

Oligocene Fossils Bearing on the Origins of the Todidae and the Momotidae (Aves: Coraciiformes)

Storrs L. Olson

ABSTRACT

A new genus and species of today, *Palaeotodus emryi*, is described from the "middle" Oligocene (Orellan land mammal stage) of Wyoming, providing the first record of the modern family Todidae outside the West Indies. The fossil bird *Protornis glarniensis* from the lower Oligocene of Switzerland is removed from the Alcedinidae to the Momotidae to provide the first occurrence of the latter family outside the New World. The Todidae and Momotidae appear to be more closely related to each other than either is to any other family of Coraciiformes. The Momotidae were evidently derived from the Old World. The Todidae appear to have been derived from a momotid-like ancestor in the Oligocene or earlier. The present distribution of these two families in the New World tropics is relictual. The Coraciiformes appear to have been one of the prevalent groups of small land birds in the Oligocene.

Introduction

The five modern species of todies (Todidae), endemic to the Greater Antilles, are among the most intriguing birds of the West Indies. The Momotidae of Central and South America and the Todidae are the only families of Coraciiformes confined to the New World. Apart from late Pleistocene remains of modern species, there has hitherto been no fossil record of either family.

Storrs L. Olson, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Now, a recently discovered fossil and a new interpretation of one of the first fossil birds to be described, provide us with increased information bearing on the evolution and geographic origins of both the Todidae and the Momotidae.

ACKNOWLEDGMENTS.—I am indebted to Robert J. Emry for calling the Wyoming specimen to my attention, permitting me to work on it, and providing much information and assistance. The manuscript has had the benefit of his comments and those of John Farrand, Jr., Alan Feduccia, and Pierce Brodkorb. Robert W. Storer (University of Michigan Museum of Zoology) kindly lent me a skeleton of *Hylomanes* for study, and casts of Swiss fossils were generously lent by Malcolm C. McKenna (American Museum of Natural History). I am grateful to L. B. Isham for his skillful illustrations accompanying this paper and to Anne Curtis for rendering Figure 3.

An Oligocene Tody from Wyoming

In June of 1972, Dr. Robert J. Emry of the Smithsonian Institution collected several blocks of matrix containing great concentrations of bones of small vertebrates from a deposit of Orellan age ("middle" Oligocene) in east-central Wyoming. Present in these samples are the abundant remains of at least two species of squirrels, various smaller rodents, small marsupials, and insectivores. That this great concentration of bone may be attributed to the work of owls is virtually certain since the blocks also contain the beautifully preserved skeletons of at least four small owls, possibly of two species.

On the surface of one of these blocks, Dr. Emry noticed the bill of a small bird and later found a crushed avian cranium that fit perfectly with the bill. After the two portions had been reunited, an incomplete avian humerus was found attached to the lower surface of the skull. There is no reason to believe that the humerus and skull are not from the same individual. Were they not, the owl that cast the pellet containing these remains would have had to eat two different birds at the same time, since it is rare for elements from a single prey item to be found in two successive pellets (Raczyński and Ruprecht, 1974). This would seem unlikely, particularly in view of the absence of birds other than owls in the remainder of the samples.

The distinctively shaped, flattened bill of the fossil was immediately reminiscent of the Todidae, but since bills of similar shape have evolved independently in several groups of birds, many of them passerines, identification was made cautiously. After careful comparisons, I concluded that this specimen is indeed referable to the family Todidae.

Palaeotodus, new genus

TYPE.—*Palaeotodus emryi*, new species.

DIAGNOSIS.—Similar to modern *Todus* but with different proportions, the wing apparently being better developed. Bill proportionately shorter and broader, not as pointed as in *Todus*. Mandibular rami not as flattened, the anterior portions grooved, so as to form a distinct dorsal shelf. Three ridges on the ventral side of the interorbital bridge separate, rather than coalesced as in *Todus*.

ETYMOLOGY.—Greek, *palaeos*, ancient, plus *Todus*, the genus of modern todies. See Newton (1896:970, footnote) for the etymology of *Todus*.

Palaeotodus emryi, new species

FIGURE 1

HOLOTYPE.—Incomplete and partially crushed skull with most of the anterior portions of the rostrum intact, including the mandibular symphysis and parts of both rami; crushed posterior portion of cranium with ventral surface of interorbital bridge well preserved; much of the rest of the skull crushed, jumbled, and displaced ventroanteriorly. Vertebrate Paleontological Collections of the Na-

tional Museum of Natural History, Smithsonian Institution, USNM 205608. Collected in NW 1/4, SE 1/4, Sec. 27, T32N, R71W, about 5.6 km SSE of Douglas, Converse County, Wyoming (42°42'55"N; 105°21'15"W) on 12 June 1972 by Robert J. Emry (Field No. WYO. 72-246) and Leroy Glenn.

HORIZON.—Brule Formation, Orellan land-mammal stage, "middle" Oligocene.

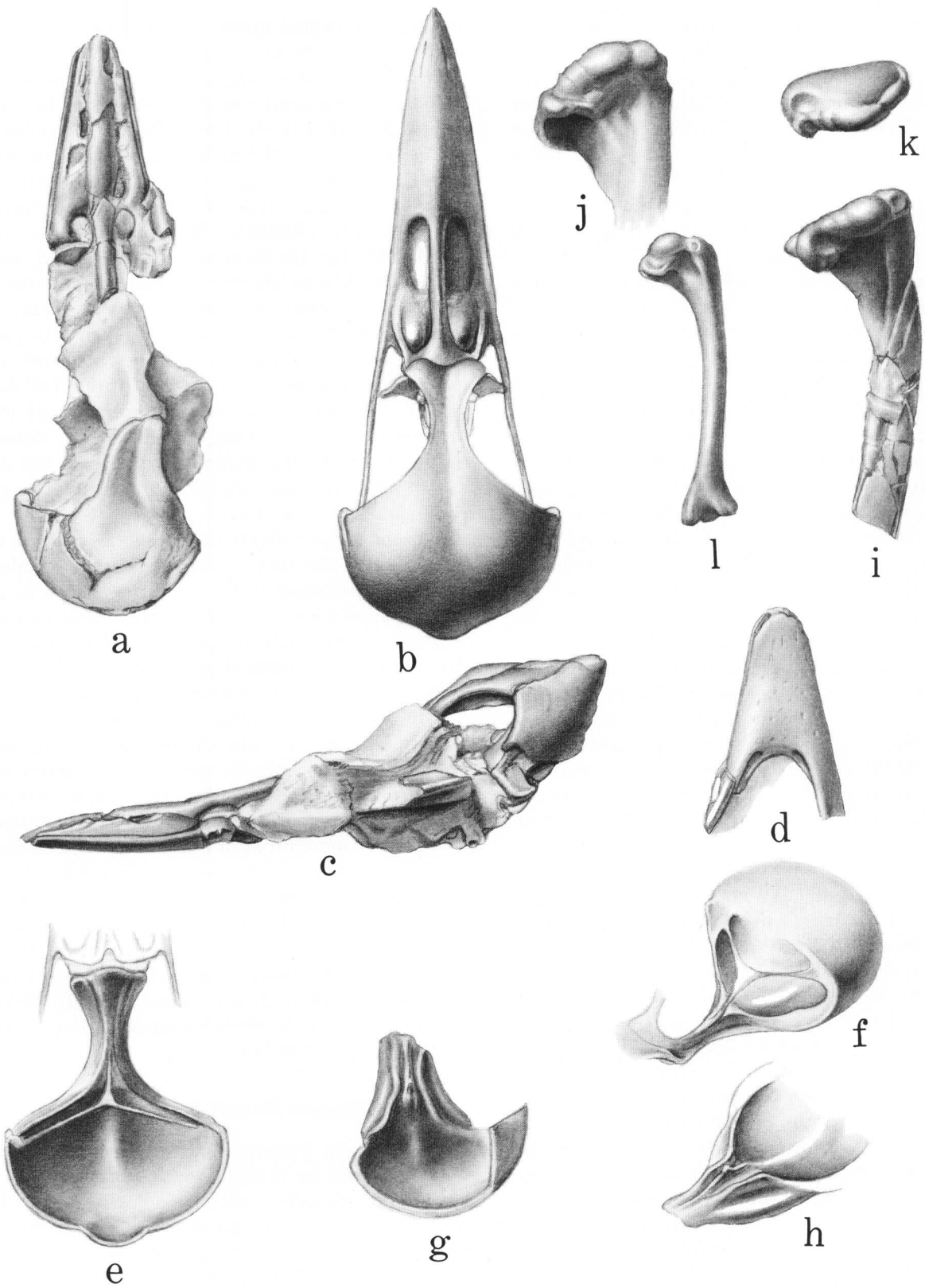
PARATYPE.—Somewhat distorted right humerus with the shaft crushed and lacking the distal end; same number and data as the holotype.

MEASUREMENTS.—Overall length of skull as preserved 34.5 mm, length of bill from anterior of nostril 10.0, length of mandibular symphysis 7.8, width of mandible at beginning of symphysis 5.6, width of mandibular ramus 1.7, proximal width of humerus 6.7.

ETYMOLOGY.—After Dr. Robert J. Emry, the collector, in recognition of his significant contributions to our knowledge of the Oligocene fauna of North America.

DESCRIPTION.—Bill flat, broad, nearly spatulate, with a broader more rounded tip than in *Todus*. Internarial bar long, slender, terete, and somewhat heavier than in *Todus*, continued out the rostrum as a slightly elevated ridge. Mandible flattened, the symphysis shorter and broader than in *Todus*; mandibular rami deeper than in *Todus*, grooved anteriorly to form a dorsal shelf. Ventral surface of interorbital bridge with three ridges, the middle one terminating in a pointed process (tip broken off in the type), the outer ones flaring laterally to form the edges of the huge anterior cranial fenestra. The condition in *Todus* is essentially similar, but the three ridges are not as distinct anteriorly and coalesce to form a narrower, deeper interorbital bridge. The middle process in *Todus* is a

FIGURE 1.—Skull (holotype) and humerus (paratype) of *Palaeotodus emryi*, new genus and species (USNM 205608), compared with the same elements of *Todus subulatus* (USNM 292589): a, dorsal view of skull of *P. emryi*; b, dorsal view of skull of *T. subulatus*; c, lateral view of skull of *P. emryi*; d, ventral view of mandible of *P. emryi*; e, f, cutaway views of ventral side of interorbital bridge and dorsal part of anterior cranial fenestra of *T. subulatus*; g, h, same views of *P. emryi*; i, anconal view of humerus of *P. emryi*; j, proximal end of humerus of *P. emryi*, viewed with distal portion tilted further upward; k, proximal view of same; l, anconal view of humerus of *T. subulatus*. (All figures approximately $\times 3$.)



point of attachment for a narrow ligament that joins with similar ligaments from the parasphenoid rostrum and the lateral edges of the cranial fenestra to form a tenuous cross holding the anterior part of the brain in place. The humerus of *Palaeotodus* is similar to that of *Todus*, but is much larger; the internal tuberosity is heavier and much less lateromedially elongate; and the ligamental furrow and the scar on the external tuberosity are both considerably deeper.

REMARKS.—Few nonpasserine landbirds have the bill anywhere near as flattened as in *Todus* and *Paleotodus*. Those with the most flattened bills are *Electron*, *Hylomanes*, and *Aspatha* (Momotidae), *Jacamarops* (Galbulidae), and *Myioceyx* (Alcedinidae). In all of these forms the bill is deeper and the internarial bar broader and shorter than in either of the two genera of Todidae. The bony structure of the bill in passerines, as for example in *Todirostrum* (Tyrannidae), is quite different from that of *Todus* and *Palaeotodus*, being deeper and more arched, with a more troughlike mandible and a shorter, wider, and less terete internarial bar.

Palaeotodus agrees with *Todus* and differs conspicuously from the Momotidae, Alcedinidae, Galbulidae, and indeed from all of the rest of the Coraciiformes and Piciformes, in having the anterior wall of the cranium and the interorbital septum unossified. In the Momotidae, Alcedinidae, and Galbulidae the interorbital septum is partially or very heavily ossified. The anterior wall of the cranium is ossified in all of these families, whereas in *Todus* and *Palaeotodus* there is a great, open fenestra.

The humerus of *Palaeotodus* is broken and distorted, with the head crushed down distally relative to the internal and external tuberosities. Although in *Todus* there is slightly more of a depression beneath the head than in other Coraciiformes, the humerus can in no sense be regarded as having a double fossa, as stated by Bock (1962), and has a single pneumatic opening beneath the internal tuberosity. *Palaeotodus* is similar to *Todus* in this respect. The humerus of *Palaeotodus* differs from that of the Passeriformes in the less bulbous head, the much lesser development of the bicipital crest, the higher and more pronounced external tuberosity, and the narrower, more ventrally projecting internal tuberosity. In the Piciformes the deltoid crest is much more expanded, the head more

bulbous, the capital groove much deeper, and the internal tuberosity less perpendicular to the shaft than in *Palaeotodus*, although these differences are considerably less pronounced in the Galbulidae and Bucconidae. Within the Coraciiformes the humeri of the Upupidae, Phoeniculidae, and Meropidae have larger, more triangular deltoid crests than in *Palaeotodus*, while in the Coraciidae the bicipital crest is more extensive. The humerus in the Alcedinidae has the head more bulbous and situated much higher above the external tuberosity, the shaft straighter, the internal tuberosity much heavier, and the bicipital surface much less produced than in *Palaeotodus*. The humerus of *Palaeotodus* is most similar to that of the Todidae and the Momotidae. In the conformation of the internal tuberosity it is more similar to the Momotidae, whereas in the greater excavation of the external tuberosity and ligamental furrow it more closely resembles the Todidae.

The manner in which the skull was crushed in the type of *Palaeotodus* makes it appear smaller, while the distortion of the humerus is such as to make it appear wider and thus larger. Nevertheless, it is quite evident that the proportions of *Palaeotodus* are different from those of *Todus*, the wing being much larger in relation to the head.

This difference in proportions may be due at least in part to the small size of *Todus* being secondarily derived, since the species of this genus are the smallest members of the order Coraciiformes. In the evolution of vertebrates, body size usually changes at a more rapid rate than head size, so that small forms derived from larger ones tend to have proportionately larger heads, and vice versa. Many authors have remarked on the large-headed appearance of *Todus* in life. In the Oligocene, the Todidae were possibly more diverse than at present and probably included larger, more actively flying forms with better developed wings than the strictly sedentary modern todies.

An Oligocene Motmot from Switzerland

In 1839, von Meyer called attention to the remains of what he thought to be a passerine bird from slate deposits (Glarner Fischschiefer) in Switzerland, then considered to be of Cretaceous age. In a subsequent publication he named this specimen *Protornis glarniensis* (von Meyer, 1844).

Later (von Meyer, 1856), he emended the name to *P. glaronensis* and this spelling was in general use until Brodkorb (1971), whom I have followed, revived the original orthography. Lambrecht (1933) maintained *Protornis* as a genus incertae sedis in the Passeriformes. At that time the deposits from which the type of *P. glarniensis* was derived were regarded as upper Eocene in age. Subsequent studies have shown them to be of lower Oligocene age (Peyer, 1957).

The type of *P. glarniensis* consists of a slab containing the bones of all four limbs, the pectoral girdle, a complete mandible, the quadrates, and a few vertebrae and ribs. These were insufficiently exposed when von Meyer studied them, but Peyer (1957) undertook further preparation of the type, illustrating his results with numerous photographs and x-radiographs. The fossil is slightly distorted from stresses imposed on the rock after deposition; Stüssi (1958) and Baumann (1958) have offered mathematical and optical corrections, respectively, for this distortion. Another less complete specimen was referred to *Protornis*, possibly *glarniensis*, by Peyer (1957). I have had access to casts of both these specimens, as well as to Peyer's excellent illustrations. The casts were made by a copper electroplate process and appear to be very accurate representations of the original specimens.

After his study of the type of *P. glarniensis*, Peyer (1957) concluded that it belonged with the Alcedinidae (kingfishers) and more particularly that it was nearest to *Dacelo*. I agree with the assignment of this form to the Coraciiformes, but numerous characters of its skeleton show conclusively that *Protornis* cannot be a kingfisher.

Protornis glarniensis is a small bird, slightly smaller than the modern motmot *Hylomanes momotula*. As detailed by Peyer, many aspects of its structure demonstrate that it does not belong with the Passeriformes and the clearly anisodactyl feet eliminate the Piciformes from consideration. The mandibular symphysis is broad, flattened and somewhat spatulate, differing from most non-passerine landbirds except the Momotidae and Todidae. The overall conformation of the mandible is in fact, markedly similar to that of the motmot genera *Electron* and *Hylomanes* and is quite distinct from that of the kingfishers, including the flat-billed genus *Myioceyx* (Figure 2). The symphysis is broader than in the Todidae and

somewhat shorter than in the modern genera of Momotidae, being most similar in this respect to *Hylomanes*, which genus is generally conceded to be the most primitive of living motmots.

In the mandibular articulation of *Protornis* the internal process is a long, thin splint set off from a well-developed retroarticular process by a distinct notch, with the actual articulating surface for the quadrate much reduced. This is exactly the condition seen in the Momotidae and Todidae. In the Alcedinidae the articular cup for the quadrate is large and deep, the retroarticular process virtually absent, and the internal process wide, heavy, and triangular, quite unlike *Protornis* or the motmots and todies. Bee-eaters, Meropidae, have a fairly long, slender internal process, but it is not set off from the retroarticular by a notch, and the articular cup is deep, as in kingfishers. Furthermore, the bill shape of *Protornis* is not at all like that of the Meropidae.

The shape of the hypotarsus in *Protornis* is exactly as in motmots and differs from that of the kingfishers, in which it projects above the cotylae in a distinct point. The tarsometatarsus of *Protornis* is only slightly shorter than the middle toe with claw, as in the motmots. In todies the tarsus is longer than the middle toe with claw, whereas in the kingfishers and bee-eaters the tarsus is squat and much shorter than the middle toe. The coracoid process appears to be nearly absent in *Protornis*, as in motmots and todies, whereas it is better developed in kingfishers.

From the evidence detailed above it is clear that *Protornis* does not belong with the Alcedinidae, where Peyer (1957) placed it. The proportions of the bill and of the hindlimb and toes preclude its assignment to the Todidae. In all of its important features it agrees with the Momotidae. It differs from the modern forms of the family mainly in the shorter mandibular symphysis and the higher, more expanded sternocoracoidal process of the coracoid. *Protornis glarniensis* should, therefore, be assigned to the family Momotidae.

A second fossil from the Glarner Fischschiefer, consisting of a slab with both hindlimbs, the right wing, some ribs, and portions of the pelvis superimposed on the sternum, was assigned to the genus *Protornis* by Peyer (1957), who suggested that it might be referable to the species *P. glarniensis*. This is plainly impossible, for the second specimen

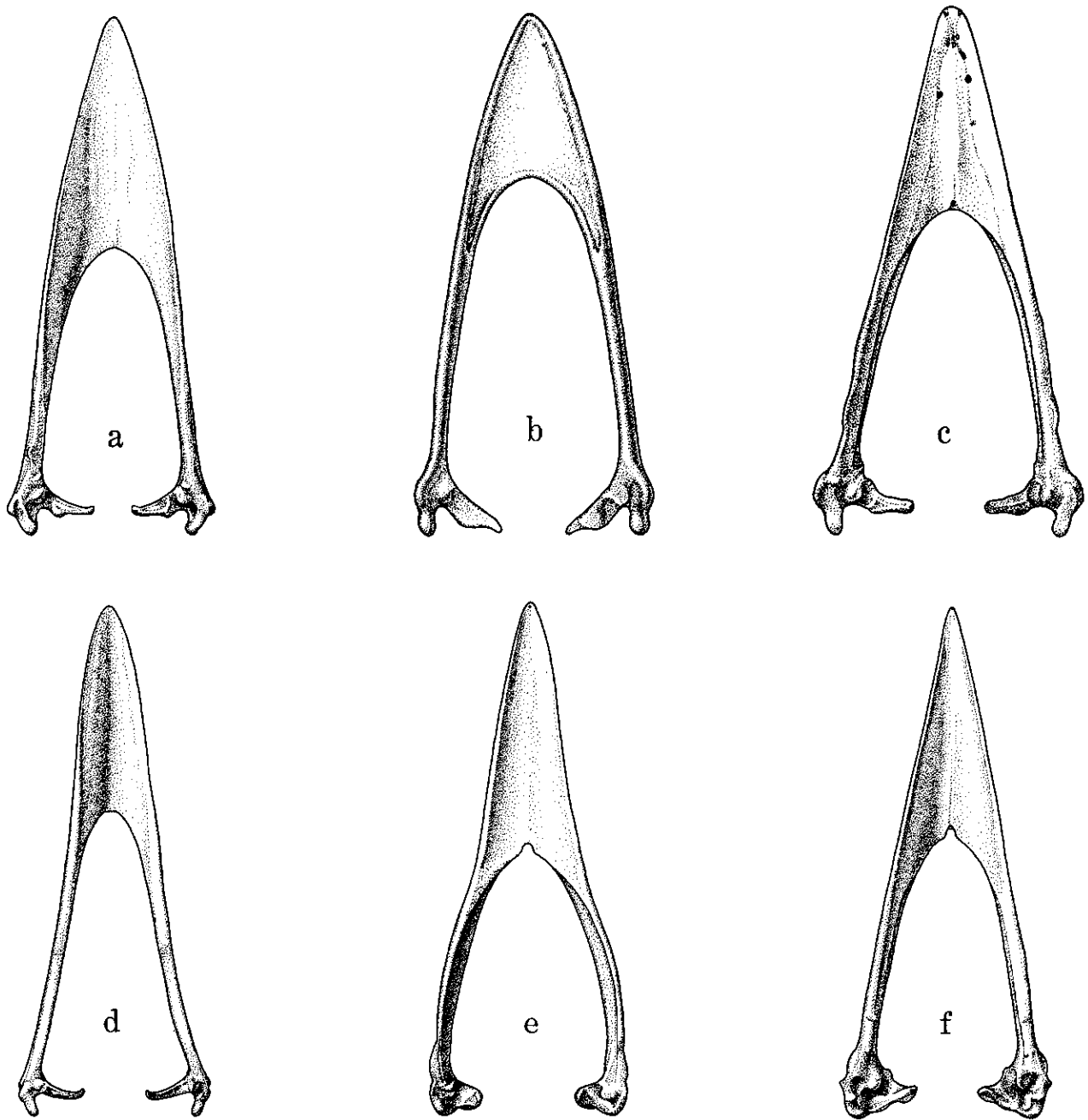


FIGURE 2.—Dorsal views of mandibles: *a*, *Electron platyrhynchum*; *b*, *Protornis glarniensis* (adapted from Peyer, 1957); *c*, *Hylomanes momotula*; *d*, *Todus subulatus*; *e*, *Myioceyx lecontei*; *f*, *Dacelo novaeguineae*. (Not to scale.)

is much too large to belong to the same species as *P. glarniensis*; the carpometacarpus, for example, is twice as long. Furthermore, in the right foot of this specimen it can be clearly seen that both digits I and II are reversed (Figure 3)—a condition

found only in the Trogonidae among modern birds. The rest of the skeleton of this specimen is generally similar to that of modern trogons, although differing in some details. This specimen deserves a great deal more attention since it provides the

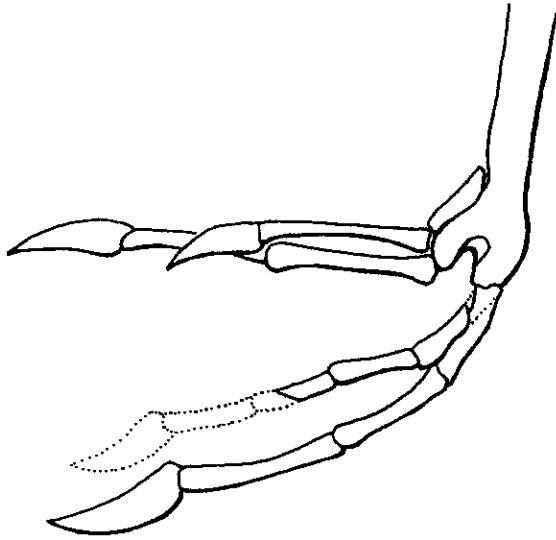


FIGURE 3.—Diagram of right foot of the so-called second specimen of *Protornis* showing the heterodactyl condition typical of the Trogonidae. (Adapted from Peyer, 1957, and a cast of the specimen; the distal portion of the fourth toe is present as an impression in the matrix.)

earliest evidence of the occurrence of the heterodactyl foot. It obviously cannot be assigned to *Protornis* or the Momotidae and for the present should be regarded as belonging to the Trogonidae. Four fossil species of trogons are known—all from France (Brodkorb, 1971). Three of these, in the genus *Archaeotrogon*, are from the Phosphorites du Quercy, which range in age from upper Eocene to lower Oligocene, and are thus possibly contemporaneous with the Swiss specimen. The fourth species, *Paratrogon gallicus*, is from lower Miocene (Aquitanian) deposits at Langy.

A second species of *Protornis*, *P. blumeri*, was described from the Glarner Fischechiefer in 1865 by Heer (1876). The type appears to have been poorly preserved and has not been restudied, its whereabouts being unknown. Brodkorb (1971) placed this species, along with *P. glarniensis*, in the Alcedinidae, but considered its position uncertain. From the original illustration one cannot even ascertain that the specimen was avian. In view of this, and since more than one family of birds occurs in the Glarner deposits, *P. blumeri* should be relegated to the category of *Aves incertae sedis*.

Discussion

The ten families of the order Coraciiformes fall into several diverse groups whose relationships within and without the order are as yet uncertain. Sibley and Ahlquist (1972:230) maintained that, "no compelling evidence exists to ally any group of the Coraciiformes more closely to a non-coraciiform than to other members of the Coraciiformes." On the basis of biochemical analysis of egg-white proteins, Sibley and Ahlquist concluded, as have other taxonomists in the past, that within the Coraciiformes, the Alcedinidae, Todidae, Momotidae, and Meropidae appear to form a natural but distantly interrelated group. Feduccia (1975) discovered that these families possess a highly derived stapes, which is shared only with the Trogonidae, and concluded that all five families are closely related. Contrary to most earlier opinions, Sibley and Ahlquist (1972:230) suggested that the Todidae are more closely allied to the Alcedinidae than to the Momotidae. The osteology of these families does not support this contention, and along with their distributional history strongly indicates that a fairly close affinity exists between todies and motmots and that these families differ considerably from the kingfishers.

Seven of the ten families of Coraciiformes are confined to the Old World. Of approximately 89 Recent species of Alcedinidae, only six, in two genera, are found in the New World. Of these, two are in the genus *Ceryle*, which also contains two Old World species, while the genus *Chloroceryle*, which is only weakly differentiated from *Ceryle*, contains four species endemic to the New World. Clearly the kingfishers are an Old World family that has only recently invaded the Americas. Thus, the Todidae and Momotidae are the only truly New World families of modern Coraciiformes.

Recent motmots are neotropical in distribution, ranging from southern Mexico south through Brazil. In a classical exercise in zoogeography, Chapman (1923) analyzed the distribution of the genera, species, and subspecies of motmots, concluding that they had originated in Central America, the few South American forms having been derived from the north. Lönnberg (1927), noting that Central and North America probably presented a more or less continuous tropical environment in the Tertiary, felt that the motmots could as easily be con-

sidered North American in origin. A North or Central American origin of the modern members of the family, as opposed to a South American one, has properly gained general acceptance. Nevertheless, this leaves unanswered the question of the origins of ancestral motmots.

The modern todies, confined to the West Indies, are also thought of as being North American in origin. This is due in part to their presumed relationship with the motmots and in part to the North American derivation of most of the rest of the Antillean avifauna (Bond, 1966). It might then be asked whether the todies evolved their distinctive characteristics from some momotid-like ancestor after arriving in the Greater Antilles, or had already assumed these characteristics before colonizing the islands.

Because of the small size and feeble flight of modern todies, Bond (1966) expressed reservations about their ability to cross even narrow water gaps and suggested that they might have been rafted to the West Indies from Central America. However, because the five species of modern todies are very similar in plumage and morphology, one must assume that members of the genus *Todus* have been able to cross the water barriers between the Greater Antilles within relatively recent geologic time. Moreover, since there are two species of *Todus* on Hispaniola, one must either assume sympatric speciation or a double invasion of the island. Bond's own remarks (1974) on the greater similarity of the voice of Hispaniolan *T. angustirostris* to that of Cuban *T. multicolor* than to that of the other Hispaniolan species, *T. subulatus*, suggest a double invasion. Thus, if todies were able to cross the water barriers between the islands of the Greater Antilles they might as easily have crossed from the mainland. Furthermore, the evidence provided by *Palaeotodus* shows that in the Oligocene, todies were larger and had proportions suggestive of greater powers of flight. It therefore seems possible that todies might have colonized the West Indies over water as easily as, say, kingfishers, and it is not necessary to invoke rafting to explain their present distribution.

Without doubt, the order Coraciiformes, as traditionally conceived, arose in the Old World. The existence of *Protornis* in the lower Oligocene of Switzerland now provides evidence that the family

Momotidae, presently confined to the New World, actually had its origins in the Old World. The place and time of origin of the Todidae are uncertain. The Orellan land-mammal stage represents a geologically very short span of time following the much longer Chadronian stage and preceding the Whitneyan stage, the latter also representing a very short span of time. The deposits from which *Palaeotodus* was recovered are about 30 million years old and have traditionally been regarded as middle Oligocene, although there is as yet no paleontological correlation between the North American terrestrial deposits of so-called Oligocene age and those of Europe. By the reduced ossification of the skull, *Palaeotodus* certainly seems to be referable to the Todidae rather than the Momotidae, but perhaps with material from earlier in the Oligocene it would not be possible to distinguish the two families, the family Todidae having assumed its characteristics since that time.

Probably through a combination of climatic change and competition with more advanced land birds, the motmot-tody group was entirely supplanted in the Old World. The deterioration of tropical conditions in North America in the late Tertiary left motmots only in Central America, from whence they have spread into South America since the closing of the Panamanian seaway in the late Pliocene. Similar factors affected the North American todies and only the isolated West Indian relicts of the genus *Todus* have survived up to the present.

Feduccia and Martin (p. 110, herein) have shown that the predominant order of small land birds of the Eocene in North America was the Piciformes. It is now becoming evident that the Oligocene was similarly important in the evolution of the Coraciiformes. Although the evidence is far from conclusive, if the Coraciiformes (including the Trogonidae) were not the predominant perching land birds of the Oligocene, they were certainly much more prevalent than today. Recently I have examined a number of fragments of small land birds of Chadronian and Orellan age from the western United States. All of these appear to be referable either to the Coraciiformes or Piciformes and definitely are not passerine. Thus, it would appear that the Passeriformes may not have gained a strong foothold in North America until the Miocene.

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