Discovery of a Cretaceous Bird, Apparently Ancestral to the Orders Coraciiformes and Piciformes (Aves: Carinatae)

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ABSTRACT

Alexornis antecedens, new genus and species, is described from the Bocana Roja Formation, Upper Cretaceous (Campanian age), near El Rosario, Baja California, Mexico. The humerus, ulna, scapula, coracoid, femur, and tibiotarsus are represented. The fossil is referred to a new family, Alexornithidae, and a new order, Alexornithiformes, thought to be ancestral to the Tertiary and Recent orders Coraciiformes and Piciformes. Since *Caenagnathus collinsi* Sternberg and *C. sternbergi* Cracraft are reptiles, and *Gobipteryx minuta* Elżanowski appears to be reptilian also, *Alexornis* is the only certain land bird known from the Cretaceous.

Introduction

The major deficiency in our knowledge of the history of birds is their inadequate Mesozoic record. The only known Jurassic genus is *Archaeopteryx,* which was certainly a land bird, whether it was arboreal (Brodkorb, 1971b) or a ground-dweller (Ostrom, 1974). In the Cretaceous period we have records of about 37 species of water birds, distributed among 18 genera, 12 families, and 7 orders. Because many groups of land birds occur early in the Tertiary, they must also have been present and undergoing radiation during the Cretaceous. However, none of the hitherto known alleged birds from terrestrial Cretaceous deposits is certainly referable to the class Aves.

Three species of supposed land birds have been described from the late Cretaceous. These are: *Caenagnathus collinsi* Sternberg (1940), *Caenagnathus sternbergi* Cracraft (1971), and *Gobipteryx minuta* Elżanowski (1974). Each was described from a single specimen of jaw or skull. Although not comparable with any living or fossil bird, the describers of *Caenagnathus* and *Gobipteryx* made them the types of new families and orders of Aves.

Sternberg (1940) based *Caenagnathus collinsi* on a mandible from the Belly River Series of Alberta, and regarded it as representing a new order of birds. Wetmore (1960) transferred it to the theropod dinosaurs, near Ornithomimidae, an assignment in which Romer (1966) concurred. Cracraft (1971) returned the genus to Aves and founded a second species, *C. sternbergi,* on a scrap of a lower jaw from the same formation as *C. collinsi.* White (1973) included *Caenognathus* [sic] and Caenognathidae [sic] as a valid genus and family of coelurosaurian theropods. Dale A. Russell of the National Museum of Canada (pers. comm.) informs me that new material of *Caenagnathus,* plus specimens of related forms from Mongolia, confirms that the Caenagnathidae are theropod dinosaurs having affinities with *Oviraptor* of the Ornithomimidae, thus vindicating Wetmore.

Gobipteryx minuta was described on a small, poorly preserved, flattened skull and mandible from the Barun Goyot Formation in Mongolia. Neither the specimen, which I have seen, nor the published illustrations, are convincingly avian.

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Elżanowski (1974) placed *Gobipteryx* in the "Superorder Palaeognathae" (i.e., Ratitae), but this is certainly wrong. The specimen is quite small, and the palate is unlike that of ratites or any other bird. Better material is needed before it can be assigned confidently to either Aves or Reptilia.

With the relegation of the above forms to Reptilia or taxa incertae sedis, there are no land birds known from the 72-million-year span of the Cretaceous period. It was therefore with great interest that I agreed to study some possibly avian remains from a terrestrial deposit of Late Cretaceous age in Baja California, Mexico. The best preserved specimens so far recovered are from a small land bird—represented by elements of the pectoral girdle, wings, and legs—the subject of the present paper.

STRATIGRAPHY.—The Rosario Group is composed of three formations, each separated by an unconformity. In descending order these are the Rosario, "El Gallo," and "La Bocana Roja." According to Morris (1972) the last two formations were defined by Kilmer in his doctoral dissertation (1963).

The Rosario Formation is a marine deposit whose invertebrate fauna was assigned an early Maestrichtian or late Campanian age by Durham and Allison (1960). The nannofossils indicate that it is situated close to the Maestrichtian-Campanian boundary (Morris, 1973).

The Gallo Formation has a thickness of more than 150 m. A potassium/argon (K/Ar) date of 73 ± 2 million years is available for the middle third of the formation (Morris, 1972, 1973). This would make it of late Campanian age. It contains the remains of hadrosaurian dinosaurs (cf. *Lambeosaurus*), smaller reptiles, amphibians, mammals, and large tree trunks with well-developed root systems. This assemblage is the only extensive Late Cretaceous terrestrial vertebrate fauna from the Pacific margin of North or Middle America.

The Bocana Roja Formation contained the remains of the bird described here. The type-specimen of the theropod dinosaur *Labocania anomala* Molnar (1974) also came from this formation, along with hadrosaur ribs and numerous small vertebrate fossils, as yet unstudied. The age of the formation is Campanian or earlier.

During the Cretaceous period the arrangement of the continents was different from that of today, Mexico being in proximity to North Africa and bordering the western part of the Tethys Sea (Deitz and Holden, 1970).

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Alexornis, new genus

TYPE OF GENUS.—*Alexornis antecedens,* new species.

DIAGNOSIS.—As for the type and only known species.

ETYMOLOGY.—From Greek *aléxō* (I defend) and *órnis* (common gender, masculine selected here) bird. On the occasion of his ninetieth birthday this genus is dedicated to my friend Alexander Wetmore, who, in addition to his many other accomplishments, has done more to foster paleornithology and has described more species of fossil birds than any other author.

Alexornis antecedens, new species

FIGURE 1

HOLOTYPE.—Distal 10 mm of right humerus, LACM 33213 (Figure 1*a,b*). From LACM locality 7256, 6 miles southwest of El Rosario, Baja California del Norte, Mexico. Bocana Roja Formation, Upper Cretaceous, Campanian age. Collected by H. Garbani and J. Loewe, 16 July 1971.

PARATYPE.—Distal 10 mm of left humerus, collected in association with the holotype and cataloged with the same number.

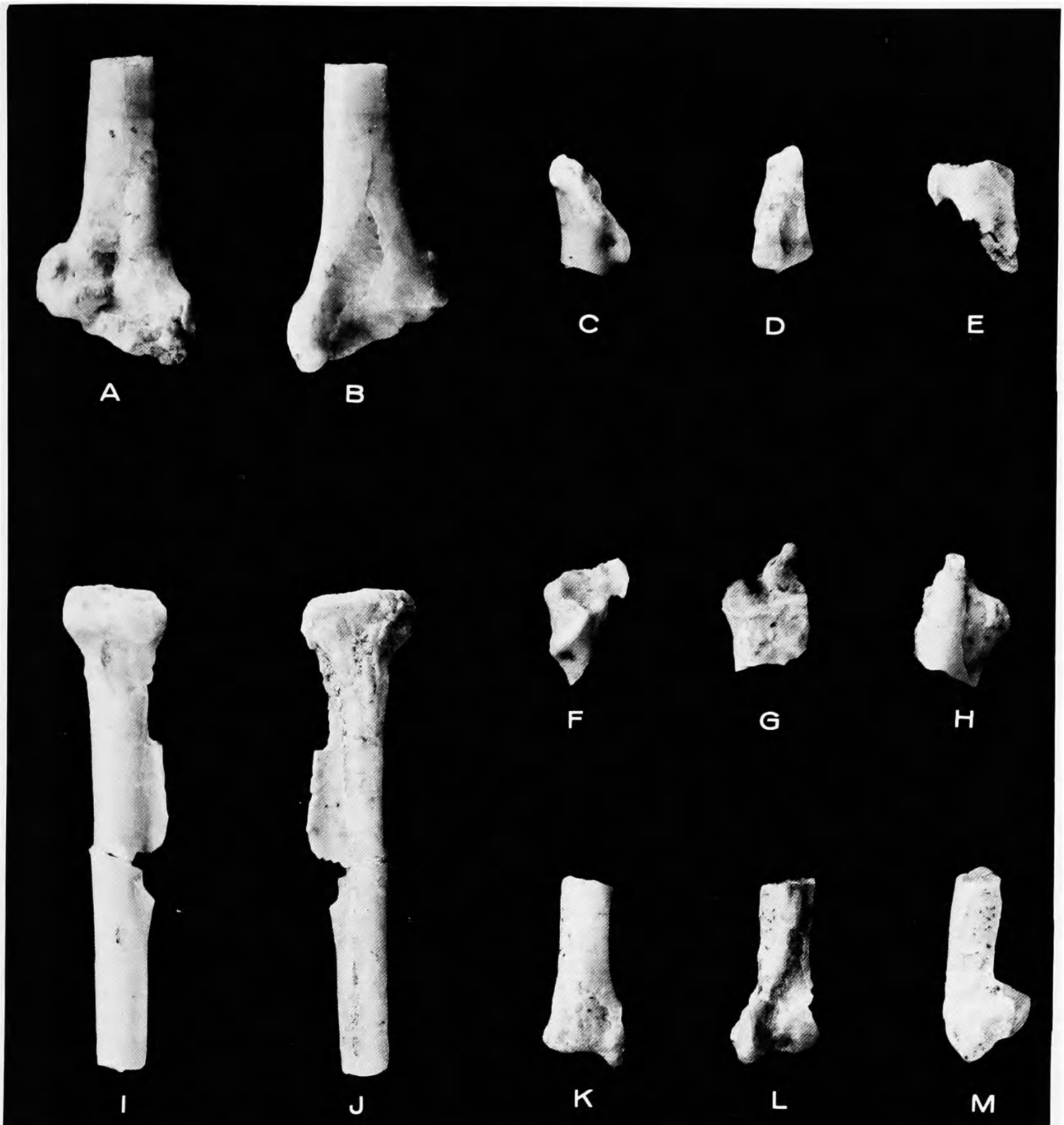

FIGURE 1.—*Alexornis antecedens,* new genus and species, Bocana Roja Formation, Campanian age, near Rosario, Baja California, Mexico (LACM 33212): *a,* holotype right humerus, palmar view; *b,* same, anconal view; *c,* left scapula, ventral view; *d,* same, dorsal view; *e,* left coracoid, anterior view; *f,* same, posterior view; *g,* right ulna, internal view; *h,* same, external view; *i,* right tibiotarsus, anterior view; *j,* same, posterior view; *k,* left femur, anterior view; *l,* same, posterior view; *m,* same, lateral view. (All × 5.)

HYPODIGM.—The holotype, paratype, and the following referred material, collected in association with the types and cataloged under the same number: proximal 4 mm of left scapula (Figure 1*c,d*), upper 4.4 mm of left coracoid (Figure 1*e,f*), proximal 3.5 mm of right ulna (Figure 1*g,h*), distal 6 mm of left femur (Figure 1*k–m*), and proximal 16.3 mm of right tibiotarsus (Figure 1*i,j*). More than 20 other fragments were also collected with the types and cataloged under the same number, but they are left unidentified at this time.

DIAGNOSIS.—Comparison of the hypodigm with the homologous skeletal elements of the known orders of birds shows that the resemblances of *Alexornis* are closest to certain members of the Piciformes and Coraciiformes. Within those two orders the piciform family Bucconidae and the coraciiform family Momotidae have the most similarity to the fossil. The fossil shares certain characters with both Bucconidae and Momotidae, some with Bucconidae alone, and some with Momotidae alone; but more of its characters are unique. In size the fossil falls between the bucconid *Malacoptila panamensis* and the motmot *Hylomanes momotula* (Table 1).

ETYMOLOGY.—Latin *antecedens,* going before in rank or time, ancestral, in reference to the supposed ancestry of this bird to the orders Piciformes and Coraciiformes.

DESCRIPTION.—Humerus: (1) Olecranal fossa deep (shallow in Bucconidae and Momotidae), and (2) wide, extending toward entepicondylar area (as in Momotidae; in Bucconidae less extended toward entepicondyle). (3) Entepicondyle produced distally, resembling Bucconidae (in Momotidae less produced; in Passeriformes much more produced). (4) External condyle bulbous as in both Bucconidae and Momotidae, but (5) oriented transversely at an angle of about 60 degrees to shaft (in Momotidae angle to shaft is about 45 degrees; in Bucconidae condyle is more upright at angle of 30 degrees to shaft). (6) Internal condyle lies inclined toward entepicondyle, resembling condition in Momotidae (in Bucconidae condyle is more transverse), (7) with a strong facet for medial cotyla of ulna, resembling both Momotidae and Bucconidae. (8) Ectepicondylar prominence large and rounded, resembling Bucconidae (less developed in Momotidae), (9) with a transverse ridge across anconal surface proximal to its base (ridge absent in Bucconidae and Momotidae).

TABLE 1.—Measurements (mm) of skeletal elements

Character	*Alexornis antecedens**	*Hylomanes momotula*	*Malacoptila panamensis*
HUMERUS			
Distal width	5.6, –	4.4	4.8
Shaft width	2.2, 2.3	1.7	2.4
Shaft depth	1.8, 1.8	1.6	1.8
Least depth through brachial depression	1.1, 1.3	1.1	1.7
SCAPULA			
Diagonal width across acromion and glenoid	4.2	3.5	4.6
Shaft width	1.7	1.6	1.5
FEMUR			
Distal width	[3.1]	3.4	3.7
Shaft width	2	1.7	2
External condyle depth	2.35	2.5	2.5
Fibular condyle depth	1.6	2.2	2.2
Internal condyle depth	2.6	2.0	2.1
External condyle height	2.5	1.5	1.6
Fibular condyle height	1.6	1.3	1.4
Internal condyle height	2	1.7	1.3
Shaft depth	1.8	1.4	1.7
TIBIOTARSUS			
Proximal width	3.7	2.6	2.9
Shaft width	1.9	1.3	1.6
Shaft depth	1.6	1.2	1.6
Width through internal cnemial crest	4.1	3.1	4
Length through fibular ridge	10.5	6.7	8.1

* The first measurement of the humerus of *Alexornis* is of the holotype, the second of the paratype.
Measurement in brackets estimated.

Insofar as preserved, the humerus of *Alexornis* has three unique characteristics (numbers 1, 5, and 9 above), shares two with Bucconidae alone (3 and 8), shares two with Momotidae alone (2 and 6), and is similar to both Bucconidae and Momotidae in two others (4 and 7).

Ulna: (1) Olecranon straight, short, stout (as in Bucconidae and Momotidae), (2) with a pit in the tip (no pit in Bucconidae and Momotidae). (3) External cotyla large and (4) strongly convex (of moderate size and moderately convex in Bucconidae; small and concave in Momotidae), (5) separated from olecranon by a deep groove (groove absent in Bucconidae and Momotidae); (6) medial rim of external cotyla thick [lateral portion of cotyla missing] (resembling Bucconidae; edge very thin in Momotidae). (7) Internal cotyla small (as in Bucconidae; large in Momotidae), (8) with surface flat (moderately concave in Bucconidae; strongly concave in Momotidae). (9) Proximal radial depression deeply undercuts entire width of rim of internal cotyla (in Bucconidae the depression falls far short of rim of cotyla; in Momotidae the depression extends to the medial edge of cotyla but fails to undercut it).

Insofar as preserved, the ulna of *Alexornis* has six unique characteristics (numbers 2, 3, 4, 5, 8, and 9 above), shares two with Bucconidae alone (6 and 7), shares none with Momotidae alone, and is similar to both Bucconidae and Momotidae in one characteristic (1).

Scapula: (1) Acromion rather short (long in Bucconidae and Momotidae), with tip slightly damaged, but (2) apparently blunt (as in Bucconidae; tip forms a recurved hook in Momotidae and Passeriformes). (3) Glenoid facet flat (cuplike in Bucconidae and Momotidae).

Thus the scapula, so far as preserved, has two unique characteristics (numbers 1 and 3), shares one with Bucconidae (2), and none with Momotidae.

Coracoid: (1) Brachial tuberosity with a recurved hook directed toward area where procoracoid process would be if preserved (slightly hooked in Bucconidae; hook absent in Momotidae). (2) Triosseal canal very deep (very shallow in Bucconidae; flat in Momotidae). (3) Scapular facet convex (as in Bucconidae and Momotidae), but (4) very broad (very narrow in Bucconidae and Momotidae).

The coracoid has three unique features (numbers 1, 2, and 4), none is shared with Bucconidae alone or with Momotidae alone, and one is shared with both Bucconidae and Momotidae (3).

Femur: The specimen shows evidence of some postmortem compression and distortion. (1) Shaft stout (resembling Bucconidae and Eurylaimidae; slender in Momotidae). (2) External condyle very long, extending both proximally and (3) distally far beyond both internal and fibular condyles (external and internal condyles of about equal extent in Bucconidae and Momotidae; in Eurylaimidae external condyle lengthened distally only). (4) Internal condyle with only very slight indication of a transverse shelf on posterior surface (resembling Bucconidae and Eurylaimidae; shelf very prominent in Momotidae). (5) Fibular condyle small (resembling Momotidae and Eurylaimidae; very stout in Bucconidae). (6) Popliteal area deeply excavated (resembling Momotidae; area nearly flat in Bucconidae and Eurylaimidae). (7) Rotular groove shallow (well developed in Bucconidae and Momotidae).

The femur has three unique features (numbers 2, 3, and 7), three are shared with Bucconidae alone (1, 4, and 5), one with Momotidae alone (6), and none are held in common with both Bucconidae and Momotidae.

Tibiotarsus: The cnemial crests are broken off, but their bases are preserved. (1) Shaft stout (resembling Bucconidae; slender in Momotidae). (2) Fibular crest wide (rudimentary in Bucconidae and Momotidae), (3) extending proximally all the way up shaft (as in Momotidae; in Bucconidae falling far short of proximal end of shaft). (4) Distal end of fibular crest merges gently with shaft (as in Momotidae; in Bucconidae distal end joins shaft at a rather abrupt angle). (5) Anterior and posterior surfaces of fibular crest concave, with an anterior and a posterior groove running along junction with shaft (a slight anterior and posterior groove in Bucconidae; in Momotidae anterior and posterior surfaces of crest flat and ungrooved). (6) Proximal internal articular surface swollen and convex (in Momotidae slightly swollen; surface more concave in Bucconidae), (7) without posterior overhang (with slight overhang in Bucconidae; in Momotidae a lip overhangs shaft posteriorly). (8) Outer cnemial crest short (as in Bucconidae and Momotidae). (9) Inner cnemial crest short, although considerably longer than outer crest (resembling Bucconidae and Momotidae).

The tibiotarsus has three unique characteristics (numbers 2, 5, and 7), shares one with Bucconidae alone (1), shares three with Momotidae alone (3, 4, and 6), and agrees with both Bucconidae and Momotidae in two features (8 and 9).

Familial Position of *Alexornis*

The characteristics described above for *Alexor-*

nis are grouped in Table 2 to show the number of features confined to a single taxon, those shared by two taxa, and those common to all three taxa. By far the strongest grouping of characteristics is of those confined to a single taxon—49 percent in *Alexornis,* 44 percent in Momotidae, and 37 percent in Bucconidae. I interpret this as indicating that the three taxa are of equal taxonomic rank and, therefore, propose *Alexornis* as the type of a new family.

TABLE 2.—Summary of shared characteristics of *Alexornis,* MOMOTIDAE, and BUCCONIDAE (+ = similar to; − = different from)

	Wing (18)	Pectoral girdle (7)	Leg (16)	Total (41)	Percentage
1. *Alexornis* + MOMOTIDAE + BUCCONIDAE	3	1	2	6	15
2. *Alexornis* + MOMOTIDAE − BUCCONIDAE	2	0	4	6	15
3. *Alexornis* + BUCCONIDAE − MOMOTIDAE	4	1	4	9	22
4. BUCCONIDAE + MOMOTIDAE − *Alexornis*	4	3	4	11	27
5. BUCCONIDAE − MOMOTIDAE − *Alexornis*	7	2	6	15	37
6. MOMOTIDAE − BUCCONIDAE − *Alexornis*	9	3	6	18	44
7. *Alexornis* − MOMOTIDAE − BUCCONIDAE	9	5	6	20	49

Numbers in parentheses represent number of characters considered.

ALEXORNITHIDAE, new family

DIAGNOSIS.—Humerus with olecranal fossa deep; entepicondylar area much produced distally; external condyle oriented transversely at an angle of about 60 degrees to shaft; ectepicondylar prominence with a transverse ridge across anconal surface proximal to its base. Ulna with a pit at the tip of olecranon; external cotyla large, strongly convex, and separated from olecranon by a deep groove; surface of internal cotyla flat; proximal radial depression deeply undercutting the entire width of lip of internal cotyla. Scapula with acromion rather short and glenoid facet flat. Coracoid with brachial tuberosity hooked; triosseal canal very deep; scapular facet very broad. Femur with external condyle very long, extending both proximally and distally far beyond both internal and fibular condyles; rotular groove obsolete. Tibiotarsus with its proximal articular surface not overhanging shaft posteriorly; fibular crest wide, with both its surfaces concave and separated from shaft by an anterior and a posterior groove.

Ordinal Position of *Alexornis*

Although possessing a large number of unique features, Alexornithidae shares some characters with the order Coraciiformes as exemplified by the Momotidae, others with the order Piciformes as exemplified by the Bucconidae, and still others with both of those orders. These similarities are summarized in Table 2, and several different hypotheses at the ordinal level could be formed from these data.

The three taxa might be combined in a single order, for which the name Piciformes would have priority (for order-group synonymies see Brodkorb, 1971a:248, 256). But of the 41 characters analyzed, only 6 are shared by the 3 families (Table 2, line 1). Such a small proportion of common characteristics militates against merging the taxa in a single order.

Alexornithidae might be referred to Coraciiformes, but such an arrangement is also supported by 6 characters only (Table 2, line 2), and this hypothesis is likewise discarded.

Alexornithidae might be placed in Piciformes, as the order is currently understood. Nine characters support this combination (Table 2, line 3), but line 4 of Table 2 argues against it, as Piciformes and Coraciiformes share more characters than any other combination of the taxa under consideration.

The conclusion thus derived from Table 2 is that the three taxa represent separate but related orders. I therefore propose *Alexornis* as the type-genus of a new order.

ALEXORNITHIFORMES, new order

DIAGNOSIS.—Same as for the only known family, Alexornithidae.

REMARKS.—The age of *Alexornis* is about 81 million years BP, much earlier than the earliest known occurrence of either the Coraciiformes and Piciformes. The earliest record of the Piciformes is early Eocene, about 51 million years BP, when bucconid-like forms appear in Wyoming (Brodkorb, 1970; Feduccia and Martin, herein). If Harrison and Walker (1972) are correct in assigning the British *Halcyornis* to the Coraciiformes, the earliest record of that order is also early Eocene. Undoubted members of the Coraciiformes occur in European deposits of middle and late Eocene age (Brodkorb, 1971a). Both morphology and the temporal sequence thus suggest *Alexornis* as the presumptive ancestor of the orders Coraciiformes and Piciformes.

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