THE AURAL ANATOMY OF BATS

by

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The fine structure of the ears of 62 species of bats from 13 families has been studied by means of serial sections. The bats were caught alive in Britain, West Indies, Panama, Central and North Africa and were intra-vitally perfused with fixative in order to obtain perfect preservation of the internal ear. Where possible, up to six specimens of each species were fixed for this study and all the ears were sectioned in the horizontal plane. This paper will survey briefly some of the results obtained.

The pinnae of bats are varied in size, shape and structure and have not been studied in detail. In many bats, e.g. *Rhinolophus* and *Hipposideros* they are mobile, the movements being correlated with pulse emission (Pye, Flinn & Pye, 1962; Pye & Roberts, 1970). These mobile pinnae are usually simple in shape, others are immobile and may be complex and have leaflets or tragi inside the main part of the ear.

Emphasis has been placed on the structure of the middle ear (Pye & Hinchcliffe, 1968; Hinchcliffe & Pye, 1969; and unpublished) and especially the structure of the cochlea (Pye, 1966a and b, 1967, and unpublished). The middle ear cavity is medium in size, but the intra-aural muscles are large, especially in the echolocating Microchiroptera. The stapedius muscle is large and fan-shaped, having a Paaw's cartilage at the junction with the tendon. This cartilage is present in Microchiroptera, but absent in all Megachiroptera. The stapedius muscle is in the same bony cavity as the facial nerve (VIIth), whereas in many other mammals, such as man, it is in separate cavity. The stapedial artery persists in all adults, contrary to many other mammals, where it is present only during development. The ossicles are medium in size.

A variety of measurements has been carried out on the cochlea in the horizontal modiolar plane. These are: the height and width of the cochlea, the number of half-turns, the width and thickness of the basilar membrane, the height of the cells of Claudius and the size of the spiral ligament. These measurements were chosen because they showed the greatest variations among the Chiroptera.

Nine species of bats representing all the superfamilies have been chosen for discussion in this paper. These are set out in figure 1 with their classification and other information.

In all Microchiroptera the cochlea is relatively large compared with other mammals and this is especially surprising when the weight of the animal is taken into account. It consists of from five to seven half-turns. In Megachiroptera the cochlea is smaller and only four half-turns are present in all the 13 species examined. The greatest height of the cochlea is recorded in *Rhinolophus fumigatus* and this is enormous for an animal which weighs only 20 g (fig. 1). Also both species of *Rhinolophus* have the widest cochleae of all the bats studies and the greatest number of half-turns.

Generally in the Microchiroptera the basilar membrane is relatively very narrow at the base of the cochlea and increases in width towards the apex. This is shown by *Noctilio, Carollia, Natalus* and *Pipistrellus* (fig. 2). An exception is found in the Rhinolophidae, where the membrane is wider at the first turn and narrowest at the second turn, increasing from there towards the apex (fig. 2). In *Hipposideros* a slight decrease occurs at the second half-turn. The overall increase in width of the membrane from the base to the apex doubles in *Noctilio* and *Carollia,* while in *Natalus* it increases only by a half. In *Rhinolophus* this increase is even less, probably due to the fact that the membrane decreases in width from the first to the second turn and only then increases again

NAME	CLASSIFICATION	PULSE TYPE	PRINCIPAL FREQUENCY	WEIGHT	HEIGHT OF COCHLEA	NUMBER OF 1/2 TURNS
Pteropus giganteus	Suborder	None	None	500g.	2.9mm.	4
Rousettus aegyptiacus	Megachiroptera	Damped click	12 kHz.	120g.	2.8mm.	4
	Superfamily					
Noctilio leporinus	Emballonuroidea	FM., CF.	60 kHz.	55g.	2.6mm.	6
	Most primitive					
Carollia perspicillata	Phyllostomatoidea	FM.-Short	80 kHz.	18g.	1.9mm.	5
	Intermediate					
Rhinolophus ferrumequinum		CF.-Long	85 kHz.	25g.	2.7mm.	7
	Rhinolophoidea					
Rhinolophus fumigatus		CF.-Long	45 kHz.	20g.	3.1mm.	7
	Intermediate					
Hipposideros caffer		CF.	150 kHz.	8g.	2.2mm.	6
Natalus tumidirostris	Vespertilionoidea	FM.	135 kHz.	5g.	1.8mm.	5
Pipistrellus pipistrellus	Most advanced	FM., CF.	45 kHz.	7g.	1.7mm.	5

Fig. 1. Some data on the bats reviewed in this paper. FM . . . frequency modulated. CF . . . constant frequency.

towards the apex. It is still a question of speculation why the width of the membrane is narrowest at the second turn. The Megachiroptera have relatively wider membranes throughout the cochlear turns and the increase in width towards the apex is gradual (fig. 2).

In Rhinolophoidea and *Natalus* the basilar membrane is thickened at the base of the cochlea. It may be as much as 50 μ in thickness at the first half-turn, decreasing towards the apex and disappearing by the third or fourth half-turns. In other species thickening is less well defined and in *Pteropus* the basilar membrane is thicker at the apex than at the base.

The supporting cells may be tall at the base of the cochlea in Microchiroptera, e.g. in *Rhinolophus fumigatus. Hipposideros caffer* and *Natalus tumidirostris.* In all cases they decrease in height towards the apex, while in Megachiroptera they remain about the same height throughout the cochlea (fig. 2).

In Microchiroptera the spiral ligament is large in size, especially at the base of the cochlea and there may be extra ossification, called the secondary spiral lamina, for instance in *Rhinolophoidea.*

None of the Megachiroptera uses echolocation, except for *Rousettus,* which produces audible pulses by clicking its tongue (Möhres & Kulzer, 1955) and because of this mechanism is the only Old World fruit bat to be able to live in caves. Of the echolocating Microchiroptera, the Rhinolophidae stand out by producing long, constant frequency pulses, which are also directional in output. As has already been described, these are also the bats which have a more modified cochlea than those which produce short, frequency modulated pulses. *Natalus* is the only other bat in this selection to produce directional pulses, which are short in duration and are frequency modulated. To some extent *Natalus* has a more modified cochlea than, for example, *Carollia,* which produces non-directional, short, frequency modulated pulses. *Noctilio* produces both frequency modulated and constant frequency pulses, depending on its hunting behaviour. It catches fish from just under the surface of water, but it is not known to what extent echolocation plays a part in this (Suthers, 1965).

In a computer correlation of cochlear dimen-

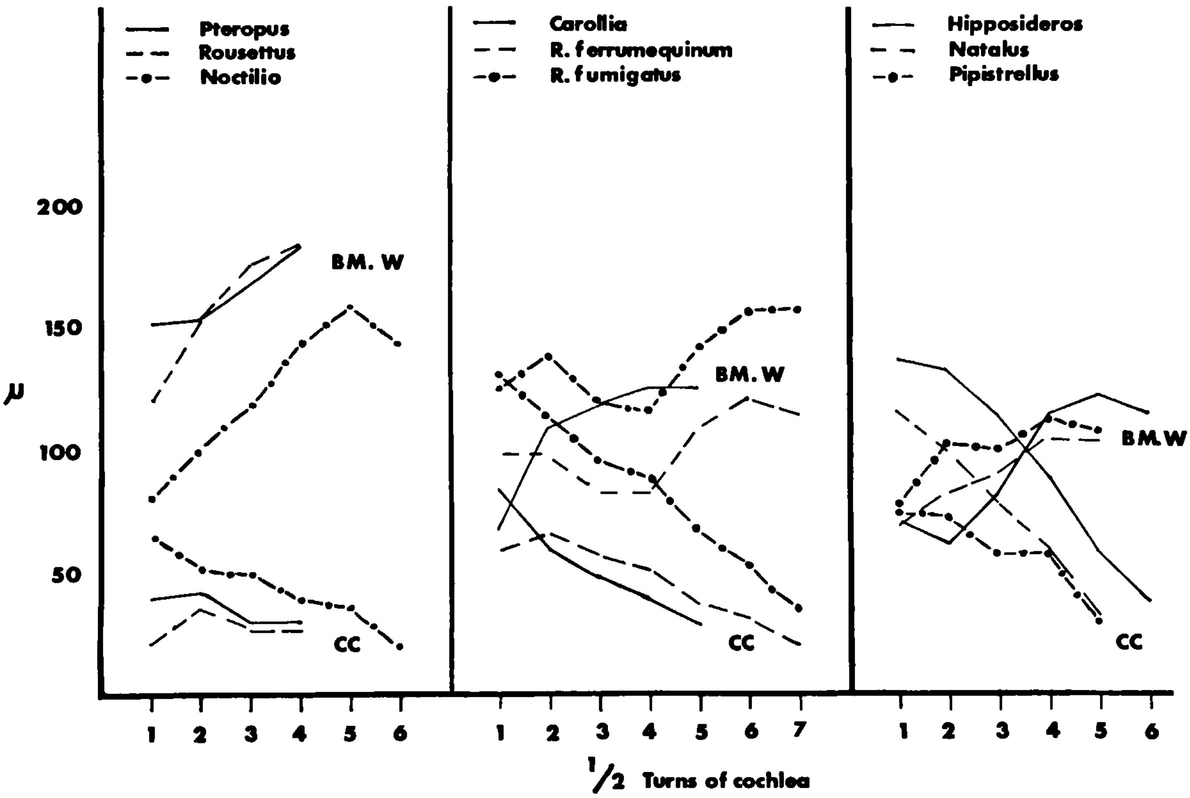

Fig. 2. Histological measurement. BM.W ... the width of the basilar membrane. CC ... the heigth of the cells of Claudius.

sions with acoustic measures (Hinchcliffe & Pye, 1968) it was established that the highest frequency of sounds emitted was significantly inversely correlated with the width measurements at the second, third and fourth half-turns. The highest frequency was also significantly inversely correlated with the widths of the basilar membrane. This is exemplified by *Natalus* and *Hipposideros* which produce the highest frequency sounds in this selection and also have the narrowest basilar membranes at the base of the cochlea (figs. 1 and 2). The highest frequency was also inversely related to the mean weights of the animals, which is again exemplified by *Natalus* and *Hipposideros*. These two bats together with *Pipistrellus* were the smallest bats studied in the whole survey, while *Pteropus* was the largest. This set of correlations is supported by the high correlation of species weight and the width of the basilar membrane found by us.

At present it seems difficult to associate the structure of the external ears with either the variations found in the structure of the cochlea or the type of pulses produced by the animal. The structure of the middle ear in the Microchiroptera is quite distinct from that of the Megachiroptera or most other mammals, but shows rather little variation within the sub-order.

In conclusion it can be said that the Megachiroptera have a fairly unspecialised cochlea and only one genus uses echolocation. Of the Microchiroptera, those bats which produce long, constant frequency pulses or which are directional in their signal output, have the more modified cochleae. It is hoped to continue this work not only by looking at more types of bats, but also by using acoustic traumatisation experiments to determine the frequency range of the cochlea in bats.

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