Occurrence and Independent Evolution of Bilateral Ear Asymmetry in Owls and Implications on Owl Taxonomy

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Phil. Trans. R. Soc. Lond. B 1977 **280**, 375-408
doi: 10.1098/rstb.1977.0116

OCCURRENCE AND INDEPENDENT EVOLUTION OF BILATERAL EAR ASYMMETRY IN OWLS AND IMPLICATIONS ON OWL TAXONOMY

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(*Communicated by B. B. Boycott, F.R.S. – Received* 13 *August* 1976)

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Vol. 280. B 973. [Published 31 August 1977

On the basis of the literature and my own examination of living and/or dead but fresh owls of 16 species, bilateral asymmetry of external ears in owls is surveyed and ear structure briefly described.

Consideration of the probability of origin of various structural similarities and dissimilarities in the ear leads to the conclusion that ear asymmetry has evolved independently in at least five lines, represented by the respective genera (1) *Tyto*, (2) *Phodilus*, (3) *Bubo*, *Ciccaba*, *Strix*, (4) *Rhinoptynx*, *Asio*, *Pseudoscops*, and (5) *Aegolius*. *Bubo*, *Ciccaba*, and *Strix* probably represent more than one line of origin of ear asymmetry.

Available evidence suggests that bilateral ear asymmetry in owls serves to make the vertical directional sensitivity patterns different between the two ears for high frequencies, thus making possible vertical localization based on binaural comparison of intensity and spectral composition of sound. When an owl localizes prey by hearing, the direction of the source usually forms a shallow angle with the ground. Therefore, a certain angle of error usually converts into a longer distance along the ground for a vertical error than for a horizontal error. This is a crucial factor that calls for good vertical localization ability of owls which rely on hearing for localization of food. Selection pressure for improvement of the ability of vertical localization of sound is believed to lie behind the evolution of all types of bilateral ear asymmetry in owls.

On the basis of comparative ear structure the current subdivision of family Strigidae into subfamily Buboninae and Striginae is rejected.

The external ears of *Rhinoptynx* and *Pseudoscops* are described for the first time and shown to be very similar to those of *Asio otus*, demonstrating affinity between these three genera.

1. INTRODUCTION

In some owl species the external ears are very large and have a complicated geometry. A most remarkable aspect of external ear geometry is the bilateral asymmetry exhibited by species of several genera. Bilateral ear asymmetry in owls involves the external ear only. In no case has asymmetry been reported to extend to the middle or internal ear.

Bilateral asymmetry of the external ears in owls is related to directional hearing, or sound localization ability (Norberg 1968, in the press; Payne 1971; this paper, § 6).

The size, structure, and bilateral asymmetry of outer ears are extremely diverse among owls. In most species with asymmetrical external ears the asymmetry is confined to soft anatomy structures. However, the bilateral ear asymmetry extends also to the temporal parts of the skull in *Strix uralensis*, *S. nebulosa*, *Aegolius funereus*, and *A. acadicus* (described in § 5).

The detailed morphology of the outer ear of owls reveals that bilateral ear asymmetry has evolved independently along several lines. However, many descriptions are brief and with few details. Further, descriptions of ear morphology are missing altogether for many species and even for whole genera. This makes it difficult to evaluate the pattern of evolution of ear asymmetry in owls.

Because of the complexity and diversity of outer ear geometry in owls, the ear has been extensively used in taxonomy. The owl classification now in wide use is essentially that given by Peters (1940). To some extent his classification is based on outer ear morphology.

The latest check-list of owls of the world is that in Burton (1973, pp. 198–199). This list follows Peters's (1940) classification except for the following deviations: (1) five monotypic genera have been merged with other genera, (2) a few species have been merged, and (3) a few recently discovered species have been added. These alterations do not concern any of the species discussed in this paper. Classification above genus level is identical between Peters's and Burton's lists. The discussion of owl systematics in this paper and my alteration of the classification (§§ 7, 8 and 9) concern aspects in which the two lists are identical. Therefore, reference is made to Peters's list throughout.

Peters (1940) distinguished two recent owl families, Tytonidae and Strigidae. This division is based on a large number of characters (17 used by Ridgway 1914, p. 598), only one of which concerns the ear (see § 7).

The family Tytonidae is divided into the two subfamilies Tytoninae and Phodilinae, including *Tyto* and *Phodilus*, respectively. The structure of the external ear is one of the several distinguishing characters used (see § 7).

The family Strigidae is divided into subfamily Buboninae and Striginae, holding 21 (16 in Burton 1973, pp. 198–199) and 6 genera, respectively. This subfamily separation is based entirely on various features of the external ear (see § 8). It is rejected in this paper and the respective groups of species are termed 'bubonine' and 'strigine' owls.

For a historical review of owl classification the reader is referred to Sibley & Ahlquist (1972, pp. 183–190). The historical development is complex and contains many confusing nomenclatural problems.

There are few explicit statements concerning the use of external ear morphology in owl classification. However, the potential merits of using the external ear were recognized early, as were also the problems. Hence, for instance, Ridgway (1914, p. 619) wrote: 'the form, size, etc., of the external ear-opening affords an excellent character, though a classification based on this alone would probably be far from perfect.'

In 1940 Kelso wrote, 'Our present-day classifications based on structure of the external ear may...need revision after the anatomy of some tropical species has been investigated....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.' He also remarked 'The subdivision of the family Strigidae has long been a source of disagreement....'

Even after Peters's revision there remain many questionable points in owl classification, and Kelso's remarks are largely currently valid. There are mainly two kinds of problem regarding the ear as a clue for classification. One is the lack of information on ear morphology for many species, notably tropical ones. It is particularly information on soft-part anatomy of external ears in living owls, or in dead but intact, fresh or preserved specimens, that is lacking. Outer ears of study skins have often been destroyed in skinning and deformed by drying and shrinkage. The other is the problem of how to interpret the information available. The owl ear is highly adaptive and hence has to be treated with great care as a taxonomical character.

To be able to judge the degree of adaptivity of various ear structures and asymmetries one needs to know (i) their function and (ii) their importance in owl ecology. Knowledge of relations between ear structure and function and the species' habitat selection and hunting technique is crucial also for the problem of ecological segregation among owls, many species of which are 'searchers' (in the terminology of MacArthur & Pianka 1966) with wide diets.

2. Aim

This paper is concerned with (1) the descriptive and comparative morphology of external ears of owls with ear asymmetries, (2) the identification of independent evolutionary lines of ear asymmetry, and (3) ensuing implications on owl taxonomy. The function of ear asymmetry is discussed elsewhere (Norberg 1968, in the press) and is touched on here only briefly (§ 6).

The description includes three tropical owl species whose ears have not been described so far. They are *Rhinoptynx clamator* of Middle and South America, *Asio capensis* of Africa, and *Pseudoscops grammicus*, endemic to the island of Jamaica. In all I have examined the ears of living and/or dead, but fresh and intact, specimens of 16 species. These studies are planned to be reported on in detail later. Only brief, preliminary information from my own studies is given here.

As a basis for a discussion of the evolution of ear asymmetries a brief survey is given of known cases of ear asymmetry among owls. It is based on the literature and my own studies. This is intended to be a fairly complete review of the literature. Although short, the morphological descriptions should give sufficient background information for the conclusions drawn in this paper. Further, the various major types of ear asymmetry are illustrated in figure 4, plate 2; figures 5–8; figures 9 and 10, plates 3 and 4.

3. Material

Ears in study skins may have been damaged and distorted during skinning and also may have shrunk during drying. Kelso (1940) noted that some ear structures are not evident in museum skins and that there is shrinkage of 1 to 3 mm in the diameter of ear openings in dried skins. I have therefore examined only living birds or dead ones that were fresh and intact (kept frozen in polyethylene bags that prevent drying). Great care was taken to examine and measure ears in what was judged to be their natural posture (without stretching soft-anatomy structures). Skulls have also been examined.

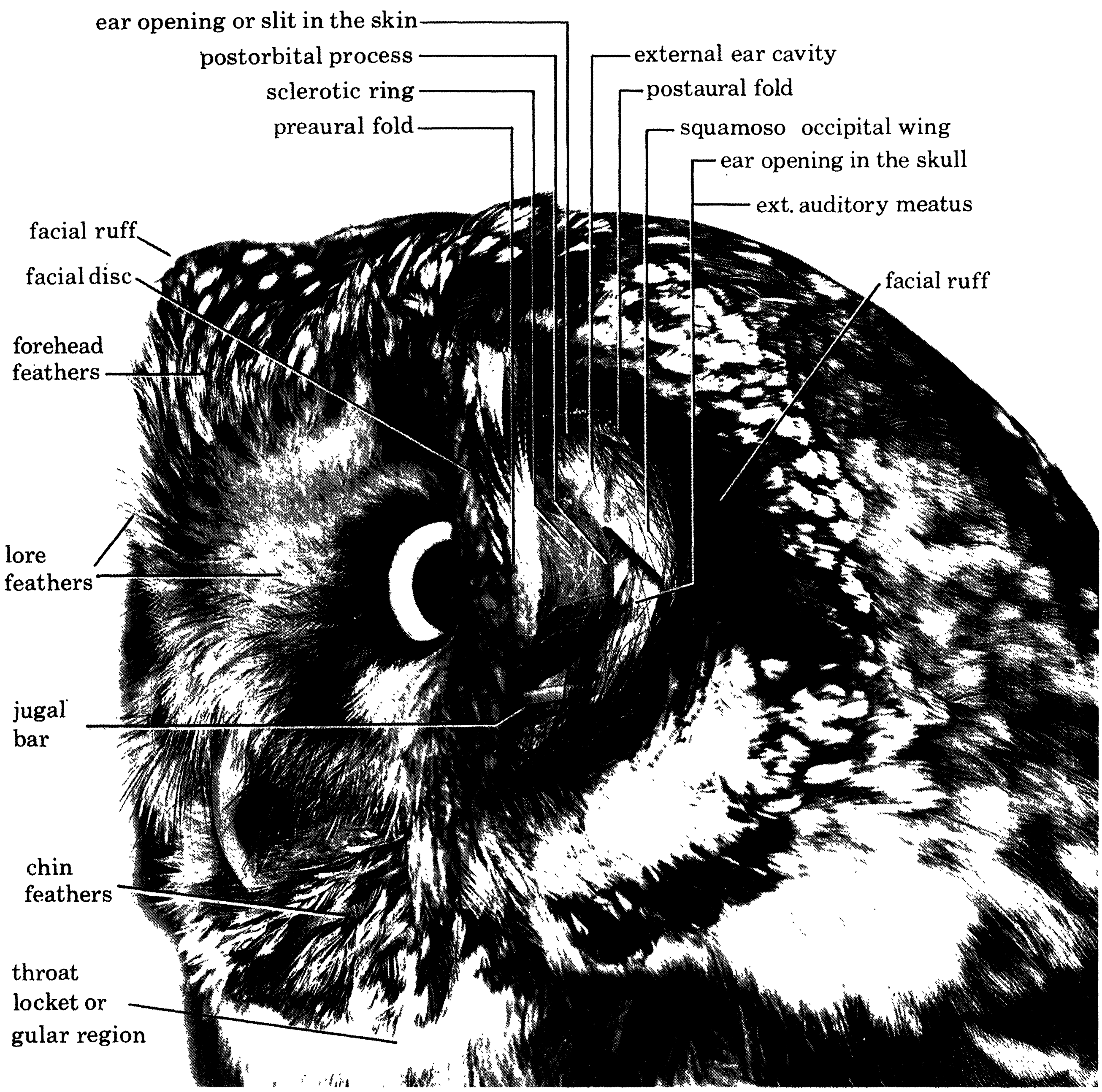
Below there is given a list of species, the outer ears of which I have examined. The number and state of the specimens examined are given in parentheses. Authors' names are given in § 5. All owls examined were adults.

Description of plate 1

Figure 1. Topography of face and external ear of *Aegolius funereus*. Living, tame specimen in a moderately alert attitude. The left facial disk is folded forwards to expose the ear opening and held forwards with the aid of a thread that is partly retouched in the photograph. 5 Jan. 1974. Photo: R. Å. Norberg.

Figure 2*a* and *b*. Left ear opening of a fledgeling of *Aegolius funereus* (about 30 days old) with a slight anomaly consisting of a small, but firm, dermal septum. As can be seen in figure 10 there are no dermal septa in the normal ears of *A. funereus*. This anomalous septum is strongly suggestive of the dermal septa responsible for the ear asymmetry in *Asio* (see figure 9). The occurrence of this septum in *Aegolius* shows how accidental may be the origin of novel ear structures that can cause binaural asymmetry and hence open up entirely new evolutionary paths (see text § 6 for further comments). 30 June 1968. Photo: R. Å. Norberg.

1

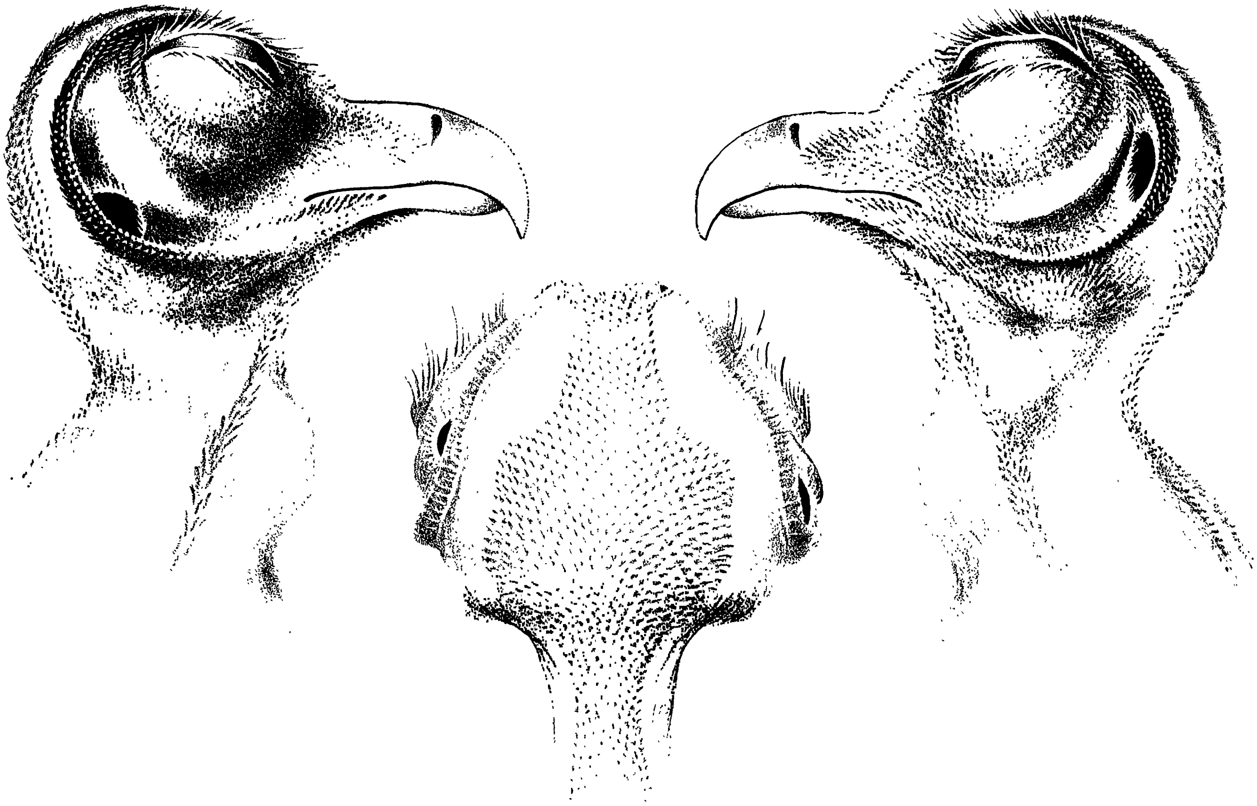


FIGURES 1 AND 2. For description see opposite.

(*Facing p.* 378)


3a


3b



FIGURES 3 AND 4. For description see opposite.

Tyto alba (two living, two dead, several skulls), *Phodilus badius* (two living), *Bubo virginianus* (one living), *Bubo bubo* (seven living, two dead), *Athene brama* (one living), *Ciccaba virgata* (one living), *Strix leptogrammica* (one living), *Strix aluco* (one living, six dead, several skulls), *Strix varia* (two living), *Strix uralensis* (one dead, several skulls), *Strix nebulosa* (several skulls), *Rhinoptynx clamator* (one living), *Asio otus* (12 dead, several skulls), *Asio flammeus* (five dead, several skulls), *Asio capensis* (one living, one dead), *Pseudoscops grammicus* (one living), *Aegolius funereus* (10 living, 10 dead, several skulls), and *Aegolius acadicus* (16 skulls).

4. Definitions, terminology, and a general description of external ear structures and head plumage in owls

A key to some terms appears in figure 1, plate 1.

External or outer ear

By *external* or *outer ear* in owls is meant ear structures outside the eardrum. Parts of the external ear are thus the *external auditory*, or *acoustic*, *meatus*, the *aural skin folds* or *flaps* bordering the ear aperture, the cavities between these skin folds and the skull, and also feathers around the ear.

Outer ear openings

I distinguish between two outer ear openings in owls.

(1) The *ear opening in the skin* is the most external opening and is bounded by a skin fold that in some species is developed into conspicuous pre- and postaural folds or flaps. In some species the ear opening is merely a small oval hole in the skin, its long axis shorter than the eye diameter (figure 6). In others the ear opening in the skin is relatively narrow but very high, reaching from the level of the lower jaw to the top of the head. The opening may then be called a *slit*. This kind of ear opening in the skin occurs, among others, in the genera *Asio* and *Aegolius* (figures 9 and 10, plates 3 and 4).

(2) The *ear opening in the skull* is the orifice of the external auditory meatus. The lateral border of the opening is usually formed at least partly by the anterior edge of the *squamoso-occipital wing*, while the medial border is formed by the lateral edge of the *postorbital process* and the *sclerotic eye ring*.

Skin flaps

Some species have a strongly developed *preaural skin fold* or *flap* that more or less overlaps the ear opening in the skin. When large and much overlapping, it is sometimes known as the *operculum*. Some species also have a specialized *postaural fold*, its anterior part being deflected laterally, forming a broad, anteriorly facing rim, the edge of which bears the most anterior facial ruff feathers.

Description of plate 2

Figure 3*a* and *b*. *Phodilus badius*. The form of its facial disk and ruff is unique among owls. The eyes are enormously large, and in this respect differ strikingly from the relatively small eyes in *Tyto alba* (figure 5). Captive owl, San Diego Zoo, July 1974. Photo: R. Å. Norberg.

Figure 4. Lateral and posterior views of the head of *Phodilus badius*. The feathers have been removed to show the different vertical locations of the ear openings in the skin. Below the left ear opening in the skin, and above the right one, there is a depression that is located immediately behind the eye and the postorbital process. Behind the ear openings in the skin there is a curved, dermal ridge on which the facial ruff feathers attach. Figures reproduced with minor changes from Pycraft (1903*b*, Plate 2).

Some muscles controlling the postaural flap, and hence the facial ruff (see below), have been described in *Strix aluco* (Stellbogen 1930) and *Aegolius funereus* (Norberg, in the press).

Feathers

Behind the ear openings there are modified, dense feathers that are densely packed and form a *facial ruff*. This is ill-defined or almost lacking in some species, prominent and almost encircling the face in others. Some of the facial ruff feathers attach to the deflected edge of the postaural skin fold and/or skin ridges behind the ears. The ruff forms an anteriorly facing concave wall, located immediately posterolateral to the ear opening in the skin, and curving anteromedially above and below the ear.

When the facial ruff is poorly developed, there is a broad, triangular *frontal tract of forehead feathers* separating the left and right parts of the facial ruff above the beak. When little developed the facial ruffs of the left and right sides are not confluent below the beak either.

In species having a strongly developed facial ruff, the left and right parts of it come very close together above the beak, curving down towards the beak and squeezing the forehead feather region into a narrow vertical strip above the beak. When strongly developed the facial ruff parts of the left and right sides are perfectly confluent below the beak. Then feathers of the *chin* (the region between the two branches of the lower jaw) participate in forming the ruff.

In front of the ear opening there are modified, sparse, sound-transparent feathers, many of which attach on the rim and anterior surface of the preaural skin fold. They are arranged radially around the eye and form a rounded *facial disk*. Usually the ruff and disk feathers are so arranged that the facial disk only partly overlaps the ruff as seen from the front. The outer part of the ruff therefore comes to enframe the facial disk. The ruff and disk feathers are very different in structure, the former being densely set with rami (barbs), the latter very sparsely so. Often the ruff and disk are strikingly differently coloured, giving the face its specific character. Indeed, the form and development of the facial ruff and disk are often good genus characters, whereas their coloration often characterizes the species.

Owing to the muscles of the postaural flap, the shape and attitude of the facial ruff are under the owl's control to some extent, very much so in some species, the appearance of the owl's face therefore varying in different situations. The most characteristic appearance of the facial ruff and disk is in the living owl when it is alert and attentive. The pre- and postaural flaps, and the facial disk and ruff attached to them, affect hearing and sound localization ability, at least in some species (Iljitschew 1960*a*, *b*; Payne 1971; Konishi 1973; and Norberg, in the press).

The development of the facial disk among different owl species parallels that of the facial ruff. The facial ruff and disk are poorly defined in many species of the 'bubonine owls', formerly subfamily Buboninae, whereas they are fairly complete in species of the subfamilies Tytoninae and Phodilinae, as well as in 'strigine owls', formerly subfamily Striginae.

On the *lore*, the region between eye and beak, there are usually more or less anteriorly directed feathers, forming a C-shaped feather configuration, its convex side against the beak. These loral feathers are coarse and relatively stiff. The tip of the rachis of the feathers closest to the beak are drawn out into long bristles, surrounding the beak like vibrissae.

Actually, these feathers are *bristles* or *semibristles* according to the terminology of Lucas & Stettenheim (1972, p. 270) and Stettenheim (1974, pp. 201, 204). In bristles the rachis tapers distally and is devoid of barbs in its outer part. There is a continuous, graded morphological series between ordinary contour feathers and bristles, the intermediate forms being recognized as semibristles. These have barbs distally, although the distal ones are reduced and spread apart, with few or no barbules.

The occurrence of these various feathers on the lore varies among different owl species (Stettenheim 1974, pp. 217, 218). In some owls also some of the peripheral feathers of the facial disk are developed into semibristles.

Dorsally the loral feathers grade more or less smoothly into forehead and/or facial disk feathers. In some 'bubonine' species the loral feathers continue in a narrow tract dorsolaterally, above the eyes, forming distinct *eyebrows* in conjunction with forehead feathers.

External auditory meatus

The *external auditory meatus* continues out to the ear opening of the skull as defined above. It includes what Pycraft (1898, p. 259) termed '*the cavernulum*', by which he apparently designated only the inner part of the external auditory meatus. The cavities outside the external auditory meatus, i.e. the more or less flat cavities between the skull and aural folds, will be termed jointly '*the outer ear cavities*'. They were called jointly '*the cavernum*' by Pycraft (1898, p. 259), who seemed to include, however, under this term also the outer part of the external auditory meatus as defined here. He did not clearly define the transition zone between 'the cavernum' and 'the cavernulum', but probably set it at the lateral edge of the quadrate, about half-way back in the external auditory meatus. His division and terms will not be used here.

Within-ear, or monaural, asymmetry

In most owl species each ear aperture in the skin is asymmetrical in the sense that there is no way in which a plane (or planes) can be oriented so as to divide one ear opening into two equal halves (or more than two equal parts). A more familiar, strongly asymmetrical structure of this kind is the human pinna.

Between-ear, or binaural, asymmetry

Species of most owl genera have each ear shaped as the mirror image of the contralateral ear, i.e. the two ears exhibit bilateral symmetry. However, pronounced bilateral asymmetry of the outer ears is known in seven owl genera, and is reported here for another two. Most species with bilateral ear asymmetry also have relatively large and geometrically complex outer ears.

In the following, bilateral asymmetry of the ears is often referred to simply as asymmetry of the ears. 'Ear asymmetry' thus should not be confused with within-ear asymmetry which will not be further considered in this paper.

Bilateral ear asymmetry is achieved in different ways and involves different structures in different owls. The following principal means, by which bilateral ear asymmetry is achieved, can be recognized (see table 1).

(*a*) *Asymmetry confined to soft anatomy structures.*

Ear apertures in the skin (1) of different size or (2) at different vertical levels. Preaural skin folds (3) of different shape or (4) at different vertical levels. Ear apertures in the skull (soft anatomy structures) (5) of different shape or (6) at different vertical levels.

(*b*) *Asymmetry of the skull.*

Ear apertures in the skull (head skeleton structures) (7) of different shape or (8) at different vertical levels.

5. OCCURRENCE OF EXTERNAL EAR ASYMMETRY AMONG OWLS

This survey includes all species that I know have bilaterally asymmetrical external ears. Also included are some species not shown to have asymmetrical ears, but which are (or are supposed to be) closely related to species with asymmetrical ears. It is very likely that most species contained in each of the genera listed below have similar ears, but the ears of many species have not been described satisfactorily if at all. I include references to descriptions of external, middle, and internal ears and also of the skull of the species presented.

The various types of asymmetry are described only briefly. The descriptions are not necessarily complete but give only the major features as extracted from the works referred to, or as ascertained by my own examinations of owl ears.

The literature review is intended to be fairly complete. It is believed to include all significant morphological reports on ear asymmetry among owls published in the period between 1859 and 1975 (inclusive). The earliest work included is Kaup's 'Review of the Strigidae' from 1859. No attempts were made at covering literature older than that.

Many descriptions of owl ears are old and thus many species appear therein under names that are different from those in current use. This makes some of the papers highly confusing and of little use without a resolution of the nomenclature. Species identification was performed with the aid of nomenclature and illustrations. For the nomenclature work the books by Sharpe (1875), Ridgway (1914), and Peters (1940) were very useful. The scientific names in the original papers are given here along with the current ones to facilitate use of these older papers.

To make the review more practical I present it in systematic order rather than by authors. The classification, nomenclature, and sequence of genera and species used by Peters (1940) in the fourth volume of 'Check-list of birds of the world' are followed throughout, except that Peters's subdivision of Strigidae into the subfamilies Buboninae and Striginae is rejected. These owls are referred to by the non-taxonomic designations 'bubonine' and 'strigine' owls, respectively.

Order STRIGIFORMES
Family TYTONIDAE
Subfamily TYTONINAE
Genus *TYTO* Billberg

Tyto alba (Scopoli) (figure 5)

The *Tyto* species and some *Strix* species (e.g. *S. nebulosa*) probably have more complete facial ruffs and disks than have species of any other owl genus. Pycraft (1898), Collett (1881, p. 11), and Stellbogen (1930) briefly described a densely feathered ridge behind the ears. The feathers of this ridge constitute the facial ruff, whose anterior side forms a curved, almost parabolic wall (Payne 1971, p. 536) below, above, and lateral to the ear opening and also forms a lateral border to the facial disk. The ear openings in the skin are very small and approximately square. They are of about the same size on both sides. The opening is covered by a big, almost square preaural skin flap, operculum, reaching far lateral to the ear opening.

The left preaural flap is located somewhat higher than the right one. The more ventrally located right flap faces *ca.* 15° more dorsally than the left one (Payne 1971, p. 536 and Plate 1F, G). According to Konishi (1973, p. 421) also the ear opening in the skin is located higher on the left side than on the right. Kaup (1859) illustrated the right side of an intact head of *T. alba* (sub nomine *Strix flammea*) with ear opening exposed (his Plate 57:8). Collett (1881, pp. 10, 11) briefly described the outer ear and the skull of *T. alba* (sub nomine *Strix flammea*), and noted that the ear openings might be slightly asymmetrical. Pycraft (1898) described and illustrated the outer ear and the pterylography of *T. alba* (sub nomine *Strix flammea* Linn.) and later (1903 *a*) also the skull. Illustrations of the asymmetrical position of the preaural flaps were given by Payne & Drury (1958), Payne (1967, 1971), and Konishi (1973).

Shufeldt (1900) described the skull of *T. alba* (sub nomine *Strix pratincola*).

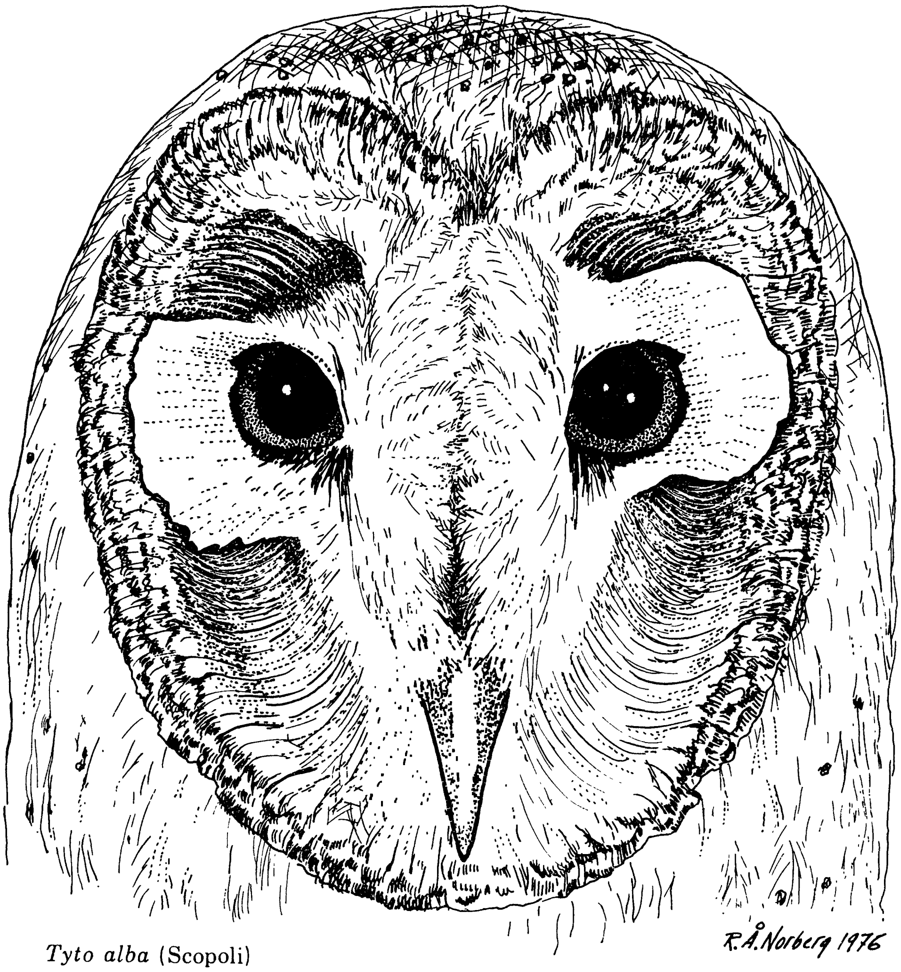


Figure 5. Frontal view of the head of *Tyto alba*. The facial disk feathers have been removed to reveal the preaural flaps which are asymmetrically located. The ear openings in the skin are small and almost square and concealed behind the preaural flaps. The facial ruff is extremely well developed in *Tyto* and forms anteriorly concave feather walls behind and around the ear openings in the skin. Normally, the facial disk feathers are attached radially around the eyes and cover the preaural flaps and the facial ruff, except for a narrow peripheral border of the ruff that comes to enframe the facial disk. The drawing is based on a photograph in Konishi (1973, Figure 11) and supplemented with details from another, similar photograph in Payne (1971, Plate 1E).

The middle ear was described by Werner (1960, p. 239), and the eardrum and stapedial complex by Freye-Zumpfe (1952/53). Dimensional data on the eardrum, footplate of stapes, and the cochlea were given by Schwartzkopff (1957). Krause (1901) described the bony stapes of *T. alba* (sub nomine *Strix flammea*), and Schwartzkopff & Winter (1960) the structure of the cochlea.

In one living specimen of *T. a. pratincola* (Bonaparte) that I examined, the left ear opening in the skin was 7.1 mm high and the right 7.7 mm.

Subfamily PHODILINAE

Genus *PHODILUS* Geoffroy Saint Hilaire

Phodilus badius (Horsfield) (figures 3 and 4, plate 2)

Pycraft (1903*b*) described the external ear of *P. badius* (sub nomine *Photodilus badius*). This little known paper contains good illustrations of the head with ear openings exposed (figure 4). The ear openings in the skin are small, oval, and of about the same relative size as in *Tyto alba*. The left ear opening is located higher than the right one and is facing nearly horizontally. The right ear opening is located immediately above the articulation between the jugal bar and quadrate and is facing obliquely upwards. Between the eye and the postaural facial ruff there is a trough, entirely open laterally, located below the ear opening in the skin on the left side, above it on the right. The bottom of this groove is formed by the skin between the eye and the postaural facial ruff. Preaural skin fold is absent. The outer ear cavities are of different forms on the left and right sides (Pycraft 1903*b*, p. 45).

Pycraft (p. 36) stated, 'In the general form and distribution of the pterylae *Photodilus* is distinctly Asionine in character, but in the form of the external ear it is unique', and (p. 46) 'The general conformation of the external ear is quite different from that of any other owl, but, externally, it may possibly be regarded as more nearly like that of *Asio* than that of any other genus.' This is discussed in § 6.

In another paper Pycraft (1903*a*) described the skull of *P. badius* (sub nomine *Photodilus baduus*).

Marshall (1966, p. 237) commented on the facial disk of *P. badius*, 'The living bird in the field reveals a facial disk unlike that of any other owl. Dorsally there are two flat Teddy-bear ears...these rounded "ears" are totally unlike the decorative ear tufts of Strigidae.'

After examination of two living owls I can verify the ear asymmetry as described by Pycraft. However, I could not examine the extension of the outer ear cavities (inside the ear opening in the skin). The ear opening is surrounded by very densely set feathers making it difficult even to find the opening in the living owl. Heights of ear openings in the skin in the two specimens were (left, right) 8.7, 7.9 and 9.0, 8.8 mm, respectively.

The shape of the facial ruff and disk gives this owl a unique and very strange appearance. The left and right parts of the ruff extend above the dorsal contour of the head. Here the ruff is directed somewhat forwards, reminiscent of prick ears of a mammal. The facial ruff most likely functions as a sound collector as does the mammalian pinna.

A tendency towards this pronounced ruff is seen in *Aegolius funereus*. When alert, its facial ruff projects above the dorsal head contour, however, not by as much as in *Phodilus*.

The ear tufts possessed by some owls are formed by modified, elongated forehead feathers and are entirely different from the dorsal extensions of the facial ruff.

Unlike *Tyto*, *Phodilus* has a broad tract of forehead feathers separating the left and right parts of the facial ruff and disk above the beak.

Family STRIGIDAE

BUBONINE OWLS (formerly subfamily BUBONINAE)

Genus *BUBO* Duméril

Bubo virginianus (Gmelin)

This species is included here because it is congeneric with *B. bubo* which has been claimed to have asymmetrical ears (see below), and because some information is available on *B. virginianus*.

Ear openings, head regions, and the skull of *B. virginianus* were described by Lucas & Stettenheim (1972, pp. 30–33). They presented good drawings and a radiograph of the head with the ear opening in the skin made visible by application of radiopaque material to the edge of the opening. The ear opening in the skin is oval and lies lateral to the sclerotic eye ring, the entire opening lying anterior to the postorbital process. Lucas & Stettenheim (1972) did not describe any ear asymmetry.

I have examined the ear of one living, *ca.* 15 weeks old Californian *B. virginianus*. Its left ear opening in the skin was 23.0 mm high, the right 23.2 mm. There was no obvious asymmetry.

Bubo bubo (Linné)

Collett (1881, p. 19) stated that the right ear opening in the skin is larger than the left one in *Bobo ignavus* Forst. (= *B. bubo*). He gave measurements for one male only. Its left ear was 26 mm high and 16 mm wide and the right 30 mm high and 19 mm wide. Collett put high confidence in this difference and even used it in a key to genera and species.

I know of no other information on ear asymmetry in *Bubo*. On the contrary, this genus has usually been included among those with perfectly symmetrical ears.

The heights of the ear openings in the skin in seven living Swedish *B. bubo* were (left, right) 29.7, 33.3 (♀), 27.1, 31.9 (♀), 27.0, 31.4 (♀), 27, 30 (♀), 25.5, 29.1 (♂), 24.7, 26.4 (♂), and 23, 25 mm (♂), respectively. The height of the left ear opening is thus on average 11% smaller that that of the right. The preaural flap was *ca.* 4 mm wide. These data support Collett's statement on ear asymmetry. (They also corroborate Collett's status as a very good observer. He made many correct observations that have been overlooked in later studies on owl ears. His papers referred to here, originally in Norwegian, are available also in English – for those preferring that, see References.)

As in *B. virginianus* the ear opening in the skin of *B. bubo* is located far forwards, most of it lying over the sclerotic eye ring. This is a more anterior position of opening than I have seen among any of the other genera treated here.

Genus *ATHENE* Boie

Kaup (1859, pp. 209, 260) stated that ear openings in the skin are asymmetrical in *Athene*. In his illustration of ear openings only (Plate 56:4), they are of slightly different size. Collett (1881, p. 12) could not verify this asymmetry in *A. noctua* (Scopoli). To my knowledge there is no information but Kaup's on ear asymmetry in *Athene*.

One living *A. brama* (Temminck) which I examined had perfectly symmetrical ears, both measuring 5 mm in height. In the absence of clear evidence to the contrary, I include *Athene* among owls with symmetrical ears and therefore make no further mention of its ears in this paper.

Genus *CICCABA* Wagler

Ciccaba virgata (Cassin) (figure 6)

The height of the left ear opening in the skin is 30–40 % smaller than that of the right. Ear openings were measured on nine study skins by Peters (1938), who obtained the mean heights 12.6 mm (s.d. 1.8) for the left and 17.9 mm (s.d. 1.4) for the right ear. Kelso (1940) remarked on the difference in size of the two ears of *Ciccaba*, but gave measurements only for the right ear in three species, thus providing no information on degree of asymmetry. Voous (1964) measured three skins and obtained the mean heights 13 mm (s.d. 2½) for the left and 20 mm (s.d. 2) for the right ear, and 2 mm for the width of the preaural skin fold.

At the bottom of table 2 in Voous (1964) individual measurements are listed separately for the left and right ear. However, the sequence of specimens is the same in the two series (Voous, personal communication), thus permitting pairing and comparison of ears on an individual basis. It thus appears, that in a few *Ciccaba* and *Strix* species the largest ear opening is on different sides of the head in different specimens, the difference in ear height being small, however. It should be kept in mind that Voous measured dry study skins. The ear sizes should therefore be checked on fresh material.

The figures from Voous (1964) given in this review are mean values that I have calculated from Voous's original data at the bottom of his table 2. The means have been rounded off to the nearest ½ mm. For some *Ciccaba* and *Strix* species these means deviate slightly from those given originally in Voous's table columns.

I have examined one living *C. virgata*. The left ear opening in the skin was 10.6 mm high, the right 17.4 mm. There is not much of a preaural flap. However, feathers attach at the skin around the ear opening and the calami thus stiffen the rim around it. When the facial disk feathers are folded forwards, the part of the anterior rim that is stiffened by calami goes with the disk and may be recognized as a narrow preaural fold or flap. This was 3½ mm wide in both ears. Except for being smaller than most *Strix* ears, and having only a narrow preaural fold, the ears of *C. virgata* resemble those of many *Strix* species.

Ciccaba nigrolineata Sclater

Peters (1938) reported the height of the left ear to be smaller than that of the right. Mean values from two skins were 13 mm for the left and 18½ mm for the right ear. Voous (1964) got about the same value for both ears, mean heights from three skins being 11½ mm (s.d. 1½) for the left and 12 mm (s.d. 2) for the right ear. Preaural skin fold was lacking.

Ciccaba huhula (Daudin)

The height of the left ear opening in the skin is 30–40 % smaller than that of the right. In one skin measured by Peters (1938) the left ear opening in the skin was 12½ mm high and the right 20 mm. Voous (1964) measured three skins and obtained the mean heights 9½ mm (s.d. 2½) for the left and 13½ mm (s.d. 2) for the right ear, and the width 1 mm for the preaural skin fold.

Ciccaba albitarsus (Bonaparte)

The height of the left ear opening in the skin was reported by Peters (1938) to be slightly smaller than that of the right. His mean values from three skins were 19 mm (s.d. 1½) for the left and 22½ (s.d. 1) for the right ear.

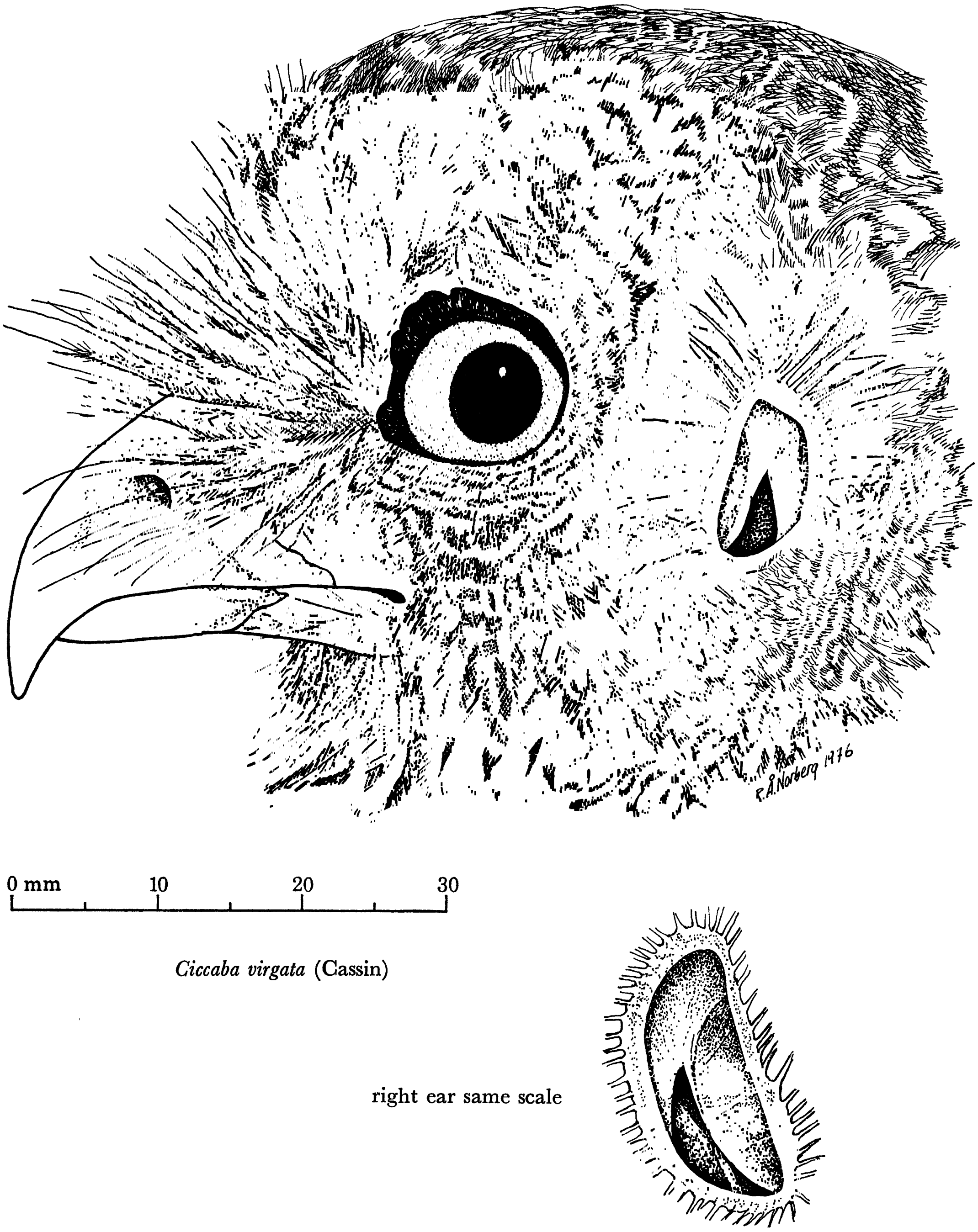


FIGURE 6. Lateral views of the head and ears of *Ciccaba virgata*. The peripheral feathers of the facial disk are folded forwards, those of the facial ruff backwards, to expose the unequally large ear openings in the skin. Drawings made from photographs of a living, captive owl in San Diego Zoo, July 1974.

Ciccaba woodfordi (A. Smith)

The height of the left ear opening in the skin is *ca.* 25 % smaller than that of the right. Mean heights in four skins measured by Peters (1938) were $8\frac{1}{2}$ mm (s.d. $1\frac{1}{2}$) for the left and 12 mm (s.d. 3) for the right ear. Voous (1964) measured five skins and obtained the mean heights 10 mm (s.d. $\frac{1}{2}$) for the left and 13 mm (s.d. $1\frac{1}{2}$) for the right ear, and the mean width 1 mm for the preaural skin fold.

Strigine owls (formerly subfamily Striginae)

Genus *STRIX* Linné

Strix selo-puto Horsfield

Three skins measured by Voous (1964) had both ear openings in the skin of about the same size, mean height being $11\frac{1}{2}$ mm (s.d. $\frac{1}{2}$) for the left and $12\frac{1}{2}$ mm (s.d. $\frac{1}{2}$) for the right. Mean width of preaural skin fold was 1 mm.

Strix leptogrammica Temminck

Among five skins measured by Voous (1964), the left ear opening in the skin was smaller than the right one in four, while they were equally large in one skin. Mean height of ear opening in the five skins was $17\frac{1}{2}$ mm (s.d. $1\frac{1}{2}$) for the left and 22 mm (s.d. $3\frac{1}{2}$) for the right ear. Mean width of preaural skin fold was 2 mm.

I have examined one living *S. leptogrammica*. Its external ears are very similar in general structure to those of *Ciccaba virgata*. The left ear opening in the skin was 15.2 mm high, the right one 21 mm, the left ear thus being *ca.* 30 % smaller than the right. The preaural skin fold was 5.4 mm wide on the left side, 4 mm on the right.

Strix aluco Linné

Ear openings in the skin are large, the left opening being slightly smaller than the right. Collett (1881, p. 25) measured the height of ear openings in the skin in one adult female of *S. aluco* (sub nomine *Syrnium aluco* (Lin.)) and got 22 mm for the left ear and 25 mm for the right. The width of the preaural skin flap was *ca.* 12 mm in both ears. Collett also remarked that the preaural skin flaps are asymmetrical. The left preaural flap is skew, the upper and lower edges slanting lateroventrally, while the upper and lower edges of the right flap are about horizontal.

Pycraft (1898) commented on the different size of the ear openings in the skin in *S. aluco* (sub nomine *Syrnium aluco*), but did not mention asymmetry of the preaural flaps. In a later paper (1903*a*) Pycraft described also the skull of *S. aluco* (sub nomine *Syrnium aluco*). Kaup (1859) described and illustrated the outer ear and the skull of *Syrnium aluco* (= *Strix aluco*). Stellbogen (1930) gave a good, detailed description of the outer and middle ear of *S. aluco* (sub nomine *Syrnium aluco*), but (curiously enough) made no remark on the asymmetry of the outer ears. Peters (1938) gave the values 20 and $23\frac{1}{2}$ mm, respectively, for the height of the left and right ear openings of one skin. Voous (1964) measured seven skins and obtained the mean heights 21 mm (s.d. 2) for the left and 23 mm (s.d. 2) for the right ear. The right ear was larger in five skins, the left in two. Mean width of the preaural skin fold was $9\frac{1}{2}$ mm.

May (1961) described the skull of an embryo (length of head 22 mm) of *S. aluco*. The eardrum and stapedial complex were described by Freye-Zumpfe (1952/53). Dimensional data on the eardrum, footplate of stapes, and the cochlea were given by Schwartzkopff (1957). Krause (1901) described the bony stapes of *S. aluco* (sub nomine *Syrnium aluco*). The structure of the cochlea was studied by Schwartzkopff & Winter (1960).

The right ear opening in the skin was larger than the left one in all six specimens that I have examined. Mean heights were 23 mm (s.d. 2) for the left ear and 26 mm (s.d. 2) for the right. The preaural flaps were 10½ mm wide in both ears but asymmetrical in their form.

Strix occidentalis (Xantus)

In one skin measured by Voous (1964) the left ear opening in the skin was slightly smaller than the right one, 17½ mm in height for the left and 22 mm for the right ear. Preaural skin flap was 13 mm wide.

Strix varia Barton

Peters (1938) gave the values 25 and 27½ mm, respectively, for height of the left and right ear opening of one skin of *S. varia* (sub nomine *Strix fulvescens*). Among five skins measured by Voous (1964), the left ear was smaller than the right in three specimens, while in two the left ear was the largest. Mean height of the opening in the skin was 24½ mm (s.d. 3) for the left, and 27 mm (s.d. 3½) for the right ear. Mean width of the preaural skin flap was 12 mm.

The right ear was larger than the left one in the two living specimens that I have examined. Heights of the ear openings in the skin were (left, right) 28.0, 29.8 and 25.0, 30.2 mm, respectively. The external ears are very similar to those of *S. aluco* and *S. uralensis*.

Strix hylophila Temminck

The left ear opening in the skin is smaller than the right one. Peters (1938) gave the heights 19 mm for the left and 24½ mm for the right ear of one skin. Voous (1964) measured the height of ear openings of another skin to 17 mm for the left and 21 mm for the right ear. The preaural skin flap was 7 mm wide.

Strix rufipes King

In one skin measured by Voous (1964) the left ear opening was larger than the right one, 17 mm in height for the left and 11 mm for the right ear. The preaural skin flap was 5 mm wide. This is the only report of the left ear being considerably larger than the right in the *Ciccaba-Strix* group.

Strix uralensis Pallas (figure 7)

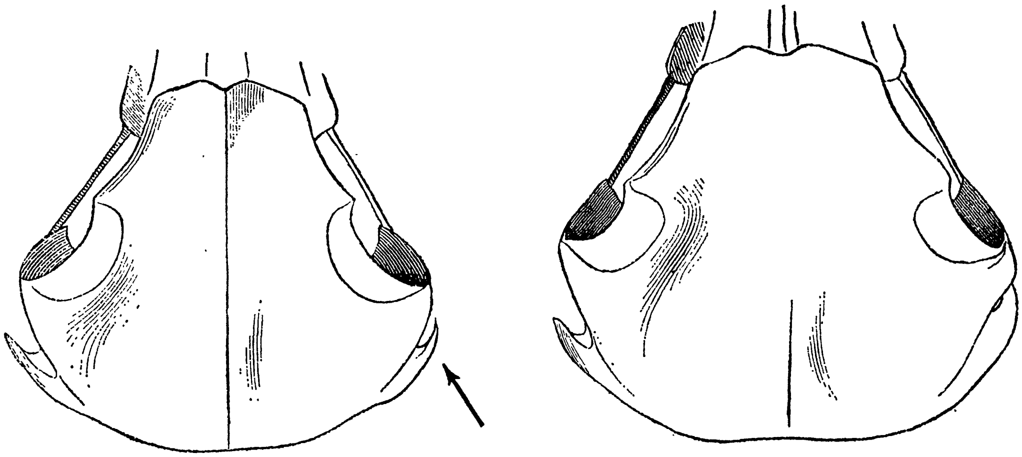
Collett (1881, p. 27) measured the height of the ear openings in the skin in one female (sub nomine *Syrnium uralense* (Pall.)) and got 23 mm for the left ear and *ca.* 27 mm for the right. According to Collett the preaural skin flaps are asymmetrical in the same way as in *S. aluco*. He also remarked on a slight asymmetry of the skull, namely a difference (1–2 mm) in development of the left and right squamoso-occipital wing (figure 7). Pycraft (1898) examined a fresh specimen of *S. uralensis* (sub nomine *Syrnium uralense*), but did not find any asymmetry in the soft parts of the ear, and reported the left and right ear openings in the skin to be equally large. He also reported that a skull that he examined was symmetrical.

Among six skins measured by Voous (1964), the left ear opening in the skin was smaller than the right in five, while the left ear was slightly larger than the right in one skin. Mean height of the ear opening in the six skins was 23½ mm (s.d. 2) for the left, and 26½ (s.d. 1) for the right ear. Mean width of the preaural flap was 13 mm.

I can confirm Collett's notes on asymmetry of the squamoso-occipital wing of the skull.

Strix nebulosa J. R. Forster (figure 8)

Collett (1881, p. 30) measured ear openings in the skin in one adult female of *S. nebulosa* (sub nomine *Syrnium lapponicum* (Thunb.)) and got 28 mm in height for the left ear and 30 mm for the right. The width of the preaural flap was 17 mm in both ears. The flaps are asymmetrical in the same sense as in *Strix aluco* but not as pronounced. Collett described and illustrated a roughly horizontal skin fold, located inside the ear opening in the skin and dorsal to the ear opening in the skull both on the left and right side. It has a slightly different orientation in the two ears. The squamoso-occipital wings are asymmetrical in a way similar to that in *Strix uralensis*, but the asymmetry is more pronounced in *S. nebulosa* (figure 8). The left squamoso-occipital wing reaches farther antero-dorsally than does the right one. The dorsal part of the right postorbital process extends farther laterally than does the left process. Because of the asymmetries, the left external auditory meatus is directed somewhat more dorsally than the right one (Collett).



Figures 7 and 8. Dorsal views of the skulls of *Strix uralensis* (7) and *Strix nebulosa* (8) showing the bilateral asymmetry of the squamoso-occipital wings which are located lateral to the ear openings in the skull (indicated by the arrow). Reproduced without change from woodcuts in Collett (1881, pp. 29 and 33, respectively).

Voous (1964) measured eight skins and obtained mean heights of about 27 mm for both ears. Mean width of the preaural flap was 15 mm.

I can confirm the skull asymmetry remarked on by Collett.

Genus *RHINOPTYNX* Kaup (Monotypic)

Rhinoptynx clamator (Vieillot)

The ear slit in the skin is higher than the height of the skull (Kelso 1940). Apart from this statement I know of no descriptions of the external ears. The structure of the external

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Description of plate 3

Figure 9. Anterolateral views of the head of *Asio otus* showing the bilateral asymmetry of the external ears. The head is oriented so that the nearest jugal bar lies in the plane of the figure and the horizontal plane of the head is perpendicular to the plane of the figure. The head and ears are intact, but the preaural flap is folded forwards and the postaural flap is displaced backwards to expose underlying structures of the external ear. Drawings made from photographs of a dead owl.

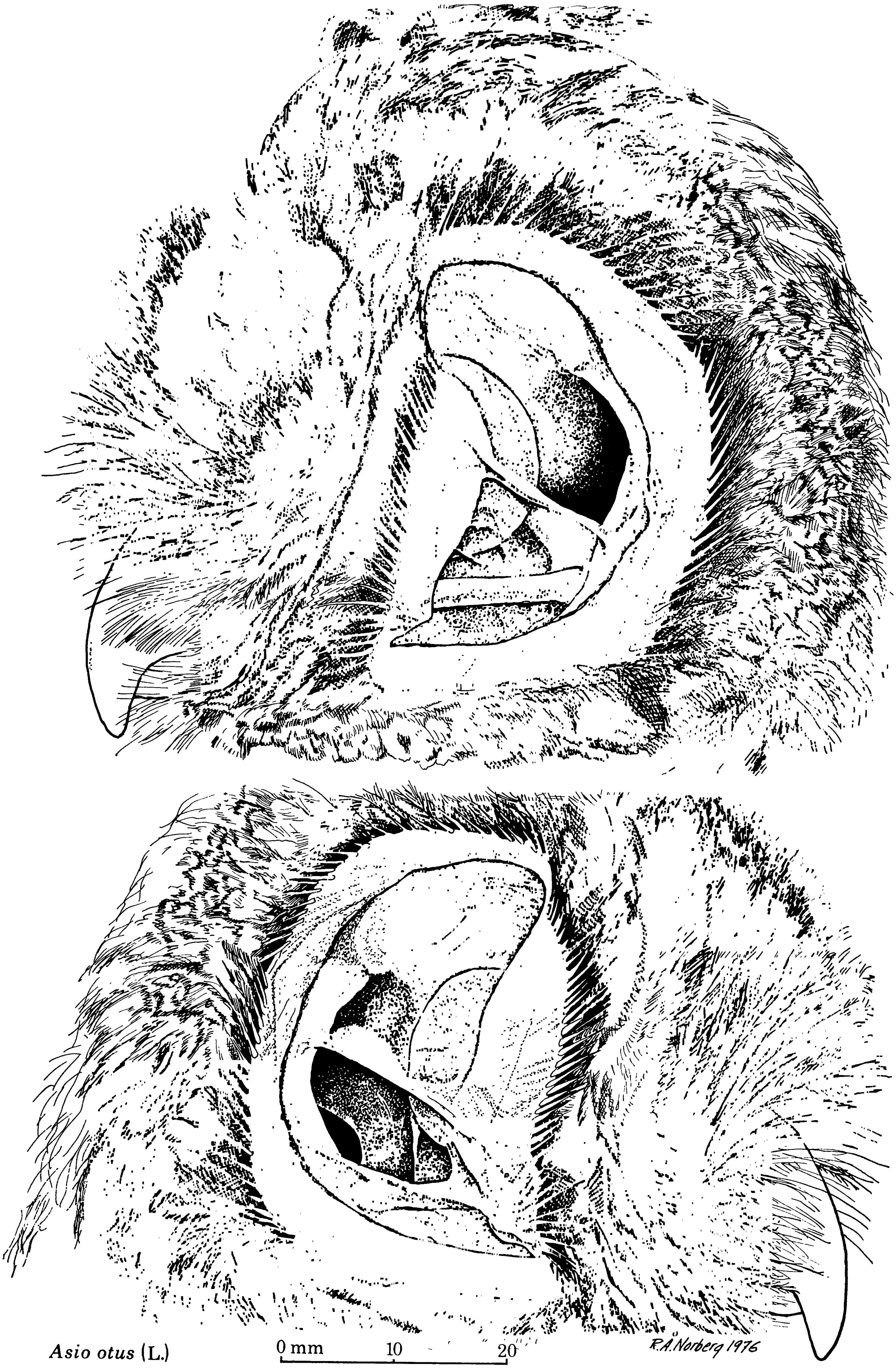


FIGURE 9. For description see opposite.

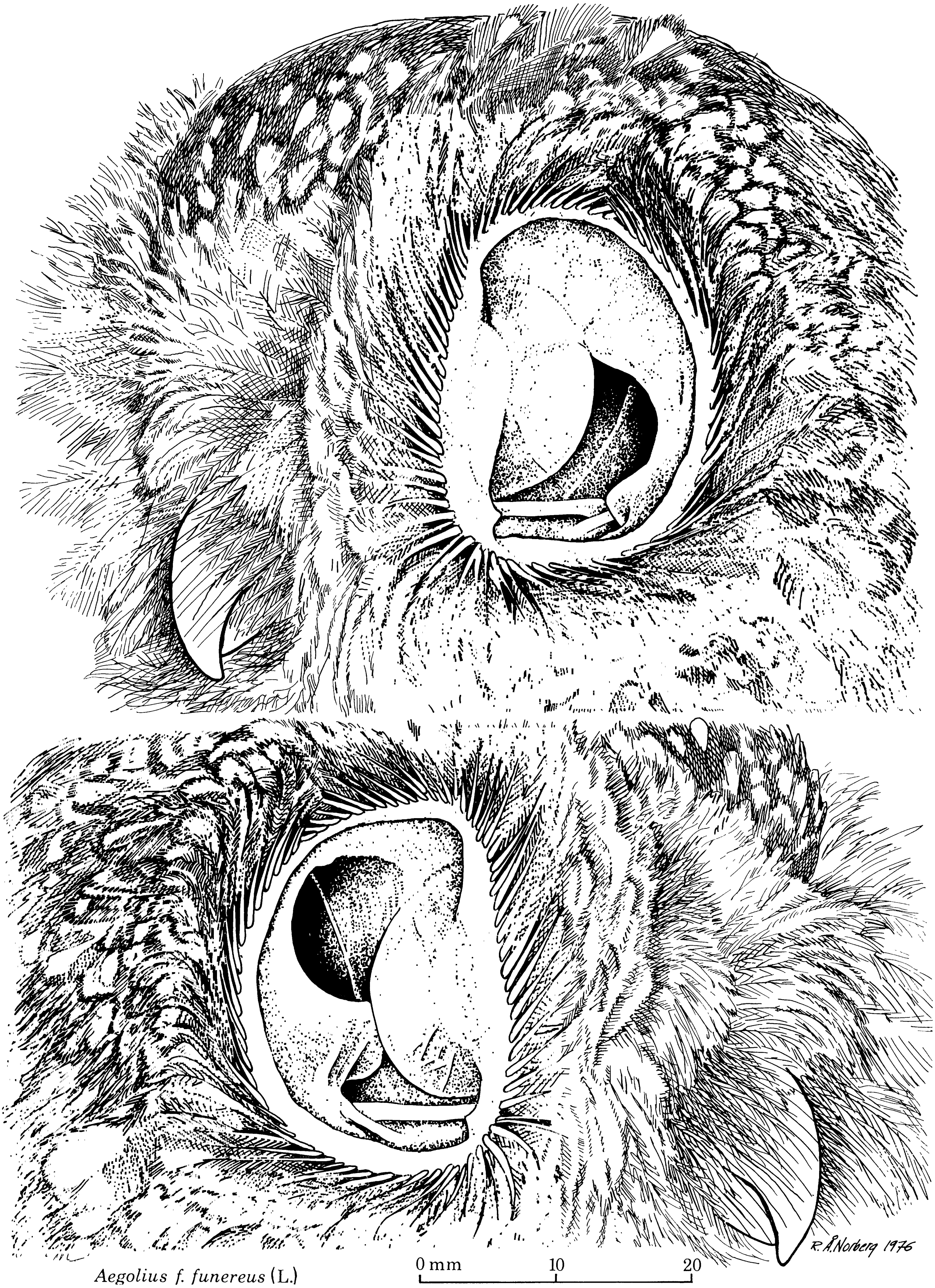


FIGURE 10. For description see opposite.

ear was assumed by Ridgway (1914, p. 620, footnote, quoted in § 9) to be similar to that of *Asio*.

I have examined one living specimen. Its external ears were like those of *Asio otus* in all essential respects, including asymmetry. The left ear slit was 37 mm high, the right 39½ mm. The left preaural fold was 9.7 mm wide, the right 11 mm. The lateral, pointed projection, present on the lateral edge of the postorbital process in *Asio flammeus* and *A. capensis*, is lacking in *Rhinoptynx*.

Genus *ASIO* Brisson

Asio otus (Linné) (figure 9, plate 3)

Ear slits in the skin are of the same size and shape on the left and right side. Ear slits are large, about as high as the skull. The height of both ear slits of one adult male measured by Collett (1881, p. 24) was 35 mm, and the width of the preaural flaps 13 mm. In both ears there is a more or less horizontal, dermal septum attaching to the posterior side of the preaural skin flap, the lateral side of the sclerotic eye ring, to the postorbital process, and to the medial and lateral walls of the external auditory meatus. This intra-aural dermal septum is differently oriented in the two ears. On the left side, the opening of the external auditory meatus (= ear opening in the skull) is above the dermal septum. Below it there is a blind cavity extending ventrally to the jugal bar. On the right side the opening of the external auditory meatus is below the dermal septum, the opening reaching ventrally to the jugal bar. On the right side the dermal septum closes off a blind cavity above the ear opening of the skull.

Pycraft (1898) described the pterylography and the outer ear. The blind cavity, located below the intra-aural dermal septum in the left ear, above it in the right, was called the *diverticulum* by Pycraft (1898, p. 262). In a later paper Pycraft (1903*a*) commented briefly on the skull. Shufeldt (1900) described the skull of *A. otus* (sub nomine *Asio wilsonianus*), and Stellbogen (1930) gave some brief notes on morphology of the outer ear. The outer ears were briefly described and illustrated with two photographs by Freye (1953). In Schwartzkopff (1962) there are diagrammatic drawings of the left and right outer ears. Kaup (1859) described the feathering of the preaural flap and illustrated the skull of *A. otus* (sub nomine *Otus vulgaris* Flem.). The stapedial complex was illustrated by Stellbogen (1930, p. 715). Dimensional data on the eardrum, footplate of stapes, and the cochlea were given by Schwartzkopff (1957). Krause (1901) described the bony stapes of *A. otus* (sub nomine *Otus vulgaris*). The structure of the cochlea was studied by Schwartzkopff & Winter (1960).

Mean height of the ear slits of 12 specimens measured by me was 38.5 mm (s.d. 2.2) for the left ear and 38.6 mm (s.d. 2.0) for the right. Mean width of the preaural fold was 8½ mm for both ears.

DESCRIPTION OF PLATE 4

FIGURE 10. Anterolateral views of the ears of *Aegolius funereus* showing their bilateral asymmetry. Orientation of head and ear flaps as described in the legend to figure 9. The light, nearly vertical bands in the ears are aponeuroses that lie along the medial wall of the external auditory meatus and are visible through the overlying, translucent skin. Different aponeuroses are visible in the two ears, the one in the left ear being apon. 2 of the M. adductor mandibulae externus, whereas that in the right ear is apon. 1 of the same muscle of the lower jaw. Drawings made from photographs of a dead owl.

Asio flammeus (Pontoppidan)

The form of outer ears is essentially as in *A. otus*, although differing in detail. Collett (1881, p. 20) measured one adult specimen (sub nomine *Asio accipitrinus* (Pall.)) and obtained 35 mm in height for both ear slits in the skin and 12 mm in width for both preaural flaps. On the lateral edge of the postorbital process, at its most lateral point, there is a small, pointed process directed posterolaterally. It is symmetrically located and supports the intra-aural dermal septum attached to it. This process is lacking in *Asio otus* (Collett 1881; Pycraft 1898) as well as in *Rhinoptynx clamator* and *Pseudoscops grammicus* (this paper).

Kaup (1859) illustrated the skull and the left and right side of an intact head of *A. flammeus* (sub nomine *Otus brachyotus* Boie) with ear openings exposed, showing their asymmetry. Pycraft (1898) described the pterylography and outer ear and later (1903*a*) also the skull of *A. flammeus* (sub nomine *Asio accipitrinus*). Kuroda (1967) described the outer ear asymmetry and published photographs of the outer ear. He also gave a number of measurements of one skull illustrated in drawings. He claimed there was a slight asymmetry of the skull, the right squamoso-occipital wing extending 1.5 mm farther laterally than the left one. Collett (1881, pp. 6, 22) and Pycraft (1898, p. 262) stated that the skull was bilaterally symmetrical.

In one owl that I measured the left ear opening in the skin was 37 mm high, the right 38 mm, and the preaural flaps $8\frac{1}{2}$ mm wide.

Asio capensis (A. Smith)

To my knowledge there are no previous descriptions of its ears.

I have examined one living and one dead, fresh specimen. The outer ears are asymmetrical and very similar to those of *A. flammeus*. As in *A. flammeus* there is a lateral, pointed process on the lateral edge of the postorbital process, supporting the asymmetrically oriented intra-aural dermal septum.

Genus *PSEUDOSCOPS* Kaup (Monotypic)

Pseudoscops grammicus (Gosse)

I know of no description of details of the outer ear. The ear slit in the skin is higher than the height of the skull (Kelso 1940). The structure of the external ear was assumed by Ridgway (1914, p. 620, footnote, quoted in § 9) to be similar to that of *Asio*. Kaup (1859, p. 231) wrote that the operculum is lacking.

I have examined one living specimen. The external ears are asymmetrical and very similar to those of *Asio otus*. The preaural flap (operculum, cf. Kaup above) is as large in *Pseudoscops* as in *Asio*. There is no lateral, pointed projection on the postorbital process.

Genus *NESASIO* Peters (Monotypic)

Nesasio solomonensis (Hartert)

I know of no description of details of the outer ear. Peters (1937) wrote about its systematic position, 'A medium sized strigine most nearly allied to *Asio* Brisson...' and 'This genus is probably derived from an offshoot of *Asio flammeus* stock...' If this is so, the external ears of this owl are likely to resemble those of the *Asio* species.

Genus *AEGOLIUS* Kaup

Aegolius funereus (Linné) (figure 10, plate 4)

Ear openings in the skin are large, about as high as the skull, and of equal size on left and right side. An adult owl measured by Collett (1881, p. 34) had *ca.* 28 mm high ear openings on both sides and 6 mm wide preaural folds. Skull is conspicuously asymmetrical. Squamoso-occipital wing is extremely large and asymmetrical. Left ear opening in the skull is located lower than the right one. In three papers Collett described and illustrated the asymmetrical skull of *A. funereus* (1871, sub nomine *Strix tengmalmi*; 1872 and 1881, sub nomine *Nyctala tengmalmi* (Gmel.)). The 1881 paper contains information also on the ear opening in the skin. Pycraft (1898) described the pterylography, the outer ear, and the skull, and later (1903*a*) again the skull of *A. funereus* (sub nomine *Nyctala tengmalmi*). Pycraft's illustration of the left ear (1898, Plate 27:5) is misleading. Probably the left ear of the specimen illustrated was damaged. In Baird, Brewer & Ridgway (1874) there are a few sketches of the head of *A. funereus* (sub nomine *Nyctale richardsoni*). The sketch on page 100, said to be of *N. richardsoni* is not, while that said to be of *Surnia ulula*, illustrating skull asymmetry, is of *Aegolius*. The brief notes by Stellbogen (1930, p. 690) and the two figures (fig. 3:6, 7) claimed to be of *Nyctala tengmalmi* Gm (= *A. funereus*) do not fit in with *A. funereus*, the underlying material certainly being misidentified. Judging by the figures I should think they are of *Athene* (or possibly *Glaucidium* Boie).

Dijk (1973, p. 161) wrote, 'members of the genus *Aegolius*...have...strongly asymmetrical external and even inner ears....' With 'inner ears', however, he actually meant the external auditory meatus (Dijk, personal communication), that owes its asymmetry to asymmetries of the skull.

The ear openings in the skin are symmetrical, but the attitude of the postaural fold may differ somewhat between the left and right side because of skull asymmetry. The skull and ear asymmetry in *A. funereus* do not extend to the middle and inner ears which are quite symmetrical. However, the superior air space that opens into the middle ear cavity, is of different shape on the left and right sides because of the skull asymmetry. A detailed description of the skull and the external and middle ear of *A. funereus* is given by Norberg (in the press).

Aegolius acadicus (Gmelin)

Streets (1870) published a brief note, without illustrations, on the asymmetry of the skull of *A. acadicus* (sub nomine *Nyctale acadica*). From this it is apparent that the skull resembles that of *A. funereus*.

I have examined 16 skulls. The skull is similar in general shape to that of *A. funereus*, but there are some marked differences in details. One is that in *A. acadicus* there is a small blind cavity in the skull, just dorsal to the left ear aperture of the skull. This blind cavity is lacking in most individuals of *A. funereus*, and is only vaguely marked in the others. In both species, however, there is, in the intact skull, a blind cavity below the right ear opening in the skull.

The occurrence of various types of bilateral ear asymmetry in owls, as described in this section (§ 5), is summarized in table 1.

TABLE 1. SCHEME SUMMARIZING THE OCCURRENCE OF VARIOUS KINDS OF EAR ASYMMETRY AMONG OWLS

The various kinds of asymmetry are ranked from left to right approximately in order of increasing complexity. The sequence of genera and species follows Peters (1940). In species having the ear apertures in the skin of different size, the vertical position of the aperture may well differ between the two sides as a secondary effect. However, differences in vertical position are indicated only when obvious. The rightmost column is intended as a guide to a minimum number of the most informative sources of documentation of ear structure in the respective species. Further references are given in § 5, which also contains brief descriptions of external ear structure.

Further study will add more species to the list, in particular species congeneric with those listed. Also the distribution pattern of various asymmetries among different species will probably be somewhat enlarged.

* The asterik refers to the present study.

ear asymmetry morphologically simple → → ear asymmetry morphologically complex

	ASYMMETRY CONFINED TO SOFT-ANATOMY STRUCTURES							ASYMMETRY OF THE SKULL		
	ear apertures in the skin			preaural skin folds		ear apertures in the skull (soft-anatomy structures)		ear apertures in the skull (head skeleton structures)		
	of diff. size		at diff. vertical levels	of diff. shape	at diff. vertical levels	of diff. shape	at diff. vertical levels	of diff. shape	at diff. vertical levels	
	left largest	right largest	left highest		left highest		left highest		right highest	SOURCE
Tyto alba Billberg	.	.	○	.	○	.	.	.	.	Payne 1971
Phodilus badius (Horsfield)	.	.	○	.	.	.	.	.	.	Pycraft 1903 *b*
Bubo bubo (Linné)	.	○	.	.	.	.	.	.	.	*
Ciccaba virgata (Cassin)	.	○	.	.	.	.	.	.	.	*
C. nigrolineata Sclater	.	○	.	.	.	.	.	.	.	Voous 1964
C. huhula (Daudin)	.	○	.	.	.	.	.	.	.	Voous 1964
C. albitarsus (Bonaparte)	.	○	.	.	.	.	.	.	.	Peters 1938
C. woodfordi (A. Smith)	.	○	.	.	.	.	.	.	.	Voous 1964
Strix selo-puto Horsfield	.	○	.	.	.	.	.	.	.	Voous 1964
S. leptogrammica Temminck	.	○	.	.	.	.	.	.	.	Voous 1964
S. aluco Linné	.	○	.	○	.	.	.	.	.	*
S. occidentalis (Xantus)	.	○	.	.	.	.	.	.	.	Voous 1964
S. varia Barton	.	○	.	.	.	.	.	.	.	*
S. hylophila Temminck	.	○	.	.	.	.	.	.	.	Voous 1964
S. rufipes King	○	.	.	.	.	.	.	.	.	Voous 1964
S. uralensis Pallas	.	○	.	○	.	.	.	○	.	Collett 1881
S. nebulosa J. R. Forster	.	○	.	○	.	.	.	○	.	Collett 1881
Rhinoptynx clamator (Vieillot)	.	.	.	.	.	○	○	.	.	*
Asio otus (Linné)	.	.	.	.	.	○	○	.	.	Pycraft 1898
A. flammeus (Pontoppidan)	.	.	.	.	.	○	○	.	.	Collett 1881
A. capensis (A. Smith)	.	.	.	.	.	○	○	.	.	*
Pseudoscops grammicus (Gosse)	.	.	.	.	.	○	○	.	.	*
Aegolius funereus (Linné)	.	.	.	.	.	.	.	○	○	Norberg, in the press
A. acadicus (Gmelin)	.	.	.	.	.	.	.	○	○	*

6. Independent evolution of external ear asymmetry among owls

Kelso (1940, p. 27) noted that the large ear openings have developed independently in *Strix*, *Asio*, and *Aegolius*. Payne (1971, p. 553) remarked that the ear asymmetry is achieved by very different means in the species *Tyto alba*, *Asio otus*, and *Aegolius funereus*, and therefore he regarded ear asymmetry to have evolved on three independent occasions among owls, with *Strix* possibly representing a fourth case. The above authors were not primarily concerned with evolutionary aspects of ear asymmetry but made the remarks in passing, without any detailed comparison of ear structure, without discussing the probability of independent acquisition of ear asymmetry, and without presenting any documentation.

I think there are five, and probably even more, cases of independent evolution of ear asymmetry among owls. There follow comparisons of the structure of ears with various types of asymmetry and discussions of their evolution, with emphasis on probabilities of independent evolution. Since outer ear structure is often part of diagnostic genus characters, ear type usually goes with genus, and so the comparison below is by genera.

Tyto – Phodilus

The ear opening in the skin is located higher on the left side than on the right in *Tyto alba* (Konishi 1973) and *Phodilus badius*. This single character, namely relative location of ear openings in the skin, thus does not preclude a common heritage of ear asymmetry in these genera, but is no proof of it whatsoever. *T. alba* has an extremely large preaural flap, operculum, whereas this is absent in *P. badius*. Further, there are differences in feathering of the facial ruff and disk. Since *Tyto* owes its ear asymmetry largely to bilateral asymmetry of the opercula, and since such are lacking in *Phodilus*, ear asymmetry is very different in *Tyto* and *Phodilus*. Another point is that the affinity between *Tyto* and *Phodilus*, suggested by their present inclusion in the same family, is not at all certain (see § 7).

After examination of their external ears I believe that the ear asymmetry has evolved independently in *Tyto* and *Phodilus*. Confirmation could arise if the genera should prove to be but distantly related.

Phodilus – Asio – Aegolius

Pycraft (1903*b*, p. 46) tried to relate the ear of *Phodilus* to that of *Asio*: 'It is, indeed, possible that the external ear of *Photodilus* [= *Phodilus*] approximately represents the primitive stage from which the complex external ear of *Asio* has been derived. The voluminous postaural fold of the latter may very well have arisen by the development of a fold of skin such as that which supports the peripheral disk-feathers [facial ruff] of *Photodilus*; but it is not easy to see how the operculum can have arisen.'...'It is possible, of course, that the operculum had its origin in a raised fold such as that which forms the anterior boundary of the auditory aperture in *Photodilus*. If we assume this to be so, then it is possible that the membranous rim bounding the aperture superiorly represents the membranous fold [intra-aural dermal septum] which in *Asio* runs from the postaural fold to the operculum and divides the "cavernum" into upper and lower moieties.'

There are certain geometrical similarities between *Phodilus* and *Asio* ears. Thus, in *Phodilus* the left ear opening in the *skin* is located higher than the right one, as is the case also of the ear openings in the *skull* in *Asio*. Further, in *Phodilus* there is a shallow depression behind the postorbital process and sclerotic ring, located below the ear opening in the *skin* on the left side, above it on the right. This is in some accordance with ear geometry of *Asio* which has a deep blind cavity below the ear opening of the *skull* on the left side, above it on the right. Structurally, however, the outer ears of *Phodilus* and *Asio* are fundamentally different. The ear openings in the skin are very small and asymmetrically located in *Phodilus*, extremely large and symmetrical in *Asio*. The depressions below the left ear and above the right in *Phodilus* are external, i.e. they lie *outside* the ear opening in the skin and are lined with the outward skin that is slightly sunk in posterior to the eyes. The blind cavities associated with the ear openings in the *skull* in *Asio* lie *inside* the aural folds and occupy part of the space between the postorbital process and squamoso-occipital wing. The cavities are lined with the thin skin that covers the skull *inside* the aural folds.

Contrary to Pycraft (1903*b*) I think the comparative outer ear morphology shows that the ear of *Phodilus* has nothing to do with that of *Asio*, neither phylogenetically nor as a developmental stage similar to any early stage in *Asio*. Speculating on evolution of ear asymmetry in *Asio*, I think it most likely that the ear openings in the *skin* increased in size first, and that horizontal folds of the skin lining the skull (*inside* the ear openings in the skin) then came to shut off the blind cavities associated with ear openings in the skull.

I once saw (1968) a slight ear anomaly in a fledgeling of *Aegolius funereus* (figure 2*a*, *b*, plate 1). In the bottom of the left external auditory meatus, near its orifice, there was a skin fold (duplication) forming an erect, small septum. It was low but rather thick. It passed from the posterior surface of the postorbital process on to the quadrate near the quadrate-quadratojugal joint. Both in its location and in its orientation the septum was strongly reminiscent of that which shuts off a blind cavity below the left ear opening in the skull in *Asio*. The ear asymmetry in *Asio* is due mainly to the septa, one in each ear (figure 9, plate 3). Usually nothing of the sort occurs in *Aegolius funereus* (figure 10, plate 4).

I think this is the way ear symmetry has originated in *Asio*. The chance occurrence of an erect skin fold in one ear immediately creates a structural ear asymmetry. If sufficiently big, the skin fold may lead also to a functional asymmetry, for instance by affecting the directional sensitivity of the ears, and possibly improve the ability of vertical localization of sound (see below, this section). Once a structural asymmetry affects function it is accessible to selection. Then selection pressure may take a new direction and lead towards optimization of the ear asymmetry. However, if an animal's ecology is such that there is no net, functional, and thus selective, advantage of ear asymmetry, then selection would merely act towards a rectification of the symmetry as soon as an incipient asymmetry becomes accessible to selection.

The observation in *Aegolius* indicates how accidental may be the origin of novel ear structures that can lead to asymmetries and hence open up entirely new evolutionary paths.

Ciccaba – *Strix*

The genera *Ciccaba* and *Strix* include species of relatively similar wood owls with big round heads without ear tufts. On account of the size of the ear opening in the skin and the width of the preaural skin flap, these wood owls fall near the border-line between the former subfamilies Buboninae and Striginae (see §8). Those thought to fall on the bubonine side are known as *Ciccaba*, those on the strigine side as *Strix* species. Although similar in general appearance *Ciccaba* and *Strix* thus came to be placed in different subfamilies, indicating relatively distant relations only.

Voous (1964, p. 472) did accept, in principle, the structure of the outer ear as a 'primary taxonomic character' but was of the decided opinion that in this case it leads to a taxonomic arrangement not reflecting the evolutionary history. He also pointed out, that if the diagnostic subfamily ear characters, underlying the present classification, are strictly followed, *Strix leptogrammica* and *Strix seloputo*, currently well-established in *Strix*, should actually belong to *Ciccaba*. Both species have poorly developed preaural skin flaps; *S. seloputo* also a relatively small ear slit. Further, *Strix rufipes*, having a preaural flap of intermediate width, is a border-line case.

Confronted with these and also zoogeographic complications, Voous turned to question the basis of separation, writing, 'It could also be stated...that the structure of the outward ear is too strictly an adaptive character for it to serve as a means of taxonomic distinction beyond genus level.' He continued, 'Could it be possible that the length of the ear slit and the size of the dermal flap [preaural fold] are directly adapted to the environment and the principal prey and therefore variable in closely related species?'

I agree that *size* of ear opening and ear flap should not be used to separate taxa above genus level, if even that high. Similarity in size of ear has high probability of occurrence in different evolutionary lines, i.e. a particular size of ear has low probability of unique occurrence and therefore has low taxonomic value (cf. discussion of adaptive characters and classification by Bock 1967). However, when the ear geometry is complicated, and many parameters are considered, the ear is potentially very useful especially in indicating affinity between species and genera. Similarity of ears with complicated structure (including details of asymmetry) has low probability of arising in separate lines, i.e. complicated ear structures have high probability of unique occurrence and therefore have high taxonomic value (see § 9).

Voous suggested that the *Ciccaba* species be transferred to *Strix* with the possible exception of *C. huhula* and *C. nigrolineata*. Because of the overall similarity between *Ciccaba* and *Strix* I think Voous is probably right (although convergence could be the reason). However, Peters's (1938) and Voous's (1964) measurements on ears (§ 5) are from dry skins, and I would like to see more detailed descriptions of the ears (not only their size) based on fresh material. I also think the general morphology of these species ought to be compared before the classification is changed. Awaiting this I have retained Peters's (1940) genera *Ciccaba* and *Strix* unchanged in this paper. Furthermore, since I reject the former subdivision of Strigidae into the subfamilies Buboninae and Striginae (see § 8), *Ciccaba* and *Strix* do not fall into different subfamilies. Assignment of a species to one or the other of these genera therefore has less systematic implications than before.

In most of the *Ciccaba* and *Strix* species the left ear opening in the skin is smaller than the right, while a few species have both ear openings of about the same size. Only one species, *Strix rufipes*, has been reported to have the left ear much larger than the right. Unfortunately, data on this species are available from one study skin only (see § 5).

There is a probability of 0.5 that two not closely related evolutionary lines, evolving unequally large ears on the left and right sides will end up with the largest ear on the same side. A coincidence in this respect between two groups therefore proves nothing as to their relatedness. If, however, the largest opening is consistently on different sides in two species, this is strong evidence of their independent acquisition of asymmetry. Thus, agreement as to which ear is the largest does not justify acceptance of a hypothesis of relatedness, whereas disagreement probably permits rejection. Which ear happens to become the largest when different ear size evolves should be purely accidental, if no genes for one case or the other pre-exist. Functionally, it is immaterial which ear is the largest. This is thus a 'paradaptive' aspect in Bock's (1967) terminology, meaning that it is not the result of selection, or literally 'besides adaptive'.

I know of no measurements on fresh material of any owl species that have shown intraspecific variation as regards the side with the biggest ear opening in the skin. Hence, left-right reversal of ear asymmetry is not known for certain to occur in any owl species (cf. § 5: *Ciccaba virgata* (Cassin)). The more complicated the bilateral ear asymmetry is, and the more structures (and hence genes) that are involved, the less likely it is that reversals of asymmetry will occur.

Because of agreement regarding the side with the largest ear opening in *Ciccaba* and *Strix*, a monophyletic origin of their asymmetry is not precluded, with the possible exception of *Strix rufipes*. Should the aberrant asymmetry present in the single study skin measured prove typical, this species should perhaps be considered a representative of a separate line of asymmetry. However, this would not cast any serious doubts on the *Strix* affinity of *S. rufipes*. This character, concerning only which ear is the largest, may well differ within a group as diverse in ear structure as the *Ciccaba–Strix* one without warranting exclusion of the species in question. Indeed, this aberrant asymmetry, if substantiated, may have originated from a left–right reversal of the ordinary *Strix* asymmetry.

Some *Strix* species have asymmetries also in the preaural flaps. Further, in *Strix uralensis* and *Strix nebulosa* ear asymmetry extends also to the skull. The slight skull asymmetry, most noticeable in *S. nebulosa*, is very similar in these two species, suggesting they have it from a common origin. In their outer appearance, however, there are notable differences between these species.

Apparently there are different lines in the *Ciccaba–Strix* group that have evolved asymmetries of a somewhat different kind and to a different degree. It was argued that the location of the largest ear does not preclude a common origin of ear asymmetry among *Ciccaba–Strix* owls (with one possible exception): neither, however, does it prove it. Considering the large diversity of ear structure in this group, it also seems entirely possible that ear asymmetries could have arisen independently by parallel evolution. The repercussions of this possibility on *Ciccaba–Strix* affinity cannot be judged with our present knowledge of these owls.

Bubo – Ciccaba – Strix

In *Bubo bubo* the right ear opening in the skin is larger than the left one (§ 5). Presence of similar ear asymmetry in *Bubo*, *Ciccaba*, and *Strix* might nourish the suspicion that this asymmetry is very ancient and that these genera have it from a common ancestor. However, let us return again to probability. It was stated above that if a difference in the size of the left and right ears originates independently in two evolutionary lines, the probability is 0.5 that both get the largest ear on the same side. Increase to three lines reduces the probability to 0.25. It is true that the probability that all three get the largest ear on the *right* side is 0.125. But if all three had had the largest ear on the *left* side, this also would have qualified as 'largest ear on same side'. Hence 0.25 is the pertinent probability here. Therefore, on the basis of ear size only, no decision is justified on common/separate ancestry of ear asymmetry in these three genera.

Tyto – Strix

Tyto alba and some *Strix* species exhibit a striking convergence of certain ear structures. Collect (1881, p. 11) remarked that the almost square preaural flaps in *T. alba* are similar to the flap of the right ear in some *Strix* species. Otherwise the ear aperture in the skin is much smaller, relative to the ear flap, in *T. alba* than in some *Strix* species. The preaural flap extends much farther above and below the ear opening in the skin in *T. alba* than in the *Strix* species.

Part of the outer ear asymmetry both in *Tyto* and *Strix* is achieved by differences between the preaural flaps of the left and right side. In *Tyto* the left flap is located higher than the right one, while in *Strix aluco* the left flap is skew, its dorsal and ventral edges slanting lateroventrally, giving the flap a more ventral extension than has the right one.

From the very good illustrations of the bony stapes appearing in Krause (1901), a striking similarity can be seen also in the unusual shape of the foot-plate of stapes in *T. alba* and *S. aluco*. In both species the inner face of the foot-plate, which is flat or nearly so in most birds, is developed into a large eminence bulging into the perilymph of the inner ear. In both species the eminence is oblique, its highest point lying off-centre. The eminence is larger in *T. alba* than in *S. aluco*.

Because of the distant relation between *Tyto* and *Strix*, as demonstrated by many features (cf. § 7), it is obvious that ear asymmetry, the large preaural flaps, and probably also the convexity of the foot-plate of stapes have evolved independently in these genera. Differences in details of outer ear structures argue for this too.

Rhinoptynx – Asio – Pseudoscops – Nesasio

Ear asymmetry is similar in the three species of *Asio* whose ears have been described. However, there are differences in detail of the outer ear between *A. otus* on the one side, *A. flammeus* and *A. capensis* on the other.

The species of the monotypic genera *Rhinoptynx* and *Pseudoscops* are reported in this paper to have ears very similar to those of *A. otus*. Because of the close agreement in the complex geometry and structure of the external ears in *Rhinoptynx*, *Asio*, and *Pseudoscops*, the probability must be considered infinitely small that the similarity is due to independent, convergent evolution. Therefore these genera must share their ear asymmetry with a common ancestor.

Nesasio solomonensis is thought to resemble *Asio* species in general ear morphology (§ 5). It is likely therefore, that the insular, monotypic genus *Nesasio* will prove eventually to be derived from the *Asio* lineage.

Strix – Asio – Aegolius

Except for the *Aegolius* species, skull asymmetry in connection with outer ear asymmetry in owls has been reported only for three species. They are *Strix uralensis*, *Strix nebulosa*, and *Asio flammeus* (cf. § 5). The skull asymmetry of the two *Strix* species is beyond any doubt. The *Asio flammeus* case seems to relate to one skull only, and the asymmetry was slight. More skulls of this species therefore must be studied and measured before the question of its symmetry condition can be settled.

There is a striking resemblance of skull asymmetry between *Strix nebulosa* and *Aegolius*. Although the asymmetry in *S. nebulosa* is much less developed than in *Aegolius*, the same trend is obvious, namely a different orientation of the anterior parts of the left and right squamoso-occipital wings. However, just as with *Asio* and *Aegolius* (below), the asymmetry is reversed between *S. nebulosa* and *Aegolius*, the left external auditory meatus being directed most upwards in *S. nebulosa*, the right in *Aegolius*. This demonstrates that their skull asymmetries evolved independently.

Skull asymmetry among owls is by far the most developed in *Aegolius*, whereas external ear asymmetry is about as pronounced in, for example, *Asio*. Morphologically, outer ear asymmetry in *Aegolius* is totally different from that in *Asio*. However, apart from the fact that the most dorsally located ear opening in the skull is on different sides in these two genera, there are certain gross similarities of outer ear geometry. Thus, the ear slit in the skin is symmetrical and very large and the preaural skin flap is symmetrical and similar in both genera. Further, the ear opening in the skull is located on conspicuously different vertical levels on left and right side. Even the blind cavities that are associated with both ear openings of the skull in *Asio* are paralleled in *Aegolius acadicus*, while present on the right side only in *Aegolius funereus* (cf. § 5). The geometry and orientation of the external auditory meatuses are rather similar too, except for the left/right difference. Hence, although evolved completely independently and achieved by quite different structural means (by soft morphology in *Asio*, by skeletal structures in *Aegolius*), ear asymmetry in *Asio* and *Aegolius* shows a general geometric similarity.

Function of ear asymmetry

Circumstantial evidence strongly suggests that bilateral ear asymmetry in owls is linked to *vertical directional hearing*. Further the fact that there is a *bilateral* asymmetry of the external ears suggests that vertical localization of sound is based on *binaural comparison* of signals from the two ears.

The left and right ear of *Aegolius funereus* have different directional sensitivity patterns in the vertical plane for high frequencies. This vertical, binaural disparity in directional sensitivity at high frequencies is an ideal cue for vertical localization on a binaural basis (Norberg 1968, in the press). The ears' directional sensitivity patterns for low frequencies, with wavelengths much longer than the dimensions of the owl's head, remain unaffected by the ears' structural asymmetry and are utilizable for azimuth (horizontal angle) determination. Further, interaural time differences should also be available for horizontal localization with asymmetrical ears (Norberg 1968).

The close geometric similarity between the *Asio*-type ear and the *Aegolius* ear (see above) strongly suggests that they function in essentially the same way. The asymmetry of the ears of *Phodilus* also shows a general geometric resemblance to that of *Aegolius*, and therefore probably has the same function.

Similarly, outer ear asymmetry has evolved independently in *Tyto* and *Strix*, but is geometrically and structurally similar in some *Tyto* and *Strix* species. Therefore, ear asymmetry probably functions in essentially the same way in *Tyto* and some *Strix* species. However, both to the acoustical and auditory mechanisms involved, the function of ear asymmetry may well be different between *Tyro* and *Strix* on the one side, and *Phodilus*, *Asio*, and *Aegolius* on the other.

The structurally and geometrically most simple ear asymmetry is that caused by the left and right ear openings in the skin simply being of different size (in some species of the genera *Bubo*, *Ciccaba*, and *Strix*). Although there is no very obvious functional explanation of this particular kind of asymmetry, it will be embraced by the following general hypothesis.

The simplest hypothesis on the function of ear asymmetry in owls is that all types of bilateral ear asymmetry serve the purpose of making the *vertical* directional sensitivity patterns *different between the two ears* for high frequencies, as postulated by Pumphrey (1948). Hence vertical localization can be based on *binaural comparison* of intensity and spectral composition of sound. This is impossible with symmetrical ears, at least in the vertical median plane of the head, leading to the median plane ambiguity (Norberg, in the press). The hypothesis advanced by Pumphrey (1948; further explained in Payne 1971, p. 566) is a bit more complicated and need not necessarily be invoked to explain the asymmetry, I think.

When an owl localizes prey by hearing, the direction of the sound source usually forms a shallow angle with the ground. Therefore, a certain angle of error usually converts into longer

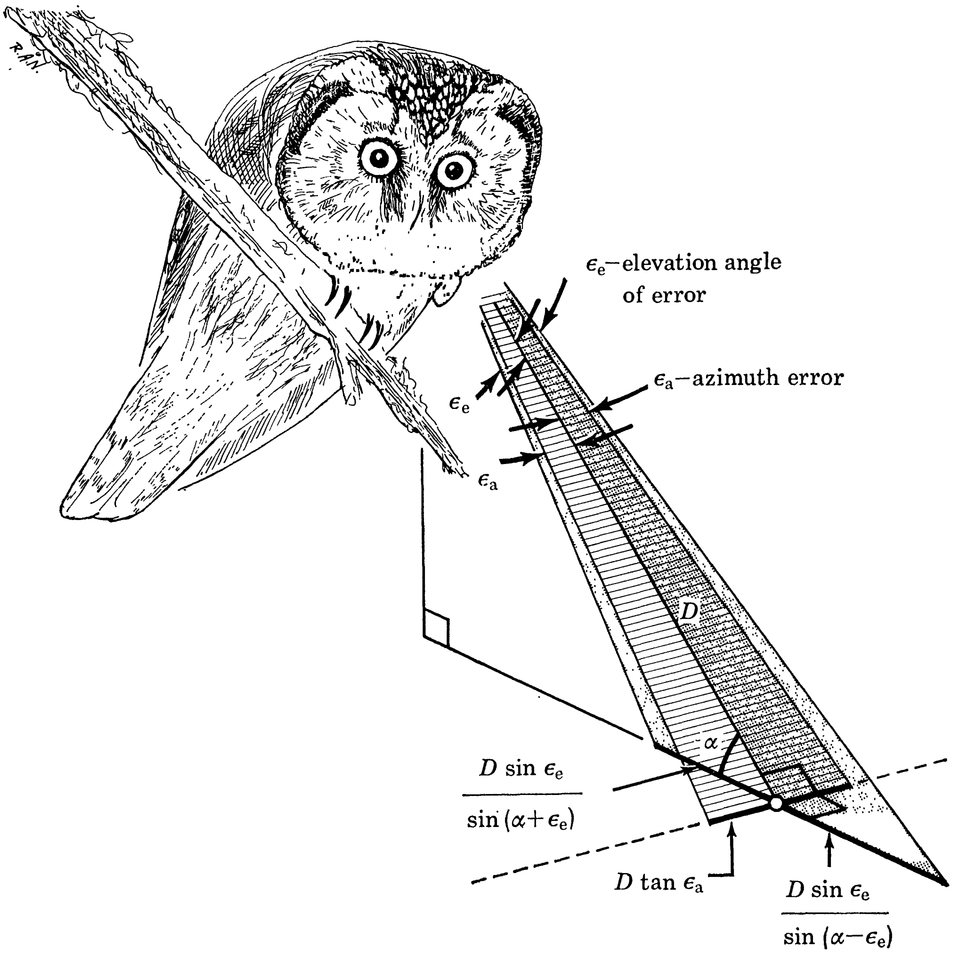


FIGURE 11. Diagram showing geometry for calculation of errors in auditory localization. Localization errors along the ground are given as functions of the angular errors in the horizontal and vertical planes, the distance D between the owl and the sound source, and the angle α which a line between the owl and the sound source forms with the (horizontal) ground.

When an owl localizes prey by hearing, the direction of the sound source usually forms a shallow angle with the ground. A certain angle of error therefore usually converts into longer distances along the ground for a vertical error than for a horizontal error. The corresponding selection pressure for improvement of the ability of vertical localization probably lies behind the evolution of all types of (vertical) binaural asymmetry of the external ears among owls.

Owl drawn from photograph of a wild *Aegolius funereus* prepared to strike.

distances along the ground for a vertical error than for a horizontal error (figure 11). This is a crucial factor that calls for good vertical localization ability of all owls which rely on hearing for localization of food.

Selection pressure for improvement of the ability of vertical localization of sound is believed to lie behind the evolution of *all* types of bilateral ear asymmetry among owls. Various evolutionary lines have produced different structural (and possibly functional) solutions which probably represent various degrees of success.

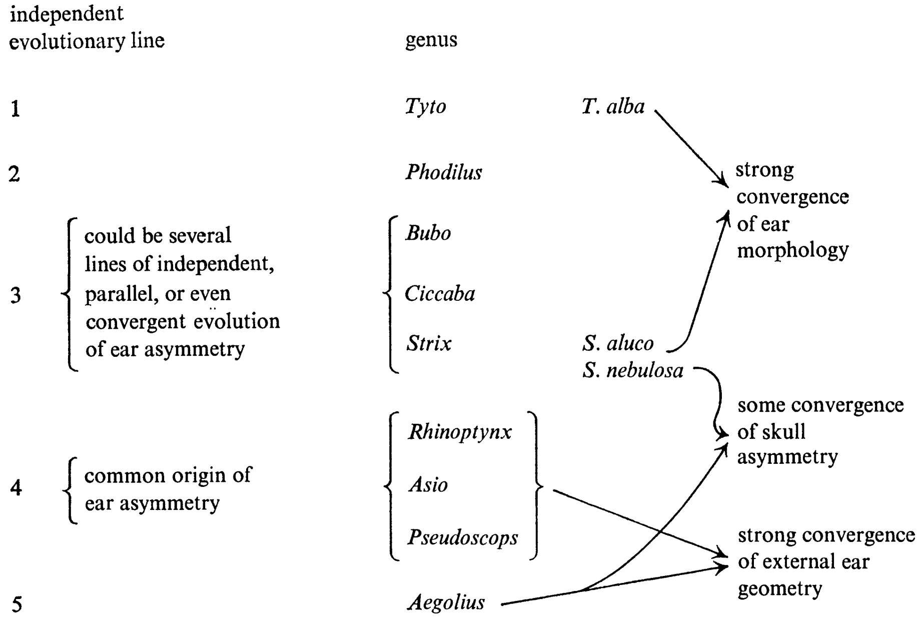
Conclusion on evolution

In conclusion then, there are probably at least five cases of independent evolution of external ear asymmetry among owls with the following generic representation (summarized in table 2).

(1) *Tyto*. (2) *Phodilus*. Its ear asymmetry probably evolved independently of that of *Tyto*, although this cannot be established with certainty until possibly after examination of certain other morphological features that could clarify the *Tyto–Phodilus* relation. (3) *Bubo*, *Ciccaba*, and *Strix*. The *Ciccaba* and *Strix* owls exhibit great diversity of ear structure and might represent more than one line of independent acquisition of ear asymmetry. The *Bubo bubo* ear asymmetry might be referable to that of *Ciccaba* and *Strix*, but may as well have originated independently. At present the question remains open. (4) *Rhinoptynx*, *Asio*, and *Pseudoscops*. (5) *Aegolius*.

TABLE 2. SCHEME SUMMARIZING THE EVOLUTIONARY HISTORY OF EAR ASYMMETRY AMONG OWLS

At least five cases of independent origin of ear asymmetry can be recognized (left column). The convergence indicated for *Tyto alba* and *Strix aluco* could be extended to include more species of the genera *Tyto* and *Strix*, the ones listed being the best known. However, several *Strix* species lack any trend towards convergence in ear structure with *Tyto alba*.



The large variation of ear asymmetry among species in the *Ciccaba–Strix* group indicates that they have not ‘decided’ on one type of asymmetry. It seems as though there is much experimentation with ear geometry, and that ear asymmetry is in a phase of rapid evolution in this group right now.

Once a near-optimum solution has evolved, it may be expected to pass unchanged through speciation processes.

In contradistinction to the *Ciccaba–Strix* case, the ear geometries of *Asio* and *Aegolius* seem to be well established. Thus, the asymmetry is very similar in *Aegolius funereus* and *A. acadicus*. Moreover, the *Asio*-type of asymmetry has remained virtually unchanged through a large number of speciations. The species differentiation, involving change of general morphology (except for that of the ear), has even gone so far that some species are regarded as generically separated from *Asio*. They are *Rhinoptynx clamator* and *Pseudoscops grammicus*. In spite of their relatively long, independent evolutionary history, as implied by their different morphology, they have retained the *Asio*-type ear structure. That they are actually related to *Asio* is in fact demonstrated by the ear structure (see § 9).

7. Family Tytonidae and Strigidae and affinity of *Phodilus*

In § 6 I used the distant relation between *Tyto* and *Strix* as one argument for regarding convergent evolution to be the cause of similarities in their ear morphology. Therefore, some data pertaining to the family distinction will be surveyed here.

Tyto has been regarded for a long time to be distinct from other owls (*Phodilus* sometimes excluded) and therefore the owls have been divided into two families. *Tyto* differs from other owls in a large number of characters involving the skull, body skeleton, claws, feathers, and facial disk. Some distinguishing characters were given in Sharpe (1875, p. 1) and many more in Ridgway (1914, p. 598), recently tabulated in a review by Sibley & Ahlquist (1972, p. 184). In all, 17 distinguishing characters are listed, only one of which concerns the ear. Hence, the facial disk is heart-shaped in Tytonidae, more or less circular in Strigidae. I refer to those works for details and for a review of literature on this subject, and engage here in a review of a few recent papers only.

The electrophoretic pattern of egg-white proteins of *Tyto* 'is distinctive but clearly similar to other [owl] genera and neither supports nor refutes the separation of the two [owl] families' (Sibley 1960, p. 102). After studies of electrophoretic behaviour of haemoglobin, Sibley (1965, p. 117) wrote, 'It is especially intriguing to find that *Falco* is more like *Tyto* than it is like any of the other diurnal birds of prey!' This might arouse doubts as to the monophyly of owls.

Bock & McEvey (1969) redescribed an enlarged sesamoid bone, the 'strigid os prominens', situated at the distal end of the radius and lengthening the moment arm of the force of M. tensor patagii longus whose tendon inserts on the sesamoid. It occurs in strigid owls but is lacking in *Tyto*. They also redescribed an osseous arch on the radius. Two muscles partly attach to the arch and a proprioreceptive organ is located beneath it (Bock 1968). As far as is known this osseous arch is unique to owls. It occurs in *Tyto* as well as in strigid owls. Bock & McEvey (1969, p. 66) concluded: 'The presence of an osseous arch of the radius and the arrangement of the tendon of the M. tensor patagii longus argue against the hypothesis that *Tyto* is related to any group within the Falconiformes...The osseous arch...argues strongly for a monophyletic origin of all owls. Sufficient evidence is available to separate *Tyto* from strigid owls...The absence of the os prominens in *Tyto* provides another bit of evidence supporting this separation....'

In a paper on electrophoresis of egg white protein, supplemented with an extensive, historical review of non-passerine bird classification, Sibley & Ahlquist (1972, p. 190) wrote, 'The pattern of *Tyto* differs from those of the Strigidae in having a third component in the ovalbumin region. The mobility of these three bands is slightly less than in the patterns of the strigid owls. The pattern of *Tyto* thus bears a strong resemblance to those of the Strigidae and also...to those of *Falco*.' In their conclusion they stated, 'The barn owls (*Tyto*) are closely related to the other owls and do not deserve familial or subfamilial distinction from them. Tribal separation may be justified.'

Since classification is supposed to reflect the evolutionary history, and *Tyto* is demonstrably different from other owls in a large number of characters suggesting a relatively long, independent evolutionary history, it should be separated taxonomically (below order level) from other owls. I therefore see no reason to change the family rank of their separation.

The inclusion of genus *Phodilus* in family Tytonidae, although given a separate subfamily, Phodilinae, is highly controversial. There are large differences between *Tyto* and *Phodilus* in the skull (Pycraft 1903*a*), pterolysis (Pycraft 1903*b*, p. 46), syrinx (Miller 1965), facial disk and body skeleton (Marshall 1966). Pycraft (1903*a*, p. 47), sharing the opinion of Beddard (1890) who studied the skeleton and soft-part anatomy, stated: '*Photodilus* [= *Phodilus*] is not a near ally of *Strix* [= *Tyto*], as has been contended on more than one occasion.' Marshall (1966, p. 238) concluded: 'Considering its unique characteristics, I recommend placing *Phodilus* in its own family, the Phodilidae.'

The only conclusion about *Tyto–Phodilus* relation to be drawn from the comparative morphology of external ears, is that there are at least no clues unequivocally suggesting affinity. However, having examined only the external ear and outer appearance of living owls, I am not prepared to change the present classification, but await further study.

8. REJECTION OF THE SUBDIVISION OF FAMILY STRIGIDAE INTO THE SUBFAMILIES BUBONINAE AND STRIGINAE

Peters's (1940) subfamily Striginae holds the genera *Strix*, *Rhinoptynx*, *Asio*, *Pseudoscops*, *Nesasio*, and *Aegolius*.

The subfamilies Buboninae and Striginae are separated on the basis of the structure of the external ears. In so doing, Peters (1940) followed Sharpe (1875, p. 2) and Ridgway (1914, pp. 619–620). Sharpe used the names 'Buboninae' and 'Syrniinae' (= Striginae) for his subfamilies, whereas Ridgway distinguished two groups of genera of his family 'Bubonidae' (= the current Strigidae) without assigning to the groups any name or taxonomic rank. Ridgeway's groups essentially coincide with Sharpe's subfamilies.

The diagnostic characters they used were as follows. The nomenclature below follows Peters (1940), and the terminology is changed according to my previous definitions.

Buboninae. Ear opening in the skin not larger than the eye, no preaural skin flap; facial disk unequal, the portion below the eye being always much greater than the area above the latter (Sharpe).

Ear opening in the skin relatively small, its vertical axis much less than half of the greatest height of skull. No horizontal partition wall and no preaural skin flap (Ridgway).

Striginae. Ear opening in the skin much larger than the eye with very large preaural skin flap; facial disk always distinct and extending as far above the eye as it does below it (Sharpe).

Ear opening in the skin extremely large, its vertical axis equal to at least half the greatest height of skull. Horizontal partition wall present as well as a preaural skin flap of greater or less width (Ridgway).

These were the subfamily criteria used also by Peters (1940) as stated explicitly in his 1937 and 1938 papers. These various characters and their taxonomic value will now be considered.

Hearing plays a very important rôle in detection and location of prey in many owl species. Therefore the owl ear must be subject to strong selection pressure and hence must be considered highly adaptive. Large ear openings and well developed facial disks and ruffs are related to good hearing ability (see § 4). There usually is a close parallelism in degree of development of the facial disk and ruff, resulting in the characteristic, big, round head and flat face of owls with good hearing ability.

Size of ear opening in the skin. This character concerns *relative sizes* only, and does not depend on structures with complicated geometry that could provide taxonomic clues. It seems obvious that similarities in such a simple, highly adaptive parameter have a high probability of occurrence through evolutionary convergence.

Width of preaural skin flap. The ear opening in the skin is always bounded by a skin fold, the edge of which bears the peripheral feathers of the facial ruff and disk. The preaural fold can be folded forwards (by manipulation) more in a big ear than in a small one, and so is more readily identified as a preaural flap when attached to a big ear. Hence, at least in the *Aegolius* and *Asio*-type ears, the width of the preaural flap is directly dependent on the size of the ear opening in the skin. In some *Strix* species, however, the preaural flap is markedly enlarged laterally to overlap the entire ear opening in the skin. A similar flap has evolved independently in *Tyto*.

Because (1) the width of the preaural flap is directly dependent on the size of the ear opening in the skin in some 'strigine' genera, and (2) the preaural flap is very dissimilar among 'strigine' owls, and, finally, because (3) wide preaural flaps have evolved independently in *Tyto* and *Strix*, demonstrating the flap's adaptivity, flap width can be discarded as a subfamily criterion.

Development of facial disk. This is again an easily modifiable character, as demonstrated by the (presumably) independent aquisition of very well developed facial disks in Tytonidae and the 'strigine' genera. Besides, the character does not hold for some *Asio* species whose facial disks extend farther below the eye than above it.

Horizontal partition wall in the ear. Many *Strix* species lack any trace of such a partition wall. Further, the partition wall is a skin septum in the *Asio*-type ear, and a bone wall (anterior part of the squamoso-occipital wing) in the *Aegolius* ear. These two wall types thus have entirely different structures and separate evolutionary histories.

Conclusion. From the above reasoning it follows that all these characters must be rejected as clues for a subfamily distinction, with the consequence that subfamily Buboninae and Striginae be suppressed. This is in line with thoughts of Kelso (1940, p. 26), Voous (1964, p. 476), and Dijk (1973, pp. 132, 163). For discussion of (former) border-line species among *Ciccaba* and *Strix* see § 6.

My arguments for suppressing Buboninae and Striginae relate to comparative morphology of the external ear only. But since the erection of these subfamilies was based on external ear morphology only, this should also be enough for a suppression. Besides, I know of no other characters unequivocally supporting the subfamily distinction here rejected.

Until phylogenetic evidence emerges, justifying change of the sequence of genera and species, I strongly suggest that the sequence given by Peters (1940) be retained.

Inspection of table 1 shows that species with the most highly organized external ears are placed last in the Strigidae list, with the 'strigine' genera arranged essentially in order of increasing ear asymmetry. I have found no explicit statement in Peters's papers that this is the principle followed in arranging the sequence of genera. However, this sequence reflects a recognition of the importance of hearing and external ear morphology in owl evolution. Peters's sequence also has the merit of being well-known. This sequence of genera and species involves no classification.

Other sequences, unless phylogenetically based, are unnecessary and confusing (except maybe an alphabetical one). One recent deviation from Peters's sequence of genera is found in the general text in the book on owls of the world, edited by Burton (1973). I can see no justification for that sequence, which cannot be defended even on ecological grounds. The check-list in Burton (pp. 198–9), however, adheres essentially to that of Peters.

9. Affinity between *Rhinoptynx clamator* (Vieillot), *Pseudoscops grammicus* (Gosse), and *Asio* (Brisson)

Rhinoptynx clamator and *Pseudoscops grammicus* have long been believed to be related to *Asio*, a genus with which both species have sometimes been merged.

One of the best distinguishing characters of *Asio* is provided by external ear morphology. However, external ear morphology has not been described before in *Rhinoptynx* and *Pseudoscops*. Ridgway (1914, p. 620, footnote) wrote: 'The details of structure of the external ear-openings, which cannot be exactly determined from dried skins, are assumed to be the same in *Rhinoptynx* and *Pseudoscops* as in *Asio*'. Kelso (1940) wrote: '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.' About ear asymmetry he noted only that it occurs in northern species of *Asio*. In passing, Peters (1937) remarked on the affinity of *Pseudoscops*: 'this bird, originally of *A. asio* [= *Asio otus*] stock...'

In this paper the external ears of *R. clamator* and *P. grammicus* are reported to be very similar in geometry and structure to those of *Asio otus* (§ 5). This similarity will now be evaluated.

When geometrical complexity of external ears evolves independently in different evolutionary lines, there are few ways in which structural similarity may arise (or be maintained) between different lines, whereas there are many ways in which dissimilarities may arise. Hence the probability is smaller that structural similarity will arise than that dissimilarities will. In general, therefore, similarity in complex structures provides strong evidence of affinity, whereas dissimilarities provide much weaker evidence of non-relatedness (see the *Ciccaba–Strix* case, § 6).

Because of the geometrical and structural complexity of their ears, the probability that the close similarity has originated independently in *Rhinoptynx*, *Asio*, and *Pseudoscops* must be infinitely small. Hence it can be stated with a high degree of certainty that *R. clamator* and *P. grammicus* are closely related to *Asio*. Strong support for this is given also by other characters.

Similarities were looked for when relating the ear asymmetry in these three genera. Now *differences* in other characters will be considered for evaluation of the validity of separation at genus level.

I am not sure that the demonstrated affinity should lead to suppression of the two monotypic genera and transfer of their species to *Asio*. At least *P. grammicus* differs strikingly from *Asio* for instance in having remarkably short and broad wings. This and some other characteristics seem to be the result of insular adaptations leading towards a generalized owl (ecologically and structurally). Parallels are found also in some other island owls. It may be as well to retain its monotypic genus and recognize its *Asio* affinity as to put it with *Asio* and recognize its distinctive characters. I plan to return to this elsewhere.

Flieg (1971) reported on a hybridization in captivity between *Tyto alba* and *Rhinoptynx clamator*, resulting in two infertile eggs and two fertile, aborting about the 15th day of incubation. This observation was given some taxonomic weight by Sibley & Ahlquist (1972, p. 189) and Mikkola (1973, p. 136). The latter wrote: 'It [*R. clamator*] appears to form a link between the two modern families of owl: a barn owl (Tytonidae) crossed in captivity with a striped owl (Strigidae) produced fertile eggs.' The discussion above on external ear morphology demonstrates that *Rhinoptynx* is not more closely related to *Tyto* than *Asio* and *Pseudoscops* are.

Acknowledgements

For providing me with material of Swedish owls and arranging for me to examine and measure dead owls before preparing them as study skins, I thank W. Berg at The Natural History Museum, Stockholm, and B. Wennerberg, E. Haack, and Monica Silfverstolpe at The Natural History Museum, Göteborg. I also thank K. Borg, Department of Veterinary Medicine, Stockholm, for material. I am most thankful to A. P. Knight, C. Pennycuick, and A. Forbes-Watson for providing me with some tropical owl species. I thank Curator K. C. Lint and Asst. Curator A. Risser for allowing me to examine living owls in the collection of the San Diego Zoo, and again A. Risser for most willingly and patiently helping me with the owls for two days. For letting me examine some living, temporarily captive owls under his care, and for helping me do that, I thank P. Bloom. B. Broo kindly let me examine some living, captive *Bubo bubo* under his care in connection with his project of reintroducing eagle owls in southwestern Sweden. Skeletal material was kindly lent me from several museums, and I express my gratitude to the following persons for bringing about the loans: J. Lepiksaar, Museum of Natural History, Göteborg; Greta Vestergren, Museum of Natural History, Stockholm; Hj. Munthe-Kaas Lund, Zoological Museum, Oslo; and H. Olsen, Zoological Museum, Bergen.

I am most thankful to W. J. Bock, Columbia University, New York, for critically reading the manuscript and for suggesting many improvements.

This study was supported by grants from 'Lennanderska Fonden', 'Längmanska Kulturfonden', and The Faculty of Natural Sciences of the University of Göteborg.

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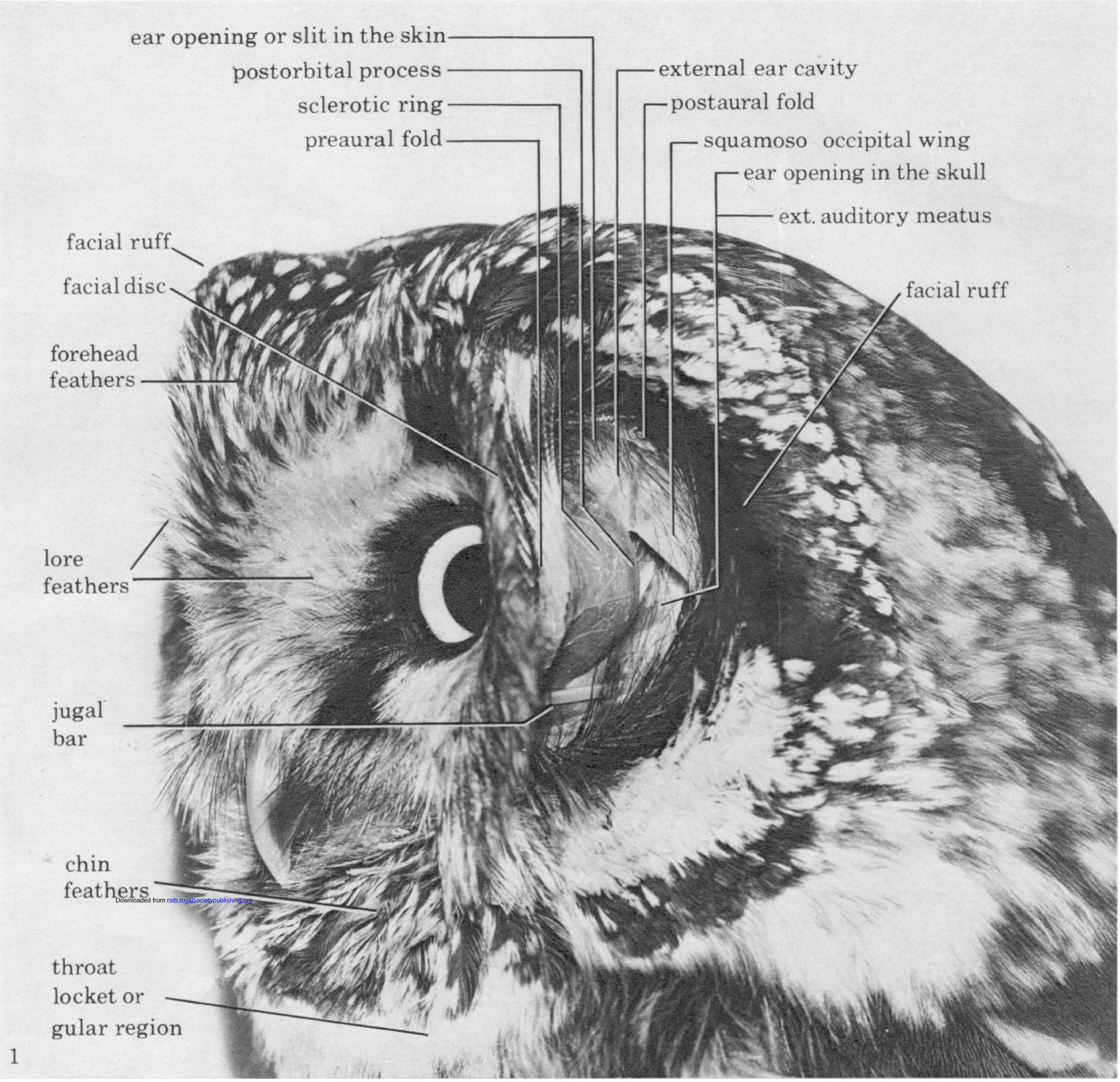
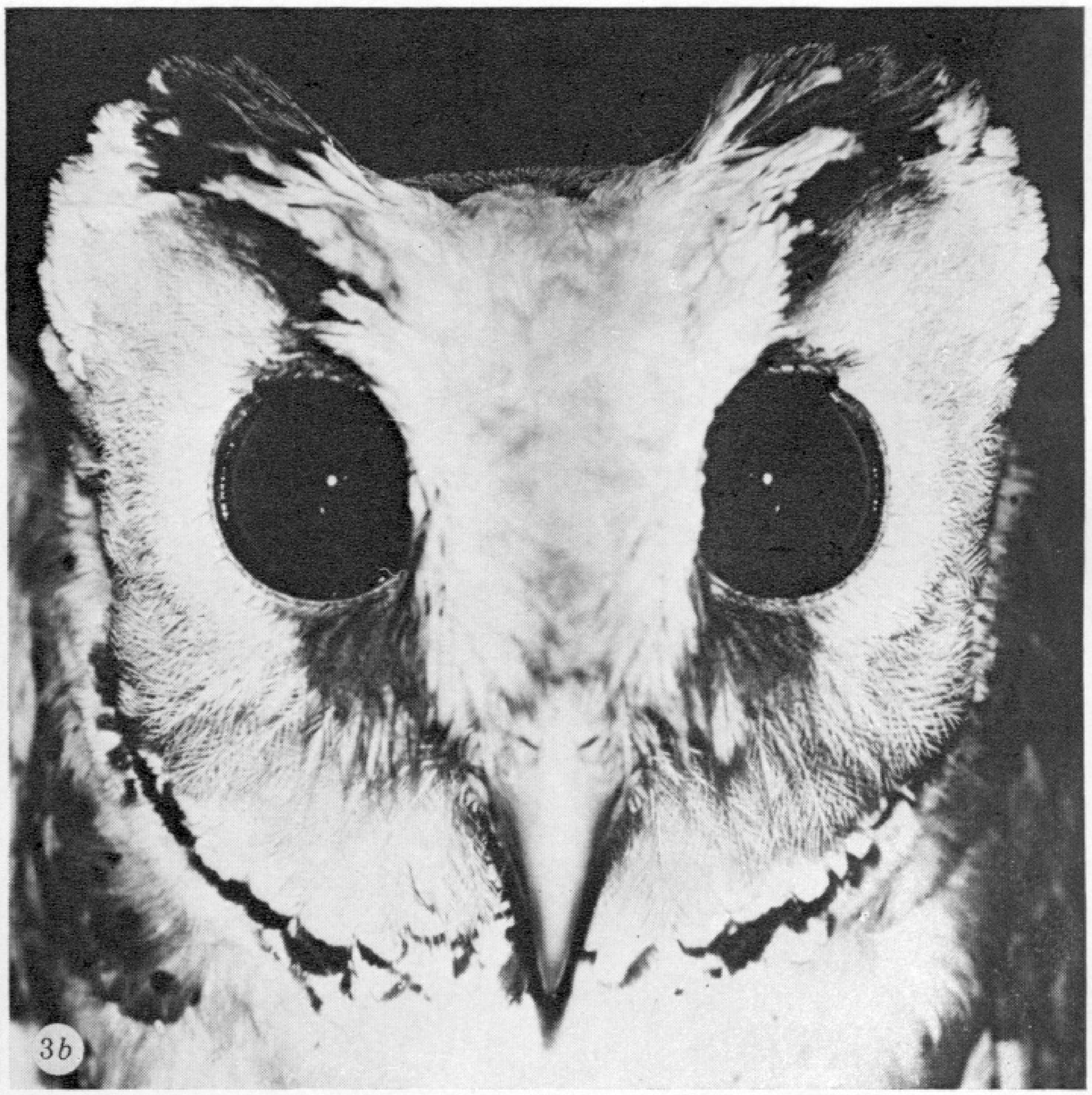


FIGURES 1 AND 2. For description see opposite.


3a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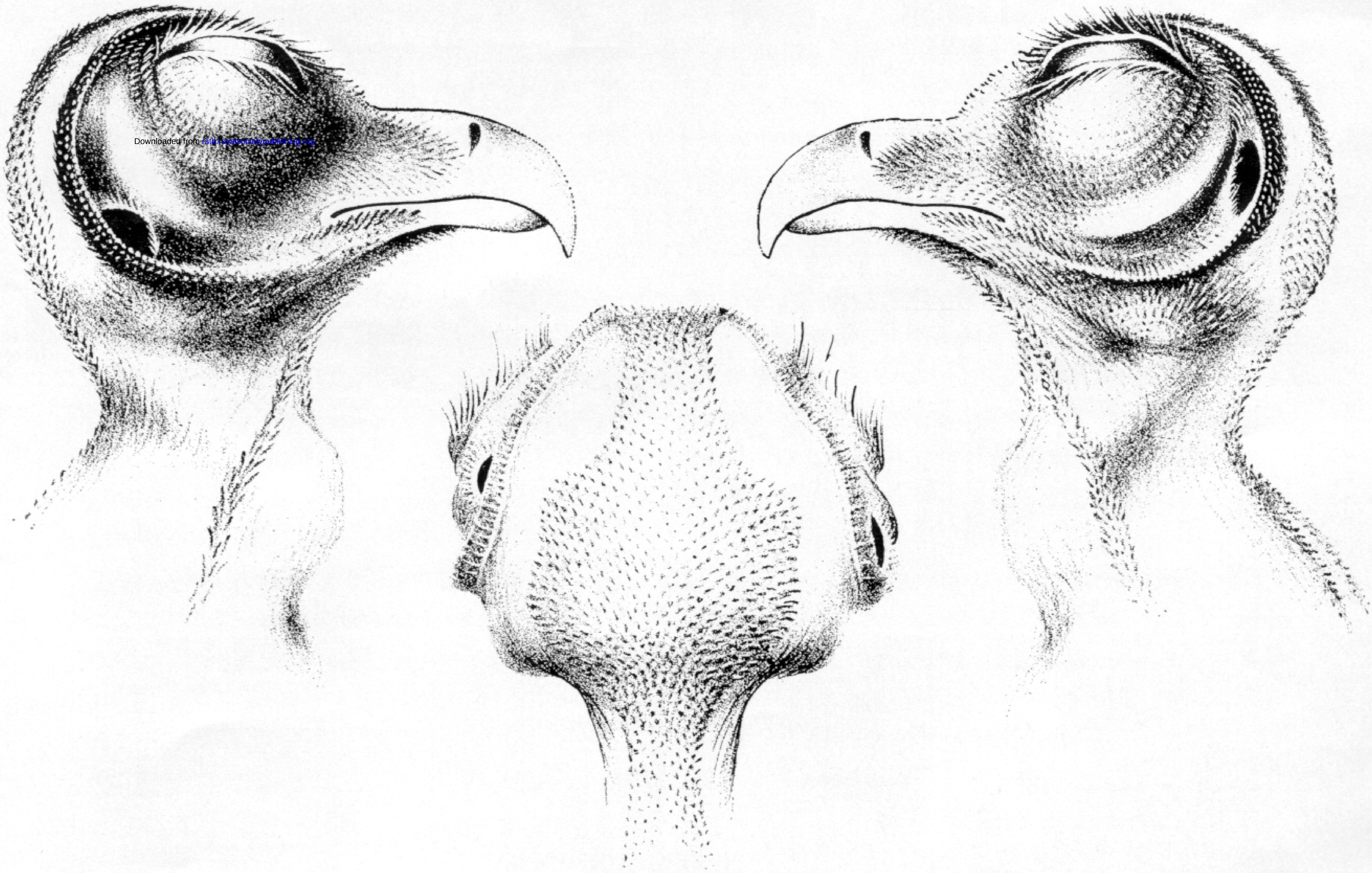

FIGURES 3 AND 4. For description see opposite.