

EVIDENCE FOR A POLYPHYLETIC ORIGIN OF THE PICIFORMES

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ABSTRACT.—Despite two recent anatomical studies to the contrary, the order Piciformes appears to be polyphyletic. The structure of the zygodactyl foot in the Galbulae is very distinct from that in the Pici, and no unique shared derived characters of the tarsometatarsus have been demonstrated for these two taxa. The supposedly three-headed origin of *M. flexor hallucis longus* shared by the Galbulae and Pici is doubtfully homologous between the two groups, leaving only the Type VI deep flexor tendons as defining the order Piciformes. This condition is probably a convergent similarity. Evidence is presented supporting a close relationship between the Galbulae and the suborder Coracii and between the Pici and the Passeriformes. There are fewer character conflicts with this hypothesis than with the hypothesis that the Piciformes are monophyletic. Problems concerning fossil taxa are also addressed. Received 24 September 1981, accepted 15 May 1982.

A MONOPHYLETIC origin of the Piciformes appears to have gained support from the simultaneous appearance of two cladistic, anatomical papers (Swierczewski and Raikow 1981, Simpson and Cracraft 1981) that concur in the traditional concept of the order—a concept that has prevailed at least since the time of Gadow (1893). I depart from this view in considering each of the two major subdivisions of the Piciformes, the Galbulae (Bucconidae, Galbulidae) and the Pici (Capitonidae, Ramphastidae, Indicatoridae, Picidae), to be more closely related to another group than to each other. My purpose here is (1) to show that the evidence for monophyly is weak, uncorroborated, and has in part been misrepresented by Simpson and Cracraft (1981), and (2) to make preliminary suggestions as to the probable closest relatives of the Galbulae and the Pici.

THE WEAKNESS OF THE EVIDENCE FOR PICIFORM MONOPHYLY

Zygodactyly.—Obligate zygodactyly, the condition in which the fourth toe is permanently reversed and has an enlarged accessory articulating process (the "sehnenhalter"), occurs in cuckoos (Cuculidae, Cuculiformes), parrots (Psittacidae, Psittaciformes), and in the Piciformes. This is obviously a derived condition in birds that could be used to define these taxa as a monophyletic group in a cladistic sense, unless it were shown that each of these zygodactyl taxa shares derived characters

with outside groups in a manner indicating that the zygodactyl condition in cuckoos, parrots, and Piciformes had arisen independently, through convergence.

Although I certainly do not advocate a monophyletic origin of zygodactyl birds, the arguments that Simpson and Cracraft (1981) and Swierczewski and Raikow (1981) present against such a hypothesis do not meet the requirements of their cladistic methodology. Simpson and Cracraft (1981: 484) conclude only that "the relationships of cuckoos and parrots remain among the most enigmatic within ornithology . . .," although "there is a general acceptance among avian systematists . . . that piciforms are most closely related to coraciiforms or to passeriforms and that cuckoos and parrots are not." They concede that "this hypothesis has yet to be tested cladistically . . ." Swierczewski and Raikow (1981: 469) state that: "The muscular component of the foot mechanism is quite different in [the Cuculidae, Psittacidae, and Piciformes] . . . which supports the contention (Bock and Miller 1959: 30) that those groups became zygodactyl independently." Both sets of authors have thus tacitly accepted differences between taxa as evidence of non-relationship, a procedure of which Cracraft has been outspokenly critical (see Olson 1982).

The most complete and original work on the nature of the zygodactyl foot is that of Steinbacher (1935), whose results have seldom been accurately represented (a notable exception being Sibley and Ahlquist 1972). Steinbacher

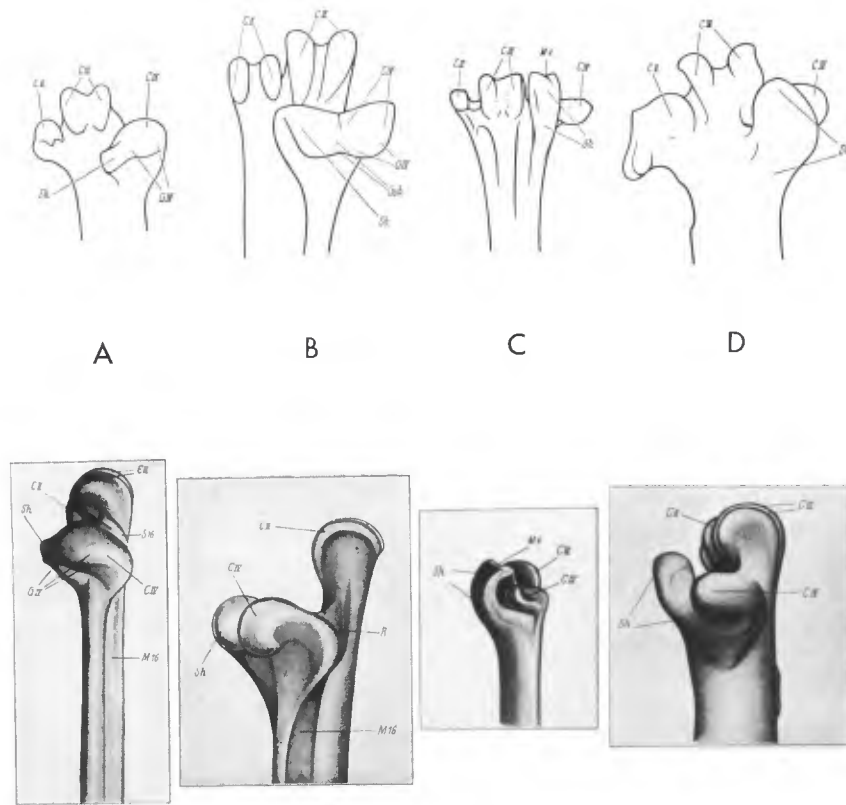


Fig. 1. Posterior (top row) and lateral (bottom row) views of the distal end of the tarsometatarsus in the four groups of birds with obligate zygodactyly (illustrations from Steinbacher 1935). A, cuckoo, *Centropus ateralbus* (Cuculidae, Cuculiformes); B, jacamar, *Galbula ruficauda* (Galbulidae, Galbulae, "Piciformes"); C, toucan, *Ramphastos toco* (Ramphastidae, Pici, Piciformes); D, parrot, *Amazona ochrocephala* (Psittacidae, Psittaciformes). Abbreviations: Sh = sehnenhalter, C II = trochlea for digit II, C III = trochlea for digit III, C IV = trochlea for digit IV, G IV = articulating surface for digit IV, Gsh = articulating surface of sehnenhalter, M 16 = depression for origin of *M. extensor brevis digiti IV*, R = groove for tendon of *M. extensor brevis digiti IV*, M 4 = depression for tendon of *M. flexor perforatus digiti IV*. It can be seen that the form of zygodactyly in the Galbulae is completely different from that in the Pici, and the two can in no way be regarded as homologous. The best interpretation of the evidence from the tarsometatarsus is that zygodactyly evolved independently in all four of these groups.

showed that there were *four* distinct types of morphology of the tarsometatarsus in birds with obligate zygodactyly, with that in the Galbulae being as different from that in the Pici as either of these two is from parrots or cuckoos (Fig. 1). In each of these four groups there is a sehnenhalter. Steinbacher (1935: 234) even identified a sehnenhalter in owls (Strigiformes), which are facultatively zygodactyl. Thus, the statement by Simpson and Cracraft (1981: 485) that "zygodactyly and the presence of a sehnenhalter can be interpreted as derived characters defining the piciforms as monophyletic" is disingenuous. In citing Steinbacher (1935) as pro-

viding evidence "that osteological . . . characteristics of zygodactyly are distinct for the piciforms and different from cuckoos and parrots," Simpson and Cracraft (1981: 484) have clearly misrepresented the facts and Steinbacher's interpretation of them.

Nowhere do Simpson and Cracraft, nor any other authors (e.g. Bock and Miller 1959), show that there are derived characters of the tarsometatarsus that will distinguish the Galbulae and Pici from parrots and cuckoos and that will establish the Piciformes as a monophyletic group. In fact, the apparently less modified trochlea IV and sehnenhalter in the Galbulae

are actually more similar to the condition in cuckoos, whereas the larger, more discrete, and distally projecting *sehnenhalter* in the Pici is more like that in parrots (Fig. 1). There simply is no evidence in the structure of the tarsometatarsus that will demonstrate a close relationship between the Galbulae and the Pici.

Swierczewski and Raikow (1981) present six myological characters to define their Clade B (= Galbulae) and six additional myological characters to define their Clade G (= Pici). Thus, these two taxa differ from each other in at least 12 myological characters of the hind limb, as well as having a completely different structure of the tarsometatarsus associated with their respective forms of zygodactyly. May we not, then, apply the same statement that Swierczewski and Raikow used against monophyly of all zygodactyl birds to argue against monophyly of the Piciformes, namely that "the muscular component of the foot system is quite different in those groups," a difference supporting the contention that they "became zygodactyl independently" (Swierczewski and Raikow 1981: 469)?

Origin of M. flexor hallucis longus.—Swierczewski and Raikow state that *M. flexor hallucis longus* has three heads in the Piciformes, which they interpret as a derived condition that supports monophyly. Simpson and Cracraft (1981: 483) imply this condition to be unique to the Piciformes by stating that "the muscle arises by one or two heads in other birds," whereas Swierczewski and Raikow discuss the fact that *M. flexor hallucis longus* also has three heads in most passerines. Because the lateral head has a different relationship to the tendon of *M. iliofibularis* in Passeriformes, Swierczewski and Raikow (1981: 473) consider that the "condition in the two orders is therefore probably not homologous." At this point I would also question whether the condition in the Galbulae and Pici has been established as being homologous.

Before I was able to consult Swierczewski's (1977) unpublished dissertation for details, I dissected one specimen each of the barbet *Trachyphonus darnaudii* (Capitonidae: Pici) and the puffbird *Hypnelus bicinctus* (Buconidae: Galbulae) in order to assess the configuration of *M. flexor hallucis* in each. In the normal avian condition, this muscle originates in the popliteal fossa of the femur. In the specimen of *Hypnelus* that I examined, the origin was

expanded so that fibers also originated from the proximal end of the fibula and from the median raphe of the adjacent *M. flexor perforatus digiti III*. [Incidentally, Fig. 6d in Simpson and Cracraft (1981) is mislabelled—"Fpp3" should read "Fp3."] In *Trachyphonus* the fibers originating on the fibula, and those originating on the raphe of *M. flexor perforatus digiti III*, are slightly separated from the main belly of the muscle that originates in the popliteal fossa, thus making the muscle three-headed. Clearly, *M. flexor hallucis longus*, in contributing to the flexion of two toes in addition to the hallux, has become strengthened by expanding the area of its origin to the two nearest available structures. This is directly correlated with the Type VI arrangement of the flexor tendons and is part of the same character complex.

I could not detect any separate heads of origin in the buconid *Hypnelus*, however. Indeed, Swierczewski (1977: 57) states that in the Galbulidae and Buconidae the heads are "somewhat difficult to separate from each other." He also notes that the "common belly extends only about two-thirds the length of the tibiotarsus" in the Galbulae, versus almost the entire length of the tibiotarsus in the Pici. Thus, it seems far from certain that the nature of the origin of this muscle is homologous between the Galbulae and the Pici or even that it can really be said to have three heads in the Galbulae.

Type VI flexor tendons.—Gadow (1893) defined the Piciformes by their possession of the Type VI configuration of the deep flexor tendons, whereby *M. flexor hallucis longus*, which ordinarily has a direct tendinous connection only with the hallux (digit I), flexes digits II and IV as well, and *M. flexor digitorum longus* flexes only digit III. This condition must have arisen when digit IV was reversed and began to function as a second hallux (zygodactyly). That parrots and cuckoos are zygodactyl but do not have the Type VI flexor tendons is evidence that different evolutionary pathways can produce similar functional results.

The Type VI tendon arrangement was used originally to define the Piciformes, and it is still the only character that can be cited to unify the order. Given that the condition of origin of *M. flexor hallucis longus* is part of the same complex and is doubtfully homologous in the Galbulae and Pici anyway, then it may fairly be said that the new studies of osteology and

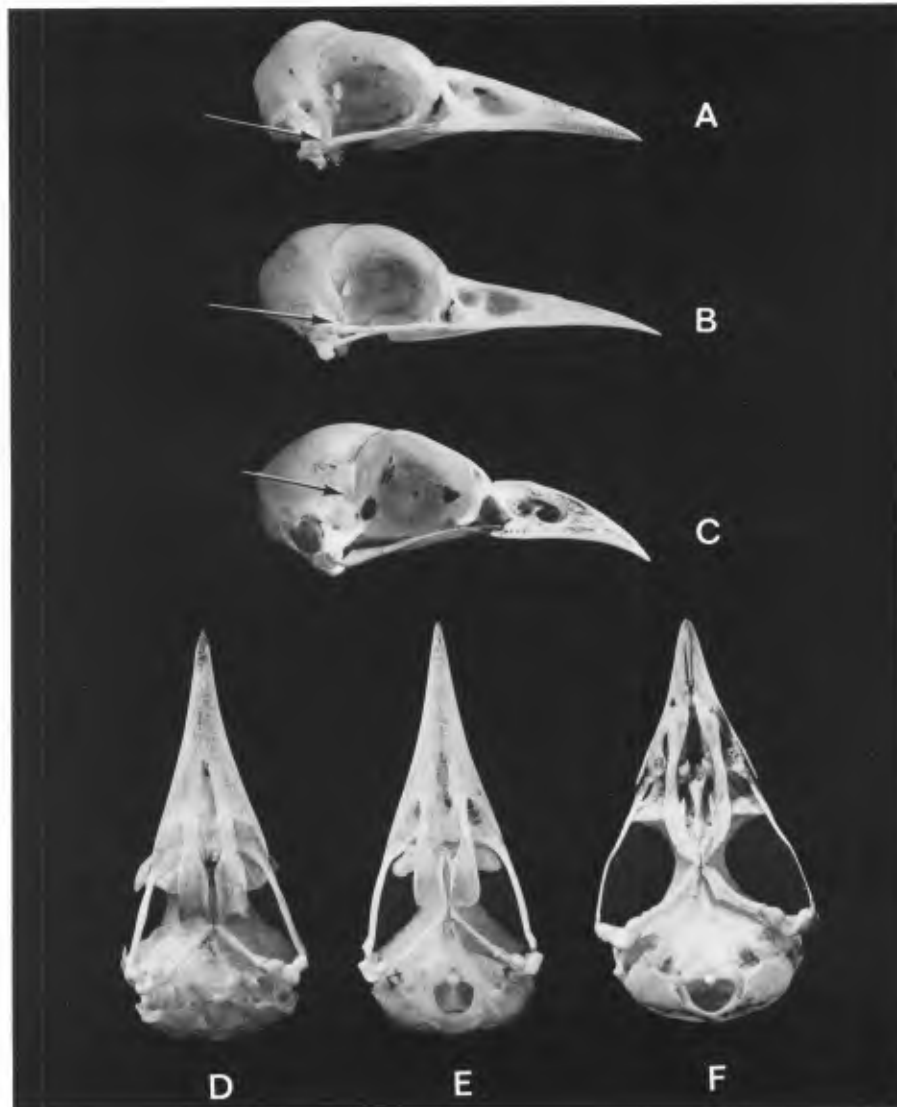


Fig. 2. Lateral and ventral views of skulls of a roller, *Coracias benghalensis* (A,D); a puffbird, *Malacoptila panamensis* (B,E); and a barbet, *Trachyphonus purpuratus* (C,F). Note the great overall similarity between the roller (Coraciidae) and the puffbird (Bucconidae), whereas neither closely resembles the barbet (Capitonidae). The arrows indicate the ventral extent of the postorbital process, which is greatly developed in the Coracii and Galbulae. Not to scale.

myology of the Piciformes have failed to reveal a single new character that independently corroborates the hypothesis of monophyly.

If we consider that the Piciformes are *not* monophyletic, then the Type VI condition of the flexor tendons must have arisen more than once. This is not at all an unreasonable hypothesis. Convergence in myological characters occurs with great frequency, as Swier-

czewski and Raikow (1981) amply demonstrate. Of the 43 myological characters presented in their Table 1, 40% evolved more than once *just within the Piciformes*. With the probability of convergence being so high, it is clearly impractical to justify an entire order of birds with a single myological character. In another situation, Berman and Raikow (1982: 55) found that only colies (Coliidae) and parrots have a branch

of the *M. extensor digitorum longus* tendon extending to the hallux; yet, they considered that "this character alone cannot demonstrate a common ancestry for the Coliiformes and Psittaciiformes . . ." Why, then, should a single tendinal character be accepted as demonstrating the common ancestry of the Piciiformes?

THE RELATIONSHIPS OF THE GALBULAE AND THE PICI

Here, I will briefly outline my reasons for believing the Galbulae to be closely related to the rollers, or Coracii of Maurer and Raikow (1981), which includes the Coraciidae, Brachypteraciidae, and Leptosomidae. The Pici, on the other hand, I believe are more closely related to the Passeriformes. These observations are preliminary; a more complete assessment of the interrelationships of all the higher orders of land birds requires more evidence than is now available. For example, it is difficult to make myological comparisons of the Piciiformes and Coraciiformes from the existing literature because Swierczewski and Raikow (1981) and Maurer and Raikow (1981) have presented only the evidence that supports their classifications, while omitting the descriptive observations of actual dissections. Even with access to the unpublished dissertations of Swierczewski (1977) and Maurer (1977), cross comparisons are difficult, because a character that was deemed important in one group was often not considered significant in the other, so that certain descriptions may be inadequate for comparison, necessitating the re-examination of specimens.

Sibley and Ahlquist (1972) have previously suggested a relationship between the Galbulae and the Coraciiformes, but they particularly singled out the kingfishers (Alcedinidae) as possible affines. The kingfishers, however, belong to the alcedinine group of Coraciiformes that is characterized by a derived morphology of the stapes (Feduccia 1975) and several derived myological characters (Maurer and Raikow 1981) that do not occur in the Galbulae. A lack of relationship between the Galbulae and the Alcedinidae does not, however, preclude a relationship between the Galbulae and some other section of the Coraciiformes.

The skull and mandible in the Galbulae, particularly in the less-specialized family Bucconidae, show a remarkable similarity to those of

Coracias (Coraciidae) in almost every aspect (Fig. 2)—bill shape, truncate palatines, straight and narrow pterygoids, heavily ossified nasal septum, shape and position of the temporal fossae, the inflated ectethmoid plate, and the greatly exaggerated and ventrally produced post-orbital process. In all of these characters the Bucconidae are consistently different from the Pici.

The major differences between the skulls of the Bucconidae and *Coracias* are in the reduced lacrimal and the dorsal expansion of the palatines onto the parasphenoid rostrum in the Bucconidae. These differences are more like those observed between genera within a family than between different orders. They are less profound than the differences observed between the four families of Pici, for example. In many respects, the skull of *Coracias* differs less from that of the bucconid *Malacoptila* than it does from *Eurystomus*, the only other modern genus in the Coraciidae.

In the Galbulae, and in all of the Coracii, the postorbital process is greatly enlarged and extends straight ventrally as far as the jugal bar (Fig. 2). From this there is a very strong, short, post-orbital ligament that attaches to a process on the medial surface of the mandible just anterior to the articulation (Fig. 3). The *M. adductor mandibulae* complex is correspondingly narrowed, enabling it to pass through the relatively small foramen formed by the enlarged postorbital process (Fig. 3). On the other hand, the postorbital process is quite small in the Pici, most Passeriformes, the Trogonidae, and in the remainder of the Coraciiformes except the Bucerotidae and some of the Momotidae. In the last two instances, the postorbital process is well developed but does not extend nearly as far ventrally as it does in the Coracii and the Galbulae. In the one example of barbet (*Trachyphonus darnaudii*) that I dissected, the postorbital ligament was very weak and was scarcely differentiated from the overlying fascia.

In the elements of the postcranial skeleton of the Galbulae, there is greater similarity to the Coracii than to the Pici. The coracoid in the Galbulae is almost identical to that in the roller group (Fig. 4) and is very different from that found in the Pici. The humeri and carpometacarpus in the Galbulae are also more similar to those in the rollers than to the Pici (see below).

Those who have experience identifying

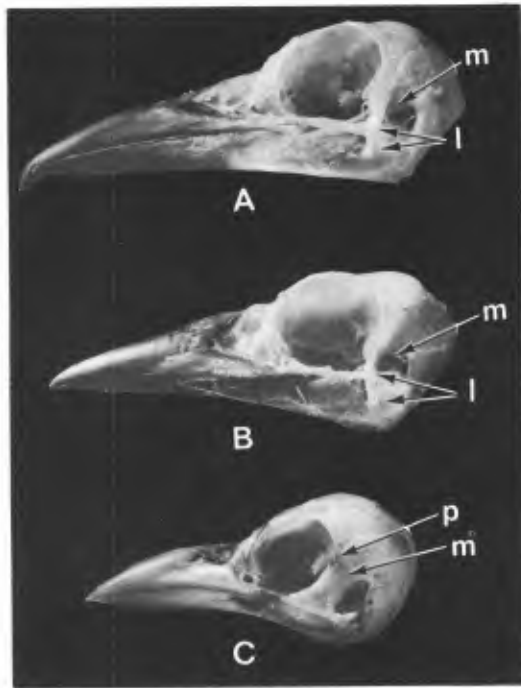


Fig. 3. Dissected heads of a roller, *Coracias garrrulus* (A); a puffbird, *Notharchus pectoralis* (B); and a barbet, *Trachyphonus darnaudii* (C). Note the marked similarity between the roller and the puffbird in the very strong ligament (l) from the enlarged postorbital process to the mandible and in the narrowed adductor mandibulae complex (m), whereas in the barbet the postorbital process (p) is very small, the ligament is vestigial, and the adductor mandibulae complex is of more normal development. Not to scale.

isolated bird bones are aware of the skeletal similarities between the Pici and the Passeriformes; a possible relationship between these two groups has long been recognized (see Sibley and Ahlquist 1972). Lowe (1946) considered the Pici to be but a suborder of the Passeriformes and did not include or even mention the Galbulae.

The coracoid in the Pici and Passeriformes is very slender and elongate, with the sternal end and head narrow, the sterno-coracoidal process reduced, and the procoracoid process usually vestigial or even absent (Fig. 4). This contrasts with the condition in the Galbulae and most Coraciiformes, in which the coracoid is comparatively short, the head and sternal end expanded, and the sterno-coracoidal and procoracoid processes well developed. The car-

pometacarpus in the Pici differs from that in the Galbulae and Coraciiformes in having a broad and very well-developed intermetacarpal tubercle, a condition shared only with the Passeriformes among the higher land birds. The humerus in the Pici differs from that in the Galbulae and Coraciiformes and resembles that in the Passeriformes in having the shaft short and stout, the proximal end broader, and the deltoid crest squared, rather than triangular or rounded.

Whereas we have seen that no characters independent of the deep flexor tendons could be found to corroborate piciform monophyly, most other characters, whatever their "polarity" may be, are concordant when the Galbulae are allied with the Coracii and the Pici are allied with the Passeriformes. Thus, the oil gland is covered with down and lacks a tufted orifice in the Galbulae and Coracii but is nude, with a tufted orifice, in the Pici and Passeriformes (Gadow 1896). The caeca are well developed in the Galbulae and Coracii but absent or rudimentary in the Pici and Passeriformes (Gadow 1896; pers. obs. for Galbulae). The structure of the down in the Galbulae is like that of the Coracii, whereas that of the Pici is similar to that of the Passeriformes (Chandler 1916). Of the six derived myological characters that Swierczewski and Raikow use to define the Pici, four (characters 1, 33, 39, and 41) are found in most, some, or all passerines. Mm. popliteus, adductor digiti II, and extensor brevis digiti IV are absent in the Pici (characters 33, 39, and 41) and in Passeriformes, whereas each of these muscles is present in both the Galbulae and the Coracii. If my interpretation of Maurer's (1977) descriptions is correct, four characters (15, 29, 31, and 32) of the six that Swierczewski and Raikow (1981) use to define the Galbulae as monophyletic also occur in the Coracii, whereas only two (14 and 42) appear to be unique (autapomorphous). When all of the data can be analyzed, I am confident that there will be far fewer character conflicts when the Piciformes are split apart, as I have proposed here, than when they are maintained as monophyletic.

COMMENTS ON FOSSIL TAXA

Simpson and Cracraft's (1981: 491) discussions of the Primobucconidae and Zygodactylidae are misleading. Their statement that the

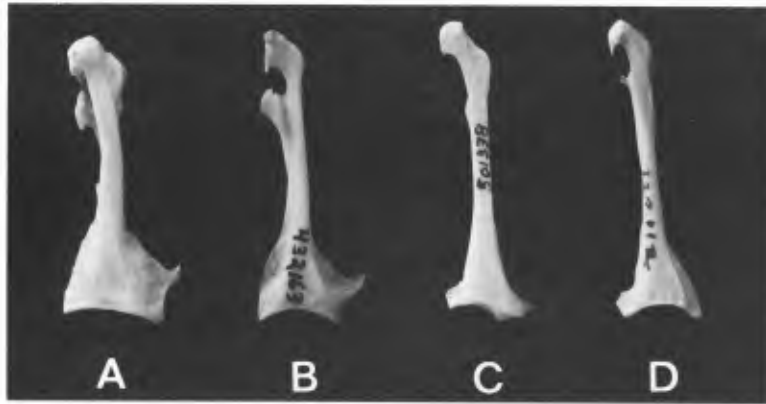


Fig. 4. Ventral view of coracoids to show the similarities between the ground roller *Brachypteracias leptosomus* (A), and a puffbird, *Malacoptila panamensis* (B). These differ greatly from the coracoid in the Pici (C, the woodpecker, *Colaptes auratus*), which is more like that in passerines (D, a rhinocryptid, *Pteroptochos megapodius*). Not to scale.

Primobucconidae have not been shown to be a monophyletic group is irrelevant. Such a statement could truthfully be made about the vast majority of groups of birds or other organisms. Simpson and Cracraft present no information to suggest that the primobucconids are *not* monophyletic. Their contention that "the bucconids and galbulids are fully zygodactyl," but that the "Eocene genera [of primobucconids] are not," hinges entirely on the definition of "fully zygodactyl," which they do not provide. Two specimens of primobucconids (the holotype of *Neanis kistneri*, Feduccia 1973; and the holotype of *Primobucco olsoni*, Feduccia and Martin 1976) are preserved with the outer toe completely reversed, in the zygodactyl manner. Perhaps by "fully zygodactyl" Simpson and Cracraft mean that the primobucconids do not have the fourth trochlea and sehnenhalter as modified as in other zygodactyl birds, but the primobucconids were certainly functionally zygodactyl. [Note also that Simpson and Cracraft (1981: 491) misquote Feduccia and Martin (1976)—the description of the primobucconid tarsometatarsus should read "a distinct groove separating the posterior portion of the trochlea" not "supporting" it.]

Simpson and Cracraft contend that the more primitive tarsal morphology of the primobucconids argues against their being placed within the Galbulae, but this follows only if one defines the Galbulae solely by the possession of a completely modified fourth trochlea. At some point, the Galbulae obviously had ances-

tors that were not zygodactyl, and forms transitional between those ancestors and the fully zygodactyl modern Galbulae must have existed. The Galbulae would have to be included at some taxonomic level with birds that did not have the fourth trochlea as modified as do the modern members of the suborder. Because Simpson and Cracraft present no evidence to show that the primobucconids are more closely related to some other group, there is no reason not to follow Brodkorb (1970) and Feduccia and Martin (1976) in considering the Primobucconidae to be primitive members of the Galbulae that share more similarities with the Bucconidae than with any other extant family of birds.

Simpson and Cracraft (1981: 492) tentatively suggest "placing the Zygodactylidae as a basal member of the Pici," but they present no evidence for this either. Ballmann (1969a, b) deliberately did not put *Zygodactylus* in any existing order, because he considered that its affinities could not be determined from the tarsometatarsus and tibiotarsus, the only elements yet known. For descriptive purposes he made comparisons not only with the Pici-formes but also with the Psittaciformes. Ballmann (pers. comm.) has emphasized verbally to me his belief that *Zygodactylus* is not pici-form. If *Zygodactylus* tells us anything at this point, it is probably that the specialized zygodactyl condition of the tarsometatarsus, in which the fourth trochlea becomes enlarged and bears a sehnenhalter, has evolved yet another time.

CONCLUSION

As I have indicated elsewhere (Olson 1981), the higher level systematics of birds has a very poor foundation. The questions of whether or not currently recognized orders are monophyletic and what the interrelationships of these orders may be are still largely unanswered. Although the studies of Swierczewski and Raikow (1981) and Maurer and Raikow (1981) are useful in documenting the monophyly of some of the subunits of Coraciiformes and Piciformes, at the level of ordinal and interordinal systematics they are less successful. Despite these workers' accumulation of much new data, they could recognize the orders Piciformes and Coraciiformes as monophyletic only by the configuration of the deep flexor tendons—the same character that had been used to define these orders nine decades ago. Their studies were designed only so as to test hypotheses that had previously been formulated, whereas they seem to lack the means to generate alternative hypotheses. Herewith, I have supplied one for the Piciformes, and there is every reason to expect alternative hypotheses of relationships for the Coraciiformes and for other orders based on single characters or that are otherwise poorly defined.

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