VARIATION OF THE EXTERNAL EAR-OPENING IN THE STRIGIDAE

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IN WILLUGHBY'S ORNITHOLOGIA and other early works the few known species of owls were classed according to presence or absence of ear-tufts. When more species became known and the structure of owls was studied in greater detail it was realized that a classification based on ear-tufts alone was not entirely satisfactory. Our present-day classifications based on structure of the external ear may likewise need revision after the anatomy of some tropical species has been investigated.

The subdivision of the family Strigidae has long been a source of disagreement and the present paper does not attempt to settle the matter. The study of the classification of owls has always been handicapped by a lack of preserved specimens and skeletons of the tropical species. Until these are available a final phylogenetic arrangement must wait. The aim of this paper is to show the general variation tendencies in the external ear-opening or ear-conch.

As a Subfamily Character

Savigny (1809) and Cuvier (1817) seem to have been the earliest to use the ear-conch in subdividing the Strigidae. Macgillivray (1836, 1840) published the first illustrated studies of the ears of owls. Kaup (1859) made use of ear characters in his revision, as did Sharpe (1875). Collett (1881), whose work was translated by Shufeldt (1900), made a detailed study of the ear-openings and crania of ten species of boreal Europe. Pycraft (1898:259-263) described the ears of 18 species of owls, placing less emphasis on the ligamentous bridge than did Collett. Later (1903:44, 45) he described the ear of *Phodilus*. Ridgway (1914: 618–622) made extensive use of external ear characters in his key and diagnoses of owl genera represented in North and Middle America. He warned however that a classification based on ear structure alone would probably be far from satisfactory. Peters (1938) measured the ear-conches of a number of species.

The inner details cannot be studied in all species at present because they are not evident in skins and whole preserved specimens are not available. There is a shrinkage of 1 to 3 mm. in diameter of ear-openings in dried skins.

On the basis of the above studies Sharpe and some subsequent writers have separated the Strigidae into two subfamilies: Striginae, characterized by having the ear-conch at least half height of skull in vertical diameter, or larger than eye, its margin produced into a dermal flap of varying width, with a ligamentous or muscular bridge across the opening; and Buboninae, characterized by openings less than half height of skull, without flap and bridge.

The dermal flap is an outward extension of the skin along the bases of the feathers surrounding the opening. The bridge is an outward extension of a ridge or shelf below or behind which the auditory passage enters the skull.

The ten boreal species studied by Dr. Collett do indicate that the proposed subfamilies are quite distinct. The Strigidae are not primarily a boreal family however, and their taxonomy cannot be finally determined on the basis of the northernmost species. Just as the genus *Phodilus* tends to bridge the gap between Tytonidae and Strigidae, so some tropical species tend to merge the proposed subfamilies.

The writer would call attention to the following points:

1. There is a distinct though narrow dermal flap on the posterior margin of the ear-conch in living or preserved specimens of such bubonine species as *Otus asio, O. choliba, O. leucotis, O. vermiculatus, Bubo bubo, B. lacteus,* and *B. coromandus,* and species of *Ciccaba.*

2. The ligamentous bridge is apparent in *Otus asio, O. choliba,* and *Bubo bubo* as a shelf above the entrance of the auditory passage into the skull. According to Hodgson (1837:372), there is a very distinct bridge in *Bubo cavearea* [= *B. bengalensis*].

3. *Pulsatrix melanonota* and *P. koeniswaldiana* (subgenus *Novipulsatrix*) are intermediate between the proposed subfamilies, their ear-openings having the small size of the bubonine group but the oval shape, dermal flap (particularly on the posterior margin), and interior transverse ligament of the strigine group. They are intermediate in iris color, ear, and plumage characters between the admittedly strigine *Strix rufipes* and the bubonine *Pulsatrix perspicillata.* The skeleton of the latter species has both bubonine and strigine characters but is closer to *Bubo.*

On the basis of ear characters, facial feathering, and bare toes, *Novipulsatrix* could well be considered generically distinct,—as much so as *Mimizuku, Nesasio, Lophostrix, Jubula, Rhabdoglaux, Berneyornis, Rhinoptynx, Gymnasio,* and *Ketupa.* It has the recommendation of not being monotypic.

4. The genus *Ciccaba* shows affinity to both *Bubo* and *Strix* although usually classed as bubonine. The right ear openings of *Ciccaba virgata* (about 22 mm.), *C. borelliana* (21 mm.), *C. nigrolineata* (20 mm.), *C. albitarsis* (23 mm.), *C. hylophila* (24 mm.), in dry skins, are over half the height of the skull in greatest diameter, a strigine character. The smaller left ear opening is another strigine character. While skins of all of them do not show the transverse ligament and dermal flap, freshly killed or preserved specimens might show traces of such. The skeletal characters of *Ciccaba* place it closer to *Strix* than to *Bubo. Ciccaba albitarsis* is a step toward *Strix fulvescens* in size and character of ear openings and in its Temperate Zone habitat.

5. *Strix indranee* and *S. leptogrammica* (Subgenus *Bulaca*) of the

Indian Region are intermediate between *Bubo* and *Strix* in build, relative length of primaries, shape of facial disk, and color of the iris. While there is a dermal flap present, the vertical axis of the ear-conch scarcely equals half the height of the skull.

6. In the living *Otus asio naevius,* and in *Bubo bubo* (Macgillivray, 1836:344b) the vertical axis of the right ear-conch is fully half the height of the skull, 12-15 and 26-31 mm. respectively. Furthermore, in *Bubo bubo* the hollow of the conch proper, or cavernum, extends upward between the skin and the skull to the crown (Pycraft, 1898:260). The same is true in *Surnia ulula.*

It is thus evident that some species of four different genera have a combination of the supposedly diagnostic ear-opening characters of both of the proposed subfamilies.

As Correlated with the Environment

Among closely related species of owls the size of the ear-opening shows a parallel variation similar to that of wing length and foot feathering. In closely related groups the northern species have relatively larger ear-openings with more conspicuous dermal flaps than the southern.

As shown in the following table, large-eared species (those with ear-conch at least half height of skull in vertical axis) comprise a higher percentage of the owls in the Temperate and Boreal Zones than in the Tropical Zones. The Tytonidae (Barn Owls) and *Phodilus* (Bay Owls), which are mainly tropical and have uniformly small conches, are not included. Only non-migratory continental Strigidae are considered.

TABLE 1

Regional Ratios of Large-eared to Small-eared Strigidae

Region	No. of species	Species with large ear-conch	Species with small ear-conch
Transition, Canadian, Hudsonian, Temperate, and Boreal Zones of the Americas	22	12 (54.5%)	10 (45.5%)
Subtropical and Tropical Zones of the Americas	51	8 (15.6%)	43 (84.4%)
Boreal Europe and Asia	10	6 (60.0%)	4 (40.0%)
Tropical Africa	23	2 (8.7%)	21 (91.3%)
Tropical India	30	6 (20.0%)	24 (80.0%)

The resident owls of New Zealand, Australia, and the Philippines are all small eared.

The following evidence of southward reduction in ear size may be noted. In *Otus asio naevius* the ear-conches are 8-12 mm. in vertical

axis, while those of the southern *O. a. asio* are 6-8 mm. *Otus choliba, O. vermiculatus,* and *Ciccaba albogularis* of tropical America are as large as *O. a. naevius* in body size but the ear-conches are smaller, 6-9 mm. *Lophostrix cristatus* and *Strix woodfordi,* tropical species twice the size of *naevius,* have ear-openings just as small, 10-12 mm. Tropical *Pulsatrix perspicillata saturata* is as large and stout as boreal *Bubo v. virginianus* but the ear-conches are only slightly larger than in *Otus,* 10-14 mm., instead of 16-20 mm. as in *Bubo v. virginianus. Bubo nipalensis* and *B. orientalis* of the Indian tropics have ear-openings as small in relative size as those of *P. p. saturata.* In *Ninox, Athene,* and *Glaucidium* they are even smaller.

This tendency is contrary to Allen's (1877) rule of variation in mammals, according to which, in related forms the external ear is relatively larger southward, instead of northward.

Closely correlated with the larger ear-openings and dermal flaps of northern owls is the occurrence of a more broadly rounded facial rim which extends farther above the eye, wings with fewer emarginate primaries, more extensively feathered feet, and (in *Strix uralensis, Scotiaptex, and Cryptoglaux*) an unsymmetrical skull.

The asionine genera (*Asio, Rhinoptynx,* and *Pseudoscops*) have ear-conches with vertical axis greater than the height of the skull, narrow and slit-like, with dermal flaps continuous around the margin. In northern species of *Asio* the auditory canal enters below the bridge in the right ear, above the bridge in the left ear. This group may prove separable when preserved material of the tropical species is examined. The aegoline genera (*Cryptoglaux* and *Gisella*) having ear-conches about equaling the height of the skull or greater, oval in shape, with continuous dermal flap, and unsymmetrical skulls, may also be separable as a subfamily when their tropical species have been studied anatomically.

It seems likely that in the asionine, aegoline, and strigine groups, the large ear-openings, like the dense feathering of their feet, developed independently through parallel evolution.

A few remarks on the relative importance of external ear structure and foot feathering as taxonomic characters may be in order here. It has been proposed that, for owls, foot feathering be considered a character of subspecific significance only. Many tropical species have bare toes. There are three facts to remember when considering this view.

(1) Among species, foot feathering shows less correlation with climate than does size of ear-opening. The species with bare toes comprise 74.51, 65.22, and 36.67 per cent of the owl species in continental tropical America, Africa, and India respectively, while small-eared species comprise 84.4, 91.3, and 80.0 per cent in those regions.

(2) In *Asio otus, Cryptoglaux funerea, Otus asio,* and *Tyto alba*

the final extent of foot feathering is established at or before time of hatching, while the dermal flaps, and final shape of the ear-opening are then scarcely evident.

(3) Several characters of tropical genera—shorter, more rounded wings; more primaries emarginated; stouter bill and feet; shorter, less compact feathering—are strongly correlated with tropical climate throughout the Strigidae, and indeed, the whole class Aves. Dismiss these along with size and coloration, and nothing is left to support many long-recognized tropical genera.

Summary and Conclusions

1. The ear-conches of some species of *Pulsatrix* and *Ciccaba* are intermediate in structure between those of *Bubo* and *Strix*. The ear-conches of some species of *Otus, Bubo,* and *Strix* are likewise intermediate in character. The proposed subfamilies Buboninae and Striginae, as defined on the basis of these ear characters, are therefore not perfectly distinct.

2. In the Strigidae there is some correlation between size of ear-opening and climate. Among closely related genera or in genera of wide distribution, the species confined to tropical climates usually have relatively smaller ear-conches. In cold climates species having large ear-openings with large dermal flaps are more numerous, while in tropical climates species having small ear-openings with scarcely any dermal flap greatly predominate. This is contrary to the tendency in mammals (Allen's Law), according to which the external ear is relatively larger in southern forms.

3. Those species of Strigidae having larger ear-openings usually have a more complete facial disk and rim, and more extensively feathered feet. In a few cases (*Strix uralensis, Scotiaptex,* and *Cryptoglaux*) the large ear is associated with an unsymmetrical skull.

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FIELD BOOK OF ANIMALS IN WINTER. By Ann H. Morgan. G. P. Putnam's Sons, New York, 1939: 4 x 6¾ in., xv + 527 pp., 283 illus., including 4 color pls. $3.50.

All of the four colored plates and more than 60 pages of the text of this excellent little manual are devoted to the winter birds of the northeastern states. The engravers have handled Roger Peterson's paintings so well that in spite of their extreme reduction in size most of the 81 species shown on the plates are very successfully represented. The text includes very brief discussions of such topics as winter food, migration, and winter flocks but most of it is devoted to details of identification points, habits, and distribution of the several species.

Unfortunately the author follows the modern but confusing custom of not capitalizing the English proper names of birds. This, combined with the occasional use of such purely literary synonyms as "white-vested nuthatches," will surely be confusing to beginners. When a new edition is needed the author should ask some ornithologist to go over the bird nomenclature, both scientific and common, and remove its many small but annoying inconsistencies. At least the misspelling of *Arquatella* should be corrected and if most birds are to be listed under trinomial scientific names the reader should not be told that all "horned larks" are called simply *Otocoris alpestris* and breed "in the Arctic zone of Canada and Newfoundland."

We regret that the author has repeated the old legend that because of past importations of Texas Bob-white "most of the present northern quail are small as compared with birds captured sixty years ago, and they are probably more easily killed off by hard winters." There seems to be no real proof of this and Milton Trautman and others have presented strong evidence against it.

Few bird students are so specialized in their interests that they will not be led irresistibly, to their own great benefit, into reading the other sections of this attractive book which recount the characteristics and habits of the surprisingly large vertebrate and invertebrate fauna to be found in winter in our northeastern states.—J. Van Tyne.