus, Saurothera*) there is a single ventral abdominal tract on each side. In a second group (*Chrysococcyx, Scythrops, Carpococcyx, Centropus, Eudynamis, Phaenicophaeus, Geococcyx, Crotophaga, Guira, Morococcyx*), the ventral abdominal tracts are paired bilaterally. Furthermore, the ventral cervical tract may bifurcate in the region of the chin (*Piaya, Saurothera, Coccyzus, Phaenicophaeus*), about midway down the neck (*Cuculus, Clamator, Tapera, Crotophaga, Guira, Carpococcyx, Geococcyx, Morococcyx*), or at the base of the neck (*Centropus, Ceuthmochares*, and probably *Surniculus*). Beddard (1898*b*:280) separated certain Old World cuckoos from certain New World cuckoos because the ventral cervical tract in the New World cuckoos is "double at [its] commencement." This latter group is the one for which I have stated that the ventral cervical tract bifurcates in the region of the chin. There is some minor variation in these tracts among the four genera that I have listed above, and this character is perhaps most striking in the Old World genus *Phaenicophaeus*. In *Phaenicophaeus* there are two interramal feather tracts, separated by a median apterium, and each tract is bounded laterally by a pronounced marginal apterium.

Similarly, there are differences in the pattern of the dorsal feather tracts. In *Cuculus canorus*, for example, the dorsal cervical tract is continuous with the interscapular tract, and there is a large median apterium in the latter tract (Lowe, 1943: Fig. 6). In *Coua, Geococcyx, Morococcyx, Carpococcyx, Guira*, and *Centropus*, however, the dorsal cervical tract ends abruptly at the base of the neck, and the interscapular tract begins as two independent, anteriorly-directed tracts, which fuse posteriorly to form a single median pelvic tract. There are some differences among these genera and it seems pertinent to describe both the dorsal and ventral tracts of *Carpococcyx*. I have already described these tracts in *Coua caerulea* and *C. ruficeps* (1953*b*, 1954); Shufeldt (1886) illustrated the pterylosis of *Geococcyx*; and Beddard (1885) illustrated feather tracts of *Centropus, Eudynamis, Piaya*, and *Cacomantis*. Shelford (1900) described and illustrated the pterylosis of the embryo and nestling of *Centropus sinensis*, and Hartley (in Beebe *et al.*, 1917) illustrated the feather tracts in both the embryo and adult of *Crotophaga ani*.

A median frontal apterium is wanting and the feathers of the capital feather tract are a little more sparse in *Carpococcyx radiceus* than they are in *Coua*. A large lateral apterium surrounds the orbit. The spinal cervical tract ends abruptly at the junction of the neck and thorax, and there is a relatively wide

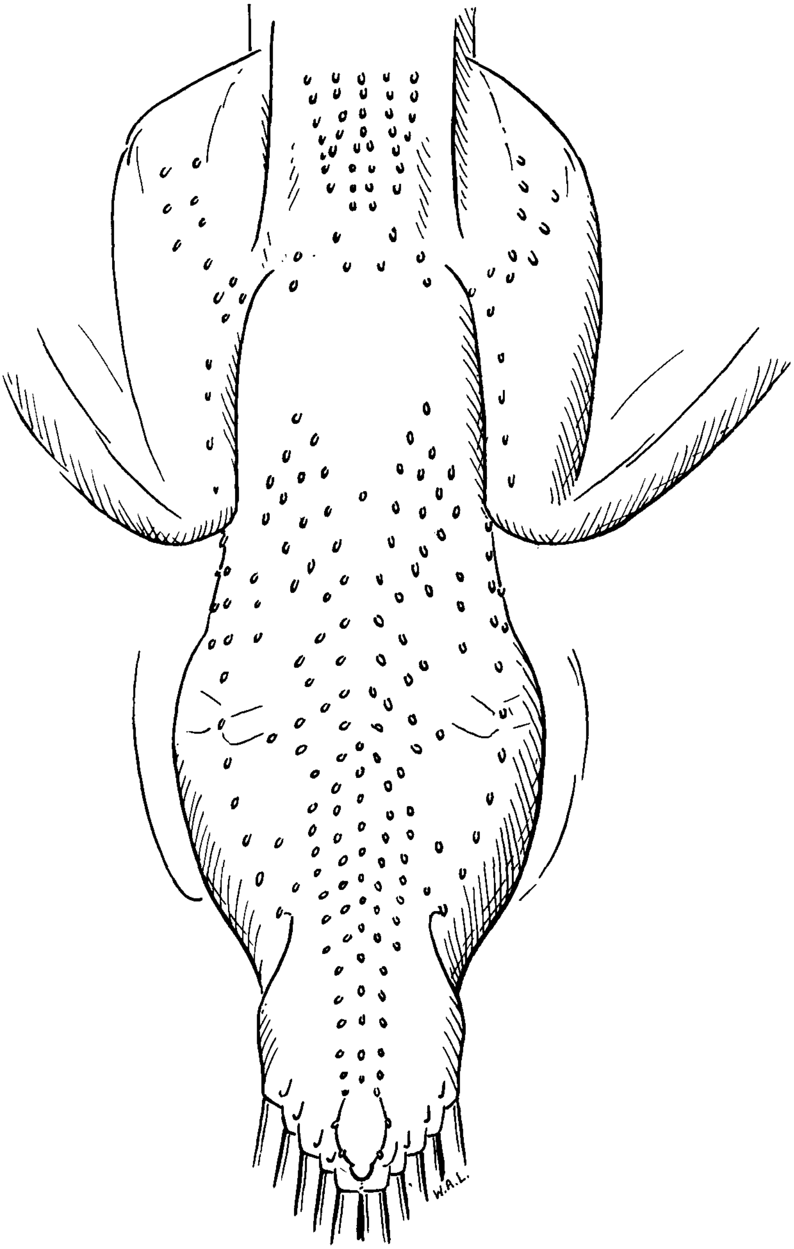

FIG. 3. Dorsal feather tracts of *Carpococcyx radiceus*.

(20 mm.) apterium between this tract and the interscapular tracts. These tracts (Fig. 3) differ from those found in other cuckoos thus far studied, as pointed out by Beddard (1901:201) but not precisely in the way that he stated. There does appear to be a short, narrow, V-shaped median apterium between the two interscapular tracts anteriorly, although in shape and extent it is unlike that in *Coua* (Fig. 4). The two interscapular tracts are continuous posteriorly with the dorsal spinal tracts, which join to form a single, median pelvic tract. In addition, lateral dorsal tracts, essentially single-rowed, pass caudally from the anterolateral edge of the dorsal spinal tracts to the area over the posterior iliac crests. There is an almost featherless area between these bilateral tracts and the median pelvic tract.

Turning now to the ventral feather tracts of *Carpococcyx,* we note first that the marginal apteria are very small, if present at all (an incision had been made along the mandible, thus making this determination somewhat unreliable). The presence or absence of the marginal apteria on either side of the interramal feather tract was one of the diagnostic features used by Beddard (1898*b*:281): (1) ventral tract occupying the entire space between the mandibles; or (2) ventral tract occupying only the median region between the mandibles, that is, the interramal tract is bounded by marginal apteria. Judging from what I have seen to date, I would say that Beddard's criteria for separating the Old World *Centropus* (= "*Pyrrhocentor*") and *Coua* from the New World *Geococcyx, Crotophaga,* and *Guira* are untenable. The pattern in *Cuculus* certainly is not precisely like that illustrated by Lowe (1943) in that there are definite small apteria on either side of the interramal tract; nor, in this character, is there such a close similarity between *Cuculus* and *Musophaga* as Lowe illustrated. The marginal apteria in *Centropus* are like those in *Coua caerulea* and *C. ruficeps.* It seems to me that we are dealing here with the degree to which the marginal apteria are developed. The narrowest interramal tract, and therefore the widest marginal apteria, seems to be found in *Crotophaga.* Thus between *Crotophaga* and *Cuculus* or *Centropus* there is a marked difference in the development of the marginal apteria, but *Tapera* (Figs. 5 and 6), *Guira, Geococcyx,* and *Morococcyx* are intermediate between the two extremes, And, as pointed out above, *Phaenicophaeus* and certain other genera have two interramal tracts, each of which is bounded laterally by a marginal apterium.

The ventral cervical tract of *Carpococcyx* bifurcates at about the midlength of the neck. Opposite the head of the furcula, two rows of feathers pass dorsocaudad to join the humeral feather tract. The ventral tract bifurcates at about the level of the anterior end of the sternum, forming an inner and an outer ventral abdominal tract bilaterally. The inner tract is composed of a double row of feathers anteriorly, but of a single row in the posterior half of

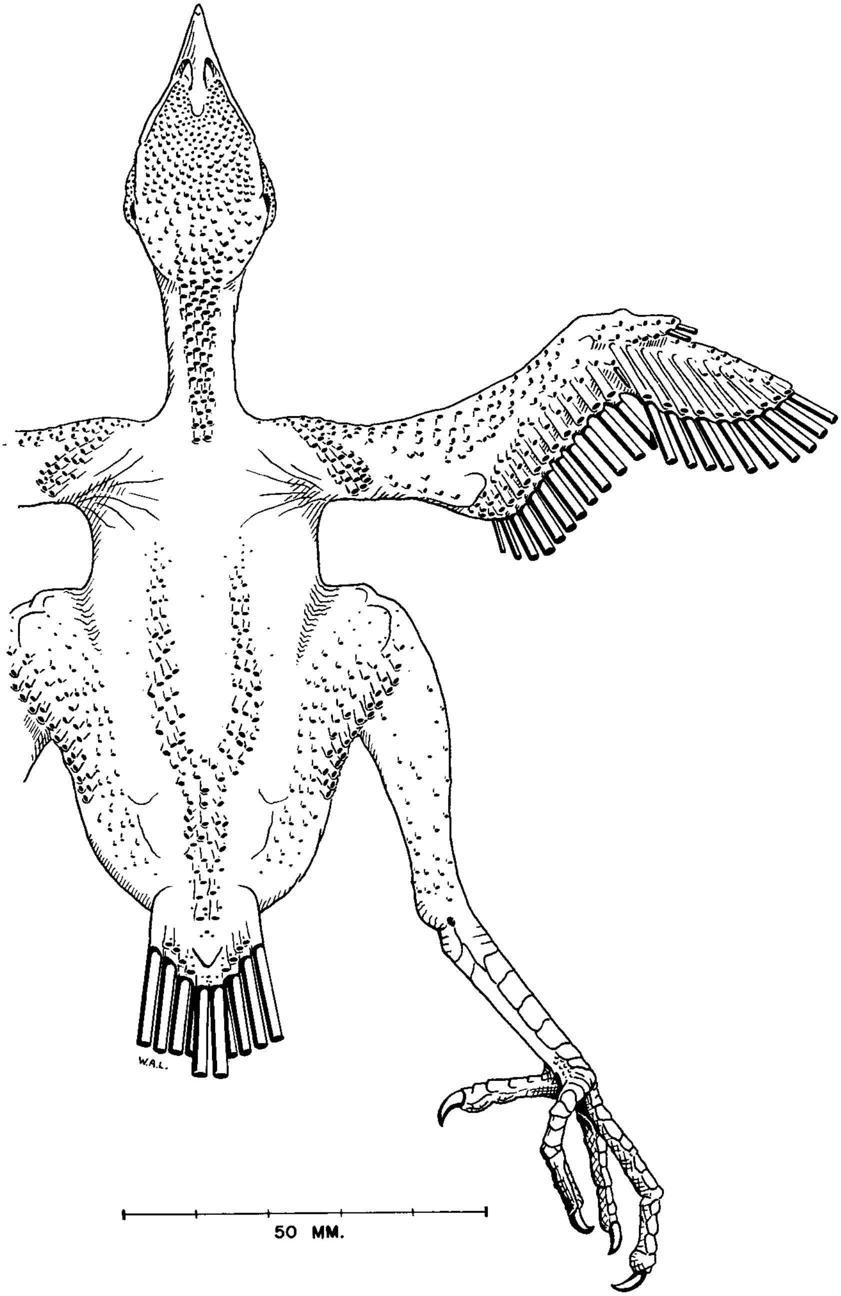

Fig. 4. Dorsal feather tracts of nestling *Coua ruficeps*.

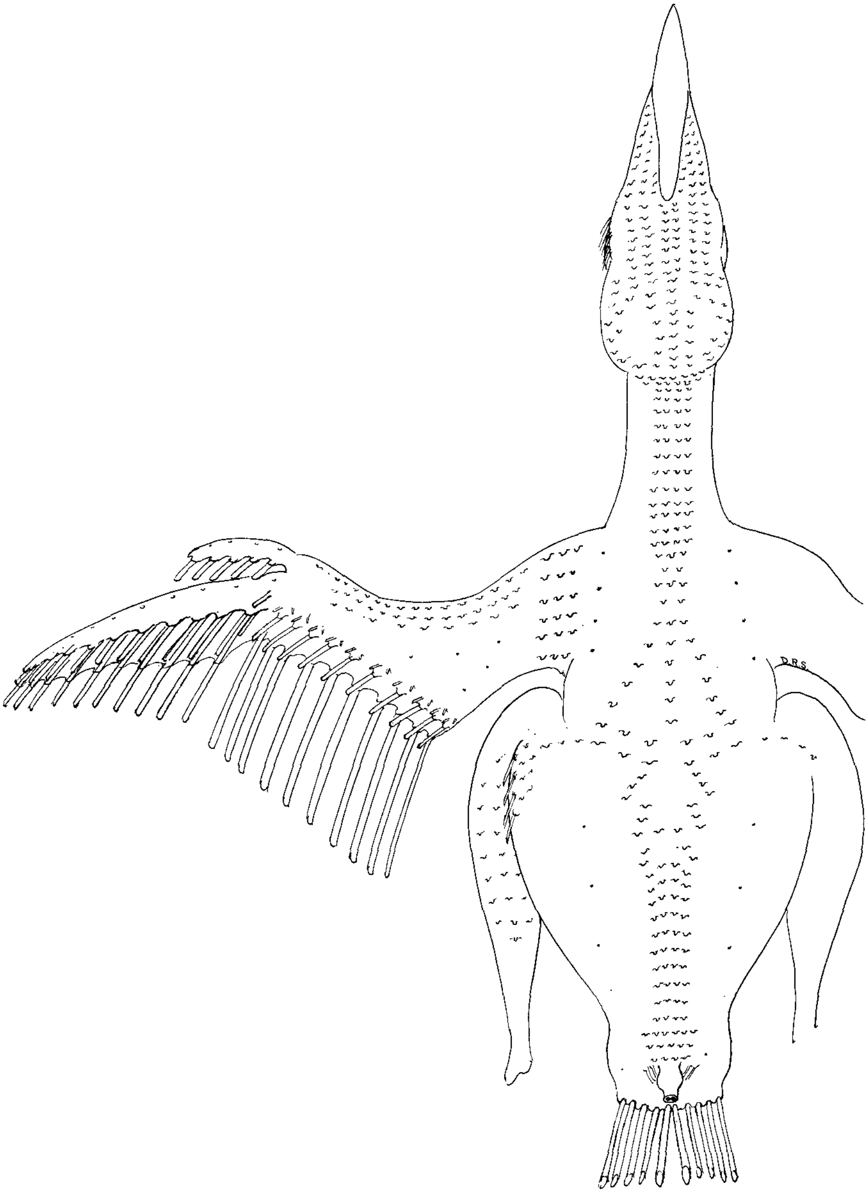

FIG. 5. Dorsal feather tracts of *Tapera naevia*.

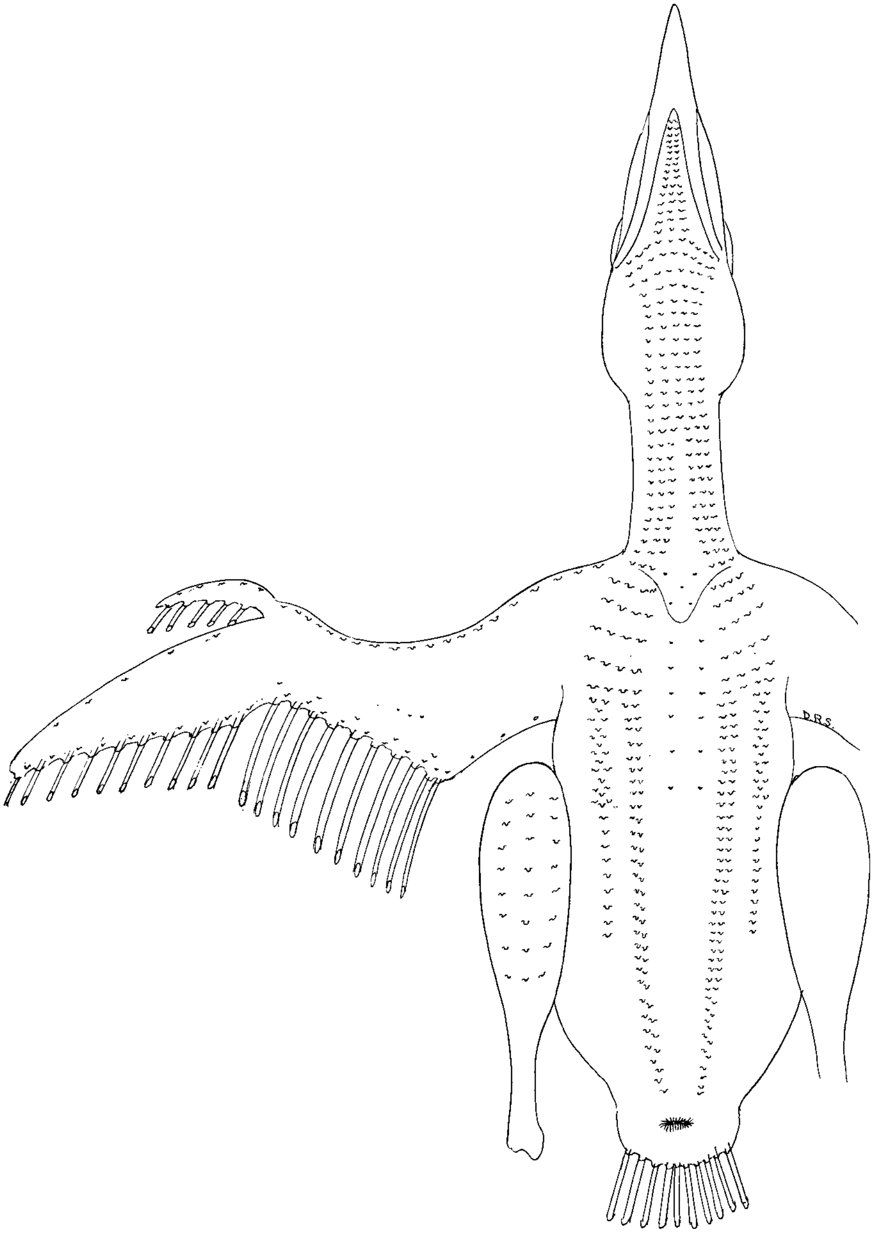

FIG. 6. Ventral feather tracts of *Tapera naevia*.

its extent; this tract terminates a short distance (about 6 mm.) in front, and a little anterolateral, of the vent. The outer abdominal tract anteriorly is composed of three rows of four feathers each, but throughout most of its extent it is composed of a single row of feathers. This row ends about midway between the posterior margin of the sternum and the vent; it does not turn inward to meet the inner abdominal tract. From the lateral margin of the anterior part of the outer abdominal tract, a single row of feathers passes dorsolaterad to the posteoventral surface of the arm (humerus).

There are 10 primaries in *Carpococcyx.* The wing is eutaxic. There are apparently 11 secondaries; the outer eight have large quills, whereas the inner three are progressively smaller and are more like coverts in size, but they are in direct line with the outer secondaries. Beddard considered only the distal eight feathers to be secondaries. There are five alula quills; the molt was in progress when the specimen was collected so that it was not possible to determine the relative lengths of the alula feathers. A relatively well-developed (40 mm. long) carpal remex was found bilaterally, but no evidence of the carpal covert. There are 10 rectrices and 10 upper tail coverts. The femoral tract laterally is developed as in *Coua ruficeps*; medially, the thigh is almost devoid of feathers. The crural tract is best developed anteriorly, where there is a triple row of feathers proximally (somewhat irregular in pattern) and a single row distally; there are three rows of widely-spaced feathers on the lateral side of the crus; medially, there are a few scattered feathers; and posteriorly, there is a single row of small feathers. The crural tracts do not extend downward on to the tarsometatarsus, as they do in *Cuculus*, *Chrysococcyx*, and *Clamator*. Sharpe (1873:579) spoke of *Cuculus*, *Chrysococcyx*, and *Clamator* as having "accipitrine thigh-feathers," and he reported that the rim around the external naris is swollen in these genera; *Surniculus lugubris* also exhibits both of these characters.

Apparently all cuckoos have 10 primaries. Most cuckoos have either 9 or 10 secondaries; *Scythrops* is said to have 13; *Carpococcyx* and *Centropus* appear to have 11; and the nestling *Coua ruficeps* seems to have 12 (see, however, the discussion by Berger and Lunk, 1954). *Guira* and *Crotophaga* have 8 rectrices; all other cuckoos are said to have 10.

Despite the variation in pattern of both the dorsal and the ventral feather tracts among the cuckoos, no cuckoo yet studied has feather tracts (particularly dorsally) like those of the touracos. The oil gland is tufted in touracos; it is nude in cuckoos. An aftershaft is present in touracos; it is absent or vestigial in cuckoos (Miller, 1924). Well-developed "eyelashes" are characteristic of cuckoos. The eyelashes may be featherlike, as in *Cuculus*, *Chrysococcyx*, *Clamator*, and *Surniculus*, or they may be "hairlike," as in *Coua*, *Geococcyx*, *Morococcyx*, *Dromococcyx*, *Tapera*, *Guira*, *Crotophaga*, *Piaya*, *Saurothera*, *Ceuthmochares*, *Centropus*, and *Phaenicophaeus*. The small, black, hairlike eyelashes are least conspicuous in *Phaenicophaeus pyrrhocephalus*; those of *Dasylophus* (= *Phaenicophaeus*?) *superciliosus* are said to be large and scarlet. Eyelashes are absent in *Tauraco leucotis donaldsoni*, and both eyelids are covered by fleshy caruncles which are especially prominent dorsal to the upper eyelid. There appear to be seven alula quills attached to the pollex in *Tauraco*; these increase in length from proximal to distal: No. 1 is 23 mm. long; No. 2, 28 mm.; No. 3, 33 mm.; No. 4, 36 mm.; No. 5, 44 mm.; No. 6, 50 mm; No. 7, 52 mm. Cuckoos apparently have either four or five alula quills. The innermost, the outermost, or one of the intermediate feathers may be the longest in the series.

THE CUCULINE SYRINX

There are few anatomical structures throughout the families of birds that need study as badly as the syrinx. Except for a very few isolated instances, our knowledge of both the passerine and the nonpasserine syrinx is based largely on work published during the last century (e.g., Müller, 1878). Such pioneers as Müller, Garrod, Forbes, Fürbringer, and Gadow were remarkably astute scholars of the old school and any thorough anatomical study must begin with a careful analysis of their papers. Nevertheless, the work of the past needs to be corroborated and extended, using both gross and microscopic techniques. We need detailed comparative studies of the syrinx interpreted in terms of modern concepts of anatomy and of systematics. For such studies, one needs a number of specimens of each species in order to work out all relationships carefully. The intrinsic syringeal muscles usually are very small and they often are poorly preserved in alcoholic specimens. In addition to gross descriptions, microscopic analyses and embryological studies of developmental stages of the syrinx *in both sexes* would undoubtedly add much to our understanding of the significance of the adult configuration of the syrinx and its relation to muscles and to the tracheobronchial tree.

I can do little more here than verify statements in the literature and summarize present knowledge of the cuculine syrinx. The following cuckoos are known to have a bronchial syrinx: *Centropus*, *Carpococcyx*, *Coua*, *Geococcyx*, *Morococcyx*, *Dromococcyx*, *Crotophaga*, and *Guira*. Within this group, however, there is a considerable difference as to the location of the syrinx within the bronchi, as pointed out by Beddard (1885:170–174). Beddard reported (1901:202) that "the syrinx of *Carpococcyx* . . . is the most purely bronchial syrinx that exists among the Cuculidae; it is even more exaggerated than that of *Crotophaga*," and he added that the syringes of *Centropus* and *Geococcyx* "present us with an intermediate stage between the typical tracheo-bronchial syrinx of the Phoenicophainae and the extraordinarily specialized bronchial syrinx of *Crotophaga* and of *Carpococcyx*." The syrinx of *Centropus superciliosus* (Fig. 11), however, approaches the "exaggerated" condition found in *Carpococcyx* (Beddard, 1901:203), and it appears to be different from the syrinx of *Centropus ateralbus* (Beddard, 1885:172). This suggests that a comparative study of the syrinx among the many species of *Centropus* would be a fruitful project.

All other cuckoos studied, including *Tapera*, have a tracheobronchial syrinx. Beddard remarked (1902:605–606) that the syrinx of *Rhamphococcyx* (= *Phaenicophaeus* according to some writers) exhibits "a hint of a development into the bronchial syrinx of the Centropine Cuckoos." Hence, as with other anatomical information, we seem to know just enough about the anatomy of the cuculine syrinx to suggest many intriguing problems for further study and not enough to understand completely the significance of the data that are available. My material was not suitable for microscopic study, and I present here figures (Figs. 7–11) illustrating the gross differences in the syrinx of one series of cuckoos. A knowledge of the finer structure of the cuculine syrinx would undoubtedly be instructive. It should be noted that M. sternotrachealis inserts very near the tracheal bifurcation in *Centropus*, whereas it inserts some distance from the bifurcation in the other genera. Only in the syrinx of *Crotophaga* (a female) did I find two pairs of intrinsic syringeal muscles; there is a single pair of intrinsic muscles in the other genera.

Discussion

There has been a tendency by some contemporary writers to state flatly that certain anatomical features in birds are so stable in an evolutionary sense that similarities in these characters "prove" relationship among the birds concerned. One may make such a basic assumption about a single character and then proceed to "prove" all sorts of inter-relationships that then permit the construction of an elaborate phylogenetic tree, which the author may state or imply is to be accepted without qualification or question. Most often such authors base their conclusions on a smattering of information about a particular anatomical character. When, for example, an author purports to "explain" the course of evolution in all oscine passeriform birds on the basis of a single bone of the skull and on the size of the birds, I believe that we have reached the ultimate in this type of systematic approach, one which might aptly be termed "the pseudo-anatomical approach." Other examples could be cited. The naive confidence in, and the exaggerated positive interpretation of, inadequate data expressed by such authors does a great disservice to anatomical studies and to the application of anatomical information to avian taxonomy.

I doubt that we know enough about avian anatomy or about the interrelationships between structure and function—and all of the related problems

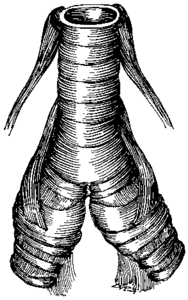

FIG. 7

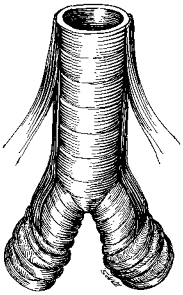

FIG. 8

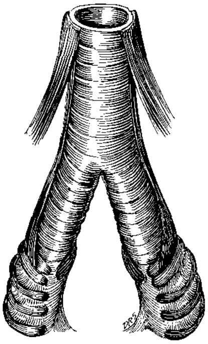

FIG. 10

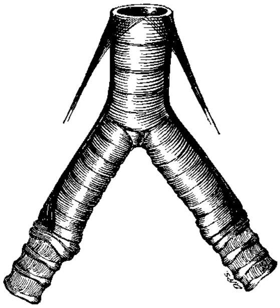

FIG. 9

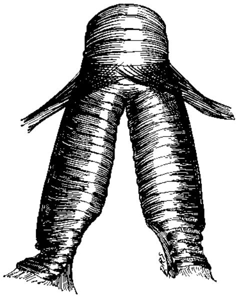

FIG. 11

FIG. 7. Tracheobronchial syrinx of *Piaya cayana.*
FIG. 8. Bronchial syrinx of *Guira guira.*
FIG. 9. Bronchial syrinx of *Morococcyx erythropygus.*
FIG. 10. Bronchial syrinx of *Crotophaga sulcirostris.*
FIG. 11. Bronchial syrinx of *Centropus superciliosus.*

of convergence and divergence among birds—to justify such confidence. Miller (1937:58–59), Rinker, and others have discussed this problem and that of the inequality of values to be assigned to anatomical features in the study of both birds and mammals. Thus, Rinker (1954:117), in speaking of rodents, wrote: "Even the segregation of characters into adaptive and nonadaptive categories, or a classification based on current survival value, is, in my opinion, a highly subjective approach. I do not believe that the present state of knowledge will allow this approach to be used with any appreciable degree of certainty. It appears to me that success in such an attempt would require much greater insight into the relationships of structure and function, into the basis of habitat preferences (or restrictions), and into many more phenomena than is possible at present." It does not seem to me to be an exaggeration to make a similar statement about birds, particularly when it seems that we know less about the significance of anatomical characters in birds than in mammals. Moreover, we can agree wholeheartedly with Enlow and Brown (1958:221) when they caution: "The projection of preconceived concepts and prejudices of evolutionary mechanics into the interpretation of observations is a consideration that must consciously, and continually, be recognized and evaluated. It is a constant temptation to look for, and thereby find, a logical, uni-linear assemblage of structural changes that conform with and confirm some preexisting idea on how things should be happening."

Before summarizing the data presented in this paper, it will be instructive to consider Peters' (1940) classification of the cuckoos. There seems to be general agreement that Peters' classification is unsatisfactory. He had little published information on cuculine anatomy to rely on, and I suspect that his system was based primarily on two factors: parasitism and geographical distribution. An analysis of his subfamilies will give further insight into some of the problems involved and will reveal where further work is needed.

Peters' subfamily Cuculinae is composed of Old World cuckoos that have parasitic breeding habits. For most of the included genera the muscle formula is AXYAm, but for *Eudynamis* and *Scythrops* it is ABXYAm. *Clamator* has 13 cervical vertebrae; so far as is known, the other genera have 14. There is a single ventral abdominal feather tract on each side in *Cuculus*, *Cacomantis*, *Clamator*, and *Surniculus*; these tracts are paired bilaterally in *Chrysococcyx*, *Scythrops*, and *Eudynamis*. Baker (1927) erected the subfamily Eudynaminae for the single genus *Eudynamis*.

An analysis of Peters' subfamily Phaenicophaeinae—which he admitted was a "catch-all" group—is even more interesting. He included in this subfamily three nonparasitic American genera and nine nonparasitic Old World genera. Each of the American genera (*Coccyzus*, *Piaya*, *Saurothera*) has a muscle formula of AEXYAm, a single ventral abdominal feather tract bilaterally, and, apparently, 13 cervical vertebrae. Six of the nine Old World genera are known to have the muscle formula of ABXYAm. Of the two genera studied for this paper, *Ceuthmochares* has a single ventral abdominal feather tract bilaterally, whereas *Phaenicophaeus* has paired tracts bilaterally. Both genera have 14 cervical vertebrae and a muscle formula of ABEXYAm. It should be pointed out that Delacour and Mayr (1945) did not recognize eight of the nine Old World genera (including *Ceuthmochares*) listed by Peters, and, therefore, placed all of the species in the genus *Phaenicophaeus.* Bannerman (1933), on the other hand, placed *Ceuthmochares* in his subfamily Centropodinae.

The Crotophaginae (*Crotophaga* and *Guira*) are New World cuckoos that have eight rectrices, a muscle formula of ABEXYAm, and social nesting habits.

Peters' subfamily Neomorphinae contains one Old World genus (*Carpococcyx*) and five New World genera. All except *Tapera* (AXYAm) have a muscle formula of ABXYAm. *Tapera* and *Dromococcyx* are parasitic; so far as is known, the other genera are not parasitic, although Makatsch (1955:34) suggested that *Neomorphus* might have parasitic nesting habits (but see, Sick, 1949). Shelley (1891:423) placed *Tapera* (= "*Diplopterus*") and *Dromococcyx* in the subfamily Diplopterinae (= Taperinae), whereas Gadow and Selenka (1893:214) put *Tapera* in their subfamily Cuculinae (parasitic, AXYAm, syrinx tracheobronchial).

The subfamily Couinae presumably was established because the single genus is restricted to Madagascar. There is little in the internal anatomy to separate *Coua* from *Geococcyx* or *Morococcyx.*

Peters' last subfamily, the Centropodinae, contains the single Old World genus *Centropus* with some 27 species and 55 subspecies. These are widespread (from Australia, the Philippines, and China to Africa and Madagascar), nonparasitic cuckoos that have a very long, straight and sharp claw on the hallux (of many, but not all, of the species), thus the name of Lark-heeled Cuckoos. The coucals build a bulky globular nest that has a side entrance (Delacour, 1947; Loke, 1953), but I suspect that most authors have erected the subfamily primarily on the basis of the long claw on the hallux.

Both Beddard (1898*b*) and Pycraft (1903) adopted several anatomical features—leg-muscle formulae, patterns of the feather tracts, skeletal characters, and the structure of the syrinx—in an attempt to determine cuculine relationships, but, as in the present paper, each author had information from less than half of all the genera. Beddard placed primary emphasis on the syrinx and the leg-muscle formulae (and omitted skeletal characters) in assigning cuckoos to three subfamilies. Pycraft omitted consideration of feather tracts and used skeletal characters (sternum and pectineal process) and the syrinx in arranging the genera. The divergence in the placement of genera between these two systems was considerable.

The difficulty of deciding relationships among the genera of cuckoos seems to result largely from the fact that anatomical characters often presumed to be very stable in an evolutionary sense exhibit several patterns among the cuckoos. Thus, the muscle formula may be AXYAm or ABXYAm; the syrinx may be bronchial or tracheobronchial; the sternum may be single-notched or double-notched; there may or may not be an apterium between the dorsal cervical and the interscapular feather tracts; and the ventral abdominal feather tracts may be either single or double bilaterally. Similarly, parasitic breeding habits have developed in genera possessing both types of muscle formula, both types of syrinx, both types of sternum, both types of ventral feather tracts, and, perhaps, both types of dorsal feather pattern. Moreover, genera with a bronchial or a tracheobronchial syrinx, those with a single-notched or a double-notched sternum, etc., are found in both the Old World and the New World. These points may be illustrated by constructing a key using such anatomical features rather than using only parasitic breeding habits, geographical distribution, or the appearance of the study skin as a basis for classification. It is obvious that an author can focus the reader's attention on certain relationships by the relative weight placed on anatomical characters in constructing such keys. To demonstrate this point, I present three different keys (Tables 1–3), which embody anatomical features used by Beddard and Pycraft, as well as other features discussed in this paper; by using information reported by Beddard, I have added a few genera not examined for this paper. It is obvious, also, that the data in the tables can be arranged in several other ways.

If we consider only Table 1 for the moment, we can say, in addition, that the genera in Group I have a well-developed peroneus longus muscle; the genera in Group II, except for *Tapera*, have a weakly-developed peroneus longus muscle. M. iliacus ("E") is absent in the Old World genera of Group I. All the genera in Group I have a bronchial syrinx, bilaterally paired ventral abdominal feather tracts, and 14 cervical vertebrae; most of the genera are nonparasitic, but two have developed social nesting habits. Sick (1953*a*, 1953*b*) reported that *Tapera* and *Dromococcyx* are similar in certain external features and in general habits, but the two genera are unlike in internal characters. One would conclude that the superficial similarities in appearance are the result of convergence.

I mentioned above (p. 90) that four genera (*Cuculus*, *Chrysococcyx*, *Clamator*, and *Surniculus*) have "accipitrine" thigh feathers and raised narial rims, but these genera differ considerably in other morphological features. All four genera have parasitic nesting habits.

After examining the tables, one can see why it would be much easier to classify the cuckoos on the basis of breeding habits or on geographical distribution rather than on the basis of internal anatomical characters.

Still other anatomical features of the cuckoos need to be studied: the morphology of the head, particularly the jaw muscles and nerves (see, for example, Barnikol, 1953, and Starck, 1959); a comparative study of the viscera, the vascular system, and the brachial and lumbosacral plexuses.

SUMMARY

As a result of this introduction to an anatomical study of cuckoos and touracos, I agree with those who have proposed that the touracos (Musophagidae) deserve ordinal rank, the Musophagiformes. Table 4 presents comparative data on the cuckoos and on *Tauraco leucotis donaldsoni.* Because they are present in all genera studied for this paper, I have not placed emphasis on two muscles that I recently (1959) proposed be added to muscle formulae: "F," M. plantaris; "G," M. popliteus. They are included in Table 4.

The following wing muscles are absent in *Tauraco leucotis donaldsoni*: cucullaris, pars propatagialis; biceps slip; anconaeus coracoideus; entepicondyloulnaris; flexor metacarpi brevis. The following leg muscles are absent in *Tauraco*: iliotrochantericus medius ("C"); iliacus ("E"); extensor brevis digiti III; adductor digiti II; adductor digiti IV.

The relatively large assemblage of zygodactyl birds that have been grouped together as cuckoos contains genera exhibiting a considerable diversity in internal morphology. It is an old group, first reported from the Oligocene Epoch. One might speculate that the ancestral cuckoos had a more complete complex of thigh muscles than do the modern forms, that they had a tracheobronchial syrinx, and that they had a propensity for developing parasitic nesting habits. Two lines of specialization might then be proposed. One group, with primarily terrestrial habits, tended to retain the thigh muscles but developed a bronchial syrinx. The other, more arboreal, group retained the tracheobronchial syrinx, tended to lose certain thigh muscles, and tended to develop parasitic breeding habits. However, there seems to be little correlation between the type of sternum and the other anatomical characters studied. Some of the cursorial genera (e.g., *Geococcyx*) have a double-notched sternum, whereas others (e.g., *Carpococcyx*) have a single-notched sternum. Similarly, both types of sternum are found among the more arboreal cuckoos. In view of the presumed occurrence of the bronchial type of syrinx in some, but not all, owls (as well as in a few other birds), one might question the significance of the bronchial syrinx, especially because of the several patterns found among the cuckoos.

Data presented in this paper reveal some of the pitfalls encountered when

TABLE 1

ANATOMICAL RELATIONS OF CUCKOOS

- Group I. Bronchial syrinx; ABE(±)XYAm; ventral abdominal feather tracts double bilaterally; 14 cervical vertebrae.
  1. Sternum double-notched; dorsal cervical and interscapular feather tracts separated by an apterium; M. flexor hallucis longus inserts on hallux.
     - a. M. flexor metacarpi brevis absent: *Coua* (E absent), *Geococcyx. Morococcyx, Neomorphus*?
     - b. M. flexor metacarpi brevis present; parasitic; E?; dorsal feather tracts?: *Dromococcyx*
  2. Sternum single-notched
     - a. M. flexor hallucis longus inserts on hallux
       - 1) dorsal cervical tract is continuous with interscapular tract; social nesting habits: *Crotophaga*
       - 2) dorsal cervical tract separated from interscapular tract by an apterium
         - a) M. flexor metacarpi brevis present; social nesting habits: *Guira*
         - b) M. flexor metacarpi brevis absent; E absent; nonparasitic: *Carpococcyx*
     - b. M. flexor hallucis longus does not insert on hallux; E absent; nonparasitic: *Centropus*
- Group II. Tracheobronchial syrinx; dorsal cervical feather tract is continuous with interscapular tract.
  1. ABE(±?)XYAm
     - a. Sternum double-notched; nonparasitic; E present.
       - 1) ventral abdominal tracts double bilaterally: *Phaenicophaeus*
       - 2) ventral abdominal tracts single bilaterally: *Ceuthmochares*
     - b. Sternum single-notched; parasitic; ventral abdominal feather tracts double bilaterally (from Beddard): *Scythrops, Eudynamis*
  2. AEXYAm; sternum double-notched; ventral abdominal tracts single.
     - a. 14 cervical vertebrae; parasitic: *Tapera, Surniculus*
     - b. 13 cervical vertebrae
       - 1) parasitic: *Clamator*
       - 2) nonparasitic: *Coccyzus, Saurothera, Piaya*
  3. AXYAm; parasitic
     - a. Sternum double-notched; ventral abdominal tracts double: *Chrysococcyx*
     - b. Sternum single-notched; ventral abdominal tracts single: *Cuculus, Pachycoccyx*

TABLE 2

ANATOMICAL RELATIONS OF CUCKOOS

Group I. ABXYAm.	
1. Bronchial syrinx; ventral abdominal feather tracts double; 14 cervical vertebrae.	
a. Dorsal cervical and interscapular feather tracts are separated by an apterium.	
1) M. flexor hallucis longus does not insert on hallux; sternum single-notched; M. flexor metacarpi brevis present; nonparasitic:	*Centropus*
2) M. flexor hallucis longus inserts on hallux.	
a) Sternum double-notched	
1—M. flexor metacarpi brevis absent; nonparasitic:	*Coua, Geococcyx, Morococcyx, Neomorphus?*
2—M. flexor metacarpi brevis present; parasitic; dorsal feather tracts ?:	*Dromococcyx*
b) Sternum single-notched	
1—M. flexor metacarpi brevis absent; nonparasitic:	*Carpococcyx*
2—M. flexor metacarpi brevis present; social nesting habits:	*Guira*
b. Dorsal cervical tract continuous with interscapular feather tract; sternum single-notched; social nesting habits:	*Crotophaga*
2. Tracheobronchial syrinx; dorsal cervical tract is continuous with interscapular feather tract.	
a. Sternum single-notched; parasitic; ventral abdominal feather tracts double:	*Scythrops, Eudynamis*
b. Sternum double-notched; nonparasitic	
1) ventral abdominal tracts double:	*Phaenicophaeus*
2) ventral abdominal tracts single:	*Ceuthmochares*
Group II. AXYAm; tracheobronchial syrinx; dorsal cervical tract continuous with interscapular feather tract.	
1. Sternum double-notched	
a. Ventral abdominal tracts single bilaterally	
1) 14 cervical vertebrae; parasitic:	*Tapera, Surniculus*
2) 13 cervical vertebrae	
a) nonparasitic:	*Coccyzus, Saurothera, Piaya*
b) parasitic:	*Clamator*
b. Ventral abdominal tracts double; parasitic:	*Chrysococcyx*
2. Sternum single-notched; ventral abdominal tracts single; parasitic:	*Cuculus*

TABLE 3

ANATOMICAL RELATIONS OF CUCKOOS

Group I.	Sternum double-notched.	
	1. Bronchial syrinx; ABE(±)XYAm	
	a. M. flexor metacarpi brevis absent; nonparasitic:	*Coua, Geococcyx,* *Morococcyx, Neomorphus?*
	b. M. flexor metacarpi brevis present; parasitic:	*Dromococcyx*
	2. Tracheobronchial syrinx	
	a. ABEXYAm; nonparasitic	
	1) Ventral abdominal tracts double:	*Phaenicophaeus*
	2) Ventral abdominal tracts single:	*Ceuthmochares*
	b. AEXYAm; ventral abdominal tracts single	
	1) 14 cervical vertebrae; parasitic:	*Tapera, Surniculus*
	2) 13 cervical vertebrae	
	a) parasitic:	*Clamator*
	b) nonparasitic:	*Coccyzus, Saurothera, Piaya*
	c. AXYAm; ventral tracts double; parasitic:	*Chrysococcyx*
Group II.	Sternum single-notched.	
	1. Bronchial syrinx	
	a. M. flexor hallucis longus inserts on hallux	
	1) Dorsal cervical tract continuous with interscapular tract; social nesting habits:	*Crotophaga*
	2) Dorsal cervical tract separated from interscapular tract by an apterium.	
	a) Flexor metacarpi brevis present; social nesting habits:	*Guira*
	b) M. flexor metacarpi brevis absent; E absent; nonparasitic:	*Carpococcyx*
	b. M. flexor hallucis longus does not insert on hallux; E. absent; nonparasitic:	*Centropus*
	2. Tracheobronchial syrinx; parasitic	
	a. ABXYAm; ventral abdominal tracts double:	*Scythrops, Eudynamis*
	b. AXYAm; ventral abdominal tracts single:	*Cuculus, Pachycoccyx*

one compares only a few anatomical characters in single representatives of two or more families of birds. To illustrate that it is unwise to draw broad conclusions on relationships after dissecting only one or two representatives of each of several families, we may cite as examples the relative development of M. iliotibialis in *Tauraco* and in *Cuculus* and the intergeneric differences in relative development of M. peroneus longus or M. pronator superficialis and M. pronator profundus among the cuckoos.

TABLE 4

ANATOMICAL CHARACTERS OF CUCKOOS AND TOURACOS

Cuculidae	**Tauraco leucotis**
1. AFGXYAm, AEFGXYAm, ABFGXY Am, ABEFGXYAm	1. ABDFGXYAmV
2. Expansor secundariorum is cuculine	2. Expansor secundariorum is ciconine
3. 2 bony canals in hypotarsus	3. 1 bony canal in hypotarsus
4. 17 or 18 presynsacral vertebrae; 4 dorsal vertebrae typical	4. 19 presynsacral vertebrae; 5 dorsal vertebrae typical
5. Perforated atlas	5. Notched atlas
6. Typical furcula present	6. Furcula absent
7. No bony canal formed by coracoid	7. Bony canal is formed by the dorsal processes of the coracoid
8. Lacrimal bone is "cuculine"	8. Lacrimal bone is "musophagine"
9. Oil gland is nude	9. Oil gland is tufted
10. Aftershaft is absent or vestigial	10. Aftershaft is present
11. Eyelashes are characteristic	11. Eyelashes are absent
12. Pattern of dorsal feather tracts is dissimilar	

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