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This volume is dedicated to Dr. Rainer Zangerl

The External Morphology of The Inner Ear In Bats From the Phosphorites of Quercy

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ABSTRACT

Camera lucida drawings of the cochlea and the fenestra cochleae of various species of a number of genera (*Pseudorhinolophus, Palaeophyllophora, Paraphyllophora, Vespertiliavus, Nycterobius,* and *Nyctinomus*) from the Phosphorites of Quercy have been measured and compared with measurements of the same structures in Recent chiropters. In each case other morphologic details have been noted.

The length of the cochlea was measured according to Gray, the width according to my own method. In the majority of chiropters, Recent and fossils, length and width of the cochlea is about equal, although the size of the cochlea differs. These facts let me assume that the shape of the cochlea in chiropters approaches the geometrical figure of an equiangular spiral.

In graphs, in which length against width of the fenestra cochleae have been used, representatives of the same species or closely related species are located in close proximity.

If two chiropter specimens show a marked difference in the dimensions and shape of the cochlea and the fenestra cochleae, they cannot belong to the same or to closely related species. However, they do belong to the same or closely related species if the dimensions are equal or nearly so.

INTRODUCTION

In the last century a number of authors (Pictet et al., 1885; Filhol, 1876; Schlosser, 1887-1889) studied fossil bats from the Quercy (Late Eocene-Middle Oligocene). Revilliod in this century, had a great amount of such material from the museums of Basel, Geneva, and Lausanne at his disposal. Among the specimens which he used were a number of complete skulls, a

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large number of mandibles, and other bony elements. He published the result of his research in three articles in the memoirs of the Swiss Palaeontological Society (Revilliod, 1917, 1920, 1922). None of the mentioned authors considered the auditory region, except Revilliod and he did it in a very superficial way. The Rhinolophidae are especially numerous in the Phosphorites of Quercy and are represented by the extinct genera *Pseudorhinolophus, Palaeophyllophora,* and *Paraphyllophora* and the extant genus *Rhinolophus,* of which the first two are the most frequent. Three other families appear first in the fossil record in the Quercy deposits. The Emballonuridae with the genus *Vespertiliavus;* the Vespertilionidae with the genus *Nycterobius* and the Molossidae with *Nyctinomus.*

ANATOMICAL REMARKS

The cochlea in chiropters varies greatly in shape and size. The latter is not related to the weight of the bat (Pye, A. 1967). Since in most microchiropters the cochlea is only loosely connected with the rest of the skull, it is often missing or dislocated in the prepared skulls of Recent and fossil bats. The number of well preserved fossil skulls suitable for my studies was therefore very limited. Preliminary investigations showed that specimens with the same or very similar dimensions and shape of the cochlea and the fenestra cochleae belong to the same or to a closely related species, and this is here investigated in greater detail.

The dimensions of the cochlea in microchiropters can be determined relatively easily since the cochlea is covered only by a thin layer of bone. Repeated measurements gave the interesting result that length and width of the cochlea in the majority of specimens are equal or close to equal; only occasionally is there a marked difference between them. D. W. Thompson (1966) refers to Descartes who in 1638 studied the growth of a shell. Thompson says (1966, p. 179): "The shell, like the creature within it, grows in size but does not change its shape; and the existence of this constant relativity of growth or constant similarities of form is of the essence, and may be made the basis of a definition of the equiangular spiral." As the shell grows in size during life, the geometric relationship of the spiral remains constant. The cochlea of the microchiropters is also a spiral and shows a great range of sizes between different species of the same genus. With few exceptions the length/width ratio is 1.0 or close to it. This suggests that also throughout the microchiropters the cochlea maintains a constant shape at least for adult stages.

The left cochlea of *Paraphyllophora robusta,* Basel Q.P. 1000 (fig. 4) is fortuitously broken and so positioned that the inside of the cochlea can be inspected from above and measurements taken.

Several radii drawn from the center of the modiolus apparently intersect the whorls of the cochlea at nearly the same angle. This angle is understood to be the angle between two straight lines, the radius vector and the tangent to the curve in the intersecting point. This seems to suggest that the cochlea in the majority of chiropters approaches an equiangular spiral.

It is of interest that, on one hand, the chiropter cochlea and, on the other, *Nautilus* should have forms based on spirals with similar geometric properties.

The fenestra ovalis (**f.o.**) of bats is in most instances oval shaped; in some taxa the width of the posterior half is wider than the anterior. Such a shape has also been observed in other orders. Since the variation in the dimensions and the shape of the f.o. in chiropters is rather limited and the f.o. in most fossils poorly defined, it was not used in this study.

In contrast to the f.o., the fenestra cochleae (**f.c.**) shows great variation in size and shape and therefore proves itself an important factor for this study. In a few specimens the inner and the outer rims of the opening of the f.c. differ slightly in their dimensions. In several species of chiropters a bony projection of variable size and shape is present. It originates very close to the posterior edge of the f.c. and extends superficially over part of the latter. This projection was never observed in fossil chiropters but is especially well developed in the Recent genus *Taphozous* (fig. 5E′). The edges of the f.c. may be very fragile and easily broken in the process of preparation. This can be deceptive and may lead to wrong observations and conclusions.

The canaliculus cochleae begins in the scala tympani and leads to the apertura canaliculi cochleae located medial and slightly posterior to the f.c. The apertura externa canaliculi shows variations in shape and size but proved itself difficult to prepare in Recent and still more so in fossil chiropters; it was therefore not used in this study.

METHODS

In fossil bats rarely is the middle ear preserved. In the species available to me for detailed study the middle ears were lost: inner ears alone were present. These museum specimens had to be kept intact, so that only the external morphology of the inner ear could be studied.

It is quite common to find isolated inner ears in collections. This is because in many chiropters they are only loosely connected with the rest of the skull. Generally, they are not used for research because their taxonomy has not been determined. Comparative morphological studies of the inner ear of known taxa may be helpful in the taxonomic identification of such specimens.

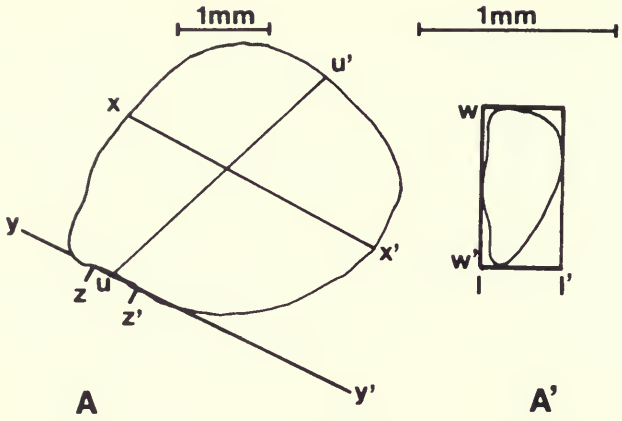


FIG. 1.A, Outline of the ventral aspect of the right cochlea in *Pseudorhinolophus*, Art 2, Schlosser: zz′ circumference of the basal part of the rim of the fenestra cochleae; uu′ length of the cochlea; yy′ vertical projection of zz′; xx′ width of the cochlea.
A′, Outline of the postero-lateral aspect of the right fenestra cochleae: ww′ width of the fenestra cochleae; ll′ length of the fenestra cochleae.

Camera lucida drawings of a representative series of cochleae were made and from them measurements taken and noted in tables in millimeters. For that purpose the skulls were oriented in such a way that the symmetry plane was vertical and the Frankfurter plane placed in a horizontal position, i.e. normal to the microscopic axis. I used Gray's (1907) method for measuring the length of the cochlea (**uu′**) that is the maximum dimension from the middle (**u**) of the ventral part of the circumference of the rim (**ZZ′**) of the f.c. to the extreme upper end of the cochlea (**u′**) (fig. 1A).

I measure the width of the cochlea (**xx′**) by first drawing a line (**yy′**) through the vertical projection of the line (ZZ′) of the f.c. and then the maximum width (**XX′**) of the cochlea parallel to (yy′) was determined. The measurement of the width of the cochlea proved to be more difficult than the measurements of the length and repeated measurements of the width gave slightly different results. Values used are averages of several measurements.

Differences in the dimensions of the cochlea and the fenestra cochleae between closely related specimens of the same genus may stem from human error in the classification of the taxon or defects due to the preparation of the specimen. Distortions due to the fossilisation process are considered to be minimal, since obviously distorted specimens were intentionally excluded from the study.

The materials used were inadequate to enable me to detect or demonstrate any sexual dimorphism.

The f.c. (fig. 1A′) is usually wider than long. When using a binocular microscope to view it, and because of the conformation of adjacent bony elements it is often more readily viewed if rotated approximately 90°. However, in the drawings of the f.c. length (**LL′**) and width (**WW′**) conform to the axis of the head and body.

Although the fenestra ovalis (f.o.) is not used in this study, some remarks about it are in place. In an earlier study in which length and width of the f.o. were given as a ratio (=stapedial ratio) marsupials and insectivores were compared. It was shown that most marsupials have a stapedial ratio between 1.1 and 2.1, while in insectivores the ratio varied from 1.8 to 3.0 (Segall, 1970). In both orders, Marsupialia and Insectivora, with specialization of the middle ear, the length of the f.o. increases while the width remains more static.

It was found that in Recent bats the ratio of the f.o. varies only between 1.5 and 1.8 with about 1.7 as the mean (Segall, 1971b). The chiropters take up a relatively small area, somewhat between the areas of the marsupials and the insectivores because of the minor variations of the angle of the ossicular functional axis with the Frankfurter horizontal and the small differences in the f.o. ratio (op. cit., fig. 2.), both of which are important factors in the transmission of the soundwaves from the eardrum to the inner ear. One may conclude from it that the middle ear in chiropters is generalized and static.

In contrast to the chiropters, gliding mammals, be they marsupials or rodents, have as specialized a middle ear as non-gliding members of the same family. The Dermoptera which have only one genus are all gliders with a specialized middle ear. There are no non-gliding members with which they can be compared. In all three groups the o.f.a. angle with the Frankfurter horizontal is small and the f.o. ratio is rather high (Segall, 1971a,b). These characteristics of the middle ear in gliding mammals provide a strong argument against the theory that gliding may have been a prestage to flying in the origin of bats.

As stated above in the great majority of Recent and fossil chiropters the l/w ratio of the cochlea is 1.0 or close to it, and therefore are not useful in this context. However, the l/w ratio of the f.c. varies greatly and thus these figures have been used in graphs.

HISTORY

The greatest number of fossil mammals from the Quercy belong to the family of the Hipposideridae. Schlosser (1887-1889) established the genus

MATERIAL

FOSSIL[1]

		Institution	*Catalogue*
		Montauban	uncatalogued 1 my reference
	schlosseri	München	1879 XV 10 C
Pseudorphinolophus		Basel	QP 874 QP 852
	cf. *schlosseri*	Montpellier	UM 5133
Palaeophyllophora	*oltina*	Basel	QP 784 QP 793
Paraphyllophora	*robusta*	Basel	QP 1000
	indeterm		8602
	bourguignati	Paris	8603 8604, 8605, 8606, 8608
		Lyon	8127
Vespertiliavus	*schlosseri*		
		Geneva	81018, 81020
	wingei	Montauban	uncatalogued 4 my reference
	gracilis	Montpellier	UM 5135
Nycterobius	*gracilis*	Basel	QP 632
Nyctinomus	*stehlini*	Basel	SG 6240

RECENT

All Recent specimens are taken from the mammal collection of the Field Museum of Natural History (FMNH) and are listed in the tables.

[1]Fossils are indicated in the graphs with *.

TABLE 1. Dimensions of the cochlea and the fenestra cochleae and the ratios (length/width) of the fenestra ovalis in four specimens of *Pseudorhinolophus*.

	Institution	Catalogue no.	Side	Cochlea length	Cochlea width	Fen. cochleae length	Fen. cochleae width	Fen. ovalis l/w
Ps. Art 2 of Schlosser	München	1879 XV 10C	r	3.25	3.25	0.4	0.9	1.7
Ps. schlosseri	Basel	Q.P. 852	r	2.5	2.3	0.4	0.64	1.7
			l	2.58	2.25	0.4	0.625	
Ps. schlosseri	Basel	Q.P. 274	l	2.5	2.5	0.4	0.6	
Ps. cf. *schlosseri*	Montauban	uncatalogued 1 my reference	l	2.91	2.916	0.32	0.6	1.7

Pseudorhinolophus and included within this genus *Rhinolophus antiquus* Filhol (1872) and *Vespertilio morloti* Pictet (1855). Revilliod (1917), who had much Quercy material at his disposal, was able to distinguish on the basis of the length of the dental structures two genera, *Pseudorhinolophus,* the most numerous among the Quercy mammals, and *Palaeophyllophora,* both belonging to the family Hipposideridae.

Pseudorhinolophus Schlosser (1888)

Revilliod established four species in the genus *Pseudorhinolophus: Ps. (Vespertilio) morloti* (Pictet); *Ps. schlosseri; Ps. weithoferi;* and *Ps. egerkingensis.* The genus exists in the Lutetien superior of Egerkingen and in the Bartonien-Ludien of Mormont (Dechasaux, 1958). Revilliod concluded that *Pseudorhinolophus* is a genus of the family Hipposideridae which became detached from the main trunk earlier than the genus *Hipposideros.* Some recent *Hipposideros* are similar to *Pseudorhinolophus,* others to *Brachipposideros* of a later age (Bouzigues). Sigé (1968) has recently included *Pseudorhinolophus* and *Brachipposideros* subgenera within the genus *Hipposideros* and he reports that *H. (Ps.) bouziguensis,* the most frequent mammal on the border of Oligocene and Miocene, is the last representative of the subgenus *Pseudorhinolophus.*

The *Ps.* skull (Art 2) pictured by Schlosser (1887-1889) has a cochlea of larger dimensions than that of one of the skulls of *Ps. schlosseri* (Q.U. 852)

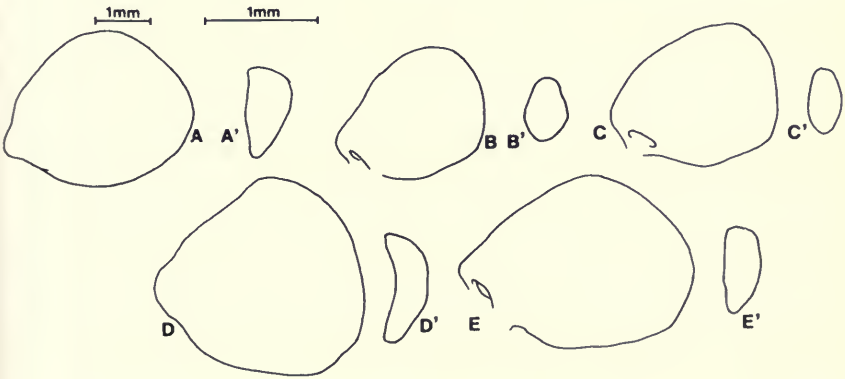
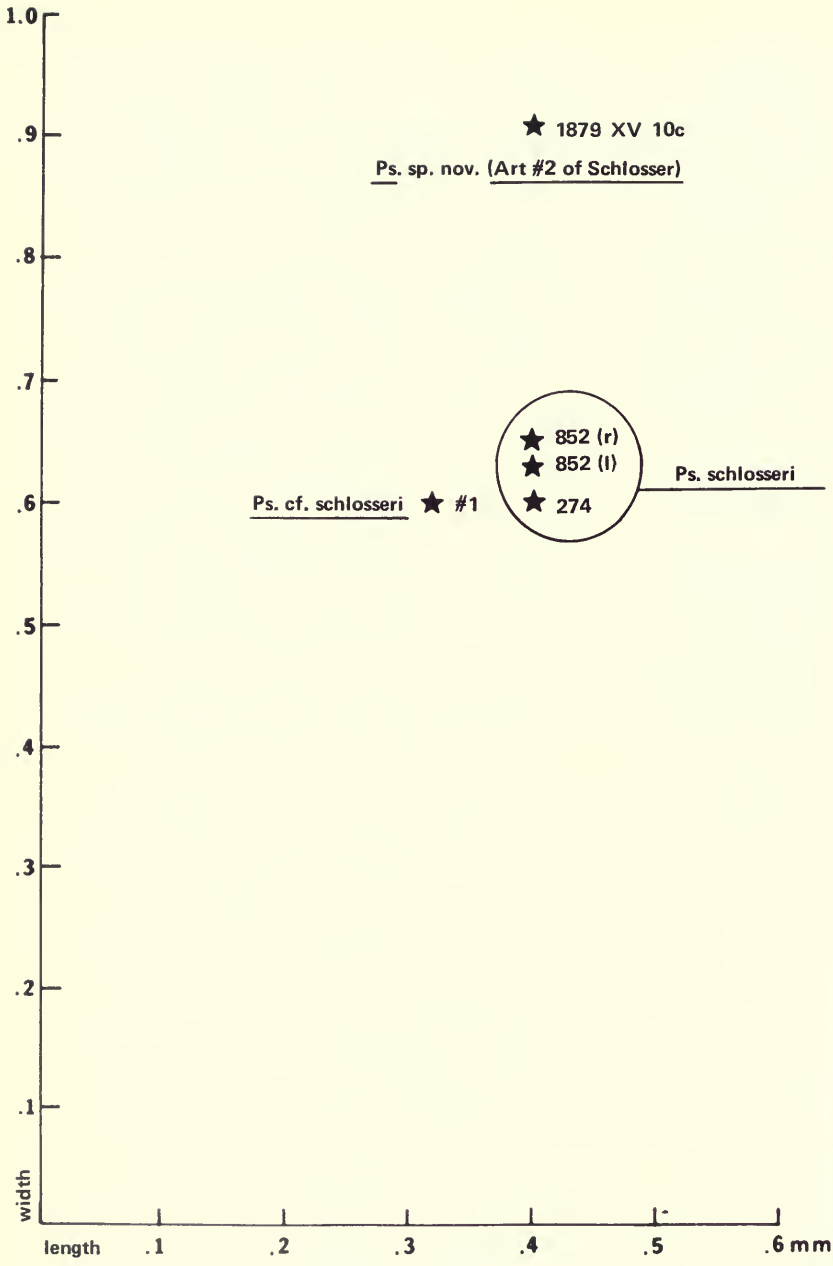


FIG. 2. Outline of the basal view of the cochlea and the postero-lateral aspect of the fenestra cochleae in **A** and **A'**, *Pseudorhinolophus,* Art 2 of Schlosser, München, 1879 XV 10c; **B** and **B'**, *Pseudorhinolophus schlosseri,* Revilliod 1917, Basel Q.P. 852; **C** and **C'**, *Pseudorhinolophus* cf. *schlosseri,* no. I my reference *Montauban;* **D** and **D'**, *Hipposideros commersoni* FMNH 95153; **E** and **E'**, *Hipposideros diadema griseus* FMNH 80367.



GRAPH 1. Length against width of the fenestra cochleae in several *Pseudorhinolophus* specimens.

TABLE 2. Available dimensions of the cochlea and the fenestra cochleae in some Recent *Hipposideros*.

		cochlea		*fenestra cochleae*	
	catalogue no. (FMNH)	*length*	*width*	*length*	*width*
Hipposideros commersoni	95153	4.0	4.0	0.44	1.0
H. commersoni	95152	4.0	4.0	0.44	1.0
H. commersoni merungensis	67928	3.75	3.75	0.56	0.92
H. diadema griseus	80367	3.75	3.7	0.24	0.68
H. diadema vicareus	76960	3.91	3.5	0.28	0.68
H. diadema	1118	3.75	3.75	0.28	0.68
H. armiger	39537	3.66	3.66	0.24	0.64
H. armiger	39540	3.58	3.58	0.2	0.6
H. caffer	104522			0.28	0.52
H. caffer	104532			0.28	0.52
H. caffer	104521	2.41	2.41	0.32	0.52
H. larvatus	82660	2.66	2.58	0.2	0.48
H. larvatus	32109	2.66	2.58	0.2	0.48
H. cineraceus	82706			0.16	0.28
H. cineraceus	32224			0.16	0.28
H. cervinus	31617	2.6	2.15	0.2	0.36
H. cervinus	31618	2.17	2.17	0.2	0.4

used by Revilliod (compare figs. 2A, B and table 1). The width of the f.c. in the Schlosser specimen (fig. 2A') is greater than in Revilliod's specimen (fig. 2B') but the length of the f.c. is equal in both.

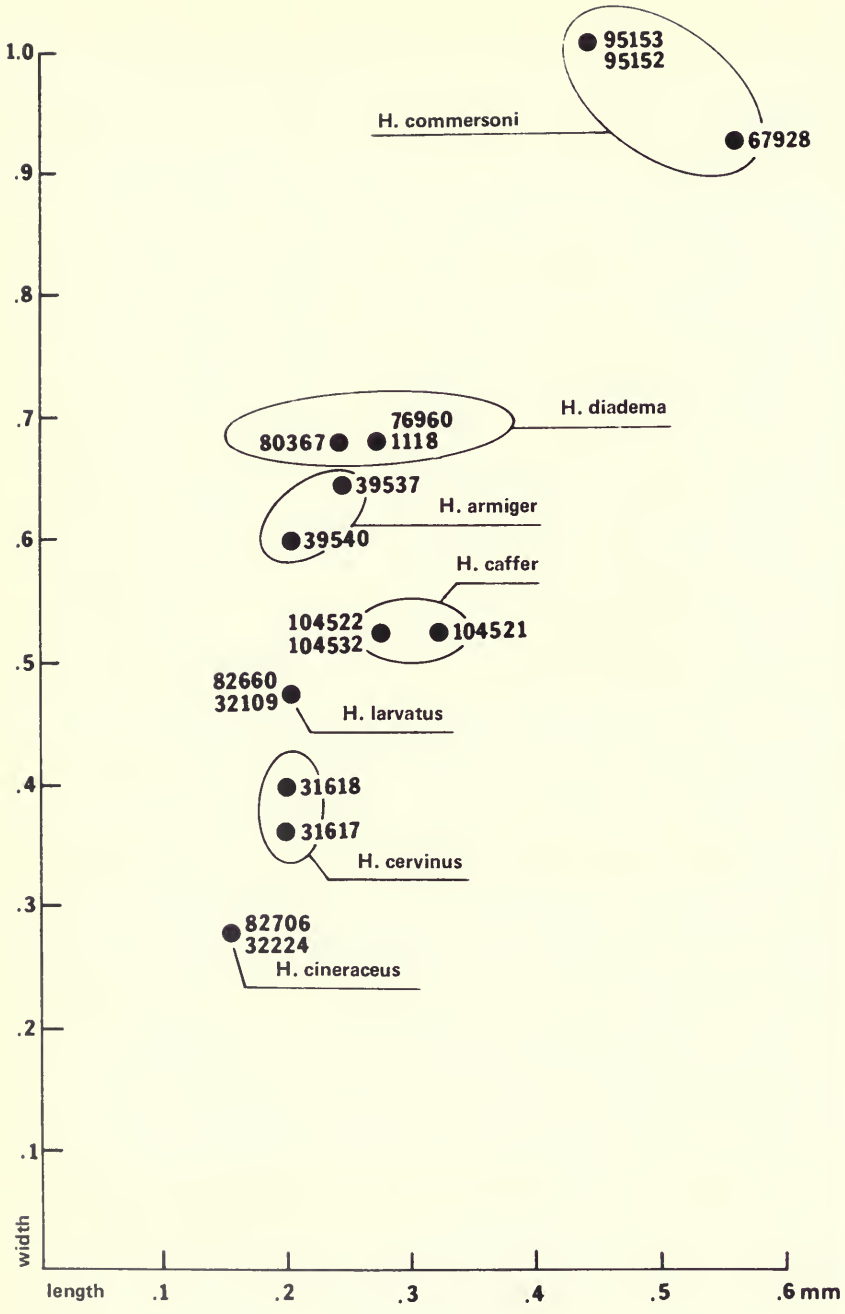
The *Ps.* cf. *schlosseri* from the Montauban collection (1 of my reference) has a cochlea of a size between Schlosser's and Revilliod's specimens.

Although there is a marked difference in the dimensions of the cochlea (c.) and f.c. between these three specimens there is no difference in the ratio of the f.o.; it is in all *Pseudorhinolophus* specimens studied 1.7. The small variations of the f.o. in chiropters has been pointed out already in a former paper (Segall, 1971b).

Revilliod found some similarities between *Pseudorhinolophus,* on one hand, and *Hipposideros commersoni* and *H. diadema,* on the other. The similarities resp. dissimilarities in the dimensions of the cochlea and the fenestra cochleae between these taxa are shown in Tables 1 and 2, Figure 2 and in the Graphs 1 and 2.

Palaeophyllophora Revilliod (1917)

This is the second genus which Revilliod (1917) established among the fossil Hipposideridae from the Quercy. It is known at least since the Bartonien-Ludien because one finds it in the Mormont which is of that age (Dechasaux, 1958). It does not exist after the Quercy and has no Recent



GRAPH 2. Length against width of the fenestra cochleae in several species of *Hipposideros*.

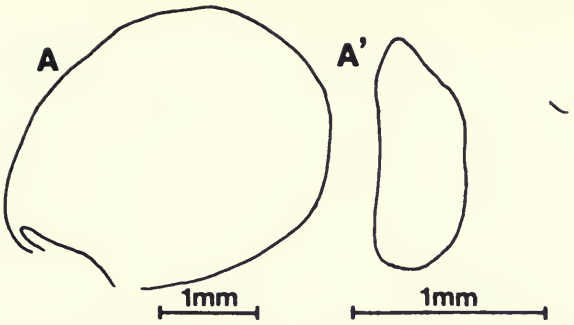


FIG. 3. Outline of A the basal view of the cochlea and A' the posterolateral view of the left fenestra cochleae in *Palaeophyllophora oltina,* Basel Q.P. 793.

representatives. Revilliod (1917) distinguished two species: *P. quercyi* and *P. St. Nebulae.* The latter was recognized (Revilliod, 1922) to be a synonym of *P. oltina* (Delfortrie). Two *P. oltina,* both from the Basel collection were available for my study (fig. 3).

The cochlea of *Pseudorhinolophus* used by Schlosser (table 1) is about the same size as that of *Palaeophyllophora oltina,* while *Pseudorhinolophus* used by Revilliod has a smaller cochlea. The width of the f.c. is smaller in *Ps. schlosseri* than in *P. oltina* while the length is about equal in both.

Paraphyllophora Revilliod (1922)

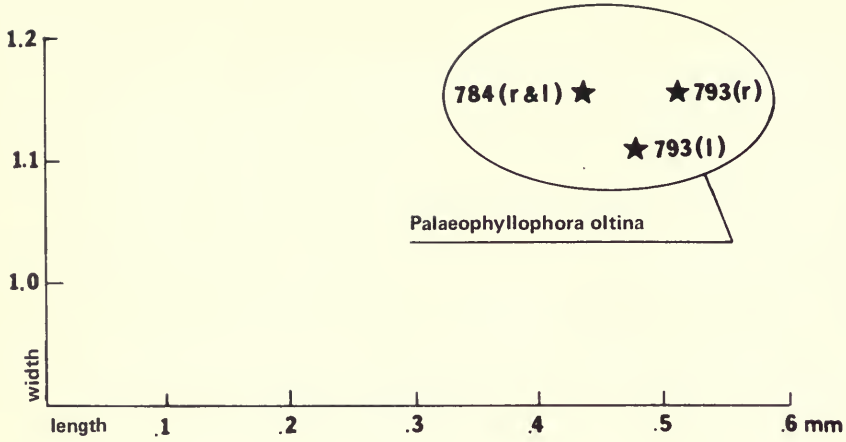
Revilliod (1922) established the genus *Paraphyllophora* and the species *P. robusta.* The left cochlea of this specimen from the Basel collection (Q.P. 1000) is clearly not *in situ;* the right appears to be *in situ* but is broken; therefore exact measurements can not be taken. Width and length are about 3.3 mm. (fig. 4).

Vespertiliavus Schlosser (1888)

Filhol (1876) had an incomplete upper jaw of a specimen which he called *Vespertilio bourguignati.* It differed from the then known genera

TABLE 3. Dimensions of the cochlea and the fenestra cochleae in two specimens of *Palaeophyllophora oltina.*

			cochlea		*fenestra cochleae*	
Catalogue no.	*Institution*	*side*	*length*	*width*	*length*	*width*
784	Basel	r	3.5	3.5	0.44	1.16
		l	3.5	3.5	0.44	1.16
793	Basel	r	3.41	3.41	0.52	1.16
		l	3.41	3.41	0.48	1.1



GRAPH 3. Length against width of the fenestra cochleae in two specimens of *Palaeophyllophora oltina.*

FIG 4. Photo of a basal view of both cochleae in *Paraphyllophora robusta,* Basel Q.P. 1000; Right cochlea *in situ,* approximately its basal half is broken off; left cochlea dislocated, its tip broken off.

from the Phosphorites at his disposal.

Schlosser (1888) who studied six lower jaws which also differed from the then known genera of the Phosphorites, assigned them to a new genus *Vespertiliavus.* He also included the Filhol specimen of *Vespertilio bourguignati* within his new genus. However, beyond *Ve. bourguignati* he did not name any of these specifically. Instead he indicated that to judge from their size differences they belong to four species, and he was not certain which, if any of them, were to be correlated with *Ve. bourguignati,* the genotype species. The new genus *Vespertiliavus* was primarily based on the dentition differences from *Vespertilio.*

According to Revilliod (1920), *Vespertiliavus* is a palaeontological precursor of the Emballonuridae which derive from a very primitive group; the Messel forms are representatives of this ancestral group (Russell and Sigé, 1970).

Revilliod accepted *Ve. bourguignati* (Filhol) and added to it the materials of Schlosser species 2. He also named three new species of the genus *Vespertiliavus: Ve. wingei, Ve. schlosseri,* and *Ve. gracilis.* All taxonomic arrangements were based on measurements of maxillae and mandibulae.

Four *Ve. bourguignati,* three *Ve. schlosseri,* one *Ve. gracilis,* one *Ve. wingei,* and one undetermined species were at my disposal (see fig. 5 and table 4).

TABLE 4. Dimensions of the cochlea and the fenestra cochleae in three species of *Vespertiliavus.*

				cochlea		*fenestra cochleae*	
species	*institution*	*catalogue no.*	*side*	*length*	*width*	*length*	*width*
Ve. sp. indetermined	Paris	8602	dext.	3.58	3.34	0.84	1.28
Ve. bourguignati	Paris	8603	sin.	3.4	3.75	0.64	1.04
Ve. bourguignati	Paris	8604	sin.	3.4	3.4	0.6	1.08
Ve. bourguignati	Paris	8605	sin.	3.4	3.4		
Ve. bourguignati	Paris	8606	sin.	3.41	3.41		
Ve. bourguignati	Paris	8608	sin	3.4	3.4	0.6	1.12
Ve. schlosseri	Geneva	81019	sin.	3.0	3.0	0.56	1.04
Ve. schlosseri	Geneva	81020	sin.	3.0	3.0	0.52	1.0
Ve. schlosseri	Lyon	8127	sin.	3.0	3.0	0.56	0.92
Ve. wingei	Montauban	uncatalogued 4 my reference	sin.	3.416			
Ve. gracilis	Montpellier	5135	dext.	2.91	2.85		

Table 4 shows similarity in the dimensions of the cochlea, slightly less in those of the f.c., between specimens of *Ve. bourguignati;* part of the

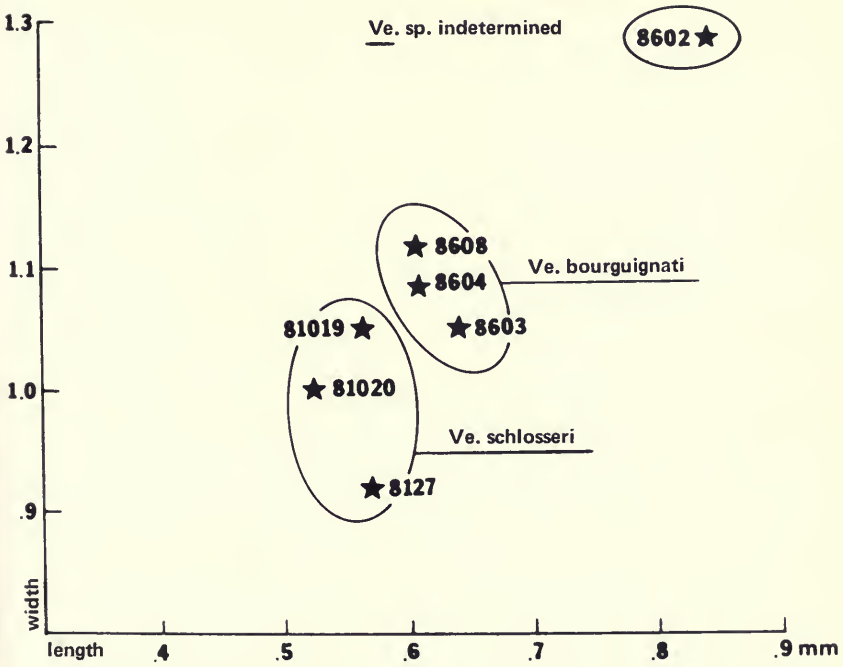
differences in the f.c. can be explained by small uncertainties in the measures.

The dimensions of the cochlea in *Ve. wingei* hardly differ from those in *Ve. bourguignati.* In both, the cochlea is larger than in *Ve. schlosseri* and *Ve. gracilis.* However, the f.c. in *Ve. bourguignati* has similar dimensions as in *Ve. schlosseri.* The dimensions of the cochlea and f.c. in the *Ve.* indet. (8602) are larger than in all the above mentioned species; it could be the representative of a different species of *Vespertiliavus.*

The similarity of *Vespertiliavus* with *Taphozous,* noted by Schlosser and later by Revilliod, was confirmed by my comparative studies, especially a similarity with *Taphozous liponycteris* (tables 4, 5; graphs 4, 5; fig. 5). Revilliod states further that in the characters of skull and dentition *Vespertiliavus* is much more primitive than the Recent Emballonurids and that it is a phylum which has developed in parallel with the other Emballonurids similar to the relationship of *Palaeophyllophora* with Recent Hipposideridae. However, one cannot place *Vespertiliavus* in the

TABLE 5. Dimensions of the cochlea and the fenestra cochleae in some Recent Emballonuridae.

	FMNH	*cochlea*		*fenestra cochleae*	
	catalogue no.	*length*	*width*	*length*	*width*
Emballonura semicaudata	31659	2.41	2.0	0.36	0.6
E. semicaudata	31651	2.4	2.0	0.36	0.6
E. monticola	77010	2.25	2.25	0.28	0.52
E. meeki	54080	2.25	2.25	0.4	0.68
E. meeki	54078	2.25	2.25	0.4	0.68
E. nigrescens	8249	2.25	2.0	0.2	0.63
Taphozous melanopogon	32257	3.08	3.0	0.56	0.96
T. melanopogon	98694	2.91	3.0	0.64	1.0
T. perforatus	67550	2.75	2.75	0.64	1.04
T. liponycteris	82785	3.25	3.17	0.64	1.08
T. liponycteris	82784	3.0	3.0	0.6	1.12
Coleura gallarum	67344	2.58	2.5	0.4	0.76
C. gallarum	67345	2.58	2.58	0.4	0.76
C. gallarum	67348	2.5	2.5	0.46	0.76
C. afra	78178	2.57	2.57	0.48	0.88
C. afra	78179	2.58	2.58	0.48	0.88
Rhynchonycteris naso	43118	2.08	2.0	0.14	0.48
R. naso	21993	2.16	1.91	0.14	0.48
R. naso	62136			0.16	0.52
Saccopteryx bilineata	19213	2.5	2.5	0.32	0.84
S. bilineata	68340	2.58	2.5	0.32	0.84
S. bilineata	19211			0.28	0.84
S. canescens	18707	2.16	2.16	0.28	0.7
S. leptura	43122			0.32	0.76
S. leptura	21659			0.36	0.8



GRAPH 4. Length against width of the fenestra cochleae in three species of *Vespertiliavus.*

direct ascendancy with the Recent *Taphozous* or any other genus of the Emballonurinae by comparing the skull only.

In *Taphozous* there is a process of the periotic which projects over a part of the f.c. (fig. 5E'); this process appears not to be present in *Vespertiliavus.*

Nycterobius Revilliod (1922)

Revilliod (1922) established a new genus *Nycterobius* and the species *N. gracilis* which he included in the family Vespertilionidae. The specimen which he studied came from the Phosphorites of St. Neboule Savin, near Cajarc. I had the opportunity to study this specimen (Q.P. 632) of the Basel Collection.

Revilliod noticed several similarities between the skull of *N. gracilis* and some species of the small *Myotis* group, especially with *Myotis capaccinii,* on one hand, and also with *Chilonatalis tumidifrons,* a natalid, on the other. He came to the conclusion that *N. gracilis* is closer to *M. capacinii* than to *Ch. tumidifrons.* My comparative studies of the inner ear agree with Revilliod's findings (table 6, fig. 6, graph 6). The

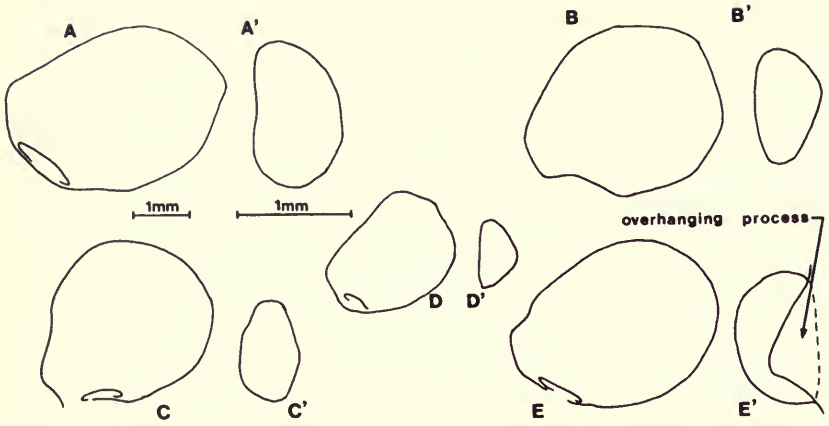


FIG. 5. Outline of the basal view of the cochlea and the postero-lateral view of the fenestra cochleae in **A** and **A'**, *Vespertiliavus* spec. indet. Paris 8602; **B** and **B'**, *Vespertiliavus bourguignati* Paris 8604; **C** and **C'**, *Vespertiliavus schlosseri* Geneva 81020; **D** and **D'**, *Emballonura semicaudata FMNH 31651;* **E** and **E'**, *Taphozous liponycteris nudiventris* FMNH 79567.

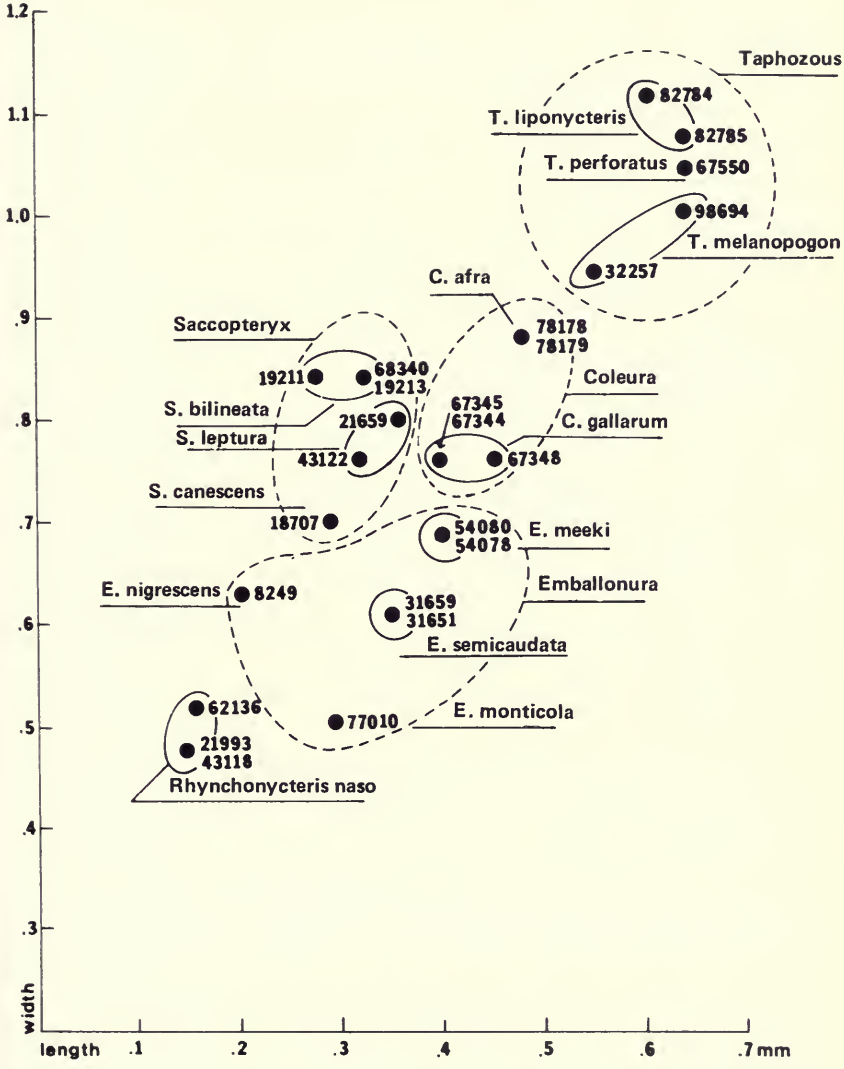
dimensions of the cochlea in *N. gracilis* and *M. capaccinii* are quite similar. This applies also to the f.c. when the inner opening of the f.c. in *M. capaccinii* (FMNH 44105) is considered. The outer opening is slightly larger (table 6). Revilliod also pointed out differences in the skull between the three taxa. Since my studies show that specimens with the same or very similar dimensions and shape of the cochlea and the fenestra cochlea belong to the same or to a closely related species, I conclude that *N. gracilis* and *M. capaccinii* are closely related. Both specimens come from southern Europe, *N. gracilis* from the Quercy and *M. capaccinii* from Lugano, Italy. It would be interesting to see how other parts of the skeleton compare.

Nyctinomus Revilliod (1920)

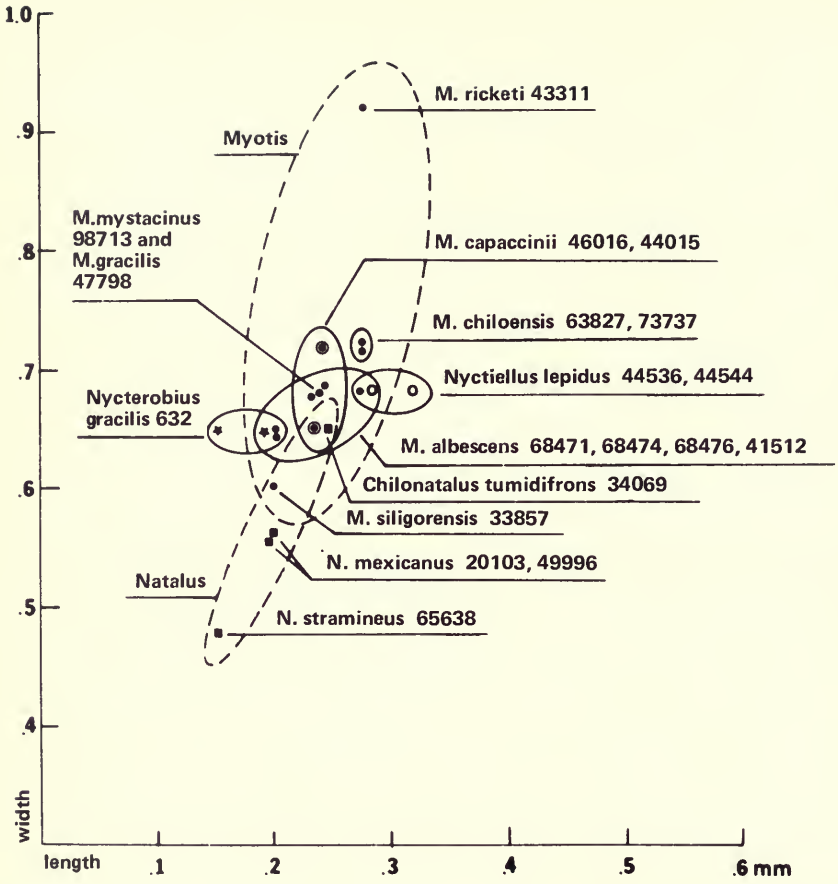
Revilliod described the genus *Nyctinomus* and the species *Ny. stehlini* which was recovered from Montaigu-le-Blin, north of St. Gerand-le-Puy. He found in the form and size of the skull similarities with small Recent Molossidae, especially with *Mormopterus*. The cochlea and the fenestra cochleae were drawn and measured in a number of Molossidae. The results are shown in the Table 7, Graph 7 and Figure 7.

DISCUSSION AND CONCLUSION

The cochlear lengths and widths have been measured. In the majority of the chiropters studied length and width of the cochlea are equal or close to



GRAPH 5. Length against width of the fenestra cochleae in several Recent Emballonurinae.



GRAPH 6. Length against width of the fenestra cochleae in *Nycterobius gracilis* compared with several Recent species representing *Myotis* (Vespertilionidae), *Natalus,* and *Nyctiellus* (Natalidae).

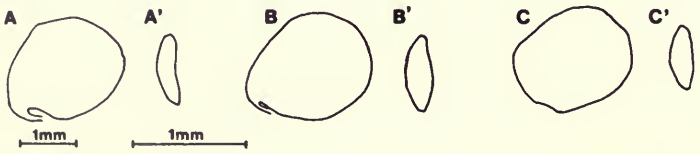


FIG. 6. Outline of the basal view of the cochlea and postero-lateral view of the fenestra cochleae in **A** and **A'**, *Nycterobius gracilis* Basel Q.P. 632; **B** and **B'**, *Myotis capaccinii* FMNH 44105 and **C** and **C'**, *Chilonatalus tumidifrons* FMNH 34069.

TABLE 6. Available dimensions of *Nycterobius gracilis* and some Recent Vespertilionidae and Natalidae.

		FMNH catalogue no.	*cochlea length*	*cochlea width*	*fenestra cochleae length*	*fenestra cochleae width*
Nycterobius gracilis	r	Q.P. 632	2.16	2.16	0.2	0.64
	l				0.16	0.64
Myotis capaccinii		44105	2.16	2.16	0.24	0.64*
					0.24	0.8 **
M. capaccinii		44106	2.16	2.16	0.24	0.72
M. ricketi		43311	2.25	2.25	0.28	0.92
M. chiloensis		73737	1.91	1.91	0.28	0.72
M. chiloensis	r	63827	1.91	1.91	0.28	0.72
	l					
M. albescens		41512	1.91	1.91	0.2	0.64
M. albescens		68476	1.91	1.91	0.2	0.64
M. albescens		68474			0.24	0.68
M. albescens		68471			0.28	0.68
M. mystacinus		98713	1.83	1.83	0.24	0.68
M. gracilis		47798	1.83	1.83	0.24	0.68
M. siligorensis		33857	1.66	1.66	0.2	0.6
Natalus stramineus		51160	1.91			
N. stramineus		65638	1.91	1.91	0.16	0.48
N. mexicanus		20103			0.2	0.56
N. mexicanus		49996			0.2	0.56
Chilonatalus tumidifrons		34069	1.84	1.84	0.24	0.64
Nyctiellus lepidus		44539	1.75	1.75		
N. lepidus		44544			0.32	0.68
N. lepidus		44536			0.28	0.68

* Inner rim of fenestra cochleae

** Outer rim of the fenestra cochleae

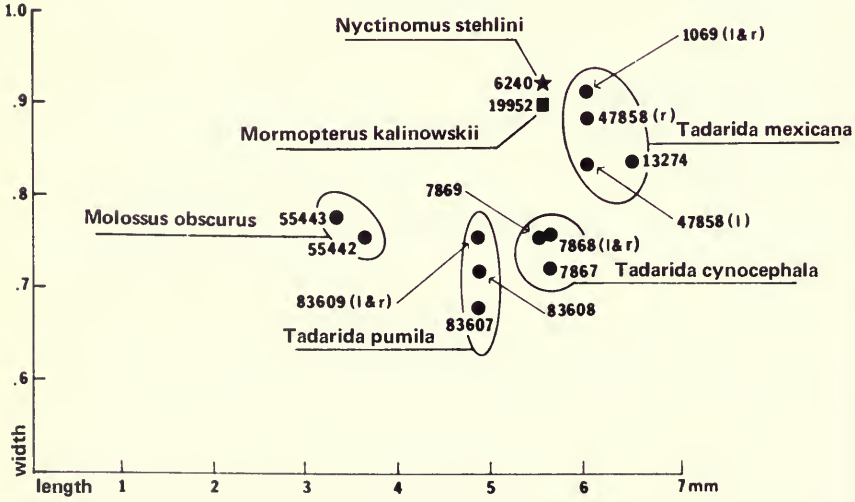
it and therefore the ratio is constant. This lets me assume that the chiropter cochlea approaches the geometric shape of an equiangular spiral.

The fenestra cochleae in the different genera, however, behaves differently. The length/width ratios are much more varied; while the width measures vary considerably, corresponding length measurements do not. Therefore the f.c. ratio was more useful than the cochlear ratio in this study.

If two chiropter specimens have cochlear and fenestra cochleae dimensions and shapes which are identical or close to it, it is very probable that they belong to the same species or to closely related species of the same genus. I have obtained this result in a wide sampling of the dimensions of these structures in a number of families, genera, and species. This result is not surprising, when one considers the importance of the cochlea with the fenestra cochleae in chiropters. For instance, several specimens of *Vespertiliavus bourguignati* were studied (table 4) and the dimensions of their cochleae and fenestrae cochleae were found to be quite similar.

TABLE 7. Available dimensions of the cochlea and the fenestra cochleae in *Nyctinomus stehlini* and some Recent Molossids.

		institution	*catalogue no.*	*cochlea length*	*cochlea width*	*fenestra cochleae length*	*fenestra cochleae width*
Nyctinomus stehlini		Basel	S.G.6240	2.41	2.41	0.56	0.92
Mormopterus kalinowskii		FMNH	19952	2.5	2.5	0.56	0.88
Tadarida cynocephala		FMNH	7867	2.58	2.5	0.56	0.72
T. cynocephala	r	FMNH	7868			0.56	0.76
	l					0.56	0.76
T. cynocephala		FMNH	7869			0.56	0.76
T. mexicana	r	FMNH	47858			0.6	0.88
	l					0.6	0.84
T. mexicana	r	FMNH	1069	2.41	2.41	0.6	0.92
	l			2.46	2.41	0.6	0.92
T. mexicana		FMNH	13273	2.41	2.41		
T. mexicana		FMNH	13274	2.41	2.41	0.64	0.84
T. pumila		FMNH	83610	2.35	2.35		0.76
T. pumila	r	FMNH	83609			0.48	0.76
	l					0.48	0.76
T. pumila		FMNH	83607			0.48	0.68
T. pumila		FMNH	83608			0.48	0.72
Molossus obscurus		FMNH	55443	2.66	2.57	0.32	0.78
M. obscurus		FMNH	55442			0.36	0.76
M. obscurus		FMNH	55440	2.75	2.66		



GRAPH 7. Length against width of the fenestra cochleae in *Nyctinomus stehlini* and some Recent Molossids.

Of even greater interest are the instances in which such similarity exists between a Recent and a fossil chiropter, as has been shown to be the case in *Nycterobius gracilis* and *Myotis capaccinii.* My studies show that their cochleae and fenestrae cochleae have similar shape and size (fig. 6, table 6,

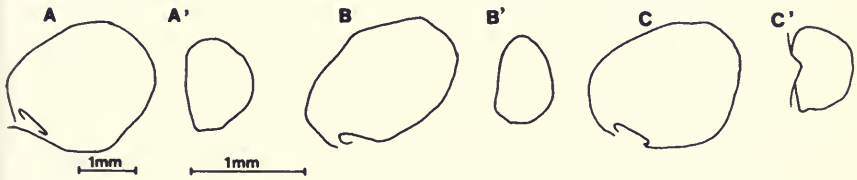


FIG. 7. Outline of the basal view of the cochlea and the postero-lateral view of the fenestra cochleae in **A** and **A'**, *Nyctinomus stehlini* Basel S.G. 6240; **B** and **B'**, *Mormopterus kalinowskii* FMNH 19952; and **C** and **C'**, *Tadarida cynocephala* FMNH 7867.

graph 6) and I have, therefore, assumed that the two taxa are closely related in spite of their other cranial differences. The phylogenetic implications of this are that the inner ear remains stable while the facial region evolved (see Revilliod, 1922, table, p. 135, for cranial and facial measurements). Apparently, the hearing mechanism adequately serves the Recent *Myotis capaccinii* about as well as it did the fossil *Nyterobius gracilis,* in spite of the changes in proportions of the facial structures necessary for food procurement and processing.

A marked difference was noted in the dimensions of the cochlea and the fenestra cochleae between the *Pseudorhinolophus* (sp. indet.) which Schlosser (1887, Art. 2) used for his illustration and the *Ps.* which Revilliod (1917) used for the description of *Pseudorhinolophus schlosseri* (table 1). This discrepancy indicates clearly that these materials belong to different species.

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REFERENCES

Dechasaux, C.
1958. Chiroptera. *In* Traité de Paléontologie, VI, 2d.

Filhol, H.
1872. Recherches sur les mammifères fossiles . . . Ann. Sci. Geol., T. III.
1876. Recherches sur les phosphorites du Quercy. Ann. Sci. Geol., T. VII.

Gray, A. A.
1907. The labyrinth of animals. Vol. I. Churchill, London.

Pictet, F. J., C. Gaudin and Pii. De La Harpe
1855. Mémoir sur les animaux vertébrés trouvés dans le terrain sidérothique du Canton de Vaud; Materiaux pour la paléontologie suisse, Genéve.

Pye, A.
1966. The structure of the cochlea in Chiroptera. I. Microchroptera, Emballonuroidea and Rhinolophidea. Jour. Morphol., **118,** pp. 495-511.
1967. The structure of the cochlea in Chiroptera. III. Microchiroptera: Phyllostomatoidea. Jour. Morphol., **121,** pp. 241-255.

Revilliod, P.
1917. Mémoires de la Societé paléontologique suisse. Vol. 42.
1920. Mémoires de la Societé paléontologique suisse. Vol. 44.
1921-1925. Mémoires de la Societé paléontologique suisse. Vol. 45.

Russel, D. E. and B. Sigé
1970. Révision des chiroptéres lutetiens de Messel, Palaeovertebrata. Vol. 3, fasc. 4. Montpellier.

Schlosser, M.
1887-1889. Die affen, lemuren, chiroptéren etc. des europäischen Tertiärs. Beiträge zur Paläontologie Osterreich-Ungarns und des Orients. Vol. 6-7.

Segall, W.
1970. Morphological parallelism of the bulla and auditory ossicles in some insectivores and marsupials. Fieldiana: Zool., **51,** no. 15, pp. 169-205.
1971a. The auditory region (ossicles, sinuses) in gliding mammals and selected representatives of non-gliding genera. Fieldiana: Zool., **58,** no. 5, pp. 27-59.
1971b. Auditory region in bats including *Icaronycteris index.* Fieldiana: Zool., **58,** no. 9, pp. 103-108.

Sigé, B.
1968. Les chiroptéres du Miocéne inférieur de Bouzigues. Palaeovertebrata, vol. 1, fasc. 3, Montpellier.

Thompson, D. W.
1966. On growth and form, 2nd ed. Vol. 2. Cambridge University.