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COMMENTS ON THE PHYLOGENY OF PERCHING BIRDS

Alan Feduccia

Abstract.—The bony stapes (columella) is a unique character in birds in that the primitive condition is the retained reptilian condition of the element, and derived "pockets" of stapedial morphologies occur that may be of importance in clarifying certain phylogenetic relationships. Scanning electron micrographs (SEM's) of various views of stapes of suboscines, certain coraciiforms and trogons are here presented and reveal with clarity the manifest differences betweeen suboscines and the alcediniform coraciiforms. These new data, combined with new data from sperm morphology of suboscines, suggests that the Passeriformes is a monophyletic assemblage, that the suboscine and alcediniform stapes evolved independently, and that the suboscines are more closely related to the oscines than to the alcediniforms.

In a previous paper (Feduccia, 1977), I proposed a hypothetical phylogeny of the passerines and related avian groups, birds that have presented difficult phylogenetic problems because of their morphological uniformity and the probability of massive convergent evolution. My reconstruction was based primarily on the discovery of a new avian taxonomic character, the configuration of the bony stapes or columella, which had until recently been overlooked because of its minute size (one to several mm) and its location in the recesses of the middle ear cavity. In addition, it is often broken or lost in skeletal preparations. The avian stapes is perhaps unique as an avian morphological character in that the primitive condition is the retained reptilian stapedial morphology, which is characteristic of most groups of birds. In some groups, however, the stapes exhibits peculiar derived morphologies. Where these "pockets" of derived stapedial morphologies are found they are considered as strong indications of evolutionary affinity, unless there are compelling reasons to assume that the morphological similarities are due to convergent evolution.

I made the following broad conclusions (Feduccia, 1977). First, the hoopoes (Upupidae) and wood-hoopoes (Phoeniculidae) are monophyletic within the Coraciiformes (*sensu* Wetmore 1960); previously there was considerable dispute as to their relatedness. These two families are characterized by a stapedial morphology that is termed the "anvil" stapes and is illustrated in Fig. 1. Second, the coraciiform families containing the bee-eaters (Mer-

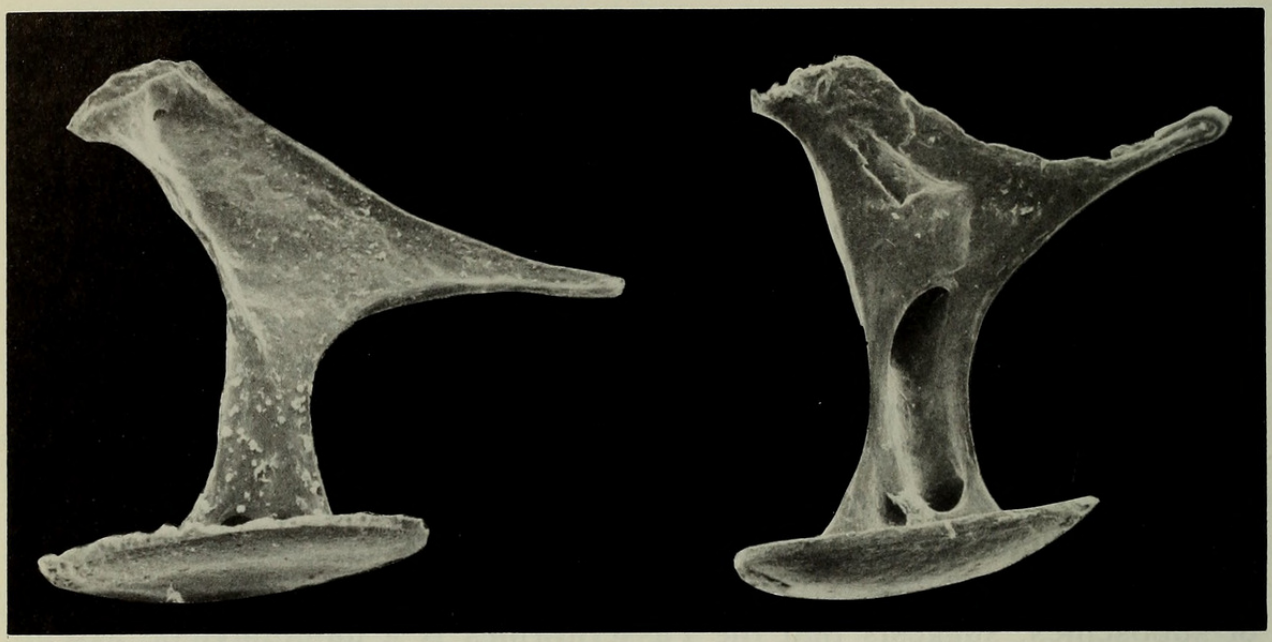

Fig. 1. Views along the lengths of the bony stapes of a hoopoe (*Upupa epops*), **left**; and a wood-hoopoe (*Phoeniculus purpureus*), **right**. SEM's × 40, and reduced here ×1/3.

opidae), kingfishers (Alcedinidae), motmots (Momotidae), and todies (Todidae) all possess a peculiar derived stapedial morphology characterized by a bulbous footplate (with particular conformations; see Feduccia, 1975) that is shared with the trogons (Trogonidae). I concluded that this bee-eater/kingfisher/motmot/tody assemblage is monophyletic, and that the trogons are allied with it. Trogons had until then been placed in a monotypic order, the Trogoniformes, and there was little but speculation as to their phylogenetic relationships. I proposed that these families (including the trogons) be combined in a separate order Alcediniformes close to the old order Coraciiformes, clearly their sister group. The separation of the Alcediniformes as a distinctive order is a matter of personal taxonomic preference. Figure 2 illustrates three views of the stapes of a kingfisher, *Ceryle rudis*, and a trogon, *Priotelus temnurus*. There is more stapedial variation within the families of the coraciiform "alcediniforms" than between the trogon and kingfisher illustrated here.

The third conclusion, which now demands modification in view of new evidence that has recently come to light, was that the suboscines (classically the suborder Tyranni of the Passeriformes) and the oscines (Passeres) did not share an immediate common ancestor, and that the classical order Passeriformes was not monophyletic.

The point focal to the discussion of passerine relationships involves the fact that while the morphologically uniform (and presumably more advanced structurally) oscines retain the primitive condition of the stapes, the suboscines have a derived stapedial morphology characterized by a bulbous footplate region with certain peculiarities. Suboscines, structurally more prim-

itive than oscines, are a real "South American" group that has been eliminated in the Old World (presumably by competition with oscines) except for two highly specialized, small families, the Pittidae and Eurylaimidae, and some relicts restricted to Madagascar. My point was that although the suboscines and oscines exhibit many osteological and other similarities, the stapes of suboscines was more similar to that of the "alcediniforms" than to the oscines (though different from the former). Since then, however, information has forced me to view the hypothesis of a polyphyletic order Passeriformes as improbable.

Scanning electron micrographs (SEM's) of suboscine and alcediniform stapes reveal many differences, especially in the footplate region (Figs. 2 and 3), which do not argue for homology of the two and, in fact, would seem to indicate a high probability that the two morphologies evolved independently. In the alcediniforms there is a relatively much larger footplate fossa that is more rounded and bulbous in appearance. The major difference, however, is seen in the conformation of the footplate (Fig. 3). In the alcediniforms the region of the footplate near the shaft of the stapes is smoothly rounded, so that when these specimens are placed in a depression slide filled with liquid, the large fossa will face upward. In the suboscines the same region tapers to a point, so that when suboscine stapes are placed in a similar preparation the fossa turns and lies to one side.

We (Henley *et al.*, 1978) have revealed characters in oscine sperm that make the group perfectly definable. Oscines have non-motile sperm that occur in bundles in the testes when placed in warm saline; other birds have non-bundled motile sperm within the testes under similar conditions. In addition, in oscine sperm cross sections are characterized by a tripartite structure of an undulating membrane. The components are a relatively straight axoneme with the 9 + 2 arrangement of the microtubules, a helically wound strand of mitochondria, and a longitudinal array of singlet microtubules. These sperm are highly derived and unique among vertebrates. At the time of our study we had not examined suboscine sperm, but I have recently discovered that suboscines have the sperm bundles (Fig. 4) characteristic of, and previously thought to be unique to, the oscines. Only two species, the Eastern Wood Pewee (*Contopus virens*) and the Eastern Kingbird (*Tyrannus tyrannus*) have been examined, but because of the uniformity observed and the extreme difficulty in making these preparations, it was felt that the data should be presented here.

The ultrastructure of suboscine sperm (Fig. 5) while showing an undulating membrane, is different in many important details from that of oscines. Suboscine sperm differ in the geometry of the microtubules that surround the axoneme. The axoneme is separated from the bundle of singlet microtubules by double plasma membrane as indicated in Fig. 5, and the entire unit is surrounded by another plasma membrane. In addition, the singlet

Fig. 2. Three views along the lengths of the bony stapes of: **right**, a trogon (Trogonidae: *Priotelus temnurus*), **middle**, a kingfisher (Alcedinidae: *Ceryle rudis*), and **left**, a suboscine (Cotingidae: *Rupicola peruviana*). SEM's were taken so as to have all to the approximate same scale; they are from approximately ×25–×35, and are here reduced ×1/3.

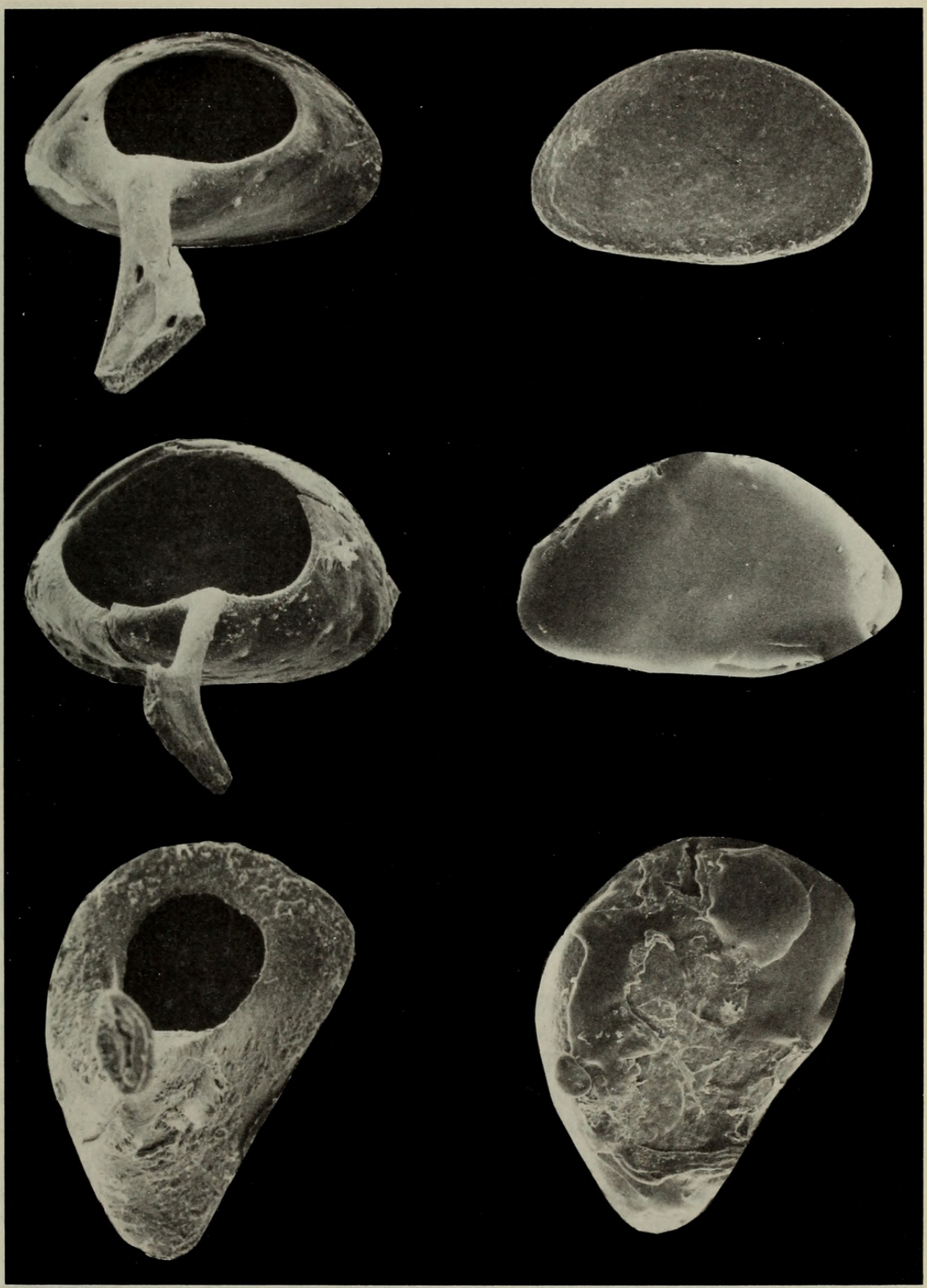

Fig. 3. Views of the tops, **left**, and bottoms, **right**, of the footplates (region of insertion into the oval window) of, from upper to lower, a trogon, kingfisher, and suboscine (same as in Fig. 2). SEM's are from ×45–×55, and are here reduced ×⅓.

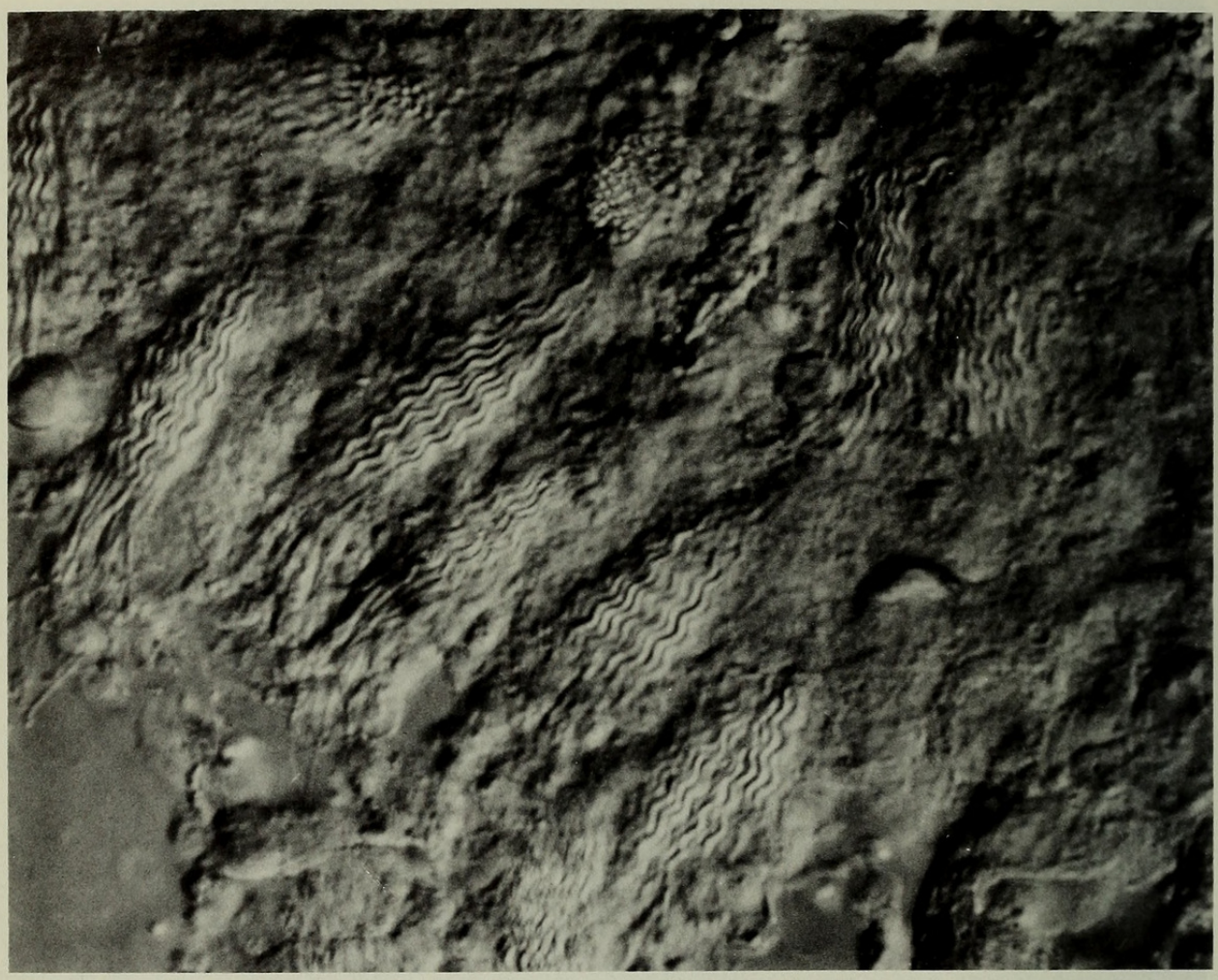

Fig. 4. Zeiss differential interference contrast micrograph of several bundles of spermatozoa from the Eastern Wood Pewee (*Contopus virens*). Approximately ×700.

microtubules are not arranged in a helical array with a mitochondrial component bound around the axoneme, and a mitochondrial component is not distinguishable. The undulating membrane characteristic in light microscopy of both oscine and suboscine sperm is due in the former case to a helically wound tripartite membrane, in the former to an undulating band of singlet microtubules that completely surround the axoneme. These data would not support a polyphyletic order Passeriformes, but would suggest that a common ancestor had already evolved the sperm bundling and that the details of the ultrastructure underwent different changes in the two lines of evolution.

It might be added that while there is currently no completely satisfactory definition of the Passeriformes, most have characteristic "aegithognathous" palates and are generally similar osteologically. From the foregoing it now seems to me more probable that the order Passeriformes is monophyletic and the similar suboscine and alcediniform stapes evolved independently. This revised view would envisage a common ancestor for the suboscines and oscines before the late Cretaceous split of Gondwanaland, suboscines

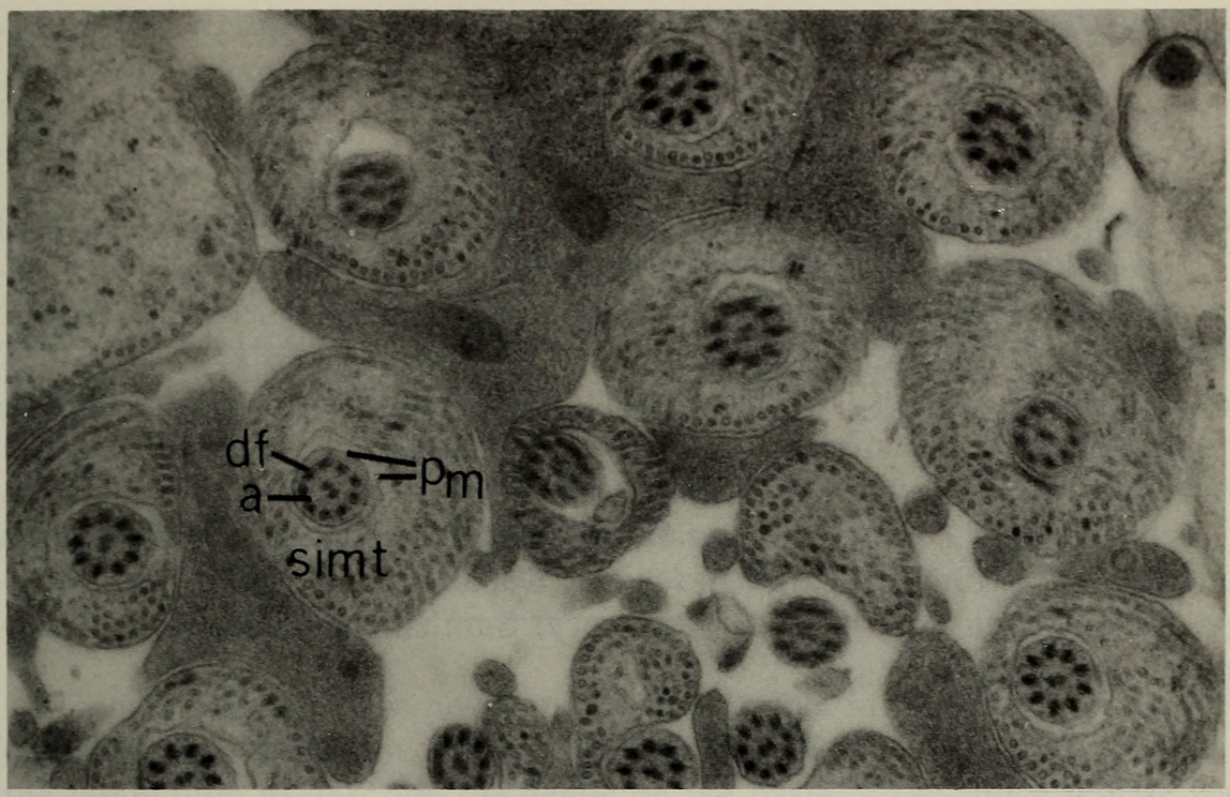

Fig. 5. Electron micrograph of a transverse section through a bundle of spermatozoa of the Eastern Wood Pewee (*Contopus virens*) at a level posterior to the region of the nuclei. Abbreviations are as follows: **simt**, singlet microtubules; **pm**, plasma membrane; **df**, dense fibers; and **a**, axoneme. Approximately ×27,000.

as a Southern Continent group, and oscines evolving in the Old World and not getting into South America before the rifting of the southern continents.

Perhaps the most instructive insight into passerine relationships that the stapes has shown is that: (1) New World suboscines and Old World forms (Eurylaimidae, Pittidae and the Madagascan Philepittidae) are part of a monophyletic group, (2) oscines and suboscines are very distinctive groups, easily separable from one another, and (3) the two groups are separated by a broad and ancient evolutionary gulf. It may also be among the coraciiforms rather than piciforms that we need to search for the true sister group of the passerines.

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Department of Zoology, University of North Carolina, Chapel Hill, North Carolina 27514 (and Research Associate, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560).