

A MODEL FOR THE EVOLUTION OF PERCHING BIRDS¹

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Abstract

Feduccia, A. (Department of Zoology, University of North Carolina, Chapel Hill, North Carolina 27514) 1976. A model for the evolution of perching birds. Syst. Zool. 26:19-31.—The Passeriformes and related avian orders (here termed “perching birds”) have presented almost insurmountable problems in resolving phylogenetic relationships. New evidence from the morphology of the avian stapes (columella) permits a reassessment of the phylogenetic relationships of the advanced perching birds. Though the stapes represents but a single character, the primitive condition for the element can be established beyond reasonable doubt as that condition found in the reptilian ancestors of birds and present in the vast majority of living birds. Therefore, where unique, *derived* morphologies of the stapes occur, they may be of great importance in establishing evolutionary relationships within these groups, as no other characters are presently available for which primitive-derived sequences can be established beyond doubt. A cladistic approach to stapedial morphology permits a number of probable evolutionary statements concerning the “perching birds” as follows: 1) New and Old World suboscines are a monophyletic assemblage, and this group, now termed the Tyranniformes, includes the previously classified suboscines of Madagascar, but not those of Australia (the lyrebirds and allies, and the New Zealand Wrens), which are shown to be oscines; 2) the wood-hoopoes and hoopoes are monophyletic and possess a unique “anvil” stapes; 3) the bee-eaters, motmots, kingfishers, and todies possess a common derived stapedial morphology and almost certainly represent a monophyletic assemblage; 4) trogons possess a stapedial morphology identical to that of the above assemblage (in 3) and are probably derived from that particular group, all of which are now termed the Alcediniformes; 5) the oscines and suboscines could not have shared a common ancestor because suboscines show a myriad of primitive characters with respect to the oscines, are relictually distributed, and yet possess a derived stapedial morphology, while the otherwise structurally advanced oscines possess the primitive condition of the stapes; for that reason the order Passeriformes is restricted to include only the oscines; 6) the Tyranniformes (suboscines) and Alcediniformes may have shared a common ancestor; both groups possess derived morphologies of the stapes that share many common features, but establishing beyond all doubt that the morphologies are strictly homologous is difficult.

New evidence from the fossil record (particularly from the Western Hemisphere) provides a new basis for a paleobiogeographic analysis of “perching birds.” This new evidence indicates that: 1) The Eocene of North America was a period during which structurally primitive piciform birds were the predominant, if not the only, perching birds. Eight species are now known from the Lower and Middle Eocene of North America, including one previously thought to represent a passerine. 2) The piciforms are probably New World in origin, and could have dispersed into the Old World via Beringia or across the North Atlantic. 3) The alcediniform birds are almost certainly Old World in origin; trogons, motmots, and perhaps todies crossed over into the New World using the Beringia route; alcediniforms were probably predominant during the Oligocene. 4) Suboscines are probably a Southern Continent group, and probably did not arrive into North America until relatively late, perhaps late Pliocene or early Pleistocene, when a Central American land bridge became established. 5) The Bering route probably served as a corridor for the arrival of oscines in the New World that gave rise to the New World nine-primaried oscine radiations. Apparently North America did not reciprocate to any significant degree. Oscines probably did not become established firmly in North America until the Miocene and are late arrivals into Central and South America; they probably entered these regions as late as late Pliocene or early Pleistocene when the Central American land bridge became established. [Phylogenetic relationships; “perching birds”; Passeriformes; stapes; paleobiogeography.]

As a morphologically uniform group of

vertebrates, birds present more problems in resolving phylogenetic relationships than any other group of tetrapods (Bock, 1963). The major difficulties are due to such fac-

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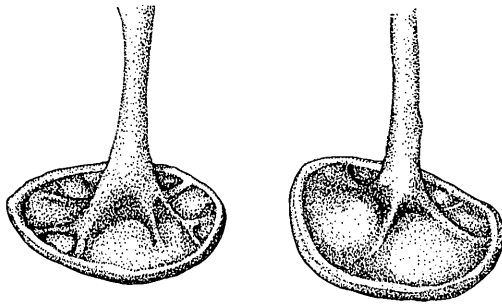


FIG. 1.—The primitive condition of the avian stapes or columella as illustrated by the kiwi, *Apteryx* (left), and an oscine passerine bird, *Coracina* (right). Both are drawn to the approximate same size. Most avian stapes are one to several mm in length (but sometimes longer in large birds).

tors as: 1) the restrictive physical demands of flight, causing massive convergence; 2) the shortage of morphological features (such as teeth) that vary sufficiently among the major groups to be of useful taxonomic value; and 3) the lack of a good fossil record because of the fragility of the bones and the arboreal nature of most forms. These factors have been particularly insidious in the Passeriformes and related groups (here termed “perching birds”), birds that are among the most advanced in perching and flying adaptations. These groups of perching birds are morphologically extremely similar, yet present certain clues that indicate possible lack of common ancestry (in contrast to commonly accepted opinion). Despite over a century of comparative morphological and other studies, little is presently known of the phylogenetic relationships of these birds. Therefore, discoveries of new characters that can be shown to be *derived* within major groups may be extremely important in assessing phylogenetic relationships.

Recent evidence from studies of the avian middle ear ossicle, the stapes or columella (Feduccia, 1975a), combined with new discoveries of fossils (Brodkorb, 1970; Feduccia, 1973; Feduccia and Mar-

tin, 1976; Olson, 1976), and reanalyses of previously described forms (Feduccia, 1976b; Olson, 1976), makes possible a reinterpretation of the evolution of the Passeriformes and related groups and provides the basis for a new paleobiogeographic analysis, particularly in the Western Hemisphere. In this article I present phylogenetic evidence from the avian stapes (columella) for a reinterpretation of the evolution of these advanced perching birds based on a cladistic analysis, often termed phylogenetic systematics (Hennig, 1966; Cracraft, 1972), and combine this evidence with new information from the fossil record. Possible functional aspects of the stapes are discussed elsewhere (Feduccia, 1975a).

The stapes is one of the last remaining elements of the avian skeleton to be examined, no doubt because of its minute size (one to several mm), fragility, and its remote location in the recesses of the middle ear. In addition, it is often lost in skeletal preparations. I have examined more than 2,000 specimens, representing nearly all of the living families of birds. Nearly all cladistic studies of birds have suffered from one major drawback: the inability to establish unequivocally the primitive nature of the particular character or characters involved. The stapes provides an exceptional and perhaps unique opportunity for phylogenetic analysis in that: (1) the primitive condition occurs in most birds; (2) the primitive nature of the element can be established beyond reasonable doubt as that found in the reptilian ancestors of birds. The primitive condition of the stapes (Fig. 1) is a simple structure, consisting of a flat footplate that fits into the oval window of the inner ear; its straight bony shaft connects via an extracolumellar and its ligaments to the tympanic membrane.

Two assumptions are made in this analysis. First, I assume that the primitive condition of the avian stapes, which is found in the vast majority of birds, is homologous with the same element in

reptiles, and represents a retained primitive condition. Second, I assume that structurally similar, derived morphologies of the stapes indicate evolutionary relationships, unless there are compelling reasons to assume convergence.

MORPHOLOGY OF THE STAPES

The orders placed close to the "passerines" (true perching or song birds) in the linear sequence of most classifications are the Apodiformes (swifts and hummingbirds), Coliiformes (mousebirds), Trogoniformes (trogons), Coraciiformes (rollers and allies, hornbills, hoopoes, kingfishers, bee-eaters, motmots, and todies), and Piciiformes (yoke-toed or zygodactyl perching birds, and the scansorial woodpeckers and allies) (Mayr and Amadon, 1951). Swifts and hummingbirds are most probably monophyletic as demonstrated by their possession of common structural features as well as a unique form of malate dehydrogenase (Kitto and Wilson, 1966). All Apodiformes possess the primitive condition of the stapes, as do the Coliiformes.

The Coraciiformes (*sensu* Wetmore, 1960) are one of the most morphologically heterogeneous orders of birds, whose various groups have presented insurmountable problems in resolving phylogenetic relationships. Our knowledge of the relationships within the order are perhaps best summarized by Lowe (1948): "... The Coraciiformes have for many years been loaded with a heterogeneous collection of forms which custom has blindly accepted." The morphologically most primitive members of the order, the Leptosomatidae (cuckoo-rollers) and Brachipteraciidae (ground-rollers) of Madagascar, and the more widespread, but Old World tropical Coraciidae (rollers) and Bucerotidae (hornbills) all possess the primitive condition of the stapes. In contrast, the hoopoes (Upupidae) and wood-hoopoes (Phoeniculidae) possess an "anvil" stapes (Fig. 2), which is functionally intriguing and structurally unique in the class Aves. This

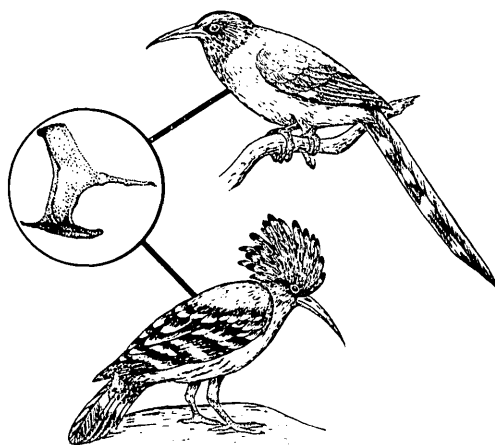


FIG. 2.—The hoopoes, represented by *Upupa* (lower), and the wood-hoopoes, represented by *Phoeniculus* (upper) are here considered to be monophyletic because of their common possession of a unique, derived "anvil" stapes, illustrated in the circle.

common derived condition argues strongly for their monophyly.

The Meropidae (bee-eaters: Old World tropics), Alcedinidae (kingfishers: nearly world wide in range), Momotidae (motmots: New World tropics, particularly Central American), and Todidae (todies: endemic to West Indies), all possess a different, derived morphology of the stapes (Fig. 3b), in which a large, hollow, bulbous basal and footplate area exhibits a large fenestra (or excavation) only on one side (the posterior aspect). The fenestra (sometimes divided) leads to a large hollow fossa; the stapelial shaft is shifted to the periphery of the footplate, thus producing a different lever system (Feduccia, 1975a). The Trogoniformes (trogons: pantropical) possess an identical derived morphology of the stapes, which argues strongly for monophyly of the trogons and the bee-eater/kingfisher/motmot/tody assemblage. Sibley and Ahlquist (1972) deduced from studies of egg-white proteins that, "... the affinities of the trogons remain obscure, but, in our opinion, the Coraciiformes should receive close scrutiny in seeking evidence of relationship."

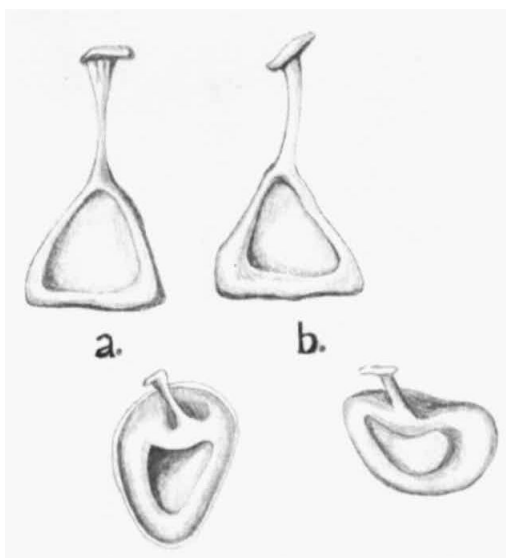


FIG. 3.—Posterior views (uppers) and views looking down upon the stapedial footplate regions (lowers) of the stapes or columellae of a, a typical suboscine passerine bird (*Tyranniformes*), and b, a typical member of the bee-eater/kingfisher/motmot/tody/trogon assemblage (*Alcediniformes*). All drawn to the approximate same size.

The trogons are probably an early offshoot of the bee-eater/kingfisher/motmot/tody assemblage which reversed digit II to the posterior to produce their unique heterodactyl foot. I propose the term *Alcediniformes* for this assemblage, including the trogons (see addendum). The type of stapes illustrated in Fig. 3b is present in all of the alcediniform birds (including the trogons); there is no indication of an intermediate condition in any of the species examined.

The order *Piciformes* is perhaps best characterized by their yoke-toed, or zygodactyl, foot arrangement, in which there are two anterior and two posterior toes, digit III being reversed (instead of II as in the heterodactyl trogons). In addition to the structurally advanced woodpeckers (*Picidae*), the order consists of a number of ancient families of perching forms, which, though once widespread in northern latitudes (Brodkorb, 1970; Feduccia, 1973; Feduccia and Martin, 1976;

Olson, 1976), are now restricted to New and Old World tropics. These include the puffbirds (*Bucconidae*: New World tropics), jacamars (*Galbulidae*: New World tropics), barbets (*Capitonidae*: pantropical), honeyguides (*Indicatoridae*: Old World tropics), and the toucans (*Ramphastidae*: New World tropics). The scansorial woodpeckers and their allies constitute a distinctive suborder *Pici*. Most forms within the *Piciformes* have the primitive condition of the stapes, but a few have derived morphologies, some with rather tubular stapes perforated by numerous fenestrae, but all have the stapedial shaft still emanating from the center of the footplate. It thus appears that within the *Piciformes* some differing morphologies of the stapes have been derived and that some evolutionary experimentation has occurred. The stapes is therefore of little use in determining the relationships of the *Piciformes* to other perching birds.

The nearly 5,000 species of "advanced" perching birds have classically been placed in a single order, the *Passeriformes*, which has been subdivided on the basis of syringeal morphology into two major divisions, the so-called "suboscines" and the "oscines." The "oscines" or suborder *Passeres* have been defined as those passerines possessing a complex syrinx with more than three pairs of intrinsic syringeal muscles, while the morphologically heterogeneous "suboscines," comprising several suborders, have an anatomically simpler syrinx (Ames, 1971). There is not total correlation between complexity of song and complexity of syringeal morphology, as the lyrebird, with its very simple syrinx is one of the world's great songsters and mimics. Phylogenetic relationships of the "Passerines" have been particularly difficult to ascertain, and their ancestry and relationships to other orders of land birds have been a complete enigma; thus, the morphology of the stapes in these forms is of particular interest.

The suboscines are thought to be the more ancient of the passerine birds be-

cause of zoogeographic (Mayr and Amadon, 1951; Amadon, 1973) and structural (Bock, 1962; Ames, 1971)¹ considerations. It was therefore surprising to discover that, whereas all of the families of oscines (sub-order Passeres) possess the primitive condition of the stapes (Fig. 1), the structurally primitive suboscines possess a unique derived stapedial morphology (Fig. 3a), differing only slightly from that of the alcediniform birds (including the trogons). The suboscine stapes, as in the alcediniforms, has a large, hollow, bulbous, basal and footplate area that exhibits a large fenestra only on one side (the posterior aspect), and the stapedial shaft is thus shifted to the periphery. The suboscine stapes is somewhat more variable within its families than that of the alcediniforms, but there is again no sign of morphological stages that approach the primitive condition. The suboscine stapes differs in only one significant aspect from that found within the alcediniforms, in the shape of the footplate (Fig. 3, lowers). In the alcediniforms the shape of the footplate is invariable, while in some suboscines the shape of the footplate resembles that of the alcediniforms, though there is no apparent pattern to this variation.

Because Old and New World suboscines have an identical, derived morphology of the stapes, these groups are probably monophyletic (Feduccia, 1974). It was of particular interest to examine the Madagascar and Australian forms thought to represent suboscine passerine birds. The suboscines of Madagascar include two species of asities (*Philepitta*)

and two species of false sunbirds (*Neodrepanis*) which are placed in a family Philepittidae. Both forms have simple syringes (Amadon, 1951), and indeed the stapedial morphology of both confirms their status as suboscines (Feduccia, 1976a); these birds probably represent very early suboscine offshoots that have survived in isolation on Madagascar. The 14 species of broadbills (Eurylaimidae) are erratically distributed over the Old World tropics, and along with the 23 species of pittas (Pittidae), also of erratic distribution throughout the Old World tropics, including Australia, are the mainstay of the Old World suboscines. Until recently, it was thought that the Australian lyrebirds (Menuridae) and scrub-birds (Atrichornithidae) and the New Zealand Wrens (Acanthisittidae) were suboscines. However, Sibley (1974) on biochemical, anatomical, and other grounds has shown that the lyrebirds are allied with the bowerbird/bird-of-paradise assemblage. Egg-white proteins of *Atrichornis* were not available, but because of anatomical similarity of the lyrebirds and scrub-birds, Sibley suggested that the two be retained close together near the bowerbird/bird-of-paradise assemblage. The stapes of the lyrebird represents the primitive condition (Feduccia, 1975b), apparently confirming its non-suboscine status. The stapes of the New Zealand rifleman (*Acanthisitta*) is also the primitive condition.

Because the present order Passeriformes is not monophyletic, I have proposed the ordinal name Tyranniformes to include the suboscines and restricted the name Passeriformes to the oscines. The question that remains is whether or not the similar morphologies of the stapes between the alcediniform and tyranniform birds are due to evolutionary relationship or convergence. One point that argues strongly for homology of the two is the fact that the stapes in both groups are bound into the middle ear cavity by a special membrane that I have termed the marginal membrane (Fig. 4). Other than the overall similarity

¹ Primitive characters found in the suboscines that support the view that they are more ancient than oscines are: simple syrinx, lack of spina externa of sternum in some forms, simple proximal end of scapula, single fossa of the humerus in all species, and variable sternal notches, including sterna with four notches in many forms. In addition, oscines possess a derived sperm morphology found in no other birds (McFarlane, 1963). For additional osteological characters that separate suboscines and oscines, see Ballman, 1973: 53.

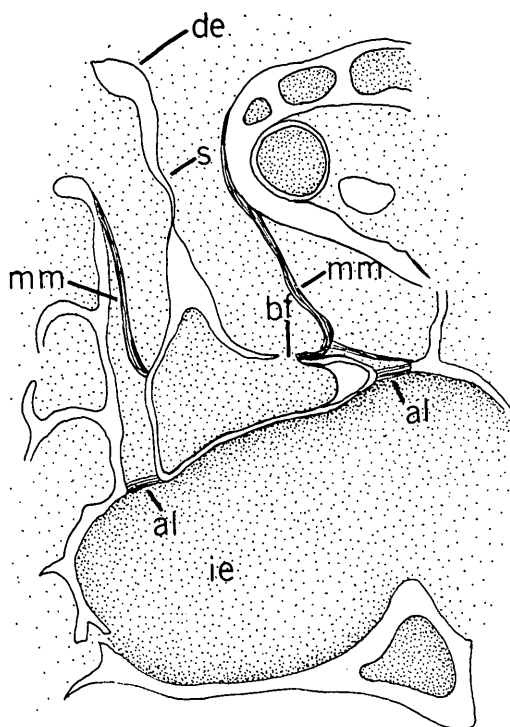


FIG. 4.—Sagittal section of the middle ear region of a suboscine (tyranniform) bird showing the marginal membrane that secures the tiny bone within the middle ear. A similar and presumably homologous membrane is found within the alcediniform assemblage. Abbreviations: de, distal end (of stapes); s, shaft; bf, basal fossa; mm, marginal membrane; al, annular ligament; ie, inner ear. The footplate extends between the annular ligament. From Feduccia (1975a).

of the stapes and the marginal membrane, no additional evidence has been proposed to suggest that the two groups are related; however, for the time being, a relationship of the Alcediniformes and Tyranniformes must remain in the form of a hypothesis. A phylogenetic hypothesis based on a diphyletic Passeriformes and homology of the alcediniform and tyranniform stapes is shown in Fig. 5.

Our inability to effectively test the phylogenetic hypotheses proposed here with previously accumulated data results for the most part from the lack of a proper framework for comparison in the past.

Workers have simply assumed that the "Passeriformes" was a natural assemblage. Future workers, particularly in biochemical and immunological studies must include alternative comparative frameworks. In a recent immunological study, Prager *et al.* (1973) compared immunological distances among transferrins within the order Passeriformes relative to Red-winged Blackbird. On their scale the oscines (excluding icterids) range from 4 to 38 ($\bar{x} = 19.4$); suboscines (broadbill, manakin, flycatcher, 2 pittas) range from 45 to 68 ($\bar{x} = 56.8$). The dramatic disparity between the suboscines and oscines is expected if we abandon the hypothesis of monophyly.

OSCINES AND SUBOSCINES

There have been two schools of thought concerning the status of suboscines. One school (see Slud, 1960; and Willis, 1966) has maintained that suboscines are not primitive within the passerine assemblage because (1) they are very successful in South America, both in terms of species diversity and adaptive radiation of morphological types; and (2) suboscines seem to be behaviorally adept in terms of competing with winter oscine migrants in the tropics. The other school, championed by Mayr and Amadon (1951) and Amadon (1973), argues that suboscines are the more primitive and have been replaced by oscines where they have been in long contact. Both schools, however, have assumed monophyly of suboscines and oscines (i.e., Passeriformes, *sensu lato*).

Suboscines are structurally primitive in most characters when compared with oscines (see footnote 1). In the Old World tropics, where suboscines have not been geographically isolated from evolving oscines, the total number of suboscines is small, and the diversity is meager, there being only two major morphological types on mainland areas. There are 23 species of pittas (Pittidae), ground-dwellers of forest or brushland floor, that are relictually distributed over many areas of the Old

The Neotropics are a different story, as there are approximately 1000 species of suboscines that represent a great diversity of morphological types in 9 families. The Neotropical suboscines were no doubt able to evolve in isolation in South America. Tropical wet forests covered much of the continent throughout much of the Tertiary (Berry, 1938; and Gill, 1961), and South America remained isolated from North America until perhaps as late as the early Pliocene (Raven and Axelrod, 1975). It must be remembered that the major Andean uplift probably did not take place until the very late Tertiary (see Haffer, 1974), providing drastic new topographic relief, new life zones, including deserts along the west coast, into which bird life could adaptively radiate; it was the suboscines that were present to invade and exploit these new habitats. The Isthmian Link connection between North and South America did not occur until early Pliocene (Raven and Axelrod, 1975), and it was probably even somewhat later that the first oscines actually invaded South America, perhaps even during the Pleistocene, when fluctuations of humid and dry periods characterized the vast Amazon Basin, resulting in very recent speciation in most of the Amazonian suboscines (Haffer, 1969; 1974). Many of the Central American suboscines are extralimital Amazonian forms. The recent massive Pleistocene speciation in the Amazon, combined with the very recent and diverse speciation in the Andes may give us somewhat of an illusion of the success of the suboscines in the Neotropics as compared with the oscines. Oscines are probably very late arrivals into South America. As Amadon (1973) has recently stated:

"All in all, I see no reason to abandon the classical view that the sub-Oscines are an early and in general less well-adapted group of Passeriformes that has persisted in South America longer than elsewhere because it was sheltered from the main wave of Oscine evolution."

The suboscines, in the form of New World flycatchers (Tyrannidae) are probably Pleistocene invaders into North America. This conclusion is indicated by a number of factors. First, suboscines are essentially absent in the West Indies, except for relatively recent invasions by some tyrant flycatchers. The suboscine avifauna of Trinidad (connected with NW South America in the Pleistocene) shows no endemism, all species are from northern South America. Second, suboscines in Central America appear (with very few exceptions) to represent not a Central American suboscine avifauna, but an extralimital suboscine avifauna from South America. Third, of more than 300 bones of passerines present in the late Pliocene Rexroad and Hagerman avifaunas (Feduccia, personal observations), none is of a suboscine, indicating that there may have been no suboscines in North America even as late as the Upper Pliocene (3.8 m.y.b.p. potassium-argon date for Hagerman; Rexroad is slightly older). If the Central American land bridge is now correctly dated at approximately 5.7 m.y.b.p. (Raven and Axelrod, *op. cit.*), the above would not be surprising. Because of relatively moderate climates in North America until the late Pliocene, and perhaps even into the Pleistocene (until the Wisconsin), it would be surprising not to have had an extensive adaptive radiation of suboscines in North America if they previously had invaded North America from the south. It would also be surprising for there not to have developed a Central American and West Indian suboscine avifauna.

To conclude, we can outline a probable history of suboscines as follows: Suboscines were probably the first attempt at an advanced passerine morphology in birds; they are probably ancient, extending back into the early Tertiary, and their ancestors were probably present in Gondwanaland before the split of the continents. They could have easily dispersed across the then-forming Atlantic Ocean, even in the Paleocene, when per-

haps no more than about 600 km separated the west coast of Africa from the eastern coast of South America, and the mid-Atlantic rift probably was dotted with volcanic islands that may have provided way stations for sweepstakes dispersal (Raven and Axelrod, 1975). Even by the end of the Eocene only 1,400 km may have separated the two continents. Six hundred km is approximately equivalent to a trans-Gulf migration route, utilized today by a number of tyrant flycatchers (Tyrannidae).

Of course, an alternative hypothesis does exist. Suboscines could have been world-wide in distribution until late Tertiary. Because of increased competition with oscines and climatic deterioration they were displaced or restricted to the present-day tropics. Suboscines may simply have become extinct in North America and the West Indies. Suboscines were once widespread in Europe as indicated by a fossil broadbill from the Middle Miocene of Bavaria (Ballman, 1969b). The Miocene was a period during which Eurasia probably had an Ethiopian avifauna; or to put it another way, Africa today has a relict Eurasian avifauna. The question of suboscine origins thus revolves around North America.

The foregoing, belabored point that the suboscines represent a more primitive and ancient form of "passerine" bird than the oscines is of great interest with respect to the stapedial morphology in the two groups and its evolutionary implications. That the more recent oscines retain the primitive condition of the stapes, while the suboscines have a derived morphology, must imply that the two groups could not have shared a common ancestor; it follows that the present order Passeriformes is a diphyletic assemblage.

Perhaps the most intriguing question raised by the foregoing model for the evolution of perching birds is the immediate ancestry of the Passeriformes (oscines). There is no modern group of birds with the primitive condition of the stapes, plus

all of the other qualifications for ancestry. Except for their zygodactyl foot, perhaps the primitive piciforms would be good candidates, both from their structure and the time of their appearance as arboreal perching birds. With Brodkorb's recent description of a Cretaceous bird apparently ancestral to the orders Coraciiformes and Piciformes (Brodkorb, 1976), one must wonder if other ancestral groups existed, intermediate between coraciiform and piciform birds, with the primitive condition of the stapes, that could have been ancestral to the Passeriformes, but which have left behind no trace of their existence. Perhaps such a bird would have at least superficially resembled the modern cuckoo-rollers (Leptosomatidae), or the rollers (Coraciidae).

THE FOSSIL RECORD

Recent discoveries of avian fossils from the Eocene of North America, combined with reanalyses of previously described fossils, provide paleogeographic support for the model proposed here for the evolution of perching birds, particularly in the Western Hemisphere. Brodkorb (1970) described a newly discovered bird from the Lower Eocene of the Green River Formation of Wyoming as the oldest representative of the avian order Piciformes. It was assigned to the structurally most primitive family of piciforms, the Neotropical Bucconidae. Because the description was based on a humerus only, it was of great interest several years later to recover a slab containing a nearly complete avian fossil from the same formation (Feduccia, 1973). It was the first avian fossil ever discovered to exhibit the yoke-toed, or zygodactyl, foot arrangement (Fig. 6). Since that time, new discoveries or reanalyses of previously described fossils have brought the total number of species of these primitive Eocene piciforms to eight, including small-, moderate-, and large-sized forms from both the Lower and Middle Eocene. In addition, one of these species, *Neanis schucherti*, was previously thought to

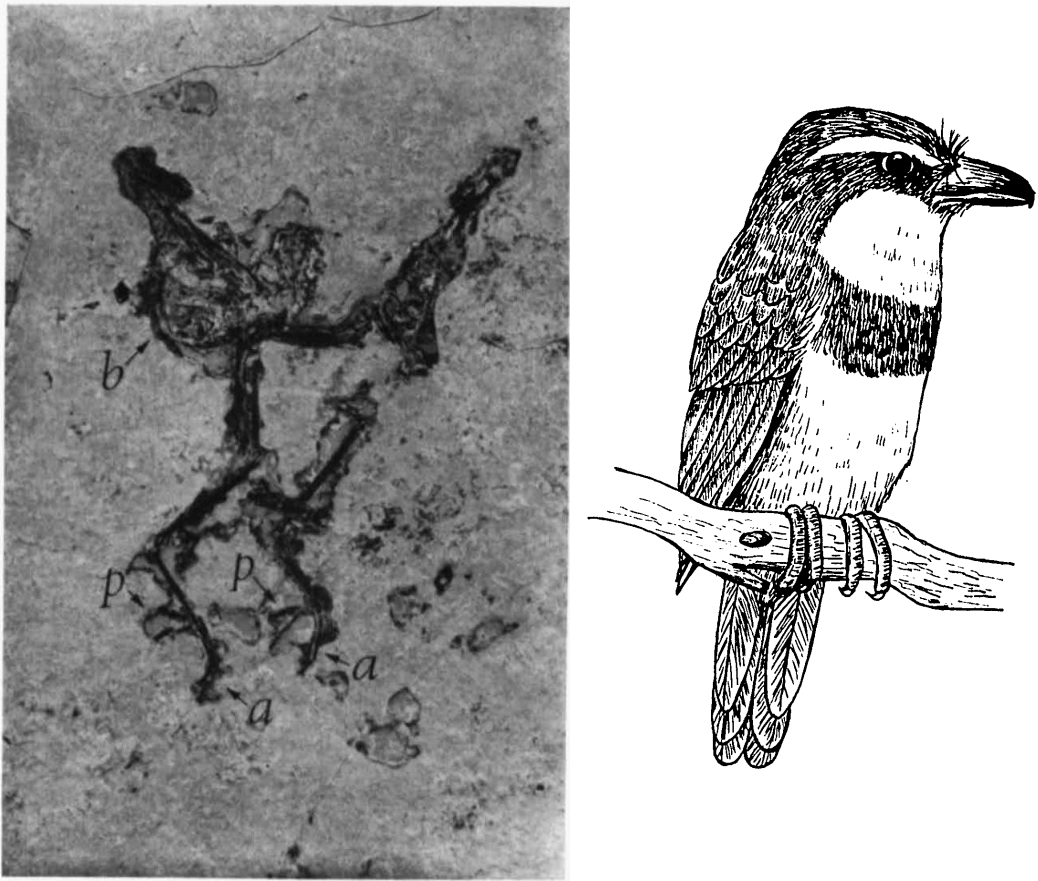


FIG. 6.—Left, the Lower Eocene fossil, *Neanis kistneri* (Feduccia), representing a primitive, perching piciform bird from the Green River Formation of Wyoming. Actual length in life was 4–5 inches. Abbreviations: b, braincase; a, anterior toes; p, posterior toes. Right, a living member of the structurally primitive piciform family Bucconidae (the Pied Puffbird, *Notharchus tectus*), now confined to the Neotropics and thought to be close allies of the North American Eocene fossil family Primobucconidae, now represented by eight species of Lower and Middle Eocene age. Note the zygodactyl (yoke-toed) foot arrangement in the living and fossil forms.

represent an Eocene passerine (Feduccia, 1976b), which would have made it the oldest representative of the order Passeriformes. The oldest passeriform from North America now is from the Upper Oligocene, and even it is of dubious identity (Wetmore, 1925). The Eocene piciforms have been described as a new family, the Primobucconidae (Feduccia and Martin, 1976). Thus, the structurally primitive piciforms were apparently the predominant and perhaps the only perching birds of the early Tertiary of North America, and the pas-

serines did not take over until the late Tertiary as the dominant perching group.

As for the Old World, supposed passerines extend back into the Eocene (Lambrecht, 1933), but their identity even to order must be reassessed. From Ballman's recent work (1969a; 1969b) it appears that as late as middle Miocene there existed a strong Ethiopian element in the European avifauna, including broadbills (Eurylaimidae), barbets (Capitonidae), members of an extinct piciform family (Zygodactylidae), wood-hoopoes (Pho-

eniculidae), turacos (Musophagidae), and passerines from faunas in Bavaria and France. Going back in time, four species of trogons are known from the Upper Eocene to Lower Oligocene of France (Brodkorb, 1971). Recently, Olson (1976) has shown that *Protornis glarninensis* from the Lower Oligocene of France is allied with the motmots (Momotidae: Central and South America), rather than with the kingfishers (Alcedinidae) as previously thought. Olson (1976) also has described a tody (Todidae: endemic to Greater Antilles) from the Middle Oligocene of Wyoming. He suggests that the Momotidae are derived from Old World stock, and that the todies are possible derivatives of the motmot stock. Both motmots and todies were probably widespread during the mid-Tertiary. With climatic deterioration and competition with more advanced "perching birds" during the late Tertiary, the motmot-tody group was entirely supplanted in the Old World and restricted to the Central American tropics and Greater Antillean tropical regions, respectively. Seven of the eleven families of the Coraciiformes and Alcediniformes are confined to the Old World. To judge from the fossil record, the trogons almost certainly originated in the Old World and probably dispersed into the New World through the Northern Hemisphere (Beringia), where they were forced southward by late Tertiary climatic deterioration. Trogons are not South American even today, their distribution is centered more in the Central American-West Indian region. In Central America and the West Indies there are 16 species in 5 genera; in South America, 14 species in 2 genera. Extralimital South American forms in Central America, and extralimital Central American forms in South America nearly cancel out. So, it appears that the trogons follow a similar pattern as the motmots and todies, that of retreat to the south with late Tertiary climatic deterioration. In addition, of approximately 89 modern species of kingfishers (Alcedinidae), only six (2 genera)

are found in the New World (Olson, 1976). The coraciiform and alcediniform groups are most probably of Old World origin.

As the Eocene of North America was a period during which the Piciformes were the dominant perching birds, so the Oligocene of the Old and New Worlds was equally a period of importance, if not predominance, of the Alcediniformes. And, while passerines may have been in the Old World in early to mid-Tertiary, they almost certainly did not become predominant in the New World until at least Miocene times, and perhaps even later.

Also, while the suboscines extended into Europe (and presumably Eurasia) during the mid-Tertiary (Ballman, 1969b), the same may not be true of the New World, as discussed before. The primitive oscines that were to give rise to the New World oscine radiations probably utilized the Bering route as a major dispersal corridor (Cracraft, 1973). Apparently North America did not reciprocate with Eurasia to any significant degree. Early piciforms might be an exception, but they could have utilized either Beringia or the North Atlantic.

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ADDENDUM

Brodkorb (pers. comm.) has kindly pointed out that the ordinal names that I have used here and

previously (Feduccia, 1975a) do not follow priority. If priority is followed, then Tyranniformes becomes Eurylaimiformes, and Alcediniformes has a number of possibilities, with perhaps Halcyoniformes being the best choice. I chose Tyranniformes and Alcediniformes because of euphony, common usage, and the fact that both are names of subgroups containing large numbers of species. The classification proposed here is as follows:

- Order Piciformes, woodpeckers and allies
- Order Coraciiformes, rollers, ground-rollers, and cuckoo-rollers
- Order Upupiformes, hoopoes and wood-hoopoes
- Order Bucerotiformes, hornbills
- Order Alcediniformes
 - Superfamily Meropoidea
 - Family Meropidae, bee-eaters
 - Superfamily Alcedinoidea
 - Family Alcedinidae, kingfishers
 - Family Momotidae, motmots
 - Family Todidae, todies
 - Superfamily Trogonoidea
 - Family Trogonidae, trogons
- Order Tyranniformes, suboscine or tyranniform birds
- Order Passeriformes, oscines or passeriform birds

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