THE PHYLOGENETIC RELATIONSHIPS OF THE PICIFORMES (CLASS AVES)

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Abstract.—The phylogenetic relationships of the avian order Piciformes were studied using a cladistic analysis of the skeletal morphology. We hypothesize that the piciforms constitute a monophyletic group on the basis of possessing a unique flexor tendon pattern in the hindlimb, a M. flexor hallucis longus with three heads of origin, zygodactyly, and a well-developed sehnenhalter on the outer (IV) trochlea of the tarsometatarsus. Two major lineages are defined by osteological characters, one (the Galbulae) consisting of the Galbulidae and Bucconidae, and the other (the Pici) comprising the remaining four families. Within the Pici, two lineages are discerned: the Ramphastoidea, consisting of the Ramphastidae and the Capitonidae, and the Picoidea, which includes the Picidae and Indicatoridae. The systematic position of the fossil families Zygodactylidae and Primobucconidae are interpreted within the framework of the phylogenetic hypothesis for the Recent families. *Received 24 September 1980, accepted 15 January 1981.*

Despite the efforts of countless investigators over the last 100 yr, corroborated hypotheses about the phylogenetic relationships of the avian higher taxa remain in short supply. Within this literature it is rare that data from different anatomical systems have been interpreted so as to provide concordant evidence supporting a specific hypothesis of genealogical relationships within a set of these higher taxa. One major reason for this is that workers have traditionally evaluated similarity without regard to the hierarchical level at which these similarities define a set of taxa, i.e. similarities have not been partitioned into derived and primitive conditions. This paper presents the results of a phylogenetic analysis of the avian order Piciformes based on a cladistic interpretation of skeletal morphology, and, along with the cladistic analysis of myological characters by Swierczewski and Raikow (1981), it represents the first time in the avian systematic literature that two independent studies of different anatomical systems have produced concordant support for the same phylogenetic hypothesis of an avian order.

Two central questions about piciform taxa repeatedly emerge from the morass that is the avian systematic literature: (1) do the families currently classified in the order Piciformes (Wetmore 1960) constitute a monophyletic assemblage, and (2), if so, what are the interrelationships of these families? The monophyly of the order was frequently questioned in the older literature, and no satisfactory hypothesis of familial interrelationships has been presented before this time.

It is not necessary to present details of the history of piciform classification; the interested reader should consult Sibley and Ahlquist (1972). We shall, however, summarize briefly some importance aspects of that history.

The earliest attempts at forming classifications of the piciforms used similarities in foot structure to group taxa together. Thus, Illiger (1811) placed all birds with modifications in foot structure into his group, the Scansores. The latter included the

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parrots, cuckoos, trogons, and the piciform families. Later workers, notably Vieillot (1816) and Temminck (1820), introduced the concept of the Zygodactyli for the cuckoos, parrots, and piciforms based on the presence of a zygodactyl foot (digits I and IV reversed). In 1840 Nitzsch placed the picids, bucconids, capitonids, and ramphastids together in one group, but he put indicatorids with cuckoos and galbulids with various coraciiform taxa. It is important to note that most 19th century systematists did not recognize the piciform taxa (*sensu* Wetmore 1960) as a natural group in their classifications (Huxley 1867; Garrod 1873–1874; Reichenow 1882; Fürbringer 1888; and Beddard 1898; are the most notable examples). The modern concept of the piciforms as a natural group apparently stems from the work of Stejneger (1885), most of all Gadow (1893), but also Ridgway (1914).

METHODS AND MATERIALS

It is now generally accepted by most systematists that monophyletic groups are defined by shared, derived characters (synapomorphies of Hennig 1966). Considerable controversy still exists, however, over the methods used to hypothesize these derived characters. In this study we have adopted the well-known method of out-group comparison (see Gaffney 1979, and Eldredge and Cracraft 1980, for more detailed discussions). After a general survey of the osteology of nearly all the families of "higher" nonpasserine birds and numerous families of the Passeriformes, we established that there were similarities shared by the piciform families that could be interpreted as unique within the larger group of taxa being compared. These characters, and others mentioned in the literature, served as the basis for the preliminary hypothesis that the Piciformes comprise a monophyletic group. In order to construct hypotheses about derived character distributions within the piciforms, we again considered all "higher" nonpasseriforms (primarily families included in the Coraciiformes, Trogoniformes, Coliiformes, Cuculiformes, and Psittaciformes) and the passeriforms to be out-groups; characters found in the out-groups and in some piciform taxa were hypothesized to be primitive within piciforms, and characters shared uniquely by piciform taxa were hypothesized to be derived and indicative of genealogical relationship.

Over a period of 2 yr, a large series of skeletons of piciforms and other taxa was examined. The specimens examined are housed in the following museums (abbreviations refer to illustrated material): American Museum of Natural History, New York City; Field Museum of Natural History (FMNH), Chicago; Louisiana State University Museum of Zoology (LSUMZ), Baton Rouge; University of Kansas Museum of Natural History; the University of Michigan Museum of Zoology; Bayerischen Staatssammlung für Paläontologie und historische Geologie, Munich; and the Laboratoire de Géologie de la Faculté des Sciences de Lyon, France.

PHYLOGENY OF THE PICIFORMES

A phylogenetic hypothesis for the Piciformes is shown in Fig. 1. In this section the different clades will be identified by the supraspecific names advocated in the Discussion. The numbers on Fig. 1 refer to the derived characters defining the various lineages.

A HYPOTHESIS OF PICIFORM MONOPHYLY

Virtually all recent classifications consider the Piciformes to represent a natural group, presumably on the basis of well-known similarities in hindlimb osteology and myology (see below). We have been unable to find additional osteological characters that could be used to corroborate the monophyly of the piciforms. Accordingly, our discussion here simply summarizes the available evidence and details how some of these characters might be interpreted in a phylogenetic context. Despite the paucity of derived characters indicating monophyly, it should be pointed out that the Piciformes are much better defined than many other orders of birds.
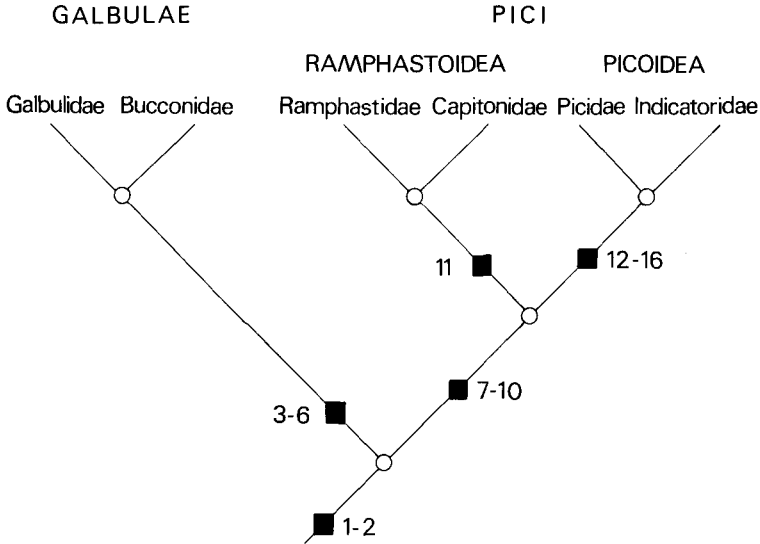
Fig. 1. A phylogenetic hypothesis of the order Piciformes. Black squares symbolize suites of derived characters (synapomorphies) defining lineages as monophyletic; numbers refer to derived characters discussed in the text.

The first characters we discuss are those of hindlimb myology (see Swierczewski and Raikow 1981).

1. The flexor tendon pattern is type VI. Garrod (1875) was the first to describe the type VI flexor tendon pattern of Gadow (1894) in which the M. flexor digitorum longus supplies digit III and the M. flexor hallucis longus supplies digits I, II, and IV. A viniculum connects the undivided portion of the flexor hallucis tendon to the flexor digitorum tendon, allowing the former to act on all four digits. Garrod noted the existence of this pattern in five out of the six piciform families. George and Berger (1966) completed the comparison by discovering the type VI arrangement in *Indicator variegatus*. In addition, the several piciform species examined by Miller (1919) confirmed Garrod's findings that there are two different flexor tendon patterns found among birds with zygodactyl feet. The type VI pattern is unique to the Piciformes and has never been reported in any other species. The cuckoos and parrots share the type I flexor tendon pattern that is found in many birds. The Coraciiformes and Passeriformes, which are most often considered closely related to the Piciformes, possess the type V and type VII patterns, respectively.

There is a second myological character corroborating monophyly. The M. flexor hallucis longus arises by three heads (Swierczewski and Raikow 1981). This is clearly a derived character, as the muscle arises by one or two heads in other birds.

At this time there is only one known derived character of the osteology that corroborates the hypothesis of piciform monophyly.

2. The foot structure is zygodactyl, and the trochlea for digit IV is enlarged and turned far posteriorly as a sehnenhalter (Fig. 2B–D). This condition has been noted often in the literature (e.g. Steinbacher 1935). In the two orders traditionally thought to be most closely related to piciforms—the Coraciiformes and Passeriformes—all three trochleae (II, III, IV) are similar in size and shape and lie more or less in the same mediolateral plane. In these orders the trochleae exhibit little curvature when
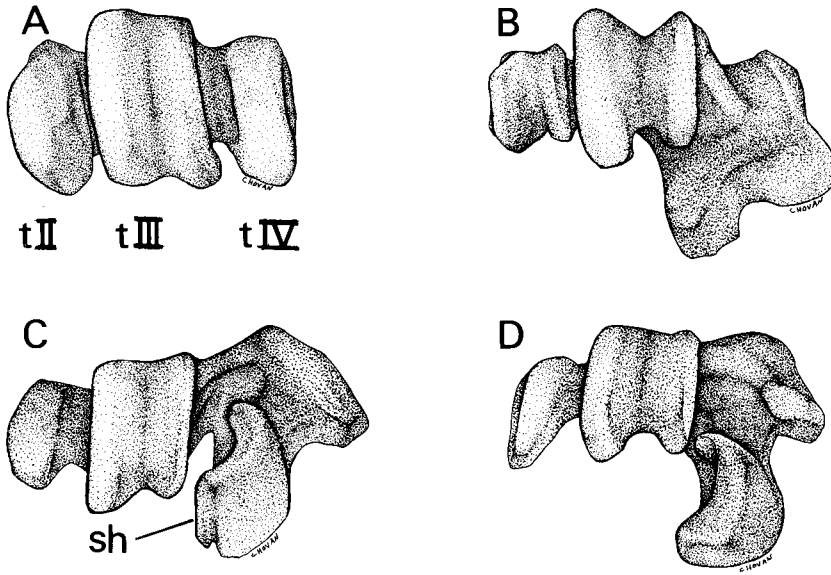
Fig. 2. Distal ends of tarsometatarsi of (A) *Cyanocorax affinis* (Corvidae), FMNH 104996; (B) *Galbula cyanescens* (Galbulidae), LSUMZ 64928; (C) *Psilopogon pyrolophus* (Capitonidae), FMNH 105407; and (D) *Colaptes auratus* (Picidae), FMNH 96113. Abbreviations: sh, sehnenhalter; t, trochlea.

viewed distally. Because of general similarities to other groups of birds, there is strong reason to infer this condition to be more primitive than that of the piciforms (Fig. 2A).

   The important systematic question is how this foot structure is to be interpreted phylogenetically, given the fact that cuckoos and parrots are also zygodactyl. There are several alternatives. It might be argued that zygodactyly evolved once, in which case that character would define cuckoos, parrots, and piciforms as a monophyletic group. The above-mentioned myological characters would then be interpretable as synapomorphies defining the piciforms as a subgroup. Another alternative is that zygodactyly has evolved more than once, the piciforms being monophyletic but related only distantly to cuckoos and parrots. We believe this second hypothesis is the most parsimonious at this time. First, there are no additional postulated synapomorphies uniting piciforms, cuckoos, and parrots and thus corroborating zygodactyly as a synapomorphy of these three groups. Moreover, there is also the well-known observation that the osteological and myological characteristics of zygodactyly are distinct for the piciforms and different from cuckoos and parrots (Steinbacher 1935, Swierczewski and Raikow 1981). Both of these reasons are less than satisfactory, however, because the first is negative evidence and the second does not constitute, in our opinion, a rigorous form of phylogenetic argumentation. The primary argument against monophyly of piciforms, cuckoos, and parrots must be support for an alternative theory of relationships that would relate these taxa to other groups rather than to each other. Unfortunately, the relationships of cuckoos and parrots remain among the most enigmatic within ornithology. There is a general acceptance among avian systematists, however, that piciforms are most closely related to coraciiforms or to passeriforms and that cuckoos and parrots are not. Although this hypothesis has yet to be tested cladistically, anatomical similarities
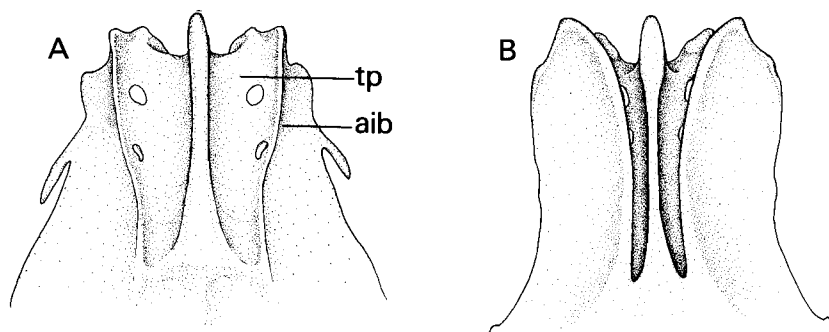
Fig. 3.   Dorsal view of the preacetabular portion of the pelvis of (A) *Galbula cyanescens* (Galbulidae), LSUMZ 64928; and (B) *Selenidera maculirostris* (Ramphastidae), FMNH 105610. Abbreviations: aib, border of anterior iliac crest; tp, transverse processes.

among piciforms, coraciiforms, and passeriforms seem to support it. This latter hypothesis, then, speaks against the monophyly of piciforms, cuckoos, and parrots.

In summary, the current evidence suggests that zygodactyly and the presence of a sehnenhalter can be interpreted as derived characters defining the piciforms as monophyletic.

MONOPHYLY OF THE SUBORDER GALBULAE

There are two major lineages within the Piciformes. One of these, the Galbulae, comprises the families Bucconidae and Galbulidae. In general overall morphology, the Galbulae appear to be relatively more primitive than the second lineage, the Pici.

Four osteological characters support the hypothesis of a close relationship between galbulids and bucconids.

3. Trochlea IV with small sehnenhalter inflected medially beneath base of trochlea III. There are two morphological conditions within the piciforms, one present in the Galbulae and one in the Pici (Fig. 2). The latter condition is clearly more derived than that of galbulids and bucconids. Accordingly, the condition of trochlea IV and the sehnenhalter in the Galbulae might be more porperly interpreted as primitive within the piciforms (Fig. 2B). We recognize this and therefore do not believe this character offers strong evidence for a relationship between galbulids and bucconids. Nevertheless, the condition of trochlea IV in some fossil taxa assigned to the family Primobucconidae (Feduccia and Martin 1976)—in which trochlea IV is much less enlarged, is bladelike, and is not turned as much posteriorly as in Recent piciforms— suggests the possibility that the conditions in the two piciform suborders might be separate, derived conditions (the primobucconids will be discussed below).

4. Anterior iliac blades greatly reduced in size and fused with vertebrae (Fig. 3). In the majority of coraciiforms, passeriforms, and in the suborder Pici, the dorsal half of the anterior iliac blade of the ilium is not fused with the vertebrae (Fig 3B). Within the galbulids and bucconids, on the other hand, the anterior blade of the ilium is greatly reduced and fused to the transverse processes to form a flat horizontal plate with only a low ridge remaining to indicate the dorsal edge of the anterior iliac crest (Fig. 3A). We hypothesize that the condition of the bucconids and galbulids represents the derived condition within the piciforms.
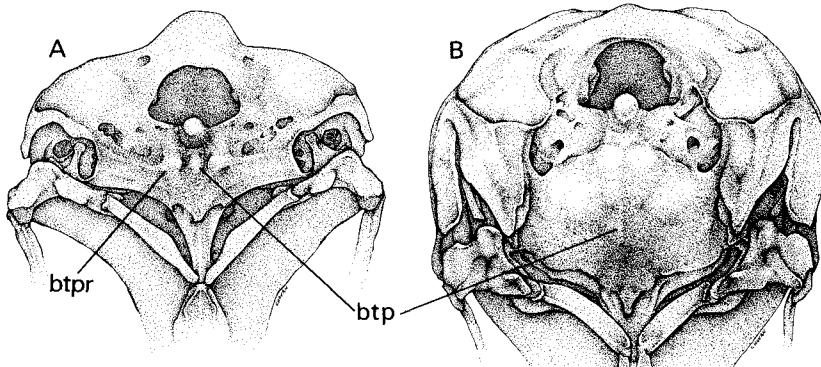
Fig. 4.   Ventral view of the skull base of (A) *Galbula cyanescens* (Galbulidae), LSUMZ 64928; and (B) *Colaptes auratus* (Picidae), FMNH 96113. Abbreviations: btp, basitemporal plate; btpr, basitemporal process.

5. Basitemporal plate greatly reduced in anteroposterior extent. In galbulids and bucconids there has been a major reorganization of the cranium so that the foramen magnum is directed relatively more ventrally than in the out-groups or the Pici. This reorganization results in a striking reduction in the extent of the basitemporal plate (Fig. 4A). To our knowledge only the coraciiform family Meropidae shows this condition. The typical avian condition is to possess a much broader (anteroposteriorly) plate (Fig. 4B).

6. Sternum with reduced sternal plate and with long, thin posterolateral processes that attach to the sternal plate relatively far anteriorly (Fig. 5). In the out-groups and other piciforms the sternal plate is longer relative to the height of the keel, and the posterolateral processes are shorter and thicker (Fig. 5B). Thus, the condition of the Galbulae is considered derived (Fig. 5A).

MONOPHYLY OF THE SUBORDER PICI

The second major lineage of the piciforms, the suborder Pici, is itself comprised of two separate lineages, one including the Ramphastidae and Capitonidae and the other the Indicatoridae and Picidae. These four families have traditionally been considered to be related, and their monophyly is strongly supported by skeletal characters.

7. Trochlea IV greatly modified with large posterodistally projecting sehnenhalter. In these four families the expanded trochlea IV possesses a large and nearly triangular-shaped sehnenhalter that projects far posteriorly and distally and is joined to the anterior portion of the trochlea by a relatively narrow stem of bone (Fig. 2C, D). This condition is unique within birds.

In the Pici, as compared to the Galbulae, the inner (II) trochlea has become narrower, more bladelike (Fig. 2C, D). In galbulids, trochlea II is broader and with a well-developed tendinal groove (Fig. 2B). In bucconids the trochlea remains fairly broad, but the tendinal groove is lacking. Various out-groups, such as some coraciiforms and passeriforms, have a narrow trochlea II; thus, the condition in the Pici may not be derived (Fig. 2A). Certainly, the condition of the Galbulae is more nearly like that of most birds, and for that reason one might surmise it to be primitive.
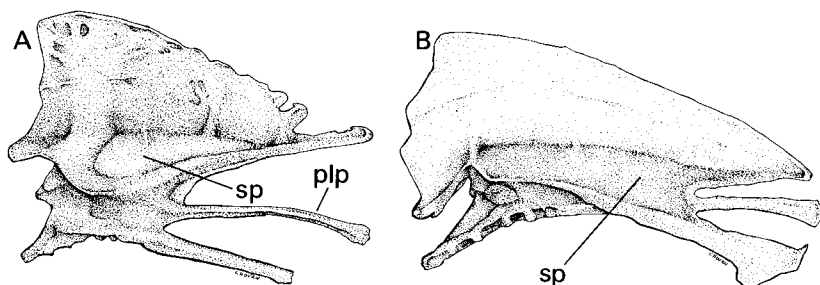
Fig. 5. Side view of sterna of (A) *Galbula ruficauda* (Galbulidae), LSUMZ 31900; and (B) *Colaptes auratus* (Picidae), FMNH 96113. Abbreviations: plp. posterolateral process; sp. sternal plate.

The shape of trochlea II is important with regard to assessing the systematic position of various fossil taxa (see below).

8. Hypotarsus with bony canals containing five flexor tendons. Within the Piciformes the primitive condition of the hypotarsus reveals a single bony tunnel or deep canal, the walls of which are formed by the medial and lateral calcaneal ridges (Fig. 6B). This condition is found in the Galbulidae, Bucconidae, and most of the Coraciiformes. This single tunnel contains the tendon of M. flexor digitorum longus in *Coracias, Chloroceryle,* galbulids, and bucconids (George and Berger 1966). In contrast, the other four piciform families, the hornbills and hoopoes, and the passeriforms each have their own unique hypotarsal tunnel pattern. It is postulated here that the pattern of bony tunnels in the Pici represents a derived condition (Fig. 6C, D); the medial and lateral calcaneal ridges extend further posteriorly than in the Bucconidae and Galbulidae and enclose four additional flexor tendons in bony tunnels. Moreover, as discussed below, we hypothesize that there exist two derived extremes within the Pici. The anteromedial tunnel in the Picidae (Burt 1930), the Passeriformes (Hudson 1937) and *Buceros* (George and Berger 1966) is considered homologous to that found in the Galbulidae and Bucconidae, because it contains the tendon of M. flexor digitorum longus (Fig. 6A, B, D). The Passeriformes, hornbills, hoopoes, and woodhoopoes also have multiple bony tunnels, but some of these tunnels uniquely enclose tendons, such as that of M. flexor hallucis longus, that lie external to the bony tunnels in the hypotarsus of piciforms (Fig. 6A).

9. Lateral hypotarsal groove significantly deepened. The lateral hypotarsal groove contains the tendon of M. flexor hallucis longus (Fig. 6D). In the primitive condition, seen in the Galbulidae, Bucconidae, and the majority of the Coraciiformes, the lateral groove, if present, is a very shallow depression (Fig. 6B). In the derived condition of the Pici, the hypotarsal groove is relatively deeper and more completely surrounds the tendon of M. flexor hallucis longus due to the posterior expansion of the rim of the lateral cotyla and the lateral protrusion of a portion of the lateral calcaneal ridge (Fig. 6C, D).

10. Fused lacrimal and ectethmoid bones (Fig. 7A). The form of the ectethmoid and the presence of the lacrimal are extremely variable within the piciforms, passeriforms, and coraciiforms. A separate lacrimal is consistently found in the galbulids and bucconids and is consistently absent from the members of the Pici. In the latter, the lacrimal is presumably fused with the ectethmoid to form an expanded plate that occupies the entire anterior end of the orbit (Fig. 7A). Embryological work is
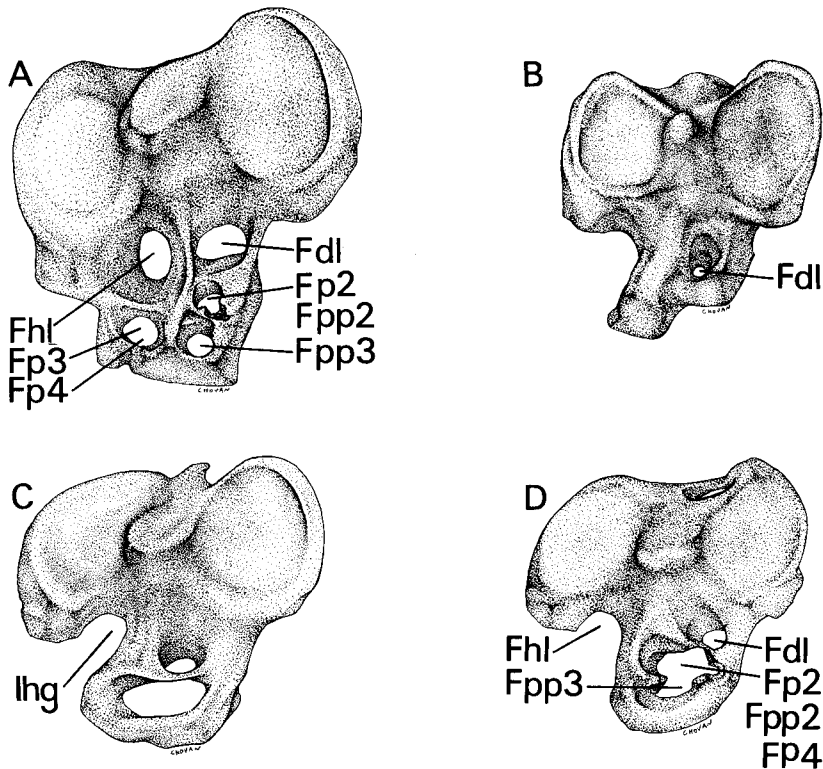
Fig. 6. Proximal ends of tarsometatarsi of (A) *Cyanocorax affinis* (Corvidae), FMNH 104996; (B) *Galbula cyanescens* (Galbulidae), LSUMZ 64928; (C) *Psilopogon pyrolophus* (Capitonidae), FMNH 105407; and (D) *Colaptes auratus* (Picidae), FMNH 96113. Abbreviations: Fdl, flexor digitorum longus; Fhl, flexor hallucis longus; Fp2, flexor perforatus digiti 2; Fp3, flexor perforatus digiti 3; Fp4, flexor perforatus digiti 4; Fpp2, flexor perforans et perforatus digiti 2; Fpp3, flexor perforans et perforatus digiti 3; lhg, lateral hypotarsal groove.

needed to verify the composition of this plate. Based upon the presence of a separate lacrimal in the majority of passeriforms and coraciiforms, the condition seen in the galbulids and bucconids is considered primitive within piciforms (Fig. 7B). The fused lacrimal-ectethmoid plate (or, the lacrimal being absent) is thus a derived condition shared by the Pici.

MONOPHYLY OF THE SUPERFAMILY RAMPHASTOIDEA

The barbets and toucans are very similar in external appearance, and few workers have doubted their close relationship. Yet there seem to be few anatomical similarities uniquely shared by these two families; Swierczewski and Raikow (1981) found only two shared, derived characters in hind-limb myology, and we found only one in their osetology.

11. Two bony canals in the hypotarsus. The hypotarsus of ramphastids and capitonids has one small, anteriorly placed canal for the tendon of M. flexor digitorum longus and a larger, posterior canal, which has its long axis oriented lateromedially, enclosing the other flexor tendons (Fig. 6C). Because this morphology is unique within the piciforms and the out-groups, we postulate it to be a derived condition.
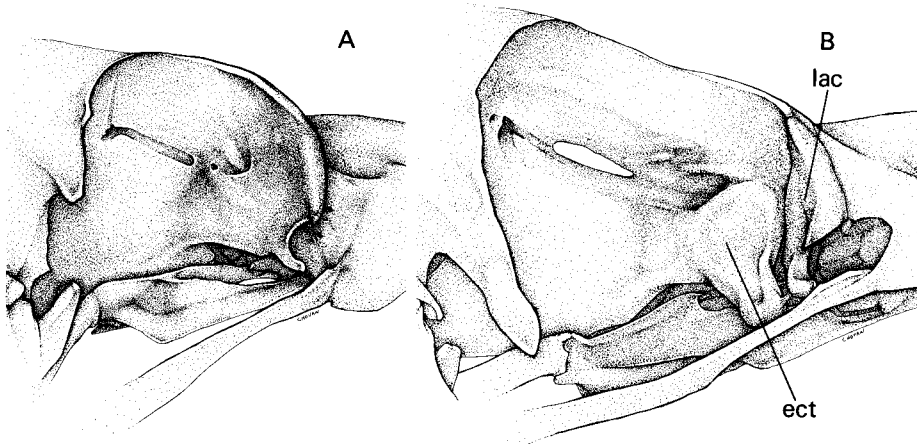
Fig. 7.   View of the orbit in (A) *Psilopogon pyrolophus* (Capitonidae), FMNH 105407; and (B) *Galbula cyanescens* (Galbulidae), LSUMZ 64928. Abbreviations: ect, ectethmoid; lac, lacrimal.

MONOPHYLY OF THE SUPERFAMILY PICOIDEA

The superfamily Picoidea consists of two families, the Indicatoridae and Picidae. The skulls of these two families share at least four characters supporting their close relationship, whereas we were able to find only one postcranial synapomorphy.

12. Maxillopalatine processes do not meet in the midline. In the derived condition the maxillopalatine process consists of a curved plate of bone, the ventral portion of which extends medially, dorsal to the rostral portion of the palatal complex, but never reaches the midline. In the primitive condition shared by the other four piciform families and the majority of the coraciiforms and passeriforms examined, the maxillopalatine processes of each side are in contact with another structure in the midline: sometimes the vomer or nasal septum and sometimes the expanded process from the other side.

13. Temporal fossa reduced in size and depth. In all the out-groups and other piciforms the temporal fossa is generally large, often extending dorsally nearly to the midline, and deep (Fig. 8B). This is the primitive condition. In picids and indicatorids, the fossa is greatly reduced, typically not being visible at all in posterior view (Fig. 8A). This condition is derived.

14. Cranium relatively more compressed lateromedially (Fig. 8A). Viewed posteriorly, the cranium of coraciiforms and other piciforms is relatively more flattened and broad lateromedially than in the Picoidea (Fig. 8B). We postulate this as the primitive condition within the Piciformes.

15. Basitemporal processes reduced or lost. In picids and indicatorids the basitemporal plate is smooth in contour, whereas in other piciforms and the out-groups basitemporal processes are generally well developed on each side of the midline (Fig. 4). We hypothesize the condition in the Picoidea to be derived.

16. Hypotarsus with single large, subdivided canal posterior to canal for M. flexor digitorum longus. In picids and indicatorids there typically is a single large canal, oriented more or less anteroposteriorly, that is subdivided into three partitions lo-
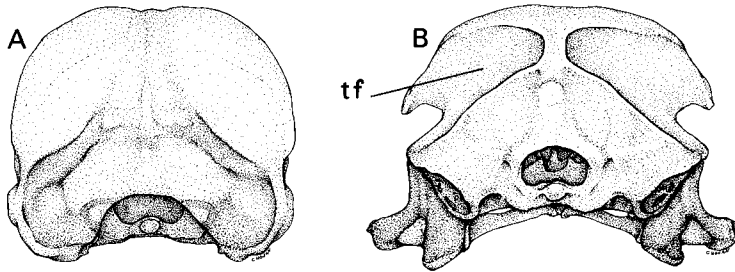
Fig. 8. Posterior view of the skull of (A) *Colaptes auratus* (Picidae), FMNH 96113; and (B) *Psilopogon pyrolophus* (Capitonidae), FMNH 105407. Abbreviations: tf, temporal fossa.

cated one behind the other (Fig. 6D). These subdivisions may be collagenous or they may become ossified. As this morphological arrangement is unique within piciforms and the out-groups, we postulate it to be derived.

DISCUSSION

ALTERNATIVE PHYLOGENETIC HYPOTHESES

Throughout this century there has been relatively little opinion, and virtually no evidence, suggesting a relationship between one or more piciform families and some other group of birds. Sibley and Ahlquist (1972: 239) suggested that indicatorids, galbulids, and bucconids may not be related to other piciforms, but no evidence was presented to support a specific alternative hypothesis. Because this study and that of Swierczewski and Raikow (1981) offer evidence of piciform monophyly, this latter hypothesis is more highly corroborated than any hypothesis of nonmonophyly. Furthermore, a pattern of interrelationships among the families is highly corroborated by both studies, and this also contributes to one's confidence in a hypothesis of piciform monophyly. Thus, for example, in order to argue that indicatorids are not piciform, it would be necessary to account for three hierarchically arranged suites of characters (characters 1–2, 7–10, and 12–16 of Fig. 1).

Relationships among the families have been much more subject to variance of opinion, but to our knowledge no study has documented a theory of relationships for all the families of piciforms. The classifications of Wetmore (1960) and Storer (1971), in which picids are placed in their own suborder and the remaining families in a second suborder, apparently reflect more a belief that morphologically distinct taxa—in this case, the Picidae—are to be distinguished by elevating them to a high rank (e.g. their separate suborder) than a conscious attempt on the part of these authors to suggest that the other five families are in fact more closely related to each other than any is to the picids. Our results and those of Swierczewski and Raikow (1981) provide strong support for the relationships shown in Fig. 1. The least corroborated lineage is the Ramphastoidea; even though there is a readily apparent close similarity in their skeletal anatomy, it is not easy to make a strong case for the hypothesis that the observed similarities are derived rather than primitive. This is the reason relatively few derived characters have been found to define this lineage. The remaining three lineages—the Galbulae, Pici, and Picoidea—are all highly corroborated by osteological and myological characters.

COMMENTS ON THE PRIMOBUCCONIDAE

Feduccia and Martin (1976) erected a new family, the Primobucconidae, for five genera (containing eight species) found in Eocene deposits of North America. The primobucconids are said to be related to the Bucconidae; this suggestion was based on an analysis of general overall similarity rather than being placed within the context of a derived character analysis and a phylogenetic hypothesis of the entire order. A consideration of the phylogenetic relationships of Fig. 1 and the evidence supporting them and of the published account about the morphology of the primobucconids elicits the following observations:

1. The primobucconids have not been shown to comprise a monophyletic group. As admitted by Feduccia and Martin (1976: 104), some of these forms are included in the family because they have general resemblances to piciform birds and because they are all Eocene in age; neither reason constitutes an argument for monophyly. Because skeletal elements cannot be compared in detail for all five genera, a unified definition of the family based on derived characters will have to await future paleontological discoveries. As discussed later, some of the characters of the tarsometatarsus said to diagnose (not define as monophyletic) the family are probably primitive.

2. At least some of the genera now included in the Primobucconidae are probably not piciforms as defined earlier in this paper. Three genera, *Uintornis, Botaurides,* and *Eobucco,* are known only from tarsometatarsi. As such, they are the only taxa directly comparable with the character analysis presented here. None of these genera can be said to have developed an enlarged trochlea IV with a sehnenhalter. Feduccia and Martin (1976) point out that these taxa more nearly resemble bucconids than any other piciform family, and certainly the Galbulae have a more primitive tarsometatarsal morphology than that of the Pici. Nevertheless, the bucconids and galbulids are fully zygodactyl, but these Eocene genera are not (Feduccia and Martin 1976: 103–104, diagnose the family as having: ". . . outer trochlea inflected inwards, without a well-developed sehnenhalter, but with a distinct groove supporting the posterior portion of the trochlea from the remainder"). In *Eobucco brodkorbi* the outer trochlea has the posterior portion inflected posteriorly and medially, but in the Galbulae virtually the entire trochlea is turned posteriorly. A condition similar to that of *E. brodkorbi* is also seen in *Uintornis lucaris.* The single specimen of the second species of *Uintornis, U. marionae,* lacks the trochlea IV and cannot be compared. The remaining taxon known from a tarsometatarsus, *Botaurides parvus,* has a small trochlea IV.

It seems, then, that the taxa included in the Primobucconidae do not possess a tarsometatarsal morphology as advanced as that characterizing the Piciformes. It may be that two or more of these Eocene species comprise a monophyletic group and that this taxon is the sister-group of the piciforms. The incipient zygodactyly may be evidence of this relationship, but, because of its primitive nature, that incipient zygodactyly cannot be used as an argument for monophyly of the primobucconids themselves. These considerations also argue against placing the primobucconids within the Galbulae.

COMMENTS ON THE ZYGODACTYLIDAE

Ballmann (1969a, b) described a new genus, *Zygodactylus,* for two species from the middle Miocene of France and Germany, as a perching bird with no apparant

affinities to any known family. Brodkorb (1971: 257) erected a new family, Zygo-dactylidae, for these species and placed it in the Galbulae. The two species of *Zygodactylus* are known from distal tarsometatarsi. That of *Z. ignotus* is damaged and does not contribute much information useful for evaluating potential relation-ships with the Piciformes. The tarsometatarsus of *Z. grivensis,* on the other hand, shows this species to be fully zygodactyl (Ballman 1969a, plate 14, Figs. 7–9).

The presence of a sehnenhalter with general resemblances to those of the piciforms suggests a relationship to that order. The morphology of *Z. grivensis* is unique, however, and an assignment of this form to a particular suborder is difficult. The general shape of the sehnenhalter (although it is not as triangular in shape as in the Pici), and its separation from the anterior portion of trochlea IV by a groove, re-sembles the condition of the Pici, but the primitive form of trochlea II, which is broad, possesses a posterior talon, and seems to have a slight rotular groove, pre-cludes a close relationship to any of the four families presently included in the suborder (J. Cracraft, pers. obs.). Likewise, the advanced nature of the sehnenhalter would seem to rule out an assignment of *Zygodactylus* to the Galbulae. Tentatively, then, we suggest placing the Zygodactylidae as a basal member of the Pici, although Ballmann's (1969a, b) opinion that *Zygodactylus* is not properly a piciform may eventually prove correct.

COMMENTS ON BIOGEOGRAPHY

Presumably as a result of their systematic conclusions about the Primobucconidae and because of the Eocene age of these fossils, Feduccia and Martin (1976: 110) concluded that the order Piciformes may have arisen in the New World. Their biogeographic scenario suggests a spread through the Northern Hemisphere to the Old World and a retreat to the tropics of both the Old and New worlds as a consequence of competition with passerines and a deteriorating environment through the Tertiary.

We suggest it may be premature to erect very specific hypotheses about piciform biogeography. We prefer to see hypotheses that have some eventuality of being evaluated empirically; hypotheses about competitive processes and their influence on distribution are probably untestable in a historical context. Two sets of phylo-genetic information, now lacking, will contribute much to our future assessment of piciform biogeography. First is knowledge about the relationships of the order to other taxa. If a relationship to primobucconid-like taxa can be established, that will imply different biogeographic hypotheses than if, for example, piciforms are found to be related to some tropical Old World coraciiform group. Second, knowledge of phylogenetic relationships within the piciform families should help clarify whether the order had a Southern or Northern Hemisphere origin.

It is clear from the fossil record that the Recent distributions of capitonids is partially relict in nature (Ballman 1969b), but the presence of fossils in the Northern Hemisphere, of any group, cannot be taken as evidence for a northern origin, only that the group in question also had a northerly distribution at a particular time: fossils should not be the arbiters of biogeographic hypotheses. Likewise, fossils of "bucconid grade" in North America do not signify a North American origin for that family.

Current distributions suggest to us that the piciforms have had a long and com-plicated history in the Southern Hemisphere. Knowledge of the intergeneric rela-

tionships within the capitonids and the picids should bear on this problem. The disjunct distributions of indicatorids, picids, and capitonids between Africa and southern Asia indicates a vicariance event associated with the deterioration of the climate (and consequently, vegetation) across northern Africa and the Arabian Peninsula in the late Cenozoic (Cracraft 1973). Finally, we note the nearly concordant distributions of galbulids, bucconids, and ramphastids in the New World and suggest that these patterns might reflect similar historical responses to changing paleogeography and paleoclimatology. An understanding of phylogenetic relationships within these families should help solve the question of whether their current distributions are primarily southern or northern in origin.

COMMENTS ON CLASSIFICATION

We believe that corroborated natural groups should be recognized formally in classification (see Eldredge and Cracraft 1980: 147–239, for reasons and discussion). Accordingly, we recommend the following classification of the Piciformes be adopted:

> Order Piciformes
>   Suborder Galbulae
>   Family Bucconidae
>   Family Galbulidae
>   Suborder Pici
>   Superfamily Ramphastoidea
>   Family Capitonidae
>   Family Ramphastidae
>   Superfamily Picoidea
>   Family Indicatoridae
>   Family Picidae

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