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Auditory Region in Bats Including *Icaronycteris index*

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ABSTRACT

A study of the auditory and neighboring regions suggests a phylogenetic relationship between the Echinosoricinae and the Chiroptera. This relationship appears to be closer to Megachiroptera than Microchiroptera. The Microchiroptera developed by further specialization of the inner ear, while the middle ear remained static. The auditory region of *Icaronycteris index*, which was examined as closely as possible, shows similarities with that of Echinosoricinae and Megachiroptera.

It has been presumed that bats evolved from an arboreal insectivore group, but the specific taxon has not been established with certainty (Romer, 1966). This study contributes new information pertinent to the determination of this taxon.

The morphology and topography of the tympanic, the malleus, the cochlea, and neighboring structures supplied by the squama have been studied and striking similarities have been noted between some Megachiroptera and the Echinosoricinae. The latter, a subfamily of the Erinaceidae is considered a generalized group of insectivores.

Jepsen (1966) meticulously prepared and described the skeleton of *Icaronycteris index* (PU 18150), a bat from the early Eocene, Green River bed of Wyoming, and he concluded that it combines megachiropteran with microchiropteran characters. My study deals in a detailed way with the auditory region and some adjoining elements of the squama and features of the posterior part of the mandible in this fossil bat.

Similarities and dissimilarities of these structures between *Icaronycteris index* and the Echinosoricinae, the Megachiroptera, and the

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Microchiroptera are pointed out and most of these structures are illustrated in Figure 1.

Several characters of the tympanic have been studied in the three higher taxa. The tympanic is horseshoe-shaped in all Echinosoricinae and in some genera of the Megachiroptera. In most Microchiroptera and in *Icaronycteris index* it is ring-shaped. The incisura is wide in the Echinosoricinae (fig. 1A), less wide in the Megachiroptera (fig. 1B), absent or small in the Microchiroptera (fig. 1C). The space between tympanic and squama is wide in the Echinosoricinae (fig. 1A), variable in the Megachiroptera (fig. 1B), and mostly absent in the Microchiroptera (fig. 1C). The inclination of the tympanic toward the horizontal is very marked in the Echinosoricinae, less marked in the Megachiroptera, and usually still smaller in Microchiroptera. The tympanic is directed antero-posteriorly in the Echinosoricinae and the Megachiroptera, and often from antero-medial to postero-lateral in the Microchiroptera.

The diameter of the malleus head in some Echinosoricinae runs antero-posteriorly (fig. 1D), in others latero-medially. Similar configurations are seen in the Megachiroptera (fig. 1B). In the Microchiroptera the malleus head shows a great variety of shapes (fig. 1F). The distal end of the tympanic plate projects antero-ventro-laterally in front of the tympanic to which it is fused posteriorly. This protuberance is present in all Echinosoricinae (fig. 1A), in some Megachiroptera (fig. 1B), but not in Microchiroptera (fig. 1C).

The relatively small cochlea is moderately convex ventrally in the Echinosoricinae and the Megachiroptera and its fenestra cochlea is directed caudo-ventrad. In the Microchiroptera the cochlea is typically inflated and wide, sometimes wider than long, and the fenestra cochlea is directed caudad, caudo-ventrad, or laterad. The

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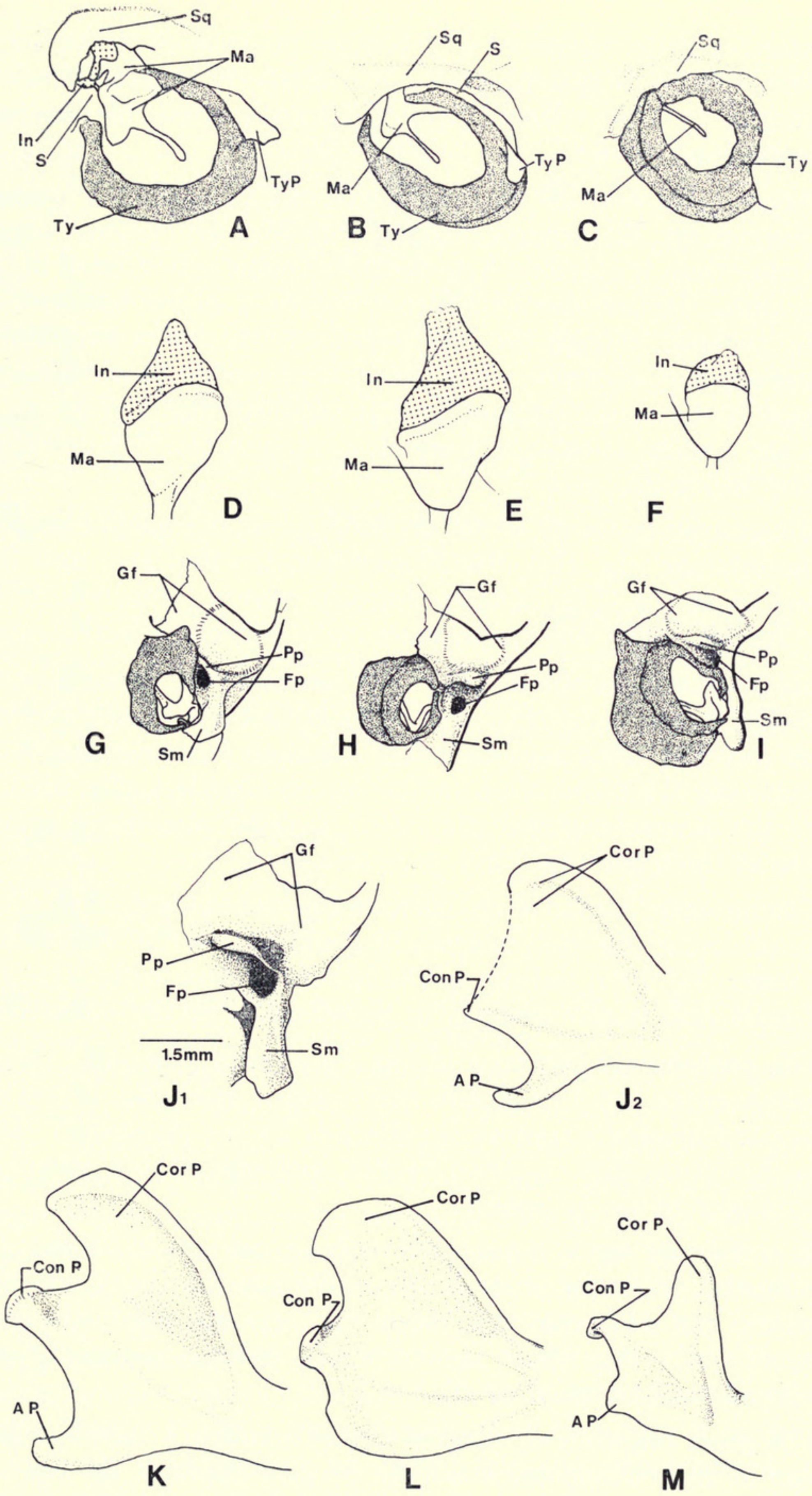
FIG. 1. (opposite)

AP	Angular process	Ma	Malleus
Con P	Condyloid process	Pp	Postglenoid process
Cor P	Coronoid process	S	Space between tympanic and squama
Fp	Postglenoid foramen	Sq	Squama
Gf	Glenoid fossa	Sm	Superficies meatus
In	Incus	Ty	Tympanic
		Typ	Tympanic plate of malleus

A. *Hylomys*
B. *Cynopterus*
C. *Hipposideros*
D. *Podogymnura*
E. *Dobsonia*
F. *Tadarida*
G. *Hylomys*
H. *Rousettus*
I. *Myotis*
J_1. *Icaronycteris* (drawn to scale)
J_2. *Icaronycteris*
K. *Hylomys*
L. *Dobsonia*
M. *Rhinopoma*


Sq
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H
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Pp
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Sm
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Gf
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Fp
1.5mm
Sm
J1
Cor P
Con P
A P
J2
Cor P
Con P
A P
K
Cor P
Con P
L
Cor P
Con P
A P
M

inner ear is tightly connected with the rest of the skull in the Echinosoricinae and the Megachiroptera, but relatively loose in many Microchiroptera. Only a small part of the cochlea can be recognized in *Icaronoycteris index.*

The straight borders of the basiocciput diverge in a posterior direction in the Echinosoricinae and the Megachiroptera, more in the former than the latter. The cochlea is not much inflated in these two groups. In the Microchiroptera the width of the basiocciput is usually reduced, though the degree of the reduction is variable. Its borders are very concave. The presence of a wide basiocciput with straight, posteriorly diverging borders suggests that in *Icaronycteris index* the cochlea is relatively small, as it is in the Echinosoricinae and the Megachiroptera.

The coronoid process of the ascending ramus mandibulae in the Echinosoricinae (fig. 1K), the Megachiroptera (fig. 1L), and *Icaronycteris index* (fig. 1J2) is high, dorsally convex, antero-posteriorly wide (Jepsen, 1966), and the incisura mandibulae is directed caudad.

In the Microchiroptera (fig. 1M) the coronoid process is more anteriorly located and the incisura mandibulae is caudo-dorsad or dorsad directed. The angulus mandibuli has a process in the Echinosoricinae (fig. 1K) and often in the Microchiroptera (fig. 1M), but not in the Megachiroptera (fig. 1L). *I. index* also has a spur-like process at the angle (fig. 1J2).

The anterior border of the glenoid fossa ascends medially in the Echinosoricinae (fig. 1G), in some Megachiroptera (fig. 1H), and also in *I. index* (fig. 1J1), but not in the Microchiroptera (fig. 1I), where the border runs latero-medially or sometimes even recedes medially.

The postglenoid foramen in the Echinosoricinae (fig. 1G), the Megachiroptera (fig. 1H), and in *Icaronycteris index* (fig. 1J1) is large, round, and located antero-dorso-laterally to the tympanic. In the Microchiroptera (fig. 1I) the foramen is elongated and located antero-dorsally to the tympanic.

Also the position and size of the horizontal lamella of the superficies meatus is similar in the Echinosoricinae (fig. 1G), some Megachiroptera (fig. 1H), and in *I. index* (fig. 1J1), but not in the Microchiroptera (fig. 1I), where the horizontal lamella is usually either very small or not present at all.

The great majority of structures mentioned are morphologically similar in the Echinosoricinae, the Megachiroptera, as well as in *I. index,* while they differ from those in the Microchiroptera.

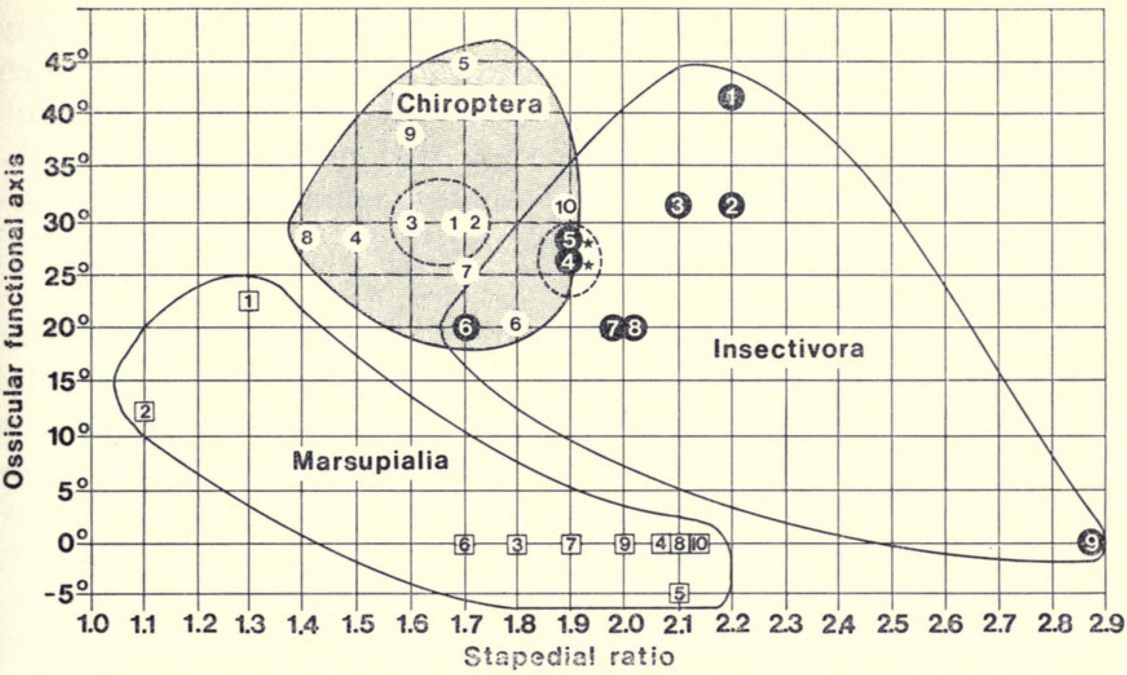

FIG. 2.

MARSUPIALS □		INSECTIVORES ●	
1. *Didelphis*	6. *Trichosurus*	1. *Oryzoryctes*	6. *Hemiechinus*
2. *Dasyurus*	7. *Petaurus*	2. *Solenodon*	7. *Erinaceus*
3. *Phalanger*	8. *Pseudochirus*	3. *Setifer*	8. *Elephantulus*
4. *Macropus*	9. *Schoinobates*	*4. *Hylomys*	9. *Tupaia*
5. *Dromiciops*	10. *Acrobates*	*5. *Podogymnura*	

BATS ○	
1. *Acerodon*	6. *Desmodus*
2. *Eidolon*	7. *Glossophaga*
3. *Epomops*	8. *Carollia*
4. *Myotis*	9. *Vampyrops*
5. *Emballonura*	10. *Artibeus*

The sound-conducting system judged by the angle of the ossicular functional axis with the Frankfurter horizontal (Segall, 1969) and by the stapedial ratio (Segall, 1970) is very similar in both suborders of bats and in the Echinosoricinae. This is demonstrated in a graph (fig. 2) combining these two factors. In this graph the Echinosoricinae and bats are located in a relatively small area in close proximity to each other, in contrast to similar graphs prepared for the marsupials and other insectivores in which a wide spread is seen. Since the angle of the ossicular functional axis with the Frankfurter horizontal and stapedial ratio are important factors in the sound conducting system, one may conclude that the evolution of this system remained conservative in the Echinosoricinae as well as in both suborders of bats. Much specialization took place, however, in the inner ear with the development of special forms of echolocation in the Microchiroptera (Griffin, 1958).

Generalized characters in the auditory region of bats are mainly found in the Megachiroptera. One group of Pteropinae to which *Pteropus*, *Rousettus*, and *Dobsonia* belong proved especially useful. Characters of specialization in the ear region are preponderantly found in the Microchiroptera. The ear region and neighboring structures of *Icaronycteris index*, as far as can be seen, has only generalized characters.

Considering the similarity in the morphology and topography of the auditory region of *I. index* with that in the Echinosoricinae and the Megachiroptera, one may assume that its audiophysiological system was similar to that found in the Echinosoricinae and the Megachiroptera, and that the complex auditory system of the Microchiroptera developed by specialization. The small cochlea, however, does not exclude the possibility that *I. index* did echolocate, a function usually correlated with an enlarged cochlea. It has been shown that *Rousettus* uses a certain form of echolocation and does not exhibit cochlear enlargement (Grifflen, 1958).

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