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**Morphology of the Bony Stapes  
(Columella) in the Passeriformes  
and Related Groups:  
Evolutionary Implications**

By

**Alan Feduccia**

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Morphology of the Bony Stapes (Columella)  
in the Passeriformes and Related Groups:  
Evolutionary Implications

BY

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## INTRODUCTION

The avian ear is of particular interest in that, although it is anatomically similar to the reptilian ear in basic structure, its sensitivity surpasses its reptilian counterpart and may even approach that of the anatomically more complex mammalian system (Manley, 1971 and 1972; Pumphrey, 1961; Schwartzkopff, 1968). Most recent studies have focused on the avian inner ear (see Konishi, 1969a, 1969b, 1970; Schwartzkopff, 1955a, 1955b, 1968), while relatively little work has been directed toward increasing our knowledge of the middle ear system, either anatomically or functionally.

The external and middle regions of the avian ear function primarily to transform aerial sound waves into fluid vibrations in the inner ear, which in turn transmits this information via the eighth cranial nerve to the higher neural centers. This transformation is accomplished first by passage of sound waves into an external ear opening. From the external ear the sound waves hit the tympanic membrane and are then transmitted through a series of cartilaginous extra-stapedial (-columellar) structures to the bony stapes or columella, which eventually terminates in a bony footplate at its junction with the oval window of the inner ear (Fig. 1).

The developmental stages and evolutionary homologies of the avian stapes, or columella auris, have been carefully studied and reported by various authors, most importantly by Brock (1932), de Beer (1937), Goodrich (1930), and Huxley (1869), and have been summarized and evaluated by Crompton (1953). Frank and Smit (1974) have presented a similar account for *Crocodylus*. All consider the entire columella auris to represent a derivative of the upper portion of the hyoid arch (II). In tetrapods (including birds) the columella auris develops from two centers, pharyngo- and epihyal elements, often

called "otostapes" and "hypostapes." In essence, the development, and for a large part the basic adult morphology of the avian stapes is typically reptilian. The skeletal structures of the columellar apparatus are in a broad way homologous to the hyomandibular cartilage (or bone) in fishes and the innermost ossicle of the mammalian middle ear, the stapes. However, both fish hyomandibular and mammalian stapes are single developmental elements, while the reptilian and avian columellar apparatus is a compound structure, consisting of both an extrastapedial portion which connects to the tympanic membrane, and a stapes proper, the footplate of which inserts into the oval window and is attached to the latter by the annular ligament (Fig. 1). A number of ligaments, as well as a tensor tympani muscle, are attached to the shaft of the stapes or the extrastapedial processes. The round window is situated just posteroventral to the oval window and at an approximate angle of 45° to it (Smith and Takasaka, 1971). It is of interest that the avian stapes lies at an acute angle with respect to the tympanic membrane; this results in a lever-like movement rather than a pistonlike action (Pumphrey, 1961).

There has been some confusion as to whether to call the avian ossicle a columella (indicating homology with the amphibian and reptilian element) or stapes (indicating homology with the mammalian innermost ossicle). As Romer (1956: 416) pointed out of the reptilian stapes, "Its medial portion is a rodlike bone, generally quite slender; this is commonly termed the columella auris; since however, it is thought that this bone is at least partially homologous with the mammalian stapes, it is frequently known by that name . . ." Pumphrey (1961: 78) distinguished the columella as, ". . . composed partly of bone (stapes) and partly of cartilage

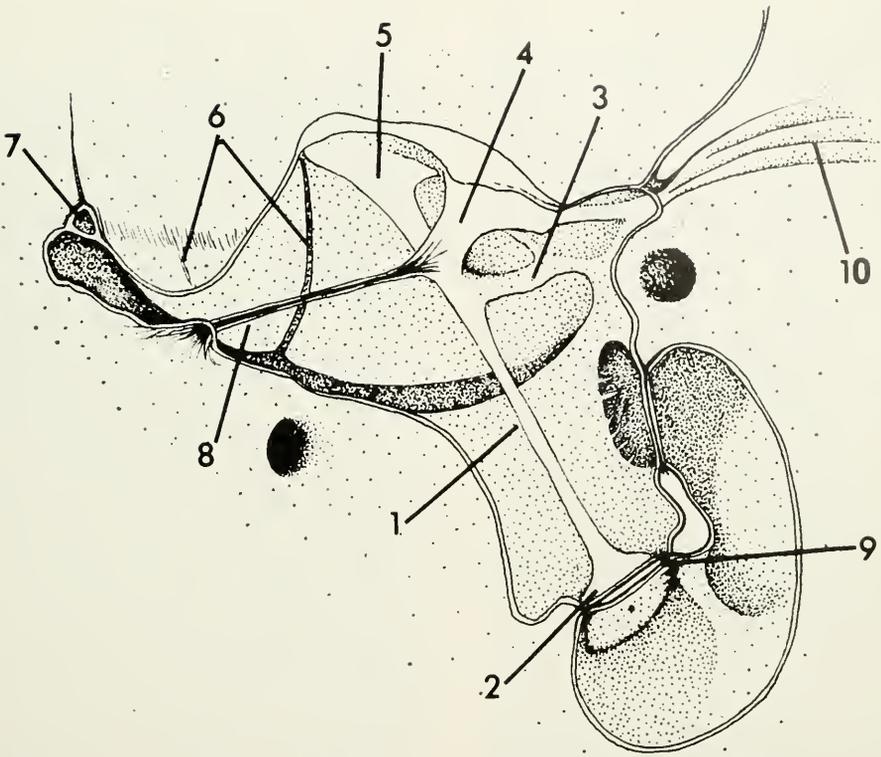


FIG. 1.—Sagittal section of the middle ear region of *Gallus*. 1, shaft of stapes (columella); 2, footplate; 3, infrastapedial cartilage; 4, suprastapedial cartilage; 5, extrastapedial cartilage; 6, middle drum-tubal ligament; 7, drum-marginal air sinus; 8, columellar-squamosal ligament; 9, annular ligament; 10, tensor tympani muscle. Redrawn and modified after Pohlman (1921).

(extrastapes) . . .” Because this paper deals only with the bony rod and footplate of the columella auris, I prefer to use the term bony stapes or simply stapes in describing the element. The nomenclature of the stapes has been described and figured by Krause (1901); the major features are illustrated here (Fig. 2), and new English terms are applied to the parts of the stapes.

Most of the work on the middle ear of birds was published before 1920 (see Gadow, 1889; Huxley, 1869; Krause, 1901; Parker, 1875; Pohlman, 1921; Pycraft, 1908; and Smith, 1904), and involved primarily a cursory view of the gross anatomy of the ear in large birds, such as domestic chickens, water birds, owls, etc., which were easily studied. The only comparative study of the stapes

was done by Krause (1901) who examined approximately 70 species. During my studies of suboscine passerine birds (Feduccia, 1973) I examined the dried bony stapes in a number of families, and much to my surprise discovered that the morphology of the stapes was quite distinctive from that of the oscine passerines. I reported this in an earlier paper (Feduccia, 1974). This study showed that the New and Old World suboscines shared a common derived morphology of the stapes, and therefore presumably a common ancestor. Subsequently, I have completed my study of the stapes in the passerines and related groups, and here present my findings on the morphology of the stapes and its evolutionary implications in these groups.

## ACKNOWLEDGMENTS

I am particularly indebted to Dr. R. W. Storer (University of Michigan Museum of Zoology), and Dr. Richard L. Zusi (U. S. National Museum) for permitting me to extract stapes from skeletal collections under their care. Dr. Robert M. Mengel (University of Kansas) permitted me to examine specimens under his care. Mr. John Cameron provided invaluable help in the sectioning of oscine and suboscine ear regions (Fig. 6), and Mrs. Yvonne Lee skillfully rendered the illustrations for Figures 1, 2, 4, and 5. Much of this study was supported by grants from the University of North Carolina Research Council. I wish to thank Drs. Frank B. Gill, Douglas M. Lay, Helmut C. Mueller, Robert W. Storer, and Richard L. Zusi for their critical review of the manuscript.

## ASSUMPTIONS

Two major assumptions are made in this paper. First, it is assumed that the type of stapes found in the majority of birds (most of the nonpasserine orders, and the suborder Passeres of the Passeriformes) is homologous with the same element in reptiles (see Baird, 1970, for a description of the reptilian middle ear), and with its flat footplate and slender bony shaft (Fig. 2) represents a retained primitive condition of the element. Second, it is assumed that where derived morphologies of the stapes occur they are indicative of evolutionary relationships, unless there are compelling reasons to assume convergence.

## VARIATION OF THE PRIMITIVE CONDITION

Considerable variation characterizes the primitive condition of the stapes, most of which involves the relative shape and size of the footplate and bony shaft. The ratio of size of the cardrum to size of the footplate seems to correlate with functional acuity of the ears, as owls and song birds have very high

ratios. In contrast, diving birds have robust stapes with large footplates (Schwartzkopff, 1968). It does not seem profitable to search for evolutionary affinities using characters correlated with size of footplate or variation in the shaft. Therefore, only a primitive condition is recognized for the purposes of this paper; it is defined in general as a stapes similar to that illustrated in Fig. 2, in which the footplate is flat, and the shaft is a straight bony rod emanating approximately from the center of the footplate. The stapes of the kiwi, *Apteryx* (Fig. 3), illustrates the primitive condition of the avian stapes. In this case the basal struts and fossae are absent, and the shaft runs directly into the footplate. Many oscine passerine birds have similar stapes (Plates 11-13), but the form may vary from the extreme illustrated in Fig. 3 (e.g., Plate 11e,f) to one in which basal struts and fossae are well developed (e.g., Plate 11e,d). In addition, many oscines exhibit a thin but wide shaft that connects to the footplate by a number of basal struts (e.g., Plate 12e,f). In all cases, however, the shaft connects to the footplate at its center; this is an important character with respect to the type of level system.

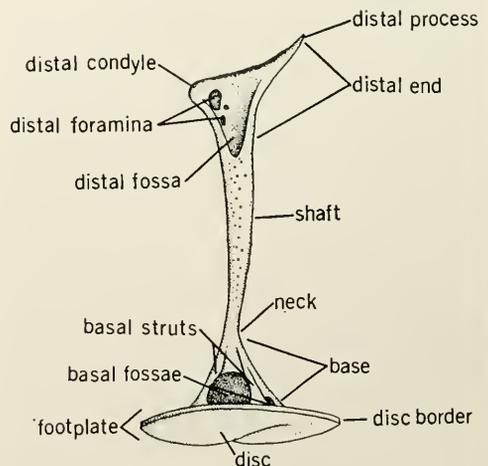


FIG. 2.—Diagrammatic drawing of a lateral view of the primitive condition of the avian stapes. Terminology is that of the author. Redrawn from Krause (1901).

### OCCURRENCE OF THE PRIMITIVE CONDITION

I have examined specimens of a large number of genera and species of all the living nonpasseriform families. Only the primitive condition occurs in the vast majority of birds. Slightly derived morphologies of the stapes were found in certain Procellariiformes, Pelecaniformes, Ciconiiformes, and Falconiformes; these will be covered in a separate paper. All of the ratites, the gaviiforms, and podicipediforms, most ciconiiforms (except storks), all anseriforms, most falconiforms (except some eagles), all galliforms, all gruiforms, all charadriiforms, all columbiforms, all psittaciforms, and all musophagiforms possess the primitive condition, essentially as illustrated in Fig. 3. In addition, slightly derived morphologies are found in certain cuculiforms, strigiforms and caprimulgiforms; these will be covered in a separate paper. This paper focuses on the morphology of the bony stapes in the Apodiformes, Coliiformes, Trogoniformes, Coraciiformes, Pici-

formes (all *sensu* Wetmore, 1960), and the "suboscine" passeriform birds, the suborders Eurylaimi and Tyranni.

### METHODS AND MATERIALS

The bony stapes (excluding the cartilaginous extrastapedial structures) may be extracted from museum skeletal specimens, prepared and studied without damage to the skeleton itself. The stapes is extracted by placing several drops of a 50% glycerine solution over the stapes and oval window area. Extraction is accomplished under a dissection scope with the aid of very fine forceps. Stapes are stained for one half hour in a solution of approximately 5% alizarin red S and sodium hydroxide, and stored in a vial filled with a solution of 50% glycerine. The bone (which is extremely fragile in the dried state) becomes pliable, and the stain facilitates observation of minute details under ordinary light microscopy. Most stapes of passerines and related groups are usually several millimeters in length (but often slightly larger). For the purposes of this paper I attempted to photograph stapes under an M5 Wild dissecting scope, each at approximately the same size, so that size would not influence the comparisons.

I prepared several stapes for scanning electron microscopy (see Feduccia, 1974), but the procedure is expensive and provides no new information about the element.

The ear regions from specimens of *Hylocichla mustelina* (Timaliidae: Turdinae) and *Dendrocolaptes certhia* (Furnariidae: Dendrocolaptinae) were removed from alcoholic specimens, decalcified, and embedded in paraffin for sectioning. Sagittal sections were made with a rotary microtome at thicknesses of 10  $\mu$ , and stained with hematoxylin for five to ten minutes. These sections, illustrated in Fig. 5 were redrawn from photomicrographs. The sections were made to determine if the area of the attachment of the stapes to the oval



FIG. 3.—Photograph of the stapes of the kiwi, *Apteryx*, to illustrate the primitive condition.

windows varies between the suboscines and oscines. A variety of nonpasserine specimens were dissected to compare with these findings.

More than 2,000 specimens, representing nearly all of the living families of birds (and a majority of the genera), were examined in the collections of the U.S. National Museum, the University of Michigan Museum of Zoology, and the University of Kansas Museum of Natural History. Although only slightly fewer than 1,000 specimens of stapes were extracted and prepared, one can easily determine the form of the stapes by simply examining a skeleton under a good dissecting scope; this was done for most of the forms examined. Right stapes are not distinguished from left in this paper. Except perhaps in some owls they are mirror images of each other, and in most cases are not distinguishable (see Plate 3); second, stapes are extremely difficult to extract and frequently only one will remain in skeletal specimens, either right or left. Third, stapes are frequently encountered in skeletal boxes, having dropped out of the skull. I have attempted to resolve any problems where they were clearly evident by reversing the side of the negatives for printing; this procedure seems to have solved most of the potential problems.

#### A "SINGLE CHARACTER" PHYLOGENY

In recent years there have been a considerable number of studies that focused on the variation and evolution of single characters or character complexes. These include papers on the bacula of mammals (Burt, 1960), the palatine process of the premaxilla of the Passeres (Bock, 1960), the pneumatic fossa of the humerus in the Passeres (Bock, 1962), avian sperm (McFarlane, 1963), sternal notches of passerine birds (Heimerdinger and Ames, 1967), the amphirhinal condition in passerine birds (Feduccia, 1967), middle ear walls and cavities in some microtine rodents (Hooper, 1968) and the syrinx in pas-

serine birds (Ames, 1971), to mention only a few. Some of the above studies found nothing more than what seemed to be meaningless and fortuitous variation along a broad spectrum of possible forms, while others resulted in the reconstruction of "single character phylogenies."

Most of the above studies failed to establish the nature of the primitive condition for the particular character under consideration. Conclusions based on comparison of what may be primitive states of characters are invalid indices of evolutionary relationships, because retention of the primitive condition of a character carries no phylogenetic information. For that reason, the bony stapes represents an exceptional character, for determining the primitive state presents no problem; it is in essence the reptilian form of the element. Therefore, where pockets of "derived" morphologies of the stapes occur they may provide important clues to evolutionary relationships, particularly in the enigmatic Passeriformes and related groups where so few reliable characters are known.

The cladistic approach, often termed phylogenetic systematics (Hennig, 1966; also see Cracraft, 1972) is followed to some degree in this paper, but principally in establishing relationships based on derived rather than primitive characters. In birds, establishing primitive and derived sequences for most characters, and establishing the directionality of the trends, is often nearly impossible. In this paper groups are assumed to be allied on the basis of similar "derived" morphologies on the stapes. It is assumed that this approach will provide the correct phylogeny unless the characters are of multiple origin.

#### MORPHOLOGY OF THE STAPES<sup>1</sup>

##### Apodiformes

The apodiform stapes (Plate 1, a-k)

<sup>1</sup>The number of specimens examined in each order is given in Table 1.

is uniform and represents the primitive condition for birds. However, the shaft is typically a relatively shorter and more robust structure than that of most oscine passerines.

### Coliiformes

All four species of the genus *Colius* examined have the primitive condition of the stapes (Plate 1, 1).

### Upupiformes

All of the hoopoes (*Upupidae*) and wood-hoopoes (*Phoeniculidae*) examined possess an "anvil" type of stapes (Fig. 4), which represents a derived stapes unique to birds, and is in a sense convergent with the middle bone in the mammalian ossicular chain, the incus (anvil). The form of the upupiform stapes is reported elsewhere (Feduccia, 1975a), where I recommended ordinal status for the two families because of the unique nature of the stapes, and the lack of evidence relating them to other coraciiform families.

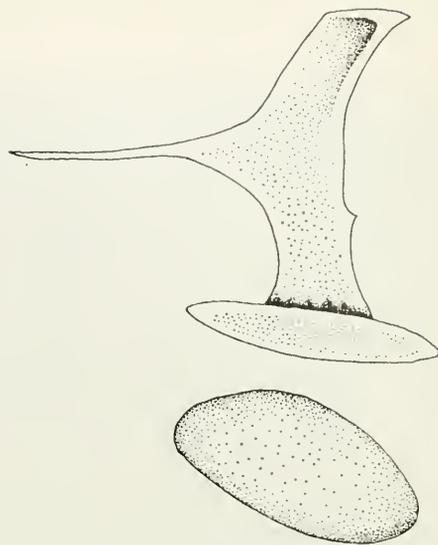


FIG. 4.—Camera lucida drawing of the "anvil" type of stapes that characterizes the Upupiformes (*Upupidae* and *Phoeniculidae*). The complex lever of this stapes appears to be convergent in a functional sense with the mammalian incus (anvil).

### Leptosomatidae, Brachypteraciidae, and Coraciidae

The cuckoo-rollers (*Leptosomatidae*), *Leptosomus* (Plate 2, a), ground-rollers (*Brachypteraciidae*), *Atelornis* examined (Plate 2, b) and true-rollers (*Coraciidae*), *Coracias* and *Eurystomus* (Plate 2, c-f), all exhibit the primitive condition.

### Bucerotidae

Most of the hornbills exhibit the primitive condition (Plate 2, g), but in some the basal struts are well formed (Plate 2, h), and in a few (e.g., *Buceros*) the basal struts are welded together to present a basal tubular effect (Plate 2, i).

### Trogonidae, Alcedinidae, Todidae, Meropidae, and Momotidae

All of the species of trogons examined exhibit a derived morphology of the stapes not diagnostically different from the same element in the coraciiform families *Alcedinidae*, *Todidae*,

TABLE 1.—FAMILIES OF THE GENERA AND SPECIES OF SPECIMENS EXAMINED.<sup>1</sup>

|                         | Number examined |         |
|-------------------------|-----------------|---------|
|                         | Genera          | Species |
| Apodidae .....          | 4               | 12      |
| Hemiprocnidae .....     | 1               | 1       |
| Trochilidae .....       | 12              | 32      |
| Coliidae .....          | 1               | 4       |
| Trogonidae .....        | 6               | 20      |
| Alcedinidae .....       | 9               | 28      |
| Todidae .....           | 1               | 2       |
| Momotidae .....         | 6               | 7       |
| Meropidae .....         | 4               | 7       |
| Coraciidae .....        | 3               | 10      |
| Leptosomatidae .....    | 1               | 1       |
| Brachypteraciidae ..... | 1               | 1       |
| Upupidae .....          | 1               | 1       |
| Phoeniculidae .....     | 2               | 3       |
| Bucerotidae .....       | 9               | 20      |
| Galbulidae .....        | 3               | 6       |
| Bucconidae .....        | 6               | 10      |
| Capitonidae .....       | 10              | 23      |
| Indicatoridae .....     | 1               | 4       |
| Ramphastidae .....      | 5               | 19      |
| Picidae .....           | 15              | 26      |
| Jyngidae .....          | 1               | 1       |

<sup>1</sup> Specimens of passerines are listed elsewhere (Feduccia, 1974).

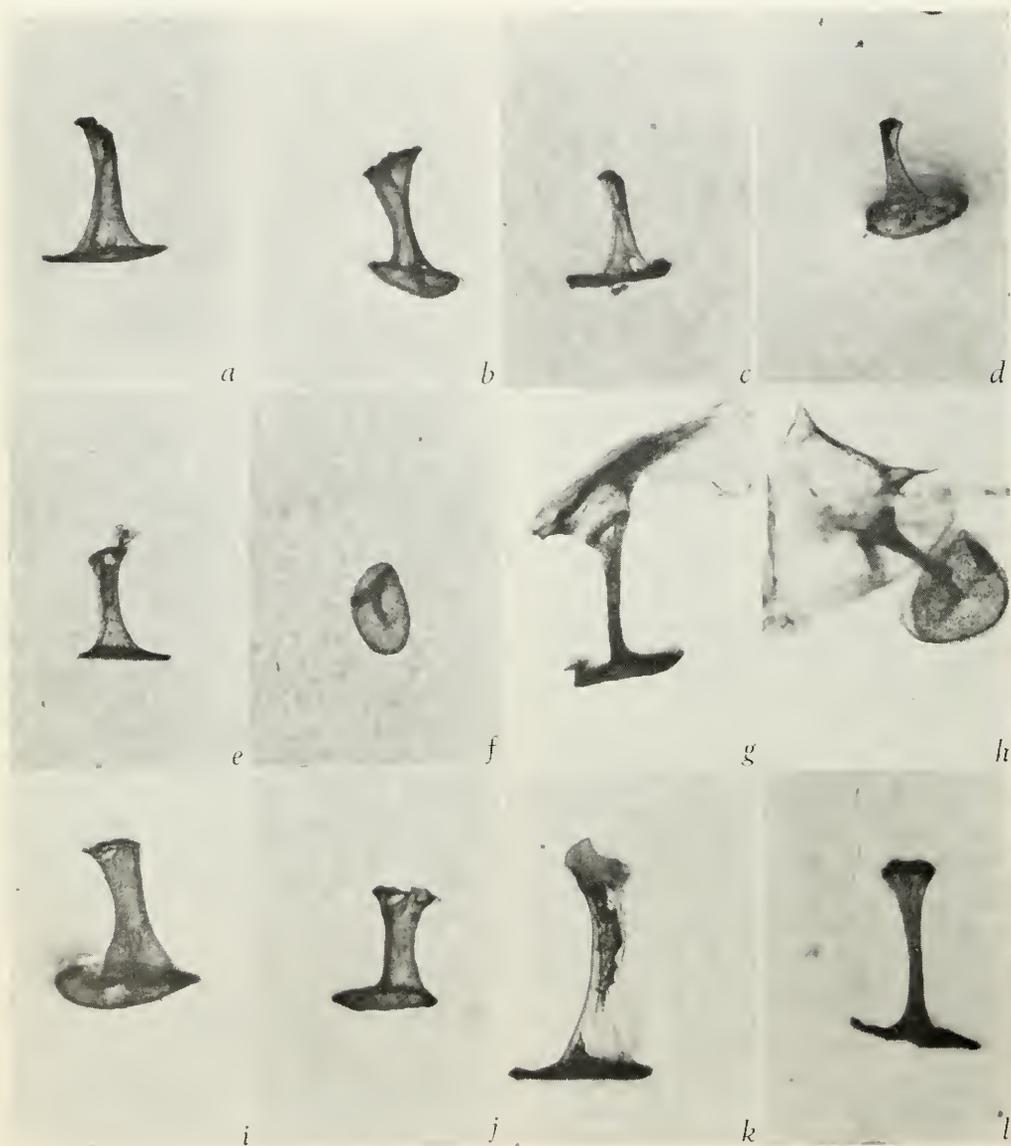


PLATE I

Photographs of the stapes of the Apodiformes and Coliiformes. Trochilidae: *a* & *b*, *Patagona gigas*; *c* & *d*, *Phaethornis superciliosus*; *e* & *f*, *Phaeochroa cuvierii*; Hemiprocnidae: *g* & *h*, *Hemiprocne coronata*; Apodidae: *i*, *Chaetura pelagica*; *j*, *Collacalia troglodytes*; *k*, *Aeronautes saxatalis*; Coliidae: *l*, *Colius striatus*. All stapes in this and the following plates were photographed to approximately the same size,  $\times 15-40$ .



PLATE 2

Photographs of the stapes of the Leptosomatidae, Brachypteraciidae, Coraciidae, and Bucerotidae. Leptosomatidae: *a*, *Leptosomus discolor*; Brachypteraciidae: *b*, *Atelornis pittoides*; Coraciidae: *c*, *Coracias temminckii*; *d*, *Coracias caudatus*; *e*, *Coracias noevia*; *f*, *Enrystomus glaucurus*; Bucerotidae: *g*, *Tockus flavirostris*; *h*, *Bereuicornis albocristatus*; *i*, *Buceros bicornis*.

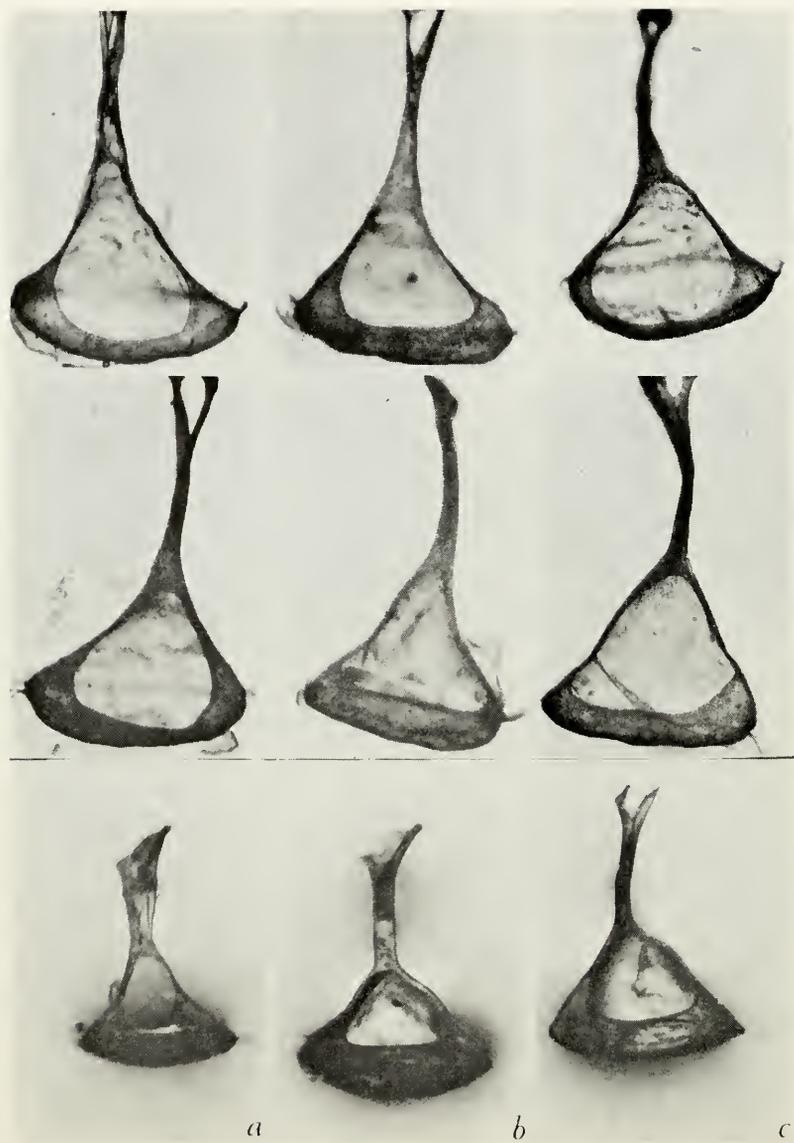


PLATE 3

Photographs of the stapes of the Trogonidae. Individual variation in the stapes of the Quetzal, *Pharomachrus mocinno*. Photographs of left stapes (uppers) and right stapes (middle row) from three individuals. Lower row, Trogonidae: *a*, *Priotelus temnurus*; *b*, *Trogon elegans*; *c*, *Trogon surrucura*. Photos of the derived subosine and alcediniform stapes (Plates 3-5 & 7-10) are of the posterior aspect of the bone (showing the fenestra). However, some are tilted slightly to one side as it was impossible to obtain other photographs.

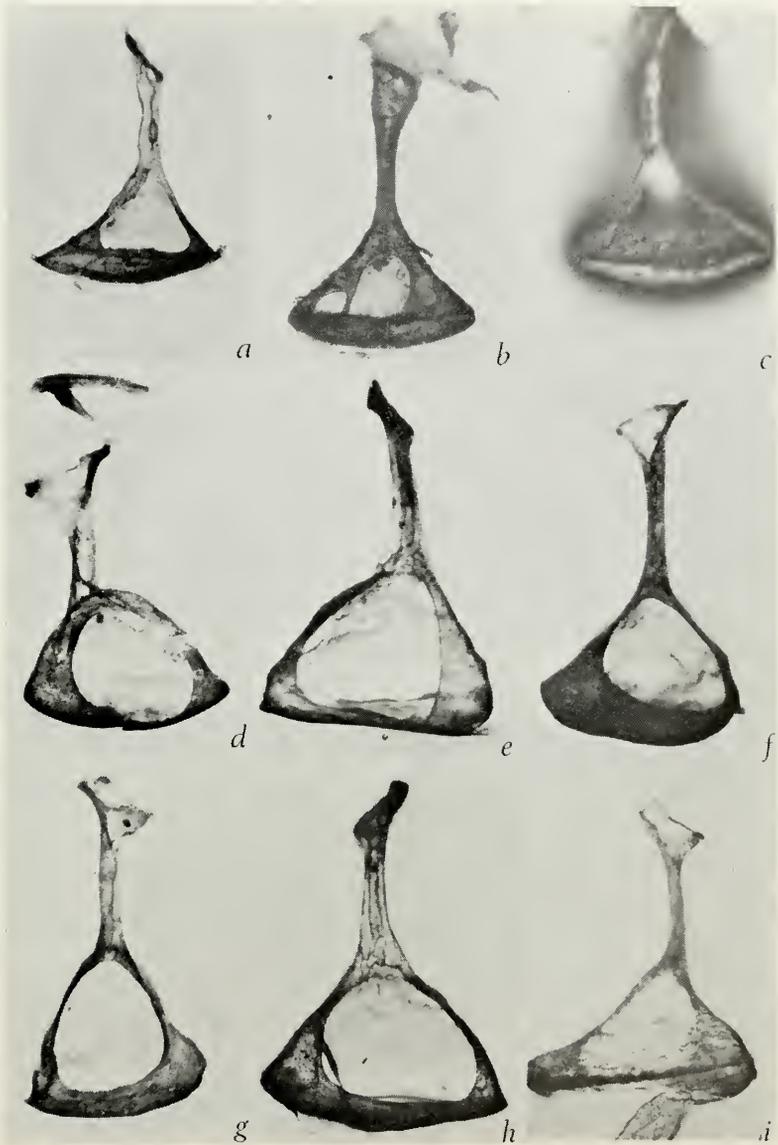


PLATE 4

Photographs of the stapes of the Trogonidae, Alcedinidae, and Todidae. Trogonidae: *a*, *Trogon collaris*; *b*, *Trogon citreolus*; *c*, *Harpactes duvauceli*; Alcedinidae: *d*, *Dacelo novaeguineae*; *e*, *Ceryle torquata*; *f*, *Ceryle rudis*; *g*, *Chloroceryle inda*; *h*, *Alcedo semitorquata*; Todidae: *i*, *Todus multicolor* (footplate damaged). See legend to Plate 3.

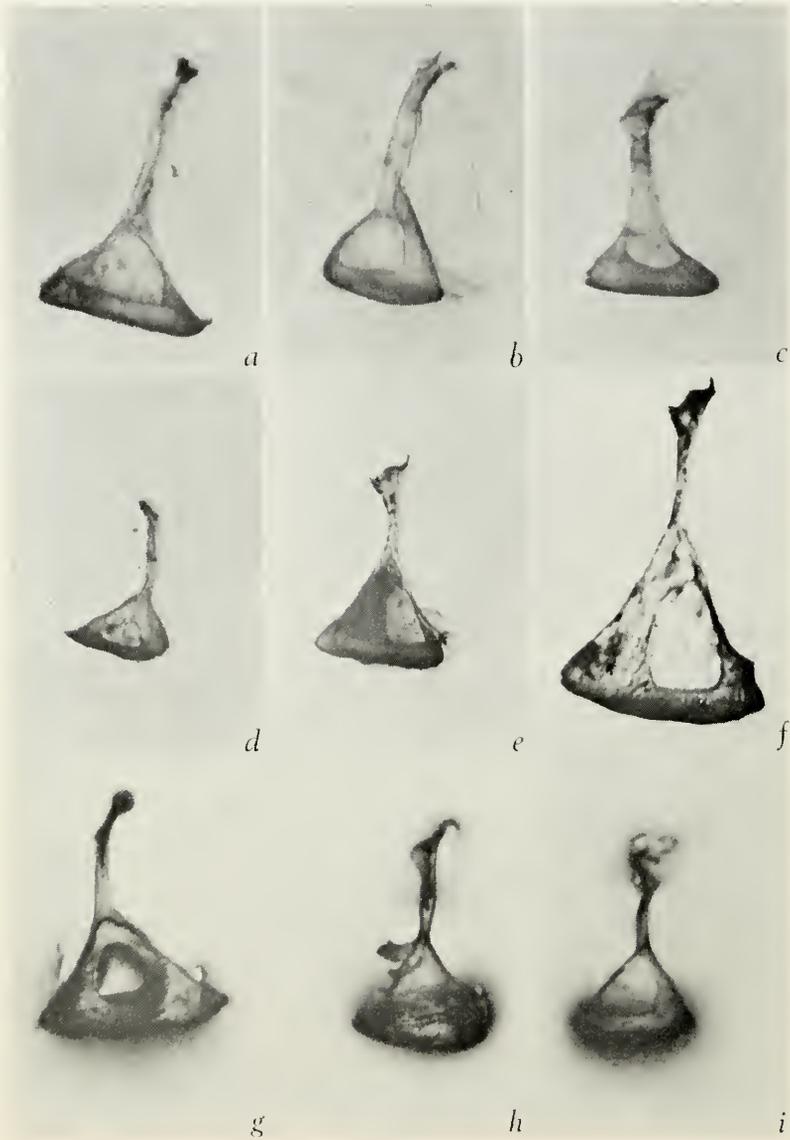


PLATE 5

Photographs of the stapes of the Meropidae and Momotidae. Meropidae: *a*, *Nyctiornis ather-toni*; *b*, *Merops orientalis*; *c*, *Merops nubicus*; Momotidae: *d*, *Baryphthengus ruficapillus*; *e*, *Electron platyrhynchum*; *f*, *Momotus momota*; *g*, *Eumomota superciliosa*; *h*, *Aspatha gularis*; *i*, *Hylo-manes momotula*. See legend to Plate 3.

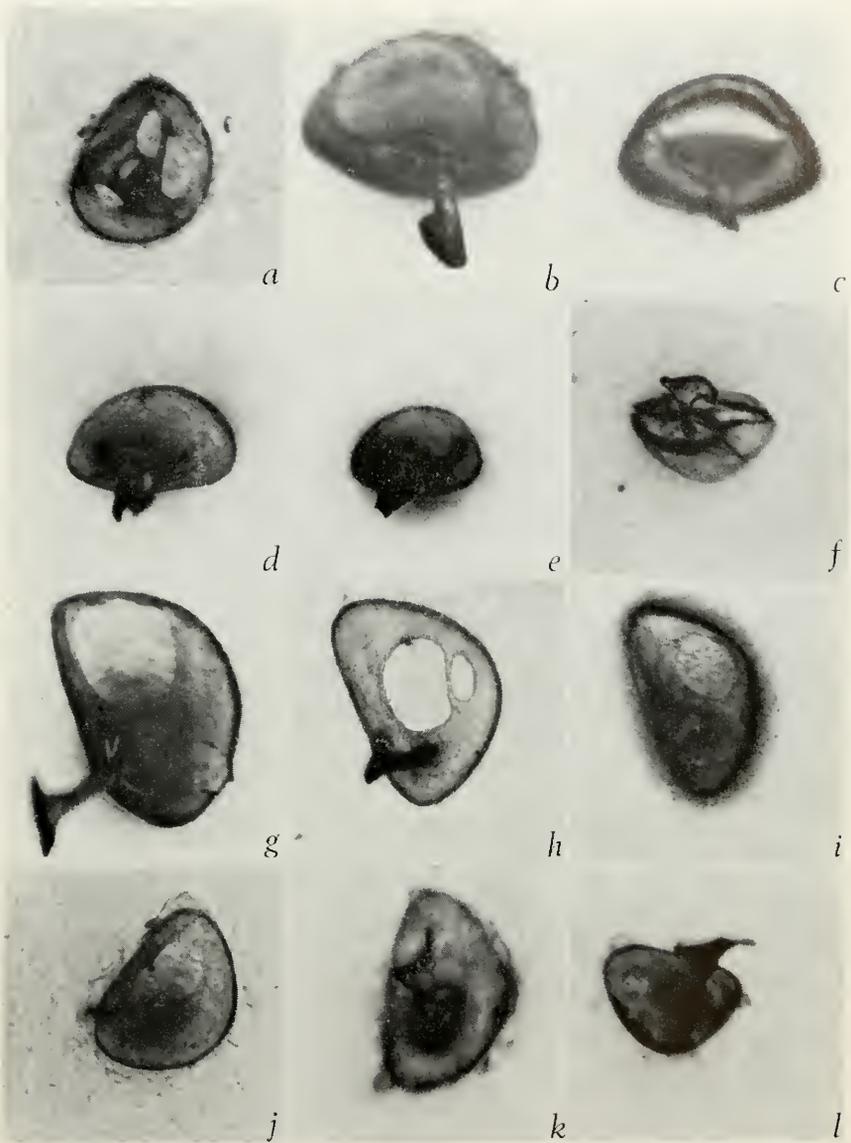


PLATE 6

Photographs of the basal regions of the right stapes of: *a*, *Centurus carolinus* (Picidae); *b*, *Ceryle rudis* (Alcedinidae); *c*, *Trogon surrucura* (Trogonidae); *d*, *Aerops albicollis* (Meropidae); *e*, *Electron platyrhynchum* (Momotidae); *f*, *Todus multicolor* (Todidae); *g*, *Corydon sumatranus* (Eurylaimidae); *h*, *Pitta brachyura* (Pittidae); *i*, *Geositta cunicularia* (Furnariidae); *j*, *Manacus manacus* (Pipridae); *k*, *Querula purpurata* (Cotingidae); *l*, *Colonia colous* (Tyrannidae).

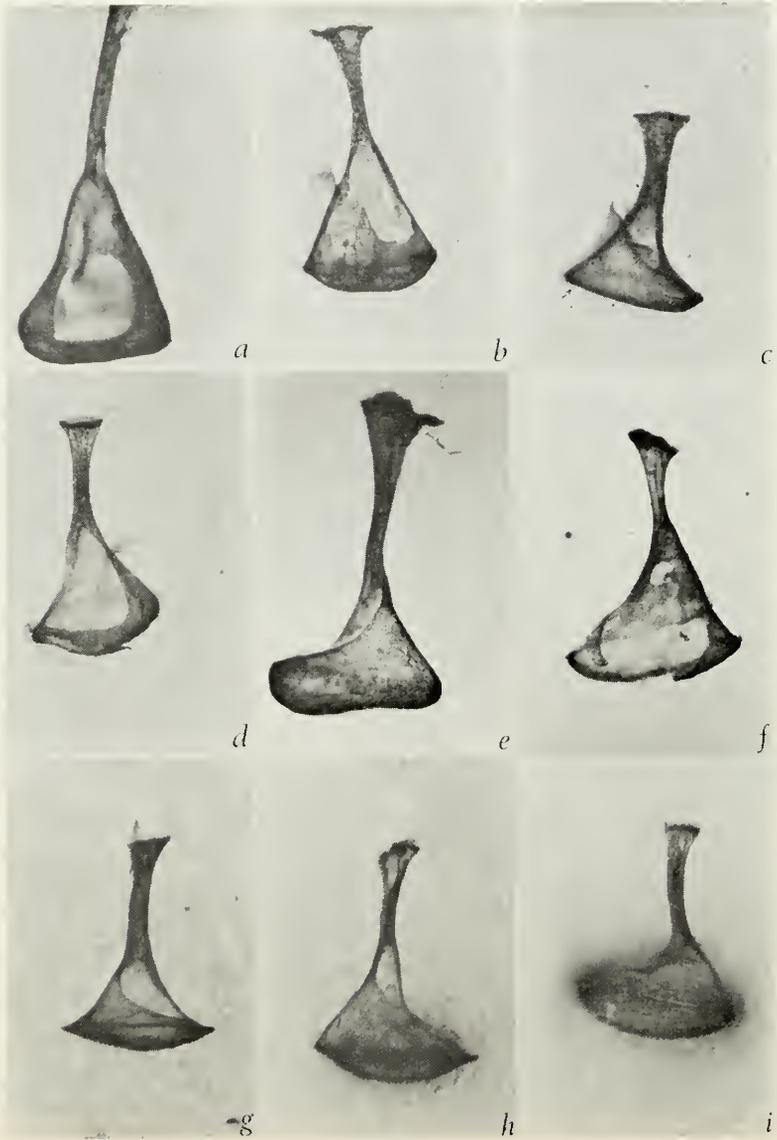


PLATE 7

Photographs of the stapes of the Eurylaimidae and Furnariidae (including woodhewers). Eurylaimidae: *a*, *Calyptomena viridis*; Furnariidae: *b*, *Furnarius rufus*; *c*, *Geositta cunicularia*; *d*, *Dendrocincla anabatina*; *e*, *Dendrocolaptes platyrostris*; *f*, *Xiphorhynchus triangularis*; *g*, *Cinclodes fuscus*; *h*, *Philydor rufus*; *i*, *Phacellodomus striaticollis*. See legend to Plate 3.

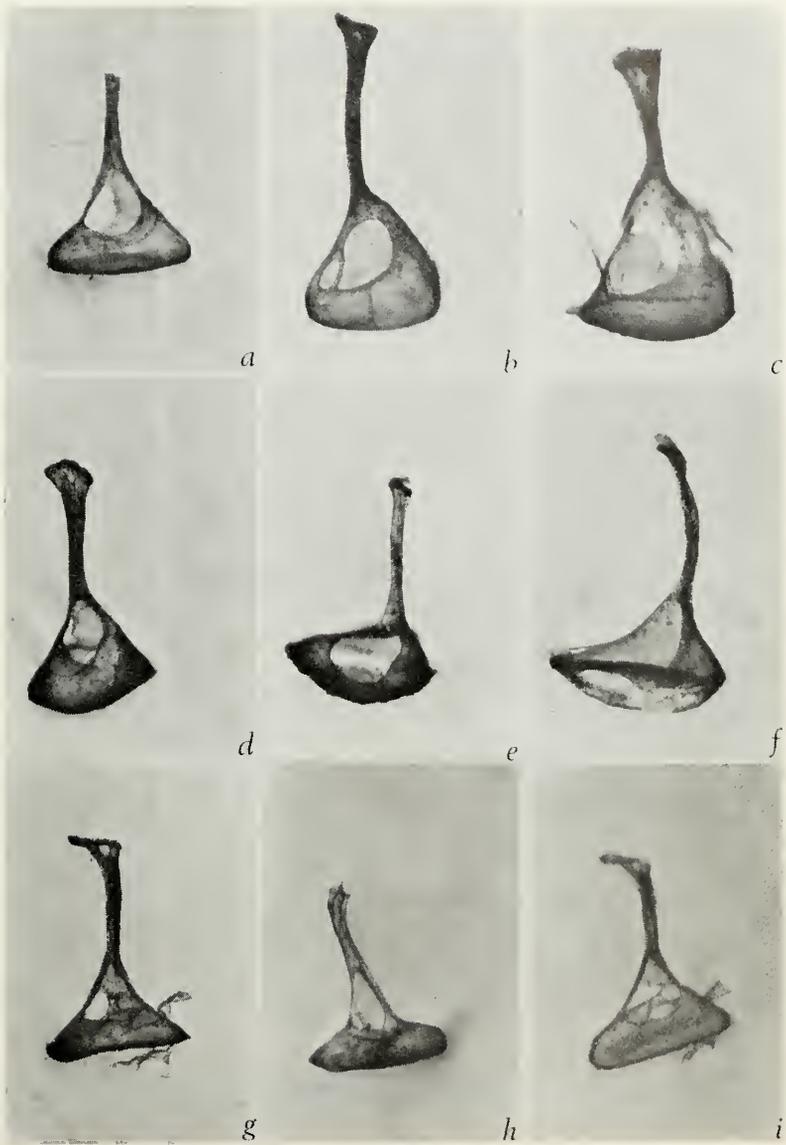


PLATE 8

Photographs of the stapes of the Formicariidae and Pipridae. Formicariidae: *a*, *Sakesphorus melanonotus*; *b*, *Taraba major*; *c*, *Grallaria quitensis*; *d*, *Myrmeciza exul*; *e*, *Pyriglena leucoptera*; *f*, *Formicarius analis*; Pipridae: *g*, *Chiroxiphia lanceolata*; *h*, *Manacus manacus*; *i*, *Pipra mentalis*. See legend to Plate 3.



PLATE 9

Photographs of the stapes of the Cotingidae, Conopophagidae, and Rhinocryptidae. Cotingidae: *a*, *Procnias nudicollis*; *b*, *Pyroderus scutatus*; *c*, *Querula purpurata*; *d*, *Pachyramphus cinnamomeus*; *e*, *Rhytipterna simplex*; *f*, *Tityra semifasciata*; Rhinocryptidae: *g*, *Pteroptochos megapodius*; *h*, *Scytalopus unicolor*; Conopophagidae: *i*, *Corythopis delalandi*. See legend to Plate 3.

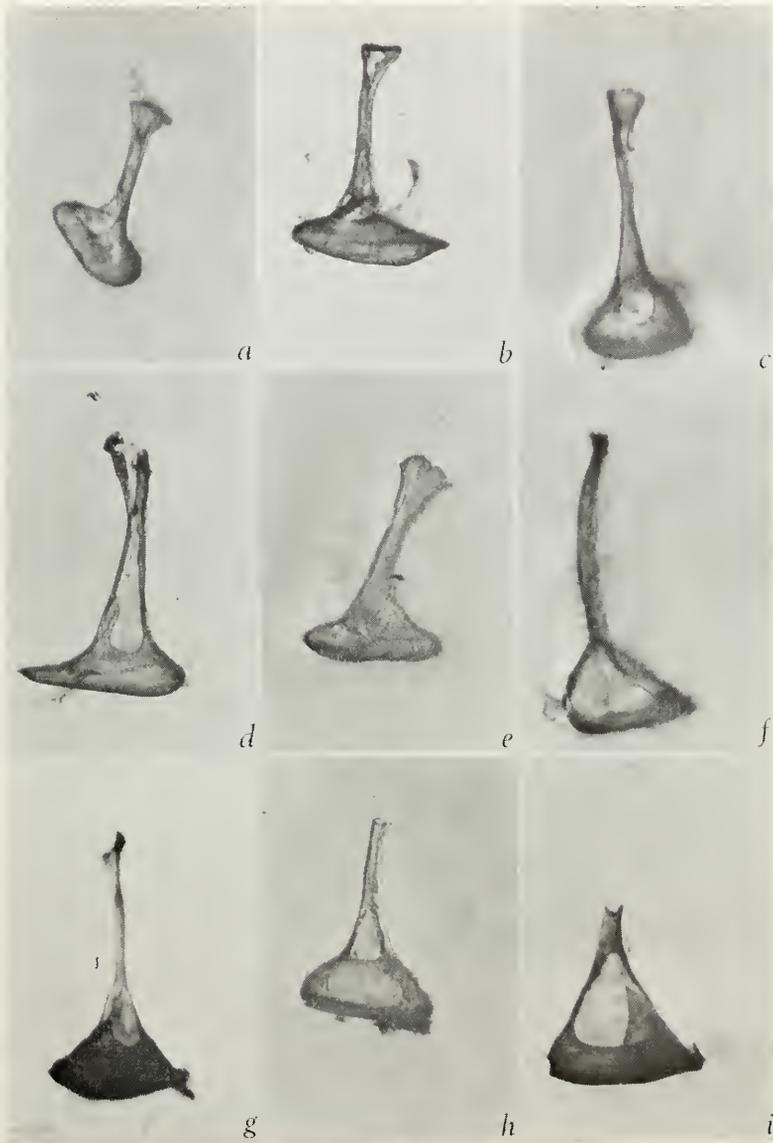


PLATE 10

Photographs of the stapes of the Tyrannidae, Phytotomidae, and Pittidae. Tyrannidae: *a*, *Colonia colonus*; *b*, *Tyrannus tyrannus*; *c*, *Myiarchus tyrannulus*; *d*, *Myiodynastes maculatus*; *e*, *Myiozetetes similis*; *f*, *Pitangus sulphuratus*; Phytotomidae: *g*, *Phytotoma rara*; *h*, *Phytotoma rutila*; Pittidae: *i*, *Pitta cucullata* (shaft broken). See legend to Plate 3.

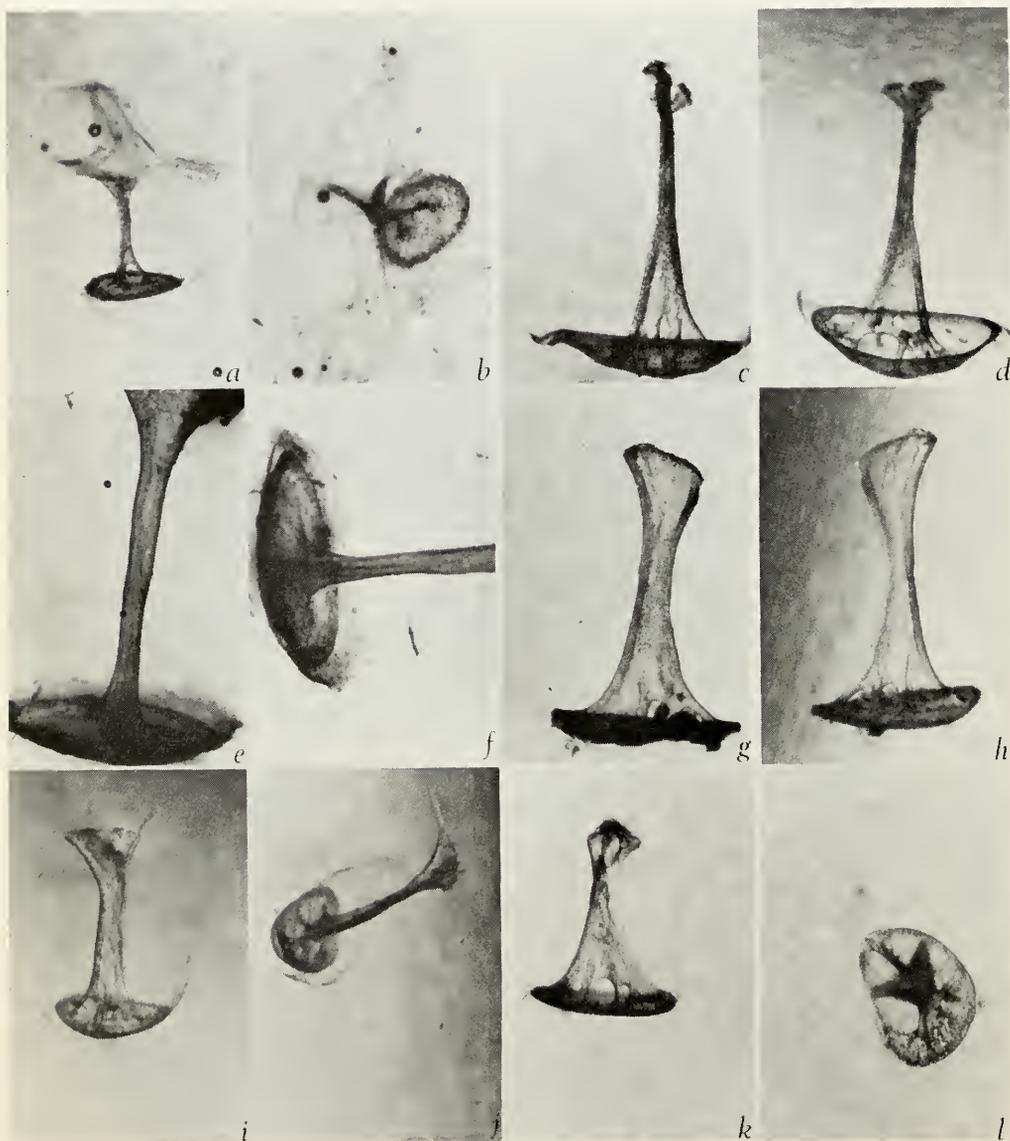


PLATE 11

Photographs of the stapes of the Timaliidae and related forms. Timaliidae: *a* & *b*, *Paradoxornis paradoxa* (tympanic membrane attached to distal end); *c* & *d*, *Pomatorhinus schisticeps*; *e* & *f*, *Picathartes gymnocephalis*; *g* & *h*, *Turdoides bicolor*; *i* & *j*, *Chamaea fasciata*; *k* & *l*, *Geocichla citrina*.

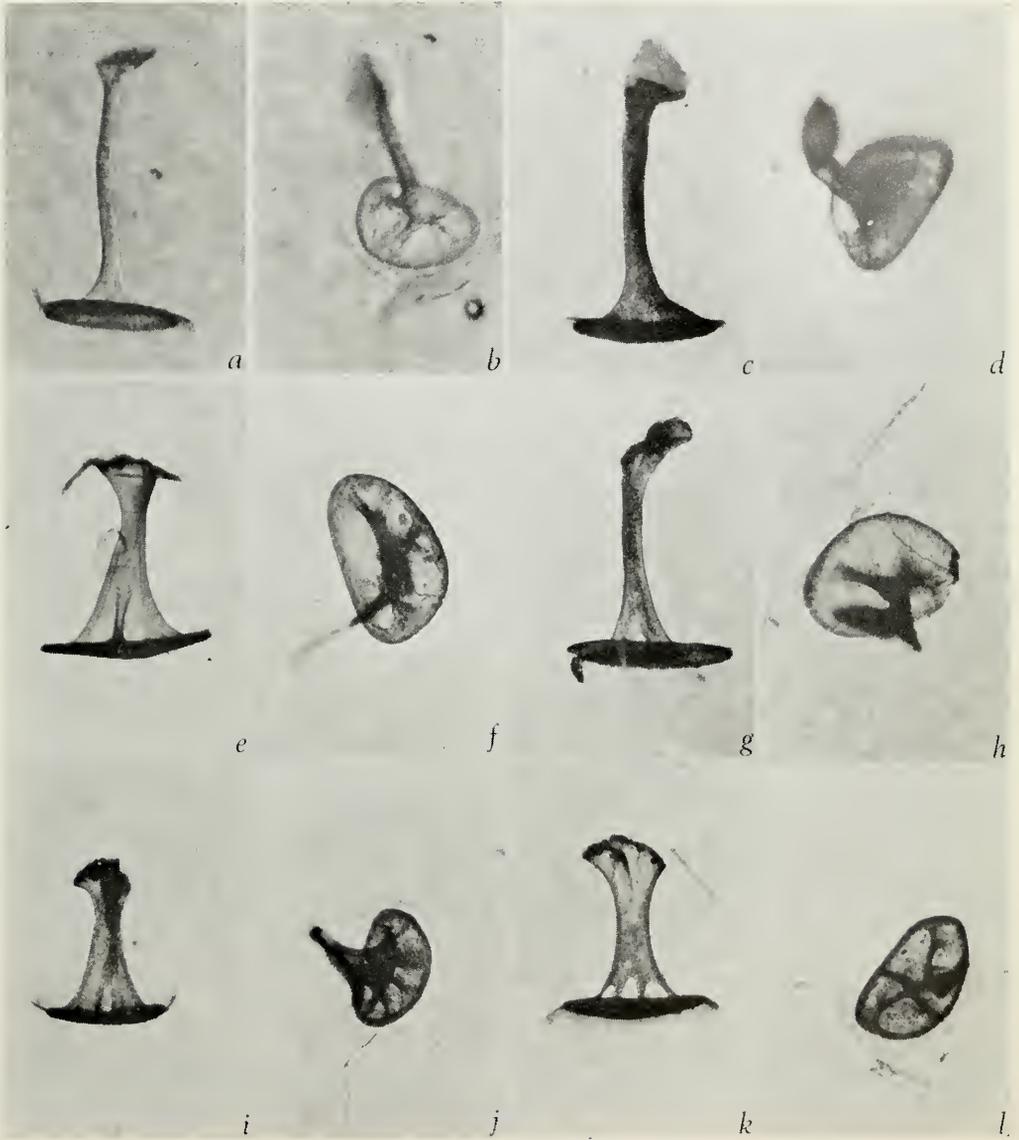


PLATE 12

Photographs of the stapes of various oscines. Campephagidae: *a* & *b*, *Coracina striata*; Cinclidae: *c* & *d*, *Cinclus cinclus*; Mimidae: *e* & *f*, *Cinlocerthia ruficauda*; *g* & *h*, *Donacobias atricapillus*; Thraupidae: *i* & *j*, *Iridosornis rufivertex*; *k* & *l*, *Ramphocelus dimidiatus*.

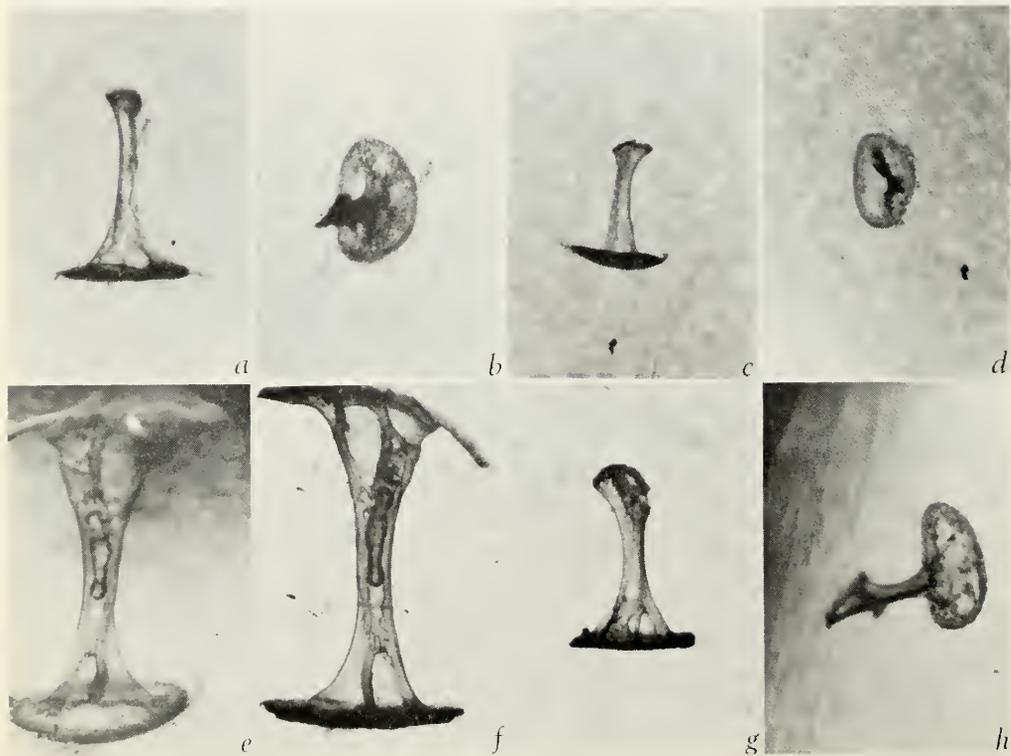


PLATE 13

Photographs of the stapes of various oscines. Cyclarhidae: *a* & *b*, *Cyclarhis gujanensis*; Nectariniidae: *c* & *d*, *Anthreptes singalensis*; Sturnidae: *e* & *f*, *Aplonis atrifusca*; Bombycillidae: *g* & *h*, *Bombycilla garrulus*.

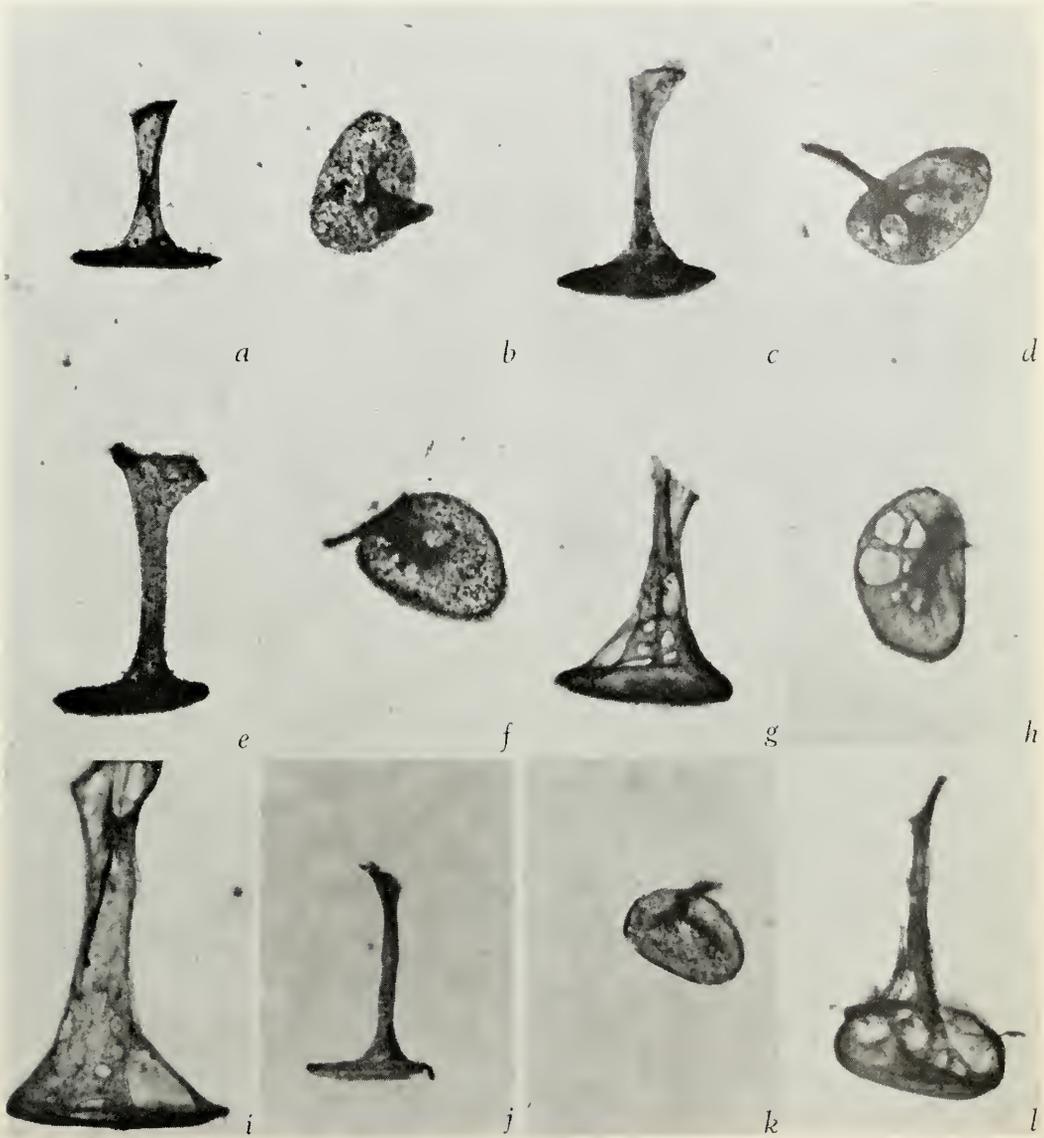
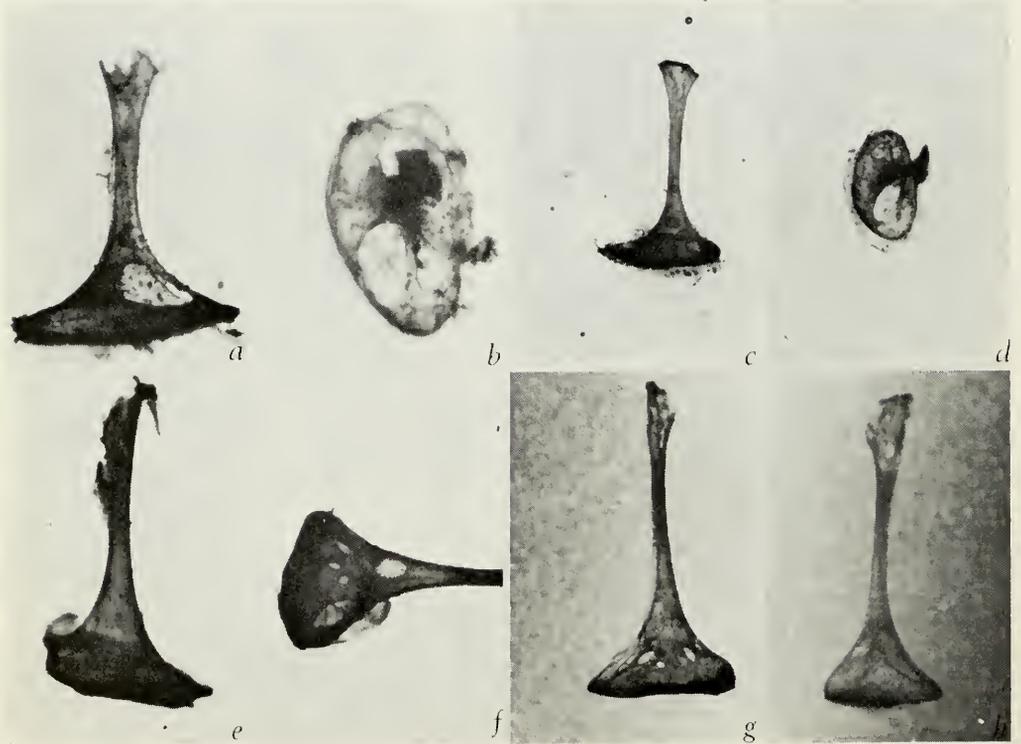


PLATE 14

Photographs of the stapes of the Piciformes. Capitonidae: *a* & *b*, *Tricholaema leucomelas*; *c* & *d*, *Gymnobucco peli*; *e* & *f*, *Semnoris ramphastinus*; *g* & *h*, *Megalaima asiatica*; *i*, *Megalaima virens*; Galbulidae: *j* & *k*, *Brachygalbula lugubris*; *l*, *Jacamerops aurea*.



## PLATE 15

Photographs of the stapes of the Piciformes. Ramphastidae: *a* & *b*, *Aulacorhynchus sulcatus*; *c* & *d*, *Pteroglossus torquatus*; *e* & *f*, *Ramphastos tucanus*; *g* & *h*, *Ramphastos toco*.

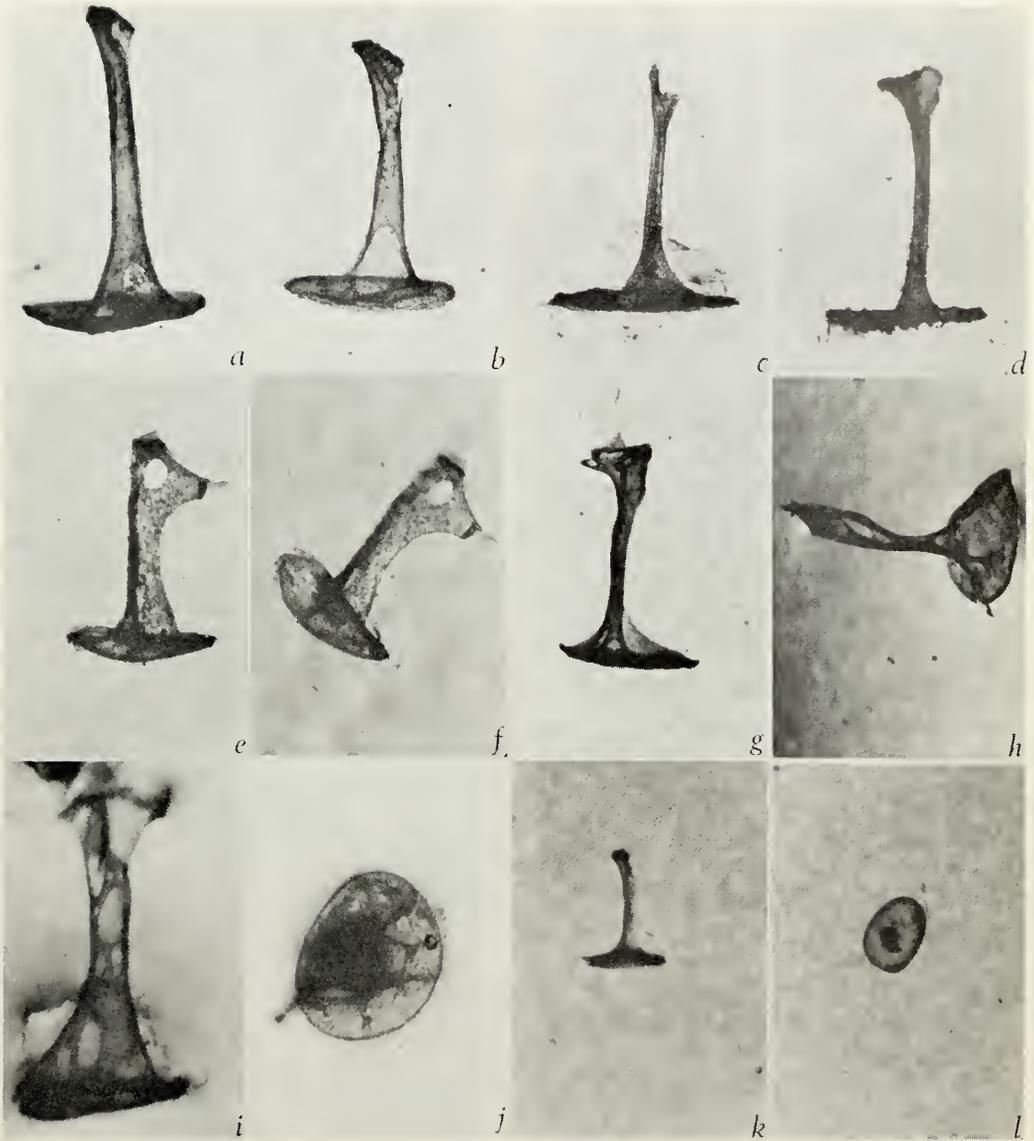


PLATE 16

Photographs of the stapes of the Piciformes. Bucconidae: *a*, *Malacoptila panamensis*; *b*, *Monasa nigrifrons*; *c*, *Indicator maculatus*; *d*, *Indicator indicator*; *e* & *f*, *Jynx torquilla*; *g* & *h*, *Centurus aurifrons*; *i* & *j*, *Colaptes auratus*; *k* & *l*, *Picumnus exilis*.

Meropidae, and Momotidae (Plates 3-5); and, it differs in only one major respect from the type of stapes found in "suboscine" passerine birds (see suboscine section). Individual variation in the stapes of the quetzal, *Pharomachrus*, is illustrated in Plate 3. This type of stapes differs from the primitive condition in having a large, hollow, bulbous basal and footplate area that exhibits a large fenestra only on one side (perhaps best termed the posterior aspect). Sometimes the fenestra is subdivided (Plate 4, b). The fenestra leads to a large hollow fossa. Because of this morphology of the basal and footplate areas, the stapedial shaft is shifted in position from the middle of the base to the periphery, thus seemingly producing a different type of lever system. Variation between the Trogonidae, Alcedinidae, Todidae, Meropidae, and Momotidae ("alcediniform birds") is depicted by the photographs in Plates 3-5. The Alcedinidae have the most expanded basal area, and are generally distinguishable from other families by that character.

The families under consideration may also be characterized by the position of the shaft of the stapes with respect to the base (Plate 6, b-c). This character is perhaps best described by imagining the form of the base of the stapes as a protractor with a slightly rounded base, from the middle of which the shaft emerges.

### Passeriformes

Suboscine species examined have a derived stapedial morphology only slightly different from that of the Trogonidae, Alcedinidae, Todidae, Meropidae, and Momotidae; this morphology is illustrated in Plates 7-10. The number of specimens of suboscine birds examined is given in Feduccia (1974); only the Oxyruncidae was not available for examination. In the oscine passerine birds (*sensu* Wetmore) the primitive condition is found in all families (see Plates 11-13). There is some variation in the basal region (see discussion under the

primitive condition), but it is fundamentally similar in all forms. As in the coraciiform families given above, the suboscine stapes has a large, hollow, bulbous basal and footplate area that exhibits a large fenestra on one side only (sometimes the fenestra is subdivided, e.g. Plate 8, b, and 9, c, d, f) which leads into a large fossa. As in the coraciiform groups, the shaft attaches to the periphery of the base. The "suboscine" stapes differs from the coraciiform derived stapes in the shape of the base and therefore the position of the shaft (Plate 6, g-k). In the suboscines, the footplate is nearly triangular, with three unequal sides, but with the shaft usually emerging from the area where the two longest sides meet. The shape of the footplate, and the point of emergence of the shaft of the stapes is highly variable in suboscines, while in the coraciiform groups possessing the derived stapes it is a static character. By this character alone one can separate suboscines from the "derived" coraciiform groups with a confidence of over 90%; however, in some suboscines the base resembles the coraciiform type (Plate 6, l). This difference in the form of the base of the stapes may also be demonstrated by placing specimens in a finger bowl or depression slide filled with a 50% glycerine solution. Coraciiform "derived" stapes will turn so that the fossa faces upward, while "suboscine" stapes will tend to fall on their "sides." Plate 6 will enable the reader to visualize the above.

It should also be noted here that while I have attempted to photograph all of the derived suboscine and coraciiform stapes in their posterior aspect, some of the suboscine stapes have shifted to one side because of the basal conformation.

In order to determine if the basic arrangement of the areas of middle and inner ears differs between oscine and suboscine birds, I sectioned the ear regions of a woodhewer (suboscine) and a thrush (oscine) (Fig. 5). One can see that the basic arrangement is similar, but

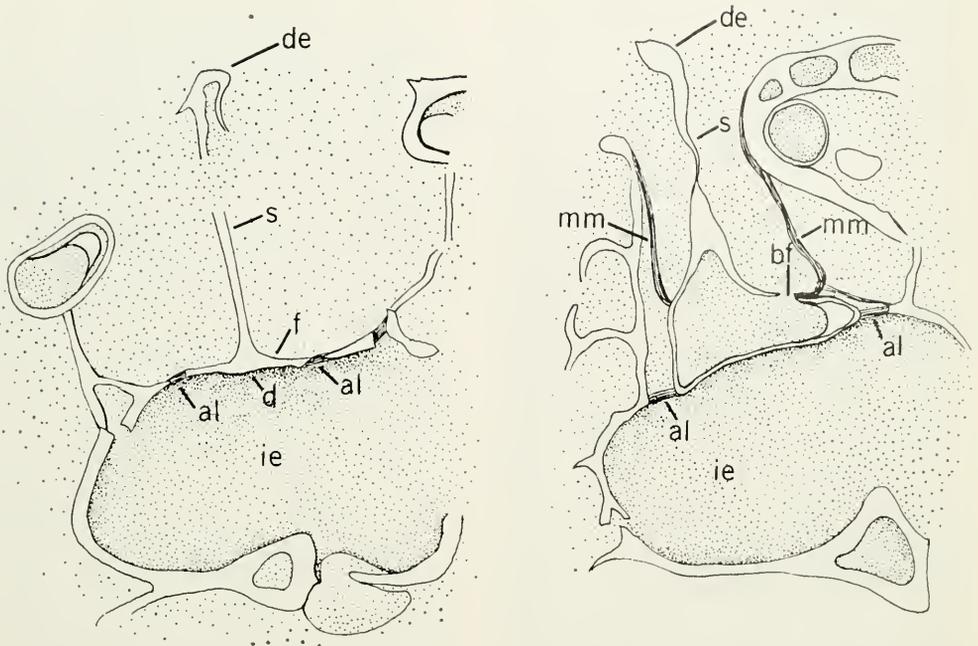


FIG. 5.—Sagittal sections of the middle ear region of (left) *Hylocichla mustelina* (Timaliidae: Turdinae), and (right) *Dendrocolaptes certhia* (Furnariidae: Dendrocolaptinae). Abbreviations: de, distal end (of stapes); s, shaft; bf, basal fossa; mm, marginal membrane (new term); f, footplate; al, annular ligament; d, disc; ie, inner ear. Drawn from photomicrographs.

Displacement of the ear drum induces a rocking movement of the stapes, which may act as a lever. Its fulcrum is one edge of the oval window; its short arm is the radius of the footplate, and its long arm is the length of the stapes. The effect of the derived type of stapes is that the short arm of the lever becomes the diameter (rather than the radius) of the footplate; therefore, any excursion of the distal end of the stapes will result in a relatively greater excursion of the posterior aspect of the footplate. One would imagine that *b* represents a more sensitive middle ear, and it might follow that the suboscines and alcediniform birds hear better than the oscines. However, there are many ways of changing an ear in an evolutionary sense, and as a consequence it would be improper to draw conclusions on hearing acuity based on the stapes alone. Indeed, it may still be that oscines have more sensitive ears than suboscines or alcediniforms; electrophysiological studies will be needed to answer these questions.

differs in certain details. First, the bony walls of the middle ear cavity form a smaller channel for the passage of the shaft of the stapes. I first recognized this difference because of the relatively greater difficulty in extracting the suboscine stapes as compared to that of the oscines. Second, there is a membrane, called here the marginal membrane, which secures the suboscine stapes within the cavity; it is lost in most skeletal preparations, but remnants remain in some (see Fig. 6). Only suboscines and the alcediniform families under consideration have the marginal membrane,

arguing for homology of the derived stapes in the two groups.

### Piciformes

The piciform birds examined exhibit either the primitive condition (Plates 14-16) or derived type of stapes which is characterized by a tubular shaft, perforated by numerous small fossae, and with the basal struts merging together (Plate 14, g, h, i; 16, i, j). The shaft (Plate 14, h; 16, j) emerges from the middle of the footplate (see Plate 6, a, for comparison), though the shaft is elevated by the expanded basal region.

Thus, it has basically the same type of lever system as in the primitive condition. I have not examined a sufficient number of piciform species because of the difficulty in extracting the stapes from their almost closed auditory bullae. I shall report on the piciform stapes in more detail when more specimens are obtained. The primitive condition occurs in all of the Capitonidae except the genus *Megalaima*; both *M. virens* and *M. asiatica* (Plate 14, g, h, i) have the derived condition described above. All of the species of the Galbulidae examined have the primitive condition, but *Jacamerops* (Plate 14, l) appears to be intermediate. All of the species of the Bucconidae and Indicatoridae have the primitive condition (Plate 16, a-d). *Jynx* has the primitive condition, but with a distal end pierced by a foramen, which may represent ossified extrastapedial cartilages. The woodpeckers and piculets (Plate 16, g-l) possess either the primitive condition (*Picumnus*, Plate 16, k, l), an intermediate stage with well-developed basal struts (*Centurus*, Plate 16, g, h), or the "derived" piciform condition (*Colaptes*, Plate 16, i, j). All of the toucans (Plate 15) possess the derived piciform stapes.

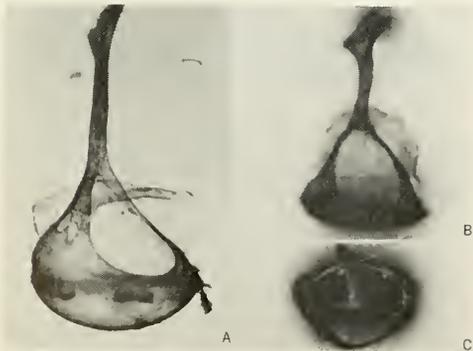


FIG. 6.—Photographs of the stapes of A, *Xiphocolaptes promeropyrhyuchus* (Furnariidae: Dendrocolaptinae); B, *Ceryle torquata* (Alcedinidae: Cerylinae); and C, view looking down on the footplate of *C. torquata*, to show the marginal membrane present in both a subsoscine and alcediniform bird. The marginal membrane is not preserved in most dried skeletal preparations.

## TAXONOMIC SUMMARY

### Coraciiform Birds and Trogons

Because of the excellent review of the vicissitudes of avian classification for passerine birds (Sibley, 1970), and non-passerine birds (Sibley and Ahlquist, 1972), it is not necessary to repeat a voluminous literature here. After evaluating both the anatomical and egg white protein data, Sibley (1972: 230) concluded that, "Our study seems to support a distinct, but rather distant, alliance among the Alcedinidae, Todidae, Momotidae, and Meropidae." Sibley (op. cit.) continued by stating that, ". . . the affinities of the Coraciidae to other members of the order are uncertain." These are identical to conclusions based on the morphology of the stapes; however, the stapes data now reveal a rather close affinity among the kingfishers, todies, motmots, and bee-eaters, which I will refer to as the alcediniform birds.

In their summary of the systematics of trogons, Sibley and Ahlquist (1972: 217) state, "The consensus is clear; the trogons constitute a distinctive group whose closest relatives are unknown but are to be sought among the 'higher' non-passerines and, possibly, the passerines." They further state (p. 218), "The affinities of the trogons remain obscure, but, in our opinion, the Coraciiformes should receive close scrutiny in seeking evidence of relationship. . . . The trogons are poorly known in many ways, and we suggest that a thorough anatomical study of them might bring to light new characters of value in assessing their relationship." The morphology of the stapes indicates a very close relationship of the trogons to the alcediniform birds.

Hornbills (Bucerotidae) have the primitive condition of the stapes with some species exhibiting a slightly derived "tubular" type. Hornbills are distinctive birds, and until new evidence can be engendered to link them with other coraciiform families, ordinal status for the group seems desirable.

Sibley (1972) was unable to support or deny a close relationship between the Upupidae and Phoeniculidae. Their unique, derived, "anvil" stapes argues strongly for their monophyly (Feduccia, 1975a), and ordinal status is recommended for the hoopoes and wood-hoopoes until *new* evidence linking them with the other coraciiform families (*sensu* Wetmore) can be engendered.

Cracraft's (1971) study of the rollers based on a variety of anatomical characters revealed that (as many previous authors had thought) the Brachypteraciidae and Coraciidae are more closely allied to each other than either is to the Leptosomatidae. As all forms possess the primitive condition of the stapes, no valid conclusions can be based on that element. Rollers could represent the ancestral condition leading to the alcediniform groups, but they must have diverged before the evolution of the derived stapes.

A classification reflecting the above discussion of the coraciiform birds is presented below. The points supported by the morphology of the stapes are: 1) the inclusion of the alcediniform birds and the trogons in a single order;<sup>1</sup> and 2) the inclusion of the hoopoes and wood-hoopoes in a single order.

- Order Coraciiformes
  - Superfamily Coracioidea
    - Family Coraciidae
    - Family Brachypteraciidae
  - Superfamily Leptosomatoidea
    - Family Leptosomatidae
- Order Bucerotiformes
  - Family Bucerotidae
- Order Upupiformes
  - Family Upupidae
  - Family Phoeniculidae
- Order Alcediniformes
  - Superfamily Meropoidea
    - Family Meropidae

- Superfamily Alcedinoidea
  - Family Alcedinidae
  - Family Todidae
  - Family Momotidae
- Superfamily Trogonoidea
  - Family Trogonidae

#### Suboscine Birds

The suboscine birds have conventionally been treated as three suborders, the Eurylaimi (Eurylaimidae), Tyranni (Furnariidae, Formicariidae, Conopophagidae, Rhinocryptidae, Cotingidae, Pipridae, Tyrannidae, Oxyruncidae, Phytotomidae, Pittidae, Acanthisittidae, and Philepittidae), and the Menurae (Menuridae and Atrichornithidae).

Recently evidence has accumulated to indicate that the Menurae is not of suboscine, but probably of oscine affinity (Sibley, 1974; Feduccia, 1975b). Further, I was able to illustrate that *Acanthisitta* lacks the stapes characteristic of the suboscines, and has the primitive condition for the element, as in the oscines (op. cit.). Though possession of the primitive condition of the stapes in these forms does not prove their oscine affinities, it suggests that they are not close allies of the modern suboscines, or at least would have had to evolve before the derived stapes type. Therefore it seems more likely that the species of the Menurae are probably oscines. The suboscines of Madagascar have the suboscine type of stapes; thus confirming their status within the Tyranni (Feduccia, 1975c).

Olson (1971) has shown that the recognition of a suborder Eurylaimi is invalid, that the broadbills are among the more primitive of the suboscine birds, and that they are most appropriately placed at the beginning of the Tyranni, perhaps followed by the primitive philepittine suboscines. On the basis of syringeal morphology (Ames, 1971) the pittas are distinct from the other suboscines, but they have a very simple type of syrinx; it is therefore not reliable as an indication of relationship. The zoogeographic probability of a pitta-broad-

<sup>1</sup> The fact that trogons are heterodactyl is, in my opinion, insufficient for ordinal recognition. After all, the zygodactyl leptosomatids have always been placed with the anisodactyl coraciids.

bill affinity seems great, though of course highly speculative. The Old World broadbills are surely convergent with the New World Cotingidae owing to their fruit-eating habits. Until data appear to the contrary, I would prefer to group all of the Old World suboscine families in close proximity in the linear sequence, at the beginning of the Tyranni. The morphology of the stapes argues for common ancestry of all suboscine families, both Old and New World groups.

It seems to be highly improbable that the suboscines and oscines shared an immediate common ancestor. First, oscines are probably of more recent vintage than suboscines. This assumption is based on: (1) the relict distributional patterns of suboscines, and (2) the relatively wide taxonomic gaps in suboscines, compared to the oscines. The fact that the oscines possess the primitive condition of the stapes, and the suboscines a derived condition, combined with the assumption of relatively greater antiquity of the suboscines draws one to the conclusion that the two groups could not have had an immediate common ancestor. The only reasonable conclusion is that the Passeriformes as presently defined constitute a diphyletic assemblage.

The fact that the oscine passerine birds are narrowly monophyletic according to preponderance of evidence, combined with the demonstrable monophyly of the "suboscines" argues strongly for separation of the two groups at the ordinal level. The following classification reflects this view of a diphyletic passerine assemblage.

- Order Tyranniformes, suboscines
  - Suborder Tyranni
- Order Passeriformes, oscines
  - Suborder Passeres

#### EVOLUTION OF THE DERIVED CONDITIONS

It is not difficult to imagine a series of events leading to either the alcediniform or suboscine derived types of

stapes. The anatomical stages might be as follows: (1) basal struts merge and fuse; (2) basal fossa enlarges; (3) basal region expands; and (4) basal fossa enlarges, causing a shift of the stapedial shaft to the periphery of the base. Usually in dealing with characters whose anatomical derivation is easily envisioned, one is met immediately with a myriad of intermediate stages; the lack of stapes intermediates in both the alcediniform and suboscine birds is truly remarkable, and probably indicates that the character was "fixed," that is, a successful morphology evolved, very early in the evolution of these groups. The different forms of the footplate regions and points of emergence of the stapedial shaft might also lead one to conclude that the alcediniform birds and suboscines "fixed" the morphology of their stapes immediately after they diverged. In the piciform birds, on the other hand, there are many intermediates, and one might imagine that a great deal of evolutionary experimentation is occurring within the group. However, the piciform derived type is in no way intermediate between the primitive condition and the alcediniform and suboscine types of stapes; it is a distinctive derived morphology.

#### POSSIBLE RELATIONSHIP OF ALCEDINIFORM AND SUBOSCINE BIRDS

The morphology of the stapes in the trogons, alcediniform birds, and suboscines argues for monophyly of these groups. Because of the radical nature of this assertion, I have posed the problem in the form of one major question: Do data exist that negate the possibility of monophyly of alcediniform and suboscine birds?

All recent studies of the oscine passerine birds indicate the remarkable homogeneity of that group. Ames (1971: 164) makes a special point of oscine cohesiveness on the basis of the syringeal musculature, and suggested in his abstract (op. cit., p. 2) that, "The sub-

order Passeres has been extensively studied. It is far less variable in syringeal structure than the Tyranni or Furnarii. The syrinx is complex but uniform throughout the suborder, suggesting that the group is narrowly monophyletic. . . . The pessulus is present in most suboscines and in the nonpasserine orders Piciformes and Coraciiformes, and was probably present in the ancestor of the Passeres." In his discussion of the primitive condition, Ames (op. cit., p. 133) states that, "In both the Piciformes and the Coraciiformes, the syrinx is a slightly modified tracheo-bronchial junction (Beddard, 1898) in which some elements may be fused into a drum and the pessalus is usually, but not always, present. . . . There is only a single narrow lateral muscle, which I have found to be *M. tracheolateralis*. . . ." The following discussion by Ames (op. cit.) of the above described syrinx is crucial to the possibility of a suboscine-coraciiform relationship and is cited in entirety.

It is likely that this type of syrinx, widely distributed in modern non-passerines, was present in the stock ancestral to the Passeriformes, Piciformes, and probably Coraciiformes. In the following discussion, I will consider it primitive and will refer to it as the "pico-passerine" type. In summary, the characters of the pico-passerine syrinx are: 1) simple tracheobronchial junction, with or without fusion, and without accessory cartilages; 2) pessulus present; 3) intrinsic muscles lacking; 4) *M. tracheolateralis* narrow and laterally situated; 5) *M. sternotrachealis* inserting laterally and usually in continuity with *M. tracheolateralis*.

Among the recent passerines, syrinxes of the pico-passerine type are found in the Eurylaimidae, Philepittidae, Pittidae, Phytotomidae, and Acanthisittidae, and in some members of the Tyrannidae, Cotingidae and Pipridae.

Thus, while the syringeal evidence may not strongly advocate a common ancestry of suboscines and alcediniform birds, neither does it negate the possibility.

With respect to osteological char-

acters, the suboscines are thought to be closer to the Passeres than to any non-passerine groups; however, this may well be owing to lack of a framework for comparison. For example, it is well known that the piciform and coraciiform birds are "closest" osteologically to the passeriform birds. Additional comparative osteological studies will be needed to answer this question. It is of some interest here that the oscine sternal structure is like the syrinx in its extreme uniformity within the group. As Heimerdinger and Ames (1967: 17) pointed out, "Oscines which have a specialized form of locomotion such as creeping on vertical surfaces (*Certhia*, *Sitta*), or which are partially terrestrial (*Eremophila*, *Cinclus*), have exactly the same sternal characters as the more typical oscines." On the other hand, the suboscines have a highly variable sternum (Heimerdinger and Ames, op. cit., and Feduccia, 1972), as do the coraciiform birds. There are a number of suboscine birds that lack the spina externa of the sternum (Olson, 1971) as in the alcediniform birds. The suboscine humerus appears to be more like that of the oscines than the alcediniforms, except perhaps in having a single fossa (Bock, 1962).

Other characters that have been historically important, such as pelvic musculature formulae, deep plantar tendons, palatal structure, intestinal convolutions, carotid arteries, and the fifth secondary have been shown to be highly variable and must be used with extreme caution (see Sibley and Ahlquist, 1972, for an excellent discussion of these characters).

In summary, there is no current evidence that negates the possibility of an alcediniform-suboscine common ancestry. A total cladistic analysis will be needed to exhibit properly the classical anatomical characters. However, at present, the evidence from the morphology of the stapes strongly suggests that the derived alcediniform element is homologous with that of the suboscines and the most parsimonious hypothesis

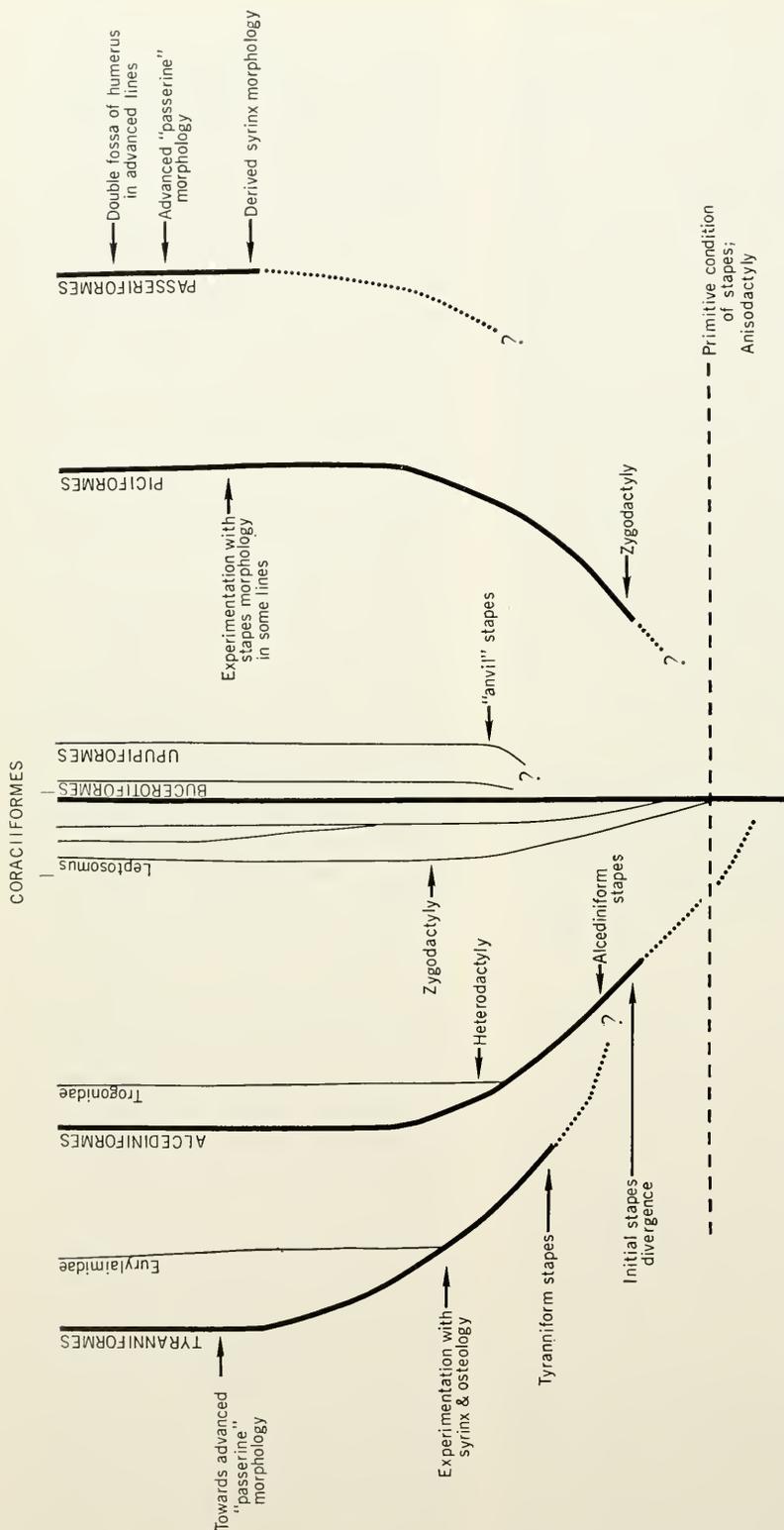


FIG. 7.—Hypothetical phylogeny based on the homology of the derived tyranniform and alcediniform stapes, and a diphyletic Passeriformes. A conventional phylogeny would show the "suboscines" (here called the Tyranniformes) interposed between the Piciformes and Passeriformes, and joined with the latter by a basal phyletic line, perhaps shared with the Piciformes. In order for the conventional phylogeny to conform with the stapes evidence, either the "suboscines" must be considered to be of equal or younger age than the "oscines," or the stapes of the "oscines" must be assumed to have undergone an evolutionary reversal to the primitive avian condition. The Eurylaimidae is shown here as an early branch of the Tyranniformes, being the "suboscine" family sharing the largest number of characters with the alcediniform groups.

is that the two groups are closely related. A classification reflecting a monophyletic alcediniform-suboscine assemblage would require little alteration from that suggested before. An infra-order Alcedini, including the Alcediniformes and Tyranniformes, would reflect the monophyly of the group. The highly specialized Piciformes would have to be removed from its conventional position between the coraciiform groups (*sensu* Wetmore) and the Passeriformes (*sensu* Wetmore) and be placed before or after the Coraciiformes (as delimited here), or after the passerines.

A phylogeny reflecting the homology of the derived suboscine and alcediniform stapes, and a diphyletic Passeriformes is shown in Fig. 7. Sibley (1970: 114-117) has used the headings "Highly Probable," "Probable," "Possible," and "Improbable," to express differing degrees of confidence which one can attach to systematic "conclusions." This seems to be a reasonable approach be-

cause we are dealing with probability estimates in any assessment of evolutionary relationships. Thus, I would summarize my systematic conclusions as follows:

It is Highly Probable that:

- (1) the bee-eaters, motmots, todies, and kingfishers are monophyletic.
- (2) trogons are derived from the above lineage.
- (3) the Upupidae and Phoeniculidae are monophyletic.
- (4) New World and Old World suboscines are monophyletic.

It is Probable or Possible that:

- (1) the alcediniform birds and suboscines are monophyletic.

It is Improbable that:

- (1) *Menura* is a suboscine.
- (2) *Acanthisitta* is a suboscine.
- (3) suboscines and oscines shared an immediate common ancestor.

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