HIND LIMB MORPHOLOGY, PHYLOGENY, AND CLASSIFICATION OF THE PICIFORMES

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ABSTRACT.—The phylogenetic relationships of the order Piciformes were studied by a cladistic analysis of variations in the hind limb muscles. Forty-four species in 30 genera were dissected. The two main questions addressed are (1) is the order Piciformes monophyletic, and (2) what are the phylogenetic relationships within the order? Monophyly of the order is corroborated by the presence of a complex synapomorphic specialization of the foot, the combination of zygodactyly and the Type 6 deep plantar tendon arrangement of Gadow. These traditional characters, now seen as derived states, are augmented by a derived condition of M. flexor hallucis longus. Arguments refuting an alternative hypothesis are presented.

The phylogenetic hypothesis is presented in a cladogram. There are two main lineages, one including the Bucconidae and Galbulidae, the second the remaining families. The second lineage is further subdivided dichotomously, one lineage including the Capitonidae and Ramphastidae, and the second the Indicatoridae and Picidae.

A new higher-level classification of the order is proposed. Only clades are recognized as taxa, and sister groups are classified at the same categorical level. The suborder Galbulae includes the families Bucconidae and Galbulidae. The suborder Pici includes two superfamilies. The Ramphastoidea contains the families Capitonidae and Ramphastidae, while the Picoidea includes the Indicatoridae and Picidae. The Picidae is divided into subfamilies Jynginae and Picinae, the latter being further divided into the tribes Picumnini and Picini. The pattern of taxa in the classification is based on the nested arrangement of clades in the hypothesis of phylogeny. *Received 25 June 1980, accepted 1 October 1980.*

THIS is a study of the phylogenetic relationships in the order Piciformes, based mainly on a cladistic analysis of morphological variation in the muscles of the hind limb. The order has traditionally included the families Bucconidae (puffbirds), Galbulidae (jacamars), Capitonidae (barbets), Ramphastidae (toucans), Indicatoridae (honeyguides), and Picidae (woodpeckers and allies). We will address two questions regarding the relationships of the order: is it monophyletic, and what are the relationships among the various families and genera? By "relationship" we mean genealogy; two taxa are considered more closely related to each other than either is to a third if they share a more recent common ancestor than either shares with the third. This definition is independent of any concept of overall general similarity and is determined by the presence of shared derived characters (synapomorphies).

Sibley and Ahlquist (1972: 232–238) present a thorough literature review of the history of piciform classification; rather than repeat this, we will offer only a brief review of major studies since about the turn of the century, which will suffice to establish the ideas and questions that our findings will test. Beddard's Pici (Beddard 1898: 183–196) included the Capitonidae, Ramphastidae, Bucconidae, and Picidae. Beddard considered the honeyguides a subfamily of the Capitonidae and placed the Galbulidae with the Coraciae (p. 213). Ridgway (1911: 297) defined an order Coraciiformes, comprising the modern orders Apodiformes, Trogoniformes, Piciformes, Coraciiformes, Coliiformes, Camprimulgiformes, and Strigiformes. Later (1914: 1–2), he defined a suborder Picariae (called "Zygodactylae" in his 1911 volume), which

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included the superfamilies Pici, Capitones, Ramphastides, and Galbulae. The Pici contained the woodpeckers and wrynecks, the Capitones included the barbets and honeyguides, the Ramphastides the toucans, and the Galbulae included the jacamars and puffbirds. Ripley, in a study of barbets (1945: 543), placed the Galbulidae and Bucconidae in the superfamily Galbuloidea, with the Bucconidae containing the Bucconinae, Capitoninae, and Indicatorinae. Lowe (1946: 113) proposed a classification in which the Passeriformes included suborders Passeres and Pici, the latter containing the Picidae, Indicatoridae, Capitonidae, and Ramphastidae. The Bucconidae and Galbulidae were not mentioned.

Currently accepted ideas of the Piciformes follow Peters (1948), who defined an order that includes the suborders Galbulae and Pici. The Galbulae contains the superfamilies Galbuloidea, Capitonoidea, and Ramphastoidea. The Galbuloidea contains the families Galbulidae and Bucconidae; the Capitonoidea contains the Capitonidae and Indicatoridae, the Ramphastoidea only the Ramphastidae. The suborder Pici includes the Picidae, with subfamilies Jynginae (wrynecks), Picumninae (piculets), and Picinae (woodpeckers). Wetmore (1960) followed this arrangement down to the level of family.

The first problem to be considered is whether the Piciformes is a monophyletic group. This is important for several reasons. First, it has been questioned by some authors. Sibley and Ahlquist (1972: 239) suggest that the Galbulidae (and perhaps the Bucconidae) may not be piciform but may be closely allied to the Alcedinidae (Coraciiformes). Second, before we can analyze the pattern of radiation within the Piciformes, we must determine that it is possible for such a pattern to exist. It is not sufficient to accept monophyly as given simply because the several families are currently classified together in a single order. Third, analysis of the relationships within the order involves techniques in which comparisons are made of character states within the order and their counterparts in nonpiciform birds. The logical validity of this method requires the prior and independent demonstration that the order is monophyletic.

The general purposes of this study are to test the hypothesis of piciform monophyly, to reconstruct the phylogenetic history of its subgroups, and to revise the higher-level classification of the group based on the foregoing analyses.

This study originated as a Ph.D. dissertation written by Swierczewski (1977) under the direction of Raikow. Subsequent commitments made it impossible for Swierczewski to prepare the work for publication. Accordingly, it was agreed that Raikow would condense and revise the manuscript into a shorter article emphasizing the phylogenetic and taxonomic aspects of the study.

MATERIALS AND METHODS

The hind limb muscles of 44 species in 30 genera were dissected with the aid of a dissection stereomicroscope and an iodine muscle stain (Bock and Shear 1972). The species studied are listed below, as classified by Morony et al. (1975). The data resulting from this study include a detailed description of the structure of each of 38 muscles in a reference species, *Semnornis ramphastinus* (Capitonidae), a comparison of similarities and differences of the homologous muscle in the other species studied, and a discussion of variations in nonpiciform birds used in identifying the primitive and derived character states. Numerous drawings were made with a camera lucida attached to the microscope in order to illustrate the musculature and its variations. This descriptive material, including the drawings, is too lengthy to publish here, but it is on record for those specialists in anatomy who may require it (Swierczewski 1977). Myological nomenclature conforms to the Nomina Anatomica Avium (Baumel et al. 1979). For the purposes of the present paper, the only part of the anatomical data to be analyzed will be the

characters used in the construction of the cladogram. Some of these variations are structurally simple and need only be listed, while others are sufficiently complex to require discussion.

For most species only one specimen was dissected, but for several more than one were used in order to assess individual variation. Such variation was rare and minor. The following species were dissected (the number in parentheses is the number dissected if more than one): Galbulidae: *Jacamaralcyon tridactyla, Galbula galbula, G. ruficauda* (3), *Jacamerops aurea*; Bucconidae: *Notharchus macrorhynchos, N. pectoralis, Nystalus maculatus, Malacoptila fusca, M. panamensis, Nonnula frontalis* (2), *Chelidoptera tenebrosa*; Capitonidae: *Capito maculicoronatus, C. niger* (2), *Semnornis ramphastinus, Megalaima zeylanica, Pogoniulus bilineatus, Tricholaema lacrymosum, T. diadematum, Lybius torquatus* (2), *L.* (species?), *Trachyphonus darnaudii*; Indicatoridae: *Indicator exilis* (2), *I. indicator*; Ramphastidae: *Aulacorhynchus prasinus* (2), *Pteroglossus torquatus* (3); *Ramphastos sulfuratus* (3); Picidae: *Jynx torquilla* (2), *Nesoctites micromegas, Picumnus temminckii, P. cirrhatus, Colaptes auratus* (3), *Picus vittatus, Dryocopus javensis, D. pileatus, D. lineatus, Melanerpes (Melanerpes) erythrocephalus* (2), *M. (Centurus) carolinus* (2), *M. (Centurus) aurifrons* (2), *Sphyrapicus varius* (4), *Picoides (Dendrocopos) albolarvatus, P. (Dendrocopos) pubescens, P. (Picoides) arcticus* (2), *Chrysocolaptes lucidus, Campephilus magellanicus. Centurus* and *Dendrocopos*, now lumped into *Melanerpes* and *Picoides* respectively, were treated as genera during the study.

The construction of the cladogram was carried out by the usual methods of cladistic analysis. The key procedure is the determination of which variations are primitive and which are derived. This was done by methods usually called outgroup and ingroup analysis. It must first be determined that the group under study is monophyletic. If this is done, then comparisons may be validly pursued between character variations in the Piciforms and those in other groups. Information on the muscular anatomy of various nonpiciform birds was taken from the reviews given by Hudson (1937) and George and Berger (1966) and from various studies underway in our laboratory. In a muscle that shows variation, the primitive state within the Piciformes is considered to be that which is also found in nonpiciform birds. The derived state is that variant restricted to some piciforms and/or that which occurs in a restricted group of species associated with some specialization also regarded as derived. See Hecht and Edwards (1977) and Gaffney (1979) for reviews of cladistic methodology and literature.

PHYLOGENY OF THE PICIFORMES

A cladogram representing our hypothesis of the phylogenetic relationships in the Piciformes is given in Fig. 1; the following discussion is keyed to that figure. In Fig. 1 clades (monophyletic groups) are identified by letters. The basic taxa shown (terminal taxa in the cladogram) are the genera of the species dissected. Although the validity of these taxa is accepted as given for the purposes of this study, corroborating derived states for many of them were discovered and are included in the results (Table 3). The data used in constructing the cladogram are given in Tables 1, 2, and 3. In Table 1 the characters are listed with their primitive and derived states, the latter being the basis for the cladogram. Each character is given a number, and all clades and basic taxa exhibiting the derived state are listed. This reveals how often and in what taxa various characters are believed to have undergone multiple evolution to the derived state. In Table 2 the clades are listed in alphabetical order, and the numbers (from Table 1) of the derived characters that corroborate the group are listed for each. This table thus serves to identify the characters upon which each group in Fig. 1 is based, while the number of characters at each node is also readily apparent. Table 3 similarly lists the characters corroborating basic taxa.

MONOPHYLY OF THE PICIFORMES

The basic argument for monophyly of the Piciformes (Clade A) is the presence of a derived type of foot structure specialized for perching (Fig. 2). The toe arrangement is zygodactyl (modified to ectropodactyl in woodpeckers, according to Bock and
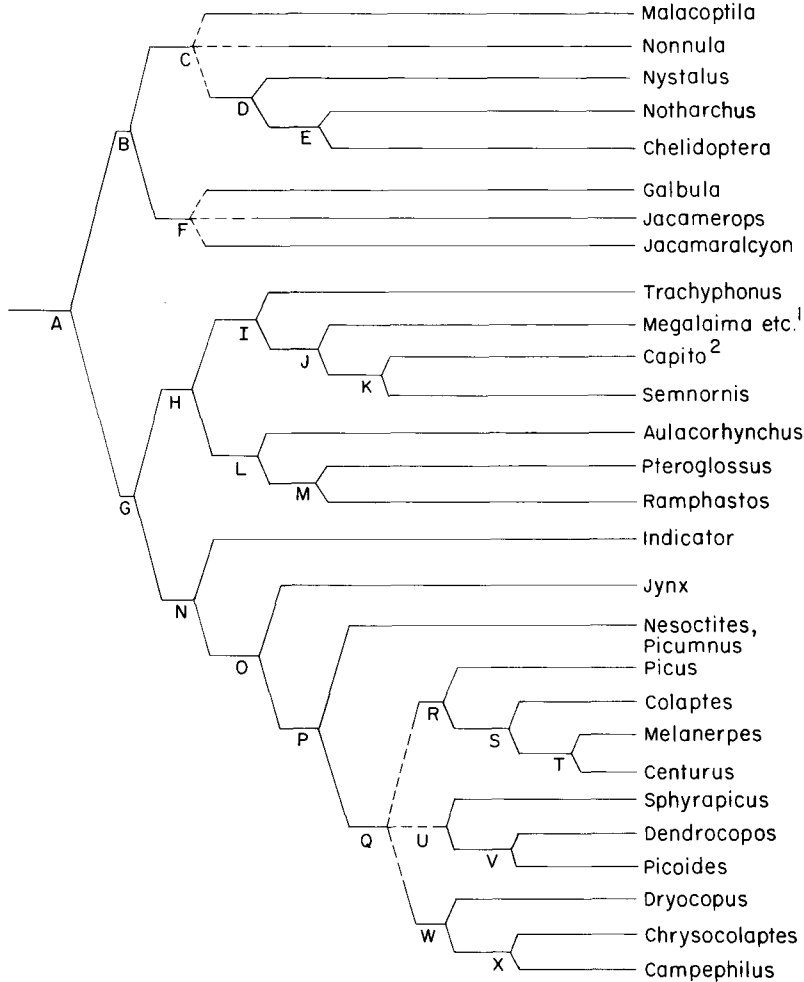
Fig. 1. A cladogram hypothesizing phylogenetic relationships in the Piciformes. Clades are designated by letters. Derived characters corroborating clades and characterizing basic (terminal) taxa are given in Tables 1, 2, and 3. Footnote 1: *Megalaima* = *Megalaima, Pogoniulus, Tricholaema, Lybius,* and *Capito niger.* Footnote 2: *Capito* = *Capito maculicoronatus.*

Miller 1959). This derived state in birds evolved from the ancestral anisodactyl arrangement (Bock and Miller 1959) but occurs in Cuculidae and Psittacidae as well as in Piciformes. The muscular component of the foot mechanism is quite different in those groups, however, which supports the contention (Bock and Miller 1959: 30) that those groups became zygodactyl independently. The muscular arrangement in piciforms involves the deep plantar tendons of two large shank muscles and consti-tutes the Type 6 arrangement of Gadow, based on Garrod (1875: 346). In this arrangement the tendon of M. flexor hallucis longus supplies digits I, II, and IV, while that of M. flexor digitorum longus supplies only digit III. A vinculum connects these tendons as they pass down the plantar surface of the tarsometatarsus. All species studied had this arrangement. In the typical avian condition flexor hallucis longus supplies only digit I, while flexor digitorum longus supplies digits II, III, and

TABLE 1. Characters used in phylogenetic analysis.

Character	Primitive state	Derived state	Groups having derived state
1	Iliotibialis cranialis origin by one head	By two heads	Clade G
2	Iliotibialis cranialis origin restricted	Origin extended along cranioventral border of ilium	Clade V Clade X
3	Iliotibialis cranialis insertion single	Insertion double	*Chrysocolaptes*
4	Iliotibialis cranialis insertion on femorotibialis internus lacking	Present	Clade V *Chrysocolaptes*
5	Iliotibialis lateralis, postacetabular part entire	Reduced	Clade E
6	Iliotibialis lateralis, all parts entire	All parts reduced	*Sphyrapicus*
7	Iliotibialis lateralis, acetabular and postacetabular parts present	Absent	Clade F *Nonnula* *Chelidoptera*
8	Femorotibialis externus pars distalis present	Absent	Clade H[a] Clade P *Indicator*
9	Femorotibialis internus with two bellies	One belly	Clade O
10	Iliofibularis origin from dorsal iliac and dorsolateral iliac crests	From dorsolateral iliac crest only	Clade S *Chrysocolaptes*
11	Flexor cruris lateralis pars accessoria present	Absent	Clade U *Jacamerops*
12	Flexor cruris lateralis and flexor cruris medialis tendons of insertion connected	Separate	Clade R *Jacamerops*
13	Caudofemoralis tendon of insertion short and wide	Long and narrow	*Ramphastos*
14	Flexor cruris medialis origin from ischium	From ischium and pubis	Clade B
15	Pubo-ischio-femoralis bellies separate	Fused distally	Clade B *Indicator*
16	Pubo-ischio-femoralis bellies separate	Fused entirely	Clade Q[b]
17	Obturatorius lateralis pars dorsalis present	Absent	Clade N
18	Obturatorius medialis oval	Triangular	Clade P[c]
19	Obturatorius medialis triangular	Secondarily oval	Clade T
20	Iliofemoralis internus present	Absent	Clade K *Jacamaralcyon* *Aulacorhynchus*
21	Extensor digitorum longus tendon first bifuration distal	Proximal	Clade G
22	Extensor digitorum longus tendinous slip to digit IV absent	Present	Clade H
23	Peroneus longus present	Absent	Clade F *Chelidoptera*
24	Peroneus longus long branch present	Absent	Clade N
25	Peroneus brevis tibiotarsal ligament present	Absent	Clade D Clade F *Indicator*

TABLE 1.   Continued.

Character	Primitive state	Derived state	Groups having derived state
26	Flexor perforatus digiti II tendon perforated by FPPD2 and FHL tendons	Not perforated	Clade F Clade M
27	Flexor perforatus digiti II present	Absent	Clade J *Aulacorhynchus*
28	Flexor perforans et perforatus digiti II tendon perforated by FHL tendon	Not perforated	Clade G[d]
29	Flexor perforatus digiti III with 2 tendons of origin	One tendon of origin	Clade B
30	Flexor perforatus digiti III heads fused	Separate	Clade O
31	Flexor perforatus digiti IV with 2 heads of origin	One head of origin	Clade B
32	Plantaris belly short	Long	Clade B
33	Popliteus present	Absent	Clade C Clade G
34	Flexor perforans et perforatus digiti III cranial head present	Absent	Clade W *Picoides*
35	Flexor digitorum longus supplies digits II, III and IV; flexor hallucis longus digit I	Flexor digitorum longus supplies digit III; flexor hallucis longus digits I, II, IV	Clade A
36	Flexor hallucis longus arises by one or two heads	Three heads	Clade A
37	Flexor hallucis brevis present	Absent	*Jacamaralcyon* *Picoides*
38	Flexor hallucis brevis tendon of insertion single	Bifurcate	Clade C
39	Adductor digiti II present	Absent	Clade G
40	Extensor proprius digiti III belly larger	Smaller	*Chrysocolaptes*
41	Extensor brevis digiti IV present	Absent	Clade G
42	Abductor digiti IV retinaculum on trochlea IV absent	Present	Clade B
43	Extensor hallucis longus present	Absent	*Jacamaralcyon* *Picoides*
44	Foot anisodactyl	Zygodactyl	Clade A
45	Chin and rictal bristles not prominent	Prominent	Clade I
46	Cerophagy absent	Present	*Indicator*
47	Nest parasitism absent	Present	*Indicator*
48	Rectrices soft	Stiffened	Clade Q
49	Hallux present	Absent	*Jacamaralcyon* *Picoides*
50	Bill smaller, simpler	Bill enlarged, serrate	Clade L

[a] Except *Aulacorhynchus*.
[b] Except *Dendrocopos*.
[c] Except *Melanerpes* and *Centurus*.
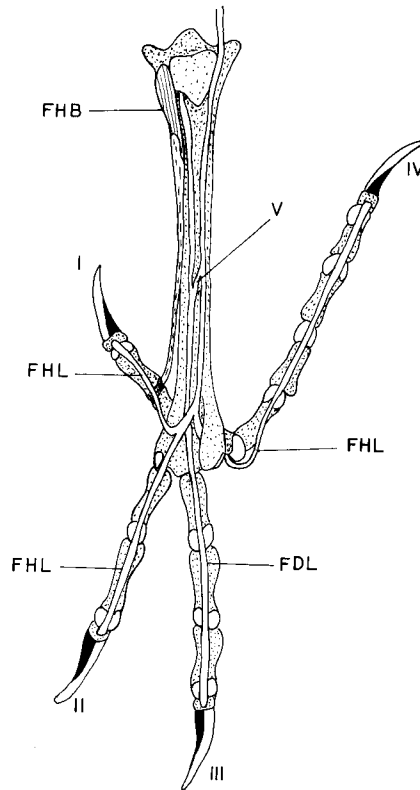[d] Except *Trachyphonus*.

Fig. 2. Plantar view of the tarsometatarsus and digits of the right hind limb of *Semnornis ramphastinus* (Capitonidae) illustrating features characteristic of the Piciformes. The foot is zygodactyl. The bellies of M. flexor hallucis longus and M. flexor digitorum longus are situated in the shank but send their tendons of insertion into the foot as shown. The tendons of the two muscles are connected by a vinculum (V). Flexor hallucis longus supplies digits I, II, and IV (FHL), while flexor digitorum longus supplies only digit III (FDL). FHB is M. flexor hallucis brevis.

IV. The flexor tendons of digits II and IV have thus been transferred from flexor digitorum longus to flexor hallucis longus.

Thus, the order Piciformes is clustered by a complex derived structural modification of the foot involving the combination of zygodactyly and the Gadow Type 6 tendon arrangement. Sibley and Ahlquist (1972: 20, 239) suggest that the Galbulidae and Bucconidae may be more closely related to the kingfishers (Alcedinidae) of the order Coraciiformes than to the order Piciformes, which is an argument against monophyly of the latter group. They point out that kingfishers have a variety of tendon arrangements and suggest that the Type 6 arrangement could be derived from some kingfisher arrangements. They also report that, in the electrophoretic behavior of the egg-white proteins, the jacamar *Galbula* and the puffbird *Chelidoptera* are more like kingfishers than woodpeckers.

We have two hypotheses to consider. The first is that the order Piciformes is monophyletic; the second is that it is not so, one or two families being perhaps independently derived from the Alcedinidae. We prefer the hypothesis of monophyly for several reasons. First, a study of alcedinid limb muscles carried out in our

laboratory fails to support the Sibley and Ahlquist hypothesis (Maurer 1977, Maurer and Raikow in prep.). Second, the traditional foot-structure characteristics, long regarded as phenetic similarities, are now recognized as constituting a structurally complex synapomorphy. Third, the biochemical data contain no information about the direction of evolutionary change in molecular structure, so that the similarities shown by Sibley and Ahlquist could well be symplesiomorphic or homoplasious and thus poor indicators of relationship. Fourth, the suggested independent evolution of the Type 6 arrangement is an *ad hoc* hypothesis with no supporting evidence; the hypothesis of piciform monophyly is more parsimonious. Fifth, Sibley and Ahlquist's hypothesis of the independent origin of the Type 6 arrangement fails to account for the coincidental occurrence of zygodactyly; it is the combination of these two features that characterizes the Piciformes. Sixth, the present study has uncovered a new derived character in the hind limb musculature that supports the hypothesis of monophyly: M. flexor hallucis longus arises by 3 heads, rather than the 1 or 2 heads found in many other birds (character 36, Table 1). Three heads also occur in most Passerines, but in that case the iliofibularis tendon passes medial to the lateral head, while in Piciformes it passes lateral to the lateral head. The condition in the two orders is therefore probably not homologous. Seventh, Simpson and Cracraft (1981) report that the tarsometatarsus shows a derived condition in the Piciformes, in which the trochlea for digit IV is enlarged, turned far posteriorly, and develops a sehnen-halter. For these reasons we conclude that the order Piciformes is monophyletic.

PHYLOGENETIC RELATIONSHIPS

Clade B.—This includes the families Bucconidae and Galbulidae. It is clustered by six myological synapomorphies (14, 15, 29, 31, 32, 42; Table 1) and is therefore strongly corroborated on the basis of hind limb morphology, being set distinctly apart from the rest of the order. This corresponds well with the opinions of previous workers (see Sibley and Ahlquist 1972) and to the separation of the two families as a superfamily, Galbuloidea, by Peters (1948) and Wetmore (1960).

Clade C.—The family Bucconidae is defined by two derived states in the hind limb musculature (characters 33 and 38). Three lineages arise from this node; the dashed lines in Fig. 1 mean that we cannot determine whether this represents the simultaneous origin of three groups or an unresolved pair of dichotomous branchings. *Malacoptila* is the most primitive genus among those studied and has no distinguishing derived states in our analysis. *Nonnula* has a derived condition of M. iliotibialis lateralis (7).

Clades D and E.—Clade D is defined by one character (25), and *Nystalus* is not distinguished further. Clade E is defined by character 5: in M. iliotibialis lateralis *Notharchus* has a reduced postacetabular portion; this is entirely lost (7) in *Cheli-doptera*, which is further distinguished from *Notharchus* by the loss of M. peroneus longus (23). The sequence of genera used by Peters (1948), followed by Morony et al. (1975), does not reflect the relationships here described and should be reconsidered.

Clade F.—The family Galbulidae is clustered by derived characters 7, 23, 25, and 26. We found no synapomorphies clustering any two of the three genera studied, hence the trichotomy shown in Fig. 1. A few differences were noted, however. In its hind limb musculature, *Galbula* is the most primitive genus studied. *Jacamerops* has derived states 11 and 12. *Jacamaralcyon* has lost the hallux (49) and several

muscles (20, 37, 43). It obviously belongs after rather than before *Galbula* in the generic sequence within the family, contrary to Peters (1948).

Clade G.—This includes the families Capitonidae, Ramphastidae, Indicatoridae, and Picidae and is clustered by several synapomorphies (1, 21, 28, 33, 39, 41), which makes it a strongly corroborated monophyletic group. Clade G is the sister group of the bucconid/galbulid cluster, Clade B.

Clades H, I, J, and K.—The families Capitonidae and Ramphastidae are linked by synapomorphies 8 and 22. The Capitonidae (Clade I) possess a specialization in their prominent chin and rictal bristles (45) but have no additional hind limb muscular novelties. *Trachyphonus* is the most primitive genus studied. Clade J includes several genera clustered by the loss of M. flexor perforatus digiti II (27), while Clade K is further distinguished by the loss of an additional muscle, M. iliofemoralis internus (20). Again, the generic sequence in Peters (1948), which *ends* with *Trachyphonus*, needs revision.

Clades L and M.—The family Ramphastidae is easily defined by the characteristically large serrate bill (50) but not by any hind limb muscular synapomorphies. *Aulacorhynchus* lacks two muscles (20, 27). Clade M is defined by character 26, nonperforation of the flexor perforatus digiti II tendon. The genus *Ramphastos* is further marked by a very long and narrow caudofemoralis tendon (13).

Clade N.—The Indicatoridae and Picidae are clustered by two myological synapomorphies. In most birds the shank muscle peroneus longus forms a tendon that bifurcates at the distal end of the shank; the short branch inserts on the tibial cartilage, while the long branch crosses the intertarsal joint and merges with the tendon of M. flexor perforatus digiti III (George and Berger 1966: 429). In the two families clustered here, the long branch is lost, an unusual derived state (24). Also lost is M. obturatorius lateralis pars dorsalis (17).

The family Indicatoridae is set apart from the Picidae by cerophagy (46) and nest parasitism (47), two derived behavioral characters. Several myological synapomorphies also characterize the honeyguides (8, 15, 25).

Clade O.—This is the family Picidae. It is clustered by complete separation of the bellies of M. flexor perforatus digiti III (30) and by the fusion of M. femorotibialis internus into a single mass (9). *Jynx* appears to be the most primitive member of the family and is not distinguished by any hind limb muscular synapomorphies. Bock and Miller (1959: 9) assume that the perching foot of *Jynx* represents the ancestral woodpecker foot, and modifications from this foot type in the Picidae were adapted for climbing specializations.

Clade P.—The Picumninae and Picinae of Peters (1948) are characterized by the absence of the distal head of M. femorotibialis externus (8). Except for *Melanerpes* and *Centurus* all members of this clade are further characterized by having a triangular obturatorius medialis (18). The Picumninae, like the Jynginae, do not climb vertical tree trunks, but they are more arboreal than the latter in confining their hunting for food to tree branches.

Clades Q, R, S, and T.—The Picinae (Peters 1948) is the most highly derived subfamily of the Picidae and is characterized by the stiffened rectrices (48) used as a brace in tree-climbing. Additionally, except in *Dendrocopos*, the two bellies of M. pubo-ischio-femoralis are completely fused together (16).

Clade Q gives rise to three lineages. This probably represents a pair of dichotomous branchings that our data cannot resolve. Clade R is characterized by the

nonconfluency of the tendons of Mm. flexor cruris lateralis and flexor cruris medialis (12). Clade S is set apart from *Picus* by the modified origin of M. iliofibularis (10). *Melanerpes* and *Centurus* (Clade T) are set apart from *Colaptes* by an oval-shaped obturatorius medialis. This is a primitive character, most woodpeckers and piculets (Clade P) having a derived triangular form (18). As *Melanerpes* and *Centurus* are undoubtedly woodpeckers, this must be a reversional apomorphy or secondarily primitive condition. Peters (1948) and later authors have synonymized *Centurus* with *Melanerpes,* a move supported by the similarities in their hind limb muscu- lature. None of the other melanerpine genera suppressed by Morony et al. (1975: 164) was examined.

   Clades U and V.—Burt (1930) studied the osteology, myology, and food of wood- peckers and concluded (p. 522) that there are two main lines of descent in the group. One line, less specialized for arboreal life, contains *Centurus, Melanerpes, Colaptes, Dryocopus,* and *Asyndesmus.* Except for *Dryocopus* this is essentially Clade R. The other line contains *Sphyrapicus, Dendrocopos,* and *Picoides.* This line is identical to the second major lineage in our cladogram, Clade U, which is characterized by the loss of M. flexor cruris lateralis pars accessoria (11). According to Garrod (1878: 630), this character could be used to divide the Picidae into two subfamilies. The genera in Clade U also possess a true scansorial foot, in which the fourth toe can be rotated to a lateral position for climbing. *Sphyrapicus* is set apart from Clade V by having an iliotibialis lateralis in which all three parts are reduced (6). It is the only form in this study having this type. Burt (1929) studied the pterylosis of certain North American woodpeckers and concluded (p. 441) that this genus is the most aberrant in feathering patterns. Goodge (1972: 83) and Short and Morony (1970: 314) concluded that *Sphyrapicus* is more closely related to the melanerpine wood- peckers. Burt (1930: 522), however, concluded that *Sphyrapicus* is a derivative of *Dendrocopos,* as did Howell (1952: 280).

   Clade V is defined by the extended connections of M. iliotibialis cranialis (2, 4). *Picoides* is set apart from *Dendrocopos* by modification of M. flexor perforans et perforatus digiti III (34) and by loss of the hallux and its short muscles (37, 43, 49). Short (1971) merged *Dendrocopos* with *Picoides* and was followed by the A.O.U. Committee on Classification and Nomenclature (1976). Short believed that the loss of the hallux and associated differences in the hind limb anatomy were not sufficient to maintain two genera.

   Clades W and X.—The third radiation includes *Dryocopos, Chrysocolaptes,* and *Campephilus* and is defined by a simplified flexor muscle (34). The ivory-billed woodpeckers and the Old World *Chrysocolaptes* (Clade X) are clustered by the extended origin of M. iliotibialis cranialis (2). The foot of these woodpeckers is also much different from that of *Dryocopus* in that digits I and IV may be rotated to the outer side of the foot until all four toes point forward, a pamprodactyl arrangement (Bock and Miller 1959). *Chrysocolaptes* and *Campephilus* are set apart from each other by several myological characters (Table 3).

   Bock and Miller (1959: 4) proposed a hypothetical morphological sequence relative to the varying degrees of specialization of the woodpecker foot for climbing, begin- ning with the least specialized, as found in *Jynx,* to the most specialized, as found in *Campephilus.* The morphocline begins with *Jynx,* followed by *Picumnus,* then by *Colaptes,* after which a dichotomy appears based on differences in the hallux. The short-hallux line is traced from *Colaptes* through *Dendrocopos,* which has a

small, functionless hallux, to *Picoides,* which lacks the hallux. The long-hallux line, again beginning from *Colaptes,* is traced through *Dryocopus* to *Campephilus,* in which the lengthened hallux is retained as a functional part of the foot. Bock and Miller state that this morphocline is not to be interpreted as an evolutionary sequence. Comparing it to the cladogram of the Picidae constructed in the present study, however, a general similarity is evident.

DISCUSSION OF THE PHYLOGENETIC HYPOTHESIS

Character conflicts.—Different derived states may suggest alternative clustering arrangements. These situations are generally attributed to the separate origin of derived states in different lineages through convergent or parallel evolution or through evolutionary reversal. The problem is how to distinguish between single and multiple origins of derived states. Sometimes they are easily recognized, but in other cases there is no satisfactory solution. The convention is to adopt a parsimonious approach and to construct the cladogram so as to minimize the number of ambiguous cases, and this is what we have done. A number of cases remain where the presence of the derived state of a character in more than one taxon betrays the assumption of multiple origin; these are explicitly displayed in the last column of Table 1.

Some cases are easily explained. Most Piciforms have four toes, but *Jacamaralcyon* of the Galbulidae and *Picoides* of the Picidae have lost the hallux, a derived state (49). The number of characters corroborating the distantly separated positions of these two genera make it certain that this is a case of independent loss. Likewise, these taxa share derived states 37 and 43. These characters are the loss of two small muscles that insert on the missing hallux, and their loss is undoubtedly correlated with the loss of the digit itself.

In most other cases the independent occurrence of derived states is less obvious, but many of them involve taxa that are widely separated by numerous other characters so that the choice appears quite reasonable. An example would be character 26, which occurs in Clade F (Galbulidae) and Clade M (two out of three genera of toucans).

Some troublesome cases remain for which we have no clearcut solutions. These are especially common among the woodpeckers, such as characters 2, 4, 10, and 34. Here we have a large group of genera in an extensive radiation, but with a common adaptive specialization. In such a case frequent parallelism may be expected. Our arrangement is the best available in terms of present understanding, but data from other systems are probably necessary to resolve some of these problems.

Levels of confidence.—The phylogeny represented in Fig. 1 is a nested set of 24 clades, each of which is an individual hypothesis of monophyly. Although in theory one synapomorphy is sufficient to define a clade, in practice the level of confidence in a hypothesis depends on the nature of the supporting evidence. One aspect is the number of synapomorphies corroborating a clade; other things being equal, a larger number of derived states is more convincing than a smaller number. The number of synapomorphies corroborating the clades in our hypothesis is shown in Table 2 (Table 3 similarly lists derived states for many basic taxa). Clades A, B, G, and F are strongly corroborated on this basis. The first three are especially satisfying, as they represent major branches of the cladogram.

Another aspect is the nature of the characters involved. Some kinds of characters

TABLE 2. Derived states corroborating clades.

Clades	Derived states	Clades	Derived states
A	35, 36, 44	M	26
B	14, 15, 29, 31, 32, 42	N	17, 24
C	33, 38	O	9, 30
D	25	P	8, 18
E	5	Q	16, 48
F	7, 23, 25, 26	R	12
G	1, 21, 28, 33, 39, 41	S	10
H	8, 22	T	19
I	45	U	11
J	27	V	2, 4
K	20	W	34
L	50	X	2

are more convincing as evidence of common ancestry than are others. A rough scale would range from structurally complex and specialized conditions at one extreme to simple modifications or losses at the other. The first are better indicators of relationship, because they intuitively seem less likely to occur independently in different lineages, while the latter are more easily subject to parallel occurrence. Hecht and Edwards (1977) discuss this matter in detail. On this basis, it is apparent that the characters used in our analysis (Table 1) vary in quality. Many are simplification or loss characters, but others are of a more trenchant nature, particularly some of the characters defining Clade A and early branchings. In any event, the data presented in Tables 1, 2, and 3 make it easy for the reader to assess the validity of each component of the overall hypothesis.

Comparison with previous studies.—Several comparisons of our results with the ideas of previous workers have been made above, but a few generalizations may be offered here. Four of the six traditionally recognized families (Bucconidae, Galbulidae, Indicatoridae, and Picidae) have also emerged in our study as clades defined by limb muscle characters. Two families (Capitonidae, Ramphastidae) did not, but the clade (H) composed of these families is so supported. Likewise, the separation of the Bucconidae and Galbulidae as close relatives (Clade B) distinctly separated from the rest of the assemblage is strongly supported by our data. Within the Picidae, the position of *Jynx* as the most primitive form, of the piculets as more advanced, and of the true woodpeckers as the most highly derived group also concur well with the ideas of previous workers. Finally, we believe that the hypothesis of piciform monophyly has been strongly corroborated by the present study.

TABLE 3. Derived states corroborating basic taxa.

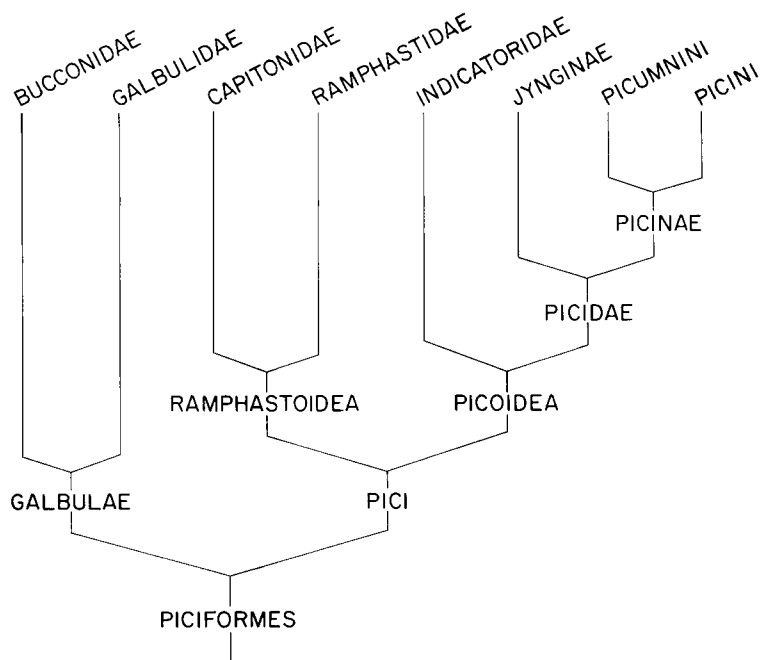| Basic taxa	Derived states
Nonnula	7
Chelidoptera	7, 23
Jacamerops	11, 12
Jacamaralcyon	20, 37, 43, 49
Aulacorhynchus	20, 27
Ramphastos	13
Indicator	8, 15, 25, 46, 47
Sphyrapicus	6
Picoides	34, 37, 43, 49
Chrysocolaptes	40
Campephilus	3, 4, 10

Fig. 3. Cladogram of the Piciformes similar to that in Fig. 1 but showing only the major branches so as to illustrate the derivation of the taxa given in the classification in the text.

CLASSIFICATION

The new higher level classification of the Order Piciformes that follows is based on the phylogenetic relationships hypothesized in Fig. 1.

> Order Piciformes
>   Suborder Galbulae
>   Family Bucconidae
>   Family Galbulidae
>   Surborder Pici
>   Superfamily Ramphastoidea
>   Family Capitonidae
>   Family Ramphastidae
>   Superfamily Picoidea
>   Family Indicatoridae
>   Family Picidae
>   Subfamily Jynginae
>   Subfamily Picinae
>   Tribe Picumnini
>   Tribe Picini

Two rules were followed in making this classification. First, only clades are recognized as taxa; no nonmonophyletic groups are named. Second, sister groups are classified at the same categorical level. Although the classification employs only monophyletic taxa, not all clades are formally named, as this would produce an

unnecessarily complicated classification. The decision as to which clades should be named is somewhat arbitrary but was done so as to retain assemblages familiar from previous classifications so long as they are monophyletic. Some groups appear at different levels than in previous classifications. For example, Peters (1948) made subfamilies of the wrynecks (Jynginae), piculets (Picumninae), and woodpeckers (Picinae). In our classification the wrynecks again constitute the subfamily Jynginae, but as they constitute the sister group of the piculets *and* woodpeckers, the latter forms together must be given subfamily status (Picinae) and are treated individually as tribes (Picumnini and Picini). Although this departs from Peters's usage, we feel that it is justified for the sake of consistency in taxonomic procedure. The taxa and their positions in a simplified cladogram are shown in Fig. 3.

LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1976. Thirty-third supplement to the American Ornithologists' Union check-list of North American birds. Auk 93: 875–879.

BAUMEL, J. J., A. S. KING, A. M. LUCAS, J. E. BREAZILE, & H. E. EVANS (Eds.). 1979. Nomina anatomica avium. London, Academic Press.

BEDDARD, F. E. 1898. The structure and classification of birds. London, Longmans, Green, and Company.

BOCK, W. J., & W. D. MILLER. 1959. The scansorial foot of the woodpeckers, with comments on the evolution of perching and climbing feet in birds. Amer. Mus. Novitates, No. 1931.

———, & R. SHEAR. 1972. A staining method for gross dissection of vertebrate muscle. Anat. Anz. 130: 222–227.

BURT, W. H. 1929. Pterylography of certain North American woodpeckers. Univ. Calif. Publ. Zool. 30: 427–442.

———. 1930. Adaptive modifications in the woodpeckers. Univ. Calif. Publ. Zool. 32: 455–524.

GAFFNEY, E. S. 1979. An introduction to the logic of phylogeny reconstruction. Pp. 79–111 *in* Phylogenetic analysis and paleontology (J. Cracraft and N. Eldredge, Eds.). New York, Columbia Univ. Press.

GARROD, A. H. 1875. On the disposition of the deep plantar tendons in different birds. Proc. Zool. Soc. London 1875: 339–348.

———. 1878. Notes on the anatomy of *Indicator major.* Proc. Zool. Soc. London, 1878 (1879): 930–935.

GEORGE, J. C., & A. J. BERGER. 1966. Avian myology. New York, Academic Press.

GOODGE, W. R. 1972. Anatomical evidence for phylogenetic relationships among woodpeckers. Auk 89: 65–85.

HECHT, M. K., & J. L. EDWARDS. 1977. The methodology of phylogenetic inference above the species level. Pp. 3–51 *in* Major patterns in vertebrate evolution (M. K. Hecht, P. C. Goody, and B. M. Hecht, Eds.). New York, Plenum Press.

HOWELL, T. R. 1952. Natural history and differentiation in Yellow-bellied Sapsuckers. Condor 54: 237–282.

HUDSON, G. E. 1937. Studies on the muscles of the pelvic appendage in birds. Amer. Midl. Natur. 18:1–108.

LOWE, P. R. 1946. On the systematic position of the woodpeckers (Pici), honey-guides (*Indicator*), hoopoes and others. Ibis 88: 103–127.

MAURER, D. R. 1977. The appendicular myology and relationships of the avian order Coraciiformes. Unpublished Ph.D. dissertation, Pittsburgh, Pennsylvania, Univ. Pittsburgh.

MORONY, J. J., JR., W. J. BOCK, & J. FARRAND, JR. 1975. Reference list of the birds of the world. New York, Amer. Mus. Nat. Hist.

PETERS, J. J. 1948. Check-list of birds of the world, vol. 6. Cambridge, Harvard Univ. Press.

RIDGWAY, R. 1911. The birds of North and Middle America. Bull. U.S. Natl. Mus. 50, part 5.

———. 1914. The birds of North and Middle America. Bull. U.S. Natl. Mus. 50, part 6.

RIPLEY, S. D. 1945. The barbets. Auk 62: 542–563.

SHORT, L. L. 1971. Systematics and behavior of some North American Woodpeckers, genus *Picoides* (Aves). Bull. Amer. Mus. Nat. Hist. 141, article 1: 1–118.

———, & J. J. MORONY. 1970. A second hybrid Williamson's × Red-naped Sapsucker and an evolutionary history of sapsuckers. Condor 72: 310–315.

SIBLEY, C. G., & J. A. AHLQUIST. 1972. A comparative study of the egg-white proteins of non-passerine birds. Bull. 39, Peabody Mus. Nat. Hist., Yale Univ.

SIMPSON, S. F., & J. CRACRAFT. 1981. The phylogenetic relationships of the Piciformes (Class Aves). Auk 98: 481–494.

SWIERCZEWSKI, E. V. 1977. The hindlimb myology and phylogenetic relationships of the avian order Piciformes. Unpublished Ph.D. dissertation, Pittsburgh, Pennsylvania, Univ. Pittsburgh.

WETMORE, A. 1960. A classification for the birds of the world. Smithsonian Misc. Coll. 139(11).