

Relative brain size and morphology of some South African bats

R.T.F. Bernard*, J. Paton and K. Sheppey**

Department of Zoology and Entomology, Rhodes University, Grahamstown, 6140 Republic of South Africa

Received 3 April 1987; accepted 13 August 1987

Measures of relative brain size and brain macromorphology are described for four species of Microchiroptera, two from the Vespertilionidae and two from the Rhinolophidae, and two species from the Pteropodidae (Megachiroptera). Four brain parameters (brain length, hemisphere length, brain width and brain height) were measured, and converted to indices of proportion to allow interspecific comparison. The megachiropteran species have relatively larger brains than the microchiropteran species, this being primarily a result of the greater development of the cerebral hemispheres in the former group. Of the microchiropteran species, *Miniopterus schreibersii* has the highest value for comparative brain size and its brain shows several characteristics of the more encephalized Megachiroptera such as reduced exposure of the mesencephalic tectum, and the presence of prominent cerebral sulci. The possibility that the differences in brain size and development between the Megachiroptera and the Microchiroptera, may be related to diet, or that they may be of phylogenetic origin, is discussed.

Relatiewe breingrootte en brein-makromorfologie word beskryf vir vier spesies van die Vespertilionidae en Rhinolophidae (Microchiroptera) en twee spesies van die Pteropodidae (Megachiroptera). Vier breinparameters (breinlengte, hemisfeerlengte, breinbreedte, en breinhoogte) is gemeet en omgesit na indekse van eweredigheid om interspesifieke vergelyking toe te laat. Die Megachiroptera-spesies het relatief groter breine as die Microchiroptera-spesies, wat primêr te wyte is aan die groter ontwikkeling van die serebrale hemisfeer van die eerste groep. Van die Microchiroptera-spesies het *Miniopterus schreibersii* die hoogste waarde vir relatiewe breingrootte en sy brein wys verskeie kenmerke van die meer ontwikkelde brein van die Megachiroptera soos verminderde ontbloting van die mesenteriese tektum en die teenwoordigheid van prominente serebrale sulci. Die moontlikheid dat die verskille in breingrootte en -ontwikkeling tussen die Megachiroptera en Microchiroptera verwant mag wees aan dieet, of dat hulle van genetiese oorsprong mag wees, word bespreek.

*To whom correspondence should be addressed

**Present address: Mammal Research Institute, University of Pretoria, Pretoria, 0002 Republic of South Africa

Studies of relative brain size (encephalization) have highlighted the variation in brain size that occurs among mammalian species, and have attempted to correlate differences in brain size with aspects of behaviour, ecology, life history strategies, and taxonomy (Bauchot & Stephan 1966; Jerison 1973; Sacher & Stafeldt 1974; Eisenberg & Wilson 1978; Clutton-Brock & Harvey 1980; Eisenberg & Wilson 1981; Mace, Harvey & Clutton-Brock 1981; Sheppey & Bernard 1985; Gittleman 1986). It has been suggested recently that since the interspecific scaling of the standard brain-body mass relationship approximates a three quarters exponent (Hofman 1982,1983), brain size may be more closely related to basal metabolic rate than ecological factors (Hofman 1983; Bennet & Harvey 1985).

Basic macromorphology and relative brain size of the Chiroptera have been studied in Australia, Europe, Africa, North and South America and Asia where differences in brain size have been correlated to feeding strategies and associated flight characteristics (Henson 1970; Pirlot & Stephan 1970; Stephan & Pirlot 1970; Stephan, Pirlot & Schneider 1974; Pirlot & Pottier 1977; Eisenberg & Wilson 1978; Stephan & Nelson 1981; see Findley & Wilson 1982 for review). However, no similar study has been carried out on the bats of South Africa.

In this paper we examine and compare the relative brain size and certain morphological measurements of the brains of six species of Chiroptera from South Africa.

Materials and Methods

The species used in this study and associated basic measurements are summarized in Table 1. The single specimen of *Epomophorus wahlbergi* came from the collection of the Albany Museum (Grahamstown) and all other specimens were collected from the eastern Cape province of South Africa (c. 33°S / 26°E) during 1985 and 1986.

Preparation of brains

Specimens were killed by asphyxiation with carbon dioxide and decapitated. Skin and excess flesh were immediately removed from the skull which was then fixed in a solution of 10% formalin for three days. The skulls were transferred to a solution of formal nitric acid (1% formalin in 0,5% nitric acid) and this solution was changed after two days. After a variable period of time the brain was carefully removed from the cranium and stored in 70% alcohol.

Comparison of linear measurements

The length of the brain (from olfactory bulb to the cerebellar uvular); the length of the cerebral hemispheres; the width of the cerebral hemispheres, which in these species is equal to the greatest width of the brain; and the height of the cerebral hemispheres (greatest height of the brain) (Figure 1) were measured using a stereo microscope and eye piece micrometer. To

Table 1 Summary of the species used in this study and their basic measurements

	N	$\bar{x} \pm 1SD$ Body mass (g)	$\bar{x} \pm 1SD$ Brain mass (g)	Indices of proportion					
				B.L.	Hem.L.	B.W.	B.H.	CBS	RBS
Suborder									
Megachiroptera									
Fam. Pteropodidae	2	114,37 ± 28,2	2,145 ± 0,1	194,5	128,5	131	93,5		+ 0,048
<i>Rousettus aegyptiacus</i>	6	134,3 ± 13,6	2,07 ± 0,2	198	120	124	90	- 0,072	
<i>Epomophorus wahlbergi</i>	1	94,44	2,22	191	137	138	97	+ 0,060	
Suborder									
Microchiroptera									
Fam. Vespertilionidae	2	12,50 ± 1,6	0,257 ± 0,004	155	83	120,5	91		- 0,103
<i>Miniopterus schreibersii</i>	5	11,4 ± 0,2	0,254 ± 0,016	158	80	120	95	+ 0,082	
<i>Myotis tricolor</i>	6	13,6 ± 0,7	0,259 ± 0,03	153	86	121	87	+ 0,045	
Fam. Rhinolophidae	2	16,45 ± 5,2	0,249 ± 0,01	181	91,5	117,5	83,5		- 0,211
<i>Rhinolophus clivovus</i>	5	20,1 ± 0,5	0,242 ± 0,03	177	88	114	82	- 0,199	
<i>Rhinolophus capensis</i>	7	12,8 ± 0,6	0,256 ± 0,01	185	95	121	85	- 0,058	
<i>Rhinolophus</i> spp.	2	16,45 ± 5,2	0,249 ± 0,01	181	91,5	117,5	83,5	- 0,135	

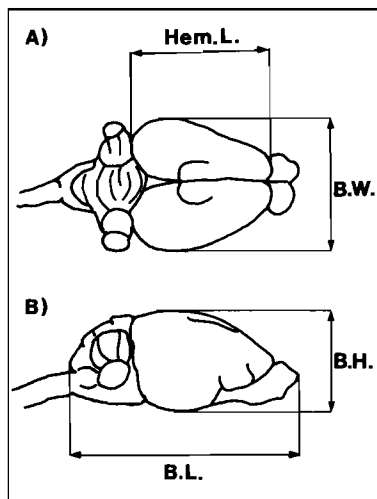


Figure 1 Dorsal (A) and lateral (B) views of the brain of *R. aegyptiacus*. The four parameters that were measured were length of the cerebral hemispheres (Hem.L.), brain width (B.W.), brain height (B.H.), and brain length (B.L.).

allow the comparison of measurements from brains of different shapes, all the linear measurements were divided by the cube root of the brain volume and multiplied by 100 to give indices of proportion (Stephan & Nelson 1981). An index of 150 means that the measurement is 1,5 times the length of a cube having the same volume as the brain.

Comparison of brain size (encephalization)

For each specimen, body mass was measured to the nearest 0,5 g, and brain mass was measured to the nearest 0,001 g. Because of the allometric relationship between brain mass and body mass, it is necessary to remove body size effects before comparing the brain size from species of differing body mass. This is done by comparing the observed brain size with an expected

value for an animal of the same body mass. The expected brain size is generated using the formula:

$$\log_{10}(\text{expected brain mass}) = \log_{10}(a) + b \log_{10}(\text{body mass})$$

where *a* is the intercept and *b* the slope of the regression of brain mass on body mass.

In the past a slope calculated from one set of data was used as the basis for calculating relative brain size in other groups of animals (Jerison 1973; Stephan & Nelson 1981). The problem with this approach is that the slope calculated for one taxonomic level will differ from the slope for a lower or higher taxon (Mace *et al.* 1981). Typically slopes increase with ascending taxonomic level (Martin & Harvey 1985). The current trend is to calculate a measure of relative brain size for one taxon based on a regression line for the next higher level (Clutton-Brock & Harvey 1980; Mace *et al.* 1981; Gittleman 1986).

We have adopted the methodology of Clutton-Brock & Harvey (1980), and in this study two measures of relative brain size have been used. At the generic level, Comparative Brain Size (CBS), defined as the mean deviation for members of a genus from their own family regression, has been used.

CBS for a given genus = $\log_{10}(\text{observed mean brain mass}) - (\text{elevation for family} + \text{slope for family} \times \log_{10}(\text{mean body mass}))$ (Clutton-Brock & Harvey 1980).

In the present study, with the exception of the genus *Rhinolophus*, there is a single species per genus and as such, CBS values can be regarded as species values. To correct this imbalance we have calculated both separate CBS values for the two rhinolophid species, and a single value for the genus.

At the family level, Relative Brain Size (RBS), defined as the mean deviation for members of a family from the regression line for the Order Chiroptera, has been used.

RBS for a particular family = \log_{10} (observed mean brain mass) – (elevation for order + slope for order $\times \log_{10}$ (mean body mass)) (Clutton-Brock & Harvey 1980).

The values for observed mean brain and body mass used in the calculations of CBS and RBS (Table 1) are arithmetic means of observed values for the constituent species when calculating CBS, and for the constituent genera, when calculating RBS.

The small number of genera used in this study made it impossible to produce statistically significant regression lines for the three families and the order, and therefore the regressions from Eisenberg & Wilson (1978) have been used (Table 2; Figure 5).

Comparison of brain macromorphology

The following characteristics, selected by Stephan & Nelson (1981) as being related to grade of brain development, have been examined: exposure of the mesencephalic tectum (roof of the mid-brain); development of sulci (grooves) in the cerebrum; and development of fissures (fine grooves) in the cerebellum. In mammals, the mesencephalic tectum is fully exposed in poorly developed brains but is covered, primarily by a caudal extension of the cerebral hemispheres, in more highly developed brains. The occurrence of prominent sulci and fissures is associated with a higher level of brain development.

Results

Comparison of indices of proportion

Indices of proportion for the six species are given in Table 1, and the indices of proportion for the three families (means of indices of proportion of the constituent species) are illustrated in Figure 2.

The brains of the Pteropodidae have the greatest indices of proportion for all four parameters (Table 1; Figure 2). Significantly, it is in the Pteropodidae only that the index of proportion for hemisphere length is greater than 100. When hemisphere length is compared to brain length (hem L / BL \times 100) the Pteropodidae have the highest value (66) the microchiropteran families lower values (Vespertilionidae, 53; Rhinolophidae, 50). Within the Pteropodidae the indices of proportion for hemisphere length and brain width are noticeably

Table 2 Slopes and intercepts of the regressions of brain mass on body mass for the order Chiroptera and the three families used in this study (from Eisenberg & Wilson 1978)

Taxon	slope (a)	intercept (\log_{10} b)
Chiroptera	0,802	- 1,368
Pteropodidae	0,661	- 1,0186
Vespertilionidae	0,589	- 1,300
Rhinolophidae	0,597	- 1,195

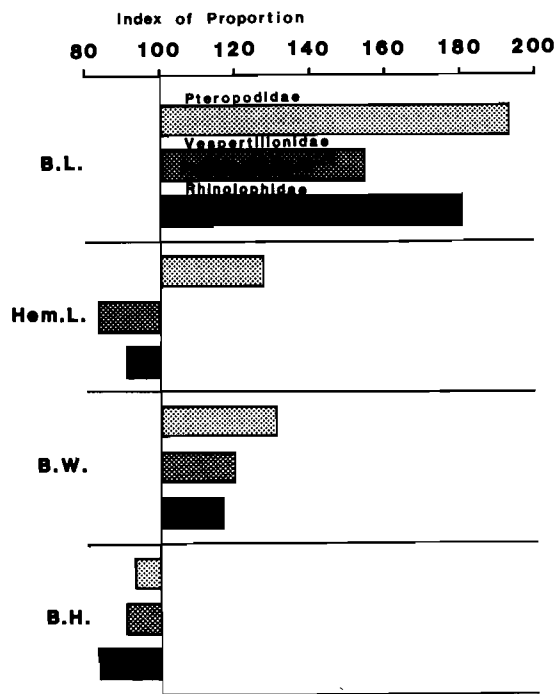


Figure 2 Indices of proportion for the families Pteropodidae (stippled), Rhinolophidae (solid black), and Vespertilionidae (cross-hatched). An index of 100 indicates that the measurement is equal to the length of the edge of a cube having the same volume as the brain.

greater in *E. wahlbergi* than in *R. aegyptiacus*, while the indices of proportion for brain height and brain length are similar (Table 1).

The brains of the Rhinolophidae have similar indices of proportion for total length, width and height to those of the Pteropodidae, the major difference being in the index of proportion for hemisphere length which is below 100 (Figure 2). The brains of the two rhinolophid species have similar indices of proportion, although those for the smaller species (*R. capensis*) are greater than those for *R. clivus* (Table 1).

The brains of the Vespertilionidae have the lowest index of proportion for brain length and hemisphere length, although the width and height are intermediate between those of the Pteropodidae and Rhinolophidae (Figure 2). The two vespertilionid species have similar indices of proportion for all four parameters, with *M. schreibersii* having greater values for brain length and height, and *M. tricolor* greater values for hemisphere length and brain width (Table 1).

As a group, the six species examined show relatively little variation in indices of proportion for brain height (82 – 97) and brain width (114 – 138), and much greater variation in brain length (153 – 198), and hemisphere length (80 – 137) (Table 1, Figure 2).

Comparison of macromorphological detail

Exposure of the mesencephalic tectum. The mesencephalic tectum comprises two pairs of lobes, the rostral and caudal colliculi. In the two members of the genus *Rhinolophus*, and *Myotis tricolor*, both lobes are

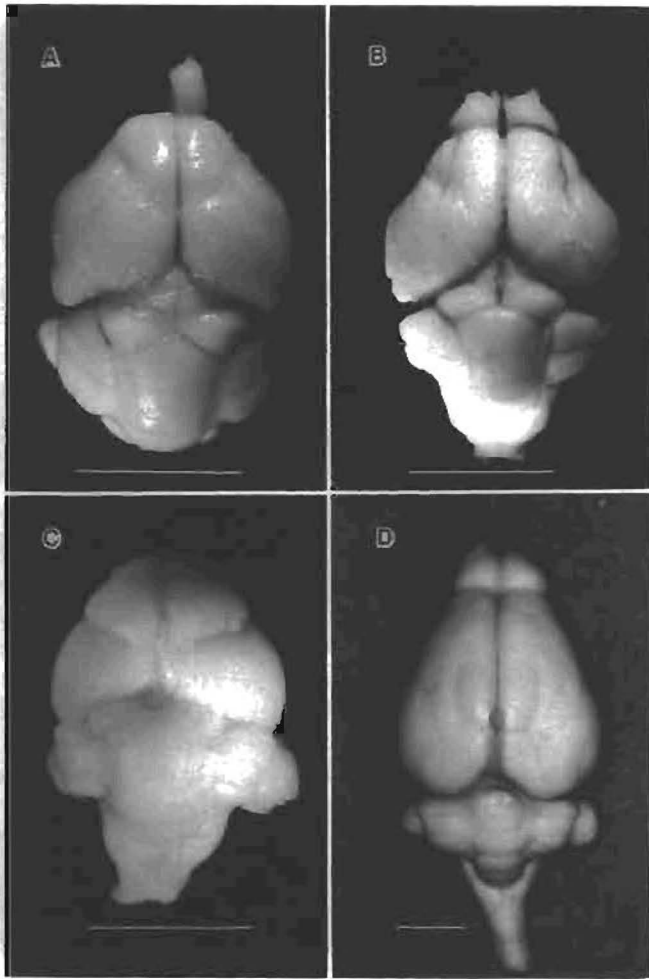


Figure 3 Light micrographs of dorsal views of the brains of *R. capensis* (A), *M. tricolor* (B), *M. schreibersii* (C), and *R. aegyptiacus* (D) showing some of the differences between the species. Scale bar = 5 mm.

fully exposed (Figures 3A,B 4A,B). However, in *Miniopterus schreibersii* the mesencephalic tectum is partly covered by a rostral extension of the cerebellar vermis (Figures 3C, 4C). In the Pteropodidae the mesencephalic tectum is completely covered by the cerebral hemispheres and the cerebellum (Figures 3D, 4D).

Cerebral sulci. These grooves in the surface of the cerebral hemispheres occur laterally, between the frontal and lateral lobes, and dorsally, running parallel to the interhemispheric fissure. *Miniopterus schreibersii* has a pronounced lateral sulcus between the frontal and lateral lobes (Figures 3C, 4C). Single lateral sulci are just discernible in the rhinolophids and *M. tricolor* and absent from the Pteropodidae (Figures 3, 4). A dorsal sulcus is present in the Pteropodidae (Figures 3D, 4D) but absent from the other species.

Cerebellar fissuration. The cerebellum of the Pteropodidae has the greatest number of fissures with the vermis having about seven, and the cerebellar hemispheres (lateral outgrowths of the cerebellum) about three. The rhinolophid species have four fissures

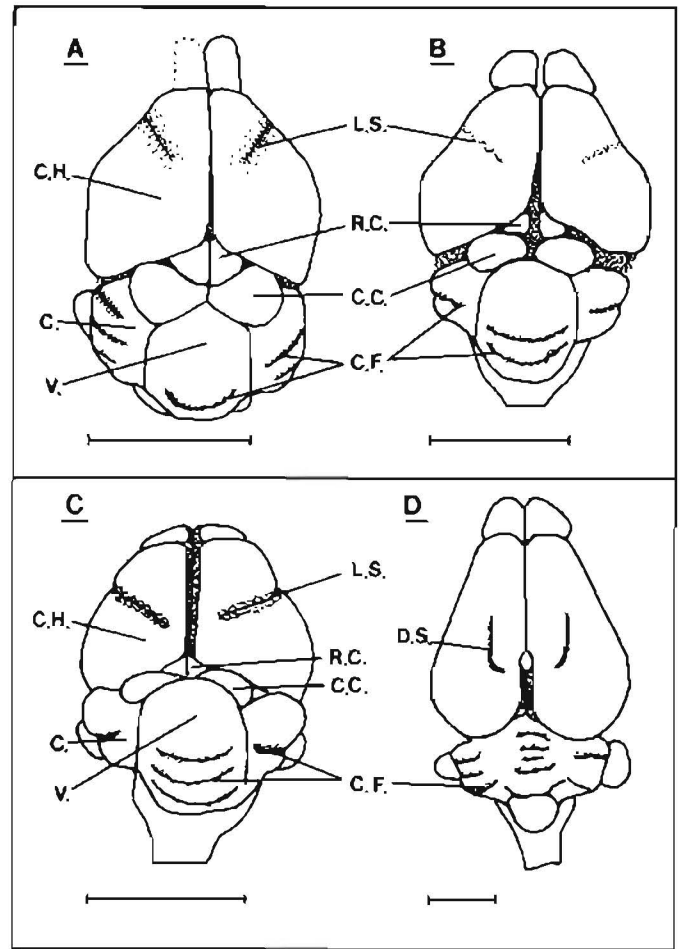


Figure 4 Diagrammatic representations of dorsal views of the brains of *R. capensis* (A), *M. tricolor* (B), *M. schreibersii* (C), and *R. aegyptiacus* (D) highlighting the differences in morphology that are discussed in the text. Scale bar = 5 mm. C = cerebellum; C.C. = caudal colliculi; C.F. = cerebellar fissures; C.H. = cerebral hemispheres; D.S. = dorsal sulci; L.S. = lateral sulci; R.C. = rostral colliculi; V. = vermis.

on the vermis and three on the hemispheres, and the vespertilionids, three on the vermis and two on the hemispheres.

Comparison of brain size

Log₁₀ brain mass has been plotted against log₁₀ body mass for all the specimens used in this study in Figure 5.

Comparative Brain Size (CBS) (Figure 6). Since CBS is calculated from separate family regressions, the values obtained can be used to compare members of the same family only. Within the Pteropodidae the CBS of *Epomophorus* is greater than that of *Rousettus* and the brain of *Rousettus* is smaller than predicted from the family regression (CBS value below zero). Both members of the Vespertilionidae have brains larger than predicted, and the CBS of *Miniopterus* is greater than that for *Myotis*. The CBS for the genus *Rhinolophus* is negative, indicating a brain size smaller than predicted and the CBS for *Rhinolophus clivosus* is lower than that of *R. capensis*.

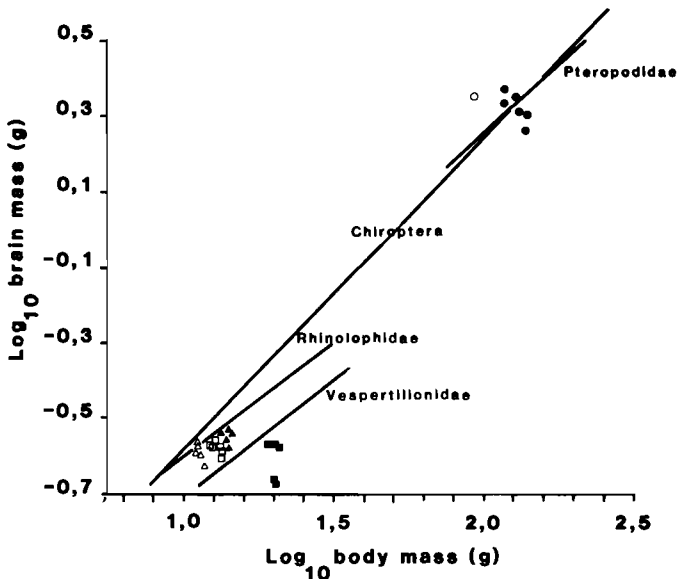


Figure 5 Plot of log brain mass against log body mass for all the specimens used in this study. (○) *E. wahlbergi*, (●) *R. aegyptiacus*, (■) *R. clivosus*, (□) *R. capensis*, (△) *M. schreibersii*, (▲) *M. tricolor*. Regression lines for the Pteropodidae, Rhinolophidae, Vespertilionidae and Chiroptera are based on the data of Eisenberg & Wilson (1978).

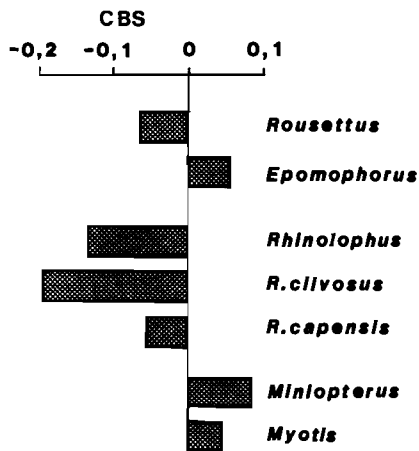


Figure 6 Comparative brain size (CBS) for the five genera of bats. Note that a CBS value of zero indicates that the observed brain size is equal to that predicted from the family regression. CBS values can be used to compare members of the same family only.

Relative Brain Size (RBS) (Figure 7). These values are calculated from a common chiropteran regression and the RBSs of the three families can be directly compared. The results indicate a trend in brain development from the Pteropodidae with the largest, positive RBS, through the Vespertilionidae (negative RBS), to the Rhinolophidae with the lowest, negative RBS.

Family characteristics

The Pteropodidae are characterized by the highest RBS, and the highest indices of proportion for all four brain

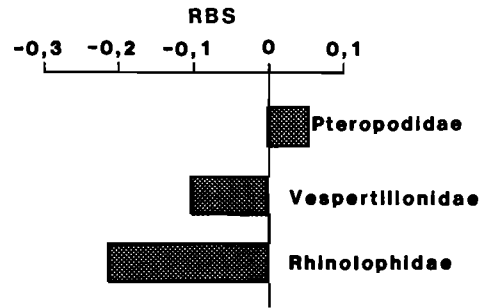


Figure 7 Relative brain size (RBS) for the three families examined in this study. RBS is calculated from the common regression for the Chiroptera and family values can be compared.

parameters. The mesencephalic tectum is completely covered, primarily by the caudal extension of the cerebral hemispheres, and the cerebellum and cerebral hemispheres have prominent sulci and fissures. The Vespertilionidae have a negative RBS that is intermediate between the Pteropodidae and Rhinolophidae, and are characterized by the lowest indices of proportion for brain length and hemisphere length. In *M. tricolor* the mesencephalic tectum is completely exposed, while in *M. schreibersii* it is partly covered. *Miniopterus schreibersii* has the most prominent cerebral sulci of all the species examined, and the Vespertilionidae have more cerebellar and cerebral sulci and fissures than the Rhinolophidae.

The Rhinolophidae have the lowest RBS, although the indices of proportion for brain and hemisphere lengths are greater than in the Vespertilionidae. Exposure of the mesencephalic tectum is always complete, and there are few cerebellar and cerebral sulci and fissures.

Feeding strategies and relative brain size

The six species used in this study represent two feeding strategies. The two pteropodid species are frugivores, and the four microchiropteran species are aerial insectivores.

Discussion

The results from this study indicate the occurrence of two levels of brain development. The first [equivalent to the A grade of development of Stephan & Nelson (1981)], is characterized by a low, negative RBS, complete exposure of the mesencephalic tectum, short and typically lissencephalic (smooth) cerebral hemispheres, and few cerebellar fissures. This group includes *M. schreibersii*, *M. tricolor*, *R. clivosus*, and *R. capensis*. Within this group *M. schreibersii* has the greatest degree of brain development and consequently has the highest CBS of the group. Stephan & Nelson (1981) reported a similar result for Australian Microchiroptera, where the brain size of the genus *Miniopterus* was the greatest of six vespertilionid species. The remaining members of this group, while having indices of proportion for brain and hemisphere

length that are similar to or greater than those of *M. schreibersii*, lack the characteristics of the more encephalized *Miniopterus* brain and consequently have lower CBS values.

The second level of development [equivalent to the C grade of Stephan & Nelson (1981)], includes the two pteropodid species. This level of development is characterized by relatively long cerebral hemispheres, the caudal extension of which is responsible for covering the mesencephalic tectum, more developed cerebellar and cerebral sulci and fissures, and high CBS and RBS values. The brain of *E. wahlbergi* is characterized by relatively larger cerebral hemispheres (as indicated by higher indices of proportion for hemisphere length and brain width) than *R. aegyptiacus* and it is presumably this development that is responsible for the former species having the higher CBS value.

The trend of increasing brain size and level of development from the insectivorous Rhinolophidae and Vespertilionidae to the frugivorous Pteropodidae has been reported by previous workers (Stephan & Pirlot 1970; Pirlot & Pottier 1977; Eisenberg & Wilson 1978; Stephan & Nelson 1981). However, Eisenberg & Wilson (1978) and Stephan & Nelson (1981) indicate that the Vespertilionidae have relatively smaller brains than the Rhinolophidae, while the opposite is the case in the present study. This reversal is probably a result of the small sample size (two species per family) in the present study, which has exaggerated the positive influence of the relatively well developed *Miniopterus* brain, and the negative influence of the poorly developed brain of *R. clivosus*.

Variation in chiropteran relative brain size has been related to feeding strategy and the results have shown that the aerial insectivores (Microchiroptera), in spite of their echolocation and highly manoeuvrable flight, have the smallest brains (A grade of development) while the frugivorous Pteropodidae (Megachiroptera) have the largest brains (C grade of development) (Henson 1970; Pirlot & Stephan 1970; Eisenberg & Wilson 1978; Stephan & Nelson 1981; present study). Intermediate between the two, but closer to the pteropodid level of development are the Microchiroptera that have evolved different feeding strategies such as the foliage gleaners, carnivores, frugivores and nectarivores (Eisenberg & Wilson 1978; Stephan & Nelson 1981).

At a macromorphological level, the most obvious difference between the C grade pteropodid brains and the A grade microchiropteran brains is the development of the cerebral hemispheres. It has been suggested that development of the cerebral hemispheres, and particularly the neocortex, is associated with the necessity for storage and retrieval of complex information involving input from several sense organs (Eisenberg & Wilson 1978). It is further suggested that the manipulation of such information would be required for locating food, such as fruit, that is unpredictable in temporal and spatial distribution (Eisenberg & Wilson 1978).

Differences such as those seen in the present study

between the Megachiroptera and Microchiroptera need not primarily be associated with differences in feeding strategy. The Chiroptera may be polyphyletic in origin with the Megachiroptera having evolved from a primitive primate and the Microchiroptera from a primitive insectivore (see Hill & Smith 1984 for review; Pettigrew 1986). If this is the case, then it is possible that the differences, as observed in the present study, are phylogenetic in origin. This type of argument could not, however, explain differences in the grade of brain development within the Microchiroptera.

In summary, within the group of bats examined in the present study, there is a range of relative brain size from small in the Rhinolophidae and Vespertilionidae, to large in the Pteropodidae. The relatively large brains of the Pteropodidae are primarily a result of development of the cerebral hemispheres, which may be associated with the type of information manipulation required by a frugivorous diet. If however, the Chiroptera are polyphyletic, then the differences between the Megachiroptera and the Microchiroptera may be of phyletic origin and not directly related to the present diet of the two groups.

Acknowledgements

We thank Robin Cross and Dale Ranchodd for technical assistance, Dr Alan Hodgson for commenting on a draft of the manuscript, the Albany Museum for loaning the specimen of *E. wahlbergi*, Dr J.D. Pettigrew for stimulating discussion, and Rhodes University for financial assistance. The comments of an unknown referee added substantially to the paper.

References

- BAUCHOT, R. & STEPHAN, H. 1966. Données nouvelles sur l'encephalisation des Insectivores et des Prosimiens. *Mammalia* 30: 160–196.
- BENNET, P.M. & HARVEY, P.H. 1985. Brain size, development and metabolism in birds and mammals. *J. Zool., Lond.* (A) 207: 491–509.
- CLUTTON-BROCK, T.H. & HARVEY, P.H. 1980. Primates, brains and ecology. *J. Zool., Lond.* 190: 309–323.
- EISENBERG, J.F. & WILSON, D.E. 1978. Relative brain size and feeding strategies in the Chiroptera. *Evolution* 32(4): 740–751.
- EISENBERG, J.F. & WILSON, D.E. 1981. Relative brain size and demographic strategies in didelphid marsupials. *Am. Nat.* 118: 1–15.
- FINDLEY, J.S. & WILSON, D.E. 1982. Ecological significance of chiropteran morphology. In: Ecology of bats (ed.) Kunz, T.H. Ch.6, Plenum Press, New York.
- GITTLEMAN, J.L. 1986. Carnivore brain size, behavioural ecology and phylogeny. *J. Mammal.* 67(1): 23–36.
- HENSON, O.W. 1970. The central nervous system. In: Biology of bats (ed.) Wimsatt, W.A., Vol.II, Ch.2, Academic Press, New York.
- HILL, J.E. & SMITH, J.D. 1984. Bats — A natural history. British Museum (Natural History), London.

- HOFMAN, M.A. 1982. Encephalization in mammals in relation to the size of the cerebral cortex. *Brain Behav. Evol.* 20: 84–96.
- HOFMAN, M.A. 1983. Energy metabolism, brain size and longevity in mammals. *Quart. Rev. Biol.* 58(4): 495–512.
- JERISON, H.J. 1973. Evolution of the brain and intelligence. Academic Press, New York.
- MACE, G.M., HARVEY, P.H. & CLUTTON-BROCK, T.H. 1981. Brain size and ecology in small mammals. *J. Zool., Lond.* 193: 333–354.
- MARTIN, R.D. & HARVEY, P.H. 1985. Brain size allometry: Ontogeny and phylogeny. In: *Size and scaling in primate biology.* (Ed.) Jungens, W.L., Ch.4, Plenum Press, New York.
- PETTIGREW, J.D. 1986. Flying primates? Megabats have the advanced pathway from eye to midbrain. *Science* 231: 1304–1306.
- PIRLOT, P. & POTTIER, J. 1977. Encephalization and quantitative brain composition in bats in relation to their life habits. *Rev. Can. Biol.* 36: 321–336.
- PIRLOT, P. & STEPHAN, H. 1970. Encephalization in Chiroptera. *Can. J. Zool.* 48: 433–444.
- SACHER, G.E. & STAFELDT, E.F. 1974. Relation of gestation time and brain weight of placental mammals: Implications for the theory of vertebrate growth. *Amer. Nat.* 5: 593–615.
- SHEPPEY, K. & BERNARD, R.T.F. 1985. Relative brain size in the mammalian carnivores of the Cape province of South Africa. *S. Afr. J. Zool.* 19: 305–308.
- STEPHAN, H. & NELSON, J.E. 1981. Brains of Australian Chiroptera I. Encephalization and Macromorphology. *Aust. J. Zool.* 29: 653–670.
- STEPHAN, H. & PIRLOT, P. 1970. Volumetric comparisons of brain structures in bats. *Z. Zool. Syst. Evolutionsforsch.* 8: 200–236.
- STEPHAN, H., PIRLOT, P. & SCHNEIDER, R. 1974. Volumetric analysis of pteropodid brains. *Acta. Anat.* 87: 161–192.