THE RELATIONSHIPS AND EVOLUTION OF THE ROLLERS: FAMILIES CORACIIDAE, BRACHYPTERACIIDAE, AND LEPTOSOMATIDAE

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THE order Coraciiformes has long been considered by many to be a heterogeneous assemblage of families. Indeed some workers have concluded that few of the families usually included in the order are related to one another, and they have recognized as many as five separate orders (Stresemann, 1959). Despite the extreme ordinal splitting of some authors, all have accepted the close relationship of three distinct taxa: the Coraciidae, or true-rollers; the Brachypteraciidae, or ground-rollers; and the Leptosomatidae, or cuckoo-rollers. The interrelationships and evolution of the rollers is the subject of this paper; their affinities to the remaining families of the order will be discussed in the future.

The Coraciidae consist of two genera, *Coracias* with eight species, and *Eurystomus* with three (Peters, 1945). The family is distributed over Africa, southern and eastern Europe, southern Asia, the islands of southeastern Asia, and Australia. The Brachypteraciidae include three genera, *Brachypteracias* and *Atelornis* with two species each, and *Uratelornis* with one. All are confined to Madagascar. The third family of rollers, the Leptosomatidae, has been erected for the monotypic genus, *Leptosomus*, found on Madagascar and the nearby islands.

The taxonomic arrangement of the rollers has varied with different authors. Some have put the Brachypteraciidae and Coraciidae in one family and *Leptosomus* in a separate family (Fürbringer, 1888; Peters, 1945; Verheyen, 1960); some would place all three taxa in a single family (Sharpe, 1871; Dresser, 1893; Beddard, 1898; Mayr and Amadon, 1951); and a third group would recognize three separate families (Stresemann, 1927–1934, 1959; Storer, 1960; Wetmore, 1960). Because of the arbitrary nature of delimiting family-rank taxa, I do not believe we shall ever reach universal agreement on the ranks to be used for the rollers. Therefore in this paper I want to emphasize the degree of relationship and the evolutionary patterns as shown by morphological criteria, in particular the osteology, rather than on the hierarchical arrangement.

The anatomy of the true-rollers has never been studied exhaustively. Except for Giebel's (1857) comments on Nitzsch's work on *Coracias garrulus*, no other investigation has been directed specifically to the Coraciidae. Milne-Edwards (1876, plates 81–82) figured the skeleton

of *Eurystomus glaucurus*. Certain points about the anatomy of the Coraciidae have been mentioned in more general anatomical papers (Fürbringer, 1888, 1902; Garrod, 1873–1874, 1875; Beddard, 1898; Lowe, 1948; Verheyen, 1955a, 1955b, 1955c).

Nor has much been written about the anatomy of the Brachypteraciidae. Milne-Edwards (1876, plates 97–99, 101–103, 104A) pictured the skeletal, and in some cases visceral, anatomy of *Brachypteracias leptosomus, B. squamigera*, and *Atelornis pittoides*. He did not discuss the anatomy of these forms, but according to Forbes (1880: 466), Milne-Edwards had planned to give a full osteological description of the ground-rollers and of *Leptosomus*; this was never published to my knowledge.

Leptosomus has been the subject of more intensive anatomical investigations than the other rollers. The first study of any importance was by Sclater (1865). He made observations mostly on the external characters but mentioned features of the sternum, coracoid, and tongue. Milne-Edwards (1876, plates 85–88) pictured the skeleton, pterylography, and viscera. Forbes (1880) discussed the pterylosis, visceral anatomy, myology, and syrinx.

MATERIALS AND METHODS

During this study I examined the following skeletal material (abbreviations as follows: AMNH—American Museum of Natural History, LSU—Louisiana State University Museum of Zoology, UMMZ—University of Michigan Museum of Zoology, and USNM—United States National Museum):

Coraciidae: *Coracias benghalensis*, USNM 343054, 343284, AMNH 2785; *C. garrulus*, AMNH 5245, 2141; *C. caudata*, USNM 321708, 18906, AMNH 3759; *Eurystomus orientalis*, USNM 223989, 319161, 343605, 291382, 226193, 18406; *E. glaucurus*, LSU 32791; *E. gularis*, USNM 292413, 292414. Brachypteraciidae: *Atelornis pittoides*, UMMZ 208409; *A. crossleyi*, USNM 223864; *Brachypteracias leptosomus*, USNM 223863. Leptosomatidae: *Leptosomus discolor*, AMNH 448, USNM 291844, 291845.

The skeletons were examined with a multiple-power dissecting microscope; the illustrations were made with the aid of a camera-lucida microscope. The terminology used in this paper follows that of Bock (1963) for the skull characters and that of Howard (1929) for postcranial features.

Study skins housed in the American Museum of Natural History were used for the external measurements, which were taken as follows: bill length, from the anterior end of the nostrils; bill width, at the anterior end of the nostrils; wing, chord, not flattened; tail, from base of central rectrix to tip of longest rectrix; tarsus, from proximal end of bone to last complete tarsal scute; hallux, from base of hallux to base of claw.

In reporting the measurements, males and females are treated as the same sample; no significant dimorphism was found. Measurements for the Coraciidae were made only on *Coracias garrulus garrulus* and *Eurystomus glaucurus afer*. These two species are admittedly only a sample of the two genera, but for the types of conclusions drawn in this study, each is probably representative of its genus.

THE ROLLERS AS A NATURAL GROUP

I am unaware of any specific discussion based on anatomical characters that points to the monophyletic nature of the rollers. Lowe (1948) and Verheyen (1955a, 1955b, 1955c) list numerous features but fail to state whether they are clearly diagnostic or not. Although a detailed treatment of this problem is beyond the scope of this paper because it would require reviewing the entire order, it is desirable to provide some rationale for considering the rollers monophyletic.

The rollers share a series of skull characters that, when taken together, tend to separate them from the other coraciiforms. Among these is a similarity in the shapes and relative positions of the basicranial features, both the lacrimal (without a supraorbital process) and ectethmoid are present, the postorbital process is elongated and touches the jugal bar, the quadrates are similar in form, the general shapes of the palatines and prepalatines are similar, the extent of ossification and the shape of the maxillopalatines are alike, and no well-developed nasal-frontal hinge is formed (best developed in the Brachypteraciidae).

In addition to the cranial features, certain aspects of the postcranial skeleton also unite the rollers. The humeri are more similar to each other than they are to any other coraciiform family. Also the rollers have the trochleae of the tarsometatarsus arranged in a curve (as seen in distal view), whereas in most other coraciiforms the trochleae are arranged more or less in a straight line.

The above skeletal characters do not prove the monophyletic nature of the rollers. Within the coraciiforms it is difficult to recognize the "primitive" and "derived" character states of many characters. It is suggested below that considerable parallelism, convergence, and multiple origins of character states have taken place in the skeletal system of the rollers. If the other coraciiform families are also studied, the problems of recognizing the evolutionary pathways of the characters are increased.

COMPARATIVE OSTEOLOGY OF THE ROLLERS

SKULL STRUCTURE

Coracias

The skull of *Coracias* (Figure 1) will serve as a standard with which to compare the other forms. The brain case is noticeably vaulted and slopes abruptly posteriorly to meet the well-developed supraoccipital crest. On the lateral side of the brain case, posterior to the postorbital process, is a well-developed temporal fossa for the adductor musculature. The brain case slopes gradually toward the nasal-frontal hinge, and a distinct groove is found between the orbits. In side view the culmen is straight and without any curve. The ventral edge of the upper jaw shows a slight upward curve; from above the bill tapers to a fine point. The nasal septum is completely ossified
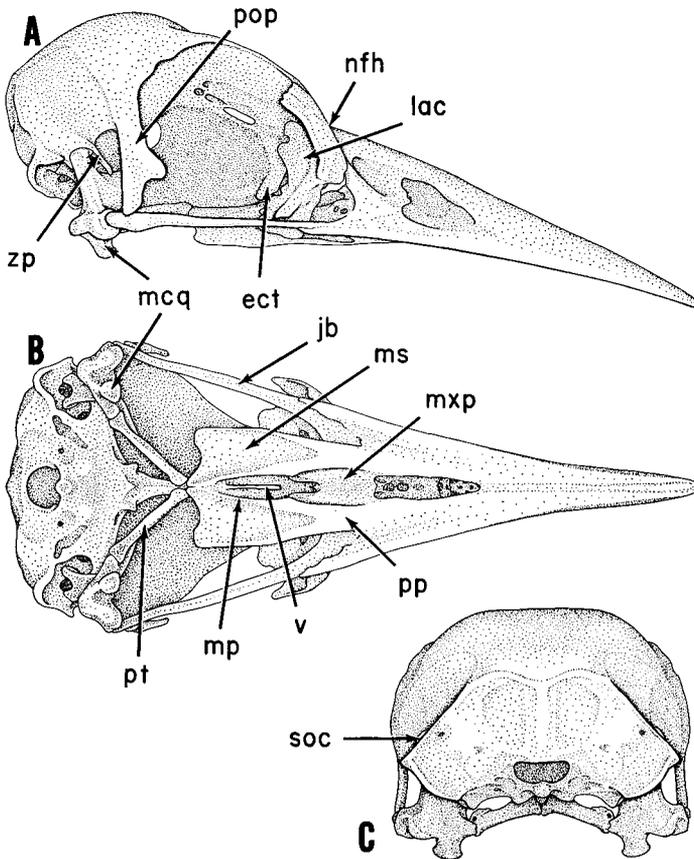
Figure 1. Skull of *Coracias benghalensis*. A, side view; B, ventral view; C, posterior view. Abbreviations: ect, ectethmoid; jb, jugal bar; lac, lacrimal; mcq, medial condyle of quadrate; mp, mediopalatine process; ms, medial shelf of palatine; mxp, maxillopalatine; nfh, nasal-frontal hinge; pop, postorbital process; pp, prepalatin; pt, pterygoid; soc, supraoccipital crest; v, vomer; zp, zygomatic process.

and the external naris is oblong in shape. At the nasal-frontal hinge the frontals and nasals apparently overlap and fuse, for the hinge shows no marked transverse groove. Posteriorly, the supraoccipital area is expansive and thus provides considerable area for the attachment of neck and jaw muscles. The lacrimal is large and its head joins the nasal-frontal hinge. Ventrally the lacrimal expands mediad into a prominent plate of bone. This plate touches or almost touches, but does not fuse with, the frontal dorsally and the ectethmoid medially; the lacrimal braces the jugal bar latero-medially. The anteroventral portion of the lacrimal lies close to the palatines. The ectethmoid is a small rectangular-shaped spur of bone passing ventrolaterally into the orbit. The ectethmoid fits into, but does not fuse with, a notch that is present on the medial side of the lacrimal. The interorbital septum is completely ossified.
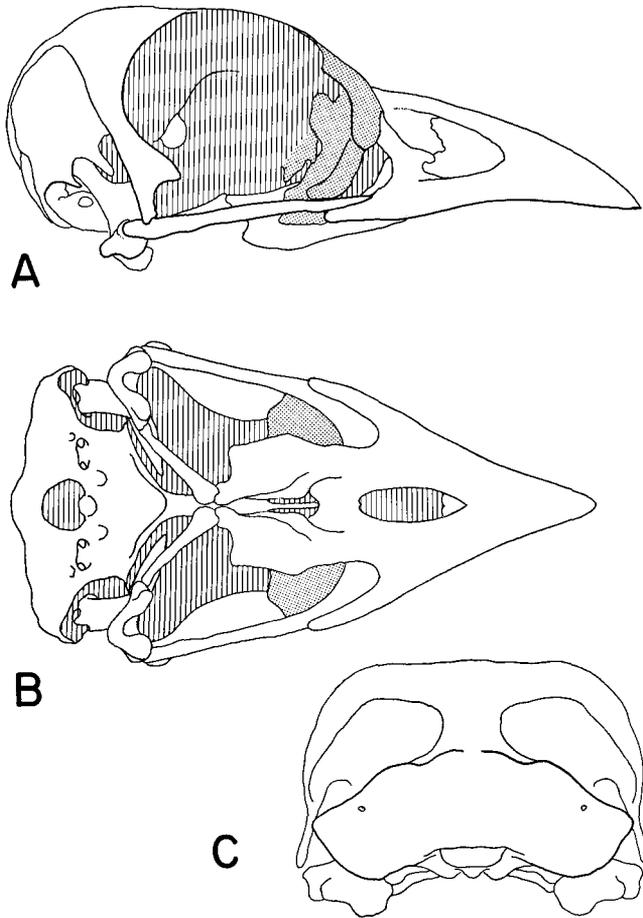
Figure 2. Skull of *Eurystomus glaucurus*. A, side view; B, ventral view; C, posterior view. For identification of structures see Figure 1.

The postorbital process is large and is produced ventrally to brace the dorsal side of the jugal bar just anterior to the jugal-quadrate articulation. The zygomatic process is short and thin. The orbital process of the quadrate is large and tapers to a fine point. The body of the quadrate is moderately broad; dorsally the otic process is short. In ventral view the medial condyle of the quadrate is very well marked and directed ventroanteriorly. The lateral and posterior condyles form a continuous articulating surface. A noticeable depression lies between the three condyles. The pterygoid is stout, somewhat flattened mediolaterally, and approaches the palatine at about a 40-degree angle. The palatines are nearly the same width throughout their length, tapering slightly in the area of the prepalatines. Posteriorly the palatines are nearly square in shape. The mediopalatine process is only slightly raised ventrad and is produced more posteriorly than anteriorly. The thickness of the palatines

appears uniform throughout; the medial shelf of the palatines is directed ventro-laterally. Anteriorly the prepalatines are rather broad and are separated a moderate distance at their junction with the maxilla. The maxillopalatines are large structures that fuse solidly at the midline. They also fuse to portions of the dorsal surface of the prepalatines. A vomer is present. The jugals are not strong in appearance; they are straight and slightly flattened dorsoventrally.

The lower jaw of *Coracias* (Figure 5A) shows a more or less continuous dorsally inflected curve. The rami are not deep in a dorsoventral direction. Anteriorly the rami are fused for slightly more than one-third their length, the symphysis being narrow but sturdy. The internal process of the mandible is long, moderately thin, and directed dorsoposteriorly. The posterior wall of the articular cavity is prominent, as is the retroarticular process; hence the articular cavity is very well-developed. The articular groove for the quadrate is well-marked.

Eurystomus

With regard to general proportions, the skull of *Eurystomus* (see Figure 2) is quite unlike that of *Coracias*. The cranium of *Eurystomus* is broader and flatter, and the bill is much shorter and broader at its base. Despite these radical changes, the detailed structure of the skull has remained essentially like that of *Coracias*. *Eurystomus* shows the following differences from *Coracias*: the temporal fossae extend more posterodorsally on the skull and approach each other at the midline; the supraoccipital crest is not located dorsally as much; the pterygoids are stouter and not so flattened lateromedially; the prepalatines are shorter and broader; the maxillopalatines are shorter; and the shelf of the palatines is shorter and broader. Long transpalatine processes are typically not present, but they were in one specimen of *Coracias benghalensis* (USNM 343054). In all other features of the skull, disregarding minor variation, *Eurystomus* is very similar to *Coracias*.

No important differences were noted in the mandible, except in proportions.

Atelornis

The skull of *Atelornis pittoides*[1] (Figure 3) shows some similarities, but also some differences, compared to that of *Coracias*. The cranium of *Atelornis* is much less vaulted and more rounded than in *Coracias*. The posterior portion of the skull curves gradually, rather than abruptly, ventrad to meet the well-marked supraoccipital crest. Laterally the temporal fossae are narrower, more horizontal, and extend more posteriorly on the cranium and almost meet at the midline. Anteriorly the groove between the orbits is much shallower. The bill is less heavy but of the same general shape. The nasal septum is somewhat less ossified. The nasal-frontal hinge is much more evident than that of *Coracias*, with a well-developed transverse groove being present. From a posterior view the skull appears less broad with the supraoccipital

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[1] The illustrations of *Atelornis pittoides* in Milne-Edwards (1876, plate 103A) are puzzling because the skull differs greatly from the specimen I examined. In his drawing the palatines are not squared posteriorly but are rounded, the prepalatines are decidedly shorter and broader, and the bill is heavier and wider. The vomer is also present, whereas it is lacking in the Michigan specimen (it may have been lost when the skull was prepared). The remainder of the illustrations, including those of the postcranial skeleton, agree in general with the specimen I studied, though the drawings differ somewhat in detailed features (possibly individual variation).

The above descrepancies are possibly explained by assuming that Milne-Edwards' drawing of the skull was poorly executed or that the specimen was damaged during preparation. That the skull features could show as much intraspecific variation as the drawings imply is unlikely. Hence I am disregarding Milne-Edwards' paper and am basing my conclusions only on the specimens that I personally examined. If the skeletons Milne-Edwards studied are still available, they should be compared with his plates to verify their accuracy.
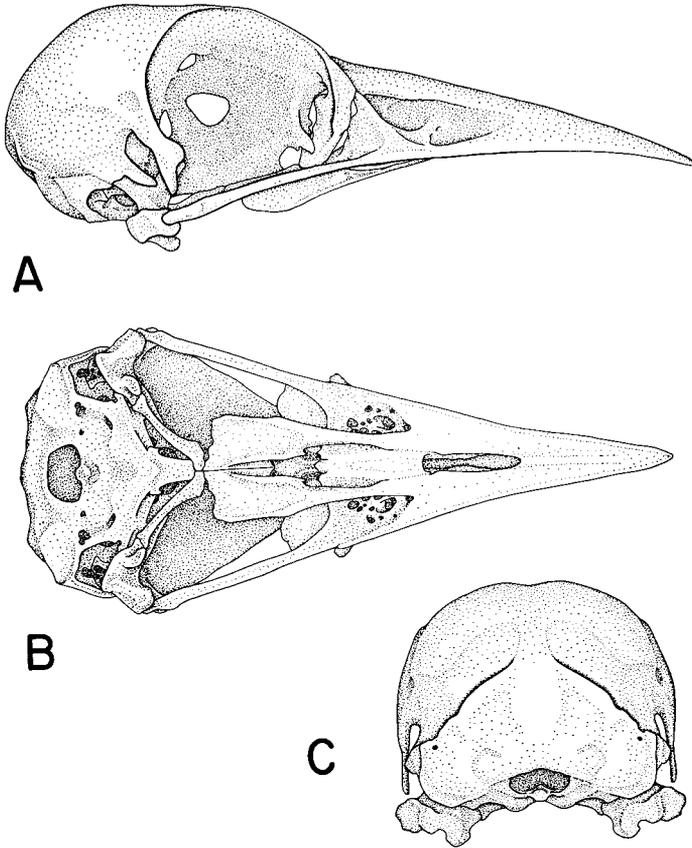
Figure 3.   Skull of *Atelornis pittoides*. A, side view; B, ventral view; C, posterior view. For identification of structures see Figure 1.

area and the foramen magnum directed more ventrally. The head of the lacrimal is smaller and has most of its articulation with the lateral nasal bar, although the dorsalmost portion of the articulation is with the frontal. Ventrally the lacrimal resembles that of *Coracias* in being expanded medially. The medial portion of the lacrimal does not extend so far dorsad toward the frontal as in *Coracias* nor does it approach as close to the palatines. The lacrimal does meet the ectethmoid and does brace the jugal. A smaller ectethmoid is present, but the bone is still spurlike. The interorbital septum is less ossified. The postorbital process is similar in shape but is somewhat thinner. The zygomatic process is shorter and slightly broader. The quadrates of *Atelornis* and *Coracias* are similar, but the otic process is shorter in the former. Ventrally, the medial condyle of the quadrate is much less developed and the shelf (depression) between the condyles is absent. The pterygoids are weaker and flattened dorsoventrally, especially near the palatine articulation. The angle of the palatine-pterygoid articulation is approximately the same as in *Coracias*. Posteriorly
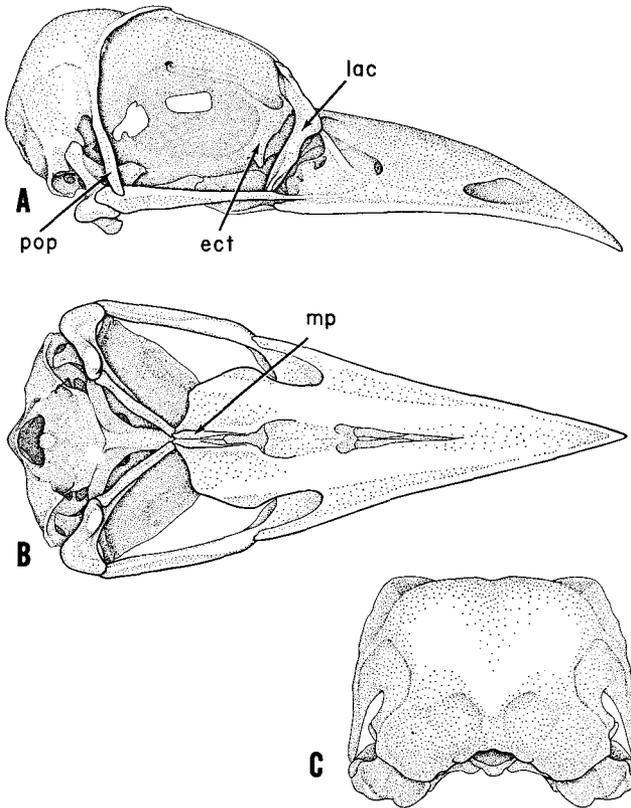
Figure 4. Skull of *Leptosomus discolor*. A, side view; B, ventral view; C, posterior view. For identification of structures and abbreviations see Figure 1.

the palatines are roughly the same shape, but anteriorly the prepalatines become much narrower and are much closer together when they meet the maxilla. Very short interpalatine processes are present (absent in *Coracias*). The mediopalatine process is more produced anteriorly in *Atelornis*, whereas they are larger posteriorly in *Coracias*. The maxillopalatines are much broader anteroposteriorly and fuse at the midline. A vomer is absent in the skull I examined but was probably lost in preparation. The jugals are similar in the two genera.

The mandibles of *Atelornis* and *Coracias* show many differences. When seen from the side, the mandible of *Atelornis* (Figure 5B) is curved downward more strongly. The internal process of the mandible is slightly longer, narrower, and directed more dorsally. The posterior wall of the articular cavity is very poorly developed, and thus so is the articular cavity itself.

Leptosomus

The brain case of *Leptosomus* (Figure 4) is greatly vaulted and more bulbous than in *Coracias*. The posterior portion of the brain case is much more vertical and

less rounded than in *Coracias*, and a supraoccipital crest is not present. The temporal fossae are like those of *Coracias* but are less extensive. A moderately deep groove is present between the orbits, and the supraorbital rim has become elevated. The upper jaw is much heavier than that of *Coracias*. The culmen is not straight but curves gradually to the tip. The area of the nasal septum is highly ossified. The nasal-frontal hinge of *Leptosomus* resembles that of *Coracias* in that a transverse groove is absent. The lacrimal differs in shape from those of *Coracias* and *Atelornis*. The head of the lacrimal joins to the nasal-frontal hinge. A long, stout descending process braces the jugal; the lacrimal is not expanded medially. The ectethmoid is not spurlike but is rectangular in shape; it joins the frontal dorsolaterally and a foramen is present dorsomedially. A large intervening space is present between the lacrimal and ectethmoid. Usually the interorbital septum is not completely ossified, but it was in one specimen. The postorbital process is like those of *Coracias* and *Atelornis*, but it is thinner and the small anterior projection is missing. A zygomatic process is absent. The orbital process of the quadrate is shortened; the otic process is also shorter but decidedly broader. Ventrally the articulating surface of the medial condyle of the quadrate is larger, but the condyle does not project ventrally as much as it does in *Coracias*. The lateral and posterior condyles merge to form a single articulating surface; the two condyles are somewhat more distinct in *Coracias*. A depression is present between all of the condyles. The pterygoids are stout and slightly flattened mediolaterally. They meet the palatines at a more acute angle (about 30 degrees) than in *Coracias*. The palatines are different in shape; the posterolateral edges are not produced as much, but the anterolateral edges are expanded more than in *Coracias* and *Atelornis*. The prepalatines are rather broad and moderately separated at their junction with the maxilla. The mediopalatine processes are much closer together and more nearly parallel than in *Coracias*, but like those of the latter genus the processes are more developed posteriorly than anteriorly. The maxillopalatines fuse at the midline and partially fuse to the prepalatines. The presence of a vomer could not be substantiated on the specimens I studied and it is probably absent. The jugals are much stouter and stronger in appearance than in *Coracias*, and they decrease in size from posterior to anterior rather than being essentially uniform in size.

The mandible of *Leptosomus* (Figure 5C) differs from that of *Coracias* in only one significant characteristic: in *Leptosomus* the lateral articulating surface is much smoother and lacks depressions.

Summary of the skull characters.—Each of the three skull types possesses its own characteristics, but also shows resemblances to the other two. Hence definite conclusions about relationships based on the skull alone are difficult.

Coracias and *Atelornis* resemble each other in many characters: the presence of a supraorbital crest, shape of the bill, shape of the jugals, the form of the postorbital and zygomatic processes, the lacrimal-ectethmoid complex, and the shape of the medial shelf of the palatines. They differ in other features: vaulting of the skull, groove between the orbits, shape of prepalatines, area of maxillopalatines, mediopalatine processes, and the shape of the pterygoids.

Although at first glance they seem to exhibit major differences, the skulls of *Coracias* and *Leptosomus* show many similarities: shape of the pterygoids, shape of the mediopalatine processes, form of the prepalatines, maxillopalatines, the vaulting skull, and the groove between the orbits. The differences are also striking: the lacrimal-ectethmoid complex, shape of the medial shelf of the prepalatines, quadrate characters, bill shape, supraoccipital crest, and the shape of the jugals.

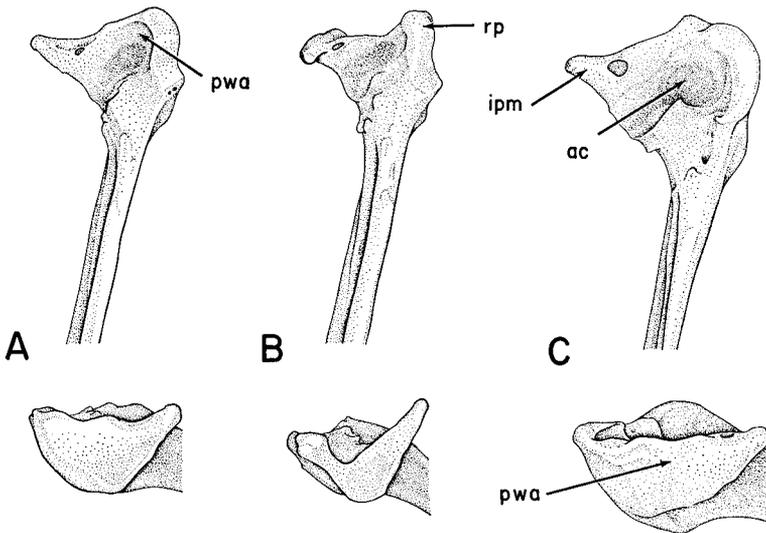In general the skull characters suggest that *Atelornis* and *Coracias* are more closely

Figure 5. Dorsal (upper figure) and posterior (lower figure) views of mandibles. A, *Coracias benghalensis*; B, *Atelornis pittoides*; C, *Leptosomus discolor*. Abbreviations: ac, articular cavity; ipm, internal process of mandible; pwa, posterior wall of articular cavity; rp, retroarticular process.

related to each other than either is to *Leptosomus*, because the former two share many features not found in other coraciiforms. Although the skulls of *Atelornis* and *Coracias* differ from each other in many characters, many of the differences can perhaps be explained on functional grounds (see below). *Atelornis* and *Leptosomus* show few, if any, similarities to each other, and these characters are common to other coraciiform families.

POSTCRANIAL SKELETON

Comments on Intrafamilial Variation

Coraciidae.—With rare exceptions the skeleton of *Eurystomus* is very similar to *Coracias* and unless there are major differences the former is not characterized in detail.

Brachypteraciidae.—Unfortunately, only four elements—coracoid, femur, sternum, and pelvis—of *Atelornis crossleyi* (USNM 223864) were available for comparison with *A. pittoides*. No differences were noted in the femur or sternum, but the brachial tuberosity of the coracoid was less enlarged, and the posterior iliac crest of the pelvis was slightly better developed in *A. crossleyi*. The skeletal material of *Brachypteracias leptosomus* (USNM 223863) also consisted of only a few elements, and although they were essentially like those of *Atelornis*, some differences were found: humerus, (1) entepicondyle less well-pronounced anconally and slightly more massive, and (2) median crest slightly better developed; coracoid, (1) area of the brachial tuberosity more massive, and (2) sternal facet slightly larger (almost, if not entirely, absent in
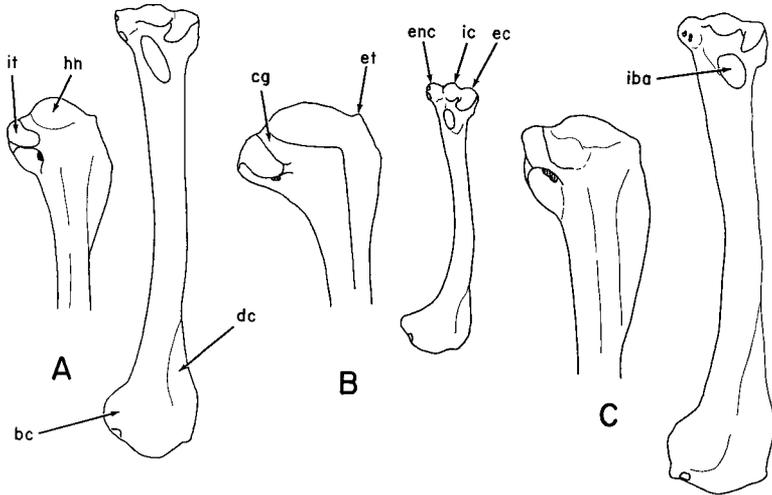
Figure 6. Humeri. A, *Coracias benghalensis*; B, *Atelornis pittoides*; C, *Leptosomus discolor*. Left, anconal view of proximal end; right, palmar view. Abbreviations: bc, bicipital crest; cg, capital groove; dc, deltoid crest; ec, external condyle; enc, entepicondyle; et, external tuberosity; hh, head of humerus; iba, impression of brachialis anticus; ic, internal condyle; it, internal tuberosity.

Atelornis); sternum, no important differences; femur, (1) popliteal area slightly less deep, less well-marked, and (2) obturator ridge slightly less pronounced.

   Leptosomatidae.—No significant differences were noted in the three skeletons I examined.

Interfamilial Comparison

   The postcranial elements are not described in detail; the reader can refer to the figures for a basis of comparison. The following discussion compares *Atelornis* and *Leptosomus* with *Coracias* in terms of both similarities and differences.

Humerus (Figure 6)

   The humerus of *Leptosomus* differs from that of *Coracias* as follows: (1) deltoid crest more elongate, (2) head less pronounced proximally and is broader, (3) internal tuberosity better developed and oriented more nearly along axis of shaft, (4) external tuberosity less well-marked, (5) capital groove deeper, especially distally, (6) median crest more pronounced, (7) bicipital crest projects more internally (anconal view), (8) bicipital furrow more depressed at its proximal end (at base of head), (9) ligamental furrow slightly more developed, (10) ectepicondylar prominence much more enlarged, (11) impression of brachialis anticus not narrow but rounded, (12) internal condyle much more bulbous, less flat distally, (13) olecranal fossa deeper, and (14) external condyle flatter, less bulbous distally.

   The humerus of *Atelornis* differs from that of *Coracias* in having: (1) internal
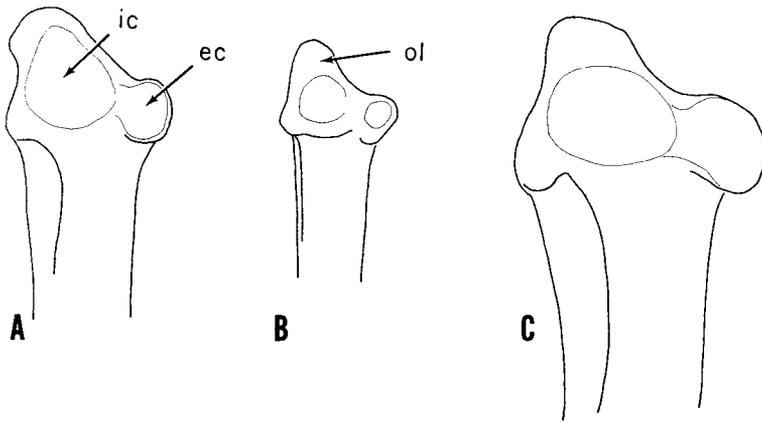
Figure 7. Palmar view of proximal end of ulna. A, *Coracias benghalensis*; B, *Atelornis pittoides*; C, *Leptosomus discolor*. Abbreviations: ec, external cotyla; ic, internal cotyla; ol, olecranon.

tuberosity curved more distally over pneumatic fossa, (2) median crest slightly less developed, (3) bicipital crest much less rounded and directed more internally, less developed distally, (4) bicipital furrow deeper proximally near head, (5) in anconal view, base of head external to median crest much more excavated, (6) impression of brachialis anticus shallower and narrower, (7) internal condyle much more abruptly raised distally relative to external condyle, and internal condyle more spherical, less elongate in external-internal direction, (8) entepicondyle more pronounced distally (seen in palmar view), (9) ectepicondyle slightly less elevated, (10) tricipital grooves less developed, and (11) olecranal fossa shallower.

The humeri of *Coracias* and *Leptosomus* resemble each other and differ from that of *Atelornis* in having: (1) a broader internal condyle that does not project as much distally beyond external condyle, (2) much less of a curve to the shaft at its proximal end, (3) the deltoid crest better developed, (4) the bicipital surface larger, (5) the entepicondyle directed less distally, and (6) the anconal surface of shaft at base of head and median crest much less depressed.

In the general form of the humerus *Coracias* and *Leptosomus* are clearly closer to each other than either is to *Atelornis*.

Ulna (Figure 7)

The ulna of *Leptosomus* differs from that of *Coracias* in that: (1) internal margin of external condyle less rounded (seen in anconal view), (2) groove between external and internal condyles slightly deeper, (3) external cotyla broader and projecting more externally, and (4) prominence for anterior articular ligament larger.

Atelornis differs from *Coracias* in the structure of the ulna as follows: (1) olecranon much larger, (2) internal cotyla protrudes more palmarily (when seen from internal side), (3) external cotyla reduced in size relative to internal cotyla, (4) internal condyle smaller, less developed, (5) groove between internal and external condyles shallower, less noticeable, and (6) carpal tuberosity more pronounced.
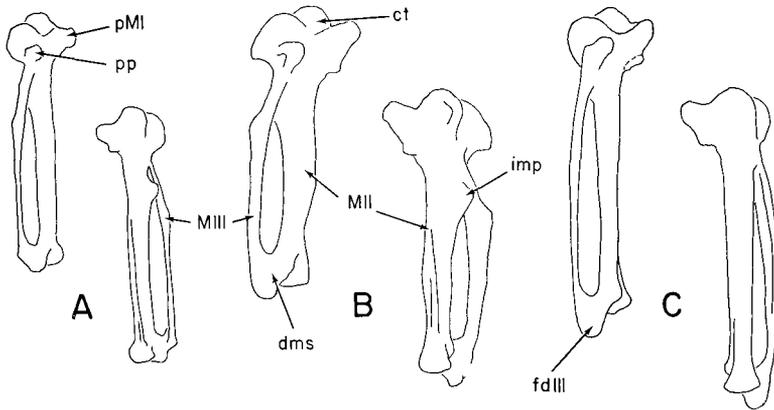
Figure 8. Internal view (left) and external view (right) of carpometacarpus. A, *Coracias benghalensis*; B, *Atelornis pittoides*; C, *Leptosomus discolor*. Abbreviations: ct, carpal trochlea; dms, distal metacarpal symphysis; fdIII, facet for digit III; imp, intermetacarpal process; MII, metacarpal II; MIII, metacarpal III; pMI, process of metacarpal I; pp, pisiform process.

Leptosomus and *Coracias* resemble each other and differ from *Atelornis* in a number of features including the shape of the olecranon, carpal tuberosity, and the cotylae. *Coracias* agrees with *Atelornis* and differs from *Leptosomus* in the shape of the internal and external condyles (internal condyle being smaller in *Atelornis*). The morphology of the ulna suggests a closer relationship between *Coracias* and *Leptosomus* than between *Coracias* and *Atelornis*.

Carpometacarpus (Figure 8)

The carpometacarpus of *Leptosomus* differs from that of *Coracias* as follows: (1) area between pisiform process and metacarpal III not so depressed to form a deep groove, (2) process for metacarpal I turned slightly more proximally, (3) intermetacarpal process (from intermetacarpal tuberosity) lacking, (4) facet for digit III projects much more, thus distal metacarpal symphysis much deeper, and (5) posterodistal edge of internal rim of carpal trochlea not rounded but more crescent-shaped.

In the characters of the carpometacarpus *Atelornis* differs from *Coracias* in that: (1) process of metacarpal I directed more proximally, (2) posterior edge of internal rim of carpal trochlea peculiar in shape, the portion just proximal to metacarpal III being absent, (3) posterior surface of metacarpal III troughlike (surface more planar in *Coracias* and *Leptosomus*), and (4) facet for digit III slightly larger.

The carpometacarpus of each genus shows its own diagnostic characters, and evidence for relationships within these birds is not strong based on this element. The carpometacarpi of *Leptosomus* and *Coracias* tend to resemble each other more than do those of *Coracias* and *Atelornis*. The fact that the intermetacarpal process is present in *Atelornis* and *Coracias*, and absent in *Leptosomus*, suggests a closer affinity of the former two genera, but the significance of this character is difficult to assess.
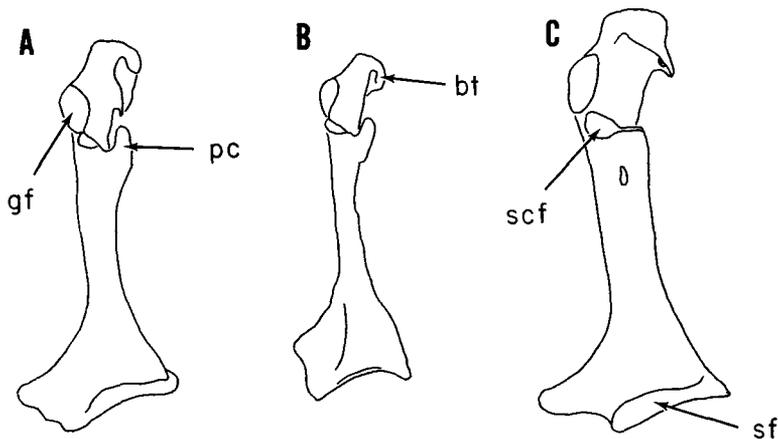
Figure 9. Dorsal view of coracoids. A, *Coracias benghalensis*; B, *Atelornis pittoides*; C, *Leptosomus discolor*. Abbreviations: bt, brachial tuberosity; gf, glenoid facet; pc, procoracoid; scf, scapular facet; sf, sternal facet.

Coracoid (Figure 9)

The coracoid of *Leptosomus* differs from that of *Coracias*, as follows: (1) brachial tuberosity less massive and less directed toward procoracoid, (2) procoracoid directed less toward brachial tuberosity, (3) shaft much broader in external-internal direction, and (4) sternal facet deeper and more elongated.

Atelornis differs from *Coracias* in the characters of the coracoid, as follows: (1) brachial tuberosity smaller, being not as massive, (2) procoracoid not as broad but same general shape, (3) sterno-coracoidal process much less pronounced externally, (4) sternal facet not present, and (5) shaft narrower.

The coracoid offers little evidence regarding relationships. *Coracias* and *Atelornis* resemble each other more in the distal end of the bone, but *Coracias* and *Leptosomus* show similarities in the proximal end (for example, in the well-developed sternal facet). Thus, each family exhibits unique characters of the coracoid.

Sternum (Figure 10)

The sternum of *Atelornis* resembles that of *Coracias* very closely and differs only in a few minor characters: (1) ventral manubrial spine larger, (2) both pairs of posterior lateral processes longer and narrower, and (3) intermuscular line more well marked.

Both *Atelornis* and *Coracias* differ from *Leptosomus* in having: (1) two pairs of posterior lateral processes whereas *Leptosomus* has only one short, broad pair, (2) ventral manubrial spine moderately developed whereas it is minute in *Leptosomus,* (3) sternocoracoidal processes directed more anteriorly whereas they are directed laterally in *Leptosomus*, (4) sternae themselves not as broad as in *Leptosomus* and more U-shaped in anterior view.

Pelvis (Figure 11)

The pelvises of *Atelornis* and *Coracias* differ from each other in only a few minor characters. Both differ from *Leptosomus* in several features: (1) pelvis is narrower;
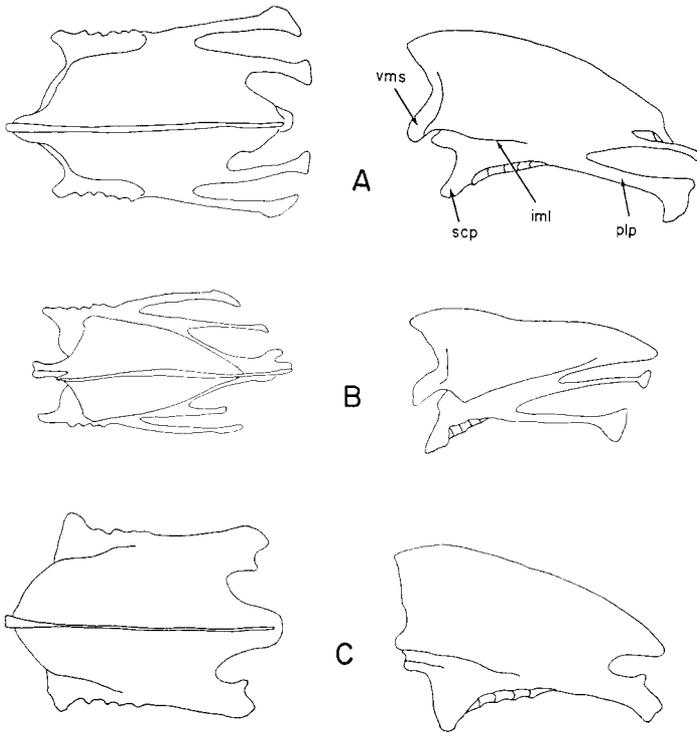
Figure 10. Ventral view (left) and side view (right) of sternum. A, *Coracias benghalensis*; B, *Atelornis pittoides*; C, *Leptosomus discolor*. Abbreviations: iml, intermuscular line; plp, posterior lateral process; scp, sternocoracoidal process; vms, ventral manubrial spine.
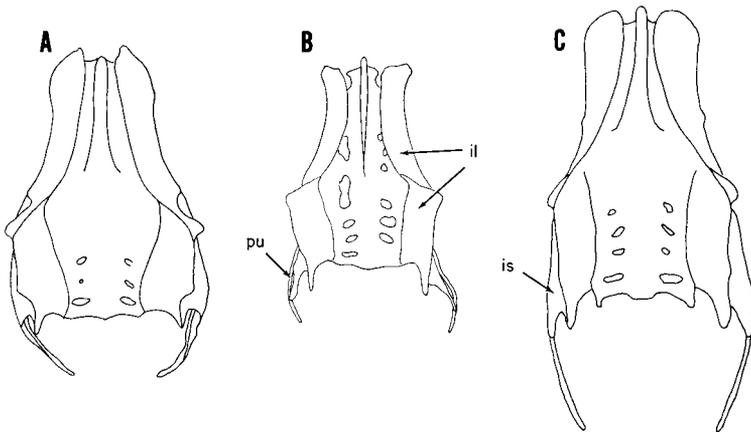

Figure 11. Dorsal view of pelvis. A, *Coracias benghalensis*; B, *Atelornis pittoides*; C, *Leptosomus discolor*. Abbreviations: il, ilium; is, ischium; pu, pubis.

in *Atelornis* and *Coracias* the sides of the pelvis are more nearly parallel (ischiae directed slightly less laterally, more ventrally), and (2) ilium is narrower, especially anteriorly.

The features of the pelvis support a closer relationship between *Coracias* and *Atelornis* than between *Coracias* and *Leptosomus*.

Femur

The femur of *Leptosomus* differs from that of *Coracias* in having: (1) trochanter more pronounced, (2) obturator ridge slightly better developed, (3) external condyle produced more posteriorly relative to fibular condyle, (4) anterior edge of internal condyle extends more proximally, and (5) rotular groove narrower.

Atelornis differs from *Coracias* in that: (1) internal condyle less rounded distally, but forms apex, (2) external condyle produced slightly more posteriorly relative to fibular condyle, (3) obturator ridge raised more, and (4) popliteal area much more depressed.

The femur does not offer much conclusive evidence about relationships. *Coracias* and *Leptosomus* do seem morphologically closer to each other, whereas *Atelornis* stands somewhat apart.

Tibiotarsus (Figure 12)

Eurystomus shows a few notable differences from *Coracias* in the structure of the tibiotarsus: (1) anteroproximal portions of external and internal condyles meet shaft at an angle approaching 90 degrees (more gradual in *Coracias*), (2) anterior inter-condylar fossa broader (condyles separated more), (3) supratendinal bridge narrower, less heavy, and (4) distal end of bone not as compressed lateromedially.

The tibiotarsus of *Leptosomus* differs from that of *Coracias* in having: (1) external condyle decidedly flatter distally and more pronounced anteriorly, (2) internal condyle flatter distally and much more pronounced anteriorly, (3) condyles much more separated and not parallel, (4) portion of shaft immediately proximal to internal condyle (anterior view) not raised to form ridge, (5) distal end compressed more anteroposteriorly than lateromedially, (6) area between outer and inner cnemial crests more depressed, (7) proximal-most portion of inner cnemial crest more pro-nounced, (8) well-developed groove present between external and internal articulating surfaces, and (9) outer cnemial crest larger.

In the characters of the tibiotarsus *Atelornis* differs from *Coracias* in that: (1) external condyle flatter distoanteriorly and more rounded and raised posteriorly, (2) internal condyle produced slightly more anteriorly, (3) condyles slightly more separated but nearly parallel, (4) portion of shaft immediately proximal to internal condyle (anterior view) not raised to form ridge, (5) outer and inner cnemial crests distinctly better developed, (6) noticeable ridge present between internal articular surface and junction of cnemial crests, and area internal to ridge is greatly depressed, and (7) external articular surface much more distinct from remainder of head of tibiotarsus.

The evidence presented by the tibiotarsus is somewhat uncertain. *Atelornis* resembles *Coracias* much more than does *Leptosomus* in the features of the distal end of the bone (in the shapes and positions of the condyles), but *Coracias* and *Leptosomus* resemble each other more in the form of the proximal end of the bone. *Eurystomus*, more than *Coracias*, tends to approach the condition seen in the distal end of *Atelornis* but maintains the *Coracias*-pattern in the proximal end. In general, *Leptosomus* resembles *Coracias* in the proximal end.
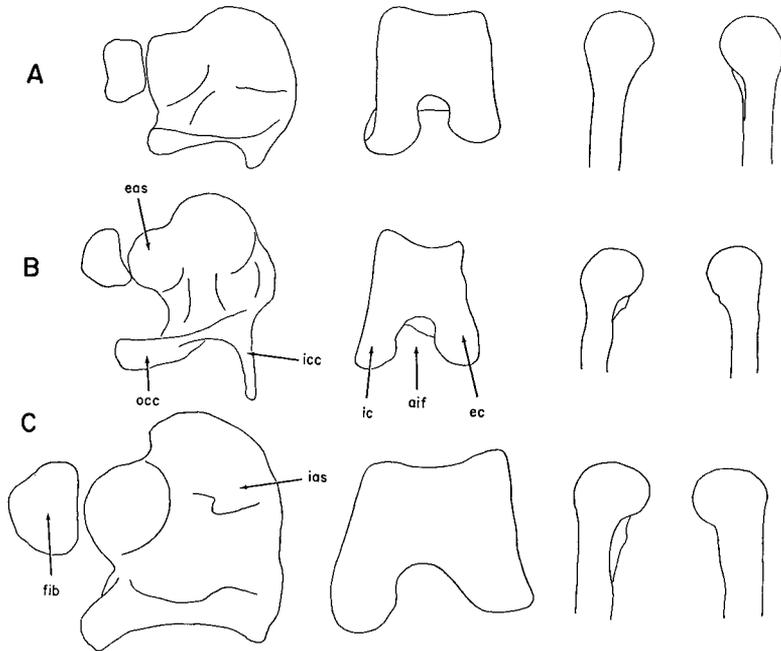
Figure 12. Tibiotarsi. A, *Coracias benghalensis*; B, *Atelornis pittoides*; C, *Leptosomus discolor*. Views of bone from left to right: proximal view, distal view, internal condyle, external condyle. Abbreviations: aif, anterior intercondylar fossa; eas, external articular surface; ec, external condyle; fib, fibula; ias, internal articular surface; ic, internal condyle; icc, inner cnemial crest; occ, outer cnemial crest.

Tarsometatarsus (Figure 13)

The tarsometatarsus of *Leptosomus* differs from that of *Coracias* in that: (1) wing of trochlea for digit 4 much larger and projects more posteriorly, (2) trochlea for digit 3 projects more distally relative to trochlea for digit 4, (3) trochlea for digit 4 located more posteriorly, (4) trochleae for digits 2 and 3 less separated, (5) posterior metatarsal groove much deeper distally and much shallower proximodistally (area surrounding inner proximal foramen much less depressed), (6) anterior metatarsal groove much deeper proximally, (7) intercotylar prominence much better developed, (8) calcaneal ridges more separated and less pronounced, and (9) hypotarsus wider at base, especially distally.

Atelornis differs from *Coracias* in the tarsometatarsal features, as follows: (1) trochleae 2 and 3 less separated, (2) intercotylar prominence much better developed, and (3) bone much longer and narrower, and flatter anteroposteriorly.

A much greater similarity exists between the tarsometatarsi of *Atelornis* and *Coracias* than between those of *Coracias* and *Leptosomus*. Despite the much elongated bone of *Atelornis*, the tarsometatarsus is very similar in detailed structures with that of *Coracias*. *Leptosomus*, on the other hand, has undergone a significant reorganiza-
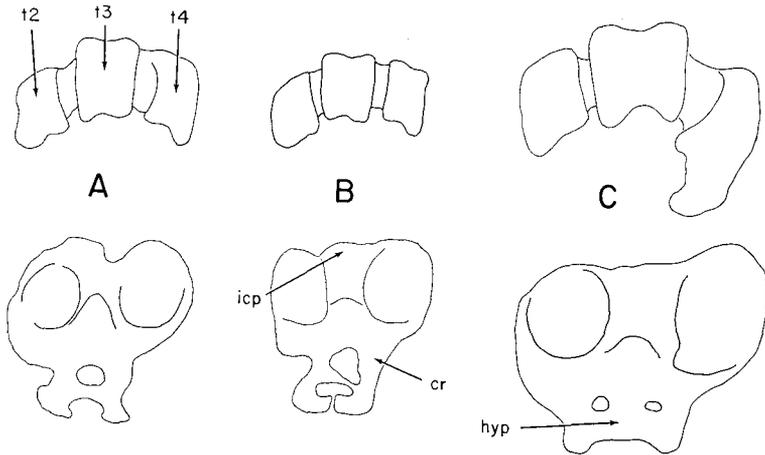
Figure 13. Distal view (upper figure) and proximal view (lower figure) of tarsometatarsus. A, *Coracias benghalensis*; B, *Atelornis pittoides*; C, *Leptosomus discolor*. Abbreviations: cr, calcaneal ridge; hyp, hypotarsus; icp, intercotylar prominence; t2, trochlea for digit 2; t3, trochlea for digit 3; t4, trochlea for digit 4.

tion of the tarsometatarsus, but yet it exhibits the same general proportions as that of *Coracias*. The distal end of *Leptosomus* has changed in response to the evolution of zygodactylism. The proximal end, which might not be expected to be modified because of the zygodactylism, is very different (e.g. the shape of the hypotarsus) from those of *Coracias* and *Atelornis*.

FUNCTIONAL INTERPRETATIONS

SKULL FEATURES

A considerable amount is known about the functional morphology of the avian skull, and the use of this information can enhance the interpretation of differences found in the roller skulls. Any discussion of functional morphology in the rollers is greatly limited by (1) our lack of knowledge of the details of food-getting behavior in these birds, and (2) the absence of comparative studies of their jaw muscles. Whereas some data are available on general feeding habits and on the food eaten, comparative myological data are lacking. Thus my conclusions must be considered tentative, but a brief discussion can still contribute to an understanding of the problem of relationships in the rollers.

The differences seen in the skull structure of *Coracias* and *Eurystomus* can be explained by their much different feeding habits. *Coracias* usually feeds on insects (especially grasshoppers), but also eats small snakes, lizards, and birds (Chapin, 1939; Mackworth-Praed and Grant, 1957). *Eurystomus* is very similar to *Coracias* in diet but is much more insectiv-

orous. The methods of feeding in these two genera also are different. *Coracias* typically flies to the ground to catch its prey (Witherby et al., 1938; McLachlan and Liversidge, 1957), whereas *Eurystomus* catches its prey on the wing (Rand, 1936; Chapin, 1939; Mackworth-Praed and Grant, 1957). Thus the short, broad bill of *Eurystomus* is almost certainly an adaptation for flycatching; the longer bill of *Coracias* is probably much better adapted for catching prey on the ground.

The well-developed temporal fossae, postorbital processes, and the orbital processes of the quadrates suggest that both genera have powerful jaw mechanisms. In addition to the general proportions of the skull, the major differences are found in the palatines, pterygoids, and jugal bars. The larger palatines of *Eurystomus* indicate a greater development of the pterygoideus muscle mass. This seems reasonable as a flycatcher like *Eurystomus* would benefit from musculature that allows rapid and forceful retraction of the upper jaw. The larger jugal bars and pterygoids of *Eurystomus* show that greater force is transmitted through them than in *Coracias*. In both genera the palatines apparently gain some dorsal support from the greatly expanded lacrimal. This would be particularly beneficial in using the roof of the mouth as a crushing device. The lacrimal braces the dorsal edge of the jugal bar and thus may act as additional protection against damage during crushing of food (Cracraft, 1968). The remainder of the skull features are essentially similar in the two genera.

The feeding behavior of the Brachypteraciidae is less well-known than that of the Coraciidae. The ground-rollers usually feed on the ground, selecting a diet of insects and various small reptiles and amphibians (Rand, 1936). These birds have undoubtedly developed the ability to pursue and capture prey on the ground to a much higher degree than has *Coracias*, which merely swoops down and picks it up.

Atelornis differs from *Coracias* mainly in having a skull that seems constructed to withstand forces of much smaller magnitude. The thinner prepalatines, less ossified orbital septum, weaker pterygoids, and the poorer ossification of the prepalatine-maxilla-maxillopalatine junction all support this conclusion. The skull of *Atelornis* is not so vaulted as in *Coracias*, and the temporal fossae are more nearly in line with the long axis of the skull. These characters suggest that the adductor musculature is at a somewhat less effective angle to the mandible for production of a forceful adduction. The minor differences already noted in the palatal area are difficult to explain.

The food of *Leptosomus* consists of caterpillars, locusts, and other insects, and especially chameleons caught in the branches and tops of trees (Rand, 1936; Benson, 1960; Forbes-Watson, 1967). Apparently *Lepto-*

somus does not typically flycatch or descend to the ground for food. The skull of *Leptosomus*, like that of *Coracias*, shows features characteristic of a strong crushing or biting habit. The temporal fossae are so situated that a powerful adductive force is probably produced (given suitable musculature, of course). The well-developed jugals and pterygoids and the broad prepalatines, which are fused strongly to the maxillopalatine-maxilla junction, reflect a mechanism adapted for resisting large forces. The most difficult feature to explain is the lacrimal-ectethmoid complex, which is very different from that of the other rollers. The lacrimal braces the jugal, thus offering some support for the jugals during the crushing of food, but the lacrimal is not expanded mediad and so does not come close to the palatines. Neither the known feeding habits nor what we know about functional anatomy can satisfactorily explain the evolution of this peculiar complex in the Cuckoo-roller.

POSTCRANIAL FEATURES

A functional interpretation of differences in postcranial osteology is presently impossible because of the almost total lack of adequate studies on joint structure and function. However in the case of the rollers some important, and probably valid, assumptions can be made regarding functional convergence.

It was noted in the descriptive section that the humeri, ulnae, and carpometacarpi of *Coracias* generally resemble those of *Leptosomus* rather than those of *Atelornis*. I think it is highly likely that the similarities of *Coracias* and *Leptosomus* are the result of convergence rather than closeness of relationship. The flight patterns of *Coracias, Eurystomus*, and *Leptosomus* are apparently very similar. *Coracias* flies very gracefully with many turning, tumbling, and plunging actions (Jackson, 1938; Witherby et al., 1938; Chapin, 1939) and it is also known to soar occasionally (Witherby et al., 1938). The flight of *Eurystomus* is even further developed than *Coracias* (Rand, 1936; Chapin, 1939). The flight of *Leptosomus* is not unlike that of the true-rollers, for according to Rand (1936: 417) the wing beats are "slow but the flight is bounding and graceful." *Leptosomus* tumbles in the air like *Coracias* and occasionally soars (Sharpe, 1871; Rand, 1936). The flight of the Brachypteraciidae, on the other hand, is different. They make quick, noisy flights usually for short distances, and although they can fly strongly (Rand, 1936), they do not have the aerial acrobatics of the other rollers. Consequently the differences in the forelimbs of *Coracias* and *Atelornis* are not unexpected. It was mentioned above that the cotylae of the ulna are greatly reduced in *Atelornis* in contrast to both *Coracias* and *Leptosomus*.

TABLE 1

RATIOS OF SKELETAL ELEMENTS OF ROLLER GENERA

	Eurystomus (1)[1]	*Coracias* (2)	*Atelornis* (1)	*Leptosomus* (2)
Femur/total leg[2]	0.35	0.32	0.25	0.24
Tibiotarus/total leg	0.41	0.43	0.43	0.44
Tarsometatarsus/total leg	0.24	0.25	0.32	0.24
Pelvis[3]/total leg	0.39	0.32	0.19	0.30
Humerus/total wing[4]	0.36	0.36	0.38	0.38
Ulna/total wing	0.43	0.44	0.44	0.44
Carpometacarpus/total wing	0.21	0.20	0.18	0.18
Coracoid/humerus	0.60	0.58	0.77	0.46
Total wing/pelvis	4.60	4.78	3.72	4.58

[1] Numbers in parentheses show number of specimens examined.

[2] Total leg equal to lengths of femur, tibiotarsus, and tarsometatarsus.

[3] Pelvis length measured along median dorsal ridge.

[4] Total wing equal to lengths of humerus, ulna, and carpometacarpus.

This surely indicates a much less effective articulation with the humerus, which in turn reflects a less developed flying mechanism in *Atelornis*. Additional work on the functional anatomy of flight may permit more accurate statements concerning detailed differences in the forelimb elements.

Table 1 shows some ratios of the skeletal elements of various genera of rollers. Several broad generalizations can be made about these ratios. Surprisingly, the ratios of the wing elements are not significantly different. Apparently all morphological changes have taken place in the muscles and in the articulations themselves. The only important differences among the four genera are the high coracoid/humerus ratio in *Atelornis* and the low coracoid/humerus ratio in *Leptosomus*. The functional significance of these two ratios is difficult to explain without additional information on the structure and function of the muscles and joints.

With respect to the hindlimb, *Atelornis* is clearly the most divergent genus, and the differences can be attributed to a cursorial way of life. In *Atelornis* the femur is proportionately shorter, the tarsometatarsus is relatively longer, and the pelvis is shorter. The relative lengths of the femur and tarsometatarsus observed in *Atelornis* are a well-known phenomenon in cursorial birds and need not be discussed further. The reduction in the length of the pelvis implies a reduction in the muscle mass. It would therefore be interesting to compare the detailed fiber arrangement of the leg muscles to see if any reorganization of the muscles has occurred to compensate for the apparent reduction in mass.

Several elements, most notably the sternum and pelvis, raise some interesting problems, for these structures are very similar in *Coracias* and *Atelornis* but are different in *Leptosomus*. Because of their different ways of life, the close similarity in *Coracias* and *Atelornis* might not be expected, whereas a general resemblance between *Coracias* and *Leptosomus* would not be very puzzling. This suggests a closer relationship of *Coracias* and *Atelornis*.

Even though the Brachypteraciidae have evolved a different locomotor pattern in the hindlimb—the elements are elongated for the more cursorial habit—they still show great similarity to the coraciids in osteological characters. This is probably indicative of the closeness of these two groups.

Many of the differences seen in the hindlimb of *Leptosomus* are probably the result of a major reorganization of the hindlimb locomotor pattern associated with the evolution of a zygodactyl foot (see below). This is especially evident in the distal end of the tarsometatarsus, but the effect is also probably reflected in the differences of the tibiotarsus. However, with present knowledge we do not know what detailed effects the shifting of a toe will have on the structure of most of the elements. In *Leptosomus* the foot is not as completely zygodactylous as in woodpeckers, and the shift of the toe apparently did not produce drastic changes in the musculature (Forbes, 1880).

DISCUSSION

ADAPTIVE RADIATION OF THE ROLLERS

The osteological data gathered in my study strongly suggest that, within the rollers, the Coraciidae and Brachypteraciidae are the most closely related and that the Leptosomatidae stand somewhat apart; the leptosomatids and brachypteraciids show few resemblances to each other. This conclusion can be reached in spite of the fact that each family is distinct osteologically. As outlined above, many of the similarities of the Coraciidae and Leptosomatidae are probably the result of convergence because of similar ways of life, whereas the differences of the Coraciidae and Brachypteraciidae are due to the very different sets of adaptations these birds exhibit. The belief that the ground-rollers and true-rollers are more closely related has been held by various authors since the last century, and my findings support it further. Still left to be discussed are the probable evolutionary pathways within these taxa.

The earliest discussion of the evolution of the rollers was by Sharpe (1871). He postulated (p. 187) that "When the osteology of *Brachypteracias* [i.e., *B. leptosomus*] becomes fully known, I believe that this form will be found to be nearer to *Leptosomus* than any other known

genus of the Coraciidae [*sensu lato*], while *Geobiastes* [*B. squamigera*] will connect *Brachypteracias* with *Atelornis*. This last named form is nearest to *Coracias*." Some support for Sharpe's contention can be found in the plates of Milne-Edwards (1876). For example the skull drawing of *B. squamigera* looks less like that of *B. leptosomus* and more like the Michigan skull (but not the one picture by Milne-Edwards) of *Atelornis*. Sharpe's belief that *B. leptosomus* is closest to *Leptosomus* is not supported by Milne-Edwards' plates nor by my study. Although the resemblance, especially in bill shape, is close between *B. leptosomus* and *Leptosomus*, the detailed skeletal features of *B. leptosomus* are definitely much closer to *Atelornis*.

The evidence from morphology and biogeography points to the coraciids as being the primitive members of the roller complex. Therefore it might be postulated that an early protocoraciid stock in Africa first reached Madagascar and subsequently evolved into *Leptosomus*. Later, after further evolution of the primitive stock to forms more closely resembling present day coraciids, another invasion gave rise to the ground-rollers. *Eurystomus glaucurus*, the only true roller on Madagascar, is clearly a late Pleistocene derivative from the same species in Africa. The morphological evidence presented earlier argues that the coraciids and brachypteraciids had a more recent common ancestor than either had with *Leptosomus*. Hence, the suggestion of Bock and Miller (1959: 35) that the ground-rollers may have given rise to *Leptosomus* is unacceptable, although the ancestors of *Leptosomus* may have had some morphological characteristics of the ground-rollers (see below). Considering the types of locomotor adaptations within the order, any terrestrial groups would most probably be derived from rather than being representative of the primitive condition.

A discussion of the evolution of *Leptosomus* must be centered around the origin and evolution of zygodactyl feet and of a strictly arboreal mode of life. Bock and Miller (1959) have argued that zygodactylism evolves as a more efficient method of perching in forms that have a weak hallux. This is a reasonable assumption, and I postulate that the ancestor of *Leptosomus* spent considerable time feeding both on the ground and in trees. The *Leptosomus* line developed a preference for feeding predominately in trees, and when their size increased (for some unknown reason, perhaps to facilitate exploitation of chameleons), zygodactylism was evolved to effect a more efficient perching foot. The hallux of the ancestor could have been moderately long (absolutely) because those of the coraciids are long and those of the brachypteraciids are not too much shorter (Table 2). Thus, it can be argued that the leptosomatids evolved zygodactylism as a response to increased size rather than because their ancestors possessed a short hallux (Bock and Miller, 1959: 35–36).

TABLE 2

EXTERNAL MEASUREMENTS OF ROLLERS[1]

	Wing			Tail			Bill length		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
Coracias g. garrulus	20	194.15	187–202	20	123.35	114–136	20	25.32	21.6–28.0
Eurystomus glaucurus afer	14	169.57	161–180	14	88.57	81–102	14	16.01	14.5–17.6
Leptosomus d. discolor	21	250.62	237–265	21	203.90	175–225	21	19.83	17.4–22.2
Atelornis pittoides	21	110.71	105–116	21	107.24	98–115	20	21.85	18.9–25.4
Atelornis crossleyi	11	92.55	87–99	11	107.91	104–118	11	17.89	16.6–20.4
Brachypteracias squamigera	13	121.92	115–128	13	97.61	90–105	11	23.02	20.1–25.4
Brachypteracias leptosomus	17	139.35	135–145	16	133.13	129–145	17	27.36	24.5–30.3
Uratelornis chimaera	9	107.11	100–112	8	236.75	200–277	9	21.88	17.5–24.5

	Bill width			Tarsus length			Hallux length		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
Coracias g. garrulus	20	9.18	7.50–10.60	20	22.75	20.7–24.4	10	11.62	9.7–13.1
Eurystomus glaucurus afer	14	10.05	9.30–11.0	14	16.86	15.4–18.8	10	10.14	9.2–11.3
Leptosomus d. discolor	21	9.76	8.7–10.9	21	27.60	24.9–29.2	10	9.38	6.8–11.0
Atelornis pittoides	20	7.55	6.7–8.5	21	39.32	36.2–42.6	10	7.89	7.0–8.8
Atelornis crossleyi	11	7.37	6.8–7.9	10	38.80	36.0–41.4	12	8.34	6.4–9.6
Brachypteracias squamigera	13	9.42	8.6–10.0	13	47.21	43.6–52.4	10	8.55	7.7–9.7
Brachypteracias leptosomus	17	12.98	12.2–14.5	17	33.12	29.2–35.3	10	11.99	11.2–13.4
Uratelornis chimaera	9	8.29	7.3–9.0	9	43.27	40.4–45.7	9	7.78	6.9–9.1

[1] Measurements in millimeters.

TABLE 3

RATIOS OF SOME MEASUREMENTS IN THE ROLLERS[1]

	Wing	Bill length	Tarsus	Wing	Tail
	tail	bill width	hallux	tarsus	tarsus
Coracias g. garrulus	1.57	2.76	1.96	8.53	5.42
Eurystomus glaucurus afer	1.91	1.59	1.66	10.06	5.25
Leptosomus d. discolor	1.23	2.03	2.94	9.08	7.39
Brachypteracias leptosomus	1.05	2.11	2.76	4.21	4.02
B. squamigera	1.25	2.44	5.52	2.58	2.07
Atelornis pittoides	1.03	2.89	4.98	2.82	2.73
A. crossleyi	0.86	2.43	4.65	2.39	2.78
Uratelornis chimaera	0.45	2.64	5.56	2.48	5.47

[1] Calculated from mean measurements of the sample.

In any case, the major selection force was probably for an increase in perching strength relative to body size.

The toes of the coraciids and brachypteraciids appear slightly syndactylous, and it is noteworthy that, at least in *Coracias*, the inner toe is more capable of freer motion than the outer. That *Leptosomus* has reversed the outer toe suggests that syndactylism may be modified easily (in a morphological sense). *Leptosomus* has not evolved zygodactylism to the degree that many other nonpasseriform families have, and this is supported by the anatomy. *Leptosomus* lacks a sehenhalter on the tarsometatarsus, a feature characteristic of the true zygodactyl foot. Many artists have shown *Leptosomus* with an anisodactyl foot (see figures in Dresser (1893) and Van Tyne and Berger (1959)), but these figures were apparently based on examination of study skins. Forbes-Watson (1967: 427) observed zygodactylism in the young of *Leptosomus*, and to my knowledge no cases of living birds perching anisodactyly have been recorded.

One of the striking features of *Leptosomus* is its sexual dimorphism in plumage pattern, whereas in the rollers the sexes have nearly identical color patterns. Why *Leptosomus* evolved sexual dimorphism is unknown, but it was probably associated with a change in the social and/or breeding behavior (Hamilton, 1961; Hamilton and Barth, 1962). Because little or no information about population ecology or behavior is available, trying to explain these plumage differences is futile.

The evolutionary patterns of the ground-rollers are reasonably clear. Within *Brachypteracias* the primitive condition is most probably represented by *B. leptosomus*. This species is unlike the other ground-rollers in having a tarsus/hallux ratio similar to those of the coraciids and *Leptosomus* (Table 3). Moderately large wing/tarsus and tail/tarsus ratios also show that *B. leptosomus* is much less "specialized" for a ter-
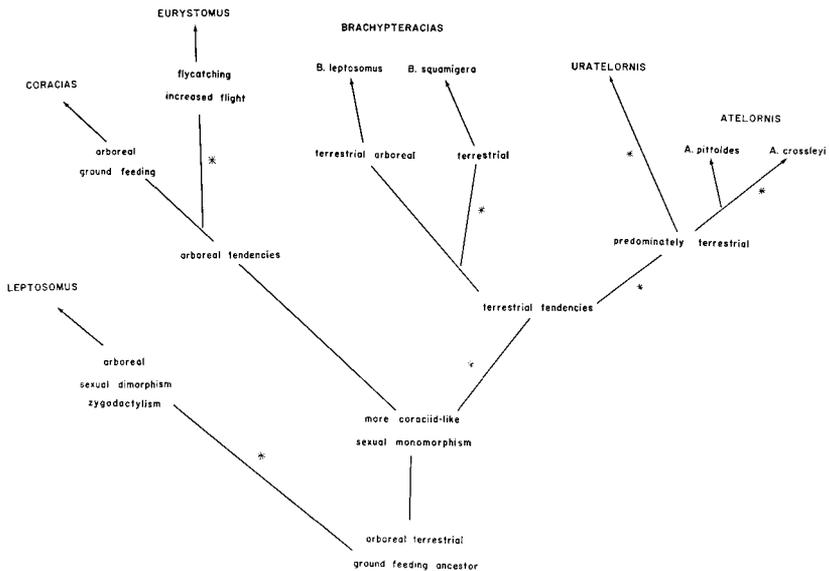
Figure 14. Diagram showing hypothetical phylogenetic relationships and adaptive pathways of various roller taxa. An asterisk indicates the lineage of a branching sequence that is apparently the most advanced from the primitive condition.

restrial way of life, and indeed *B. leptosomus* apparently perches more often than *B. squamigera* (Rand, 1936). *Brachypteracias squamigera* has the longest tarsus of any roller, and the tail/tarsus ratio is decidedly the lowest of any roller.

The genus *Atelornis* seems more terrestrial than *Brachypteracias* and is probably more advanced from the primitive ground-roller condition. *Atelornis pittoides* and *A. crossleyi* are similar in their wing, leg, and tail ratios (Table 3), and both have plumage patterns different from *Brachypteracias*. It is difficult to determine which species most closely represents the ancestral condition. That *A. pittoides* might be more primitive is suggested by some of the features of *Uratelornis*.

Uratelornis is unmistakedly closer to *Atelornis* than to *Brachypteracias*. The bill structure of *Uratelornis* and *A. pittoides* is essentially the same, and although they differ in plumage coloration (especially dorsally), the patterns of the ventral surface are similar in having a dark band on the upper breast. Apparently *Uratelornis* is predominately terrestrial (Appert, 1968), thus resembling *Atelornis* more than *Brachypteracias*.

Within the coraciids *Eurystomus* is clearly the most advanced from the ancestral condition. Whereas *Coracias* still descends to the ground to feed, *Eurystomus* has evolved the most highly developed flight behavior

of any roller and depends on flycatching for most of its food. Table 3 shows that *Eurystomus* has the largest wing/tail and wing/tarsus ratios of any roller, and reflecting its flycatching habit, the lowest bill length/ bill width ratio.

Figure 14 summarizes the phylogenetic and adaptive pathways of the different taxa in the three families.

TAXONOMIC CONSIDERATIONS

It is difficult to decide the taxonomic ranks of the higher taxa of birds, because almost any decision can be reasonably defended. With respect to the classification of the rollers, two points need emphasis. First, any classification designed to reflect phylogeny must recognize the dichotomy of the true-rollers and ground-rollers on the one hand and the cuckoo-rollers on the other. Second, each of the three groups exhibits morphological features as distinct as those characterizing other coraciiform taxa of family rank. Thus each has attained a set of adaptations different from the other two (though not always clear-cut).

Considering the above points I propose the following classification, which will have to be tentative pending further studies on the relationships of the other coraciiform families, some of which may also be included in the Coracii:

Suborder Coracii
   Superfamily Coracioidea
     Family Coraciidae
     Family Brachypteraciidae
   Superfamily Leptosomatoidea
     Family Leptosomatidae

SUMMARY

An osteological study of *Atelornis* and *Brachypteracias* (Brachypteraciidae), *Leptosomus* (Leptosomatidae), and *Coracias* and *Eurystomus* (Coraciidae) supports the previously held opinion of some authors that

the Brachypteraciidae and Coraciidae are more closely related to each other than either is to the Leptosomatidae. The similarities in the fore-limb osteology of *Coracias* and *Leptosomus* are attributed to convergence based on similar modes of locomotion. The brachypteraciids have a different flight pattern and thus differ in the features of the forelimb. The Coraciidae and Brachypteraciidae are very similar in hindlimb osteology despite differences in locomotor behavior. A primitive roller stock in Africa is postulated to have first invaded Madagascar. These primitive rollers, which were probably both terrestrial and arboreal, gave rise to a lineage that became predominately arboreal. Because of an increase in size this lineage developed zygodactylism in order to maintain an effective perching mechanism. Thus, the *Leptosomus* adaptive pattern was evolved.

A second invasion of Madagascar by a more coraciidlike stock gave rise to the ground-rollers. *Brachypteracias* is considered the most primitive genus of the family. *Atelornis* is a more advanced genus in having evolved a more terrestrial way of life. *Uratelornis* is closely related to *Atelornis*, especially *A. pittoides*.

It is recommended that three families of rollers be recognized but that the Coraciidae and Brachypteraciidae be placed in a superfamily separate from the Leptosomatidae.

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