# Comparison of the morphology of the megachiropteran and microchiropteran eye

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The structure of the eyes of two South African bat species, *Rousettus aegyptiacus* (Megachiroptera: Pteropodidae) and *Rhinolophus capensis* (Microchiroptera: Rhinolophidae) was examined and compared by means of light microscopy. The eyes of both species exhibit characteristics of a typical 'nocturnal eye' (presence of only rods in the retina; the cornea shows a marked curvature and occupies about one third of the globe; the anterior and posterior chambers are very large in relation to the vitreous) and neither possess a fovea. The main difference occurs in the choroid and the retina. The fruit bat *R. aegyptiacus* shows a marked folding of the retina, as a result of papillae that project inwards from the choroid. This does not occur in the insectivorous bat *R. capensis*, where the choroid and the retina form a smooth layer. It is suggested that this unique feature of the fruit bat, and the associated increase in surface area and hence the number of photoreceptors is probably responsible for its good nocturnal vision.

Die struktuur van die oë van twee Suid-Afrikaanse vlermuis-soorte, *Rousettus aegyptiacus* (Megachiroptera: Pteropodidae) en *Rhinolophus capensis* (Microchiroptera: Rhinolophidae) is ondersoek en vergelyk deur middel van die ligmikroskoop. Die oë van albei soorte toon kenmerke van 'n tipiese 'nagtelike oog' (teenwoordigheid van slegs stawe in die retina; die horingvlies vertoon 'n duidelik waarneembare geboë vorm en beslaan omtrent een-derde van die oogbol; die voorste en agterste kamers is baie groot in vergelyking met die glasige deel) en nie een besit 'n fovea nie. Die belangrikste verskil kom voor in die choroïed en die retina. Die vrugtevlermuis *R. aegyptiacus* toon opmerklike voue in die retina as gevolg van papillae wat vanuit die choroïed na binne uitsteek. Dit kom nie voor in die insekvretende vlermuis *R. capensis* nie waar die choroïed en die retina 'n gladde laag vorm. Daar word aan die hand gedoen dat hierdie unieke kenmerk van die vrugtevlermuis, met sy gepaardgaande vergroting vav die oppervlakte en die gevolglike groter aantal foto-reseptore waarskynlik verantwoordelik is vir die vrugtevlermuis se goeie nagvisie.

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Old-world bats of the suborder Megachiroptera (fruit bats) use vision as their major sense for orientation and consequently their eyes show several adaptations for nocturnal vision (Suthers 1970b). The fruit bat eye shows a unique feature among mammalian eyes, in that papillae project inwards from the choroid and hence the retina, which follows closely the contours of these papillae, is highly folded (Kolmer 1909). This feature is believed to increase visual acuity firstly because an increased number of photoreceptors can be packed into a given retinal area, and secondly because the nutrient and oxygen supply to the inner retinal layers is more efficient (Kolmer 1909). Insectivorous bats (suborder Microchiroptera), lack this feature, have a relatively poor eyesight and orientate mainly by echolocation (Suthers 1970b; Hill & Smith 1984).

The morphology of the eye has been described for a wide range of mammals and several authors have emphasized the differences particularly in the retina between diurnal and nocturnal species (Detweiler 1939; Feldman & Phillips 1984). By contrast, within the Chiroptera, the eye has been described for relatively few species, mainly in the genus *Pteropus* (Pedler & Tilly 1969; Suthers 1970a).

The aim of this study is to compare the morphology of the eye and in particular the choroid and retina of two nocturnal species, one of which (Egyptian fruit bat, *R. aegyptiacus*) orientates using vision and the other (Cape horseshoe bat, *R. capensis*) orientates using echolocation.

## Materials and Methods

The material was collected from the eastern Cape Province of South Africa at *c.* 26°E / 33°S. The bats (5 per species) were killed by asphyxiation, body height (length of head and body) was measured and the eyes removed.

The eyes of both species were fixed in Bouin's fixative for 24 h, dehydrated in a series of increasing alcohol concentrations and embedded in paraffin. Thin sections of 3 μm and 5 μm were cut using a rotary microtome and were stained with hematoxylin and eosin, and Mallory's trichome (1 stage). Removal of the lens of the fruit bat eye was necessary as the lens became too hard during the fixation process and prevented successful sectioning.

Eye axial length (antero-posterior mid-axial length of the sagittal section) and thickness of the retina and cornea (along the eye axial length) were measured ($n$ = 10) from histological slides using an ocular micrometer. A comparison of the axial length of fresh and sectioned material indicates that there was no distortion during histological preparation.

## Results

The eyes of both species are nearly spherical and neither possess a fovea (Figures 1, 2). The lens occupies about half of the eye's axial length and the anterior and posterior chambers are large.

The fruit bat eye is bigger than that of the insectivorous bat, the eye axial length to body height

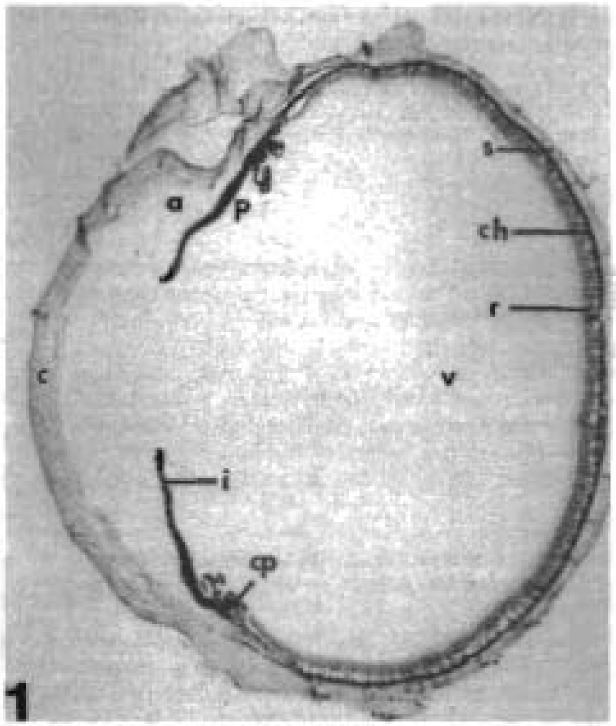


**Figure 1** Section (5 μm) through the eye of *Rousettus aegyptiacus* (lens removed), showing the major structural features. a — anterior chamber; p — posterior chamber; cp — ciliary process; v — vitreous body; c — cornea; i — iris; r — retina; ch — choroid; s — sclera. ×11.

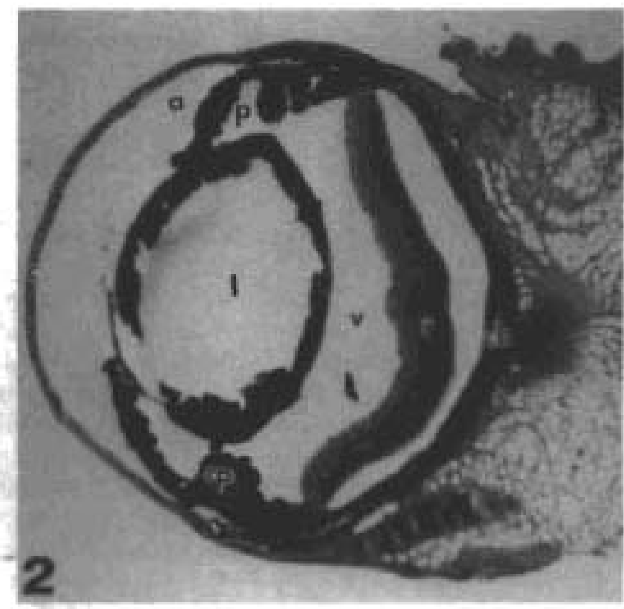


**Figure 2** Section (5 μm) through the eye of *Rhinolophus capensis*, showing the major structural features (retina detached from choroid). l — lens; a — anterior chamber; p — posterior chamber; cp — ciliary process; v — vitreous body; c — cornea; i — iris; r — retina; ch — choroid; s — sclera. ×51.

ratio being 1:20 and 1:52 respectively (Table 1).

The ciliary process in the insectivorous bat is thick and large, whereas in comparison it is thinner and smaller in

**Table 1** Body height ($\bar{x}$ and range, $n$ = 5), eye parameters ($\bar{x}$ ± $SD$, $n$ = 10) and ratios for the two bat species

| | *R. aegyptiacus* | | *R. capensis* | |
|---|---|---|---|---|
| | $\bar{x}$ | range/$SD$ | $\bar{x}$ | range/$SD$ |
| Body height | 115,00 mm | 105–125 mm | 55,00 mm | 51–59 mm |
| Eye axial length | 5,82 mm | ± 0,110 | 1,05 mm | ± 0,020 |
| Retina thickness | 0,27 mm | ± 0,010 | 0,12 mm | ± 0,010 |
| Cornea thickness | 0,23 mm | ± 0,010 | 0,03 mm | ± 0,003 |
| Ratio: eye axial length to body height | 1:19,8 | | 1:52,4 | |
| Ratio: retinal thickness to eye axial length | 1:21,6 | | 1: 8,8 | |
| Ratio: corneal thickness to eye axial length | 1:25,3 | | 1:35,0 | |


**Figure 3** Section (5 μm) through the fruit bat's cornea, showing the different layers. e — epithelium; b — Bowman's membrane; st — stroma; d — Descemet's membrane; en — endothelium. ×440.

the fruit bat. The cornea of both eyes is transparent and in the fruit bat (Figure 3) consists of an outer layer of stratified squamous epithelium; the stroma, which is made up of collagen fibres and corneal corpuscles; and an endothelium. Separating the epithelium and the stroma, and the endothelium and the stroma are the Bowman's and Descemet's membranes respectively. In the insectivorous bat eye (Figure 4), the stratified

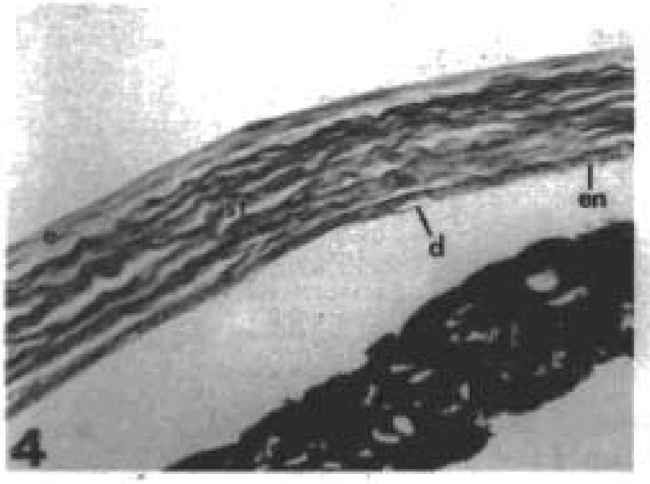


**Figure 4** Section (5 μm) through the insectivorous bat's cornea, showing the different layers. e — epithelium; st — stroma; d — Descemet's membrane; en — endothelium; i — iris. ×440.

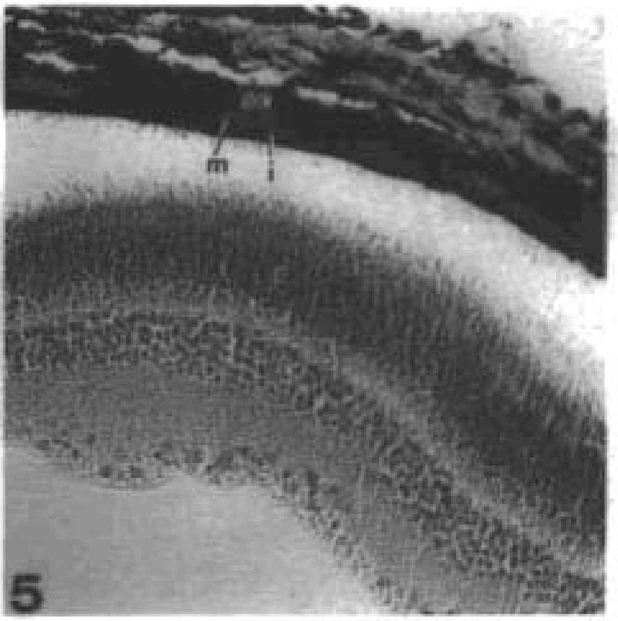


**Figure 5** Section (3 μm) of the insectivorous bat eye, showing the different choroidal layers and the retina (retina detached from choroid). s — sclera; sc — sclerad; m — middle layer; i — inner layer; r — retina. ×230.

epithelium and the stroma are thinner than in the fruit bat eye, and the Bowman's membrane seems to be absent. The relative thickness of the fruit bat's cornea is greater than that of the insectivorous bat, the corneal thickness to eye axial length ratios being 1:25 and 1:35 respectively (Table 1).

In both species the cornea has a slightly greater curvature than the rest of the eyeball and covers about one third of the ocular (Figures 1, 2). The remaining two thirds of the ocular is covered by the sclera. In the fruit bat the sclera is not pigmented and is composed of collagen fibres. The insectivorous bat sclera is thin, deeply pigmented and hardly distinguishable from the choroid (Figures 1, 2).

The main difference between the two eyes is seen in the choroid. In both species the choroid comprises three layers (Figures 5, 6). Firstly, a heavily pigmented stratum (sclerad), which lies next to the sclera; secondly, a non-pigmented middle layer, containing the blood vessels and thirdly, a heavily pigmented inner layer, which in the insectivorous bat forms a smooth even layer. In the fruit bat (Figure 6), this inner surface possesses numerous small conical projections, called choroidal papillae, which extend into the retina. Long and short papillae occur and in the long papillae, choroidal capillary loops are present which extend into the retina to the inner nuclear layer. These loops contain a pair of blood vessels. The shorter papillae penetrate only to the outer limiting membrane and contain no blood vessels. The height of the papillae decreases towards the periphery of the ocular, and their shape changes, so that the tip of each papilla is always directed to the nodal point of the dioptric apparatus (Figure 7).

Separating the choroid from the pigment epithelium (Figure 6) in the fruit bat is the thin Bruch's membrane, which can not be seen in the insectivorous bat. The pigment epithelium, which is a single layer of cuboidal cells, is devoid of pigment in the fruit bat and poorly pigmented in the insectivorous bat. The inner surface of each cell has long thin processes, that loosely surround

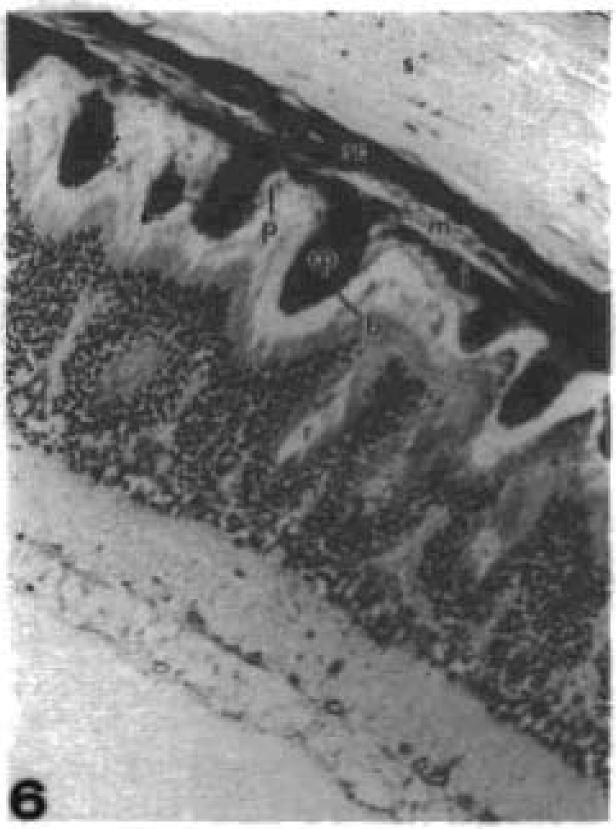


**Figure 6** Section (3 μm) of the fruit bat eye, showing the different choroidal layers and the retina. s — sclera; sc — sclerad; m — middle layer; i — inner layer; ch — choroidal papilla; r — retina; b — Bruch's membrane; p — pigment epithelium. ×230.

the surface of the photoreceptor's outer segment.

In the fruit bat the retina closely follows the contours

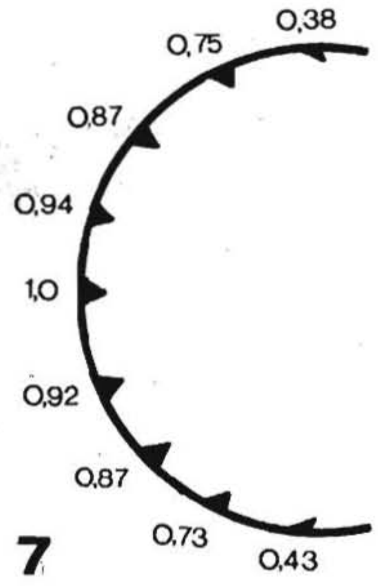


**Figure 7** Diagram illustrating the orientation and shape of the choroidal papillae. The numbers indicate the ratios of the outer and inner sides of the choroidal papillae (modified after Neuweiler 1962).

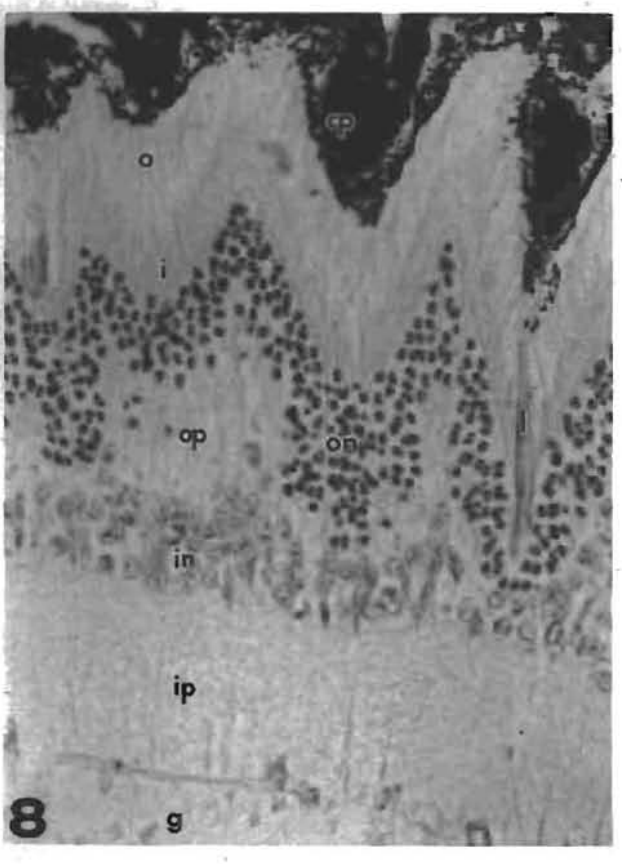


**Figure 8** Section (5 μm) of the fruit bat retina, showing the seven retinal layers. ch — choroidal papilla; l — capillary loop; o — outer segment; i — inner segment; on — outer nuclear layer; in — inner nuclear layer; op — outer plexiform layer; ip — inner plexiform layer; g — ganglion cell layer. ×490.

of the choroidal papillae and is thus highly folded (Figure 8). The retina, which thickens from the ora serrata towards the fundus, consists of seven layers, each

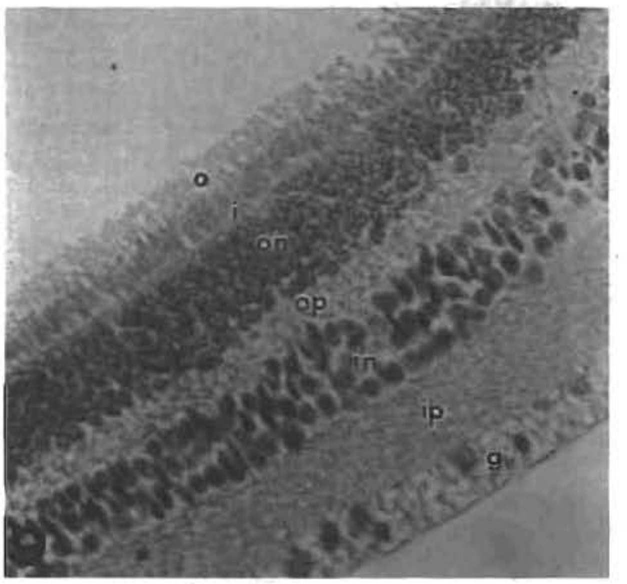


**Figure 9** Section (3 μm) of the insectivorous bat retina, showing the different retinal layers. o — outer segment; i — inner segment; on — outer nuclear layer; in — inner nuclear layer; op — outer plexiform layer; ip — inner plexiform layer; g — ganglion cell layer. ×490.

varying in thickness, and which are thickest in the depression of the folds. These layers are firstly, the outer segment, consisting of uniformly shaped receptors that are in loose contact with the processes arising from the inner surface of the pigment epithelium. This layer consists of rods only. Secondly, the inner segment, in which the photoreceptors are more tightly packed. Thirdly, the outer nuclear layer, which is separated from the inner segment by the outer limiting membrane. It contains the nuclei of the rods, which are most concentrated in the depressions of the layer. The rod axes are orientated parallel to the axes of the choroidal papillae, and are therefore also directed towards the nodal point. The outer nuclear layer is the thickest layer in the retina. Fourthly, the outer plexiform layer in which the visual cells synapse with horizontal and bipolar cells from the inner nuclear layer. This layer is not continuous, being confined to the depressions of the outer nuclear layer. Fifthly, the inner nuclear layer which is continuous and is thickest in the depressions of the outer nuclear layer. The inner surface of the layer is smooth since it evens out the irregularities of the papillae. This layer consists of horizontal, bipolar and Mueller's cells. Sixthly, the inner plexiform layer which is not folded and consists of synapses between processes of bipolar, horizontal, Mueller's and ganglion cells. And finally, the ganglion cell layer which is a continuous, non-folded layer consisting of ganglion cells, which have large cell bodies. These ganglion cells are less frequent than the cells in the inner nuclear layer. This layer terminates with the inner limiting membrane. The retina of the fruit bat is thinner than that of the insectivorous bat, the retinal thickness to eye axial length ratios being 1:21 and 1:9 respectively (Table 1). The insectivorous bat retina possesses the same layers as the fruit bat retina (Figure 9), but the layers are all continuous and not folded. As in the fruit bat, the insectivorous bat retina possesses only rods. Owing to the absence of choroidal papillae no blood vessels penetrate into the retinal layers. The eye of *R. aegyptiacus* possesses a tapetum lucidum, indicated by a faint red eyeshine observed while collecting the specimens. We were unable to find any histological evidence for this tapetum. There is no tapetum lucidum in *R. capensis*.

## Discussion

Although the fruit bat and insectivorous bat differ in their use of vision at night, both possess eyes with characteristic features of a nocturnal mammal: the cornea shows a marked curvature and occupies about one third of the globe (Detweiler 1939); the anterior and posterior chambers are very large in relation to the vitreous, resulting from the development of the large cornea with its extreme curvature (Detweiler 1939); the retina possesses only rods, which occur at a great density and enable the bats to see very well at night or dusk, but allow limited vision during the day (Feldman & Phillips 1984); no fovea is present, which implies unclear vision (Neuweiler 1962); the lens is very large and therefore the distance between the lens and the retina is short, giving the dioptric apparatus a high refractive power (Neuweiler 1962). The latter facilitates sharp vision and probably compensates for the absence of a fovea.

However the fruit bat, being highly dependent on well developed nocturnal vision, shows a significant difference in the structure of the choroid and the retina, which is probably responsible for the bat's excellent visual acuity. The choroidal papillae project from the inner choroid layer, and are all directed towards the nodal point of the dioptric apparatus. In this way, light coming in from an angle onto the papillae produces no shadow on the retina, which would otherwise result in the formation of an incomplete image. Capillary loops, present in these choroidal papillae, transport blood from the middle layer of the choroid to the inner retinal layers, which are avascular. By contrast, in the insectivorous bat eye, which does not possess these papillae, the supply of oxygen and nutrients relies on diffusion from the choroid to the retina. The efficient nutrient and oxygen supply, resulting from the occurrence of choroidal papillae probably facilitates better vision (Fritsch 1911; Kolmer 1924; Neuweiler 1962; Pedler & Tilly 1969; Suthers 1970a). Furthermore, the folding of the retina owing to these papillae increases its surface area and consequently a greater number of photoreceptors can be accommodated (Hill & Smith 1984). The outer segments of the retina all lie in a direction approximately parallel to the long axis of the papillae, which are orientated towards the nodal point. Thus it appears that most outer segments could be involved in the reception of light (Pedler & Tilly 1969), which could be important in enhancing vision in the fruit bat.

It has been suggested that the choroidal papillae provide a variable focal distance which would compensate for the absence of dioptric accommodation (Duke-Elder 1958). However, the difference in the posterior focal distance of rods at the apex and at the base of a papilla is about 1% (Neuweiler 1962) and this is probably too small to influence the vision in the fruit bat. Instead, Neuweiler (1962) suggested that the different height of the choroidal papillae changes the normally constant speed of an image passing over the retina. Although this change is small (Neuweiler 1962), it may aid in the detection of slow motion, since changes in the rate of motion may be expected to be more easily detected than slow constant motions.

The relatively larger eye of the fruit bat (1:20 as compared to 1:52 in the insectivorous bat) will result in an increased surface area of the retina, which will allow more rods to be accommodated and thus facilitate nocturnal vision. The small differences in relative thickness of the retina and cornea are unlikely to be significant in modifying visual acuity.

All results obtained were in concordance with those of other workers (Kolmer 1909; Fritsch 1911; Neuweiler 1962; Suthers 1970a), except for Pedler & Tilly (1969) who found cone receptor cells in the retina of *Pteropus giganteus* Bruennich. Using the electron microscope to study the pigment epithelium of a fruit bat eye, Pedler & Tilly (1969) revealed cells in the superior portion of the fundus, containing numerous refractile, spherical bodies with occasional pigment granules. These bodies tended to be absent from cells nearest the tip of the choroidal papilla. It is believed that these spherical bodies are responsible for the faint eyeshine in fruit bats and thus constitute a retinal tapetum. This tapetum lucidum increases the visual sensitivity by reflecting more light onto the retina (Fenton 1983). In the present study, although a tapetum lucidum is present, these refractile bodies were not detected, probably owing to examination with the light microscope only.

In conclusion, the choroidal papillae in the fruit bat provide firstly, a very effective route for nutrient and oxygen supply to the inner retinal layers, and secondly, increase the retinal surface to accommodate more photoreceptors which can be involved in light reception, hence providing an excellent nocturnal vision. Furthermore the presence of a tapetum lucidum in the fruit bat increases the visual sensitivity by reflecting more light onto the retina.

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