



SMITHSONIAN INSTITUTION
U. S. NATIONAL MUSEUM

Vol. 103

Washington : 1955

No. 3335

ON THE ANATOMY AND RELATIONSHIPS OF GLOSSY
CUCKOOS OF THE GENERA *CHRYSOCOCCYX*,
LAMPROMORPHA, AND *CHALCITES*

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The relationships of the glossy cuckoos have long been in question. Sharpe (1873, p. 579) commented that he could not "find any character in the genus *Chrysococcyx* to justify its separation from *Cuculus*, beyond the metallic plumage . . ." Shelley (1891, pp. 280, 288) recognized as distinct the genera *Chrysococcyx* and *Chalcococcyx* (= *Chalcites*), but placed *Lampromorpha* in synonymy with *Chrysococcyx*. Bannerman (1922, pp. 413-420; 1933, pp. 111-120), however, recognized both *Lampromorpha* and *Chrysococcyx*. Chapin (1939, pp. 197-201), Peters (1940, p. 29), and Friedmann (1948, p. 115) again placed *Lampromorpha* in synonymy with *Chrysococcyx*. Delacour (1951, p. 19) and Friedmann (in litt.) further suggest that the genus *Chalcites* should be united with *Chrysococcyx*, which would place all species of this complex in the genus *Chrysococcyx*.

Little has been written on the internal anatomy of *Chrysococcyx* and, so far as I know, there has been no published description of the internal anatomy of *Lampromorpha* or *Chalcites*.

I am indebted to the following for supplying alcoholic and skeletal material: Dr. Dean Amadon, American Museum of Natural History; Dr. Herbert Friedmann, United States National Museum; and Mr. John G. Williams, the Coryndon Museum, Nairobi, East Africa. I had the following spirit material for study: *Chrysococcyx cupreus* (3), *Lampromorpha caprius* (2), *L. klaas* (1), and *Chalcites*

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lucidus (2). Skeletal material was available as follows: *Chrysococcyx cupreus* (3), *Lampromorpha caprius* (2), and *L. klaas* (1). Certain information was also obtained from the skeletons of the alcoholic specimens. For reading the manuscript and for offering suggestions I am indebted to Dr. Amadon, Dr. Jean Delacour, Los Angeles County Museum, California, Dr. Friedmann, and Dr. Josselyn Van Tyne, University of Michigan Museum of Zoology.

Pterylosis

Beddard (1885, p. 187), basing his comments on manuscript notes of Garrod and Forbes, grouped *Chrysococcyx* with those cuckoos which have the "ventral tract [abdominal] of both sides single," but this arrangement is, in fact, not found in *Chrysococcyx*. Miller (1924, p. 330) reported that the nestling of *Chrysococcyx* lacks natal down. Nothing else seems to have been published on the pterylosis of the species discussed in this paper.

In general the pterylosis of the four species is similar. In each species there are 10 primaries and 10 secondaries, though secondaries 8, 9, and 10 (outermost counted as first) are progressively smaller. The fifth secondary is present, i. e., the wing is eutaxic, or quintocubital. There are four alula quills, the outermost being the longest. The carpal remex and its covert are present. There are 10 rectrices and 10 upper tail coverts. The oil gland is nude; a single, median feather at the base of the gland passes caudad, covering it. The eyelashes are featherlike rather than hairlike as in *Coua caerulea*. The tarsi are what Sharpe (1873, p. 579) spoke of as "accipitrine," i. e., feather tracts descend for a distance of about 6 mm. on the tarsometatarsus; the lateral tract shows the best development.

In the capital region, the median frontal apterium is wanting. A small supraorbital apterium is present, but it is separated from the eyelashes by a single row of feathers. The dorsal cervical feather tract is continuous with the interscapular tract. A wide lateral cervical apterium is present. A long, narrow, median dorsal apterium extends through the dorsal region and the anterior half of the pelvic region. There is a single, medium pelvic feather tract.

Bilateral submalar apteria are present; these are widest in *Chrysococcyx* and narrowest in *Lampromorpha caprius*.

The abdominal branches of the above-mentioned genera differ from those shown for *Cacomantis*, *Piaya* (Beddard, 1885), and *Cuculus canorus* (Lowe, 1943, p. 493) in that two separate tracts form at the posterior margin of the sternum. An inner abdominal tract extends to the anus; this tract is two feathers wide at the beginning, but is reduced to one row about two-thirds the distance to the anus. The outer abdominal tract turns inward to meet the inner abdominal tract about midway to the anus.

Osteology

All four species have 14 cervical vertebrae. There are two pairs of cervicodorsal ribs and, usually, only the last such rib possesses an uncinat process, though one specimen of *Chrysococcyx cupreus* has uncinat processes on both left cervicodorsal ribs, one specimen of *Lampromorpha caprius* possesses these processes on both right ribs, and an alcoholic specimen of *Chalcites lucidus* has uncinat processes on all four ribs. The atlas is perforated by the odontoid process, except in a strongly bleached skeleton of *Lampromorpha klaas*, where the atlas appears to be notched.

With one exception, each specimen has four dorsal vertebrae, four dorsal ribs, and one thoracic rib. In each case, the thoracic rib articulates with the synsacrum dorsally and fuses with the last dorsal rib ventrally. One alcoholic specimen of *Chrysococcyx cupreus*, however, has five dorsal vertebrae and five dorsal, or true, ribs. Of the latter, four articulate with the sternum, while the fifth fuses ventrally with the fourth rib; there is no thoracic rib. Of ten cuculine genera I have thus far investigated, this is the first example I have seen of intra-specific variation in the number of dorsal vertebrae. The number of ribs articulating directly with the sternum, on the other hand, is far more variable. Four, apparently, is the "normal" number of sternal ribs in these species. In one specimen of *Chrysococcyx cupreus* and two specimens of *Lampromorpha caprius*, however, only three of the four dorsal ribs articulate directly with the sternum; and in an alcoholic specimen of *L. klaas* three ribs articulate with the sternum on the left side, whereas four do so on the right.

Apparently in younger individuals the general pattern of the posterior emargination of the sternum is double-notched; it does not seem likely that the bone would be resorbed to form fenestrae in older individuals. In half of the specimens, the sternum is single-notched and bilateral fenestrae are present. In some cases, these fenestrae are bounded posteriorly by a bony bar only 1 mm. in width.

The external nares are oval to rounded and their borders are conspicuously swollen. On the floor of the narial cavity is a well-developed tubercle which has a small bony core; the latter is readily discernible in the skeleton.

A pectineal process is not developed.

Wing Myology

In all four species the following wing muscles are absent: proscapulohumeralis brevis, abductor indicis brevis, abductor digiti II, and the biceps slip to the tendon of *M. tensor patagii longus*. Gadow's pars propatagialis musculi cucullaris does not insert on the tendon of *M. tensor patagii longus*.

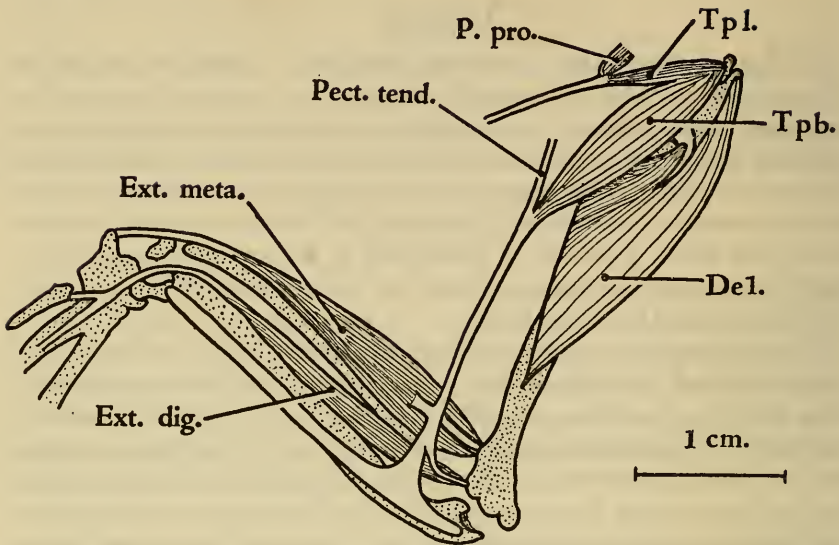


FIGURE 69.—*Chrysococcyx cupreus*. Anconal view of left arm and forearm to show the structure and relationships of *M. tensor patagii brevis*. Explanation of symbols: Del., deltoideus major; Ext. dig., extensor digitorum communis; Ext. meta., extensor metacarpi radialis; P. pro., pars propatagialis, pectoralis superficialis; Pect. tend., accessory tendon of pectoralis superficialis; Tpb., tensor patagii brevis; Tpl., tensor patagii longus.

The structure of *M. tensor patagii brevis* (fig. 69) is similar in the three genera and exhibits some differences from that found in other cuckoos studied. In *Lampromorpha caprius* the belly is 14 mm. long and 5 mm. in maximum width. The distal end of its fleshy belly has no relationship to the tendon of *M. tensor patagii longus*. A strong flat tendon (0.5 mm. wide) arises from the dense fascial envelope which surrounds the insertion of *M. pectoralis superficialis*, and fuses with the tendon of *M. tensor patagii brevis*. About 5 mm. distal to the ectepicondylar process of the humerus, part of the tendon of *M. tensor patagii brevis* fuses with the superficial surface of *M. extensor metacarpi radialis*. From this region of fusion, a strong tendon passes proximad to attach to the ectepicondylar process; distal to the area of fusion, the tendon expands and gives origin on both its superficial and deep surfaces to fleshy fibers of *M. extensor metacarpi radialis*. Posterior to the area of fusion, the tendon of *M. tensor patagii brevis* bifurcates: one branch fuses with the superficial surface of *M. extensor digitorum communis* and attaches to the humerus with that muscle; the second branch fans out, extends nearly the entire length of the ulna, attaches to the bases of the secondaries, and fuses with the antibrachial fascia. This muscle shows the same relationships in the other species, but measurements are slightly smaller in them. In its insertion, *M. tensor patagii brevis* is similar to that in *Coccyzus erythrophthalmus*.

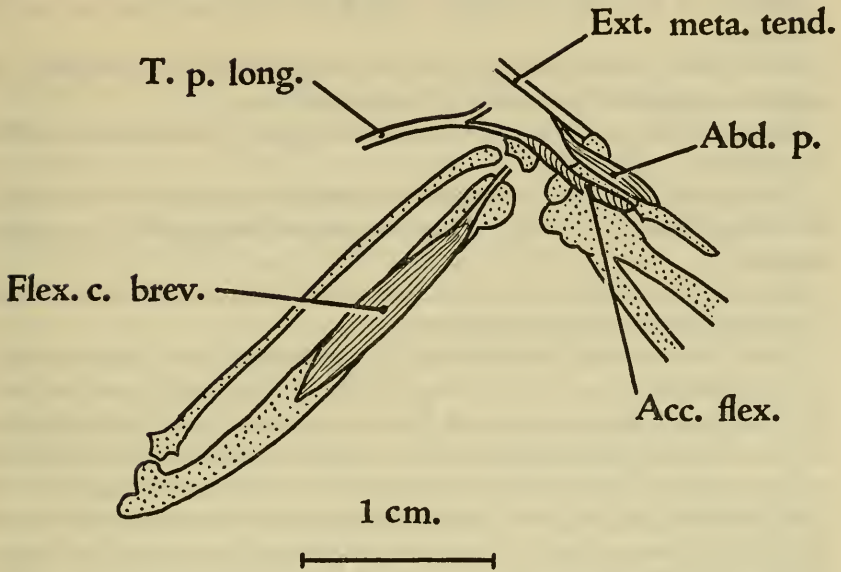


FIGURE 70.—*Chrysococcyx cupreus*. Palmar view of part of left wing to show relationships of the accessory flexor muscle of the pollex. Explanation of symbols: Abd. p., abductor pollicis; Acc. flex., accessory flexor muscle; Ext. meta. tend., tendon of extensor metacarpi radialis; Flex. c. brev., flexor carpi ulnaris brevis; T. p. long., tendon of tensor patagii longus.

Although *M. tensor patagii longus* (figs. 69, 70) has a common origin with *M. tensor patagii brevis* from the superomedial surface of the furculum, the two bellies are incompletely fused distally. In *Lampromorpha caprius*, *M. pectoralis, pars proptatagialis*, is a well-developed, fleshy fasciculus 14 mm. in length and 5 mm. wide at its base on the furculum. The belly tapers to a tendon whose direct continuation is the tendon of *M. tensor patagii longus*. The belly of the latter muscle (about 8 mm. long and 2 mm. wide) fuses with *M. pectoralis, pars proptatagialis*, just before the formation of the common tendon. The tendon runs distad in the leading edge of the propatagium and bifurcates near the distal end of the radius. The main tendon fuses with the fascia of the manus and has a minor attachment to the extensor process. The smaller tendon serves as the origin for a small (4 mm. long) fleshy belly (fig. 70) which inserts on the postero-basal corner of the pollex superficial to the insertion of *M. flexor pollicis*, which, although present, is poorly developed. *Chrysococcyx* and *Chalcites* exhibit this same structure, which I have found neither in other cuckoos nor in literature on other birds.

M. coracobrachialis anterior is similar in the four species and, as in *Coccyzus erythrophthalmus*, it is poorly developed. The belly is surrounded by a dense fascia and, in fact, the muscle almost seems to be

imbedded in the joint capsule. The belly does not fan out at its insertion.

M. *expansor secundariorum* is a single muscle with two tendons of origin: a scapular tendon and a humeral tendon.

M. *scapulotriceps* does not have an accessory attachment to the humerus.

M. *subcoracoideus* has two heads, one arises from the furculum and the other arises from the coracoclavicular membrane as in other cuckoos.

M. *deltoideus minor* is present and arises inside the triosseal canal from the inferior furcular process.

In all four species, the tendon of M. *latissimus dorsi*, pars posticus, inserts posterior to and in contact with the tendon of pars anticus. In *Chalcites*, *Chrysococcyx*, and *Lampromorpha klaas* the area of insertion of pars posticus begins about .5 mm. proximal to the insertion of pars anticus, whereas in *Lampromorpha caprius* the insertion of pars posticus begins about .5 mm. distal to the uppermost fibers of insertion of pars anticus. A dermal component is present, but is very small, and I was unable to demonstrate it in every specimen.

In each species, M. *pronator longus* is a relatively short muscle, extending distad the same distance as M. *pronator brevis*, i. e., about two-thirds the length of the radius.

M. *flexor digitorum profundus* arises on both sides of the area of insertion of M. *brachialis*.

M. *flexor carpi ulnaris brevis* (fig. 70) shows the best development yet seen in cuckoos. The fleshy belly is relatively and absolutely longer (14 mm. in *Chrysococcyx* and *Lampromorpha caprius*) than in *Coua*, *Geococcyx*, etc., and the belly is located more proximally on the ulna.

M. *flexor metacarpi brevis* is well developed in all four species. The belly is triangular in shape; it arises fleshy from the base of the carpometacarpus; it inserts on the tendon of M. *extensor indicis longus*.

M. *extensor pollicis brevis* exhibits minor variation. In *Chrysococcyx cupreus* none of its fibers appear to arise from the tendon of M. *extensor pollicis longus*. In *Lampromorpha caprius* there are two heads as in *Crotophaga sulcirostris*. In *Chalcites* the structure is intermediate between that found in *Crotophaga* and in *Coccyzus*, and a few fibers arise from the tendon of M. *extensor pollicis longus*.

M. *abductor pollicis* is a small muscle with a maximum length of 6 mm. I found two bellies to this muscle in *Chrysococcyx cupreus*, but I was unable to determine to my satisfaction in preserved material that there are two parts in *Lampromorpha* or *Chalcites*. The origin and insertion of this muscle are in each case, however, typical for cuckoos.

Leg Myology

The muscle formula in the three genera is AXYAm. The following muscles are absent: pars iliofemoralis of the piriformis, ilirotrochantericus medius, gluteus medius et minimus, iliacus, adductor digiti IV, extensor brevis digiti III, and, apparently, adductor digiti II. A vinculum is present between the tendons of Mm. flexor digitorum longus and flexor hallucis longus, but a vinculum is wanting between the tendons of Mm. flexor perforatus digiti III and flexor perforans et perforatus digiti III. The tendon of insertion of M. flexor perforatus digiti II forms a sheath for the tendon of M. flexor perforans et perforatus digiti II, but the latter tendon does not ensheath the tendon of M. flexor digitorum longus which supplies digit II. The tendon of M. flexor perforatus digiti IV does not ensheath the tendon of M. flexor digitorum longus which supplies digit IV.

In *Lampromorpha caprius*, M. iliotibialis (fig. 71) arises semitendinous from the entire anterior iliac crest, the anterior iliac process, and from approximately the anterior half of the posterior iliac crest. The muscle is composed of anterior and posterior fleshy portions separated by a central aponeurosis, which distally is intimately fused with the underlying M. femorotibialis externus. The central aponeurosis is best developed distally, where it is 13 mm. long and 3.5 mm. in maximum width; proximally, this band is only 1 mm. wide. In this central area, however, the muscle is completely aponeurotic from origin to insertion. Except for its smaller size, M. iliotibialis exhibits the same structure in *Chalcites lucidus*. In *Chrysococcyx cupreus* the distal aponeurotic portion is the same shape and size as in *Lampromorpha*, but it is separated from the aponeurosis of origin by a central fleshy portion 5 mm. long; for this short distance, therefore, the belly is entirely fleshy from anterior to posterior border. In each of the genera, the insertion of M. iliotibialis is typical and its belly conceals only the anterior and proximal half of M. biceps femoris.

M. semitendinosus (fig. 71) is similar in the three genera. It arises from the posterior third of the posterior iliac crest and from the transverse process of the first free caudal vertebra. Its insertion is typical.

M. gastrocnemius is composed of three main parts: pars externa, pars media, and pars interna. Pars externa arises by two heads, as in *Coccyzus*. Pars media is very small: 5, 7, and 8 mm. long, respectively, in *Chalcites*, *Lampromorpha*, and *Chrysococcyx*. The fleshy portions of pars externa and pars interna are nowhere in contact; the posterior aspect of the complex is a thin, tendinous sheet, which connects the fleshy bellies.

M. peroneus longus is poorly developed, resembling the structure of that muscle in *Coccyzus*. Fleshy fibers begin some distance (7 to 10 mm.) distal to the rotular crest, and the belly does not conceal any part of *M. tibialis anticus*.

M. plantaris is a long, thin muscle whose belly extends about two-thirds the distance down the tibiotarsus.

In *Chrysococcyx cupreus*, *M. extensor proprius digiti III* is a long thin muscle which begins just distal to the proximal articular surface of the tarsometatarsus and extends to the distal end of that bone. The belly does not increase much distad, as it does in *Coccyzus*. The muscle is similar in origin in *Chalcites lucidus*, but the fleshy fibers end 5.5 mm. proximal to the insertion. In *Lampromorpha caprius*, the muscle arises at the level of insertion of *M. tibialis anticus*.

M. lumbricalis exhibits its best development in *Lampromorpha* and its poorest development in *Chalcites*; in the latter genus it is limited to the distal half of the tarsometatarsus.

M. obturator internus, similar in the three genera, is triangular in shape and has only a small fasciculus arising from inside the pelvis.

Syrinx

The syrinx is tracheobronchial. There is one pair of intrinsic syringeal muscles. In *Chrysococcyx cupreus* and *Lampromorpha klaas* these muscles insert on the fourth bronchial semiring. This ring is not much wider than adjacent rings, but it has the largest diameter of any in the bronchial series. The structure is similar in *L. caprius* and *Chalcites lucidus* except that the muscles insert on the third semiring. However, not more than two syringes were suitable for study in any one species so I cannot say that the point of insertion is constant.

Viscera

In each specimen the right lobe of the liver is much larger than the left lobe. A gall bladder is not evident. The pancreas is bilobed. One can obtain only an approximate total-length measurement of the intestine. Its total length in millimeters in two specimens of *Lampromorpha caprius* is 220 and 240; in two specimens of *Chalcites lucidus*, 160 and 180; and in two specimens of *Chrysococcyx cupreus*, 170 and 260. Only insect remains were found in the stomachs. A peculiar feature is the presence of a single caecum, about 4 mm. long in *Chalcites* and 5 mm. long in *Lampromorpha* and *Chrysococcyx*.

Discussion

The genera *Chrysococcyx* and *Lampromorpha* are restricted to Africa. *Chalcites* is found in Asia, Australia, and New Zealand.

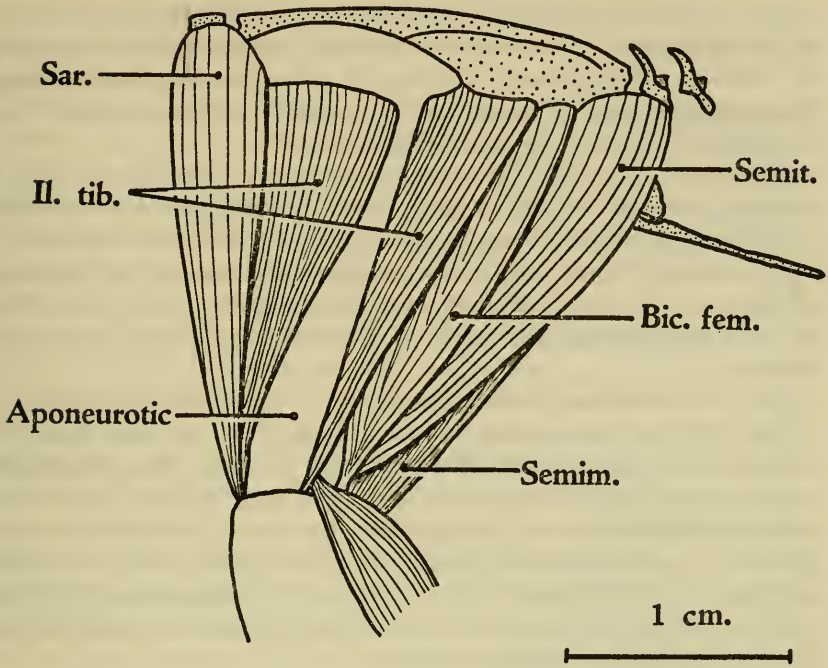


FIGURE 71.—*Lampropromorpha caprius*. Superficial muscles of the left thigh (lateral view). Explanation of symbols: Bic. fem., biceps femoris; Il. tib., iliotibialis; Sar., sartorius; Semim., semimembranosus; Semit., semitendinosus.

Except for the rare yellow-throated cuckoo (*Chrysococcyx flavigularis*), which has not been studied in the field, it is known that all of the glossy cuckoos are parasitic on other birds. A large number of hosts have been recorded, but for the African species the most important hosts seem to be members of the following families: Ploceidae, Nectariniidae, Sylviidae, Muscicapidae, and Motacillidae. Common hosts of the bronze cuckoos (*Chalcites*) in Australia are certain thornbills, wrens, and scrub-wrens of the family Sylviidae (Serventy and Whittell, 1948, p. 238). For other species of *Chalcites* in India, Baker (1934, pp. 353-354) reports the most common hosts to be sunbirds and spider-hunters (Nectariniidae).

Friedmann (1948, pp. 115-116) remarked that: "The eggs of the glossy cuckoos show far more variation in color and markings than do those of any of the other cuckoos of Africa." The eggs of Klaas's cuckoo (*Lampropromorpha klaas*), for example, have "the ground color . . . white, pale greenish blue, or pale blue, and either unspotted or quite abundantly flecked with brick red, brown, or purplish gray," (ibid., p. 136). According to Barrett (1945, p. 149), "five kinds of bronze cuckoos occur in Australia, and the eggs of four of them are bronzy-green in colour, while that of the fifth, the narrow-billed bronze

cuckoo (*Chalcites basalis*) is pinkish, with a uniform sprinkling of tiny reddish spots." Serventy and Whittell (1948, p. 238), in speaking of *Chalcites lucidus*, state: "The egg is pale olive in colour, without any markings, but this colour can be removed with water, after which the shell is found to be light bluish in colour."

Friedmann (1948, p. 115; 1949, p. 519) has called attention to a behavior pattern "unique" among parasitic birds in that the "habit of feeding of fledged young by adult parasitic cuckoos is known . . . only in some four species of the small glossy cuckoos of the *Chalcites-Chrysococcyx* group." However, Moreau (1949, p. 537) cited two references indicating that adults of *Cuculus* occasionally feed young cuckoos.

"The African glossy cuckoos also have a courtship feeding behavior," which "is otherwise known, in cuckoos, only in African forms of *Clamator* and *Cuculus*" (Friedmann, 1948, p. 115). Since this statement was published, however, Watson and Bull (1950, p. 226) have reported observations of *Chalcites lucidus* which gave them the "impression . . . that some form of communal display with courtship feeding was taking place." These authors do not agree with Friedmann (1949, p. 517) that feeding of young by adults has been proved for the New Zealand shining cuckoo.

That the species of glossy cuckoos here discussed are closely related, biologically and anatomically, is evident from an analysis of the data presented. The behavior patterns of courtship feeding and feeding of fledged young indicate close relationship. Too little is known about the detailed life history of these birds to justify further comparison. In morphological characters, also, these species exhibit a general uniformity of structure. For the most part, differences in muscles, for example, can be ascribed only to size differences of the species.

It seems certain that unsatisfactory characters have been used by some authors to separate *Chrysococcyx* and *Lampromorpha*. Jackson (1938, p. 500) used shape and length of tail to separate them: *Lampromorpha* "has the tail much shorter and slightly rounded, but not graduated." Priest (1934, p. 227) separated them on the basis of sexual dimorphism, but this surely was a misprint in his key. In establishing the genus "*Adamatornis*" for *klaas*, Roberts (1922, p. 219) stated only that *klaas* "is much smaller than *cupreus*."

Little has been written on the locomotor habits of these species. Yet, of seven differences in anatomical structure which might be useful for determining relationship, six seem definitely to be correlated to functional phenomena. These involve primarily the extent of origin or insertion and relative length of belly of the following muscles: latissimus dorsi, iliobtibialis, extensor proprius digiti III, abductor

pollicis, flexor hallucis longus, and extensor hallucis longus. It must be emphasized, however, that all differences in structure here discussed are minor in degree.

An analysis of *M. iliotibialis* will serve to illustrate the minor differences encountered and to cast doubt on the validity of them as a basis for establishing separate genera. The structure of this muscle has been discussed in some detail above (p. 591). The complete aponeurotic central portion of *M. iliotibialis* in *Lampromorpha caprius* is most like the structure of that muscle in *Coccyzus*. In each of eight other genera (*Crotophaga*, *Geococcyx*, *Coua*, etc.) the aponeurotic portion is limited to the distal half or two-thirds and there is a well-developed fleshy belly located proximal to this aponeurosis. Only in *Chrysococcyx cupreus* and *Lampromorpha klaas*, where the middle fleshy portion is very small, does the structure of the muscle represent an intermediate stage. The locomotor pattern seems to be similar in these species (Friedmann (1948, pp. 129, 150, 158) implies this as regards the manner of flight), so one might place some weight on this character as indicating degree of relationship. Also, the place of insertion of the syringeal muscles, if proven constant, would indicate relationship as follows: *caprius* with *lucidus* (insertion on the third bronchial ring); *cupreus* with *klaas* (insertion on the fourth ring). Minor differences in other muscles, however, indicate a closer relationship between *lucidus* and *cupreus* than between the former and *caprius*, so that it seems unlikely that the structure of *M. iliotibialis*, in this instance, is a valid character for judging relationship. In anatomical features *klaas* resembles *cupreus* more than it does *caprius*. Van Someren (1925, pp. 660–662) came to the same conclusion after a study of feather structure; he stated that *klaas* should either be placed with *cupreus* in the genus *Chrysococcyx* or else in an intermediate position, but that *klaas* could not be placed with *caprius* if only two genera were to be recognized. Both van Someren and Friedmann (1948, pp. 150, 151) felt that *cupreus*, *caprius*, and *klaas* are congeneric.

In reviewing the evidence presented here, I must conclude that all of the glossy cuckoos are congeneric. Following the law of priority, all the species of this complex must be placed in the genus *Chrysococcyx*. Anatomical similarities further suggest that *cupreus* and *klaas* are more closely related to each other than to either *caprius* or *lucidus*. Though *lucidus* possesses certain anatomical features exhibited by *caprius* (especially the structure of *M. iliotibialis* and the place of insertion of the syringeal muscles), in most respects *lucidus* is like *cupreus*. Therefore, *caprius* is most unlike the other species of this genus.

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