

Ecology and Conservation of Owls

***Ian Newton, Rodney Kavanagh,
Jerry Olsen & Iain Taylor***

This book is available from CSIRO PUBLISHING through our secure online ordering facility at <http://www.publish.csiro.au/> or from:

Customer Service
CSIRO PUBLISHING
PO Box 1139
Collingwood Victoria 3066
Australia

Telephone +61 3 9662 7666
Freecall 1800 645 051 (Australia only)
Fax +61 3 9662 7555
Email publishing.sales@csiro.au

© CSIRO 2002

The sample pages following are provided solely for information purposes and may not be reproduced, stored or transmitted in any form or by any means without prior permission of the copyright owner. Contact CSIRO PUBLISHING for all permission requests.

INDEPENDENT EVOLUTION OF OUTER EAR ASYMMETRY AMONG FIVE OWL LINEAGES; MORPHOLOGY, FUNCTION AND SELECTION

R. ÅKE NORBERG

Department of Zoology, Zoomorphology, University of Göteborg, Box 463, 405 30
Göteborg, Sweden. email: ake.norberg@zool.gu.se



Asymmetry of the outer ear occurs among owls belonging to five phyletic lines, represented by the following genera: (1) *Tyto*; (2) *Phodilus*; (3) *Strix*; (4) *Rhinoptynx*, *Asio*, *Pseudoscops*; and (5) *Aegolius*. Various *Strix* species differ considerably in their degree of ear asymmetry, and in the structures involved. Within each of the other groups, however, ear morphology is rather uniform among species, but strikingly different between groups. In fact, differences in the form and structure of the asymmetry are so great between groups that ear asymmetry almost certainly originated independently in each one of the five owl lineages. Ear asymmetry makes the auditory directional sensitivity pattern for high frequencies different in elevation between the two ears. This enables the owl to localize sound in the vertical plane, by comparing the intensity and spectral composition of sound between the two ears. When an owl localizes ground-living prey by hearing, it usually sits or flies low in order to be close to the sound source, thereby improving detection. The direction of the sound source then forms a shallow angle with the ground. Therefore, a vertical angle of error, with respect to the true direction to the target, converts into a longer error in distance along the ground than does an equally large, horizontal, angular error. This trigonometrical relationship causes selection for high accuracy in the vertical localization of sound, which presumably underlies the evolution of ear asymmetry in owls.

INTRODUCTION

My aims in this paper are to: (1) describe briefly the anatomy of the five major types of ear asymmetry among owls, and show why each one of them must have evolved independently in a separate phyletic line; (2) explain the functional significance of ear asymmetry; and (3) expose the selection pressures that are likely to lead to the evolution of ear asymmetry. Much of the presentation is based on Norberg (1968; 1977; 1978 and on references therein), with new material and interpretations added.

MORPHOLOGY AND TERMINOLOGY OF THE OUTER EAR OF OWLS

External or outer ear

By *external or outer ear* is meant those ear structures that are outside of the eardrum. Parts of the external ear are thus the *external auditory meatus* 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 opening

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 *preaural* and *postaural folds* or *flaps*. In some species the ear opening is merely a small oval hole in the skin, with its long axis shorter than the eye diameter. In others, the ear opening in the skin is narrow but very high, forming a *slit*, that reaches from below the lower jaw up to the top of the head.
2. The *ear opening in the skull* is the orifice of the external auditory meatus, and is formed by skeletal bone, covered by very thin skin. The lateral border of the opening is usually formed partly by a curved bone flange, the *squamoso-occipital wing*, vaulting over the ear canal, and often forming the most lateral part of the skull. The inner, medial, border of the ear opening is formed by the *postorbital process*, on which the eye rests, and by the *sclerotic eye ring*. This is a bone ring, or short tube, formed by a series of bone lamellae, encircling the eye ball and making the eye almost immobile.

Ear flaps

Most owl species have merely a narrow skin fold around the rim of the ear opening. But some species have a strongly developed *preaural skin fold* or *flap* that more or less overlaps the ear opening in the skin. And others have a well developed *postaural skin fold*, whose anterior part is deflected laterally, forming a broad, anteriorly facing rim, the edge of which bears the most anterior feathers of the *facial ruff*.

Ear feathers

Facial ruff. Behind and to the sides of the ear openings there are specialised, dense feathers that are extremely densely packed and form a *facial ruff*. Indeed, nowhere else on the owl's body are any feathers even nearly as densely packed as in the facial ruff. The ruff forms a concave surface to the sides of the ears. It is sound-reflecting and increases the sound intensity in the ear like a parabolic reflector. Some of the facial ruff feathers attach to the deflected edge of the postaural skin fold, or skin ridge, behind the ear opening, while the remaining ruff feathers are densely packed behind this rim.

The facial ruff is ill-defined or almost lacking in some species, whereas it is very prominent and almost encircling the face in those species that rely most heavily on hearing for prey localization.

Facial disc. In front of the ear opening lie modified, very sparse, 'sound-transparent' feathers, which attach to the rim and anterior surface of the preaural skin fold. They are arranged radially around the eye and form a rounded *facial disc*. The facial disc feathers easily let sound through,

their main function obviously being to protect the ear canal from objects coming into it, and probably also preventing air turbulence and aerodynamic noise from arising at the ear opening. Usually the facial disc feathers only partly overlap the ruff as seen from in front, leaving an often dark-coloured rim of the ruff visible outside the disc. The facial ruff and disc together often give the owl face a distinctive, species-specific character.

External auditory meatus or ear canal

The *external auditory meatus* or *ear canal* is the canal between the ear opening and the eardrum. Inside the ear opening in the skull the ear canal expands behind the eye and runs backwards-downwards, then contracts as it passes outside the quadrate, after which it curves sharply downwards-inwards, and finally flattens and spreads out over the eardrum, which is located to either side at the bottom of the skull.

Between-ear, or binaural or bilateral ear asymmetry

Species of most owl genera have each ear shaped as a perfect mirror image of the other, the contralateral ear. However, pronounced *bilateral asymmetry* of the outer ear, meaning that the two ears are *not* mirror images of each other, is known in seven owl genera, and is referred to below simply as *asymmetry* of the ears. This must not be confused with *monaural asymmetry*, meaning that in no way can one or more planes be oriented so as to divide one ear into two or more equal parts. The human pinna shows a familiar example of monaural asymmetry. This kind of ear asymmetry will not be further mentioned here.

The bilateral ear asymmetry among owls always concerns the outer ear only. From the eardrum and inwards, perfect bilateral symmetry prevails. This is also to be expected for theoretical reasons. Once the outer ear asymmetry has caused different, direction-dependent, transformation – coding – of the incoming sound in the two ears, that information should be transmitted unaltered through the middle ear, inner ear and onto the auditory nervous system, with no further differentiation between the ears. This is because bilateral asymmetry in the eardrum or structures inside of it could not perform any direction-dependent transformation of the incoming sound, situated far from the outside sound field as they are.

FIVE INDEPENDENT EVOLUTIONARY LINES OF EAR ASYMMETRY AMONG OWLS

The five major morphological types of outer ear asymmetry among owls will be briefly described here, presented by genera.

1. *Tyto*

The *Tyto* species have very complete facial ruffs and discs. They form a conspicuously heart-shaped face, with the ruff and disc completing nearly the full 360°. The facial ruff forms a concave surface, made up of compact and densely packed feathers. It collects sound over the entire face of the owl and guides the sound to the ear openings in the skin. The ear openings are about the size of the eye, and nearly square. They are of about the same size on both sides and each is covered by a big, almost square preaural skin flap, which reaches far lateral to the ear opening.

Ear asymmetry.

- Ear openings in the skin at different vertical levels. *Left* opening highest.
- Skin flaps in front of the ear of slightly different form on the left and right side and set at different vertical levels. *Left* flap highest. Because the flap is located further down in the concave face in the right ear than in the left ear, the right flap faces about 15° more upwards than the left flap.
- Ear asymmetry is caused by soft anatomy structures only, confined here to left-right differences in shape and position of the preaural flaps and to the position of the ear openings in the skin (Fig. 1).

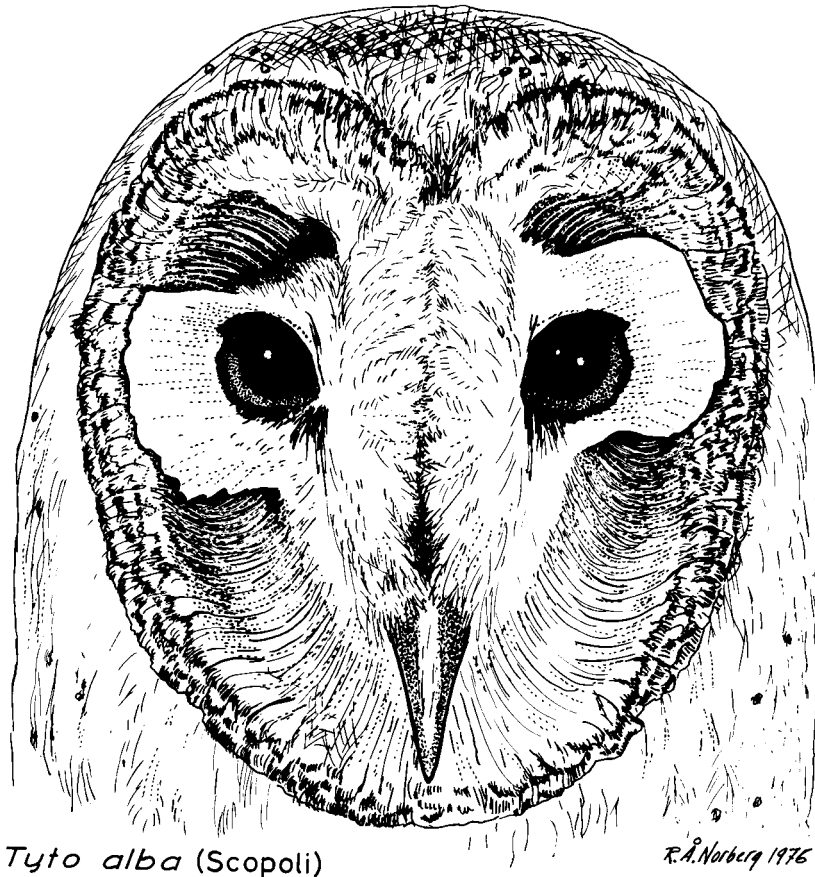


Fig. 1. Frontal view of *Tyto alba*, whose facial disk feathers have been removed from the drawing. The ear openings in the skin are small and nearly square and entirely overlapped by the preaural flaps, which are somewhat different in form in the left and right ear. The ear opening and the preaural flap are located higher on the left side. The facial ruff is extremely well developed, nearly completing the full 360°, and makes the entire face into two concave surfaces. In effect, because of the shape and structure of the facial ruff, each half-face forms a sound-collecting outer ear, which in its function, and even in its form, is like the human pinna. The facial disc feathers are normally attached radially around the eyes and onto the preaural flaps, and they overlap the facial ruff, except for a narrow peripheral border of the ruff, which comes to enframe the facial disc. All illustrations, except Fig. 2, bottom, are made by R. Å. Norberg.

2. *Phodilus*

Phodilus has a well developed facial ruff and disc, but unlike *Tyto*, *Phodilus* has a wide tract of forehead feathers, which separate the left and right parts of the facial ruff and disk above the beak. The facial ruff and disc extend upwards, above the top of the head, and are unlike those of any other owl. They give a unique and strange appearance to the owl.

The ear openings in the skin are small, oval, and of about the same relative size as in *Tyto alba*. There is no preaural skin flap.

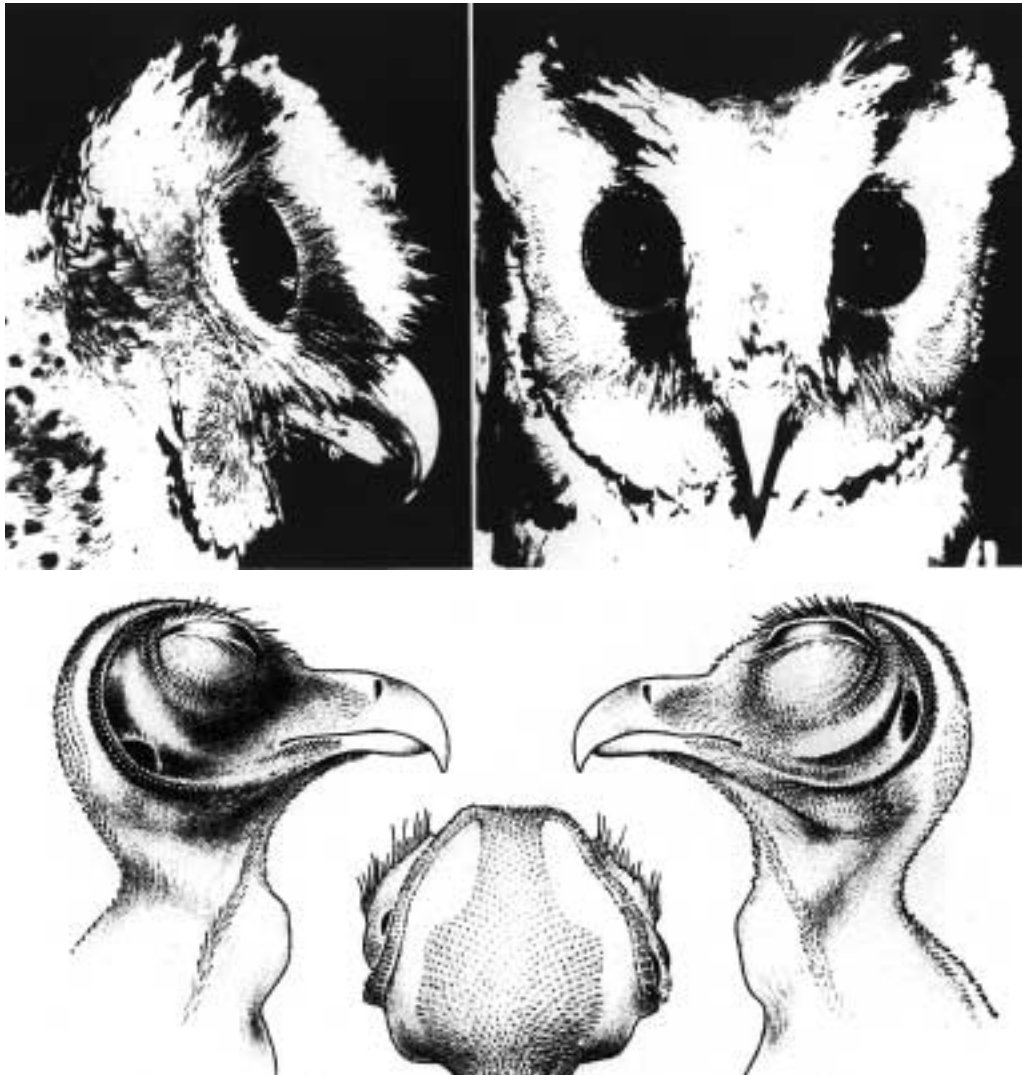


Fig. 2. *Top.* *Phodilus badius*. The form of the facial disc and ruff is unique among owls, and the eyes are enormously large. Photo: R. Å. Norberg. *Bottom.* Lateral and posterior views of the head of *Phodilus badius*. All feathers have been removed to show the different vertical locations of the ear openings in the skin, behind which lies a curved, dermal ridge on which the facial ruff feathers attach. From Pycraft (1903, Plate 2).

Ear asymmetry

- Ear openings in the skin at different vertical levels. *Left* opening highest.
- Ear asymmetry caused by soft anatomy structures only, confined here to left-right differences in vertical position of the ear openings in the skin (Fig. 2).

3. *Strix*

Among *Strix* species there is extreme diversity in ear morphology. This genus now contains all those species formerly placed in the genus *Ciccaba*. In fact, *Ciccaba* was formerly placed in subfamily Buboninae and *Strix* in subfamily Striginae. These two subfamilies were separated on the basis of the relative size of the ear openings in the skin. However, I have argued that *size* of the ear opening in the skin is a character of such small complexity, that it is much too easily modifiable by evolution to be adequate for taxonomic separation at subfamily level; so I rejected this division into subfamilies and also questioned the validity of the genus *Ciccaba* (Norberg 1977). These two former subfamilies and the genus *Ciccaba* are now suppressed. But this taxonomic history highlights the diversity of ear structure among species in the present genus *Strix* – an ear diversity once thought important enough to justify splitting at subfamily level.

The facial ruff and disc are moderately developed in some *Strix* species, like *Strix virgata*, whereas *Strix nebulosa* exhibits a facial ruff and disc that are huge in size and as well developed and complete as in *Tyto*, forming nearly a full 360°.

Ear asymmetry

Most species formerly assigned to the genus *Ciccaba* are now those *Strix* species which have the least developed ear asymmetry. Their asymmetry is the simplest and least complex in the genus *Strix*, and is exemplified here by *Strix virgata*:

- Ear openings in the skin of different size. *Right* opening largest, its height being about 55% larger than that of the left ear.
- Ear asymmetry caused by soft anatomy structures only, confined here to left-right differences only in the size of the ear openings in the skin (Fig. 3).

Between this simple kind of asymmetry, and the most complex one, there is a range of different asymmetries of varying complexity in the genus *Strix*. Below I describe the most complicated, extreme ear asymmetry, which occurs in *Strix nebulosa*:

- Ear openings in the skin of different size. *Right* opening largest.
- Skin flaps in front of the ear large, overlapping the ear opening in the skin, and of different shape in left and right ears.
- A nearly horizontal skin fold, or septum, located inside the ear opening in the skin, and above the ear opening in the skull, present in both ears, but with a slightly different position in the two ears.
- Asymmetry of the skull. The squamoso-occipital wing reaches farther antero-dorsally on the left side than on the right side, and the dorsal part of the postorbital process extends farther laterally on the right side. Because of this skull asymmetry, the ear openings in the skull are of different shape, and the left ear canal is directed more upwards than the right canal.
- Ear asymmetry caused by soft anatomy structures, but also by the skeleton of the skull; left-right differences in the size of the ear openings in the skin, in the shape of the preaural skin

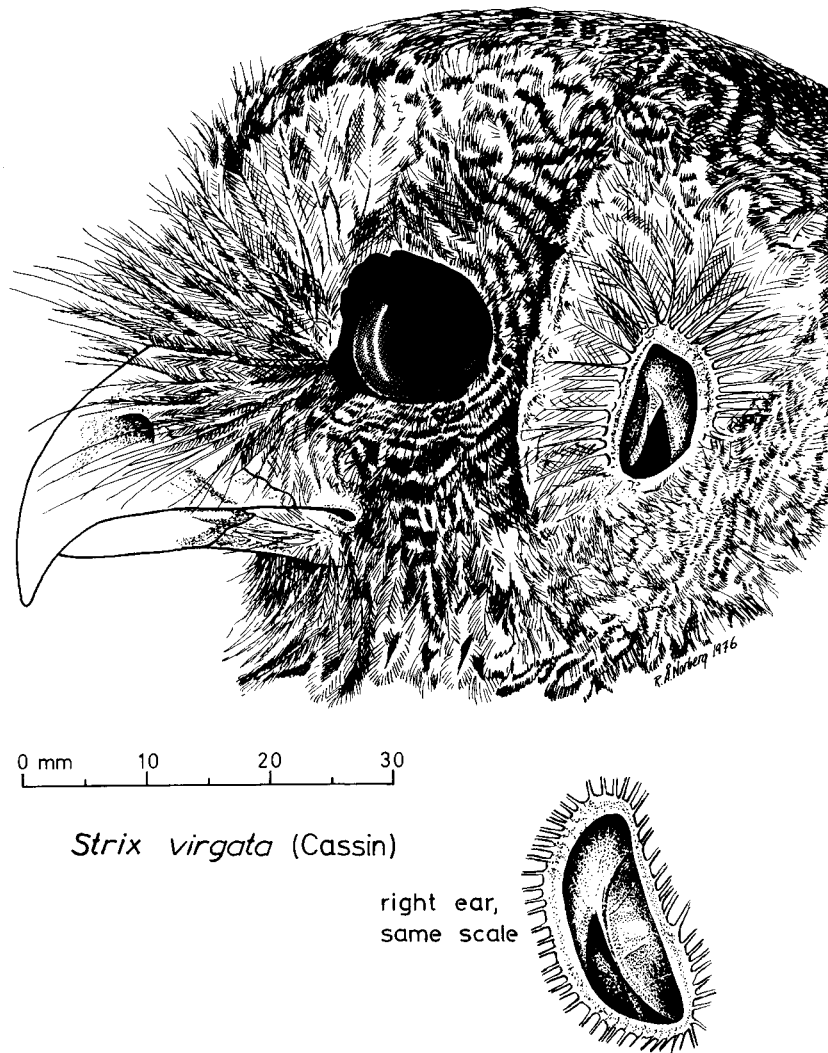


Fig. 3. Lateral view of the head of *Strix virgata*. The facial disc feathers over the ear opening are folded forwards and the facial ruff feathers behind the ear are folded backwards, to expose the unequally large ear openings in the skin.

flaps, in the position of a nearly horizontal skin septum above the ear opening in the skull, and also in the shape of the skull bones bordering the ear aperture in the skull.

4. *Bubo*

In *Bubo bubo* the right ear opening is larger than the left, just as among *Strix* species. But the right opening was only about 15% higher than the left one in the eight specimens examined. And no ear asymmetry has been reported in any other *Bubo* species. The edges of the ear opening in the skin in owls are rather lax, and the ear opening can easily be stretched and deformed, so it is rather difficult to take reliable and reproducible measurements. Therefore, I feel that the possible

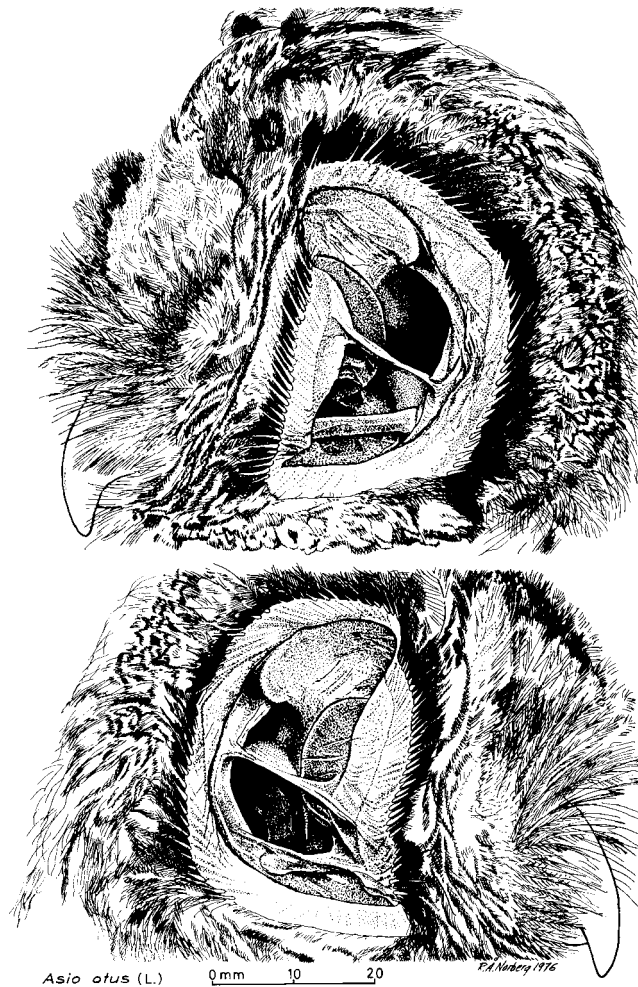


Fig. 4. Lateral view of the head and ear of *Asio otus*, with the jugal bar lying in the plane of the figure, so that the head is seen slightly from in front. The head and ears are intact, but the preaural flap is folded forwards and the postaural flap is displaced backwards to expose underlying structures of the outer ear. The bilateral ear asymmetry is caused entirely by the different orientation of the nearly horizontal intra-aural skin septum in the left and right ear.

ear asymmetry in *Bubo* needs to be examined further – for its definition, consistency and occurrence among species.

5. *Asio*, *Rhinoptynx*, *Pseudoscops*

The ear openings in the skin are slit-like and very large, extending from below the lower jaw up to the top of the head, thus occupying the entire height of the head. The preaural flaps overlap the ear openings, which therefore open towards the side of the head. The ear openings in the skin, the postaural skin folds and the preaural flaps are perfectly symmetrical between the left and right side.

Rhinoptynx clamator of the new world was formerly placed in a monotypic genus but is now

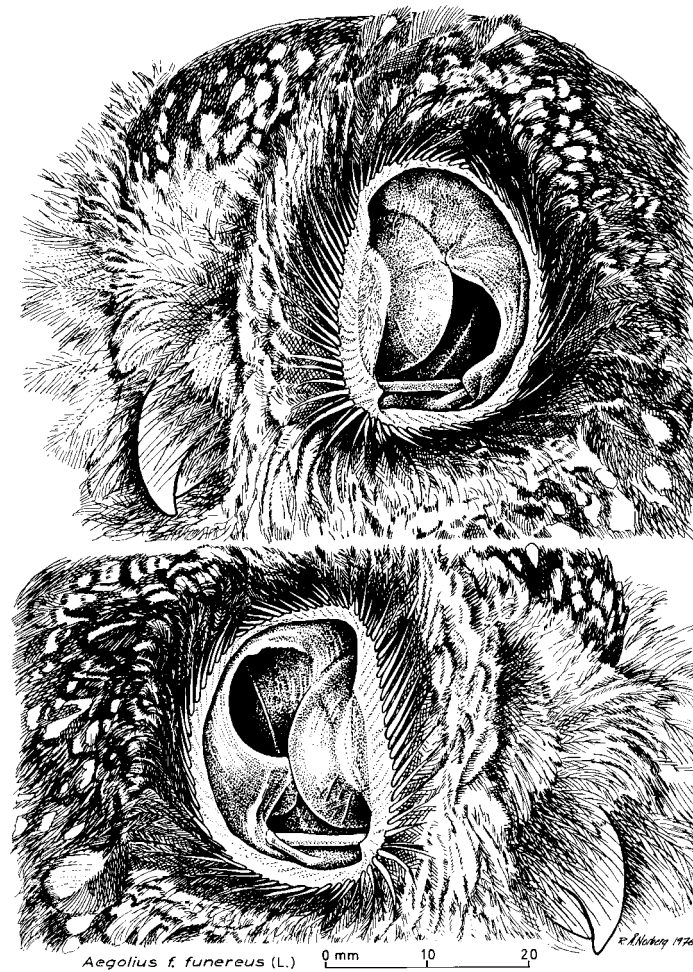


Fig. 5. Lateral view of the head and ear of *Aegolius funereus*, with the jugal bar lying in the plane of the figure, so that the head is seen slightly from in front. The head and ears are intact, but the preaural flap is folded forwards and the postaural flap is displaced backwards to expose underlying structures of the outer ear. The bilateral ear asymmetry is caused entirely by the asymmetry of the head skeleton, namely the different position and orientation of the squamoso-occipital wing.

usually referred to as *Asio clamator*. *Pseudoscops grammicus* is endemic to the island of Jamaica and has a monotypic genus named for it.

Ear asymmetry

- Ear openings in the skull are perfectly symmetrical between the left and right sides, but a nearly horizontal intra-aural skin septum is oriented in different ways in the two ears. By very simple means, namely by different attachments of the septum to the inner and outer walls of the ear opening in the skull, the septa produce dramatic bilateral ear asymmetry.
- The functional ear openings in the skull are of different form and are located at different vertical levels, due entirely to the delimitation by the skin septum; *left* opening highest,

resulting in the left ear canal being directed markedly upwards, whereas the right canal is directed horizontally.

- Ear asymmetry caused by soft anatomy structures only, confined here entirely to the different orientation of a nearly horizontal skin septum in the left and right ear (Fig. 4).

6. *Aegolius*

The ear openings in the skin are slit-like and very large, extending from the level of the lower jaw up to near the top of the head, thus occupying almost the entire height of the head, but not quite as large as in *Asio*. The preaural flaps overlap the ear openings, which therefore open towards the side of the head. The ear openings in the skin, the postaural skin folds and the preaural flaps are perfectly symmetrical between the left and right side.

Ear asymmetry

- Ear openings in the skull are located at strikingly different vertical levels, due entirely to the different positions and orientations of the squamoso-occipital wing on each side of the skull, which produces a dramatic bilateral skull and ear asymmetry.

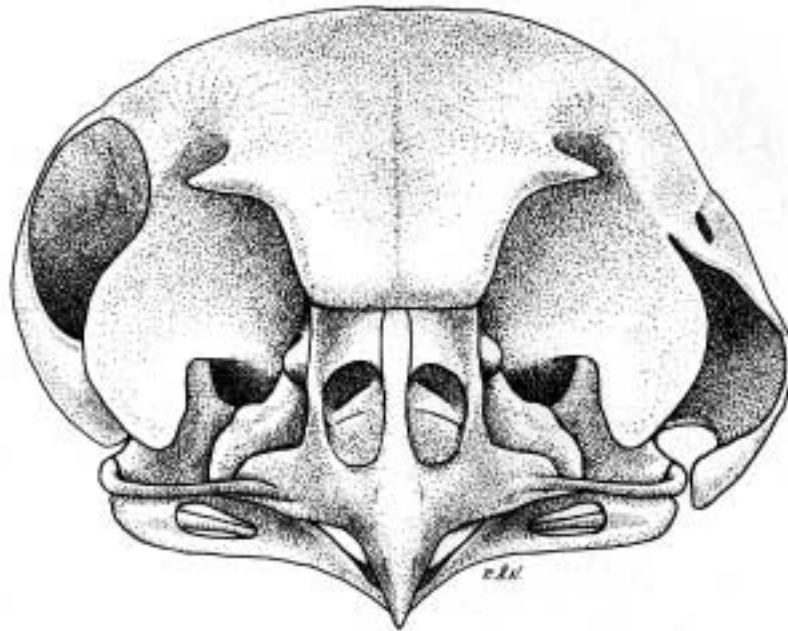


Fig. 6. Frontal view of the skull of *Aegolius funereus*, with the sclerotic eye rings and the rhamphotheca (horny beak sheath) removed. The asymmetry of the skull and of the ear openings in the skull is caused by the asymmetric position and orientation of the squamoso-occipital wings, which vault over, and form the outer wall of the ear canal. Apart from the squamoso-occipital wing, the asymmetry extends also to the neighbouring skull elements – orbitosphenoid, squamosal, parietal, and frontal. When the skull is viewed from in front, a line connecting the centres of the ear openings deviates 12° from the horizontal. And lines through the centre of the eardrum and the centre of the ear opening in each ear diverge vertically by 40° when the head is seen from the side, i.e. in a projection onto the vertical median plane of the head. This is the projected, vertical divergence angle between the left and right ear canal.

- The ear openings in the skull are of different form and are located at different vertical levels; *right* opening highest, resulting in the right ear canal being directed markedly upwards, whereas the left canal is directed horizontally – opposite to the situation in *Asio*.
- Ear asymmetry caused by head skeleton structures only, confined here entirely to the different positions and orientations of the squamoso-occipital wing and adjacent bones on the left and right sides.

Conclusion

Various *Strix* species differ considerably in their degree of ear asymmetry, and in the structures involved. Within each of the other groups, however, ear morphology is rather uniform among species, but strikingly different in structure and geometry between groups. Consideration of the probabilities that various anatomical similarities and dissimilarities in the outer ear have shared or independent evolutionary origins, leads to the conclusion that ear asymmetry has evolved independently at least five times among owls (Norberg 1977). The phylogenetic distribution of ear asymmetry supports this conclusion.

FUNCTION OF EAR ASYMMETRY

Symmetrical ears

Whenever the direction to a sound source is determined binaurally – by comparison of sounds received in the two ears – the all-important reference directions are those in which the sound is perceived equally in both ears. For animals with symmetrical head and ears these reference directions lie in the vertical, median plane of the head. When a sound source lies in this median plane, sound reaches the two ears simultaneously, and with the same intensity and spectral composition, i.e. with the same intensity in both ears for any frequency component of the sound (Fig. 7).

The *azimuth*, or *horizontal direction*, may therefore be determined, with reference to the vertical median plane, by using differences between the two ears in *arrival time* of sound, and in *intensity* and *spectral composition* of sound. The *vertical direction* can be determined *binaurally* only by tilting the head so that the reference median plane becomes oriented more or less horizontally, and then repeating the process.

Owls with symmetrical ears must determine the horizontal and vertical directions of a sound separately, one after the other, by tilting the head in between (Fig. 7). Therefore, a moving prey individual will be in a different position when the vertical localization is made.

Asymmetrical ears

The description above applies also to owls with asymmetrical ears when sound contains low frequencies only, because the morphological ear asymmetry has no effect on the ears' directional sensitivity for low frequencies. But for *high frequencies* ear asymmetry makes the auditory directional sensitivity pattern different in elevation – in the vertical plane – between the two ears, which enables the owl to localize in the vertical plane by comparing intensity and spectral composition of *high-frequency sound* in the two ears without tilting the head (Fig. 8). Rustling sounds made by prey in vegetation or snow contain low as well as high frequency components and also transients. Moving prey, can therefore be localized both in the horizontal and vertical planes

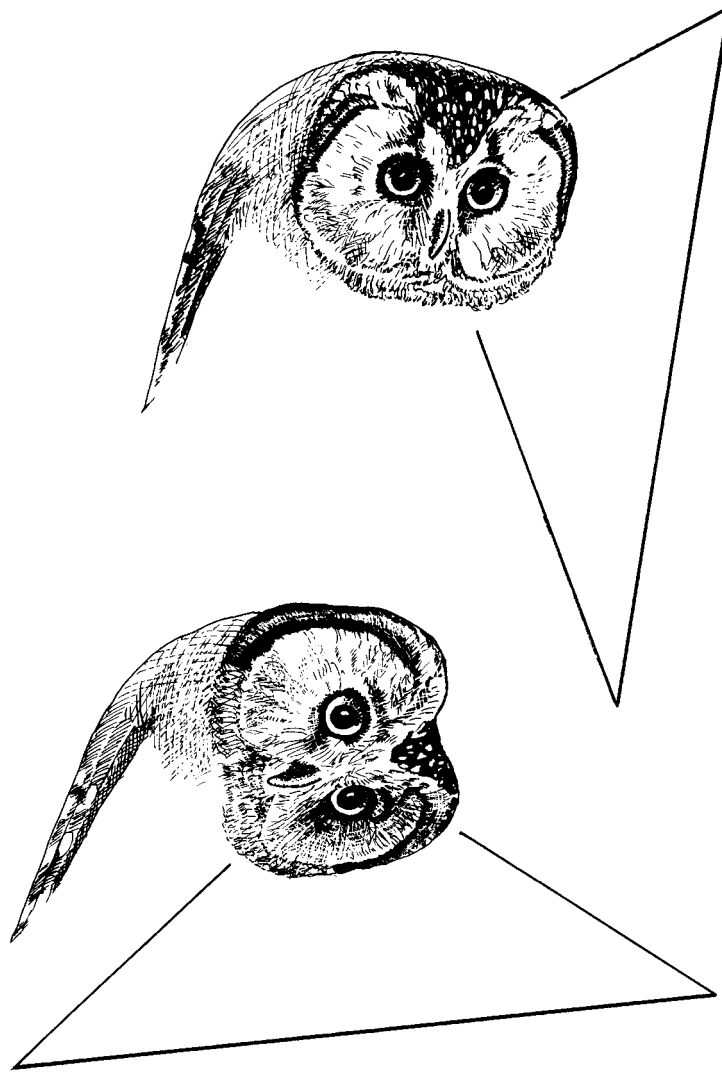


Fig. 7. With symmetrical ears, sound reaches the two ears simultaneously, and with the same intensity and spectral composition, whenever the source lies in the vertical median plane of the head – which is an all-important reference plane. Using binaural cues – differences in arrival time and intensity of sound between the two ears – and keeping the head upright, it is possible to localize only horizontally, in azimuth, i.e. with reference to the vertical, median plane of the head. Therefore, vertical direction can be determined *binaurally* only after tilting the head – again with reference to the vertical median plane of the owl's head, now tilted. And the azimuth must be remembered and combined with the succeeding vertical localization. Because of this time interval, a moving prey individual will be in different positions at the two localization events. These conditions and the associated localization difficulties apply also to owls with asymmetrical ears when sound contains low frequencies only, because then the structural ear asymmetry does not impose any vertical disparity between the directional sensitivity patterns of the two ears.

simultaneously, using binaural comparison. This is the great acoustical advantage with ear asymmetry. It saves time and avoids directional ambiguity with moving prey (Norberg 1968; 1978).

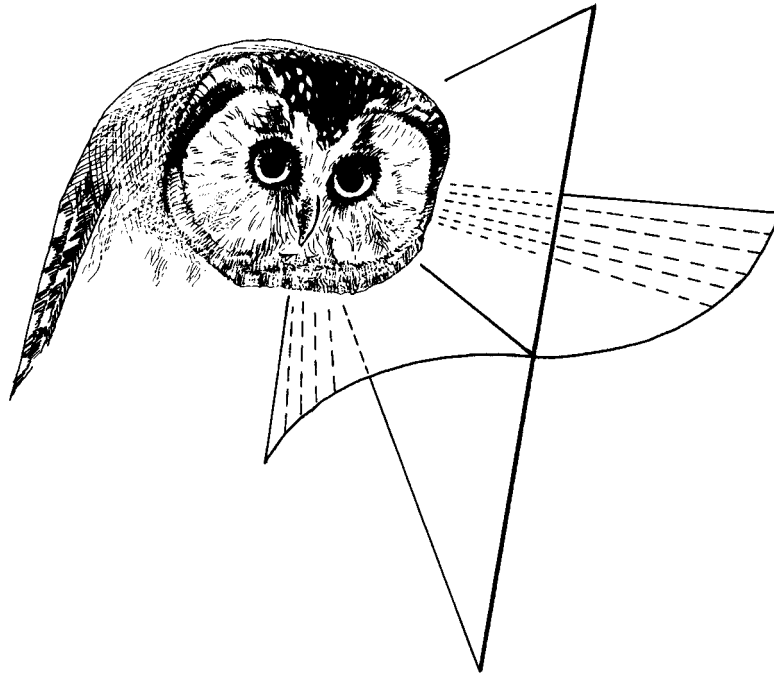


Fig. 8. With asymmetrical ears, time of arrival of sound to the two ears, and intensity of *low-frequency sound*, can still be used to localize in azimuth – horizontally, with reference to the vertical, median plane of the head. But owing to ear asymmetry, high frequency sounds are heard with equal intensity in directions lying on a curved surface that is almost horizontal near the owl's line of sight. Vertical localization can be made with reference to this surface by comparing intensity and spectral composition of *high-frequency sound* in the two ears. Therefore, broadband sound with transients can be localized *simultaneously* – without head tilting – both in azimuth and elevation, by binaural comparison of arrival time and intensity of low and high frequency sound components.

STEPS IN THE EVOLUTIONARY ORIGIN OF EAR ASYMMETRY IN OWLS

The following chain of causes and conditions must have been important for the evolutionary origin of ear asymmetry among owls.

- Selection by the owl of ground-living prey for food.
- Selection by the owl of habitats with dense forest or dense ground vegetation or with temporary snow cover.
- This makes visual hunting less useful but favours aural detection and localization.
- The use of hearing for detection requires that the owl is close enough to the sound source. In order to maximize its detection area, the owl must therefore select low perches or fly low if it hunts in flight.
- The direction to prey must be localized in two planes, both horizontally and vertically, whenever predator or prey are off ground level.
- From a low listening position, the direction to prey forms a shallow angle with the ground. Therefore, a given angle of error, with respect to the true direction to the target, converts into

a longer off-target in distance along the ground for a vertical angular error than for an equally large, horizontal angular error (Norberg 1977).

- This trigonometrical relationship causes selection for high localization accuracy in the vertical plane (in elevation).
- Directional localization must be quick, before prey reaches cover. With symmetrical ears horizontal and vertical localization can only be made successively, with head tilting in between, and with memorization of the horizontal direction, to be combined later with the vertical localization. This takes time, and allows prey to run into a new position between the two localization events.
- Ear asymmetry is an adaptive answer to the selection pressures described above. It enables the owl to localize *quickly* and *simultaneously* both in the horizontal and vertical planes.

ACKNOWLEDGMENTS

I gratefully acknowledge a travel grant from The Royal Society of Arts and Sciences in Göteborg.

REFERENCES

- Norberg, R. Å. 1968. Physical factors in directional hearing in *Aegolius funereus* (Linné) (Strigiformes), with special reference to the significance of the asymmetry of the external ears. *Arkiv för Zoologi* **20**: 181–204.
- Norberg, R. Å. 1977. Occurrence and independent evolution of bilateral ear asymmetry in owls and implications on owl taxonomy. *Phil. Trans. Roy. Soc. Lond. Ser. B.* **280**: 375–408. Plates 1–4.
- Norberg, R. Å. 1978. Skull asymmetry, ear structure and function, and auditory localization in Tengmalm's Owl, *Aegolius funereus* (Linné). *Phil. Trans. Roy. Soc. Lond. Ser. B.* **282**: 325–410. Plates 1–10.
- Pycraft, W. P. 1903. On the pterylography of *Photodilus*. *Ibis* **1903**: 36–48.