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MORPHOLOGY OF THE BONY STAPES (COLUMELLA) IN OWLS: EVOLUTIONARY IMPLICATIONS

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Abstract.—The morphology of the bony stapes in owls (Aves: Strigiformes) is examined. Similar derived stapes occur in *Tyto* and *Phodilus*, supporting the concept of their close affinity. Another type of derived stapedial morphology occurs in some species of *Strix*, but most species of Strigidae exhibit the primitive avian stapes.

The owls (order Strigiformes) represent a notably homogeneous avian assemblage. Although many are diurnal, two-thirds of the 130 living species are crepuscular or nocturnal, and all are supposed to have evolved from nocturnal ancestors (Pumphrey, 1948:40). Enhanced visual and auditory acuity is essential for their existence as predators.

The earliest reliable record dates from the Paleocene (Rich and Bohaska, 1976), and by the Eocene at least two distinct strigiform genera are known to have existed. During the early to middle Tertiary, the diversification of many forms of small mammals probably accelerated the adaptive radiation of owls (Burton, 1973:30).

Although the members of the Strigiformes may be easily distinguished from those of other orders; the familial, subfamilial, and generic relationships within the order are much less certain. At present, the most widely accepted classification is that of Peters (1940), which separates the order into two families, the typical owls (Strigidae) and the barn owls (Tytonidae). The Strigidae is further subdivided into two subfamilies, Buboninae and Striginae; the Tytonidae is subdivided into the Tytoninae and Phodilinae. The last taxon has been the source of debate for many years, with some authors choosing to ally *Phodilus* with the strigids rather than the tytonids. In hopes of resolving this controversy, the primary concern of this paper will be to determine the relationship of *Phodilus* to other owls using the morphology of the columella or stapes. The occurrence and evolution of bilateral ear asymmetry in owls and its bearing on their systematics is discussed by Norberg (1977).

Morphology of the Stapes

The avian columella, consisting of the bony stapes and the cartilaginous extracolumella (or extrastapes), functions to transform airborne vibrations. The avian element, although broadly homologous with the hyomandibular cartilage of fishes and the stapes of mammals, most closely resembles the reptilian columella. In fact, these elements are so similar that the development and the primitive adult morphology of the avian stapes may be considered typically reptilian.

Although the columella describes a piston-like motion in all birds (Pohlman, 1921), in many species it also acts as a lever. The majority of owls possess the primitive type of avian stapes, very similar to that of many other birds and consisting of a relatively flat footplate and a nearly straight shaft emanating approximately from the center of the footplate (see Feduccia, 1975). In a number of species, however, the shaft has shifted towards the periphery (for example, *Aegolius funereus*, *Otus asio*, and others), presumably functioning to lengthen the short arm of the lever and therefore increase the magnitude of response to perturbations at the distal end (for discussion of this function see Feduccia, 1975). Also, some species (e.g. *Aegolius funereus*) have the footplate slightly expanded, but such variation is not considered markedly modified.

In addition to this variation, another type of derived morphology of the stapes is known which is of particular interest here. This condition is characterized by a prolongation of the inner aspect of the footplate into an almost hemispherical knob. Krause (1901) was the first to describe this variation, and Schwartzkopff (1955:342–343) has commented on its possible function: "Since the movements of this lever (the stapes) produce considerable turning moments at the remarkable velocity of the sonic vibrations, the pressure upon the hinge, namely the elastic connection with the footplate in the oval window (annulus fibrosus), must be reduced. This is done through 'mass equilibration': the inner surface of the footplate is prolonged into a tip which projects into the perilymph of the inner ear; and the tip has a special shape which prevents the formation of eddies." Schwartzkopff was mistaken, however, in assuming that all owls possess this derived morphology of the stapes footplate. Illustrations by Krause (1901) show the presence of the flat footplate (primitive condition) in both *Athene noctua* and *Otus asio*. Although he confirms the presence of a derived morphology in *Strix aluco*, though a problem of nomenclature he attributes this variation also to *Strix flammea*, but this name was previously used for *Tyto alba* and is not equivalent to the *Asio flammeus* of modern usage. Krause's illustration clearly shows the derived stapes of *Tyto alba* and not the primitive condition of *Asio flammeus*.

We have examined the bony stapes of 27 species from 17 of the 24 living genera of the order Strigiformes (Table 1). A derived condition of the footplate occurs in only three genera: *Tyto*, *Phodilus*, and some species of *Strix* (Figs. 1 and 2). The other genera examined all possess a relatively flat footplate, although in *Ciccaba woodfordii* (the African wood owl) there is a slightly convex protuberance on the inner aspect. With the possible exception of *C. woodfordii*, all of the species possessing a derived morphology of the stapes also possess asymmetrically placed ear openings (Table 1).

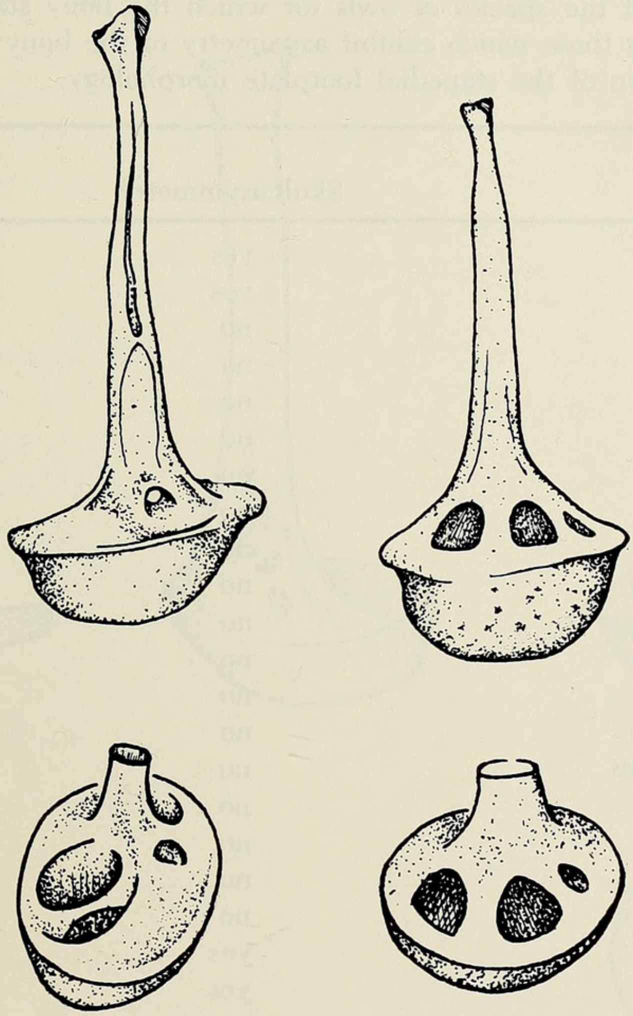

Fig. 1. Top: lateral views of the bony stapes of *Phodilus badius* (left), and *Tyto alba* (right). Bottom: views looking down upon the footplates of each, respectively. In mesial view the extended footplate region of *Tyto* tapers distally, that of *Phodilus* is more evenly rounded and does not taper so abruptly. All figures are drawn to the same approximate scale; actual lengths are 3–4.5 mm.

Upon close examination of the derived morphology of *Tyto*, *Phodilus* and *Strix* two features became obvious: (1) although the stapedial footplates of *Tyto* and *Phodilus* are very similar (Fig. 1), they differ markedly from those of *Strix*; (2) in the three species of *Strix* examined (*nebulosa*, *occidentalis*, and *varia*) the degree of protrusion of the footplate varies from almost none in *S. nebulosa* to a very marked protrusion in *S. varia* (Fig. 2).

Thus, the modified morphology of the stapes in *Strix* appears to have evolved independently of that of *Tyto*, particularly since none of the other genera of Strigidae possess such a character. There also appears to be a great deal of evolutionary experimentation with respect to stapes morphology within the genus *Strix*, evidenced by the wide range of variation of this character among the different species. The retention of the primitive condition in *S. nebulosa* also argues for independent evolution of the pro-

Table 1. A list of the species of owls for which the bony stapes was examined in this study, comparing those which exhibit asymmetry of the bony external ear openings and some modification of the stapedial footplate morphology.

Species	Skull asymmetry	Modified stapedial footplate
Phodilus badius	yes	yes
Tyto alba	yes	yes
Otus asio	no	no
Otus bakkamoena	no	no
Otus clarkii	no	no
Otus nudipes	no	no
Bubo virginianus	no	no
Bubo bubo	no	no
Bubo africanus	no	no
Pulsatrix perspicillata	no	no
Ketupa zeylonensis	no	no
Nyctea scandiaca	no	no
Surnia ulula	no	no
Glaucidium perlatum	no	no
Glaucidium cuculoides	no	no
Athene brama	no	no
Ninox scutulata	no	no
Speotyto cunicularia	no	no
Ciccaba woodfordii	no	possible?
Strix occidentalis	yes	yes
Strix varia	yes	yes
Strix nebulosa	yes	no
Asio otus	yes	no
Asio flammeus	yes	no
Asio capensis	yes	no
Pseudoscops grammicus	no	no
Aegolius funereus	yes	no

truding footplate in *Strix*. The extreme similarity of the stapes in *Tyto* and *Phodilus* suggests that the derived condition in these two genera is homologous, indicating that *Phodilus* is more closely related to *Tyto* than to any of the Strigidae. Other evidence supporting such a relationship follows later.

The derived morphology of the footplates of *Tyto* and *Phodilus* differs from that in *Strix* not only in the degree to which the footplate protrudes into the oval window, but also in the means of its attachment to the shaft. In both *Tyto* and *Phodilus* the shaft broadens at the base to meet the footplate at its periphery, making the shape of the stapes similar to that of an inverted ice cream cone (Figs. 1 and 2). In contrast, the shaft of *Strix* attaches nearer the center of the footplate, causing the stapes to appear umbrella-shaped.

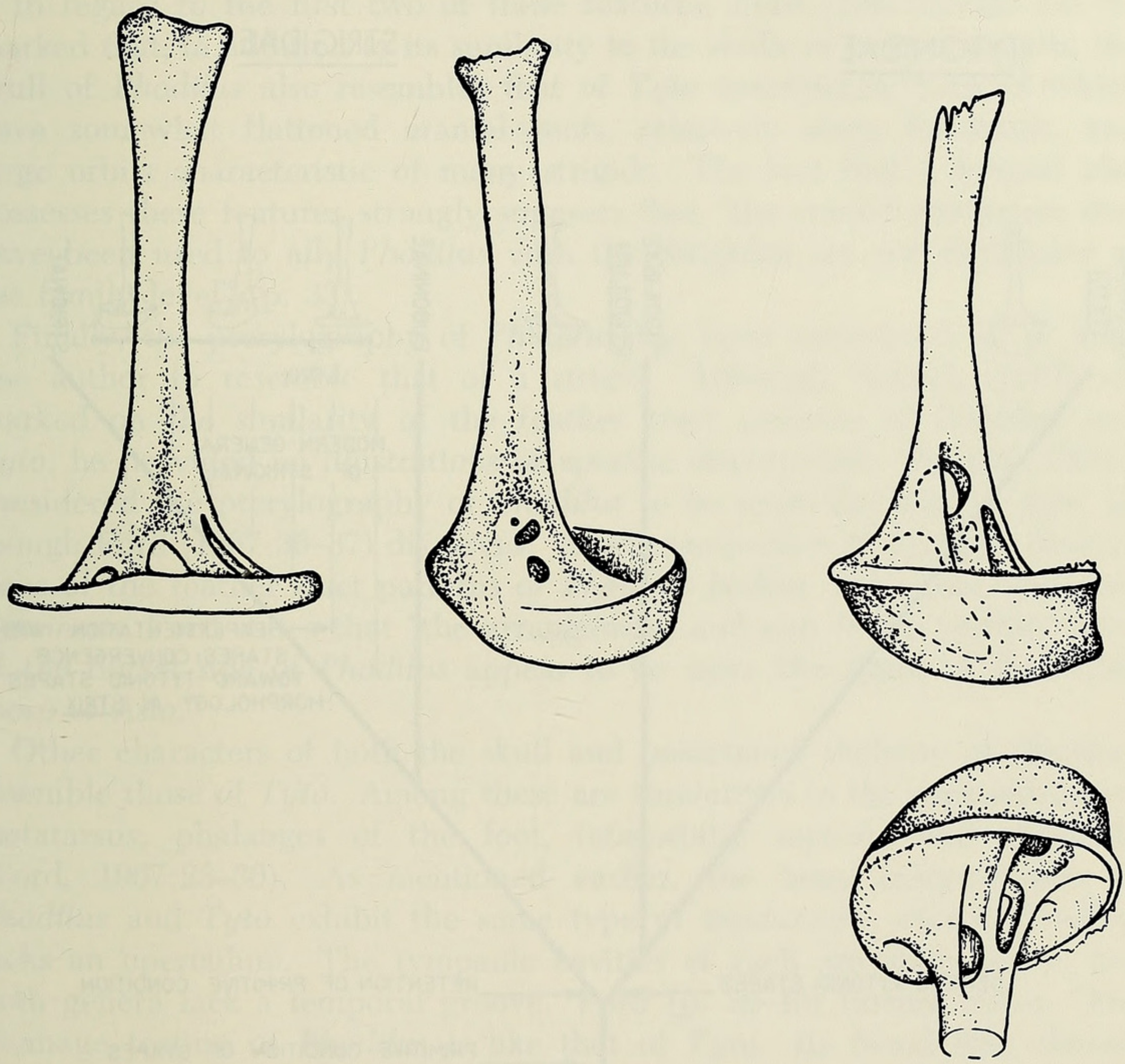

Fig. 2. Left to right: lateral views of the stapes of *Strix nebulosa* (primitive avian condition), *Strix occidentalis*, and *Strix varia*. Lower right, view looking down upon the footplate region of *S. varia* to show the "inverted umbrella" appearance of the attachment of the shaft of the bony stapes to the footplate region. All figures are drawn to the same approximate scale; actual lengths are approximately as those in Fig. 1.

Until recent years, only one species of *Phodilus* was recognized, *Phodilus badius*, ranging from northern India to Indonesia. In March, 1951, however, a second species was discovered in the eastern Congo and named *Phodilus prigoginei* (Burton, 1973:59). The genus *Phodilus* has been variously considered as a member of the Strigidae (Beddard, 1890; and Pycraft, 1903a, 1903b), a member of the Tytonidae (Nitzsch, 1867; Peters, 1940; Ford, 1967), or as a separate family (Marshall, 1966). A number of characters have been used as evidence for these various classifications, but it is often difficult to determine which of these are valid indices of evolutionary relationships. For example, the weak, unfused clavicles of

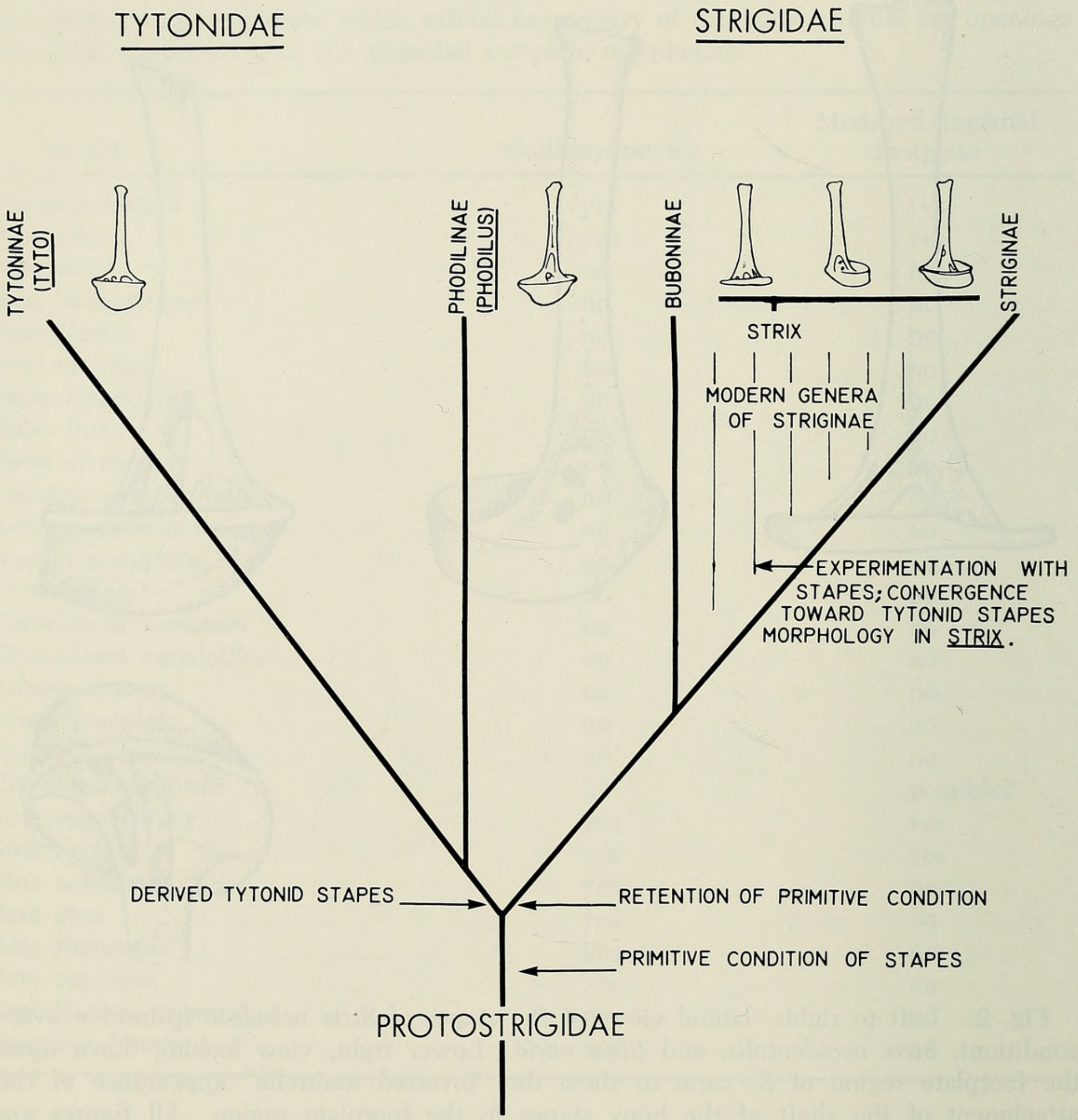

Fig. 3. Hypothetical phylogeny of the Strigiformes based on the morphology of the stapes and other lines of osteological evidence. This phylogeny assumes homology of the bony stapes of *Phodilus* and *Tyto*, and follows Ford (1967). The phylogeny also assumes convergence in the extended footplate of the stapes between certain species of *Strix* and the Tytonidae.

Phodilus have been used to ally it with the Strigidae, since some genera of this family (*Aegolius*, *Athene*, *Surnia*) possess similar characters.

Other features of *Phodilus* which have been used to indicate relationship with the Strigidae are: (1) broad, flat skull with a prominent forehead, (2) relatively large orbits, (3) posterior margin of the sternum with 4 notches, and (4) pterylography similar to that of certain strigids (Ford, 1967:31–37).

In regard to the first two of these features, Ford (1967:32–33) has remarked that, in addition to its similarity to the skulls of certain strigids, the skull of *Phodilus* also resembles that of *Tyto tenebricosa*, both of which have somewhat flattened cranial roofs, relatively steep foreheads, and large orbits characteristic of many strigids. The fact that a tytonid also possesses these features strongly suggests that "the cranial characters that have been used to ally *Phodilus* with the Strigidae are not significant at the family level" (p. 33).

Finally, the pterylography of *Phodilus* has been considered by at least one author to resemble that of a strigid. Although Nitzsch (1967) remarked on the similarity of the feather tract patterns of *Phodilus* and *Tyto*, he provided no illustrations or specific descriptions. Pycraft (1903b) considered the pterylography of *Phodilus* to be most like that of *Asio*, although Ford (1967:36–37) disagrees. After examination of Pycraft's illustrations of the feather tract patterns of *Phodilus badius*, *Tyto alba*, and *Asio flammeus*, Ford states that "the arrangement and size of the feather tracts of the dorsal side of *Phodilus* appear to be more like those of *Tyto* than those of *Asio*."

Other characters of both the skull and postcranial skeleton of *Phodilus* resemble those of *Tyto*. Among these are similarities in the coracoid, tarsometatarsus, phalanges of the foot, interorbital septum, and mandible (Ford, 1967:23–30). As mentioned earlier, the bony external ears of *Phodilus* and *Tyto* exhibit the same type of asymmetry, except *Phodilus* lacks an operculum. The tympanic cavities of each are open above, and both genera lack a temporal groove. Ford (p. 39–40) further states, "The plumage texture of *Phodilus* is like that of *Tyto*. Its facial disc, though forming unique 'teddy-bear ears' dorsally (Marshall, 1966:237 and Fig. 2), is nevertheless more similar to the heart-shaped disc of *Tyto* than to that of any strigid."

It seems that the large number of morphological similarities between *Phodilus* and *Tyto* including that of the stapes argue strongly for monophyly of the two genera. On the basis of the available evidence we believe that the genus *Phodilus* is correctly classified as a member of the Tytonidae, as reflected by the taxonomy of Peters (1940). A hypothetical phylogeny of owls based on stapedial morphology and other primarily osteological evidence is shown in Fig. 3.

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